

cover and a partially closed native understory dominated by graminoids, shrubs, and ground ferns. We also made incidental sightings of this species during the survey period. All known sightings have been on the northeast slopes of Haleakala from 1400 to 2050 m elevation in wet ohia forests with well-developed understories (Berger 1981, Conant 1981). Fossil records from Ulupalakua (S. L. Olson, pers. comm.) indicate that Poo-uli originally occupied a larger range that included dry to mesic habitat.

The total population of 140 ± 280 (95% CI) Poo-uli (Tables 11, 24) inhabits the upper Hanawi and Kuhiwa watersheds. The birds we found (0.03 birds/count period) within the species range in 1980 indicate about the same abundance as S. Mountainspring (unpub. data) found in 1981 in the upper Hanawi area (0.04 birds/count period). A decline in abundance was suggested by comparison with the upper Hanawi survey that T. L. C. Casey (unpub. data) conducted in 1976 (0.18 birds/count period). Incidental observations over the 1974–1983 period also suggest fewer Poo-uli now than a decade ago (T. L. C. Casey, pers. comm.). Correlated with this trend was an increase in pig damage to the understory of the upper Hanawi watershed (S. Mountainspring, pers. observ.).

Areas in Poo-uli range differ from nearby areas outside the range in the same elevational stratum and in the same general vegetation type. Whereas in-range areas have moderate pig damage and well-developed herb, ground fern, and moss layers, adjacent areas outside the range have significantly greater pig damage and less ground cover (S. Mountainspring, pers. observ.). Poo-uli appear to be adversely impacted by pig activity, possibly because pigs destroy microhabitat sites critical to the life cycle of the land snails and other invertebrates that species eats. Pigs are thus one probable cause of the apparent decline of Poo-uli over the past decade. The restriction of Poo-uli and Nukupuu to the wet ohia forests of the upper Hanawi watershed (Figs. 112, 159) suggests that these birds are in extreme danger of extinction. It seems imperative to remove pigs permanently from this and adjacent areas to ensure the survival of these species.

INTRODUCED SPECIES ACCOUNTS

General notes on format of the species accounts are given at the beginning of the native species section. Often only a few of the many individuals in a flock were detected for species such as Erckel's Francolin, Gray Francolin, Chukar, Wild Turkey, California Quail, House Finch, and Nutmeg Mannikin. Moreover, calling rates of gamebirds fell sharply within an hour after sunrise.

For gallinaceous birds in particular, density and population estimates are therefore best interpreted as relative indices of abundance. It should be noted that as a result of our sampling design, many introduced species entered the study areas only at the periphery of their range.

BLACK FRANCOLIN (*Francolinus francolinus*)

Black Francolins were introduced from India in 1959 (Berger 1981). They presently occur on Hawaii, Maui, Molokai, and Kauai. Black Francolins feed on plants, insects, and seeds.

We found this species in five study areas (Tables 33–35). The distribution patterns indicated that we sampled at the periphery of the range. An estimated 230 ± 40 (95% CI) birds occupy the Kona study area, mainly at low elevations on the north slope of Hualalai (near the initial release site on Puu Waawaa [Lewin 1971]) and at higher elevations in the area from Puu Lehua to Devil Country (Fig. 160). On Hawaii, Black Francolins occur from sea level to 2300 m elevation (Table 35). They occur below 2200 m in the Mauna Kea study area and are common along the Saddle Road west of Mauna Kea State Park. We consider the one bird recorded in the Kohala study area to be an extralimital record. The species is common at lower elevations on the leeward side of Kohala Mountain and Mauna Kea.

In the East Maui study area an estimated 8 ± 6 (95% CI) birds occur below 1300 m elevation in dry areas. As on Hawaii, they are more common below the study area. On Molokai 150 \pm 60 birds inhabit the study area (Table 34, Fig. 161). Here they are very widespread in dry areas on lower slopes, but also penetrate closed-canopy forests along roads, jeep trails, clearings, and grassy areas.

Highest densities occur in dry scrubland and savanna (often scrubby pasturelands) at lower elevations, with occasional birds in mesic to wet areas and in open woodlands (Table 36, Fig. 162). Most tree species have negative terms in the regression models and little response appears to understory elements. The strong tendency of this species to wander, however, makes it a potential dispersal agent for banana poka (Warshauer et al. 1983).

In the Kohala area Black Francolins typically inhabit the perimeters of sugar cane fields, irrigation ditches, and drier pasture areas where mesquite and lantana are common (Lewin 1971). These habitats are similar to areas occupied within the native range in India: dry grasslands, open brushlands, and cultivated areas with available water and cover for feeding (Ali and Ripley 1969).

TABLE 33
SUMMARY STATISTICS FOR INTRODUCED BIRDS IN THE STUDY AREAS ON HAWAII

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala
Black Francolin							
Range (km ²)	275	97	12
Stations in range	605	234	19
Stations occupied	178	1	1
Birds recorded	487	1	1
Total population	230	6	1
SE	18	6	1
Pop. by habitat type							
Ohia	159	...	1
Koa-ohia	1
Mamane-naio	11
Mamane	30	6	...
Other natives	21
Intro. trees	8
Erckel's Francolin							
Range (km ²)	...	4	42	45	325	97	...
Stations in range	...	10	75	73	820	234	...
Stations occupied	...	1	58	22	421	53	...
Birds recorded	...	1	244	72	2047	100	...
Total population	...	1	287	43	1137	326	...
SE	...	1	25	6	47	48	...
Pop. by habitat type							
Ohia	287	...	669
Koa-ohia	39	110
Koa-mamane	4	2
Mamane-naio	28	253	...
Mamane	144	74	...
Other natives	...	1	97
Intro. trees	88
Gray Francolin							
Stations occupied	2
Birds recorded	2
Chukar							
Range (km ²)	...	14	...	127	242	139	...
Stations in range	...	27	...	157	608	317	...
Stations occupied	...	11	...	43	105	66	...
Birds recorded	...	21	...	67	194	165	...
Total population	...	239	...	227	777	4243	...
SE	...	52	...	45	84	655	...
Pop. by habitat type							
Ohia	208	405
Koa-ohia	26
Koa-mamane	...	219	...	9	11
Mamane-naio	24	1620	...
Mamane	239	2666	...
Other natives	...	20	...	2	3
Intro. trees	2
Treeless	8	67
Japanese Quail							
Range (km ²)	20	17	...	32	...	97	...
Stations in range	25	17	...	35	...	234	...
Stations occupied	1	3	...	3	...	2	...
Birds recorded	1	23	...	15	...	2	...
Total population	33	31	...	52	...	17	...
SE	33	21	...	23	...	11	...

TABLE 33
CONTINUED

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala
Pop. by habitat type							
Ohia	33	24	...	18
Koa-mamane	13
Mamane	17	...
Other natives	...	8	...	21
Kalij Pheasant							
Range (km ²)	...	67	...	28	758
Stations in range	...	178	...	36	1760
Stations occupied	...	6	...	2	253
Birds recorded	...	8	...	3	432
Total population	...	174	...	23	5499
SE	...	83	...	20	461
Pop. by habitat type							
Ohia	...	80	...	3	2196
Koa-ohia	...	82	...	20	2116
Koa-mamane	527
Mamane-naio	8
Mamane	272
Other natives	3
Intro. trees	...	13	377
Red Junglefowl (Moa)							
Range (km ²)	32
Stations in range	70
Stations occupied	11
Birds recorded	21
Total population	3
SE	1
Pop. by habitat type							
Ohia	3
Ring-necked Pheasant							
Range (km ²)	71	354	81	271	933	139	19
Stations in range	156	740	219	458	2201	317	38
Stations occupied	44	185	45	265	1075	13	5
Birds recorded	101	556	110	1196	3578	17	8
Total population	1147	2088	270	2250	7452	657	45
SE	297	144	45	99	207	225	27
Pop. by habitat type							
Ohia	1142	666	252	927	3294	...	45
Koa-ohia	5	918	...	801	1287
Koa-mamane	...	171	...	324	1422
Mamane-naio	9	54	...
Mamane	1071	603	...
Other natives	...	333	...	189	81
Intro. trees	225
Treeless	18	...	54
Common Peafowl							
Range (km ²)	239
Stations in range	545
Stations occupied	175
Birds recorded	953
Total population	83
SE	5
Pop. by habitat type							
Ohia	31
Koa-ohia	21

TABLE 33
CONTINUED

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala
Mamane	17
Other natives	6
Intro. trees	8
Wild Turkey							
Range (km ²)	11	157	834	139	...
Stations in range	18	319	1960	317	...
Stations occupied	1	73	920	13	...
Birds recorded	1	222	3117	21	...
Total population	4	322	1616	42	...
SE	4	32	65	13	...
Pop. by habitat type							
Ohia	4	644
Koa-ohia	...	224	347
Koa-mamane	...	13	350
Mamane-naio	3	7	...
Mamane	231	35	...
Other natives	...	77	13
Intro. trees	...	8	27
Treeless	1
California Quail							
Range (km ²)	...	65	34	220	465	139	...
Stations in range	...	151	71	361	1101	317	...
Stations occupied	...	24	9	151	333	84	...
Birds recorded	...	69	15	545	863	372	...
Total population	...	36	49	457	820	1408	...
SE	...	9	19	30	69	337	...
Pop. by habitat type							
Ohia	...	14	47	189	287
Koa-ohia	...	13	...	74	6
Koa-mamane	...	1	...	112	219
Mamane-naio	7	745	...
Mamane	274	663	...
Other natives	...	7	...	83	14
Intro. trees	13
Treeless	2
Spotted Dove							
Range (km ²)	9	70	126	16	299	...	30
Stations in range	22	180	295	10	731	...	53
Stations occupied	9	16	60	6	145	...	2
Birds recorded	21	30	193	9	328	...	2
Total population	95	39	258	7	296	...	8
SE	35	8	35	2	24	...	6
Pop. by habitat type							
Ohia	80	10	256	7	132	...	2
Koa-ohia	15	5	58
Koa-mamane	1
Mamane	3
Other natives	...	19	4
Intro. trees	...	5	95
Treeless	2	...	2	...	6
Zebra Dove							
Range (km ²)	...	37	...	64	515
Stations in range	...	97	...	42	1235
Stations occupied	...	7	...	5	342
Birds recorded	...	16	...	14	936
Total population	...	41	...	11	1114
SE	...	13	...	3	73

TABLE 33
CONTINUED

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala
Pop. by habitat type							
Ohia	...	19	...	3	554
Koa-ohia	...	22	...	3	139
Koa-mamane	147
Mamane	90
Other natives	4	29
Intro. trees	148
Treeless	6
Mourning Dove							
Range (km ²)	75
Stations in range	203
Stations occupied	12
Birds recorded	12
Total population	8
SE	3
Pop. by habitat type							
Ohia	7
Koa-mamane	2
Common Barn-Owl							
Stations occupied	...	1	1	...	1
Birds recorded	...	1	1	...	1
Eurasian Skylark							
Range (km ²)	7	103	15	177	663	139	...
Stations in range	19	192	54	268	1571	317	...
Stations occupied	1	57	1	65	653	160	1
Birds recorded	1	124	1	186	1958	421	1
Total population	19	395	1	445	4678	4461	...
SE	19	52	1	46	161	342	...
Pop. by habitat type							
Ohia	19	17	1	168	1183
Koa-ohia	...	114	...	95	401
Koa-mamane	...	109	...	51	1240
Mamane-naio	5	724	...
Mamane	1516	3737	...
Other natives	...	154	...	131	148
Intro. trees	94
Treeless	92
Melodious Laughing-thrush							
Range (km ²)	...	896	246	5	61	97	110
Stations in range	...	2131	621	28	120	234	207
Stations occupied	...	661	355	1	9	28	109
Birds recorded	...	1412	1102	1	23	44	310
Total population	...	5406	3146	1	12	284	1445
SE	...	203	127	1	4	58	121
Pop. by habitat type							
Ohia	...	2323	3146	...	12	...	1405
Koa-ohia	...	2682
Koa-mamane	1
Mamane-naio	284	...
Other natives	...	8
Intro. trees	...	385	40
Treeless	...	8
Red-billed Leiothrix							
Range (km ²)	278	973	8	63	712	139	111
Stations in range	793	2187	15	134	1636	317	204
Stations occupied	418	1260	2	24	518	44	142

TABLE 33
CONTINUED

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala
Birds recorded	1064	4452	3	43	1681	81	550
Total population	15,398	60,547	30	582	11,289	1807	8233
SE	658	1417	21	86	474	299	624
Pop. by habitat type							
Ohia	9275	32,329	30	102	4810	...	7670
Koa-ohia	6123	26,961	...	245	3859
Koa-mamane	...	3	...	53	937
Mamane-naio	4	1709	...
Mamane	1217	98	...
Other natives	...	88	...	19	83
Intro. trees	...	1165	379	...	563
Treeless	...	2	...	162
Northern Mockingbird							
Range (km ²)	10	97	...
Stations in range	20	234	...
Stations occupied	5	34	...
Birds recorded	8	38	...
Total population	32	439	...
SE	13	85	...
Pop. by habitat type							
Ohia	32
Mamane-naio	371	...
Mamane	68	...
Common Myna							
Range (km ²)	9	138	35	72	355	97	...
Stations in range	11	307	75	136	828	234	...
Stations occupied	2	83	21	31	265	2	...
Birds recorded	9	335	71	101	1069	9	...
Total population	39	1170	337	171	2652	90	...
SE	19	117	69	23	164	63	...
Pop. by habitat type							
Ohia	39	312	337	56	712
Koa-ohia	...	355	...	25	1168
Koa-mamane	...	191	...	40	556
Mamane-naio	2	90	...
Mamane	76
Other natives	...	311	...	49	51
Intro. trees	87
Japanese White-eye							
Range (km ²)	329	1095	269	276	1228	139	121
Stations in range	868	2426	668	462	2832	317	215
Stations occupied	573	2150	643	234	2251	178	156
Birds recorded	2308	11,635	4254	1041	11,069	484	742
Total population	129,598	638,018	158,182	26,414	302,235	34,614	48,038
SE	4254	8958	3249	1259	5402	2420	2549
Pop. by habitat type							
Ohia	107,028	303,006	155,678	8769	167,170	...	46,705
Koa-ohia	22,570	300,711	...	14,261	73,416
Koa-mamane	...	3579	...	2425	18,144
Mamane-naio	650	26,671	...
Mamane	9242	7943	...
Other natives	...	9685	...	866	3402
Intro. trees	...	20,503	28,332	...	1332
Treeless	...	355	2504	93	1879
Northern Cardinal							
Range (km ²)	140	829	259	142	1232	97	81

TABLE 33
CONTINUED

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala
Stations in range	375	1944	632	275	2849	234	176
Stations occupied	68	574	346	140	2207	29	40
Birds recorded	143	1188	1030	426	7617	43	81
Total population	1359	9413	6044	1360	28,445	493	604
SE	231	419	286	85	498	94	92
Pop. by habitat type							
Ohia	1041	2269	6044	247	12,422	...	539
Koa-ohia	318	6343	...	808	7129
Koa-mamane	205	3696
Mamane-naio	81	436	...
Mamane	1869	57	...
Other natives	...	51	...	99	332
Intro. trees	...	751	2582	...	65
Treeless	1	335
Saffron Finch							
Range (km ²)	123
Stations in range	307
Stations occupied	70
Birds recorded	156
Total population	2388
SE	294
Pop. by habitat type							
Ohia	1035
Koa-ohia	80
Mamane	574
Other natives	71
Intro. trees	629
House Finch							
Range (km ²)	25	348	229	261	1181	139	61
Stations in range	36	676	554	471	2773	317	151
Stations occupied	1	214	130	246	1600	196	10
Birds recorded	1	1495	473	923	7037	735	12
Total population	47	21,898	7301	8111	65,743	23,742	253
SE	42	2201	610	533	1622	2299	83
Pop. by habitat type							
Ohia	47	2232	6901	4050	35,600	...	245
Koa-ohia	...	11,008	...	2928	12,153
Koa-mamane	...	1523	...	630	5181
Mamane-naio	351	14,482	...
Mamane	5964	9261	...
Other natives	...	6466	...	500	2241
Intro. trees	...	668	3688	...	9
Treeless	400	3	565
Yellow-fronted Canary							
Range (km ²)	134
Stations in range	301
Stations occupied	76
Birds recorded	286
Total population	4464
SE	418
Pop. by habitat type							
Ohia	3716
Koa-ohia	398
Mamane	64
Other natives	130
Intro. trees	157

TABLE 33
CONTINUED

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala
House Sparrow							
Stations occupied	...	3	2	...	2	6	...
Birds recorded	...	8	4	...	4	305	...
Red-cheeked Cordonbleu							
Range (km ²)	22
Stations in range	54
Stations occupied	2
Birds recorded	3
Total population	32
SE	23
Pop. by habitat type							
Ohia	18
Other natives	14
Lavender Waxbill							
Range (km ²)	20
Stations in range	46
Stations occupied	5
Birds recorded	9
Total population	234
SE	60
Pop. by habitat type							
Ohia	19
Other natives	18
Intro. trees	197
Warbling Silverbill							
Range (km ²)	157	97	...
Stations in range	375	234	...
Stations occupied	72	1	...
Birds recorded	127	4	...
Total population	3536	486	...
SE	669	486	...
Pop. by habitat type							
Ohia	2542
Koa-ohia	13
Mamane-naio	21	486	...
Mamane	58
Other natives	604
Intro. trees	299
Nutmeg Mannikin							
Range (km ²)	...	375	150	40	307	139	44
Stations in range	...	890	373	41	800	317	100
Stations occupied	...	61	31	11	86	4	12
Birds recorded	...	151	52	23	197	29	21
Total population	...	10,316	2449	657	6367	3703	1353
SE	...	1151	519	226	1007	2078	295
Pop. by habitat type							
Ohia	...	3181	2449	...	3538	...	1353
Koa-ohia	...	2635	...	648	806
Mamane-naio	3301	...
Mamane	281	402	...
Other natives	...	326	...	9	161
Intro. trees	...	4174	1582

TABLE 34
SUMMARY STATISTICS FOR INTRODUCED BIRDS IN THE STUDY AREAS ON MAUI, MOLOKAI, LANAI, AND KAUAI

	East Maui	West Maui	Molokai	Lanai	Kauai
Black Francolin					
Range (km ²)	4	...	67
Stations in range	15	...	313
Stations occupied	5	...	85
Birds recorded	24	...	246
Total population	8	...	151
SE	3	...	28
Pop. by habitat type					
Ohia	25
Other natives	8	...	60
Intro. trees	67
Erckel's Francolin					
Range (km ²)	4	...	14	20	25
Stations in range	19	...	74	77	140
Stations occupied	3	...	13	41	4
Birds recorded	4	...	19	108	5
Total population	2	...	10	44	4
SE	2	...	3	7	2
Pop. by habitat type					
Ohia	5	...	4
Koa-ohia	1
Other natives	1	...	4	10	...
Intro. trees	1	27	...
Treeless	7	...
Gray Francolin					
Range (km ²)	31	0.2	4	20	...
Stations in range	82	8	7	77	...
Stations occupied	22	2	2	4	...
Birds recorded	41	5	2	8	...
Total population	39	1	1	4	...
SE	9	1	1	3	...
Pop. by habitat type					
Ohia	...	1
Koa-ohia	1
Other natives	38	...	1	3	...
Intro. trees	1	1	...
Chukar					
Range (km ²)	46	0.2	14
Stations in range	262	8	56
Stations occupied	121	1	14
Birds recorded	549	1	30
Total population	1716	1	249
SE	203	1	79
Pop. by habitat type					
Ohia	31	1	239
Koa-ohia	15
Mamane	151
Other natives	617	...	10
Intro. trees	18
Treeless	883
Japanese Quail					
Range (km ²)	9
Stations in range	29
Stations occupied	9
Birds recorded	29
Total population	133
SE	63

TABLE 34
CONTINUED

	East Maui	West Maui	Molokai	Lanai	Kauai
Pop. by habitat type					
Koa-ohia	17
Other natives	115
Intro. trees	1
Red Junglefowl (Moa)					
Range (km ²)	25
Stations in range	140
Stations occupied	24
Birds recorded	63
Total population	4
SE	1
Pop. by habitat type					
Ohia	4
Ring-necked Pheasant					
Range (km ²)	153	...	14	20	25
Stations in range	425	...	80	77	140
Stations occupied	244	...	6	31	1
Birds recorded	1258	...	7	76	1
Total population	1728	...	9	162	9
SE	90	...	9	27	9
Pop. by habitat type					
Ohia	99	...	9	...	9
Koa-ohia	171
Mamane	54
Other natives	729	63	...
Intro. trees	54	63	...
Treeless	18	27	...
Common Peafowl					
Range (km ²)	25
Stations in range	62
Stations occupied	21
Birds recorded	107
Total population	8
SE	1
Pop. by habitat type					
Koa-ohia	1
Other natives	7
Wild Turkey					
Range (km ²)	9
Stations in range	24
Stations occupied	3
Birds recorded	4
Total population	2
SE	1
Pop. by habitat type					
Other natives	2
California Quail					
Range (km ²)	37	20	...
Stations in range	81	77	...
Stations occupied	25	1	...
Birds recorded	56	3	...
Total population	50	7	...
SE	10	1	...
Pop. by habitat type					
Other natives	50	7	...

TABLE 34
CONTINUED

	East Maui	West Maui	Molokai	Lanai	Kauai
Rock Dove					
Stations occupied	...	2	1
Birds recorded	...	8	2
Spotted Dove					
Range (km ²)	85	13	86	20	25
Stations in range	70	84	438	77	140
Stations occupied	44	7	148	10	14
Birds recorded	96	12	375	16	23
Total population	65	4	309	15	15
SE	9	1	29	5	5
Pop. by habitat type					
Ohia	17	4	165	...	15
Koa-ohia	2
Other natives	27	...	51	3	...
Intro. trees	18	...	93	13	...
Zebra Dove					
Range (km ²)	7	...	19	20	...
Stations in range	19	...	90	77	...
Stations occupied	15	...	22	5	...
Birds recorded	43	...	41	8	...
Total population	35	...	91	3	...
SE	4	...	32	2	...
Pop. by habitat type					
Ohia	1
Other natives	35	...	16	2	...
Intro. trees	74	1	...
Common Barn-Owl					
Stations occupied	1
Birds recorded	1
Eurasian Skylark					
Range (km ²)	87
Stations in range	220
Stations occupied	67
Birds recorded	172
Total population	381
SE	49
Pop. by habitat type					
Koa-ohia	14
Mamane	33
Other natives	274
Intro. trees	7
Treeless	2
Japanese Bush-Warbler					
Range (km ²)	17	...	27
Stations in range	48	...	172
Stations occupied	1	...	43
Birds recorded	1	...	164
Total population	5	...	202
SE	5	...	40
Pop. by habitat type					
Ohia	5	...	202
White-rumped Shama					
Range (km ²)	25
Stations in range	140

TABLE 34
CONTINUED

	East Maui	West Maui	Molokai	Lanai	Kauai
Stations occupied	8
Birds recorded	15
Total population	45
SE	18
Pop. by habitat type					
Ohia	45
Melodious Laughing-thrush					
Range (km ²)	290	19	25
Stations in range	863	135	140
Stations occupied	299	23	108
Birds recorded	724	47	450
Total population	2078	43	445
SE	138	11	37
Pop. by habitat type					
Ohia	1236	42	445
Koa-ohia	409
Mamane	2
Other natives	31
Intro. trees	370	1
Treeless	29
Red-billed Leiothrix					
Range (km ²)	332	28	63
Stations in range	1005	135	358
Stations occupied	674	60	150
Birds recorded	2858	143	759
Total population	18,652	755	1836
SE	607	116	114
Pop. by habitat type					
Ohia	11,391	755	1831
Koa-ohia	3115
Mamane	1
Other natives	1199
Intro. trees	2686	...	5
Treeless	260
Northern Mockingbird					
Range (km ²)	99	0.5	15
Stations in range	251	4	68
Stations occupied	147	2	13
Birds recorded	563	2	24
Total population	1122	1	69
SE	77	1	25
Pop. by habitat type					
Ohia	...	1
Koa-ohia	2
Mamane	12
Other natives	939	...	38
Intro. trees	7	...	31
Treeless	162
Common Myna					
Range (km ²)	24	...	11	20	...
Stations in range	63	...	46	77	...
Stations occupied	26	...	9	3	...
Birds recorded	94	...	25	3	...
Total population	185	...	136	22	...
SE	45	...	76	11	...

TABLE 34
CONTINUED

	East Maui	West Maui	Molokai	Lanai	Kauai
Pop. by habitat type					
Koa-ohia	33
Other natives	136	...	57	6	...
Intro. trees	17	...	79	16	...
Japanese White-eye					
Range (km ²)	384	43	125	20	25
Stations in range	1091	203	573	77	140
Stations occupied	818	178	554	72	138
Birds recorded	3727	773	4213	508	1471
Total population	113,968	19,230	119,092	11,380	15,231
SE	3767	1323	4518	1887	721
Pop. by habitat type					
Ohia	64,277	18,864	74,785	...	15,218
Koa-ohia	18,904
Mamane	82
Other natives	12,744	...	9751	4156	...
Intro. trees	13,666	65	34,463	5711	...
Treeless	4297	301	93	1513	12
Northern Cardinal					
Range (km ²)	311	21	116	20	25
Stations in range	896	121	488	77	140
Stations occupied	242	16	163	65	37
Birds recorded	697	31	305	304	68
Total population	2937	55	1741	1116	111
SE	187	16	142	152	20
Pop. by habitat type					
Ohia	1120	54	671	...	111
Koa-ohia	385
Mamane	1
Other natives	660	...	110	268	...
Intro. trees	713	2	959	704	...
Treeless	59	...	1	144	...
House Finch					
Range (km ²)	134	21	112	20	25
Stations in range	417	111	496	77	140
Stations occupied	157	9	174	9	1
Birds recorded	862	16	416	23	2
Total population	7635	123	5321	614	22
SE	500	68	652	202	22
Pop. by habitat type					
Ohia	11	116	2131	...	22
Koa-ohia	1013
Mamane	3
Other natives	3753	...	717	46	...
Intro. trees	2733	2	2470	332	...
Treeless	123	4	3	236	...
House Sparrow					
Stations occupied	5
Birds recorded	11
Nutmeg Mannikin					
Range (km ²)	113	26	97	...	25
Stations in range	116	122	421	...	140
Stations occupied	64	21	94	...	1
Birds recorded	190	106	444	...	4
Total population	8192	3290	10,619	...	128
SE	1507	1117	1851	...	128

TABLE 34
CONTINUED

	East Maui	West Maui	Molokai	Lanai	Kauai
Pop. by habitat type					
Ohia	2051	3290	3077	...	128
Koa-ohia	1626
Other natives	3242	...	1188
Intro. trees	1253	...	5868
Treeless	19	...	485

TABLE 35
DENSITY [MEAN (SE)] OF THE BLACK FRANCOLIN AND GRAY FRANCOLIN BY ELEVATION, HABITAT, AND STUDY AREA^a

	Black Francolin					Gray Francolin			
	Kona	Mauna Kea	Kohala	East Maui	Molokai	East Maui	West Maui	Molokai	Lanai
<i>Elevation</i>									
100–300 m	0	0	...
300–500 m	+ (+)	...	0	0	+ (+)	0	...	0	...
500–700 m	1 (+)	...	0	0	3 (1)	0	0	0	+ (+)
700–900 m	1 (+)	...	0	4 (2)	3 (1)	3 (2)	4 (4)	1 (+)	+ (+)
900–1100 m	+ (+)	...	+ (+)	2 (1)	2 (+)	2 (1)	+	+ (+)	1 (1)
1100–1300 m	2 (+)	...	+ (+)	+ (+)	+ (+)	5 (1)	+	0	...
1300–1500 m	1 (+)	...	0	0	+ (+)	1 (+)	0	0	...
1500–1700 m	1 (+)	...	0	0	...	+ (+)	0
1700–1900 m	+ (+)	0	...	+ (+)	0
1900–2100 m	+ (+)	+ (+)	...	0	...	1 (1)
2100–2300 m	+ (+)	+ (+)	...	0	...	+ (+)
2300–2500 m	0	0	...	0	...	+ (+)
2500–2700 m	...	0	...	0	...	+ (+)
2700–2900 m	...	0	...	0	...	+ (+)
2900–3100 m	...	0
<i>Habitat</i>									
Ohia	1 (+)	...	+ (+)	0	1 (+)	0	+ (+)	0	...
Koa-ohia	+ (+)	0	...	+ (+)
Koa-mamane	*
Mamane-naio	2 (+)	+ (+)
Mamane	1 (+)	+ (+)	...	0	...	0
Other natives	2 (+)	2 (1)	4 (1)	2 (1)	...	+ (+)	1 (+)
Intro. trees	1 (1)	...	+ (+)	0	4 (1)	1 (1)	0	+ (+)	+ (+)
Treeless	+ (+)	...	+	...	+ (+)	+ (+)	0	0	+ (+)

^a Densities are given in birds/km²; + indicates stratum was in the species range but density <0.5 birds/km²; 0 indicates stratum was outside range but was sampled; ... indicates stratum was not sampled in study area, * indicates stratum was not sampled in range but was sampled elsewhere in study area.

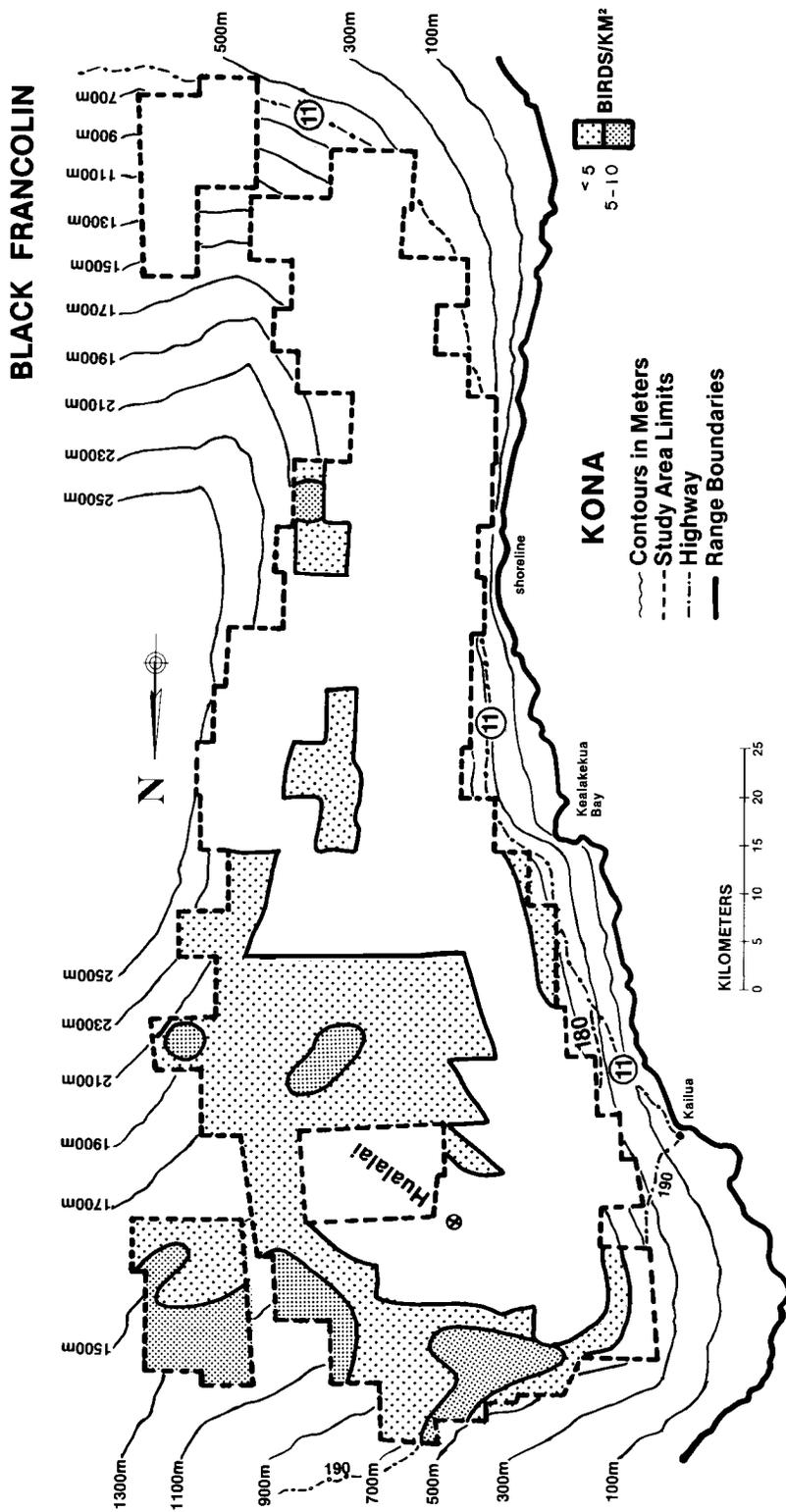


FIGURE 160. Distribution and abundance of the Black Francolin in the Kona study area.

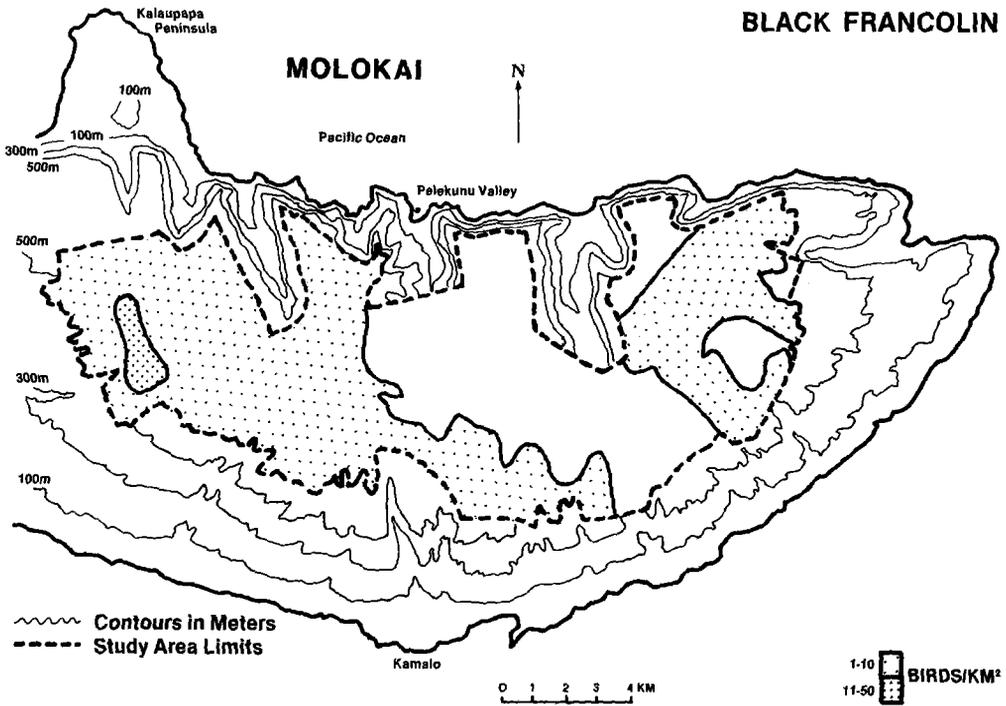


FIGURE 161. Distribution and abundance of the Black Francolin in the Molokai study area.

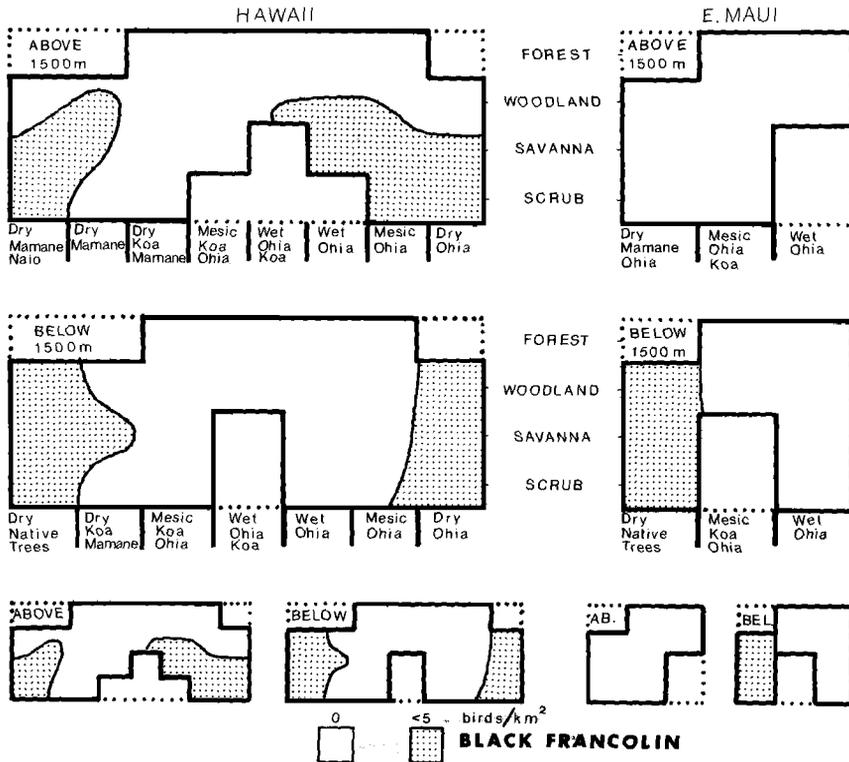


FIGURE 162. Habitat response graphs of the Black Francolin. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

TABLE 36
REGRESSION MODELS FOR HABITAT RESPONSE OF THE BLACK FRANCOLIN, ERCKEL'S FRANCOLIN, AND GRAY FRANCOLIN^a

	Black Francolin			Erckel's Francolin			Gray Francolin	
	Kona	Molokai	Puna	Kipukas	Kona	Mauna Kea	Maui	Lanai
<i>R</i> ²	0.10*	0.23*	0.60*	0.32*	0.26*	0.07*	0.24*	0.18
Moisture	-9.1*	-7.7*	-7.6*	-4.9*	-16.5*	X	-8.5*	-3.4
Elevation	4.0*	4.8*	6.5*	-11.2*	...	-2.2
(Elevation) ²	-5.6*	-4.2*	-6.6*	10.7*	-20.2*	...	-5.9*	...
Tree biomass	3.6*	3.5*	...	4.8*	...
(Tree biomass) ²	7.6*	...	-4.4*
Crown cover	-3.9*	-3.2	-3.8*	2.6
Canopy height	5.4*	...	-4.0*	...	3.9*	3.3
Koa	-5.1*	X	X	3.2	...	X	...	X
Ohia	-6.4*	...	6.9*	...	-3.3*	X
Naio	...	X	X	...	-4.6*	...	X	X
Mamane	-4.1*	X	-2.6	X
Intro. trees	-2.3	3.1	...	X	3.6*	X	-2.7	...
Shrub cover	3.9*	...	2.6	-7.7*	...
Ground cover	6.8*	...	6.1*	...
Native shrubs	6.0*	X
Intro. shrubs	-5.1*	X
Ground ferns	-3.8*	X	...	X
Matted ferns	X
Tree ferns	-6.1*	X	...	X	...	X
Ieie	...	X	...	X	...	X	...	X
Passiflora	...	X	X	X	6.7*	X	11.2*	X
Native herbs	X	...	X
Intro. herbs	2.7	-3.0	X
Native grasses	-3.4*	...	4.1*	X
Intro. grasses	3.4*

^a *R*² is the variance accounted for by the model. Entries are *t* statistics and all are significant at *P* < 0.05; * indicates *P* < 0.001; ... indicates variable not significant (*P* > 0.05); X indicates variable not available for inclusion in model.

ERCKEL'S FRANCOLIN (*Francolinus erckelii*)

Erckel's Francolins were introduced to all major islands between 1957 and 1962 (R. L. Walker, pers. comm.) and are native to northeast Africa (Berger 1981). They occur alone or in flocks, and feed on grass shoots, insects, and seeds; drinking water may also be a requirement (Mackworth-Praed and Grant 1957). In their native range, they occur in high-elevation semi-arid open scrub and open woodlands (Bohl 1972).

We found this species in all but three study areas (Tables 33, 34, 37; Figs. 163–167). On Hawaii 1800 ± 150 (95% CI) birds inhabit the study areas. Populations are well established in the Mauna Kea mamane-naio woodland, on the north slope of Hualalai, in the Puu Lehua/Devil Country area south of Hualalai, on the Kahuku Tract, on the Kapapala Tract, and along the east margin of the Kau Desert. Their range is probably still expanding on Hawaii. On Maui an estimated 2 ± 4 birds occur on the northwest slopes of Haleakala. On Molokai 10 ± 6 birds occur in the dry scrublands in the southwest part of the

study area. On Lanai 45 ± 15 birds occur throughout the study area. On Kauai, birds occur occasionally in forest clearings along trails, particularly near the tops of dry canyons. Well established populations occur on all these islands outside the study areas.

Highest densities occur in dry open woodlands at lower elevations (Table 36, Fig. 168). They are strongly associated with passiflora and are probable dispersal agents of banana poka (Warschauer et al. 1983). No variable meets the entry criteria in the Lanai regression model.

Erckel's Francolins primarily occur in dry areas. Even in the Kipukas, the driest study area, a negative relation to moisture occurs. The Kipukas model shows a curious bimodal relation for elevation that reflects the distribution of birds at the tops and bottoms of certain transects, but not in the middle. This separation may represent birds arriving at lower elevations from the population in Puna and birds arriving independently from the high elevation population. Future dispersal may close the hiatus.

In Kona, Erckel's Francolins are associated with

TABLE 37
DENSITY [MEAN (SE)] OF THE ERCKEL'S FRANCOLIN BY ELEVATION, HABITAT, AND STUDY AREA^a

	Hamakua	Puna	Kipukas	Kona	Mauna Kea	East Maui	Molokai	Lanai	Kauai
<i>Elevation</i>									
100–300 m	0
300–500 m	0	0	...	0	...	0	0
500–700 m	0	+ (+)	...	7 (1)	...	0	0	4 (1)	...
700–900 m	0	17 (2)	...	9 (1)	...	1 (1)	+ (+)	3 (1)	...
900–1100 m	0	8 (1)	...	7 (1)	...	+ (+)	1 (+)	3 (1)	...
1100–1300 m	0	+ (+)	5 (1)	5 (1)	...	+ (+)	2 (1)	...	+ (+)
1300–1500 m	0	...	+ (+)	4 (+)	...	*	0	...	+ (+)
1500–1700 m	0	...	+ (+)	1 (+)	...	1 (1)
1700–1900 m	+ (+)	...	1 (1)	1 (+)	...	0
1900–2100 m	0	...	+ (+)	1 (+)	4 (1)	0
2100–2300 m	0	...	0	+ (+)	5 (2)	0
2300–2500 m	+ (+)	4 (2)	0
2500–2700 m	2 (1)	0
2700–2900 m	3 (1)	0
2900–3100 m	+ (+)
<i>Habitat</i>									
Ohia	0	10 (1)	+ (+)	3 (+)	...	0	2 (1)	...	+ (+)
Koa-ohia	+ (+)	...	2 (+)	4 (1)	...	2 (2)
Koa-mamane	+ (+)	...	1 (+)	+ (+)
Mamane-naio	5 (1)	4 (1)
Mamane	4 (1)	3 (1)	0
Other natives	+ (+)	...	+ (+)	6 (1)	...	+ (+)	1 (+)	1 (1)	...
Intro. trees	+ (+)	7 (1)	...	+ (+)	+ (+)	4 (1)	...
Treeless	0	+ (+)	+ (+)	+ (+)	...	0	+ (+)	2 (1)	+ (+)

^a Densities are given in birds/km²; + indicates stratum was in the species range but density <0.5 birds/km²; 0 indicates stratum was outside range but was sampled; ... indicates stratum was not sampled in study area, * indicates stratum was not sampled in range but was sampled elsewhere in study area.

sparse woodland and scattered high trees. Some response to individual tree species also occurs in the regression models. Ohia generates a positive response in Puna, where birds frequent spindly open ohia groves on recent substrates in drier areas. The negative tree fern term for Puna represents absence in rainforest interiors. In Kona lower densities are associated with naio and higher ones with introduced trees.

Erckel's Francolins also respond to some understory components. In Puna they are associated with dry native shrubs on recent substrates. In Kona low densities occur in dense shrub thickets of guava and Christmas-berry at lower elevations. The strong response to passiflora in Kona is paralleled by their occurrence in Hamakua and on Maui at passiflora infestations. Little response to herbs or grasses occurs. The difference in signs for native grasses in Puna and Kona results from the distribution of native graminoids in wet forest interiors in Puna where birds are absent, and in dry grassy woodlands in Kona where birds are common. Native grasses thus indicate different habitat types in these two study areas.

GRAY FRANCOLIN (*Francolinus pondicerianus*)

Gray Francolins were introduced in 1958 (R. L. Walker, pers. comm.) and are native to India (Berger 1981). There they inhabit dry open grasslands and xerophytic thorn-scrub (Ali and Ripley 1969) and feed extensively on plants and insects (Bump 1970).

We found Gray Francolins in the Kona, East Maui, West Maui, Molokai, and Lanai study areas (Tables 33–35, Fig. 169). Although rare on Oahu (R. L. Walker, pers. comm.), Gray Francolins are well established in the drier lowland areas of all the major islands, especially from sea level to 1000 m elevation (Lewin 1971). Only the extreme upper elevations of the range of this species fall in our study areas. We considered the two birds recorded near the lower study boundary at Puu Waawaa to be extralimital.

Gray Francolins are associated with scrublands and sparse woodlands in dry low-elevation areas, but appear to avoid brushy understories (Table 36, Fig. 170). Although we had too few observations to construct a habitat response graph, the areas inhabited on Hawaii are similar

ERCKEL'S FRANCOLIN

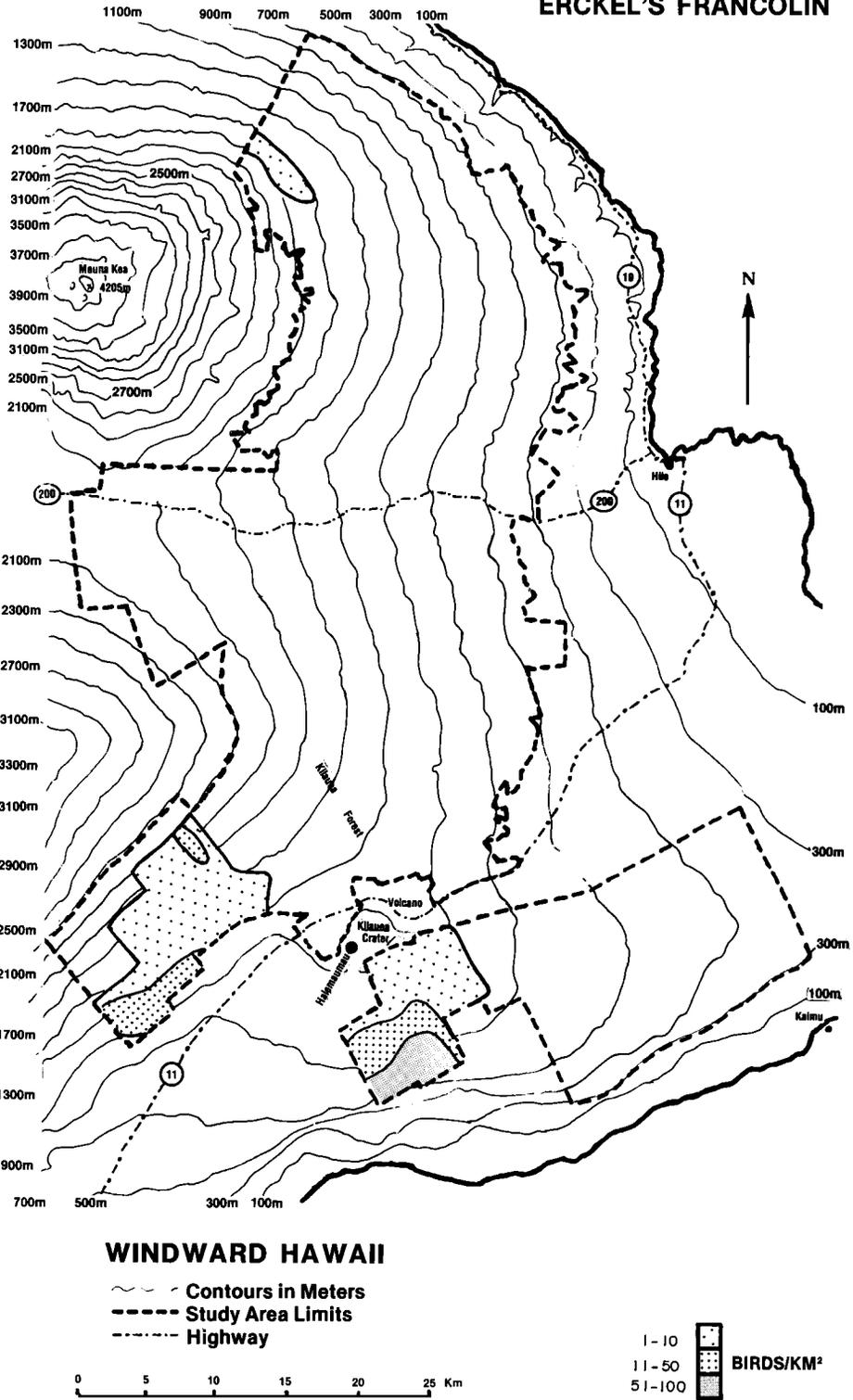


FIGURE 163. Distribution and abundance of the Erckel's Francolin in the windward Hawaii study areas.

ERCKEL'S FRANCOLIN

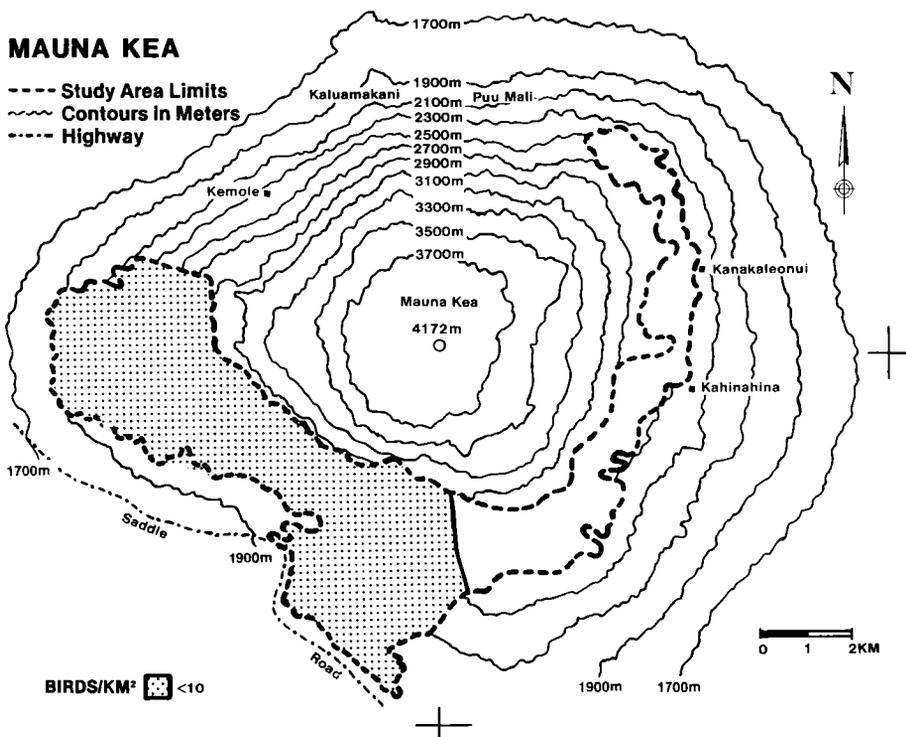


FIGURE 165. Distribution and abundance of the Erckel's Francolin in the Mauna Kea study area.

ERCKEL'S FRANCOLIN

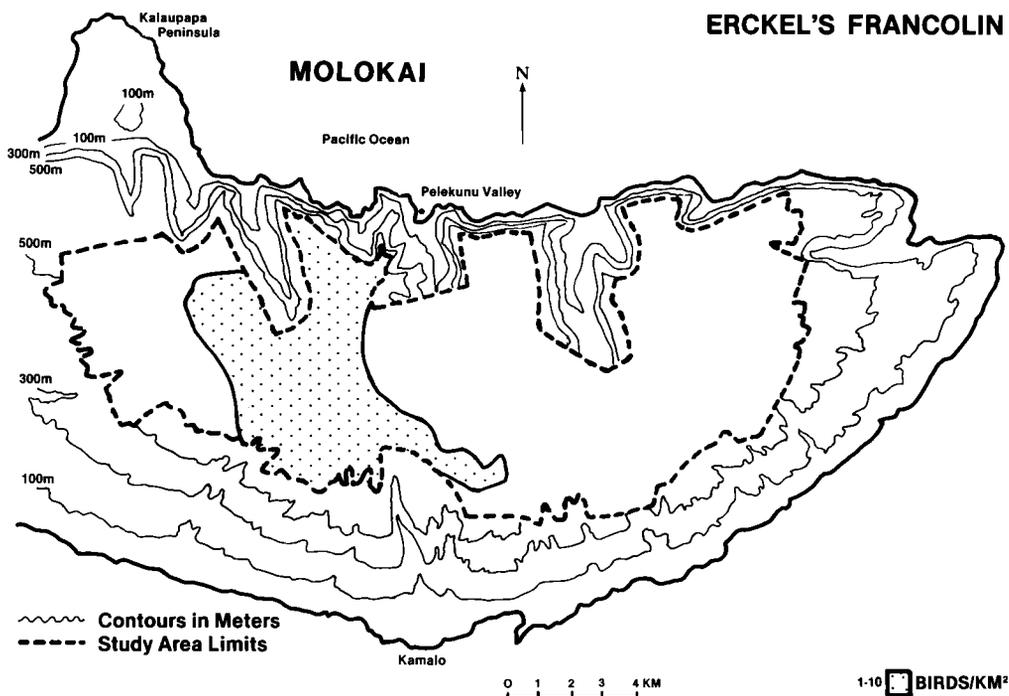


FIGURE 166. Distribution and abundance of the Erckel's Francolin in the Molokai study area.

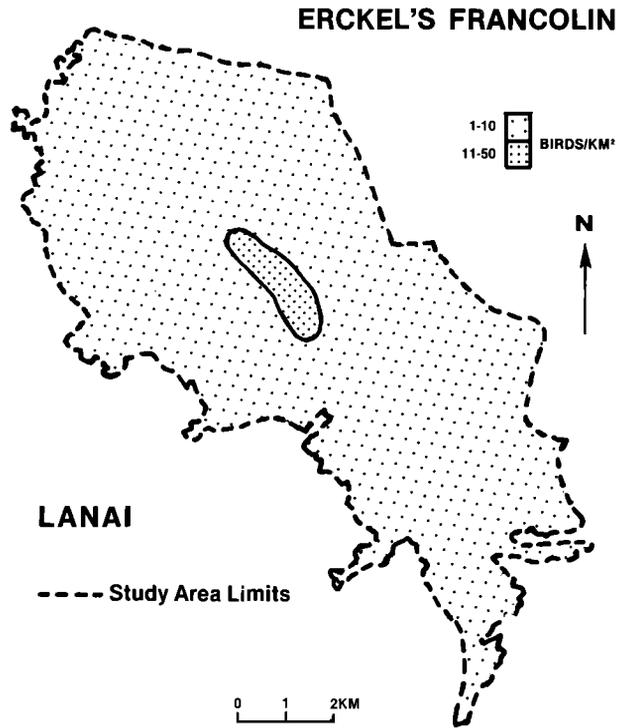
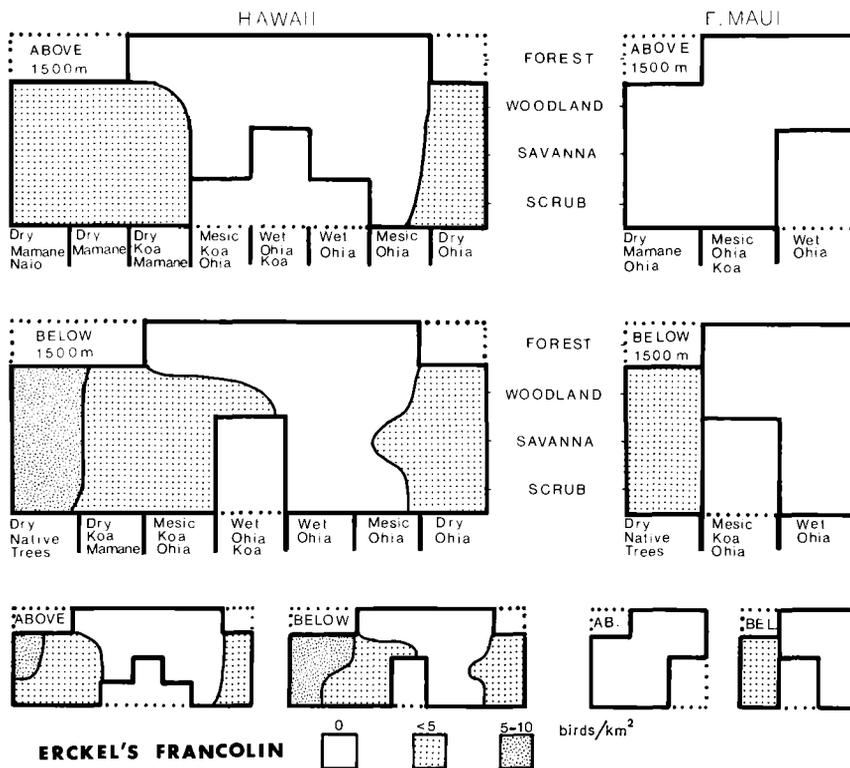


FIGURE 167. Distribution and abundance of the Erckel's Francolin in the Lanai study area.



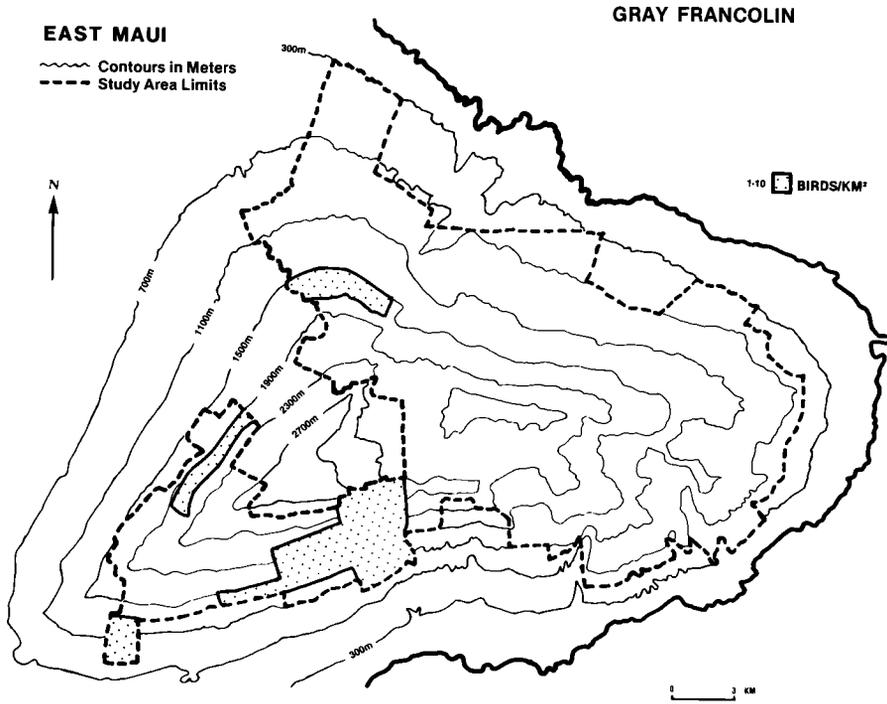


FIGURE 169. Distribution and abundance of the Gray Francolin in the East Maui study area.

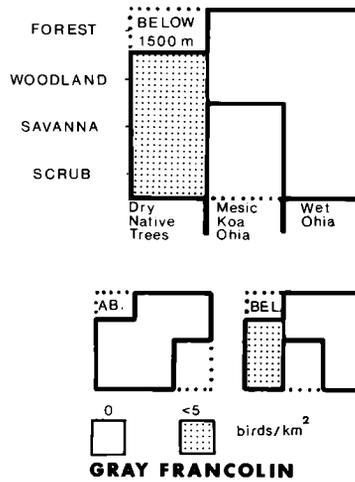


FIGURE 170. Habitat response graphs of the Gray Francolin. (Graphs give mean density below 1500 m elevation for East Maui; half-size graphs give standard deviation.)

FIGURE 168. Habitat response graphs of the Erckel's Francolin. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

to those shown for Maui. Gray Francolins are common in open mesquite woodland in lowland leeward Hawaii (Lewin 1971). The preference for passiflora is biologically significant, because Gray Francolins are possible dispersal agents for banana poka (Warshauer et al. 1983).

CHUKAR (*Alectoris chukar*)

Chukar were first introduced to the Hawaiian Islands in 1923 (Caum 1933) and are native to southern Eurasia. During their survey, Schwartz and Schwartz (1949) found very low numbers on Molokai and Lanai. Berger (1981) considered Chukar to be well established on all the main islands, although they may be absent from Oahu now, as there have been no game reports since 1979 (R. L. Walker, unpub. data). Chukar feed on grass, weeds, seeds, leaves, bulbs, fruits, berries, and insects (Bohl 1971). Because Chukar flock and we had no independent estimates of flock size, our sampling design did not yield unbiased density estimates.

Chukar have greatly increased since 1949 due to introduction. We found them well established in dry upland habitats on all study areas except Lanai (Tables 33, 34, 38, Figs. 171–175). On

Hawaii 5500 ± 1300 (95% CI) birds occupy four study areas. They are best established on the upper slopes of Mauna Kea where 4200 ± 1100 birds occur. From release sites there and on Puu Waawaa, Chukar have spread across Hualalai and the upper elevations of windward Hawaii. On East Maui 1700 ± 400 birds are well established in Haleakala Crater and on the leeward side; these birds may compete with Hawaiian Geese for browse. On Molokai 250 ± 150 birds occur sparsely in dry open habitat. Although we failed to find Chukar on Lanai, Hirai (1978) reported birds at lower elevations near release sites.

The habitat response graphs (Fig. 176) and regression models (Table 39) show that Chukar occur at high elevations in dry areas with sparse tree and ground cover. Mamane is characteristic of this habitat configuration and usually has high Chukar densities.

Rocky slopes and water are two important habitat requirements for Chukar that were not examined as variables. Rocky slopes, including talus, bluffs, or rimrock, are essential to good Chukar habitat for escape routes and roosting sites, as is the presence of drinking water within 1 km (Johnsgaard 1973). In most areas where we

TABLE 38
DENSITY [MEAN (SE)] OF THE CHUKAR AND RED JUNGLEFOWL BY ELEVATION, HABITAT, AND STUDY AREA^a

	Chukar						Red Junglefowl		
	Hamakua	Kipukas	Kona	Mauna Kea	East Maui	West Maui	Molokai	Puna	Kauai
<i>Elevation</i>									
100–300 m	0
300–500 m	0	...	0	...	0	...	0	0	...
500–700 m	0	...	0	...	0	0	0	0	...
700–900 m	0	...	0	...	0	+ (+)	44 (4)	+ (+)	...
900–1100 m	0	...	15 (5)	...	0	2 (2)	30 (15)	+ (+)	...
1100–1300 m	0	0	39 (39)	...	30 (17)	+ (+)	17 (6)	+ (+)	+ (+)
1300–1500 m	0	0	3 (1)	...	15 (15)	0	0	...	+ (+)
1500–1700 m	3 (3)	+ (+)	2 (+)	...	16 (6)	0
1700–1900 m	6 (4)	4 (1)	2 (1)	...	9 (3)	0
1900–2100 m	46 (11)	3 (1)	5 (1)	6 (4)	19 (4)
2100–2300 m	5 (5)	4 (2)	8 (2)	16 (7)	26 (7)
2300–2500 m	2 (1)	6 (3)	17 (5)
2500–2700 m	24 (7)	21 (9)
2700–2900 m	68 (14)	7 (1)
2900–3100 m	171 (82)
<i>Habitat</i>									
Ohia	0	3 (1)	4 (1)	...	5 (5)	1 (1)	28 (9)	+ (+)	+ (+)
Koa-ohia	+ (+)	+ (+)	4 (3)	...	8 (7)
Koa-mamane	29 (9)	3 (1)	1 (+)
Mamane-naio	4 (4)	24 (5)
Mamane	6 (1)	38 (9)	103 (48)
Other natives	5 (3)	3 (2)	1 (1)	...	23 (4)	...	1 (1)
Intro. trees	+ (+)	...	7 (7)	...	5 (2)	0	+ (+)
Treeless	0	11 (11)	7 (2)	...	19 (3)	0	+ (+)	+ (+)	+ (+)

^a Densities are given in birds/km²; + indicates stratum was in the species range but density <0.5 birds/km²; 0 indicates stratum was outside range but was sampled; ... indicates stratum was not sampled in study area.

CHUKAR

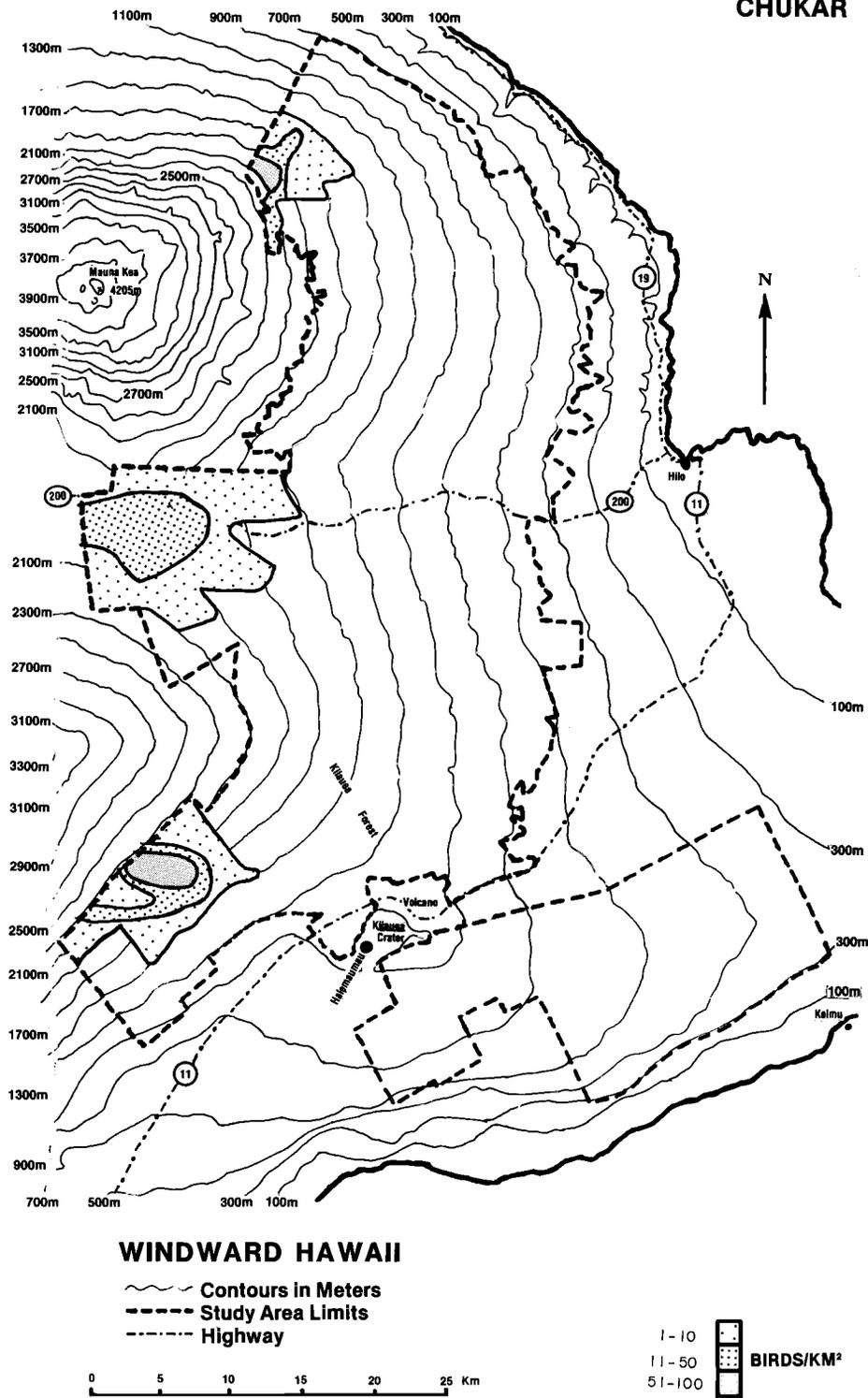


FIGURE 171. Distribution and abundance of the Chukar in the windward Hawaii study areas.

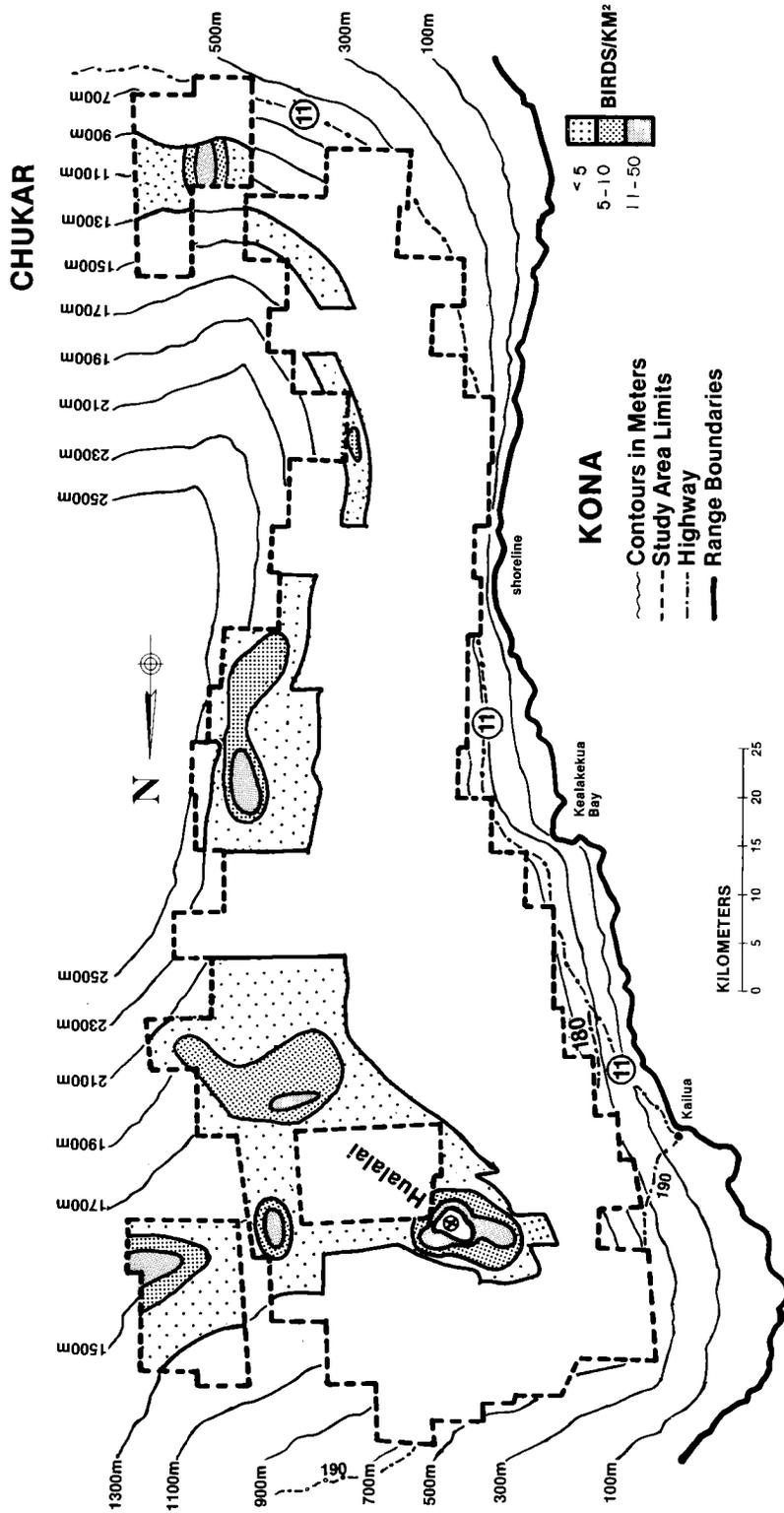


FIGURE 172. Distribution and abundance of the Chukar in the Kona study area.

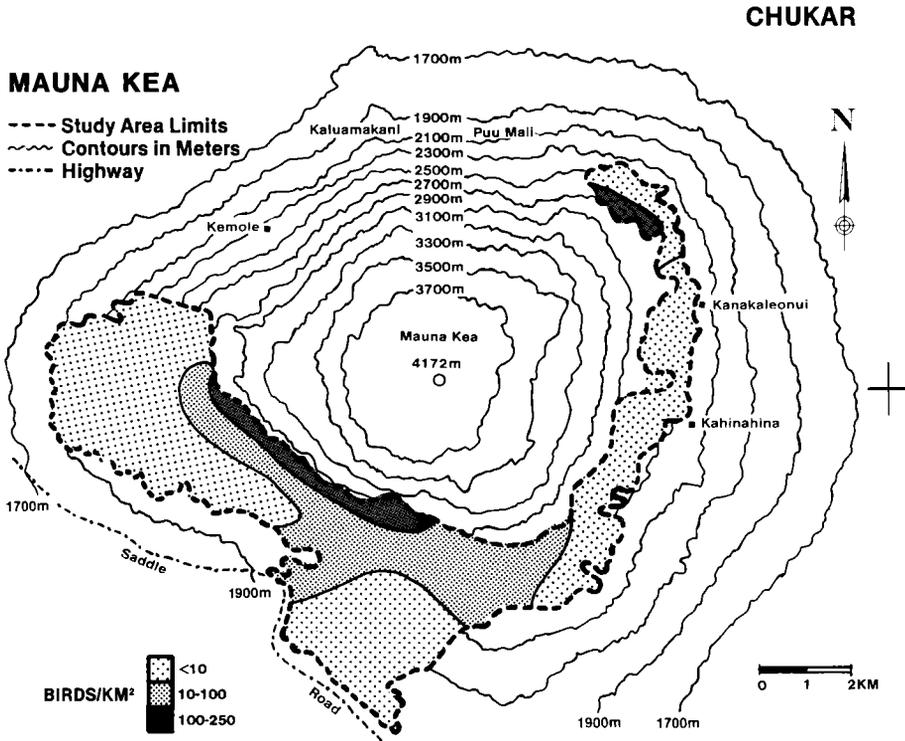


FIGURE 173. Distribution and abundance of the Chukar in the Mauna Kea study area.

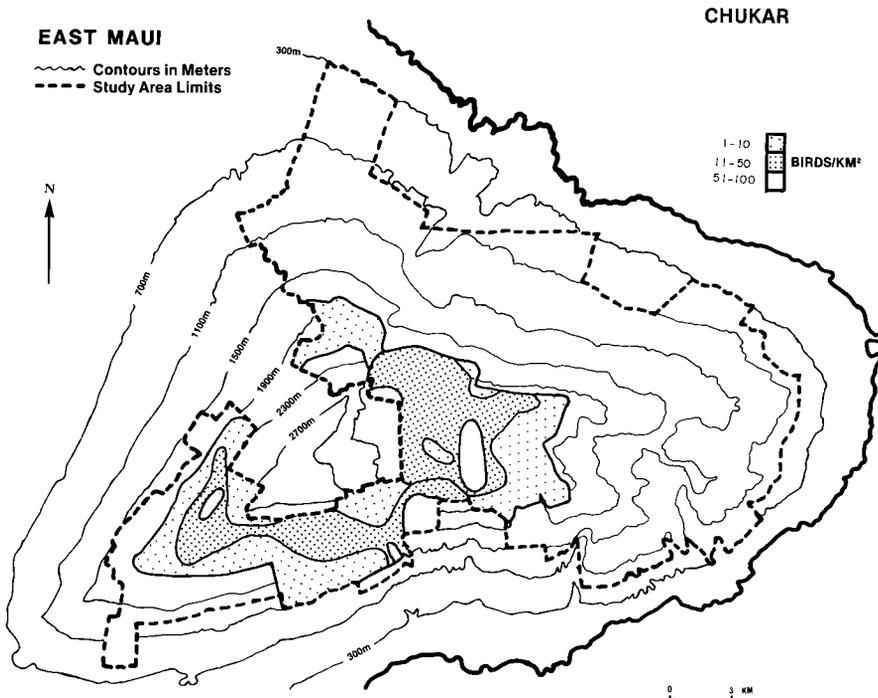


FIGURE 174. Distribution and abundance of the Chukar in the East Maui study area.

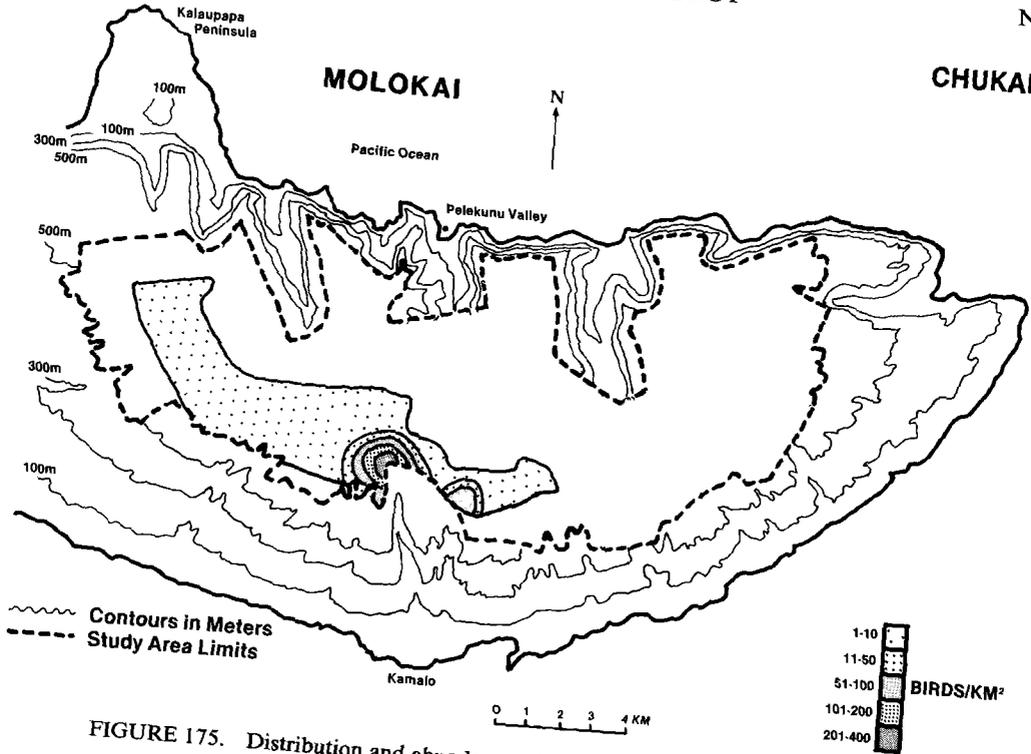


FIGURE 175. Distribution and abundance of the Chukar in the Molokai study area.

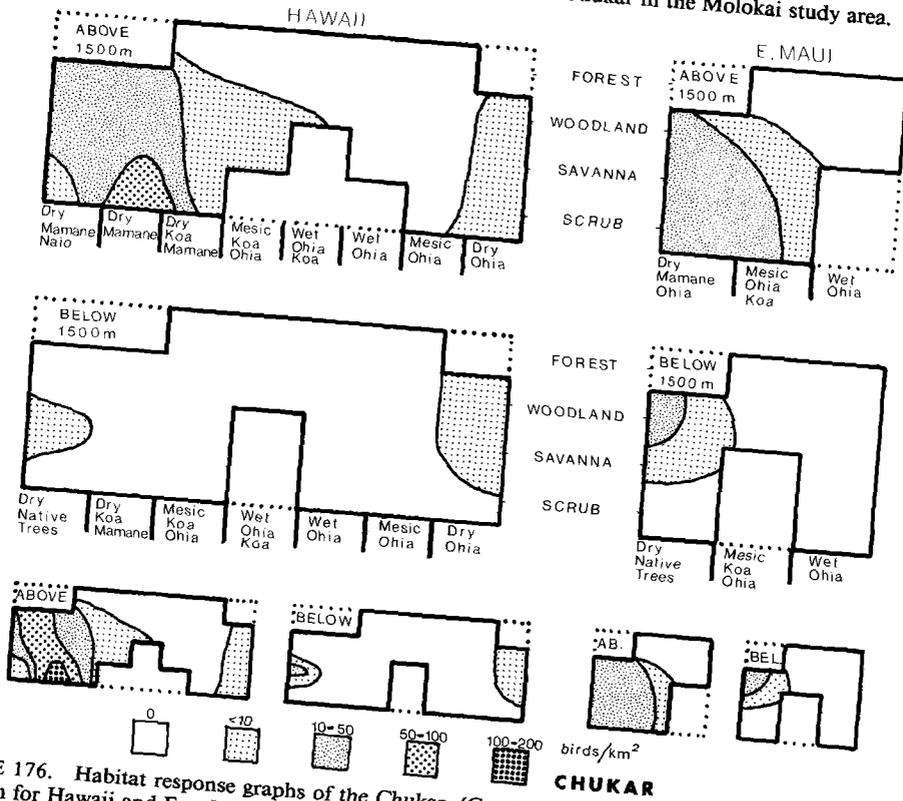


FIGURE 176. Habitat response graphs of the Chukar. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

TABLE 39
REGRESSION MODELS FOR HABITAT RESPONSE OF THE CHUKAR, KALIJ PHEASANT, AND RED JUNGLEFOWL^a

	Chukar					Kalij Pheasant		Red Junglefowl
	Hamakua	Kipukas	Kona	Mauna Kea	Maui	Hamakua	Kona	Kauai
R^2	0.21*	0.12*	0.08*	0.21*	0.32*	0.01*	0.08*	0.36*
Moisture	X	-5.8*	...	5.5*	X
Elevation	...	4.9*	-3.6*	-4.6*	4.1*	-3.1
(Elevation) ²	4.9*	5.1*	2.9
Tree biomass	-9.0*	...	-9.8*	...	3.1	X
(Tree biomass) ²	7.0*
Crown cover
Canopy height	2.5	-2.1	...
Koa	X	X
Ohia	X	X
Naio	X	X	...	X
Mamane	12.5*	7.0*	X
Intro. trees	...	X	...	X	-2.7	X
Shrub cover	-12.4*	...	3.0
Ground cover	-5.6*	-2.5
Native shrubs	...	-4.2*	...	X
Intro. shrubs	X	2.3
Ground ferns	X	-3.0	...	X	...	X	2.8	...
Matted ferns	-2.9	X	-2.5	...
Tree ferns	X	X	...	X	...	X	-4.6*	...
Ieie	X	X	...	X	...	X	...	3.5*
Passiflora	...	X	...	X	...	5.2*	9.0*	X
Native herbs	X	X	...	X	...	-2.3
Intro. herbs	X	...	-2.6	X
Native grasses
Intro. grasses

^a R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ... indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

found Chukar, rocky slopes are frequent, and water is usually available from ranching or game management activities. On Mauna Kea special watering units are maintained to support high densities of Chukar and other gamebirds. The native habitat in India is similar to areas occupied in Hawaii—barren, stony hillsides with sparse shrub cover, boulder-strewn ravines, and the nearby presence of drinking water (Ali and Ripley 1969).

JAPANESE QUAIL (*Coturnix japonica*)

Japanese Quail were introduced to Maui and Lanai in 1921 (Caum 1933). Schwartz and Schwartz (1949) found them well established on all the islands except Oahu, in grasslands, pastures, and some agricultural fields. Native to China and Japan, this species feeds primarily on seeds and insects (Schwartz and Schwartz 1949).

We found the species only on Hawaii and Maui (Tables 33, 34, 40, Figs. 177–179), with a total population of 270 ± 150 (95% CI) birds in the study areas. The Kau population was not reported by Schwartz and Schwartz (1949), but by 1984 the species had become moderately com-

mon in the subalpine scrub (S. Mountainspring, pers. observ.). Japanese Quail occur in dry woodland, savanna, and scrub (Fig. 180). Highest densities occur outside the study areas in very open tall grass pastures on the northwest slopes of both Mauna Kea and Haleakala. Since we failed to sample much of the area indicated as within range by earlier workers on Maui, we cannot state whether the abundance and range changed since 1948.

KALIJ PHEASANT (*Lophura leucomelana*)

Kalij Pheasant, native to the Himalayan foothills and northern southeast Asia, were introduced in 1962 (Lewin 1971). In the Hawaiian Islands they have been introduced only to Hawaii where the range is still expanding. The diet includes seeds, fleshy fruit, leaves, and insects (Bohl 1971).

As late as 1972 this species was listed as “possibly” established on Puu Waawaa on northwest Hawaii (Berger 1972). During the 1970s, however, Kalij Pheasant became well established throughout the wetter forests of Kona and invaded the upper-elevation forests of Hamakua

TABLE 40
DENSITY [MEAN (SE)] OF THE JAPANESE QUAIL AND KALIJ PHEASANT BY ELEVATION, HABITAT, AND STUDY AREA^a

	Japanese Quail					Kalij Pheasant		
	Kau	Hamakua	Kipukas	Mauna Kea	East Maui	Hamakua	Kipukas	Kona
<i>Elevation</i>								
100–300 m
300–500 m	...	0	0	0	...	3 (3)
500–700 m	0	0	0	0	...	5 (2)
700–900 m	0	0	0	0	...	7 (1)
900–1100 m	0	0	2 (2)	0	...	13 (4)
1100–1300 m	0	0	6 (6)	...	24 (13)	8 (8)	0	12 (2)
1300–1500 m	0	+ (+)	5 (2)	...	36 (12)	3 (2)	0	8 (2)
1500–1700 m	26 (26)	2 (1)	2 (2)	...	19 (16)	2 (2)	0	7 (1)
1700–1900 m	+ (+)	2 (2)	0	...	0	3 (3)	3 (1)	7 (2)
1900–2100 m	+ (+)	0	0	+ (+)	0	0	0	4 (1)
2100–2300 m	0	0	0	1 (+)	0	0	0	2 (1)
2300–2500 m	+ (+)	0	7 (7)
2500–2700 m	+ (+)	0
2700–2900 m	0	0
2900–3100 m	0
<i>Habitat</i>								
Ohia	7 (7)	2 (+)	6 (6)	...	0	2 (2)	1 (1)	5 (1)
Koa-ohia	0	+ (+)	+ (+)	...	34 (14)	3 (2)	13 (13)	13 (2)
Koa-mamane	...	0	3 (3)	+ (+)	0	6 (2)
Mamane-naio	+ (+)	22 (22)
Mamane	1 (+)	0	5 (2)
Other natives	...	3 (1)	3 (1)	...	15 (8)	+ (+)	+ (+)	25 (5)
Intro. trees	...	0	4 (4)	3 (3)	...	15 (+)
Treeless	0	+ (+)	0	...	0	0	0	+ (+)

^a Densities are given in birds/km²; + indicates stratum was in the species range but density <0.5 birds/km²; 0 indicates stratum was outside range but was sampled; ... indicates stratum was not sampled in study area.

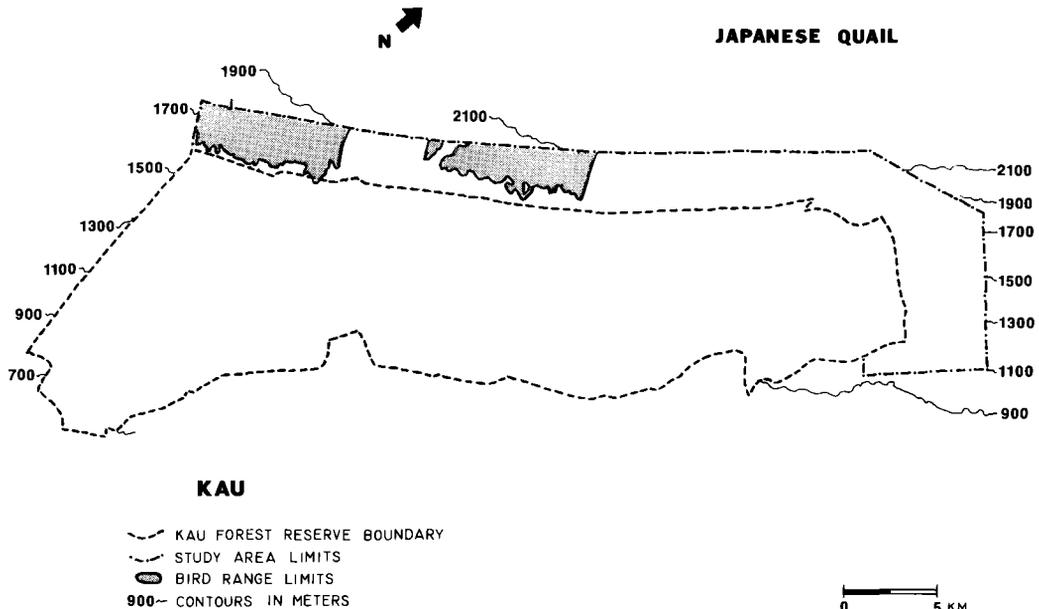


FIGURE 177. Distribution and abundance of the Japanese Quail in the Kau study area. (Density within range is less than 10 birds/km².)

JAPANESE QUAIL

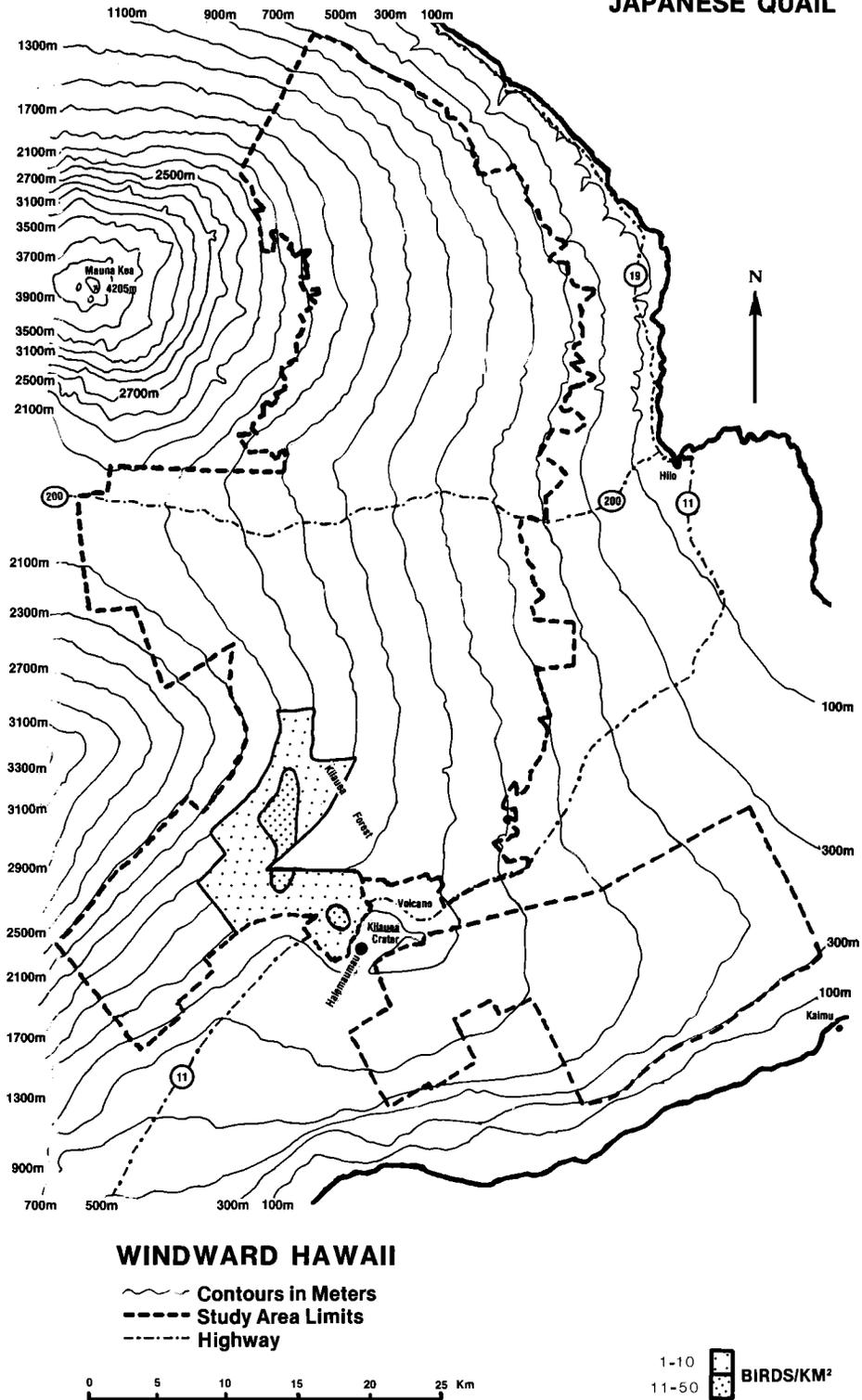


FIGURE 178. Distribution and abundance of the Japanese Quail in the windward Hawaii study areas.

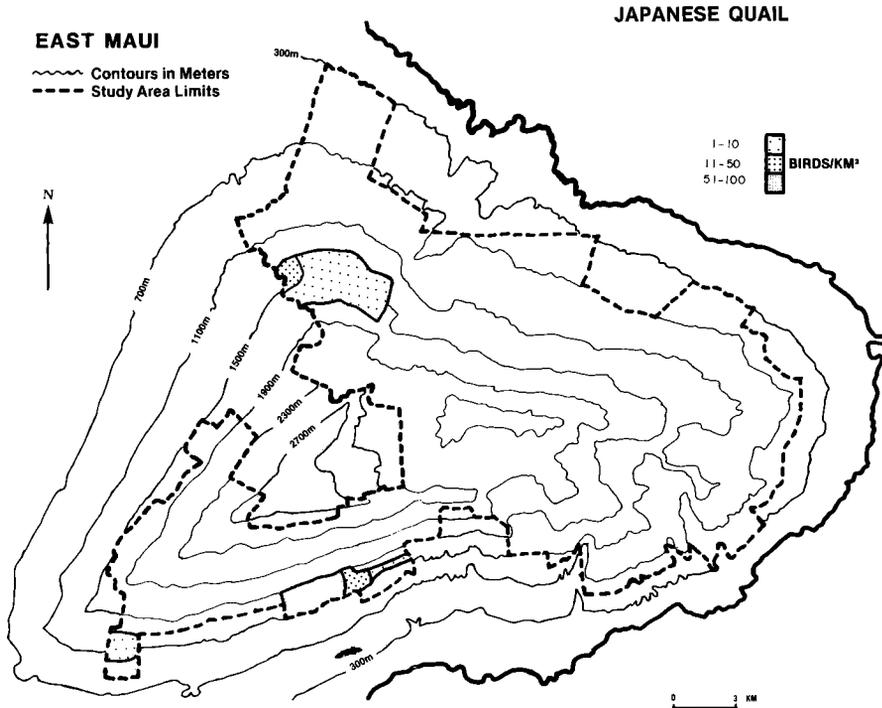


FIGURE 179. Distribution and abundance of the Japanese Quail in the East Maui study area.

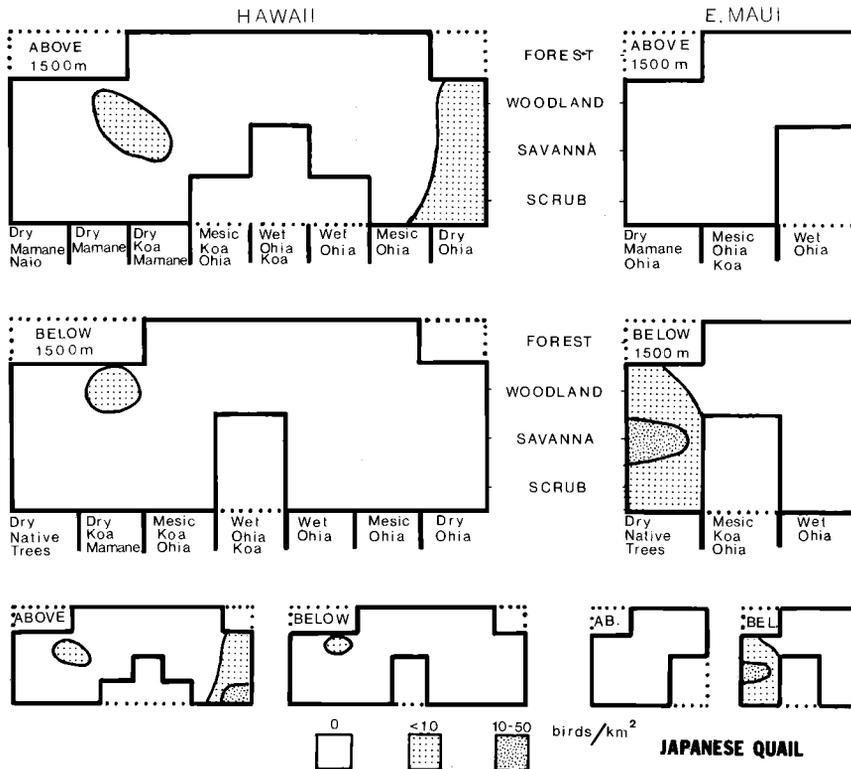


FIGURE 180. Habitat response graphs of the Japanese Quail. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

KALIJ PHEASANT

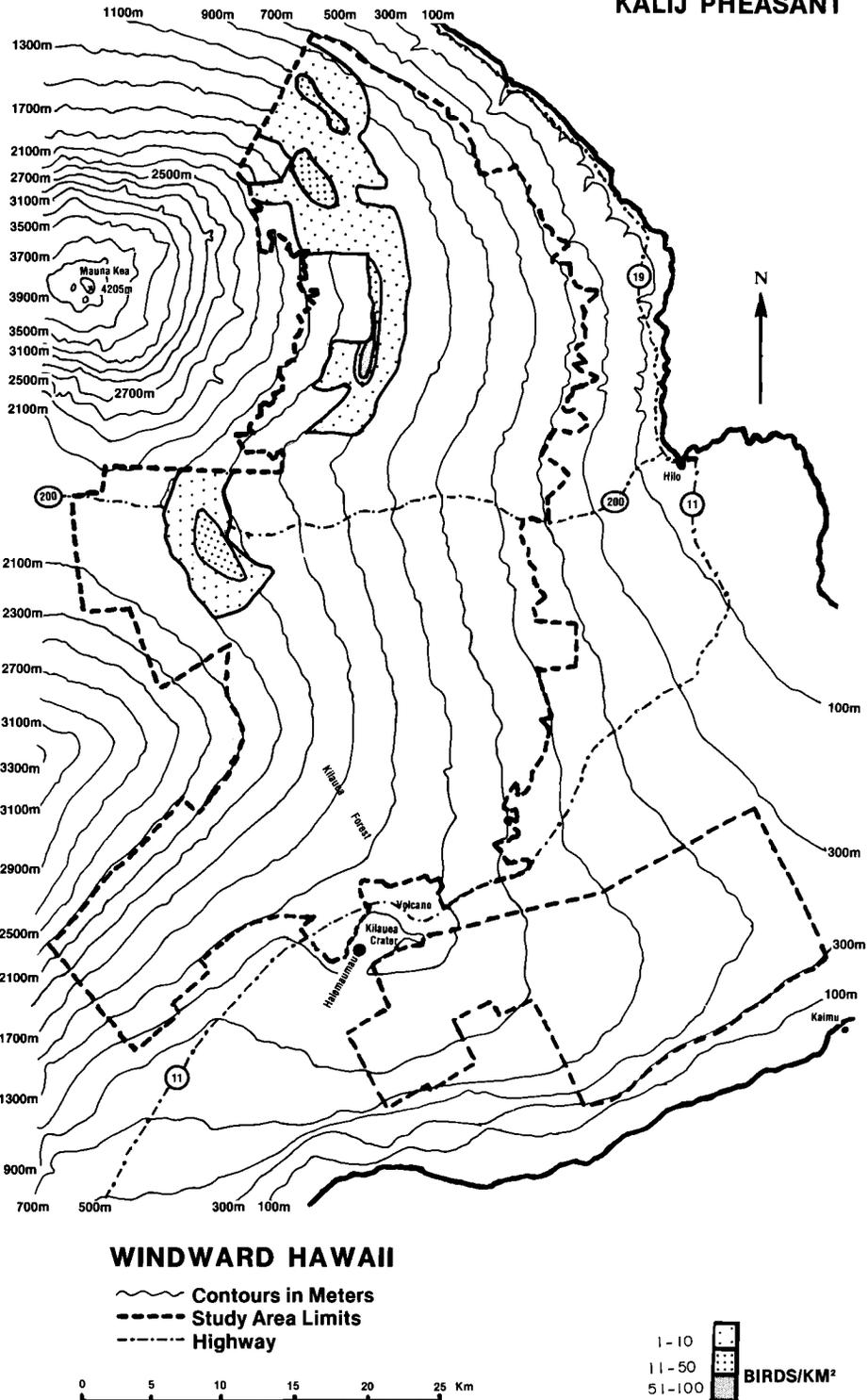


FIGURE 181. Distribution and abundance of the Kalij Pheasant in the windward Hawaii study areas.

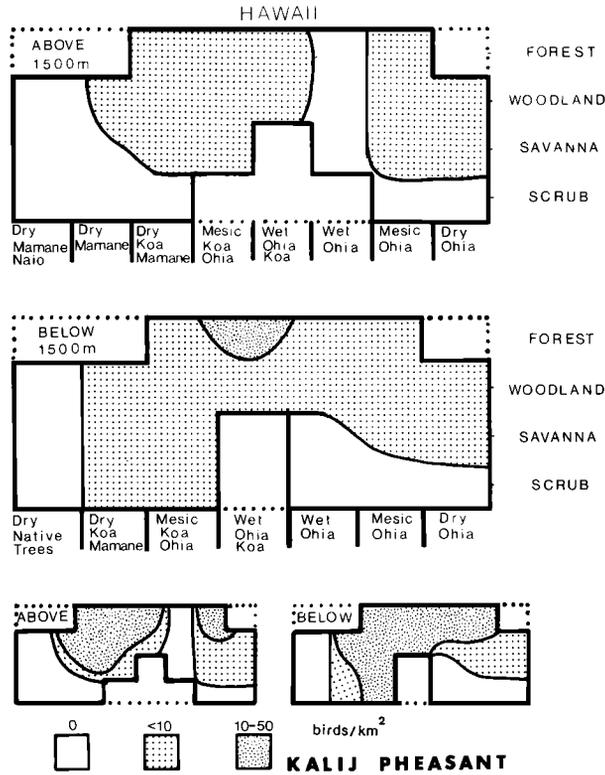


FIGURE 183. Habitat response graph of Kalij Pheasant. (Graphs give mean density above and below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

(Berger 1981; Tables 33, 40, Figs. 181, 182). We estimated 5700 ± 900 (95% CI) birds in our study areas; 97% were in Kona. Although in Kau we failed to find birds during count periods, we saw one bird in 1976 at 1670 m elevation along a jeep trail in ohia forest between transects 2 and 3. In 1984 this species was fairly common in the Kau study area (U.S.F.W.S. data). Kalij were first recorded in the vicinity of Kilauea Crater in 1977 (Katahira 1978) and have been sighted with increasing frequency in Hawaii Volcanoes National Park since 1980, particularly in kipukas along the Mauna Loa Strip Road (S. Mountainspring, J. M. Scott, pers. observ.).

Kalij Pheasant occur from 300 to 2500 m elevation in a variety of habitat types, but most often in wet ohia-koa forests (Table 40, Fig. 183). Because the range was still expanding during our survey, the observed habitat responses may change somewhat as new areas are colonized.

The regression models for Hamakua and Kona (Table 39) show that Kalij Pheasant are especially associated with passiflora. Birds actively disperse the seeds of banana poka (Lewin and Lewin 1984). Kalij Pheasant occur in moderately

dry to moderately wet forests at mid to high elevations; this resembles their foothill forest habitat in India (Ali and Ripley 1969). On Hawaii, Lewin (1971) found that Kalij often occupy dense stands of silky oak. Matted ferns are probably too dense for their activities, as reflected by the negative term in the Kona regression model.

RED JUNGLEFOWL (*Gallus gallus*)

Red Junglefowl, known as Moa by the Hawaiians, were introduced by the early Polynesians and are native to India and southeast Asia. They are most common on Kauai, although small populations occur on Hawaii and Niihau near human habitation (Berger 1981). The rarity or extinction on most islands has been attributed to predation by cats and mongooses, and to a lesser degree to excessive hunting, interbreeding with domestic stock, and forest destruction (Schwartz and Schwartz 1949, Berger 1981). Their ground nesting habits make them particularly vulnerable to predators. Red Junglefowl are omnivorous, taking seeds, fruits, insects, and other small invertebrates (Schwartz and Schwartz 1949).

During our survey we found Red Junglefowl

RED JUNGLEFOWL

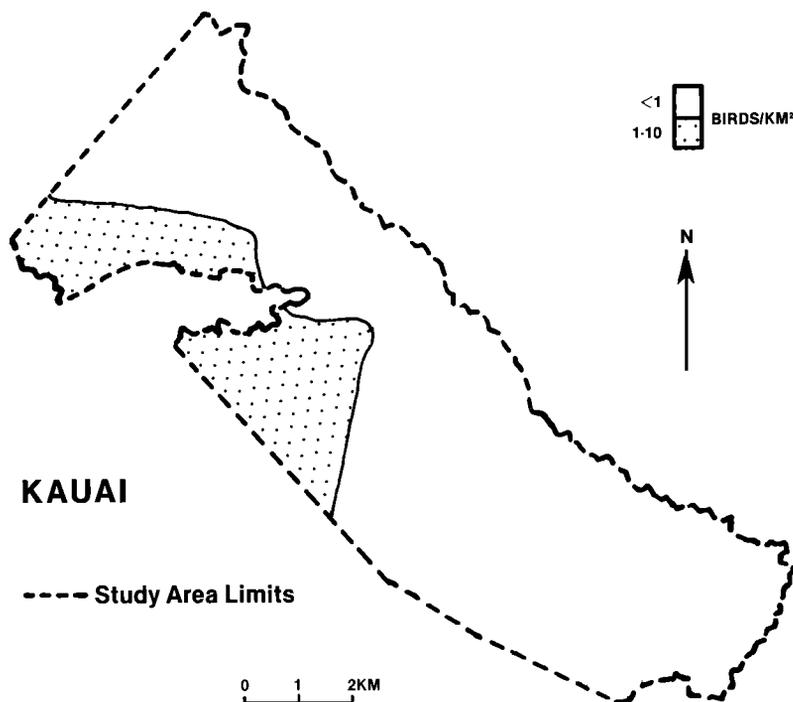


FIGURE 184. Distribution and abundance of the Red Junglefowl in the Kauai study area.

on Kauai, where they have penetrated the Alakai Swamp, and on Hawaii near Ainalou in Hawaii Volcanoes National Park (Tables 33, 34, 38, Fig. 184). We suspect that on Hawaii this species is maintained in the wild by escaped or released domestic birds. Van Riper (1973a) found a small population of birds at 600–900 m elevation on the southwest slopes of Hualalai. In native forests on Kauai, Sincock et al. (1984) found the species almost only in the Alakai Swamp and Kokee State Park area, estimated the population at 1000 ± 750 (95% CI) birds, but believed the total island population to be about 5000.

The regression model for Kauai (Table 39) is fairly inconclusive, although the positive term for ieie may reflect the large component of fruit in the diet. Schwartz and Schwartz (1949) described the habitat on Kauai as the periphery of rather mesic, partly open forests, usually of koa and ohia, although at lower elevations kukui (*Aleurites moluccana*) and guava stands are occupied. Forests that are very dense, wet, open, or dry are unoccupied. Typically the understory has a scattering of shrubs, ground ferns, matted ferns, and tree ferns. In India, Red Junglefowl usually occur in moist forests and scrub jungles interspersed with cultivated patches and clearings (Ali and Ripley 1969).

RING-NECKED PHEASANT (*Phasianus colchicus*)

Ring-necked Pheasant, introduced to the Hawaiian Islands in 1875 (Caum 1933), are native to eastern Asia. Additional introductions have been made on all the major islands since that time. In 1948, pheasant were characterized as having low densities (1–25 birds/km²) over most of our study areas (Schwartz and Schwartz 1949). Densities in Hawaii Volcanoes National Park appear to have increased over the 1940–1975 interval (Conant 1975, Banko and Banko 1980). The Green Pheasant of Japan, considered by some a distinct allospecies (*P. versicolor*), has recently been merged with *colchicus* (A.O.U. 1983).

In the Hawaiian Islands, Ring-necked Pheasant range from sea level to 3000 m elevation, from very dry to very wet habitat, and from grassland to forest (Schwartz and Schwartz 1949, 1951b). We found this species in all study areas (Tables 33, 34, 41, Figs. 185–192). An estimated $14,000 \pm 1000$ (95% CI) birds occupy our study areas on Hawaii; 1700 ± 200 on Maui; 10 ± 20 on Molokai; 320 ± 50 on Lanai; and 10 ± 20 on Kauai.

The distributional patterns we observed differ

TABLE 41
DENSITY [MEAN (SE)] OF THE RING-NECKED PHEASANT BY ELEVATION, HABITAT, AND STUDY AREA^a

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	Molokai	Lanai	Kauai
<i>Elevation</i>											
100–300 m	0
300–500 m	...	0	0	...	1 (1)	...	0	0	0
500–700 m	0	0	+	...	3 (1)	...	+	0	+
700–900 m	+	4 (1)	1 (+)	...	7 (1)	...	3 (2)	2 (1)	+	13 (5)	...
900–1100 m	2 (2)	+	13 (3)	...	8 (1)	...	+	12 (2)	+	5 (1)	...
1100–1300 m	3 (3)	8 (2)	5 (1)	27 (4)	10 (1)	...	2 (2)	18 (4)	4 (3)	...	+
1300–1500 m	+	4 (1)	...	20 (2)	9 (1)	...	0	23 (5)	0	...	+
1500–1700 m	2 (2)	3 (1)	...	19 (2)	11 (1)	...	0	28 (4)	+
1700–1900 m	15 (6)	8 (1)	...	9 (1)	8 (1)	9 (2)
1900–2100 m	17 (4)	13 (2)	...	3 (1)	10 (1)	4 (3)	...	8 (1)
2100–2300 m	18 (11)	17 (6)	...	+	5 (1)	19 (12)	...	14 (2)
2300–2500 m	+	4 (2)	...	7 (1)
2500–2700 m	4 (2)	...	15 (4)
2700–2900 m	+	...	0
2900–3100 m	+
<i>Habitat</i>											
Ohia	14 (3)	5 (1)	4 (1)	7 (1)	7 (+)	...	2 (1)	5 (1)	+	...	+
Koa-ohia	1 (1)	6 (1)	...	20 (2)	9 (+)	39 (8)
Koa-mamane	...	13 (2)	...	18 (2)	15 (1)
Mamane-naio	2 (1)	1 (1)
Mamane	14 (1)	9 (4)	...	30 (17)
Other natives	...	15 (2)	...	16 (4)	7 (1)	17 (2)	+	9 (3)	...
Intro. trees	...	2 (1)	7 (1)	...	2 (2)	6 (2)	+	7 (2)	...
Treelless	...	+	4 (2)	+	4 (1)	11 (1)	+	9 (4)	+

^a Densities are given in birds/km²; + indicates stratum was in the species range but density <0.5 birds/km²; 0 indicates stratum was outside range but was sampled; ... indicates stratum was not sampled in study area.

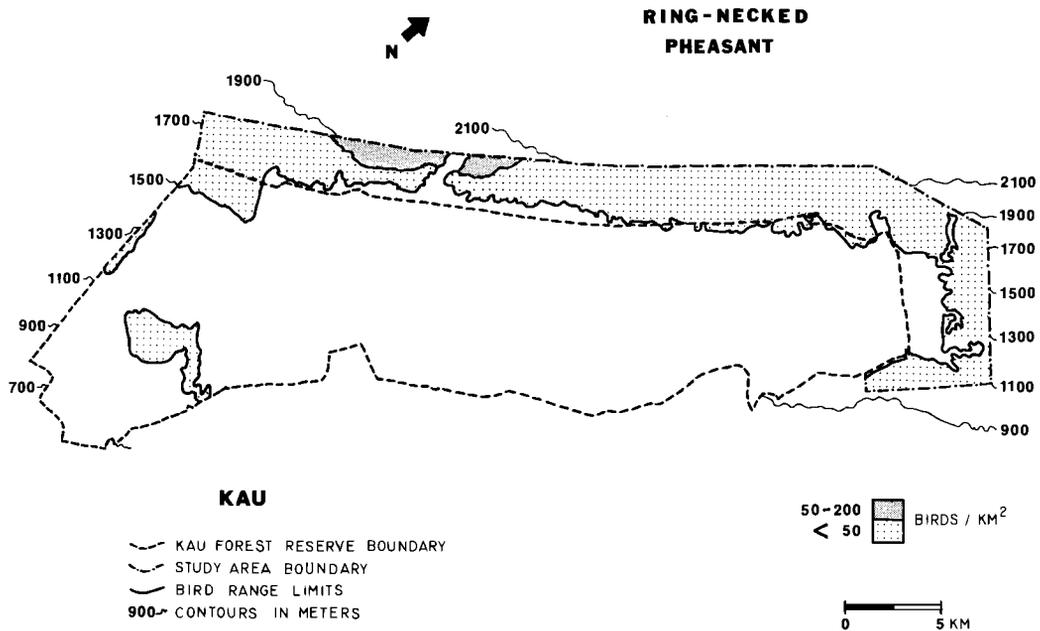


FIGURE 185. Distribution and abundance of the Ring-necked Pheasant in the Kau study area.

TABLE 42
REGRESSION MODELS FOR HABITAT RESPONSE OF THE RING-NECKED PHEASANT AND COMMON PEAFOWL^a

	Ring-necked Pheasant							Common Peafowl
	Kau	Hamakua	Puna	Kipukas	Kona	Maui	Lanai	Kona
<i>R</i> ²	0.39*	0.34*	0.26*	0.64*	0.25*	0.41*	0.12	0.19*
Moisture	-3.7*	-3.5*	-9.7*	-14.3*	...	-5.0*
Elevation	...	-5.9*	5.9*	-18.2*	9.9*	2.5	...	-13.2*
(Elevation) ²	...	6.8*	-8.4*	-2.2
Tree biomass	-10.2*	7.1*	6.4*
(Tree biomass) ²	8.4*	7.4*	-3.2
Crown cover	-7.7*	7.5*	...	-6.6*
Canopy height	...	3.9*	-3.0	-2.3
Koa	X	...	-7.2*	...	X	...
Ohia	-2.1	...	-5.4*
Naio	X	X	X	X	X	-3.0
Mamane	X	10.2*	...	X	...
Intro. trees	X	X	...	-6.0*
Shrub cover	-2.8	-8.3*	-6.7*
Ground cover	10.9*	-4.6*	4.2*	5.5*
Native shrubs	...	-10.8*
Intro. shrubs	X	5.2*	3.7*
Ground ferns	X	X	-7.8*	-4.6*	X	...
Matted ferns	-2.9	-2.9	-3.0	...
Tree ferns	...	X	...	X	X	...
Ieie	X	X	...	X	X	-2.3
Passiflora	X	-7.3*	X	X	X	8.5*
Native herbs	X	X	-4.1*	...	-2.8	...	X	...
Intro. herbs	X	X	...	5.7*	4.0*	3.1	X	...
Native grasses	...	4.0*	-3.9*	8.3*	-5.0*	4.5*	X	...
Intro. grasses	-10.7*	-3.4*

^a *R*² is the variance accounted for by the model. Entries are *t* statistics and all are significant at *P* < 0.05; * indicates *P* < 0.001; ... indicates variable not significant (*P* > 0.05); X indicates variable not available for inclusion in model.

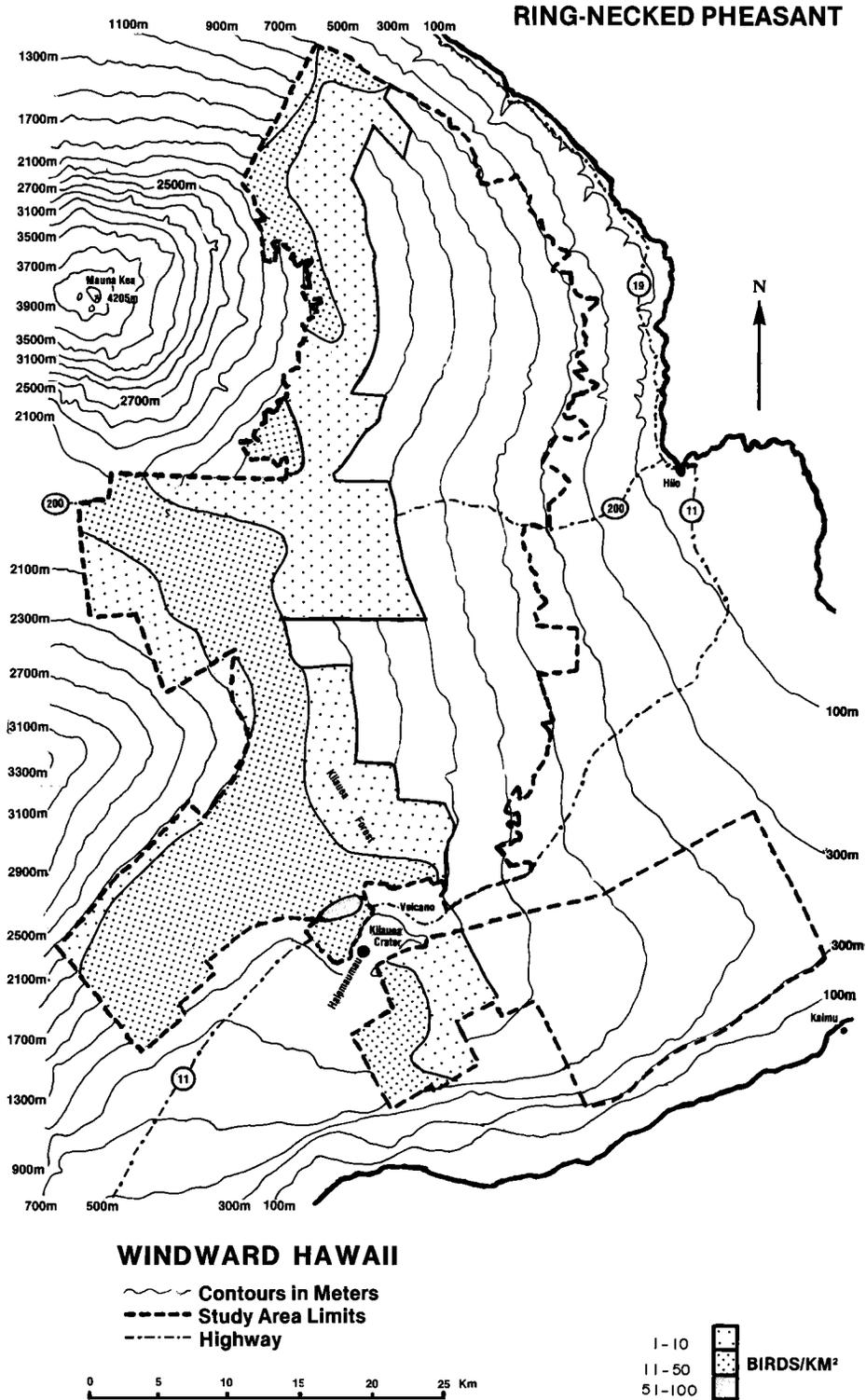


FIGURE 186. Distribution and abundance of the Ring-necked Pheasant in the windward Hawaii study areas.

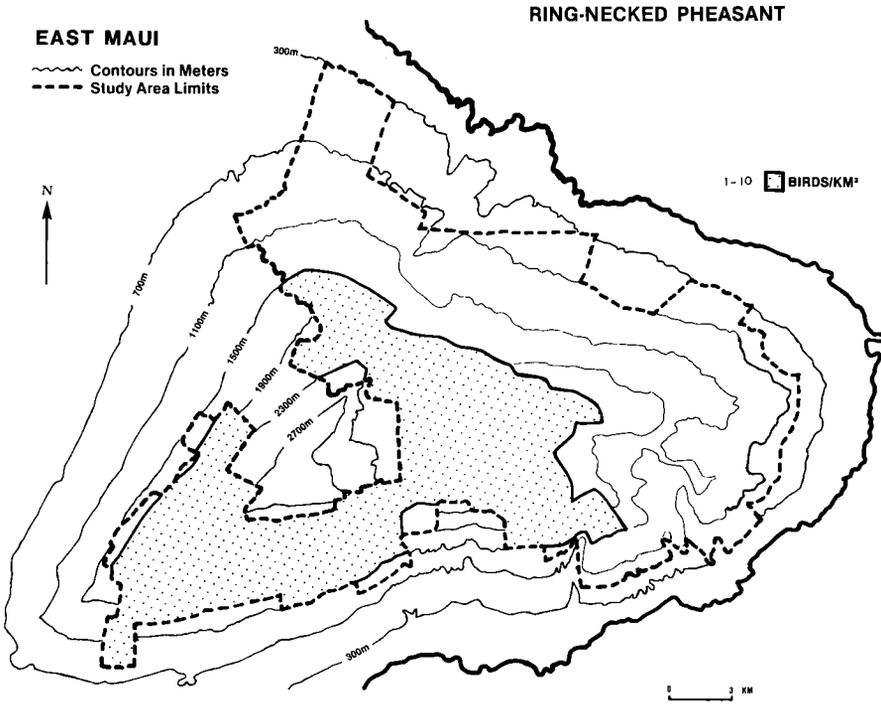


FIGURE 190. Distribution and abundance of the Ring-necked Pheasant in the East Maui study area.

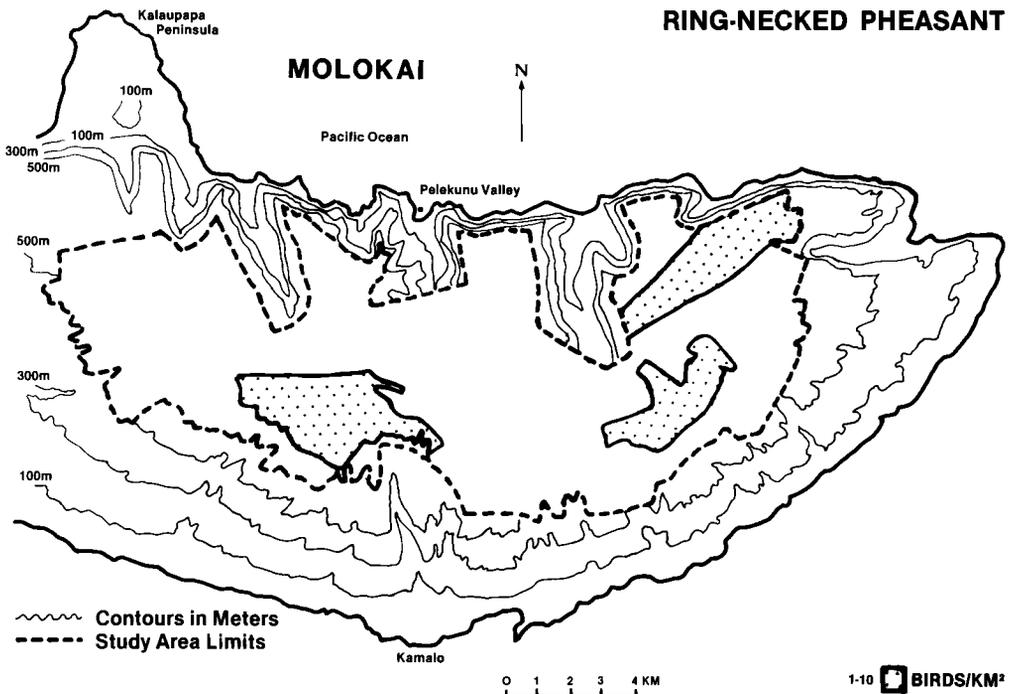


FIGURE 191. Distribution and abundance of the Ring-necked Pheasant in the Molokai study area.

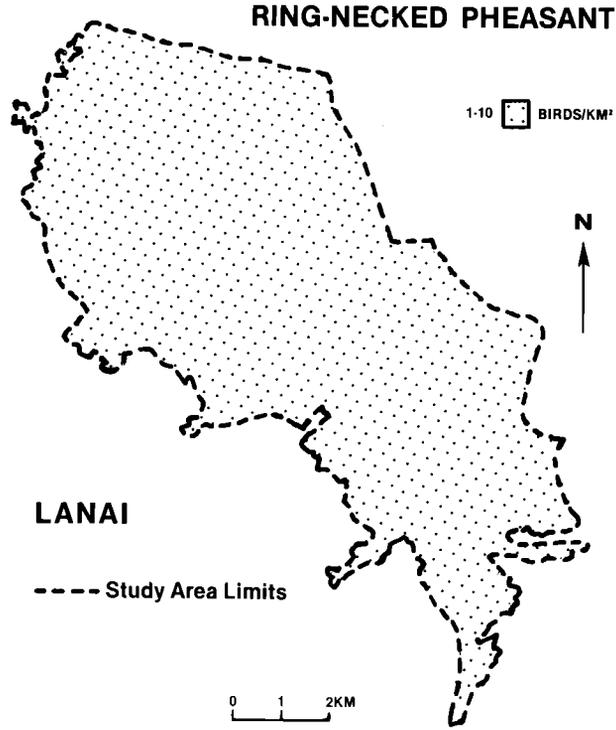


FIGURE 192. Distribution and abundance of the Ring-necked Pheasant in the Lanai study area.

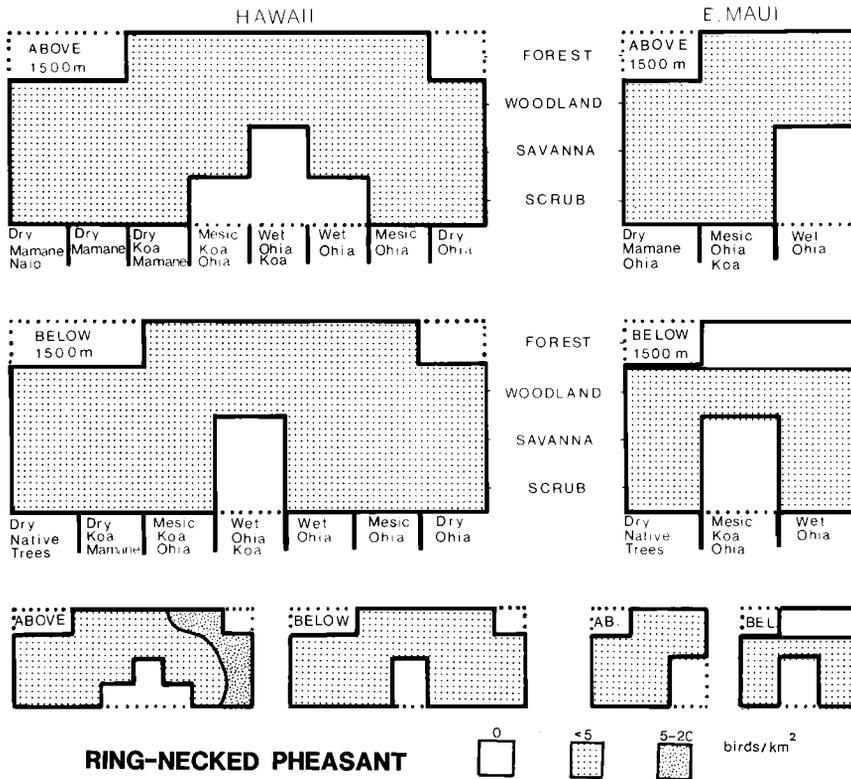


FIGURE 193. Habitat response graphs of the Ring-necked Pheasant. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

only slightly from those documented by Schwartz and Schwartz (1949, 1951b). The Mauna Kea and Mauna Loa populations are now linked at high elevations in windward Hawaii and the hiatus between upper and lower elevation populations in Kona is filled. On East Maui, pheasant filled in the Kahikinui area since 1949. On Lanai, distribution is now continuous over the entire study area.

The habitat response graphs merely indicate that Ring-necked Pheasant occur in almost every habitat type on Hawaii and Maui (Fig. 193). Crowing cocks are heard long distances, and some recorded birds were undoubtedly in a different habitat than the observer. The regression models (Table 42) show that Ring-necked Pheasant are more common in dry areas of scattered trees with little shrub cover, few matted ferns, and many introduced herbs. Wet habitats have negative responses in four of the seven models. A moisture term does not appear in the poorly-fit Lanai model, nor for the Kipukas or Kona areas where conditions are generally dry. Individual tree species have only modest effects on habitat response. The exception is mamane, strongly positive in two models and characteristic of dry open woodland.

Ring-necked Pheasant respond strongly to several understory components. Unbroken shrub cover and ground ferns are typical of many undisturbed wet native communities where birds are absent, but high densities occur where introduced shrubs reach high cover values because of disturbance by grazing or feral animals. The relation to shrub components in the regression models thus depicts positive response to disturbance, as also seen in the positive terms for introduced herbs and negative ones for native herbs. The negative terms for matted ferns in three models reflect the low forage value of dense fern understories (Schwartz and Schwartz 1949, 1951b).

In open areas, densities are generally correlated with ground cover. In the Kona regression model, the negative term for introduced grasses marks low densities in areas choked by kikuyu grass or fountain grass. Such areas may lack the diversity of fruit, browse, seeds, and insects that compose the typical diet (Schwartz and Schwartz 1949, 1951b). Moisture may ultimately limit pheasant in such areas, for fruit is a common source of water in dry areas (Schwartz and Schwartz 1949).

The picture of habitat response that developed from our analysis generally matches the range and mode of pheasant habitat response found by Schwartz and Schwartz (1949, 1951b). The typical habitat in the Hawaiian Islands is similar to

the open brush and grain field habitat of South Dakota where extremely high populations occur (Kimball et al. 1956).

COMMON PEAFOWL (*Pavo cristatus*)

Common Peafowl were introduced in 1860 (Caum 1933); they are native to the Indian subcontinent. In the Hawaiian Islands they range from sea level to 1500 m elevation (Schwartz and Schwartz 1949), occasionally higher. The diet is omnivorous and resembles that of the Ring-necked Pheasant (Schwartz and Schwartz 1949). Peafowl were established on Hawaii, Maui, Molokai, Oahu, Kauai, and Niihau in the 1940s (Schwartz and Schwartz 1949).

Common Peafowl are fairly uncommon in Kona and East Maui (Tables 33, 34, 43, Figs. 194, 195), where we estimated total populations of 80 ± 10 (95% CI) and 8 ± 2 birds, respectively. The range appears to have expanded in Kona since 1949, but elsewhere on Hawaii and Maui it has changed little. The Molokai, Lanai, and Kauai study areas lie outside the range (Schwartz and Schwartz 1949). In the Hawaiian Islands, peafowl are usually associated with ranches and stockpounds.

Common Peafowl occupy a wide range of more open habitats, and are most common in dry lower elevation areas (Table 42, Fig. 196). Because of the long distances that vocalizations carry, some birds were in a different vegetation type than the observer. In India, peafowl prefer dry woodlands with open growth (Ali and Ripley 1969). Association with open woodland is indicated in the regression model by an inverted parabola for tree biomass centered far above the range of values (i.e., nearly linear positive response) and by negative terms for crown cover and canopy height. Areas with high densities have little shrub cover but much ground cover.

Common Peafowl are commonly associated with passiflora, especially banana poka. The attraction of Common Peafowl to passiflora is reflected by the strongest term in the model, and the birds are possible dispersal agents for banana poka (Warshauer et al. 1983). Schwartz and Schwartz (1949) list passiflora as a common feature of typical habitat. In North Kona, Lewin (1971) found Common Peafowl most abundant in forests festooned with banana poka. In the East Maui study area, the main population coincides with an area of high passiflora cover.

WILD TURKEY (*Meleagris gallopavo*)

Turkeys were first introduced about 1815 from domestic stock (Caum 1933); later introductions were mostly wild stock from the subspecies *intermedia* and *merriami* of the southwest United

TABLE 43
DENSITY [MEAN (SE)] OF THE COMMON PEAFOWL AND WILD TURKEY BY ELEVATION, HABITAT, AND STUDY AREA*

	Common Peafowl			Wild Turkey			
	Kona	E. Maui	Kau	Hamakua	Kona	Mauna Kea	E. Maui
<i>Elevation</i>							
100–300 m
300–500 m	0	0	...	0	0	...	0
500–700 m	+ (+)	0	0	0	1 (+)	...	0
700–900 m	1 (+)	1 (1)	0	1 (1)	2 (+)	...	0
900–1100 m	1 (+)	1 (+)	0	+ (+)	2 (+)	...	0
1100–1300 m	+ (+)	1 (+)	0	+ (+)	2 (+)	...	1 (1)
1300–1500 m	+ (+)	+ (+)	0	+ (+)	2 (+)	...	0
1500–1700 m	+ (+)	+ (+)	3 (3)	2 (+)	2 (+)	...	0
1700–1900 m	+ (+)	+ (+)	+ (+)	2 (1)	2 (+)	...	0
1900–2100 m	+ (+)	+ (+)	0	2 (1)	3 (+)	+ (+)	+ (+)
2100–2300 m	0	+ (+)	0	+ (+)	1 (+)	1 (1)	+ (+)
2300–2500 m	0	+ (+)	0	+ (+)	+ (+)
2500–2700 m	...	0	+ (+)	0
2700–2900 m	...	0	+ (+)	0
2900–3100 m	+ (+)	...
<i>Habitat</i>							
Ohia	+ (+)	0	1 (1)	0	2 (+)	...	0
Koa-ohia	+ (+)	+ (+)	0	1 (+)	2 (+)	...	0
Koa-mamane	+ (+)	1 (+)	4 (+)
Mamane-naio	+ (+)	3 (1)	+ (+)	...
Mamane	+ (+)	0	3 (+)	+ (+)	0
Other natives	+ (+)	+ (+)	...	6 (2)	1 (+)	...	+ (+)
Intro. trees	+ (+)	0	...	1 (1)	4 (1)	...	0
Treeless	+ (+)	0	...	0	+ (+)	...	0

* Densities are given in birds/km²; + indicates stratum was in the species range but density <0.5 birds/km²; 0 indicates stratum was outside range but was sampled; ... indicates stratum was not sampled in study area.

States (Hewitt 1967). Turkeys increased in numbers on all islands (Munro 1944) and were plentiful until 1938. Between 1938 and 1941, a drastic reduction in numbers restricted Wild Turkey to a small population on leeward Hawaii (Schwartz and Schwartz 1949). By the 1970s, new releases of *intermedia* resulted in numbers sufficient to sustain public hunting (R. Bachman, R. L. Walker, pers. comm.).

Wild Turkeys are well established throughout Kona and on the upper slopes of Mauna Kea (Tables 33, 34, 43, Figs. 197–200). We estimated a total population of 2000 ± 150 (95% CI) birds in the study areas on Hawaii. On Maui, turkeys are rare on the lower slopes of Haleakala on the Auwahi Tract and in west Kahikinui (Fig. 201). Because turkeys flock, our density and population estimates are biased on the low side.

Wild Turkeys occupy a wider variety of habitats on Hawaii than on Maui (Fig. 202). This may simply reflect a population that is better established on Hawaii. The regression models (Table 44) indicate that turkeys are most common at higher elevations in open woodland with

ground cover. This generally matches the open woodland habitat of populations in Texas and the American Southwest (Bent 1932, Hewitt 1967).

In both regression models some variables act as correction terms and require careful interpretation. In Kona, crown cover and canopy height balance tree biomass. The net effect shows that turkeys are associated with open woodlands. In Hamakua three tree species balance tree biomass, but mamane actually has a positive correlation ($r = 0.11$) with turkey density. The net effect reflects the absence of turkey from treeless areas and heavy forest, and lower densities in pure mamane than in mixed mamane-naio. The discrepancy between the Hamakua and Kona mamane terms is thus a result of model mechanics.

In both regression models, turkeys are positively associated with ground cover and passiflora but negatively associated with native grasses. Shrub cover has a negative term in the Hamakua model, and shrub cover could enter the final model for Kona as a negative term sig-

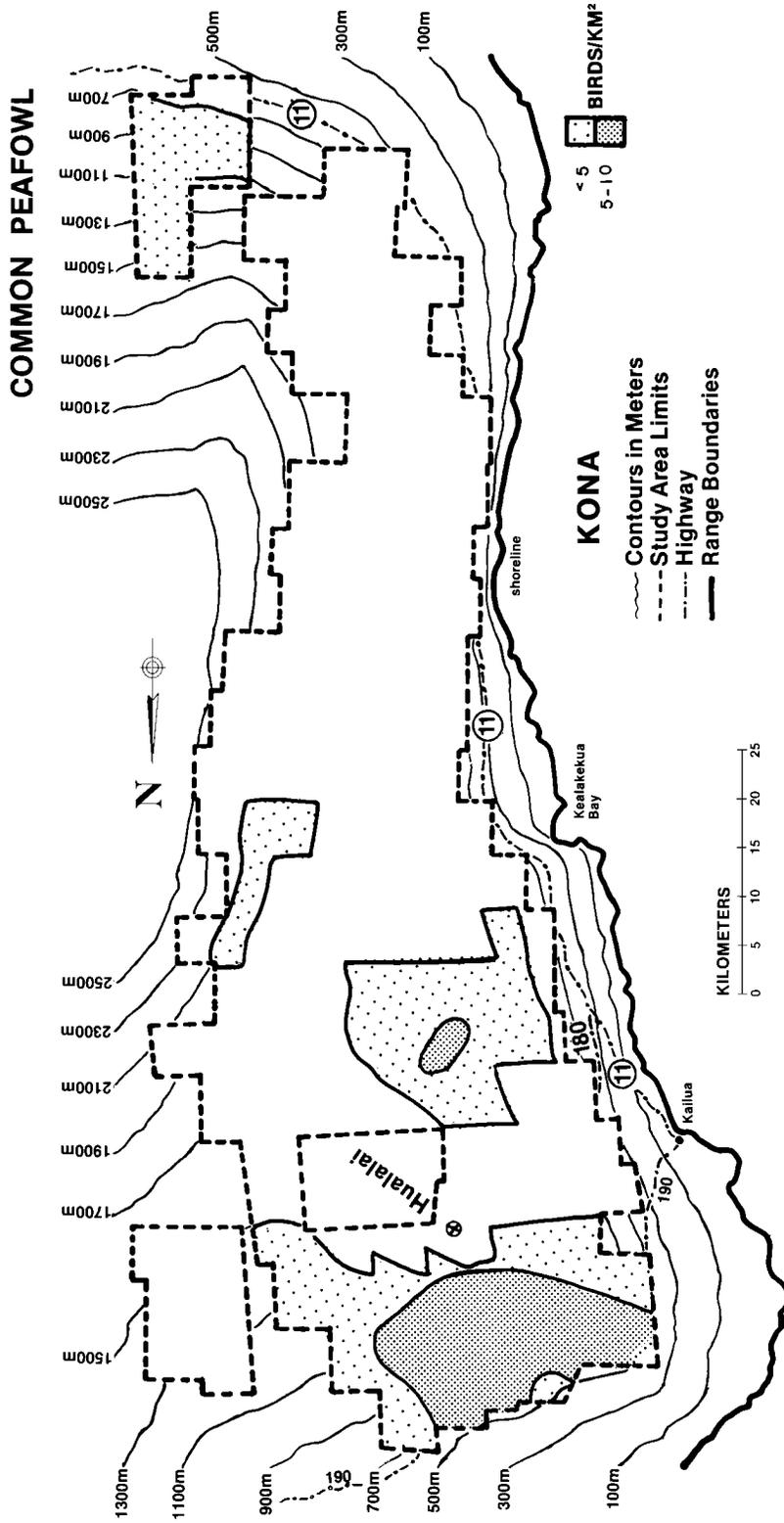


FIGURE 194. Distribution and abundance of the Common Peafowl in the Kona study area.

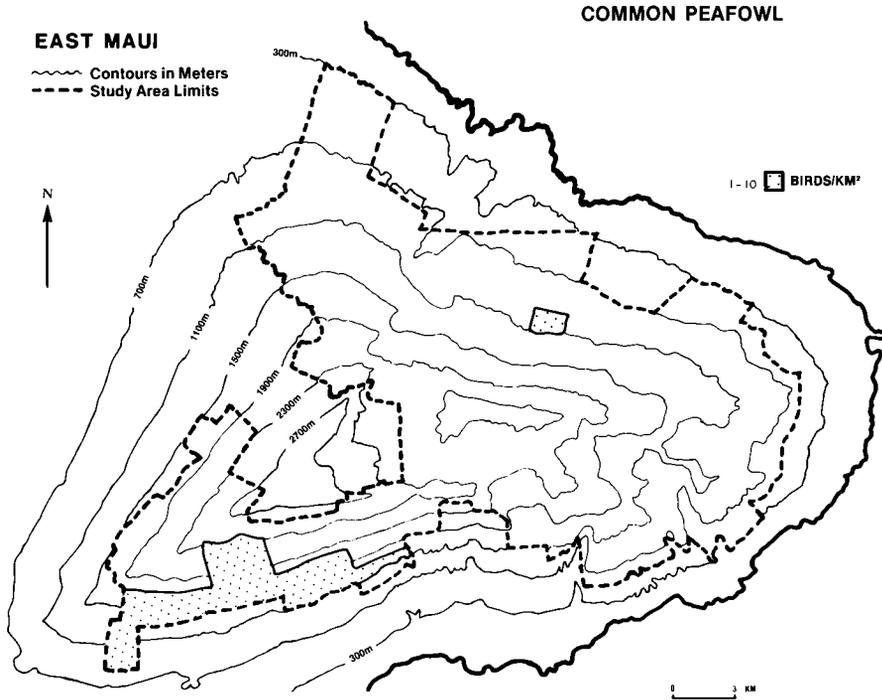


FIGURE 195. Distribution and abundance of the Common Peafowl in the East Maui study area.

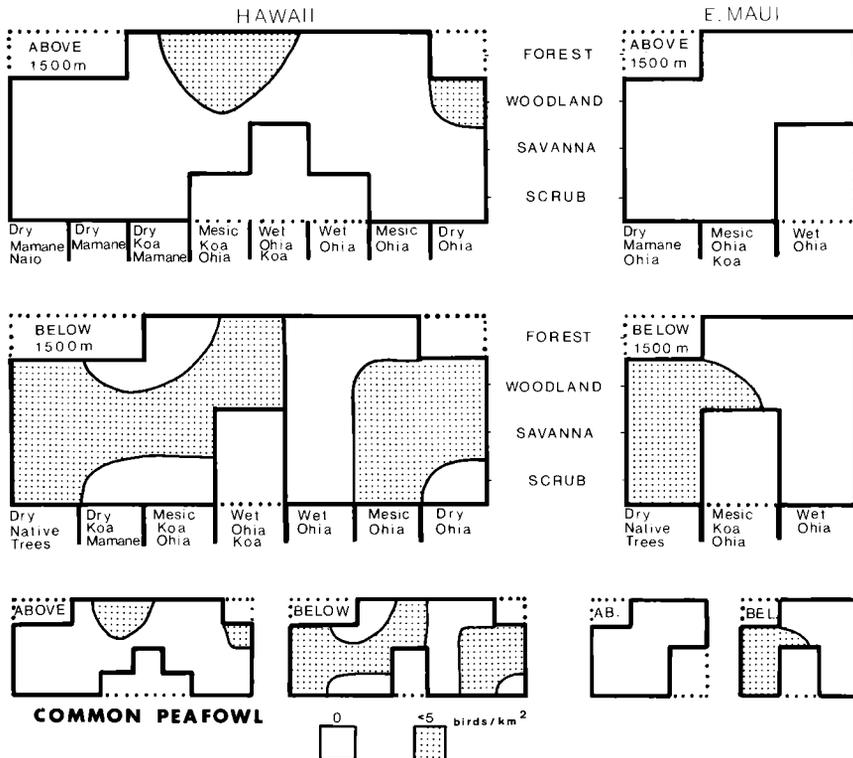


FIGURE 196. Habitat response graphs of the Common Peafowl. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

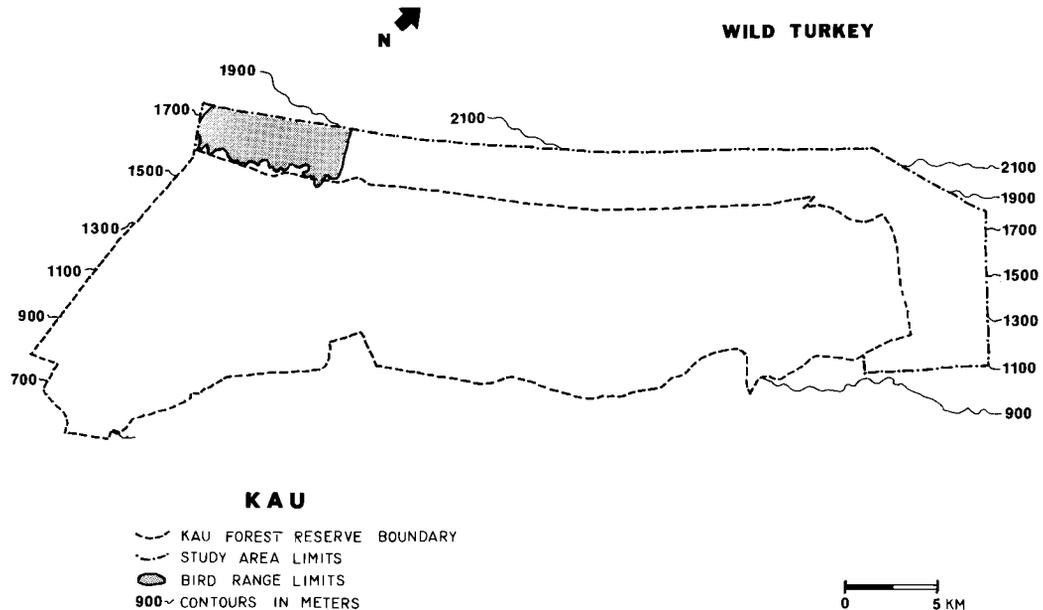


FIGURE 197. Distribution and abundance of the Wild Turkey in the Kau study area. (Density within range is less than 5 birds/km².)

TABLE 44
REGRESSION MODELS FOR HABITAT RESPONSE OF THE WILD TURKEY AND CALIFORNIA QUAIL^a

	Wild Turkey		California Quail				
	Hamakua	Kona	Hamakua	Puna	Kipukas	Kona	Mauna Kea
<i>R</i> ²	0.24*	0.19*	0.17*	0.10*	0.45*	0.22*	0.16*
Moisture	-5.5*	-4.0*	-3.2	X
Elevation	4.1*	7.0*	-7.1*	...	-3.4*
(Elevation) ²	...	-5.9*	8.1*	...
Tree biomass	4.8*	5.4*	6.4*	3.7*	...	2.0	...
(Tree biomass) ²
Crown cover	...	-5.5*	...	-2.8
Canopy height	...	-3.0	6.4*
Koa	X	2.4	-5.4*	X
Ohia	-6.9*	...	-9.3*	...	-6.5*	-3.8*	X
Naio	X	2.3	X	X	-2.6	3.2	-2.0
Mamane	-6.9*	9.4*	9.1*	7.2*	...
Intro. trees	-4.0*	...	-4.6*	...	X	...	X
Shrub cover	-8.8*	-4.5*
Ground cover	3.5*	7.4*	-6.0*	-2.6
Native shrubs	8.8*	2.6	X
Intro. shrubs	X
Ground ferns	X	-4.4*	X	2.4	X
Matted ferns	X
Tree ferns	X	-5.2*	X	...	X	...	X
Ieie	X	...	X	...	X	...	X
Passiflora	8.8*	4.6*	...	X	X	-3.3	X
Native herbs	X	...	X	-2.8	...	-2.6	X
Intro. herbs	X	...	X	...	4.9*	2.7	...
Native grasses	-7.4*	-4.3*	6.2*	...	2.7	-6.6*	...
Intro. grasses	6.0*

^a *R*² is the variance accounted for by the model. Entries are *t* statistics and all are significant at *P* < 0.05; * indicates *P* < 0.001; ... indicates variable not significant (*P* > 0.05); X indicates variable not available for inclusion in model.

WILD TURKEY

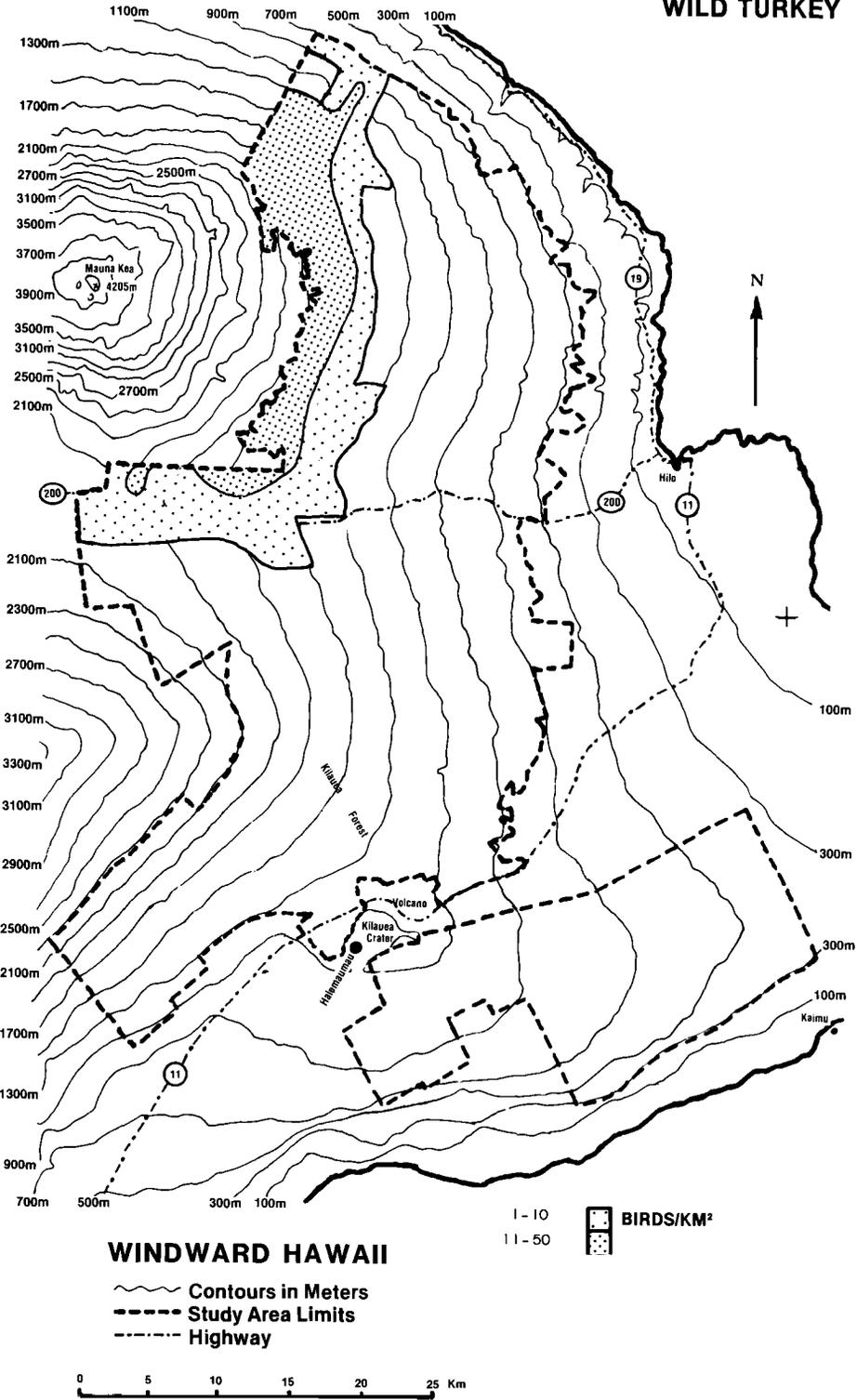


FIGURE 198. Distribution and abundance of the Wild Turkey in the windward Hawaii study areas.

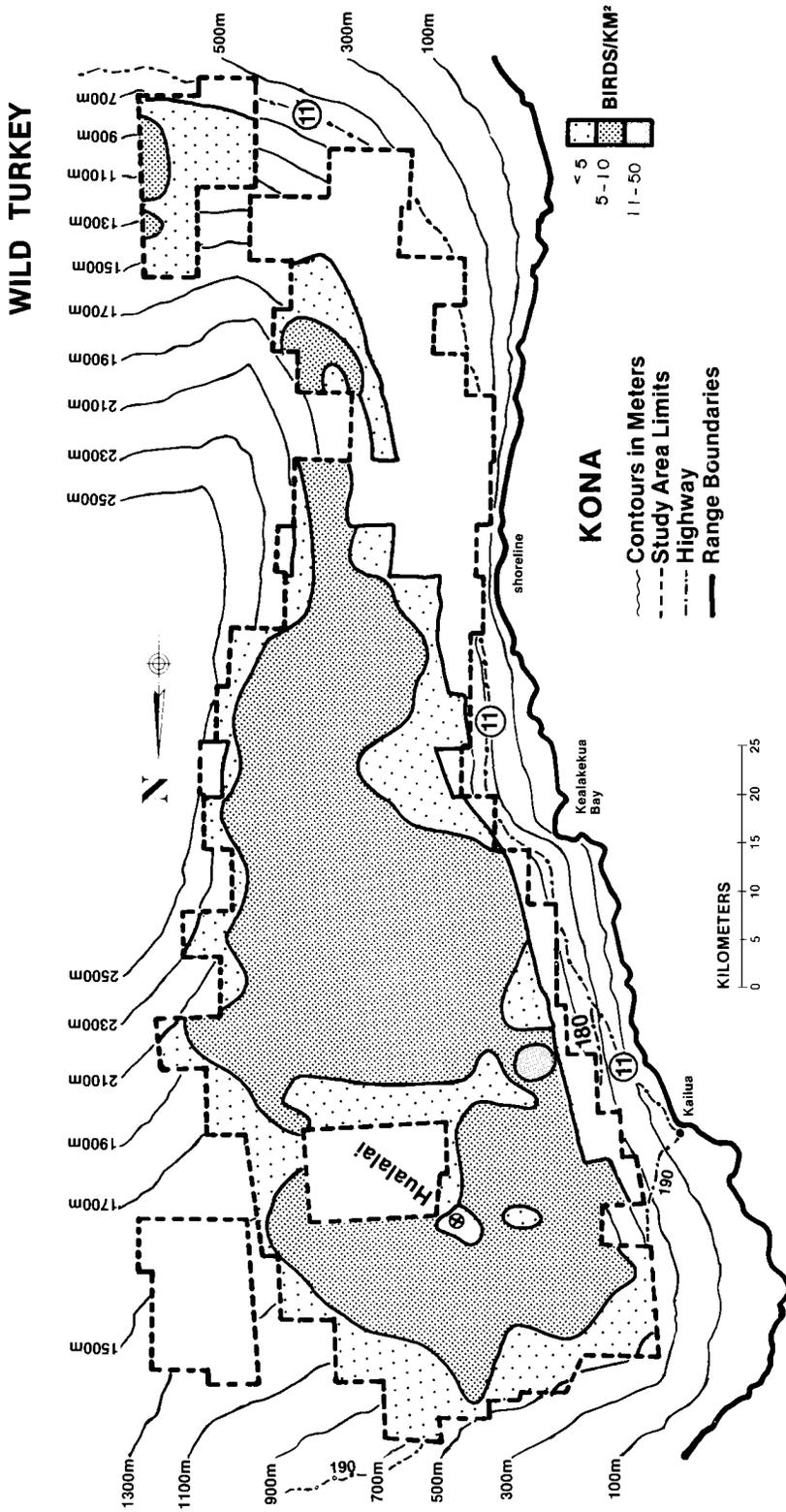


FIGURE 199. Distribution and abundance of the Wild Turkey in the Kona study area.

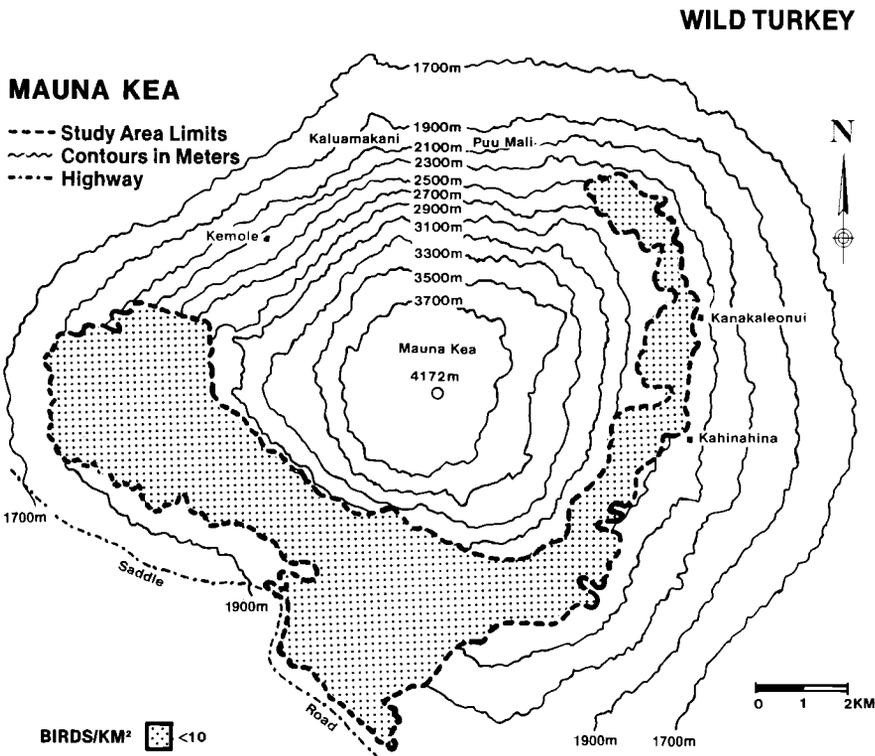


FIGURE 200. Distribution and abundance of the Wild Turkey in the Mauna Kea study area.

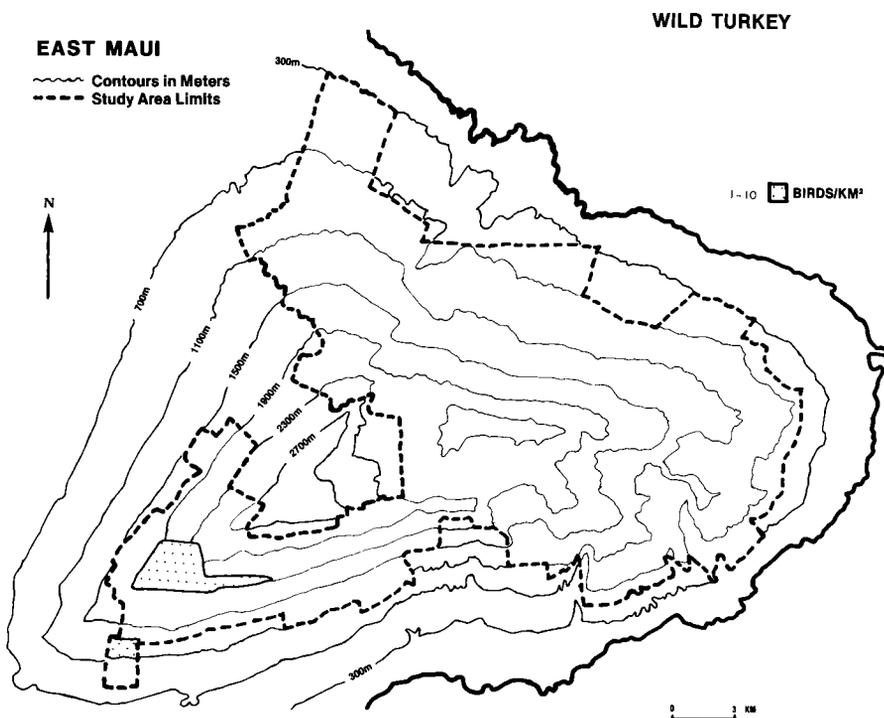


FIGURE 201. Distribution and abundance of the Wild Turkey in the East Maui study area.

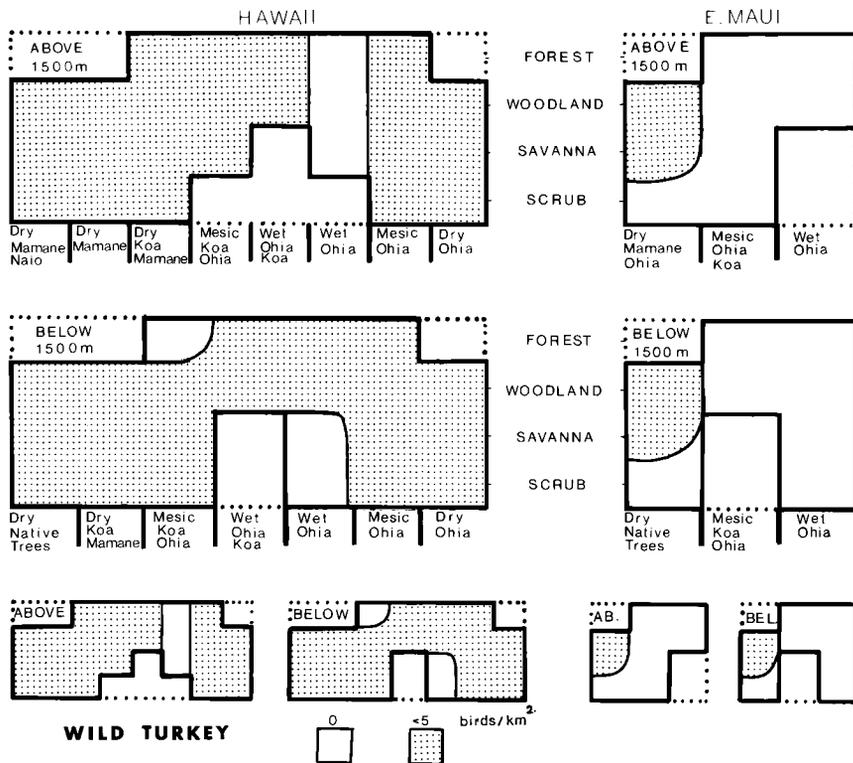


FIGURE 202. Habitat response graphs of the Wild Turkey (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

nificant at the 0.07 level. The association with *passiflora* supports the indictment of Wild Turkeys as dispersal agents of banana poka (Warsauer et al. 1983).

CALIFORNIA QUAIL (*Callipepla californica*)

California Quail were introduced to the Hawaiian Islands from California before 1855 (Caum 1933). Munro (1944) considered them well established and common on Molokai and Hawaii in the 1890s and reported birds on Kauai and Niihau. He stated that the Lanai population was extirpated. They are now present on all main islands except Oahu (R. L. Walker, pers. comm.). California Quail are native to western North America where they occur in habitats from desert scrub to open woodlands (Grinnell and Miller 1944).

Because quail flock, our density estimates are biased on the low side. We found California Quail in a variety of habitat types and over a wide elevational range in seven study areas (Tables 33, 34, 45, Figs. 203–206). On Hawaii 2800 ± 700 (95% CI) birds inhabit our study areas. Contrary to Schwartz and Schwartz (1949, 1950), we

did not find birds above 1500 m elevation in ohia scrub in Kau, nor at all in south Kona. Populations are well established in the drier upper portions of Hawaii Volcanoes National Park, in north Kona, and in the mamane-naio woodland on Mauna Kea. Densities appear to have increased in the national park over the 1940–1975 interval (Conant 1975, Banko and Banko 1980). On East Maui an estimated 50 ± 20 birds occur in west Kahikinui. Only scattered birds were observed on Lanai.

Highest quail densities are in dry mamane-naio scrublands and savannas above 1500 m (Fig. 207). The regression models (Table 44) show that quail are most commonly associated with dry areas over a range of elevation and habitat types. The models suggest that California Quail have little response to tree biomass, crown cover, or canopy height. Densities tend to be higher in mamane and lower in ohia and introduced tree habitats.

The negative response to native grasses in the Kona regression model corresponds to low densities in alpine scrub, where lack of water and cold temperatures may limit numbers. *Passiflora* infestations do not attract high densities, but in-

TABLE 45
DENSITY [MEAN (SE)] OF THE CALIFORNIA QUAIL BY ELEVATION, HABITAT, AND STUDY AREA^a

	Hamakua	Puna	Kipukas	Kona	Mauna Kea	E. Maui	Lanai
<i>Elevation</i>							
100–300 m
300–500 m	0	0	...	+ (+)	...	0	...
500–700 m	0	0	...	1 (1)	...	0	+ (+)
700–900 m	0	4 (2)	...	2 (1)	...	0	+ (+)
900–1100 m	0	1 (1)	...	+ (+)	...	0	+ (+)
1100–1300 m	1 (1)	1 (+)	5 (1)	1 (+)	...	1 (1)	...
1300–1500 m	1 (+)	...	5 (1)	1 (+)	...	+ (+)	...
1500–1700 m	+ (+)	...	5 (1)	2 (+)	...	+ (1)	...
1700–1900 m	2 (1)	...	5 (1)	2 (+)	...	2 (1)	...
1900–2100 m	0	...	1 (+)	3 (+)	19 (10)	1 (+)	...
2100–2300 m	2 (2)	...	2 (1)	4 (1)	30 (11)	1 (1)	...
2300–2500 m	1 (1)	12 (6)	3 (1)	...
2500–2700 m	3 (1)	8 (5)	...
2700–2900 m	2 (+)	0	...
2900–3100 m	1 (1)
<i>Habitat</i>							
Ohia	1 (+)	2 (1)	2 (+)	1 (+)	...	0	...
Koa-ohia	+ (+)	...	3 (1)	+ (+)	...	0	...
Koa-mamane	2 (2)	...	6 (1)	3 (+)
Mamane-naio	2 (1)	11 (4)
Mamane	5 (+)	10 (4)	0	...
Other natives	3 (1)	...	8 (+)	2 (+)	...	2 (+)	1 (1)
Intro. trees	0	1 (+)	...	0	+ (+)
Treeless	0	0	+ (+)	+ (+)	...	+ (+)	+ (+)

^a Densities are given in birds/km²; + indicates stratum was in the species range but density <0.5 birds/km²; 0 indicates stratum was outside range but was sampled; ... indicates stratum was not sampled in study area.

roduced herbs, a common food source, do. This relation is also seen in the diet; where browse and seeds are major items and fruit is unimportant (Schwartz and Schwartz 1950).

Suitable habitat for California Quail is a mosaic of cover types, food sources, and watering points (Leopold 1977). Their absence in rainforests and cultivated areas in Hawaii was noted by Schwartz and Schwartz (1949), although birds occur occasionally in ohia dieback areas with 400-cm annual precipitation (S. Mountain-spring, pers. observ.). The requirement for water, often met by stock watering troughs or game watering tanks, is essential for good population densities (Schwartz and Schwartz 1949), and appears to restrict the range at high elevations in the Kona and Kipukas study areas.

ROCK DOVE (*Columba livia*)

Rock Doves were introduced to the Hawaiian Islands as early as 1796 (Schwartz and Schwartz 1949). They occur on all main islands and are well established in many urban areas. They feed chiefly on seeds, with larval insects next in dietary importance (Schwartz and Schwartz 1949). Rock Doves were sighted flying near forest edges and occasionally in the dry mamane-naio wood-

land near Mauna Kea State Park (J. M. Scott, pers. observ.). These are assumed to be recent escapes or domestic birds, although they may be vagrants from feral populations.

SPOTTED DOVE (*Streptopelia chinensis*)

Spotted Doves, known locally as Lace-necked or Chinese Doves, were introduced before 1880 (Caum 1933) and are native to most of the Oriental zoogeographical region. Spotted Doves are most abundant from sea level to 1200 m elevation and are widely distributed on all the islands (Schwartz and Schwartz 1949, 1951a; Lewin 1971); our survey primarily sampled peripheral range. The call notes carry quite far, and some of the birds recorded may have occupied a different habitat than that of the observer. The habitat responses noted may also fail to take into account the 6–8 km distances between some roosting and feeding areas (Schwartz and Schwartz 1949). Spotted Doves feed chiefly on seeds and insects on the ground (Schwartz and Schwartz 1949, Goodwin 1970).

We found Spotted Doves on all the islands surveyed (Tables 33, 34, 46). A total of 1100 ± 150 (95% CI) birds was estimated for our study

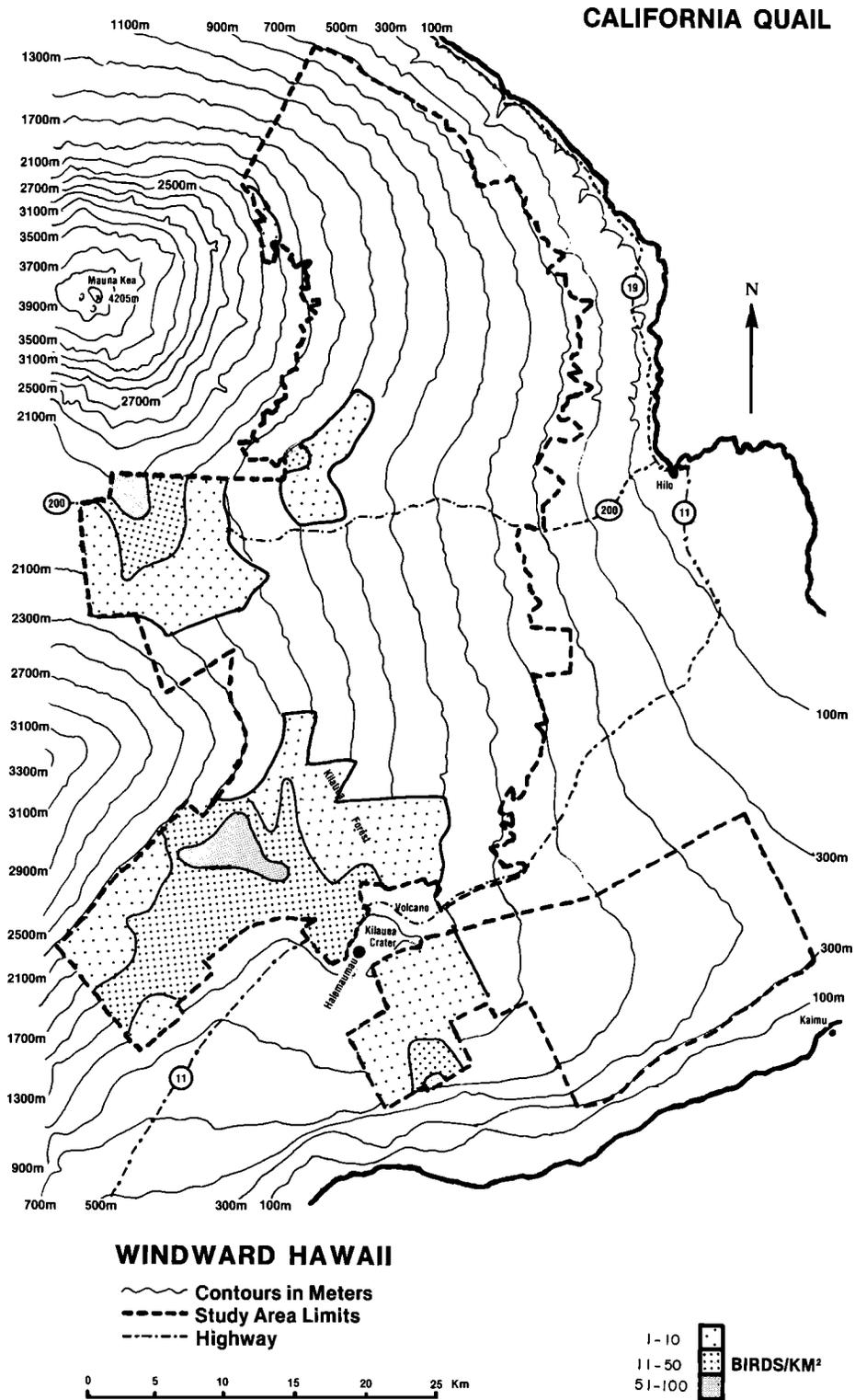


FIGURE 203. Distribution and abundance of the California Quail in the windward Hawaii study areas.

CALIFORNIA QUAIL

MAUNA KEA

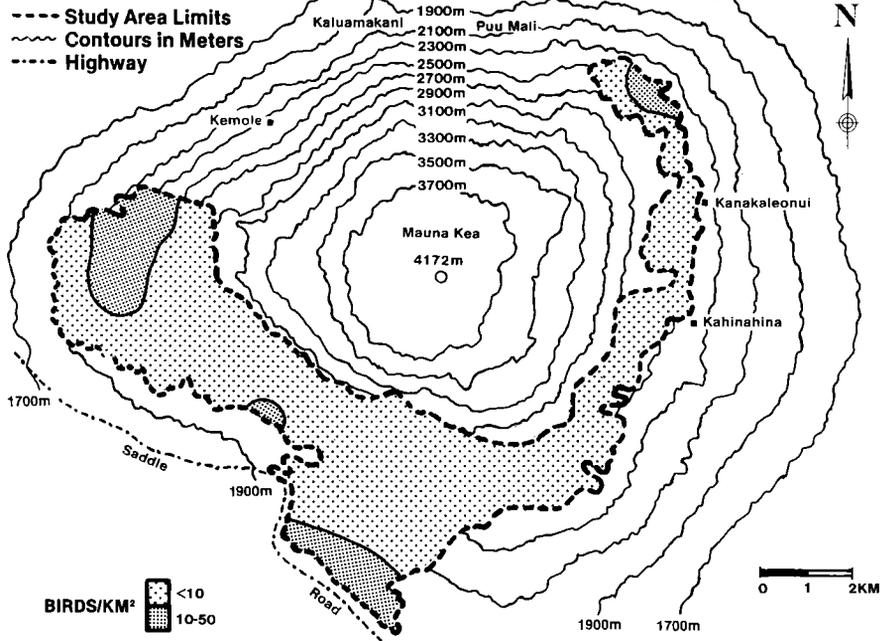


FIGURE 205. Distribution and abundance of the California Quail in the Mauna Kea study area.

CALIFORNIA QUAIL

EAST MAUI

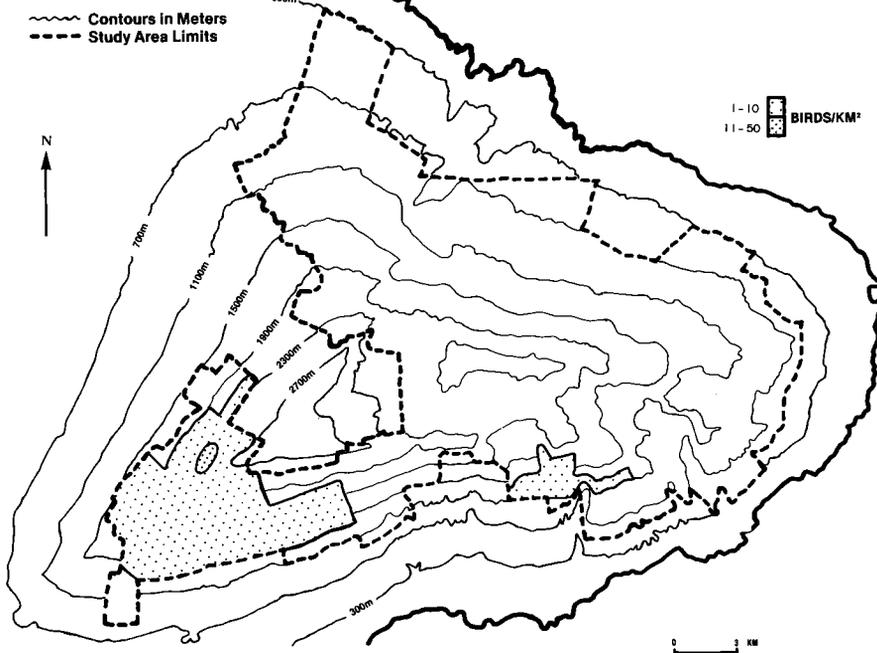


FIGURE 206. Distribution and abundance of the California Quail in the East Maui study area.

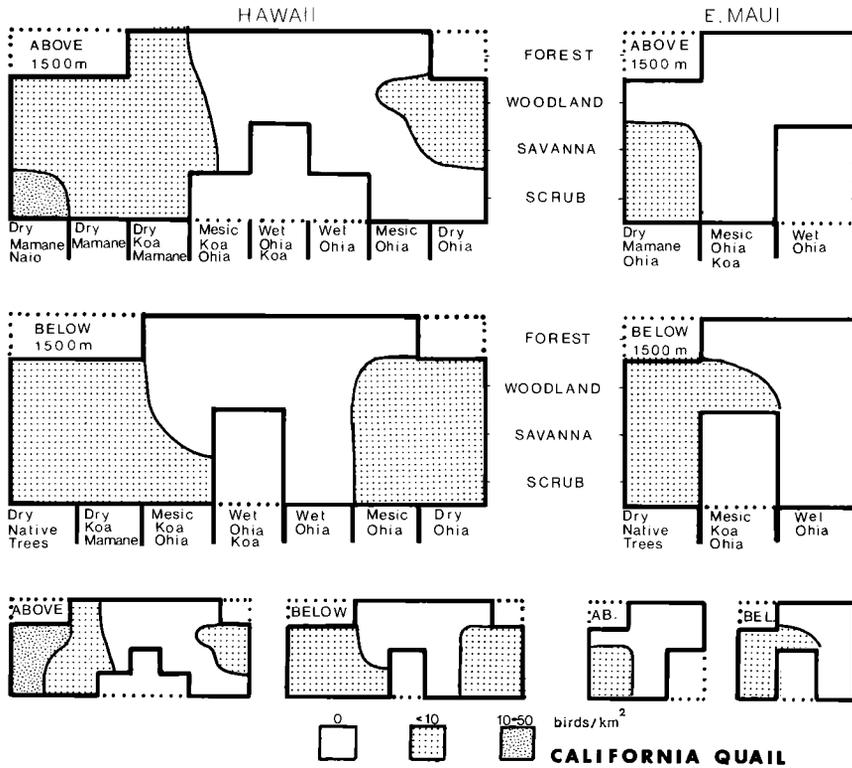


FIGURE 207. Habitat response graphs of the California Quail. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

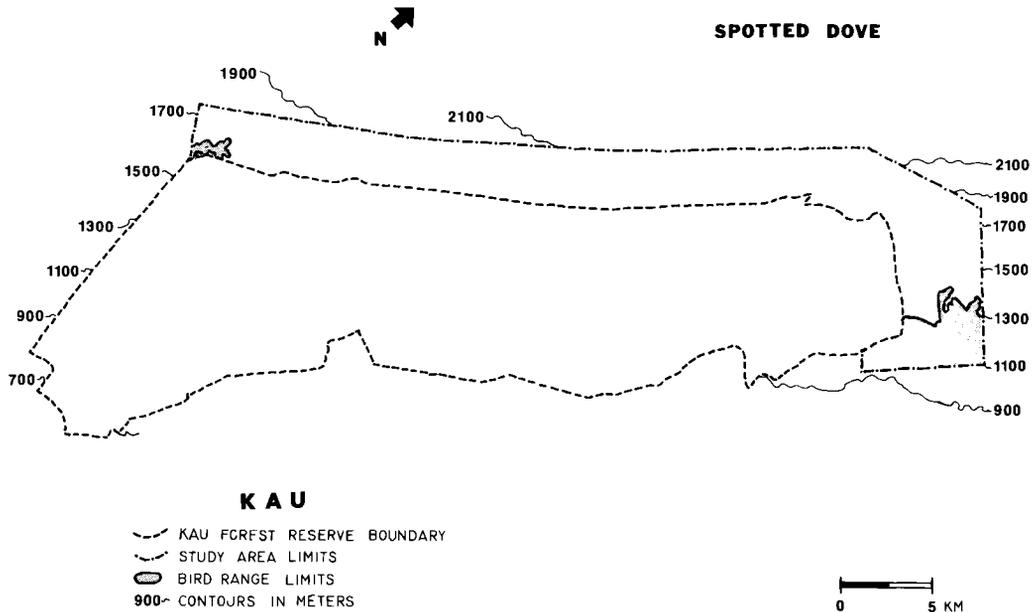


FIGURE 208. Distribution and abundance of the Spotted Dove in the Kau study area. (Density within range is less than 10 birds/km².)

SPOTTED DOVE

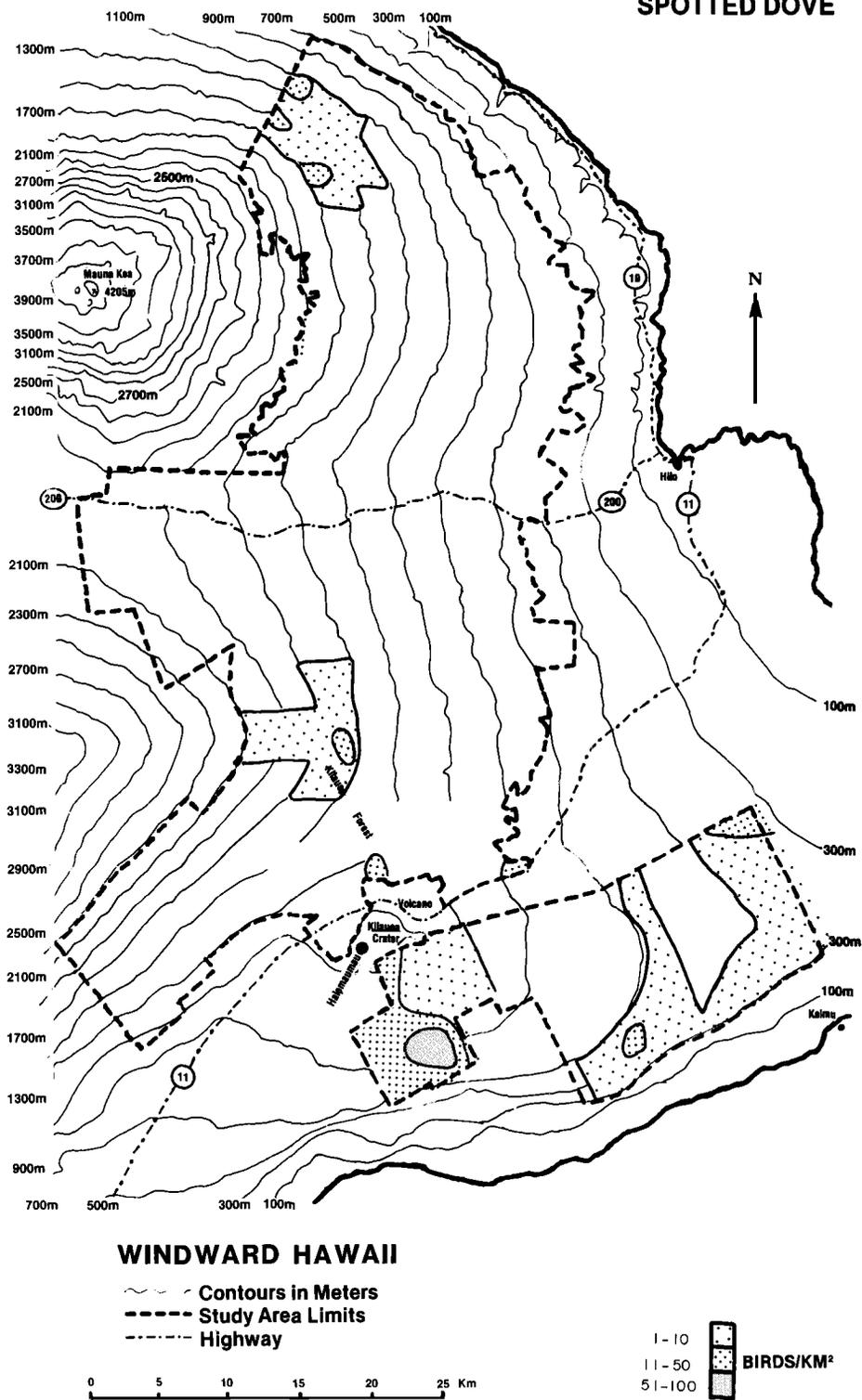


FIGURE 209. Distribution and abundance of the Spotted Dove in the windward Hawaii study areas.

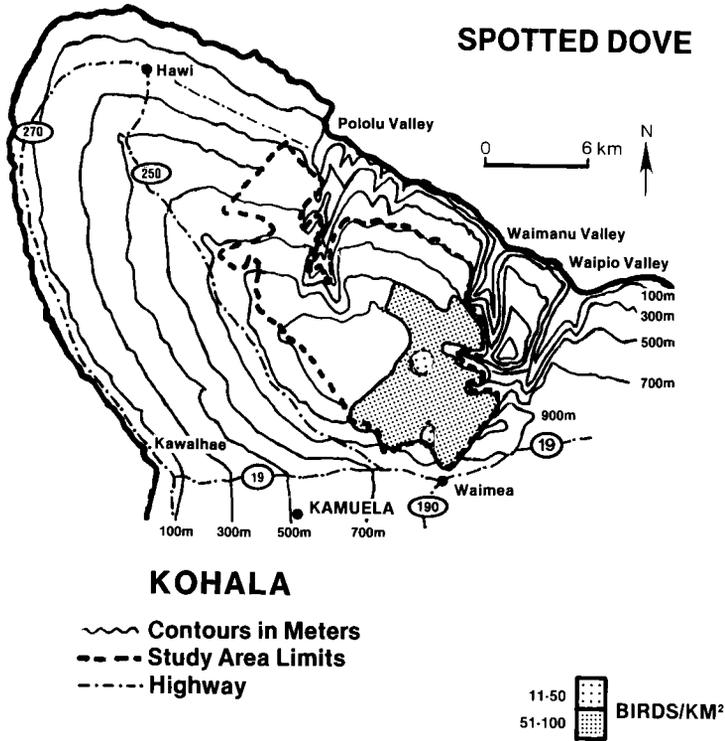


FIGURE 211. Distribution and abundance of the Spotted Dove in the Kohala study area.

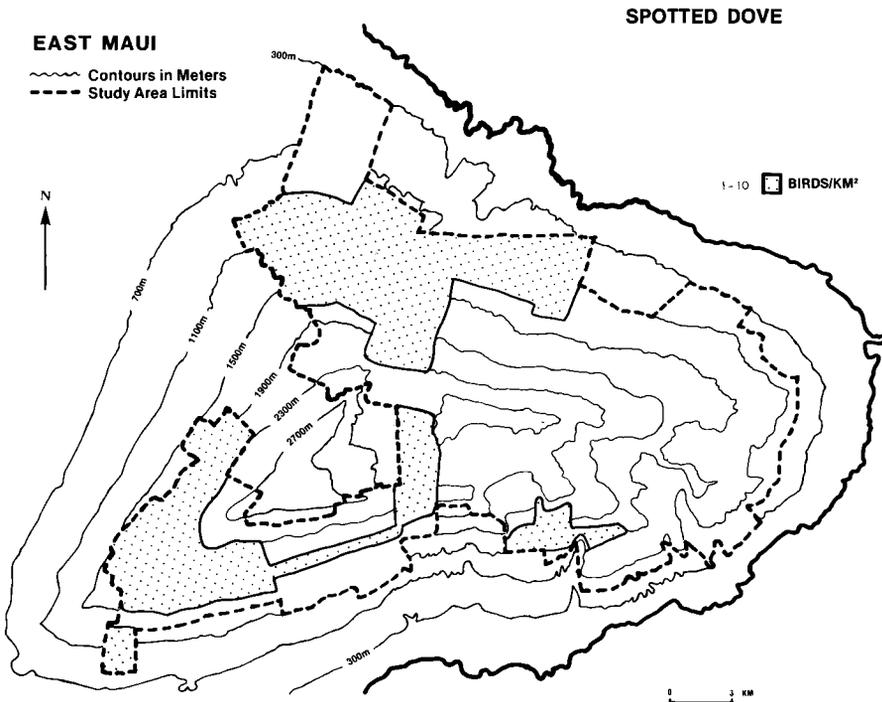


FIGURE 212. Distribution and abundance of the Spotted Dove in the East Maui study area.

WEST MAUI

SPOTTED DOVE

~~~~~ Contours in Meters  
 - - - - Study Area Limits

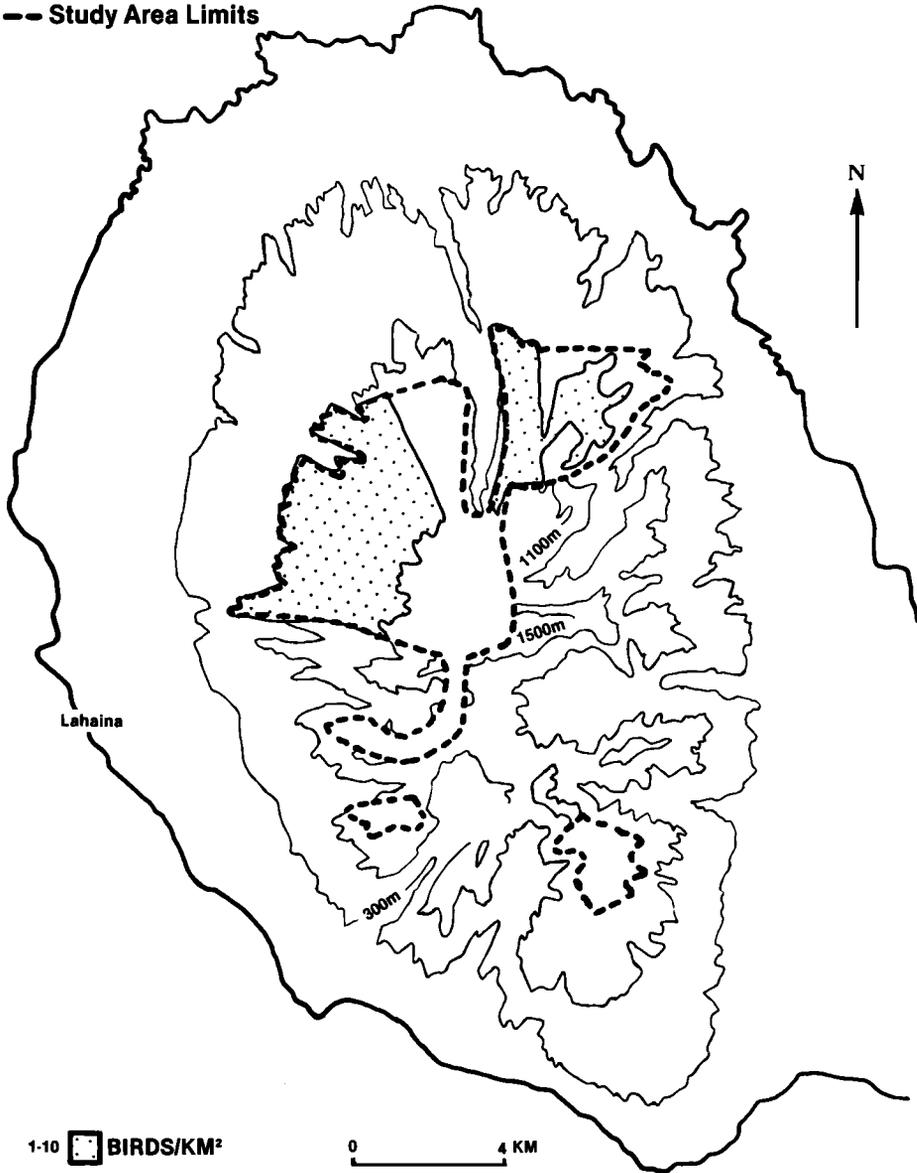


FIGURE 213. Distribution and abundance of the Spotted Dove in the West Maui study area.

areas. They are well established within the Puna, Kona, and Molokai study areas, but occur at low densities and as scattered populations in other study areas (Figs. 208–216). The range of Spotted Doves has expanded greatly on Hawaii, Maui, and Molokai since the survey by Schwartz and Schwartz (1949). In Kona, good numbers of Spotted Doves occur at Puu Waawaa, on the

Kahuku tract, and in agricultural areas in south Kona (Honomalino Tract to Manuka Tract) and south and east of Kailua. On East Maui, birds occur on the northwest slopes of Haleakala, at low elevations in Keanae Valley, and at low densities across Kahikinui. On Molokai, birds show a massive intrusion into the western half of the study area and the northern valleys; one bird was

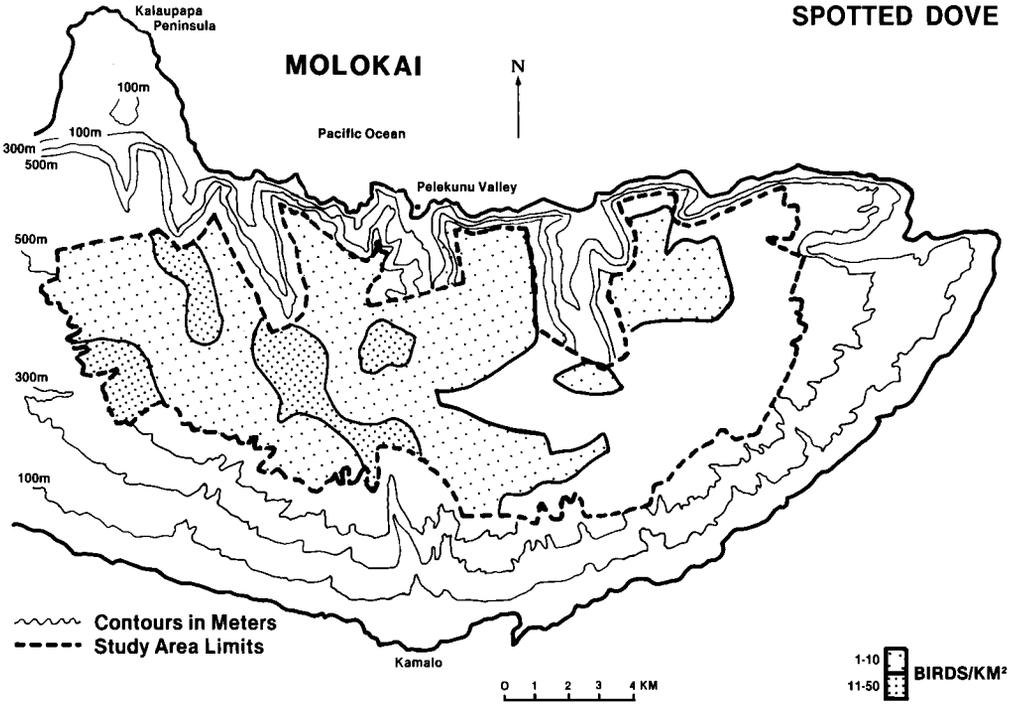


FIGURE 214. Distribution and abundance of the Spotted Dove in the Molokai study area.

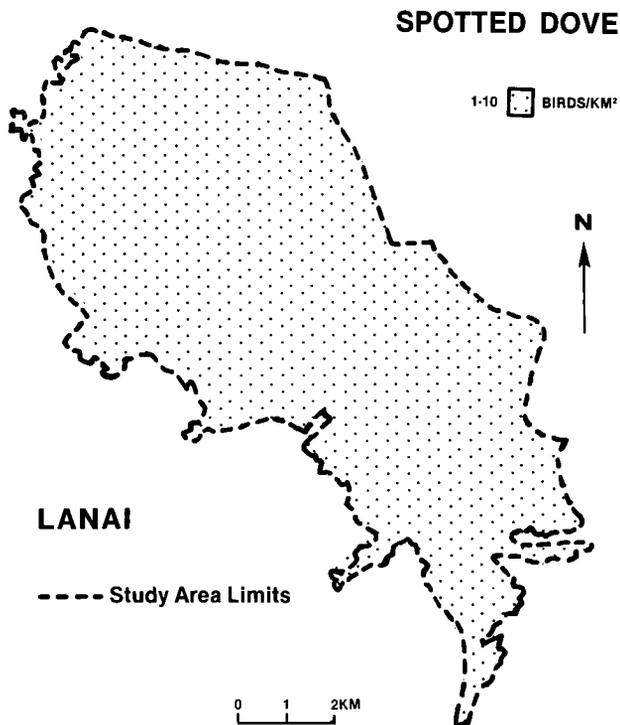


FIGURE 215. Distribution and abundance of the Spotted Dove in the Lanai study area.

**SPOTTED DOVE**

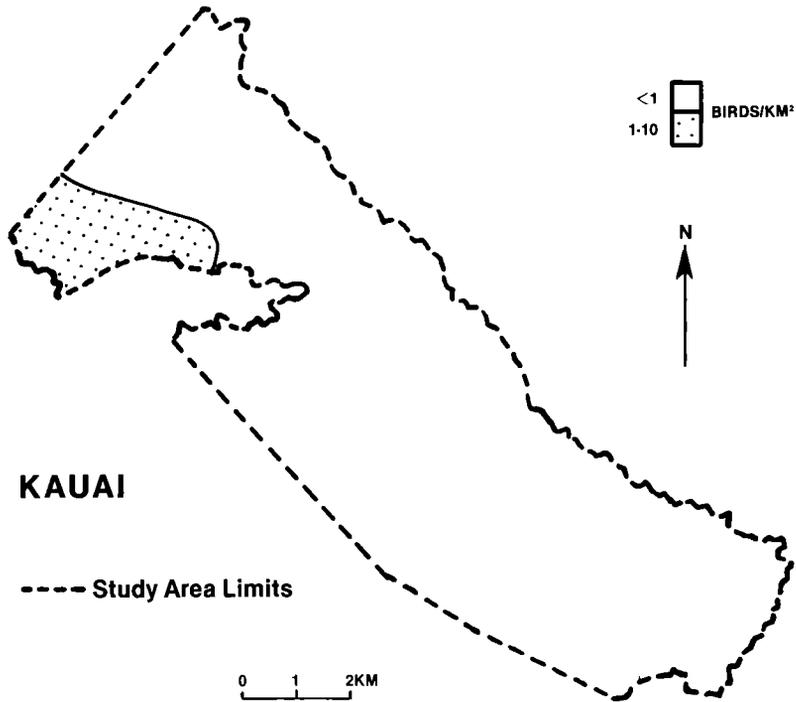


FIGURE 216. Distribution and abundance of the Spotted Dove in the Kauai study area.

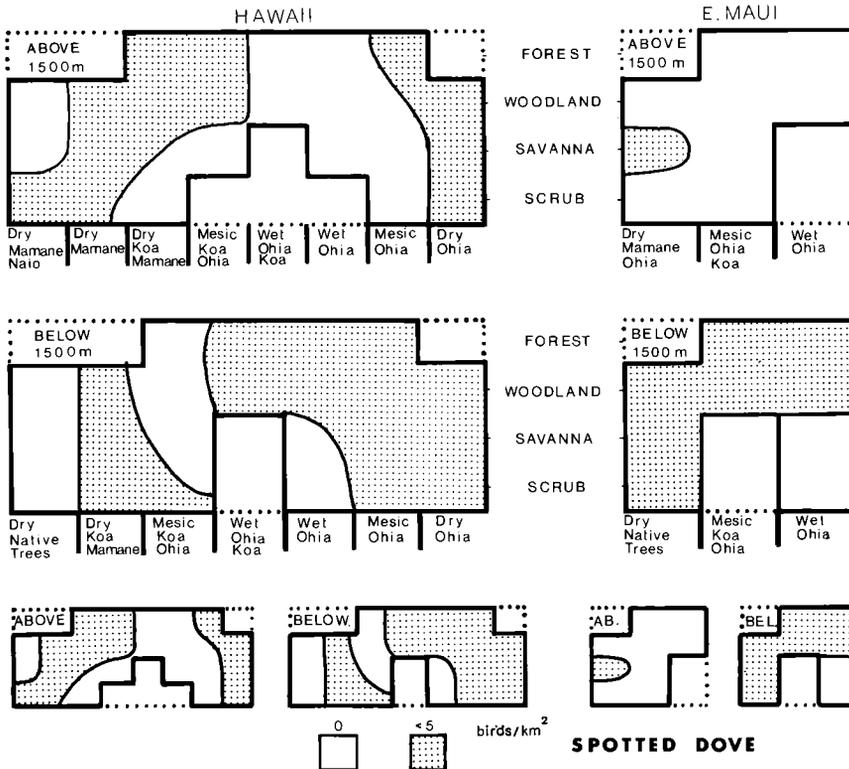


FIGURE 217. Habitat response graphs of the Spotted Dove. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

TABLE 46  
DENSITY [MEAN (SE)] OF THE SPOTTED DOVE BY ELEVATION, HABITAT, AND STUDY AREA<sup>a</sup>

| Elevation      | Kau     | Hamakua | Puna   | Kipukas | Kona  | Kohala | E. Maui | W. Maui | Molokai | Lanai | Kauai |
|----------------|---------|---------|--------|---------|-------|--------|---------|---------|---------|-------|-------|
| 100-300 m      | ...     | ...     | ...    | ...     | ...   | ...    | ...     | ...     | +       | ...   | ...   |
| 300-500 m      | ...     | +       | 0      | ...     | 6 (2) | 0      | 0       | ...     | 10 (4)  | ...   | ...   |
| 500-700 m      | 0       | +       | 0      | ...     | 2 (+) | 0      | 1 (+)   | ...     | 9 (3)   | ...   | ...   |
| 700-900 m      | +       | +       | 12 (2) | ...     | 1 (+) | 0      | 1 (+)   | 0       | 2 (+)   | 2 (1) | ...   |
| 900-1100 m     | 27 (10) | +       | 9 (2)  | ...     | 1 (+) | 3 (3)  | 2 (1)   | 1 (+)   | 5 (1)   | +     | ...   |
| 1100-1300 m    | +       | +       | 2 (1)  | 1 (1)   | 1 (+) | +      | 1 (1)   | +       | 4 (1)   | 1 (1) | ...   |
| 1300-1500 m    | ...     | 1 (+)   | ...    | 0       | 1 (+) | 3 (3)  | +       | +       | +       | ...   | 1 (+) |
| 1500-1700 m    | 37 (12) | +       | ...    | 0       | 1 (+) | 0      | 1 (+)   | +       | +       | ...   | +     |
| 1700-1900 m    | 0       | +       | ...    | 0       | +     | ...    | 1 (+)   | +       | ...     | ...   | ...   |
| 1900-2100 m    | 0       | +       | ...    | +       | +     | ...    | +       | +       | ...     | ...   | ...   |
| 2100-2300 m    | 0       | 0       | ...    | +       | 0     | ...    | +       | ...     | ...     | ...   | ...   |
| 2300-2500 m    | ...     | ...     | ...    | ...     | 0     | ...    | +       | ...     | ...     | ...   | ...   |
| 2500-2700 m    | ...     | ...     | ...    | ...     | 0     | ...    | 0       | ...     | ...     | ...   | ...   |
| 2700-2900 m    | ...     | ...     | ...    | ...     | ...   | ...    | 0       | ...     | ...     | ...   | ...   |
| 2900-3100 m    | ...     | ...     | ...    | ...     | ...   | ...    | ...     | ...     | ...     | ...   | ...   |
| <i>Habitat</i> |         |         |        |         |       |        |         |         |         |       |       |
| Ohia           | 31 (10) | +       | 3 (1)  | 1 (+)   | 1 (+) | +      | +       | +       | 4 (1)   | ...   | +     |
| Koa-ohia       | 5 (5)   | +       | ...    | +       | 2 (+) | ...    | +       | ...     | ...     | ...   | ...   |
| Koa-mamane     | ...     | +       | ...    | 0       | +     | ...    | ...     | ...     | ...     | ...   | ...   |
| Mamane-naio    | ...     | ...     | ...    | ...     | +     | ...    | ...     | ...     | ...     | ...   | ...   |
| Mamane         | ...     | ...     | ...    | ...     | +     | ...    | 0       | ...     | ...     | ...   | ...   |
| Other natives  | ...     | 3 (1)   | ...    | 0       | 1 (+) | ...    | 2 (+)   | ...     | 5 (1)   | +     | ...   |
| Intro. trees   | ...     | 1 (1)   | ...    | ...     | 3 (1) | 2 (2)  | 2 (1)   | 0       | 5 (1)   | 1 (+) | ...   |
| Treelless      | 0       | +       | 1 (+)  | 0       | 1 (+) | ...    | +       | 0       | +       | +     | 0     |

<sup>a</sup> Densities are given in birds/km<sup>2</sup>; + indicates stratum was in the species range but density <0.5 birds/km<sup>2</sup>; 0 indicates stratum was outside range but was sampled; ... indicates stratum was not sampled in study area.

TABLE 47  
REGRESSION MODELS FOR HABITAT RESPONSE OF THE SPOTTED DOVE AND ZEBRA DOVE<sup>a</sup>

|                             | Spotted Dove |       |       |       |         | Zebra Dove |         |
|-----------------------------|--------------|-------|-------|-------|---------|------------|---------|
|                             | Hamakua      | Puna  | Kona  | Maui  | Molokai | Kona       | Molokai |
| <i>R</i> <sup>2</sup>       | 0.10*        | 0.50* | 0.10* | 0.15* | 0.26*   | 0.17*      | 0.17*   |
| Moisture                    | -5.0*        | -8.1* | ...   | -7.6* | -10.1*  | -5.1*      | -4.4*   |
| Elevation                   | 2.9          | ...   | -7.2* | ...   | 5.9*    | -11.3*     | ...     |
| (Elevation) <sup>2</sup>    | -3.3*        | ...   | ...   | -6.6* | ...     | ...        | ...     |
| Tree biomass                | ...          | ...   | ...   | ...   | 4.5*    | ...        | 5.4*    |
| (Tree biomass) <sup>2</sup> | 3.5*         | 6.9*  | ...   | 7.2*  | ...     | ...        | ...     |
| Crown cover                 | -3.0         | -2.7  | ...   | ...   | ...     | ...        | ...     |
| Canopy height               | 3.8*         | -2.7  | ...   | ...   | ...     | ...        | ...     |
| Koa                         | -2.5         | X     | ...   | -4.0* | X       | ...        | X       |
| Ohia                        | -7.0*        | ...   | ...   | -4.5* | 3.5*    | ...        | -5.9*   |
| Naio                        | X            | X     | ...   | X     | X       | -2.7       | X       |
| Mamane                      | -5.6*        | 6.0*  | ...   | ...   | X       | 7.4*       | X       |
| Intro. trees                | 2.5          | ...   | 7.9*  | ...   | ...     | 7.3*       | ...     |
| Shrub cover                 | -2.7         | 3.2   | ...   | ...   | ...     | -5.6*      | ...     |
| Ground cover                | ...          | ...   | -4.6* | ...   | ...     | ...        | ...     |
| Native shrubs               | ...          | 4.3*  | ...   | ...   | ...     | ...        | ...     |
| Intro. shrubs               | -3.3         | ...   | 4.7*  | ...   | ...     | ...        | ...     |
| Ground ferns                | X            | -3.4* | ...   | ...   | -3.5*   | -4.1*      | ...     |
| Matted ferns                | ...          | ...   | -3.8* | ...   | ...     | -3.7*      | ...     |
| Tree ferns                  | X            | -3.9* | -5.6* | ...   | ...     | ...        | ...     |
| Ieie                        | X            | ...   | ...   | ...   | X       | -3.2       | X       |
| Passiflora                  | ...          | X     | ...   | 7.9*  | X       | ...        | X       |
| Native herbs                | X            | -2.6  | ...   | ...   | ...     | ...        | ...     |
| Intro. herbs                | X            | ...   | ...   | -3.5* | 2.9     | 3.6*       | ...     |
| Native grasses              | -3.0         | -3.7* | ...   | ...   | ...     | ...        | ...     |
| Intro. grasses              | ...          | ...   | ...   | ...   | 3.6*    | ...        | ...     |

<sup>a</sup> *R*<sup>2</sup> is the variance accounted for by the model. Entries are *t* statistics and all are significant at *P* < 0.05; \* indicates *P* < 0.001; ... indicates variable not significant (*P* > 0.05); X indicates variable not available for inclusion in model.

sighted from the Olokui Plateau along the sea-cliff. On West Maui, Lanai, and Kauai, the distribution of Spotted Doves has changed little from 1949. We found birds as high as 2000 m elevation on Hawaii and 2300 m on Maui.

Spotted Doves are widely distributed at all elevations in low numbers, although they are usually absent from high elevation forests and grasslands (Fig. 217). The regression models (Table 47) show that the species is most common in dry, low elevation woodlands with introduced trees and grasses. Spotted Doves occupy similar habitats in India (Ali and Ripley 1970) and southeast Asia (Smythies 1953), especially agricultural lands. No variable met the entry criteria in the Lanai model. Moisture has a negative term in four of five models, and elevation has a negative term in study areas with a mean elevation above 1000 m. Positive terms for tree biomass, balanced in most models by negative terms for crown cover, ohia, or koa, indicate association with savanna, pasture, woodland, and open forest. Spotted Doves have negative responses to all three fern variables; not only are ferns more common in wet areas and forest in-

teriors, but they also close the ground story where birds primarily feed. Higher densities are associated with passiflora, and birds may act as dispersal agents for banana poka (Warshauer et al. 1983). Introduced grasses tend to have positive terms and are an important element of the diet (Schwartz and Schwartz 1949, 1951a). Available water may limit distribution in some areas (Caum 1933).

#### ZEBRA DOVE (*Geopelia striata*)

Zebra Doves, also known as Barred Doves, were introduced to the Hawaiian Islands in 1922 (Caum 1933) and are native to the Indo-Malay and Australasian regions. The characteristic habitat is cleared, open, or lightly forested areas below 1000 m elevation (Schwartz and Schwartz 1949, Goodwin 1970, Lewin 1971); our study areas were therefore mainly on the range periphery. Berger (1981) considered this species common to abundant on all the main islands. The diet consists almost entirely of seeds from the ground (Schwartz and Schwartz 1951c).

Zebra Doves occur in six study areas (Tables 33, 34, 48, Figs. 218–221). On Hawaii an esti-

TABLE 48  
DENSITY [MEAN (SE)] OF THE ZEBRA DOVE AND MOURNING DOVE BY ELEVATION, HABITAT, AND STUDY AREA\*

|                  | Zebra Dove |         |       |         |         |       | Mourning Dove |
|------------------|------------|---------|-------|---------|---------|-------|---------------|
|                  | Hamakua    | Kipukas | Kona  | E. Maui | Molokai | Lanai | Kona          |
| <i>Elevation</i> |            |         |       |         |         |       |               |
| 100–300 m        | ...        | ...     | ...   | ...     | 0       | ...   | ...           |
| 300–500 m        | 0          | ...     | 3 (1) | 0       | 3 (3)   | ...   | 0             |
| 500–700 m        | 0          | ...     | 6 (1) | 0       | 9 (4)   | + (+) | + (+)         |
| 700–900 m        | 0          | ...     | 4 (1) | 3 (2)   | 8 (4)   | + (+) | + (+)         |
| 900–1100 m       | 0          | ...     | 1 (+) | 8 (1)   | 1 (+)   | 1 (+) | + (+)         |
| 1100–1300 m      | + (+)      | 3 (2)   | 2 (+) | 12 (3)  | + (+)   | ...   | + (+)         |
| 1300–1500 m      | 2 (1)      | 1 (+)   | 3 (+) | 0       | ...     | ...   | + (+)         |
| 1500–1700 m      | 0          | + (+)   | 2 (+) | 0       | ...     | ...   | + (+)         |
| 1700–1900 m      | + (+)      | 0       | + (+) | 0       | ...     | ...   | + (+)         |
| 1900–2100 m      | + (+)      | + (+)   | + (+) | 0       | ...     | ...   | + (+)         |
| 2100–2300 m      | 0          | 0       | 1 (+) | + (+)   | ...     | ...   | 0             |
| 2300–2500 m      | ...        | ...     | + (+) | 0       | ...     | ...   | 0             |
| 2500–2700 m      | ...        | ...     | ...   | 0       | ...     | ...   | ...           |
| 2700–2900 m      | ...        | ...     | ...   | 0       | ...     | ...   | ...           |
| 2900–3100 m      | ...        | ...     | ...   | ...     | ...     | ...   | ...           |
| <i>Habitat</i>   |            |         |       |         |         |       |               |
| Ohia             | 1 (1)      | + (+)   | 3 (+) | 0       | 1 (1)   | ...   | + (+)         |
| Koa-ohia         | 1 (1)      | 10 (3)  | 2 (+) | 0       | ...     | ...   | + (+)         |
| Koa-mamane       | 0          | + (+)   | 2 (+) | ...     | ...     | ...   | + (+)         |
| Mamane-naio      | ...        | ...     | + (+) | ...     | ...     | ...   | +             |
| Mamane           | ...        | ...     | 2 (+) | 0       | ...     | ...   | 0             |
| Other natives    | + (+)      | + (+)   | 3 (1) | 7 (1)   | 2 (2)   | 1 (+) | + (+)         |
| Intro. trees     | 0          | ...     | 3 (1) | 0       | 5 (2)   | 1 (+) | + (+)         |
| Treeless         | + (+)      | + (+)   | 1 (1) | 0       | 0       | + (+) | + (+)         |

\* Densities are given in birds/km<sup>2</sup>; + indicates stratum was in the species range but density <0.5 birds/km<sup>2</sup>; 0 indicates stratum was outside range but was sampled; ... indicates stratum was not sampled in study area.

mated  $1200 \pm 150$  (95% CI) birds occur in the Kona, Hamakua, and Kipukas study areas. The range on Hawaii has expanded considerably since the surveys of Schwartz and Schwartz (1949). Although the Schwartzes failed to find them on windward Hawaii, they are now well established in urban and agricultural areas (J. M. Scott, pers. observ.). We found birds on East Maui, Molokai, and Lanai, but only on Molokai was their occurrence more than occasional.

Zebra Doves occur in very low densities in a variety of vegetation types and over a wide range of elevations, from sea level to 2300 m on Hawaii and Maui. They were absent only from wet ohia forests. They occupy fewer habitat types above 1500 m than below (Fig. 222), probably because the range limit is near 1000 m.

The regression models (Table 47) show that within our study areas Zebra Doves are most common in dry areas at lower elevations with mamane or introduced trees, but have low densities in areas with high amounts of shrub cover, ohia, ground ferns, or matted ferns. In Asia they seldom occur in wet forests or dense brush except at forest margins and clearings, but are particu-

larly common on agricultural lands (Schwartz and Schwartz 1949, Goodwin 1970).

In the Molokai regression model, tree biomass is a balance term for ohia and serves as a "proxy" for positive responses to introduced trees; this is seen in the correlations between bird density and tree biomass ( $r = 0.04$ ), ohia ( $-0.30$ ), and introduced trees (0.29). The latter two values are the second and third highest bird-habitat correlations for this species. The mechanics of model construction entered tree biomass first, then at a lower level chose ohia over introduced trees. A more representative model might use introduced trees instead of tree biomass, but would not differ statistically from the one given.

#### MOURNING DOVE (*Zenaida macroura*)

Mourning Doves are native to most of North America (A.O.U. 1983). They were first introduced to Hawaii in 1929, but failed to establish a population. Birds from California game farms were released during 1962–1965 on Puu Waawaa Ranch in Kona (Lewin 1971). A hunting season was established in October 1969 pursuant to incidental takes by gamebird hunters in 1968, and

ZEBRA DOVE

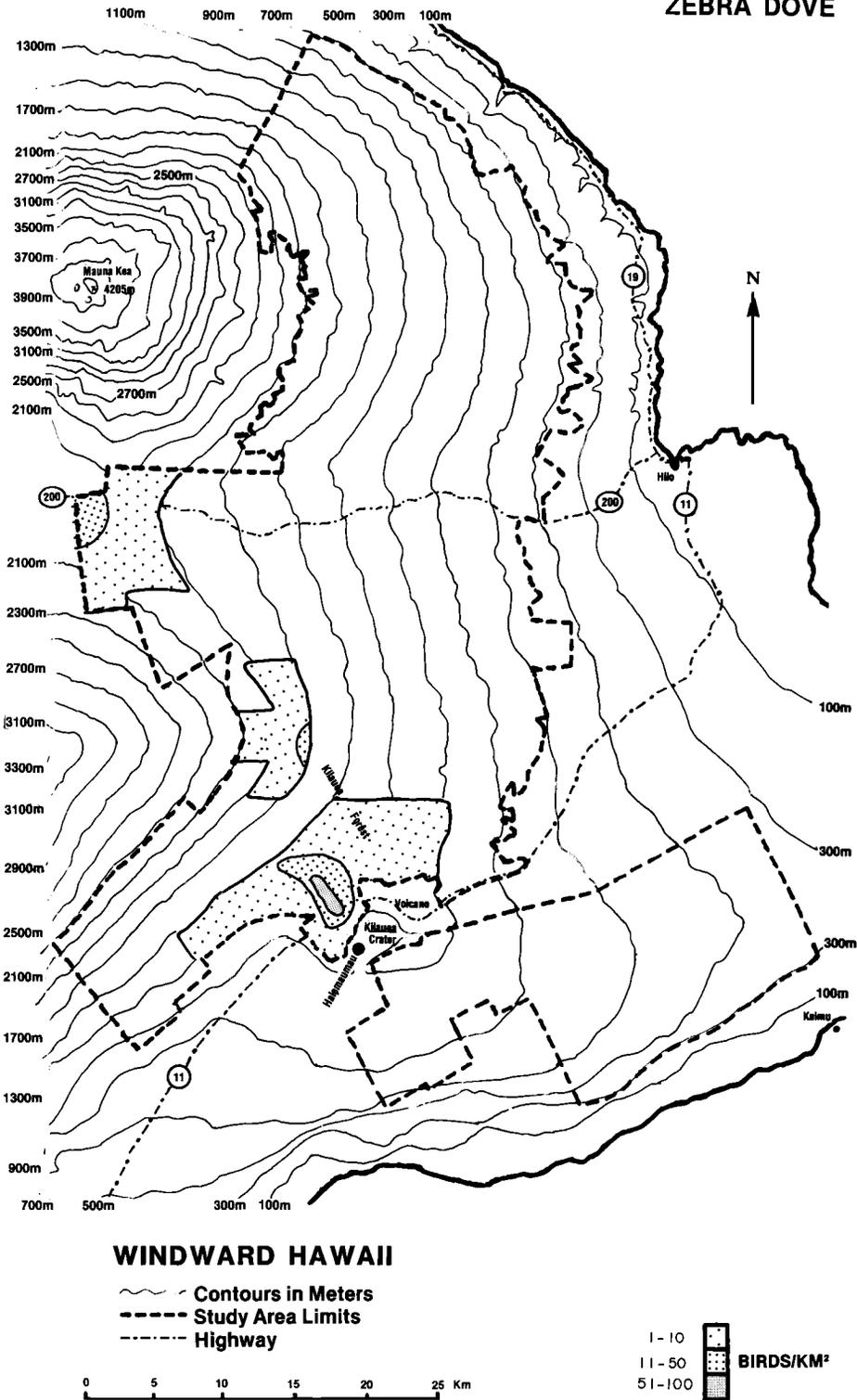


FIGURE 218. Distribution and abundance of the Zebra Dove in the windward Hawaii study areas.



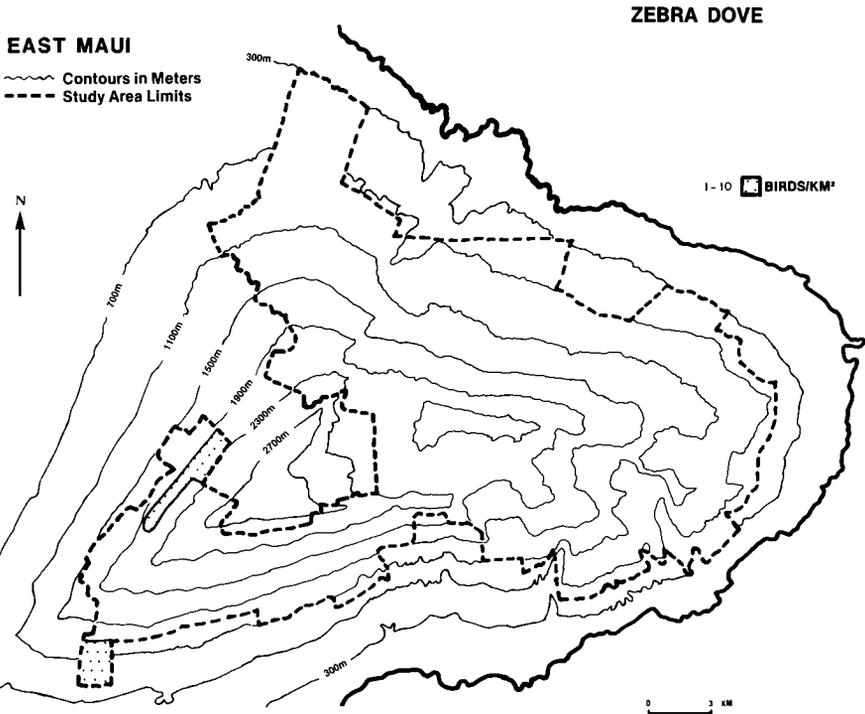


FIGURE 220. Distribution and abundance of the Zebra Dove in the East Maui study area.

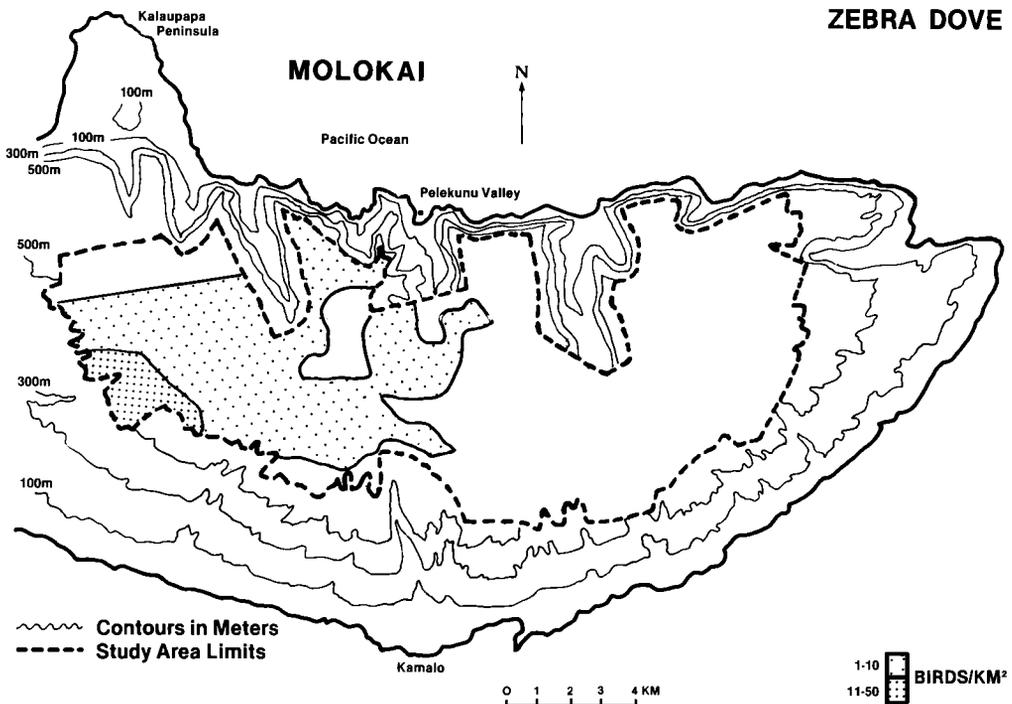


FIGURE 221. Distribution and abundance of the Zebra Dove in the Molokai study area.

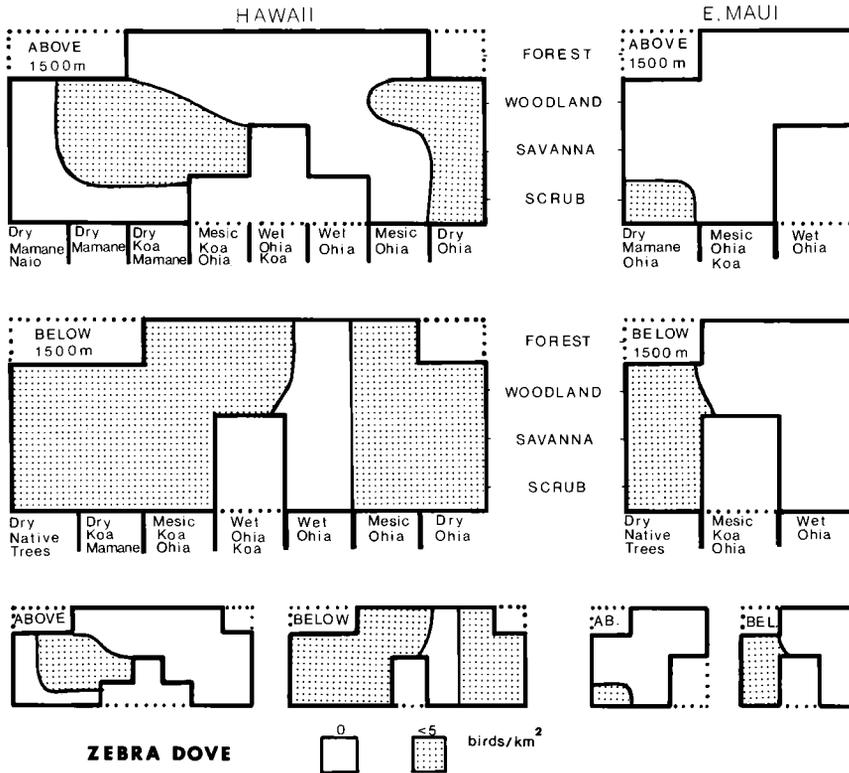


FIGURE 222. Habitat response graphs of the Zebra Dove. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

in 1974 the population was estimated at 500–1500 birds (R. L. Walker, pers. comm.).

We found Mourning Doves only in the Kona study area, restricted to the north slopes of Hualalai and the high-elevation open woodland on Mauna Loa (Table 48, Fig. 223). We estimated the population to be  $8 \pm 6$  (95% CI) birds (Table 33). Although we did not sample much of the lowland areas on Hawaii, we failed to find them outside Puu Waawaa Ranch, as have others (J. Giffin, pers. comm.). The core population is centered at low-elevation feedlots near Puu Waawaa (R. L. Walker, pers. comm.), an area we did not sample. The habitat response graphs indicate occurrence in dry open habitats below 1500 m (Fig. 224). The patchy pattern reflects the recent introduction.

#### COMMON BARN-OWL (*Tyto alba*)

This species was introduced on Hawaii in 1958 from California in hopes of controlling rats in sugar cane fields (Tomich 1962). We had only 10 incidental observations and station records for this species. Five of these were in Kona. The others were on windward Hawaii, Kohala, Mo-

lokai, and East Maui. Although its nocturnal habits may account in part for these low numbers, we suspect that this species has not yet established sizeable populations in the native forests and may be limited by suitable nesting and roosting sites in many areas. It is common in sugar cane fields and other lowland agricultural areas on Hawaii, Maui (J. M. Scott, C. B. Kepler, pers. observ.), Oahu (M. Morin, pers. comm.), and Kauai (Au and Swedberg 1966).

#### EURASIAN SKYLARK (*Alauda arvensis*)

Eurasian Skylarks were introduced from England in 1865 (Caum 1933). Munro (1944) considered them well established on all the islands as did Berger (1972). However, in recent years they have declined in abundance on Oahu and are apparently no longer found on Kauai (Berger 1981).

We found Eurasian Skylarks only on Hawaii and Maui (Tables 33, 34, 49, Figs. 225–229), where an estimated  $10,000 \pm 1500$  (95% CI) and  $400 \pm 100$  birds occur in the study areas on those respective islands. Birds occur at low densities throughout the open upper-elevation forests of

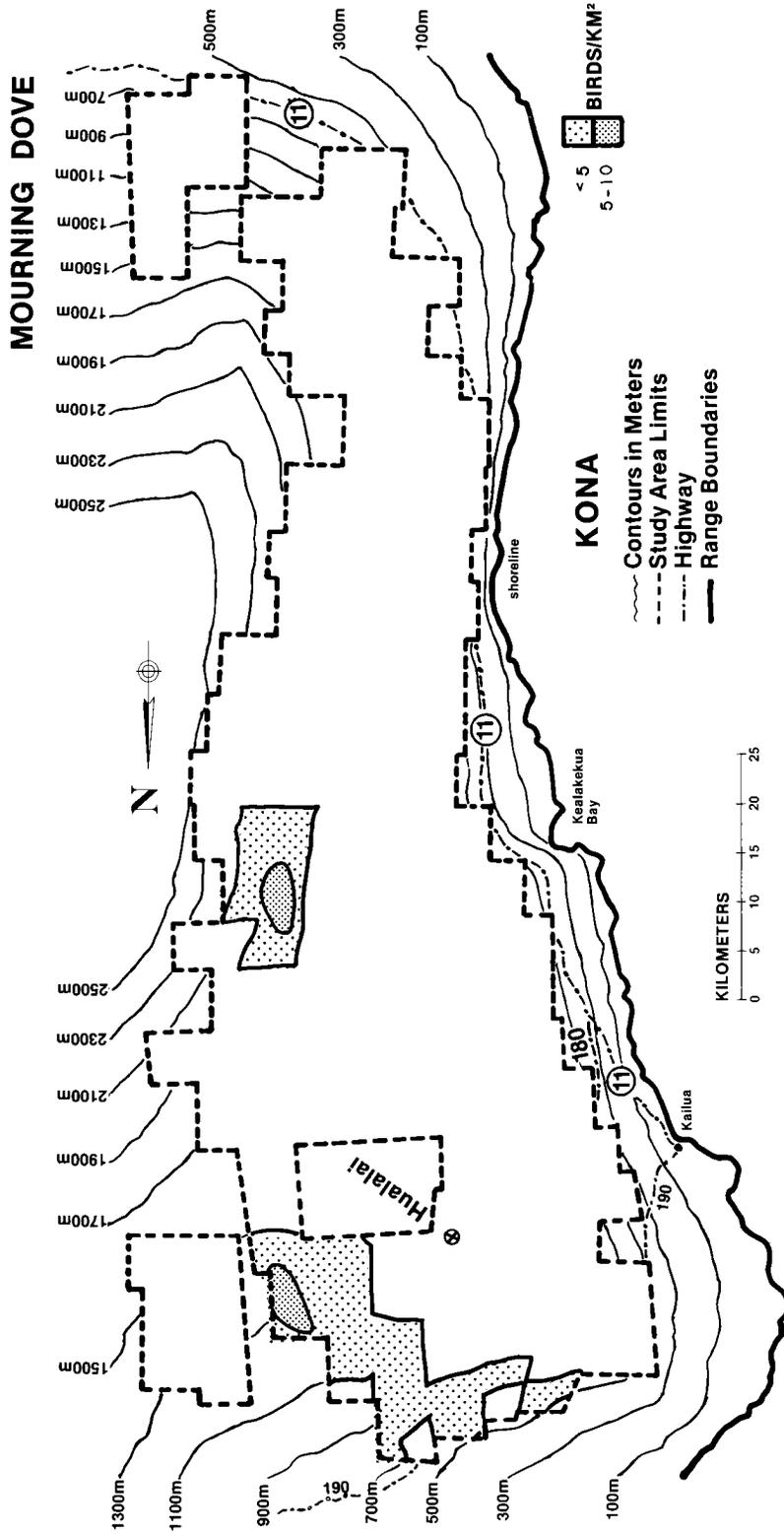


FIGURE 223. Distribution and abundance of the Mourning Dove in the Kona study area.

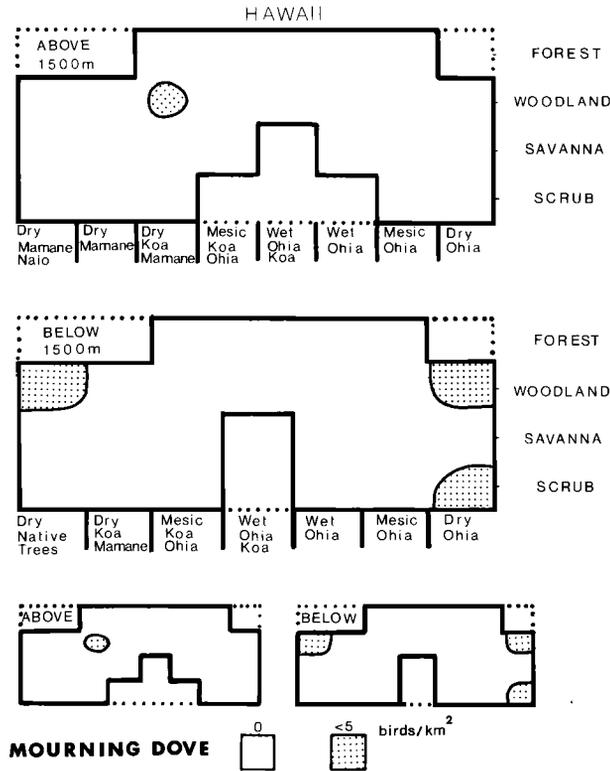


FIGURE 224. Habitat response graphs of the Mourning Dove. (Graphs give mean density above and below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

windward Hawaii and are scattered throughout Kona and Mauna Kea at higher densities. The one bird recorded in Kohala was singing from open pastures outside the study area. Skylarks are widely distributed in the crater district and drier slopes of Haleakala. They occur from sea level to 3000 m on Hawaii and to 2700 m on Maui.

Eurasian Skylarks are most common in dry scrub, savanna, and woodland, with lower densities in mesic habitats (Table 50, Fig. 230). Wet habitats are unoccupied on Maui, but small numbers occur along woodland edges on Hawaii. In general, skylarks frequent degraded, fragmented, and deforested habitat. Many observations were aural detections of birds at considerable distances from the actual station. The positive terms in the regression models for canopy height represent birds heard by observers situated in tall koa and eucalyptus groves on the edges of pastures. The negative response to ohia reflects absence in forest interiors. High densities in mamane woodlands are reflected in the positive terms in two models. Densities tend to be lower in areas with introduced trees such as guava, or with closed shrub and ground cover. Scattered

ground cover is required for nest concealment (Berger 1981).

**JAPANESE BUSH-WARBLER (*Cettia diphone*)**

Japanese Bush-Warblers, also called Uguisu, were introduced to Oahu in 1929 (Caum 1933). Native to Japan and other parts of Asia, they are largely insectivorous but also take fruit and nectar (Berger 1981). Japanese Bush-Warblers were first noted on Molokai and Lanai in 1979 (Pyle 1979, P. Conant 1980) and on Maui in 1980 (Carothers and Hansen 1982). Since our study they have dramatically increased on Molokai (C. B. Kepler, pers. observ.).

We found Japanese Bush-Warblers only on East Maui and Molokai. They were uncommon on Molokai with a fragmented distributional pattern in those areas sampled in 1979. They were well established on the Olokui Plateau during the 1980 survey (Tables 34, 51, Fig. 231). We estimated  $200 \pm 80$  (95% CI) birds in the Molokai study area. Our record for East Maui is the first for the island.

The regression model for Molokai (Table 50) shows that birds are more common at higher elevations in areas with a high cover of native

TABLE 49  
DENSITY [MEAN (SE)] OF THE EURASIAN SKYLARK BY ELEVATION, HABITAT, AND STUDY AREA<sup>a</sup>

|                  | Kau   | Hamakua | Puna  | Kipukas | Kona   | Mauna Kea | Kohala | East Maui |
|------------------|-------|---------|-------|---------|--------|-----------|--------|-----------|
| <i>Elevation</i> |       |         |       |         |        |           |        |           |
| 100–300 m        | ...   | ...     | ...   | ...     | ...    | ...       | ...    | ...       |
| 300–500 m        | ...   | 0       | 0     | ...     | 0      | ...       | 0      | 0         |
| 500–700 m        | 0     | 0       | 0     | ...     | 6 (2)  | ...       | 0      | 0         |
| 700–900 m        | 0     | 0       | 0     | ...     | 5 (1)  | ...       | 0      | 3 (3)     |
| 900–1100 m       | 0     | 0       | + (+) | ...     | 7 (1)  | ...       | 0      | 11 (3)    |
| 1100–1300 m      | 0     | 6 (4)   | 0     | 7 (2)   | 4 (1)  | ...       | + (+)  | 25 (6)    |
| 1300–1500 m      | 0     | 5 (1)   | ...   | 7 (1)   | 6 (1)  | ...       | 0      | 8 (3)     |
| 1500–1700 m      | 0     | 2 (1)   | ...   | 3 (1)   | 12 (1) | ...       | 0      | 5 (3)     |
| 1700–1900 m      | 0     | 8 (2)   | ...   | 1 (+)   | 8 (1)  | ...       | ...    | 2 (1)     |
| 1900–2100 m      | 6 (6) | 4 (1)   | ...   | 2 (1)   | 8 (1)  | 28 (7)    | ...    | 2 (1)     |
| 2100–2300 m      | 0     | 17 (3)  | ...   | + (+)   | 7 (1)  | 40 (9)    | ...    | 5 (2)     |
| 2300–2500 m      | ...   | ...     | ...   | ...     | 4 (1)  | 36 (6)    | ...    | 3 (1)     |
| 2500–2700 m      | ...   | ...     | ...   | ...     | ...    | 27 (4)    | ...    | 6 (3)     |
| 2700–2900 m      | ...   | ...     | ...   | ...     | ...    | 29 (4)    | ...    | 0         |
| 2900–3100 m      | ...   | ...     | ...   | ...     | ...    | 22 (13)   | ...    | ...       |
| <i>Habitat</i>   |       |         |       |         |        |           |        |           |
| Ohia             | 6 (6) | 2 (1)   | + (+) | 2 (+)   | 4 (+)  | ...       | + (+)  | 0         |
| Koa-ohia         | 0     | 4 (1)   | ...   | 3 (1)   | 4 (1)  | ...       | ...    | 5 (3)     |
| Koa-mamane       | ...   | 10 (2)  | ...   | 3 (1)   | 14 (1) | ...       | ...    | ...       |
| Mamane-naio      | ...   | ...     | ...   | ...     | 3 (2)  | 11 (2)    | ...    | ...       |
| Mamane           | ...   | ...     | ...   | ...     | 20 (2) | 53 (4)    | ...    | 22 (12)   |
| Other natives    | ...   | 7 (2)   | ...   | 13 (2)  | 16 (6) | ...       | ...    | 7 (1)     |
| Intro. trees     | ...   | 2 (1)   | ...   | ...     | 6 (2)  | ...       | 0      | 7 (4)     |
| Treeless         | 0     | + (+)   | + (+) | + (+)   | 8 (2)  | ...       | ...    | 2 (1)     |

<sup>a</sup> Densities are given in birds/km<sup>2</sup>; + indicates stratum was in the species range but density <0.5 birds/km<sup>2</sup>; 0 indicates stratum was outside range but was sampled; ... indicates stratum was not sampled in study area.

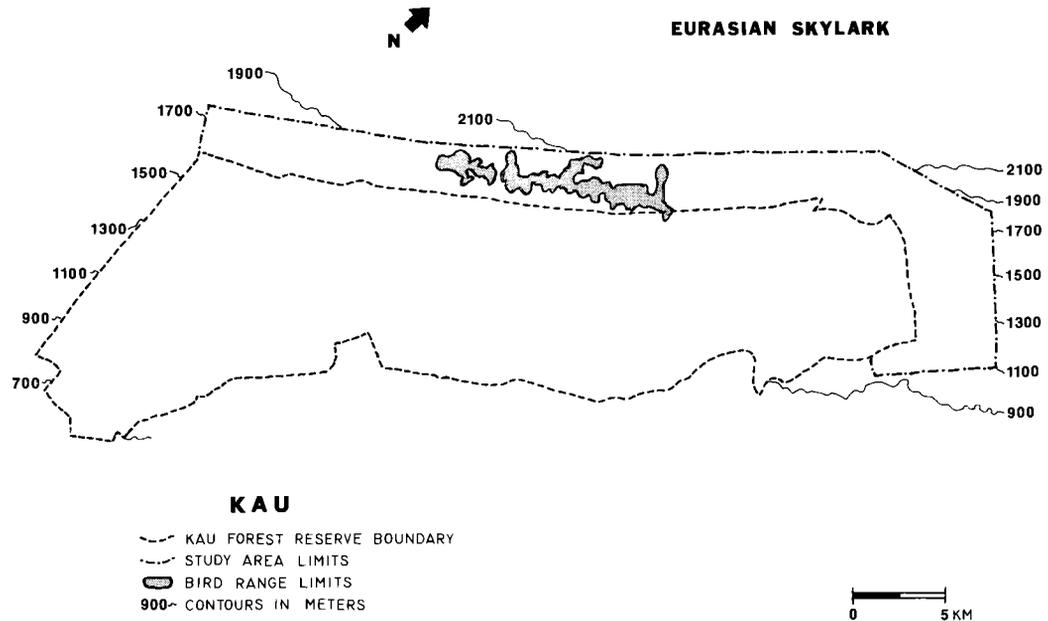


FIGURE 225. Distribution and abundance of the Eurasian Skylark in the Kau study area. (Density within range is less than 10 birds/km<sup>2</sup>.)

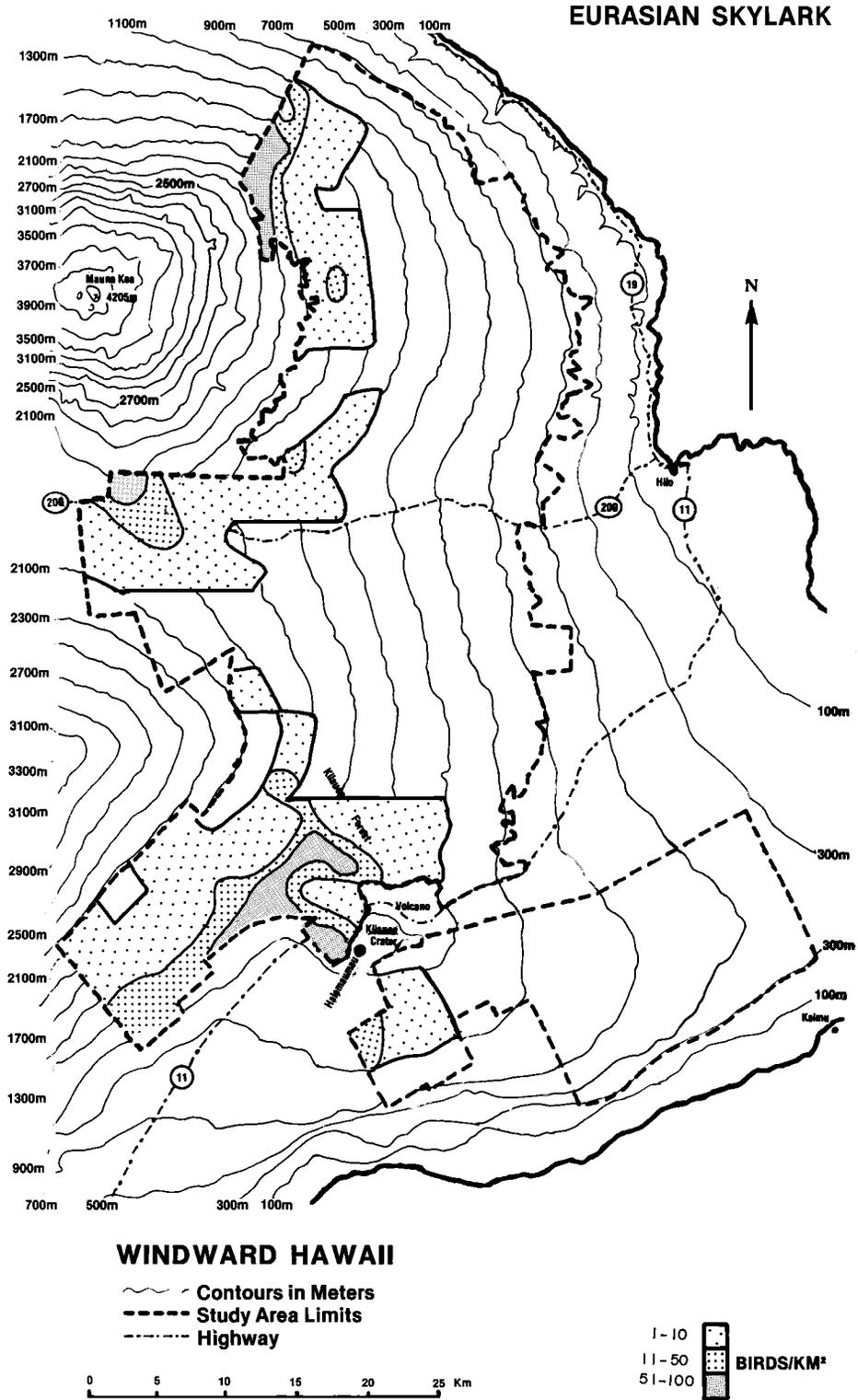


FIGURE 226. Distribution and abundance of the Eurasian Skylark in the windward Hawaii study areas.

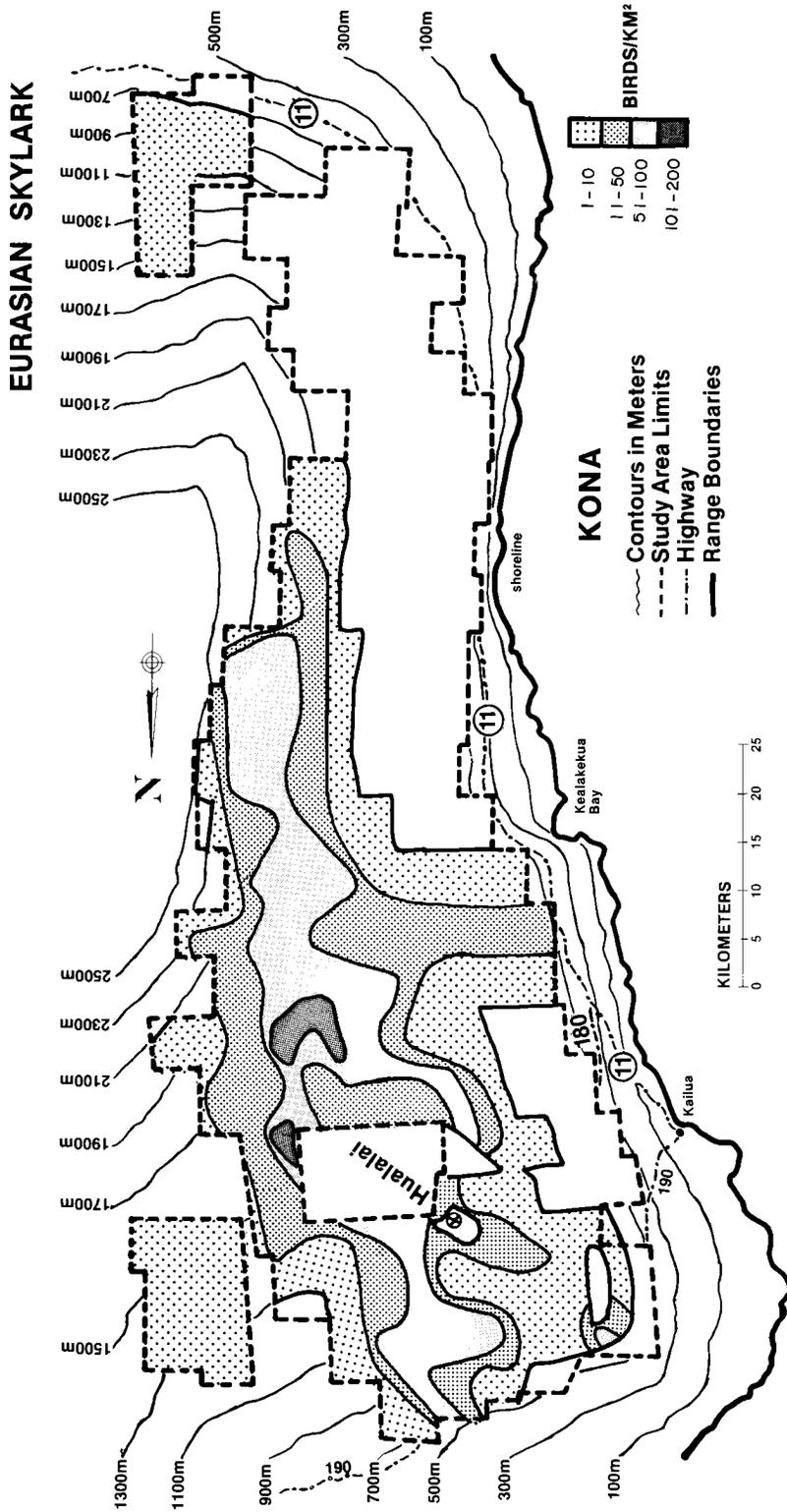


FIGURE 227. Distribution and abundance of the Eurasian Skylark in the Kona study area.

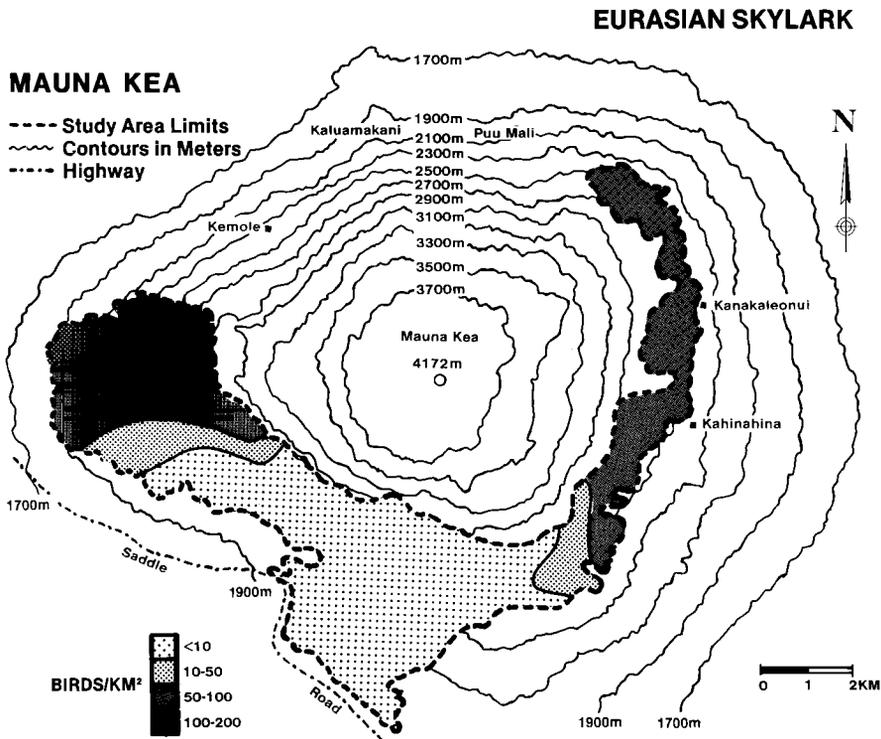


FIGURE 228. Distribution and abundance of the Eurasian Skylark in the Mauna Kea study area.

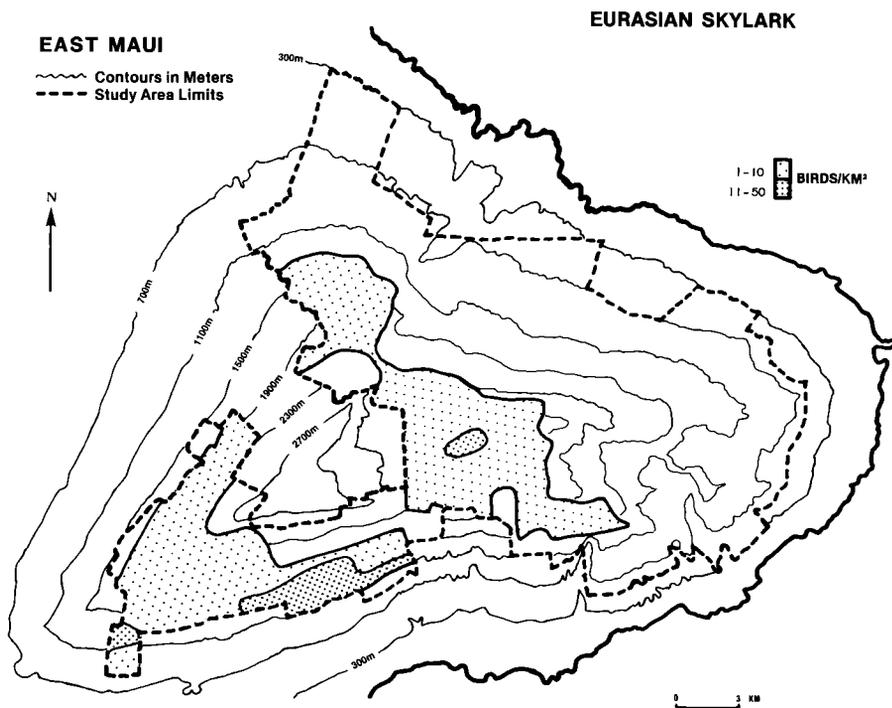


FIGURE 229. Distribution and abundance of the Eurasian Skylark in the East Maui study area.

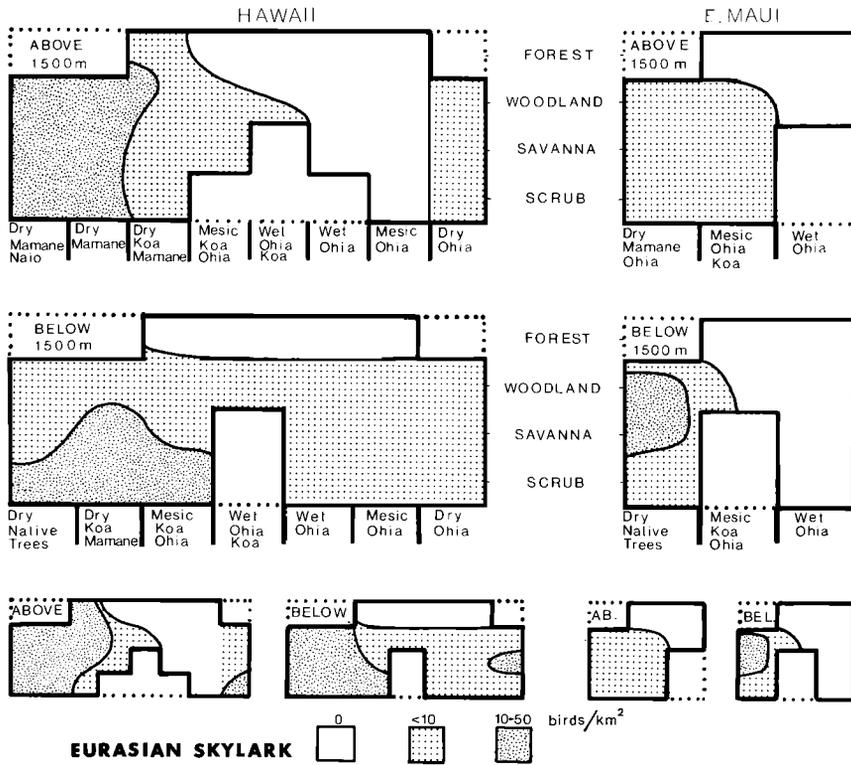


FIGURE 230. Habitat response graphs of the Eurasian Skylark. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

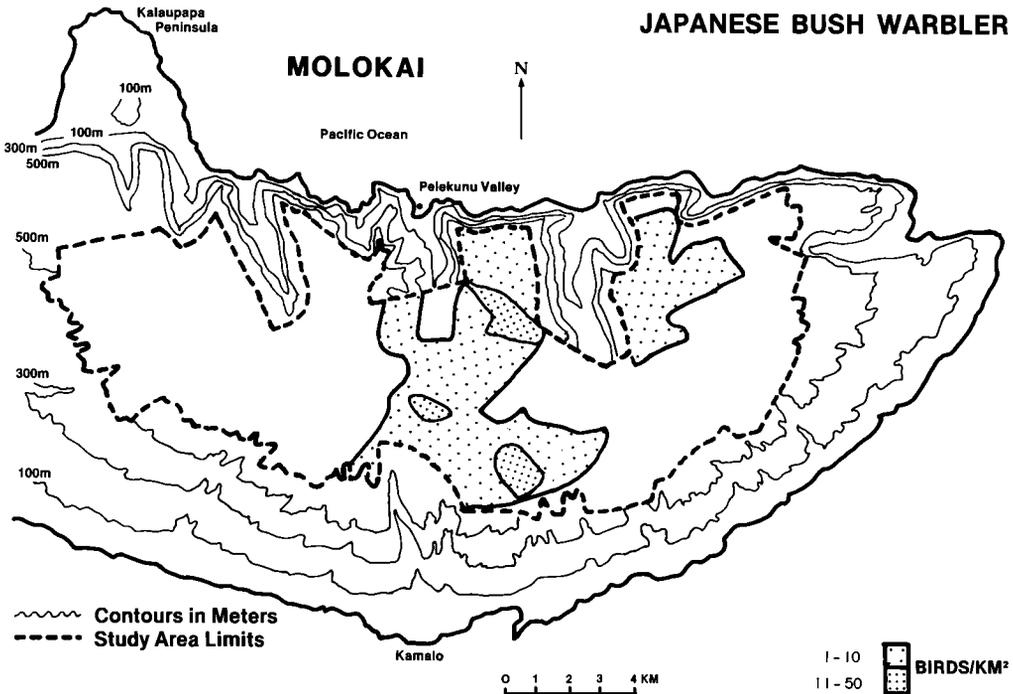


FIGURE 231. Distribution and abundance of the Japanese Bush-Warbler in the Molokai study area.

TABLE 50  
REGRESSION MODELS FOR HABITAT RESPONSE OF THE EURASIAN SKYLARK, JAPANESE BUSH-WARBLER, AND NORTHERN MOCKINGBIRD<sup>a</sup>

|                             | Eurasian Skylark |         |       |           |       | Japanese Bush-Warbler | Northern Mockingbird |       |
|-----------------------------|------------------|---------|-------|-----------|-------|-----------------------|----------------------|-------|
|                             | Hamakua          | Kipukas | Kona  | Mauna Kea | Maui  | Molokai               | Mauna Kea            | Maui  |
| <i>R</i> <sup>2</sup>       | 0.43*            | 0.29*   | 0.39* | 0.47*     | 0.20* | 0.21*                 | 0.08*                | 0.48* |
| Moisture                    | -6.0*            | -4.6*   | ...   | X         | -9.6* | ...                   | X                    | -7.6* |
| Elevation                   | ...              | -4.3*   | 4.8*  | ...       | ...   | -2.3                  | 3.8*                 | 3.9*  |
| (Elevation) <sup>2</sup>    | ...              | 3.5*    | -3.1  | -5.1*     | ...   | 2.7                   | ...                  | ...   |
| Tree biomass                | 2.4              | ...     | 5.0*  | ...       | ...   | ...                   | ...                  | -3.0  |
| (Tree biomass) <sup>2</sup> | ...              | ...     | -3.0  | ...       | ...   | ...                   | ...                  | -4.7* |
| Crown cover                 | ...              | ...     | -7.2* | ...       | ...   | ...                   | ...                  | 4.0*  |
| Canopy height               | 4.9*             | 4.4*    | ...   | 2.2       | 4.5*  | ...                   | 2.4                  | ...   |
| Koa                         | ...              | ...     | -3.6* | X         | ...   | X                     | X                    | -4.8* |
| Ohia                        | -9.8*            | -5.4*   | -6.0* | X         | ...   | ...                   | X                    | -6.3* |
| Naio                        | X                | ...     | ...   | -11.8*    | X     | X                     | 3.1                  | X     |
| Mamane                      | 15.6*            | ...     | 15.6* | ...       | ...   | X                     | ...                  | 11.4* |
| Intro. trees                | -5.8*            | X       | ...   | X         | -3.8* | ...                   | X                    | -6.6* |
| Shrub cover                 | -7.3*            | ...     | -3.8* | -4.6*     | -3.9* | ...                   | ...                  | ...   |
| Ground cover                | -3.1             | ...     | ...   | -4.6*     | 5.6*  | ...                   | ...                  | ...   |
| Native shrubs               | ...              | ...     | ...   | X         | -3.9* | ...                   | X                    | ...   |
| Intro. shrubs               | ...              | ...     | ...   | X         | ...   | ...                   | X                    | 4.4*  |
| Ground ferns                | ...              | ...     | ...   | X         | -3.6* | ...                   | X                    | -3.2  |
| Matted ferns                | ...              | ...     | ...   | X         | ...   | ...                   | X                    | ...   |
| Tree ferns                  | X                | X       | ...   | X         | ...   | ...                   | X                    | ...   |
| Ieie                        | X                | X       | 3.9*  | X         | ...   | X                     | X                    | ...   |
| Passiflora                  | -3.0             | X       | -2.6  | X         | ...   | X                     | X                    | 4.3*  |
| Native herbs                | X                | ...     | ...   | X         | ...   | 4.1*                  | X                    | -3.9* |
| Intro. herbs                | X                | ...     | ...   | ...       | ...   | ...                   | ...                  | ...   |
| Native grasses              | 3.3              | -3.2    | -5.2* | 4.2*      | ...   | 7.5*                  | ...                  | ...   |
| Intro. grasses              | 3.0              | ...     | ...   | ...       | ...   | ...                   | ...                  | -5.8* |
| Ohia flowers                | X                | X       | X     | X         | X     | ...                   | X                    | ...   |
| Olapa fruit                 | X                | X       | X     | X         | X     | ...                   | X                    | ...   |
| Mamane flowers              | X                | X       | X     | X         | X     | X                     | ...                  | -3.5* |
| Mamane fruit                | X                | X       | X     | X         | X     | X                     | ...                  | X     |
| Naio fruit                  | X                | X       | X     | X         | X     | X                     | ...                  | X     |

<sup>a</sup> *R*<sup>2</sup> is the variance accounted for by the model. Entries are *t* statistics and all are significant at *P* < 0.05; \* indicates *P* < 0.001; ... indicates variable not significant (*P* > 0.05); X indicates variable not available for inclusion in model.

herbs and grasses. The elevational response in the model is partly a sampling artifact because birds were usually recorded along cliff faces, and these sites were sampled at the top due to logistics. Cliffs may be a component of preferred habitat and appeared to be the first sites colonized on Maui and Molokai. Berger (1981) characterized this species as occurring primarily in habitats with luxuriant undergrowth, reflected in our model by the terms for native herbs and grasses. In Japan the species has a similar preference for areas with a brushy understory (Kiyosu 1965).

#### WHITE-RUMPED SHAMA (*Copsychus malabaricus*)

Native to southeast Asia, White-rumped Shammas were first released in the Hawaiian Islands

on Oahu in 1940 (Harpham 1953). In 1960 on Kauai, they were a "moderately common resident locally, usually in inhabited lowland areas" (Richardson and Bowles 1964). They are now common on leeward and windward Oahu (Berger 1981), but we know of no records for islands other than Kauai and Oahu. This species is largely insectivorous (Berger 1981).

We found White-rumped Shammas only on Kauai (Fig. 232) where they occur in low densities on the edge of the Alakai Swamp (Tables 34, 51). There were too few observations to interpret habitat response. We estimated a population of  $45 \pm 35$  (95% CI) birds in the study area. Sincov et al. (1984) had two incidental sightings during 1968-1973 in this area, and estimated a total of  $19,000 \pm 23,000$  birds in the native forests on Kauai.

TABLE 51  
DENSITY [MEAN (SE)] OF THE JAPANESE BUSH-WARBLER, WHITE-RUMPED SHAMA, AND NORTHERN MOCKINGBIRD  
BY ELEVATION, HABITAT, AND STUDY AREA\*

| Elevation      | Japanese Bush-Warbler |         | White-rumped Shama | Northern Mockingbird |           |           |           |         |
|----------------|-----------------------|---------|--------------------|----------------------|-----------|-----------|-----------|---------|
|                | East Maui             | Molokai | Kauai              | Kona                 | Mauna Kea | East Maui | West Maui | Molokai |
| 100–300 m      | ...                   | 0       | ...                | ...                  | ...       | ...       | ...       | 0       |
| 300–500 m      | 0                     | 0       | ...                | 0                    | ...       | 0         | ...       | 0       |
| 500–700 m      | 0                     | 56 (32) | ...                | 0                    | ...       | 0         | 4 (4)     | 9 (6)   |
| 700–900 m      | 0                     | 2 (2)   | ...                | 0                    | ...       | 25 (13)   | 1 (1)     | 4 (1)   |
| 900–1100 m     | 0                     | 6 (3)   | ...                | 0                    | ...       | 29 (3)    | +         | 1 (+)   |
| 1100–1300 m    | 1 (1)                 | 17 (4)  | 2 (1)              | 0                    | ...       | 31 (3)    | +         | 0       |
| 1300–1500 m    | +                     | 18 (8)  | +                  | 3 (1)                | ...       | 14 (4)    | 0         | 0       |
| 1500–1700 m    | +                     | ...     | ...                | 3 (1)                | ...       | 14 (4)    | 0         | ...     |
| 1700–1900 m    | +                     | ...     | ...                | 0                    | ...       | 11 (2)    | 0         | ...     |
| 1900–2100 m    | 0                     | ...     | ...                | 0                    | 2 (2)     | 11 (2)    | ...       | ...     |
| 2100–2300 m    | 0                     | ...     | ...                | 0                    | 5 (3)     | 8 (2)     | ...       | ...     |
| 2300–2500 m    | 0                     | ...     | ...                | 0                    | 3 (1)     | 13 (4)    | ...       | ...     |
| 2500–2700 m    | 0                     | ...     | ...                | ...                  | 5 (2)     | 21 (7)    | ...       | ...     |
| 2700–2900 m    | 0                     | ...     | ...                | ...                  | 8 (2)     | +         | ...       | ...     |
| 2900–3100 m    | ...                   | ...     | ...                | ...                  | 3 (3)     | ...       | ...       | ...     |
| <i>Habitat</i> |                       |         |                    |                      |           |           |           |         |
| Ohia           | +                     | 10 (2)  | 1 (1)              | 3 (1)                | ...       | 0         | +         | +       |
| Koa-ohia       | 0                     | ...     | ...                | 0                    | ...       | 1 (1)     | ...       | ...     |
| Koa-mamane     | ...                   | ...     | ...                | 0                    | ...       | ...       | ...       | ...     |
| Mamane-naio    | ...                   | ...     | ...                | 0                    | 2 (1)     | ...       | ...       | ...     |
| Mamane         | 0                     | ...     | ...                | 0                    | 5 (1)     | 10 (5)    | ...       | ...     |
| Other natives  | 0                     | +       | ...                | 0                    | ...       | 26 (6)    | ...       | 5 (5)   |
| Intro. trees   | 0                     | +       | ...                | 0                    | ...       | 5 (5)     | ...       | 3 (2)   |
| Treeless       | +                     | 0       | +                  | 0                    | ...       | 4 (1)     | ...       | +       |

\* Densities are given in birds/km<sup>2</sup>; + indicates stratum was in the species range but density <0.5 birds/km<sup>2</sup>; 0 indicates stratum was outside range but was sampled; ... indicates stratum was not sampled in study area.

#### MELODIOUS LAUGHING-THRUSH (*Garrulax canorus*)

Melodious Laughing-thrushes, also known as Hwa-mei or Chinese Thrushes, were liberated during the great 1900 fire in Honolulu (Caum 1933). These babblers (Timaliinae) are native to southeast Asia. Munro (1944) considered them well established even in the deepest forests but did not list the islands occupied. Berger (1981) summarized that they were apparently well established on Hawaii, Maui, Oahu, and Kauai.

Melodious Laughing-thrushes occur in nine study areas (Tables 33, 34, 52, Figs. 233–239). On Hawaii an estimated 10,000 ± 500 (95% CI) birds occupy our study areas. On Mauna Kea, Melodious Laughing-thrushes are mainly restricted to areas with naio. On windward Hawaii the species has a dynamic range. Birds were rarely reported in Hawaii Volcanoes National Park during the 1940–1975 interval (Baldwin 1953, Conant 1975, Banko and Banko 1980). The range limit running northwest of Kilauea Crater across the Hamakua study area (Fig. 233) represents the

1977 position. High densities in the southwest part of the Puna study area probably reflect changes that occurred as late as 1979. In the mesic and wet forests around Kilauea Crater and in Kipuka Puauulu, Melodious Laughing-thrushes increased from occasional vagrants to fairly common residents in the 1980–1984 period (J. M. Scott, S. Mountainspring, pers. observ.). Birds have apparently not yet colonized the Kau study area, although they occur below the area (J. D. Jacobi, pers. comm.). The pattern in Kona suggests that birds were beginning to invade in 1978, possibly from the Mauna Kea population. Although birds were fairly common in the Kohala study area in 1979 (53% of the stations occupied), they were very scarce (1 bird on 47 counts) in 1970–1972 (van Riper 1982).

On East Maui, Melodious Laughing-thrushes are fairly common in low- to mid-elevation mesic and wet forests, and in dry areas along gulches and near water. Although they are absent from high-elevation wet forests on Maui, the pattern in Hamakua suggests that they will eventually

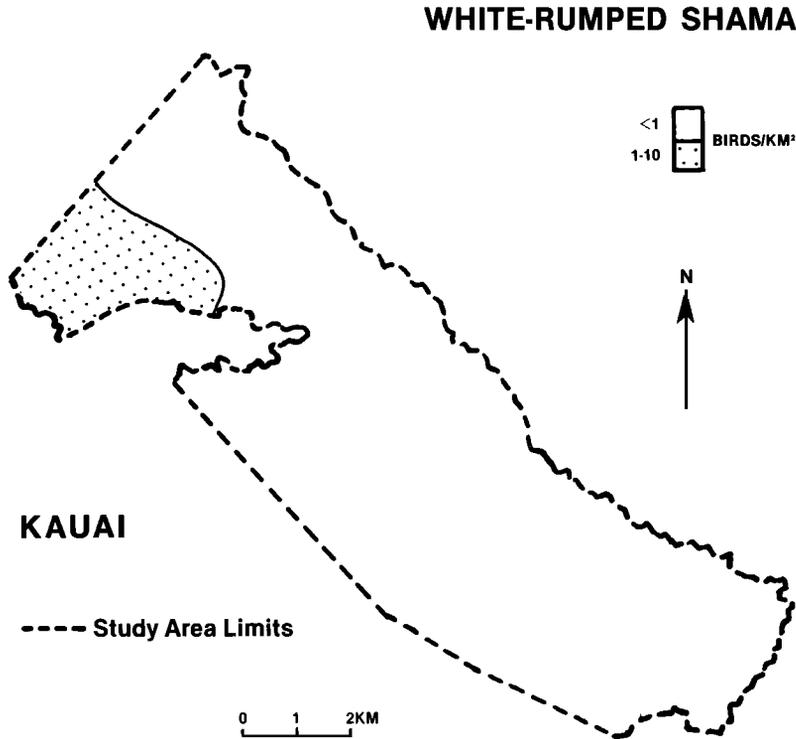


FIGURE 232. Distribution and abundance of the White-rumped Shama in the Kauai study area.

TABLE 52  
DENSITY [MEAN (SE)] OF THE MELODIOUS LAUGHING-THRUSH BY ELEVATION, HABITAT, AND STUDY AREA<sup>a</sup>

|                  | Hamakua | Puna   | Kipukas | Kona  | Mauna<br>Kea | Kohala | East Maui | West Maui | Kauai  |
|------------------|---------|--------|---------|-------|--------------|--------|-----------|-----------|--------|
| <i>Elevation</i> |         |        |         |       |              |        |           |           |        |
| 100–300 m        | ...     | ...    | ...     | ...   | ...          | ...    | ...       | ...       | ...    |
| 300–500 m        | 9 (3)   | 27 (1) | ...     | 0     | ...          | 0      | 9 (3)     | ...       | ...    |
| 500–700 m        | 9 (1)   | 14 (1) | ...     | 0     | ...          | 32 (8) | 18 (2)    | 7 (3)     | ...    |
| 700–900 m        | 15 (1)  | 7 (1)  | ...     | 0     | ...          | 17 (5) | 8 (1)     | 4 (1)     | ...    |
| 900–1100 m       | 6 (1)   | 6 (1)  | ...     | 0     | ...          | 14 (3) | 9 (1)     | 1 (1)     | ...    |
| 1100–1300 m      | 7 (1)   | 1 (1)  | 0       | + (+) | ...          | 18 (3) | 10 (2)    | 2 (1)     | 22 (2) |
| 1300–1500 m      | 2 (+)   | ...    | 0       | 2 (1) | ...          | 12 (2) | 9 (1)     | 1 (1)     | 7 (1)  |
| 1500–1700 m      | 1 (+)   | ...    | 0       | + (+) | ...          | 4 (2)  | 4 (1)     | + (+)     | ...    |
| 1700–1900 m      | 1 (+)   | ...    | + (+)   | + (+) | ...          | ...    | 2 (+)     | + (+)     | ...    |
| 1900–2100 m      | + (+)   | ...    | + (+)   | 0     | 1 (1)        | ...    | 2 (1)     | ...       | ...    |
| 2100–2300 m      | 0       | ...    | 0       | 0     | 1 (1)        | ...    | 1 (1)     | ...       | ...    |
| 2300–2500 m      | ...     | ...    | ...     | 0     | 5 (1)        | ...    | + (+)     | ...       | ...    |
| 2500–2700 m      | ...     | ...    | ...     | ...   | 5 (2)        | ...    | + (+)     | ...       | ...    |
| 2700–2900 m      | ...     | ...    | ...     | ...   | 3 (2)        | ...    | 0         | ...       | ...    |
| 2900–3100 m      | ...     | ...    | ...     | ...   | + (+)        | ...    | ...       | ...       | ...    |
| <i>Habitat</i>   |         |        |         |       |              |        |           |           |        |
| Ohia             | 5 (+)   | 13 (1) | + (+)   | + (+) | ...          | 15 (1) | 6 (1)     | 3 (1)     | 15 (1) |
| Koa-ohia         | 8 (1)   | ...    | + (+)   | 0     | ...          | ...    | 13 (2)    | ...       | ...    |
| Koa-mamane       | + (+)   | ...    | + (+)   | + (+) | ...          | ...    | ...       | ...       | ...    |
| Mamane-naio      | ...     | ...    | ...     | 0     | 4 (1)        | ...    | ...       | ...       | ...    |
| Mamane           | ...     | ...    | ...     | 0     | + (+)        | ...    | 12 (12)   | ...       | ...    |
| Other natives    | 1 (1)   | ...    | + (+)   | 0     | ...          | ...    | 2 (1)     | ...       | ...    |
| Intro. trees     | 13 (1)  | ...    | ...     | 0     | ...          | 24 (7) | 10 (1)    | 14 (14)   | ...    |
| Treeless         | 4 (1)   | + (+)  | + (+)   | 0     | ...          | ...    | 3 (1)     | + (+)     | + (+)  |

<sup>a</sup> Densities are given in birds/km<sup>2</sup>; + indicates stratum was in the species range but density <0.5 birds/km<sup>2</sup>; 0 indicates stratum was outside range but was sampled; ... indicates stratum was not sampled in study area.

**MELODIOUS  
LAUGHING-THRUSH**

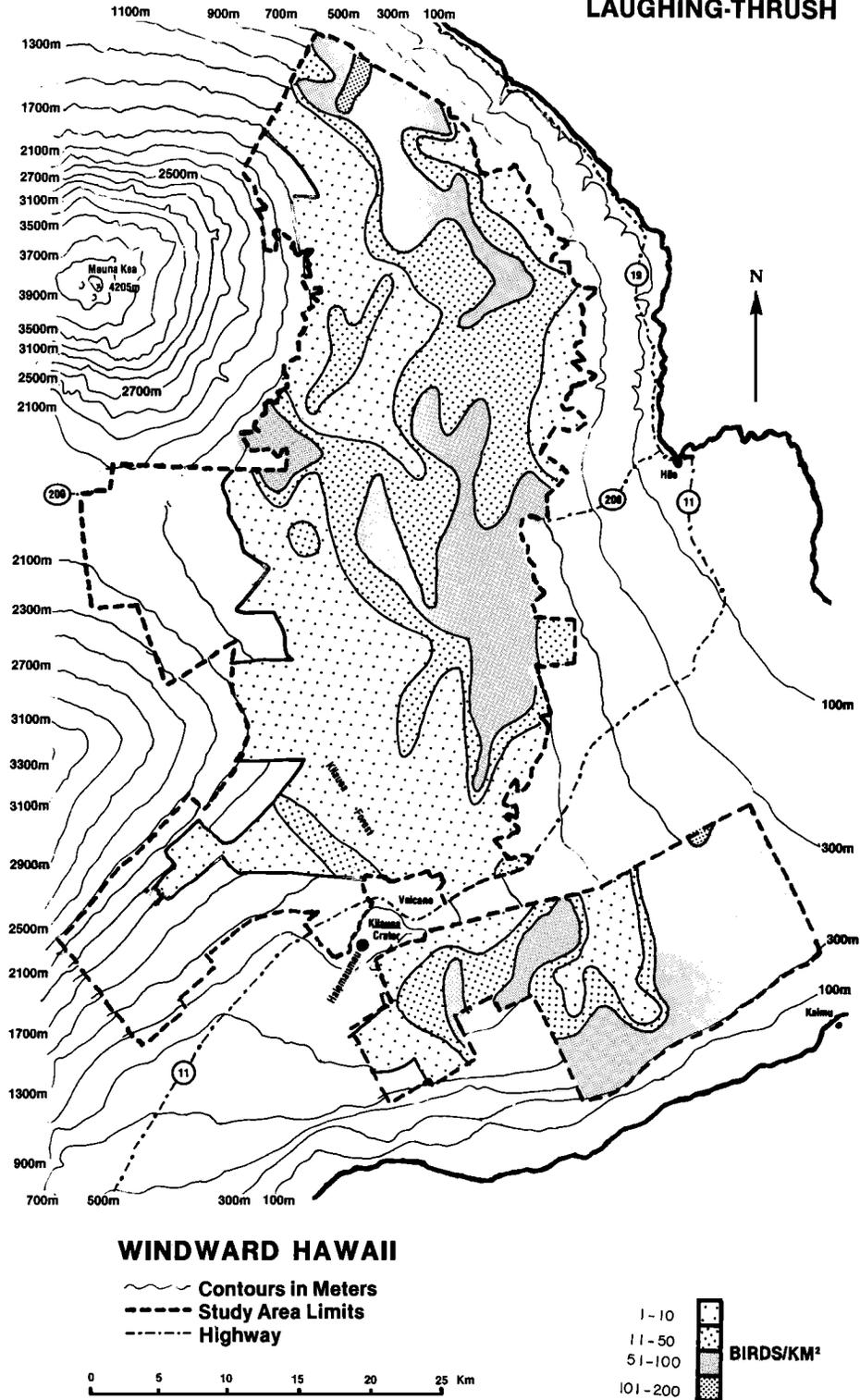


FIGURE 233. Distribution and abundance of the Melodious Laughing-thrush in the windward Hawaii study areas.

MELODIOUS LAUGHING-THRUSH

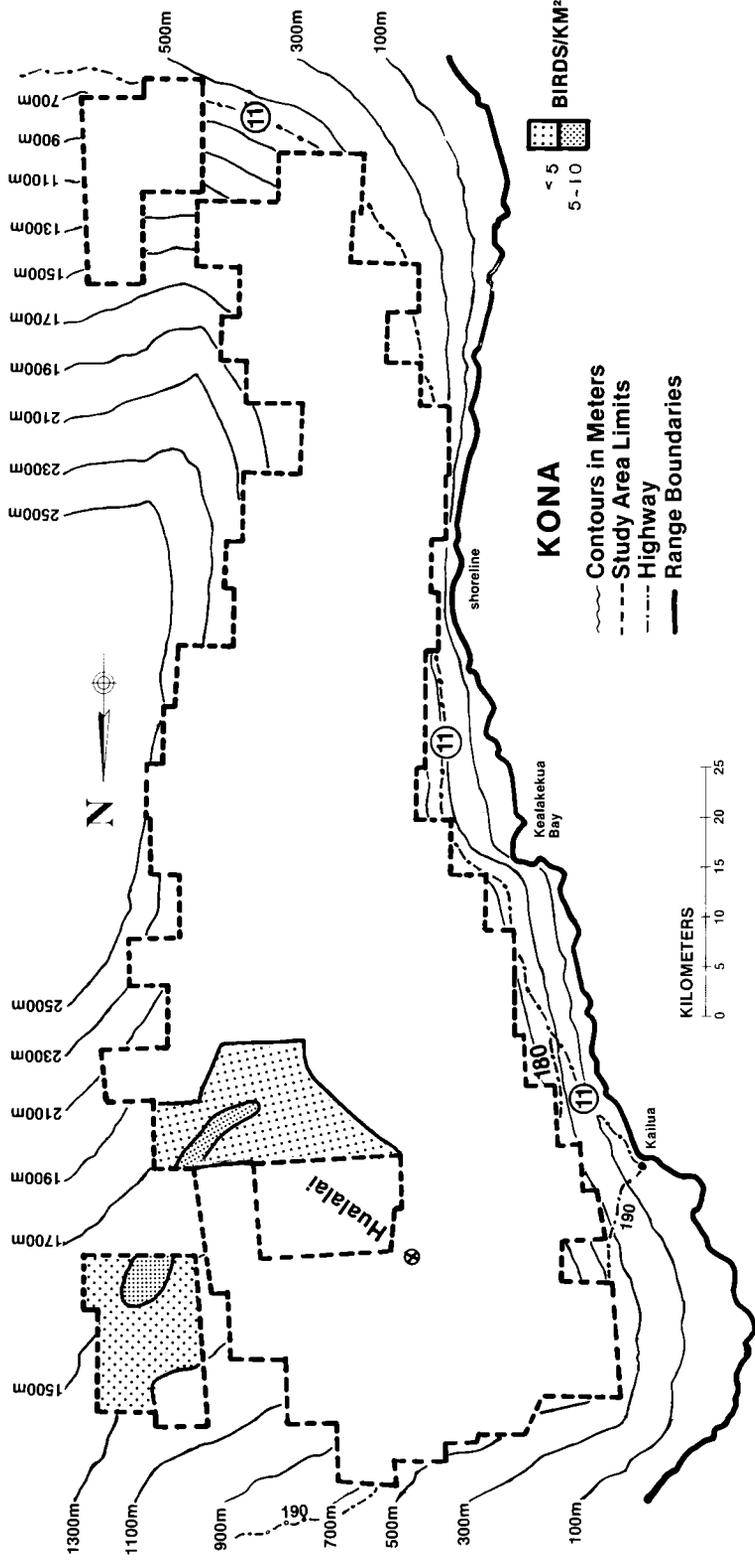


FIGURE 234. Distribution and abundance of the Melodious Laughing-thrush in the Kona study area.

**MELODIOUS LAUGHING-THRUSH**

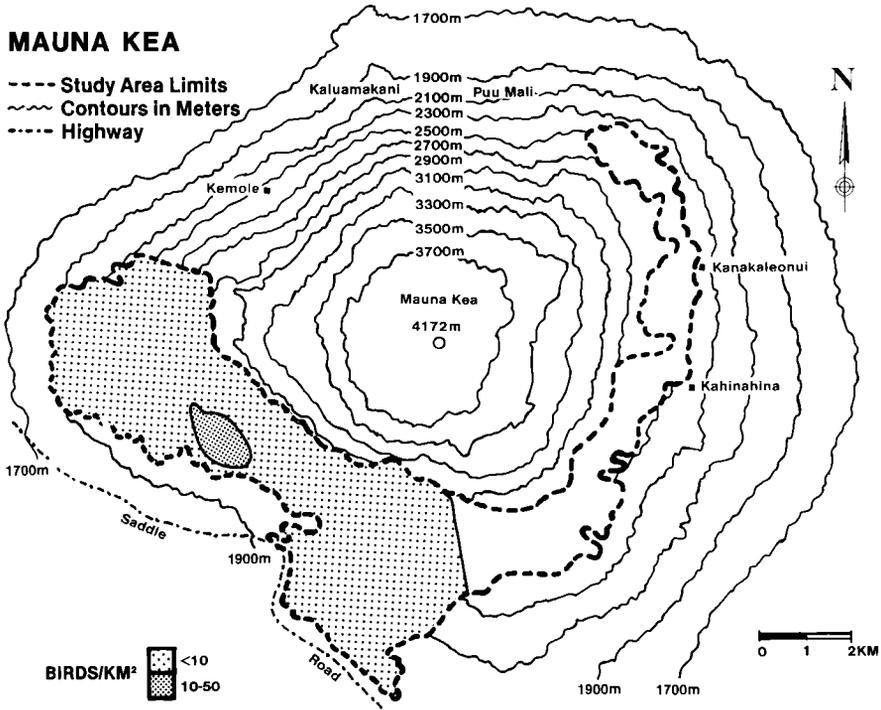


FIGURE 235. Distribution and abundance of the Melodious Laughing-thrush in the Mauna Kea study area.

**MELODIOUS LAUGHING-THRUSH**

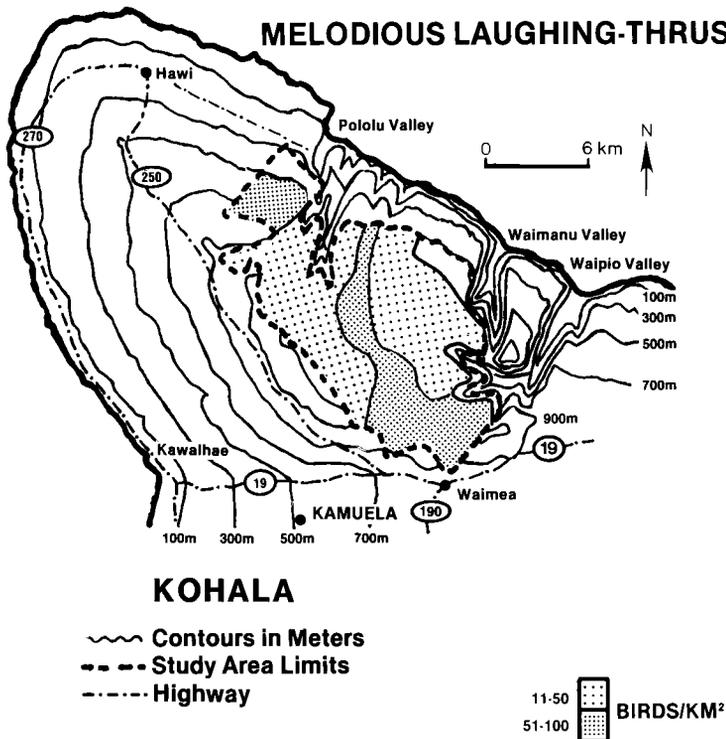


FIGURE 236. Distribution and abundance of the Melodious Laughing-thrush in the Kohala study area.

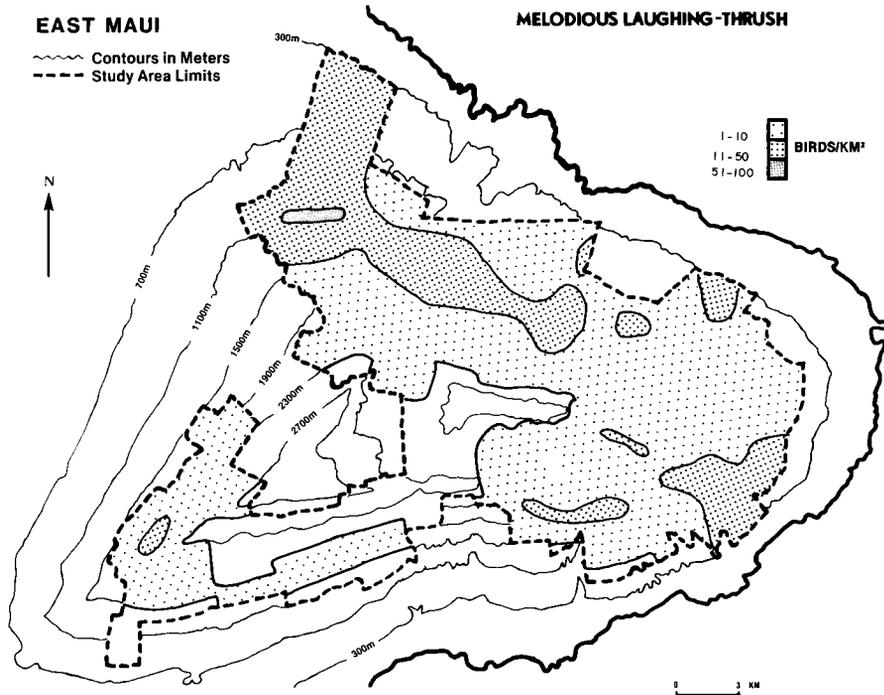


FIGURE 237. Distribution and abundance of the Melodious Laughing-thrush in the East Maui study area.

colonize this habitat on Maui. Warner (1967) reported no birds from Kipahulu Valley; 13 years later they were fairly common below 1500 m elevation. In many respects the dynamic range expansion of the Melodious Laughing-thrush paralleled the population explosion many observers reported for Japanese White-eyes 20 years earlier. We estimated a total of  $2100 \pm 300$  (95% CI) birds in the East Maui study area. Densities were lower on West Maui, and we failed to find birds on Molokai and Lanai.

On Kauai, Melodious Laughing-thrushes have low densities that decrease in the higher, wetter areas of the south Alakai. Our estimate of  $450 \pm 75$  (95% CI) birds compares well with an estimate of  $240 \pm 150$  birds for the same area in 1968–1973 (Sincock et al. 1984). Sincock estimated a total of  $13,000 \pm 4000$  birds in native forests on Kauai.

Melodious Laughing-thrushes occur from sea level to 2900 m on Hawaii and to 2500 m on Maui. They are most common below 1000 m in most areas, but reach fairly high densities up to 1500 m in the Kohala study area.

Melodious Laughing-thrushes tend to be habitat generalists that are most common at lower elevations, as seen in all regression models (Table 53). Birds occupy a wide breadth of habitat types, from very wet forests to dry scrub, with a slight

inclination for lower stature forests (Fig. 240). The regression models show little response to individual trees, another indication of generalized habitat requirements.

Although Melodious Laughing-thrushes show little response to total shrub or ground cover in the regression models, they have substantial positive response to individual understory components, notably native shrubs, introduced shrubs, ground ferns, and matted ferns. This suggests that they prefer brushy understories with structural and floristic diversity. Association with matted ferns is unusual among Hawaiian birds, but matted ferns are good habitat because birds feed and skulk low in the understory and frequent the dense impenetrable cover. In China, Melodious Laughing-thrushes likewise feed near the ground, are shy, and prefer dense understories (Étchécopar and Hüe 1983). The negative response to passiflora suggests that they are not particularly involved in the population expansion of banana poka. The positive term in the Mauna Kea model for naio fruit no doubt reflects its use for moisture and food.

#### RED-BILLED LEIOTHRIX (*Leiothrix lutea*)

The Red-billed Leiothrix, also known as the Hill Robin or Pekin Nightingale, is a babbler native to southern China and northern India; it

## WEST MAUI

## MELODIOUS LAUGHING-THRUSH

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 - - - - Study Area Limits

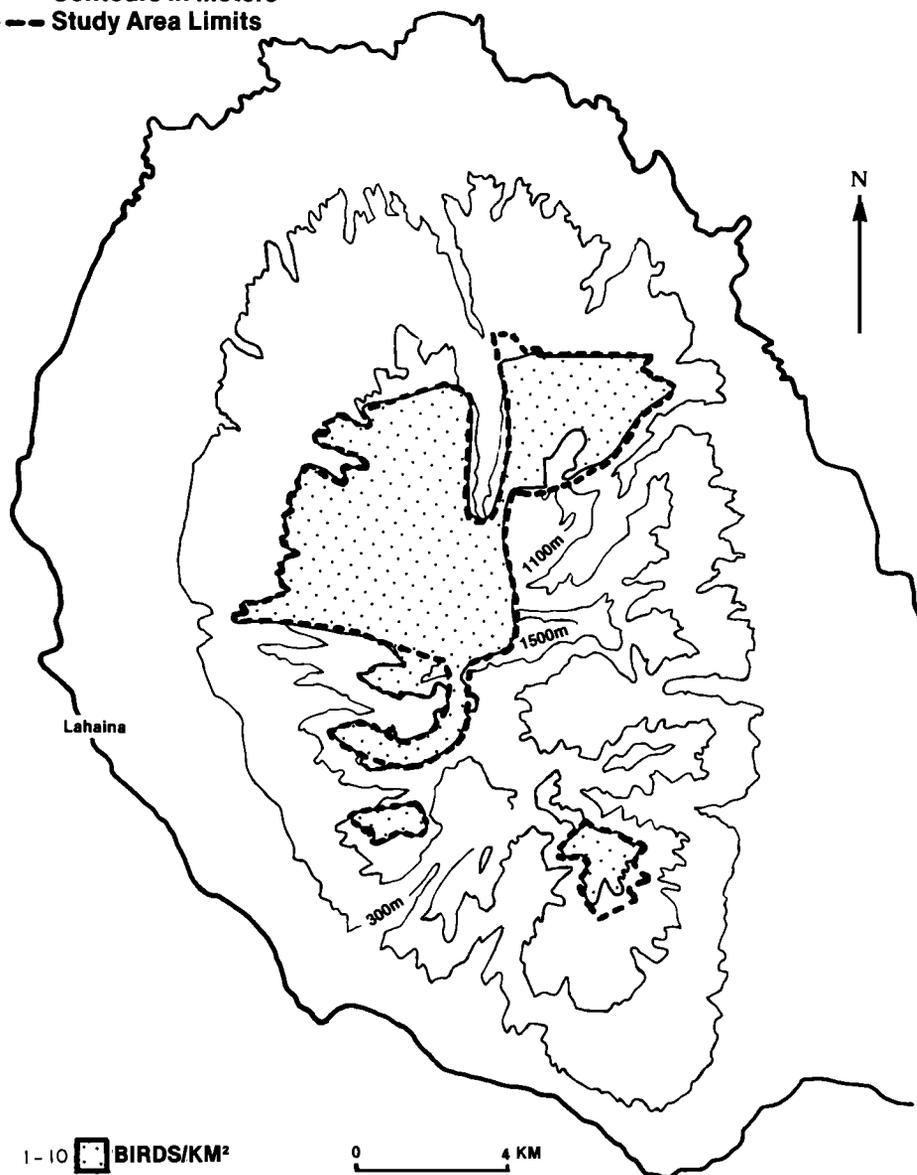


FIGURE 238. Distribution and abundance of the Melodious Laughing-thrush in the West Maui study area.

was introduced to the Hawaiian Islands as early as 1911 (Fisher and Baldwin 1947). They were first released on Hawaii in 1928 or 1929 (Caum 1933, Berger 1975b). By the 1970s they were well established on Hawaii, Maui, Molokai, Oahu, and Kauai (Berger 1972).

The Red-billed *Leiothrix* occurs in all study areas except Lanai and Kauai (Tables 33, 34, 54,

Figs. 241–248). On Hawaii $98,000 \pm 4000$ (95% CI) birds occupy the study areas. On Mauna Kea, birds occur at very low densities throughout the study area, reaching high densities only in denser woodlands with naio or water sources. Birds are well distributed on windward Hawaii above 1000 m elevation, but low densities occur at lower elevations. At elevations below 1200 m in Ha-

MELODIOUS LAUGHING-THRUSH

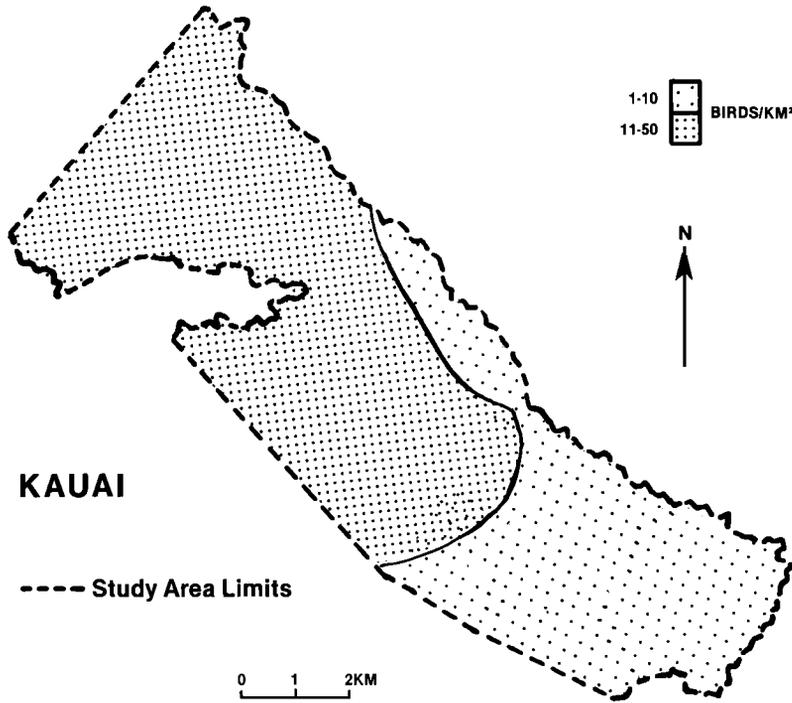


FIGURE 239. Distribution and abundance of the Melodious Laughing-thrush in the Kauai study area.

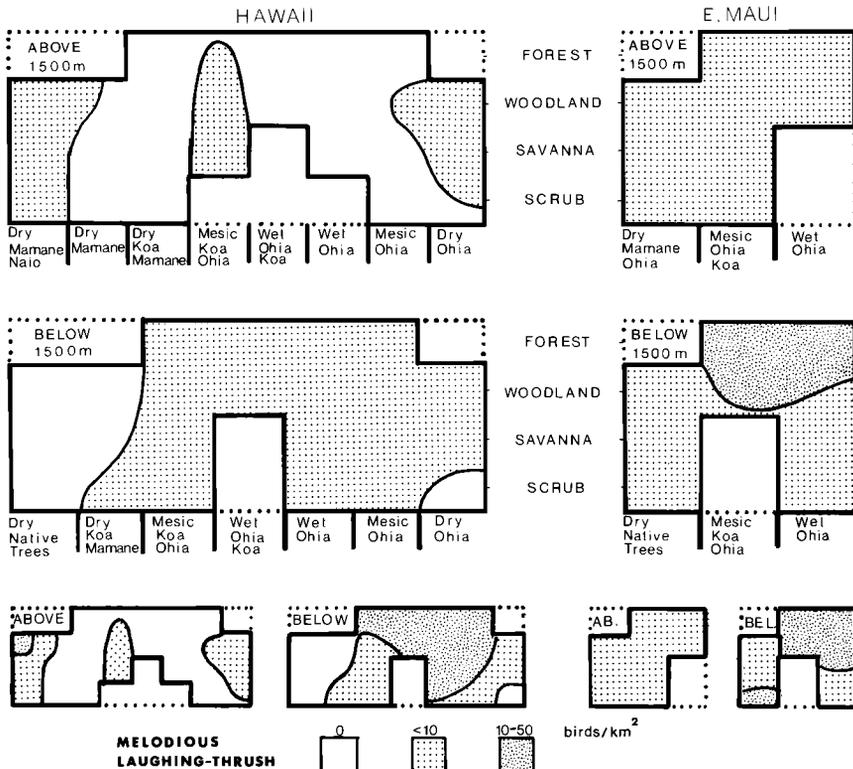


FIGURE 240. Habitat response graphs of the Melodious Laughing-thrush. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

TABLE 53
REGRESSION MODELS FOR HABITAT RESPONSE OF THE MELODIOUS LAUGHING-THRUSH^a

| | Hamakua | Puna | Mauna Kea | Kohala | Maui | Kauai |
|-----------------------------|---------|--------|-----------|--------|-------|-------|
| <i>R</i> ² | 0.23* | 0.50* | 0.19* | 0.12* | 0.22* | 0.28* |
| Moisture | -6.9* | ... | X | X | -4.9* | X |
| Elevation | 4.9* | -10.6* | 2.9 | -3.3 | -7.5* | -6.1* |
| (Elevation) ² | -7.9* | ... | -2.7 | ... | ... | ... |
| Tree biomass | ... | 3.5* | ... | ... | ... | ... |
| (Tree biomass) ² | ... | -3.3* | ... | ... | ... | ... |
| Crown cover | ... | ... | ... | ... | ... | ... |
| Canopy height | ... | -5.7* | ... | ... | ... | ... |
| Koa | ... | X | X | X | 3.9* | X |
| Ohia | ... | ... | X | ... | ... | X |
| Naio | X | X | ... | X | X | X |
| Mamane | 3.5* | ... | ... | X | ... | X |
| Intro. trees | -3.8* | 2.7 | X | ... | 7.9* | X |
| Shrub cover | ... | ... | ... | ... | ... | ... |
| Ground cover | -5.2* | ... | ... | ... | -2.2 | ... |
| Native shrubs | 6.9* | ... | X | ... | 2.7 | ... |
| Intro. shrubs | 6.1* | 3.6* | X | ... | ... | ... |
| Ground ferns | X | ... | X | 2.7 | 3.1 | ... |
| Matted ferns | 4.8* | 10.1* | X | 3.7* | 2.1 | ... |
| Tree ferns | X | ... | X | ... | 4.9* | ... |
| Ieie | X | 3.9* | X | X | -4.7* | 2.6 |
| Passiflora | ... | X | X | ... | ... | X |
| Native herbs | X | ... | X | ... | ... | ... |
| Intro. herbs | X | ... | 4.6* | ... | ... | -3.0 |
| Native grasses | 5.4* | ... | ... | ... | ... | ... |
| Intro. grasses | ... | ... | ... | ... | ... | ... |
| Ohia flowers | ... | ... | X | ... | ... | ... |
| Olapa fruit | ... | -3.9* | X | ... | 2.3 | ... |
| Mamane flowers | X | X | ... | X | ... | X |
| Mamane fruit | X | X | ... | X | X | X |
| Naio fruit | X | X | 6.3* | X | X | X |

^a *R*² is the variance accounted for by the model. Entries are *t* statistics and all are significant at *P* < 0.05; * indicates *P* < 0.001; ... indicates variable not significant (*P* > 0.05); X indicates variable not available for inclusion in model.

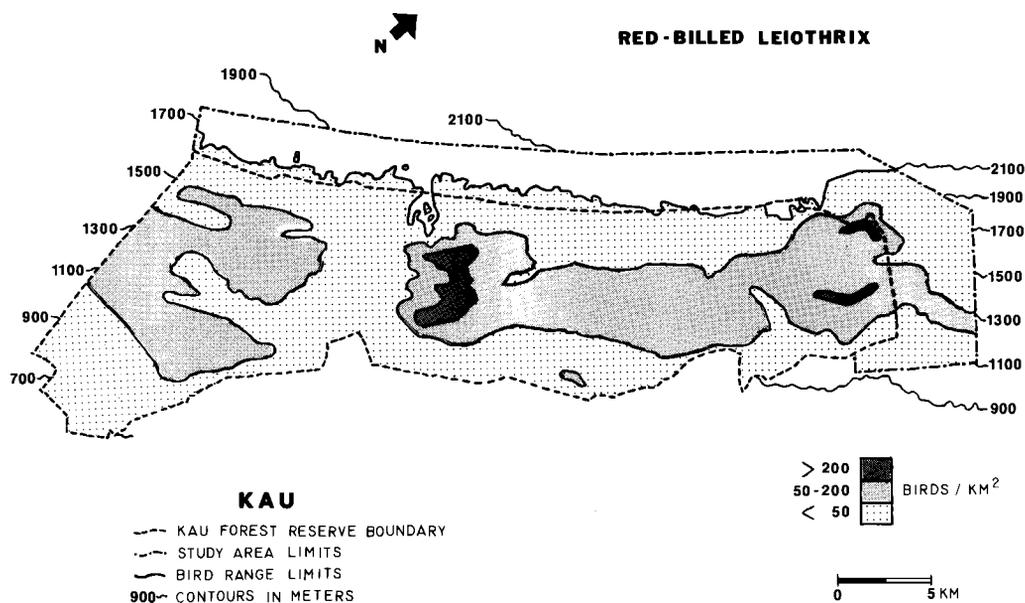


FIGURE 241. Distribution and abundance of the Red-billed Leiothrix in the Kau study area.

TABLE 54
DENSITY [MEAN (SE)] OF THE RED-BILLED LEIOTHRIX BY ELEVATION, HABITAT, AND STUDY AREA^a

| | Kau | Hamakua | Puna | Kipukas | Kona | Mauna Kea | Kohala | East Maui | West Maui | Molokai |
|------------------|--------|---------|-------|---------|---------|-----------|----------|-----------|-----------|---------|
| <i>Elevation</i> | | | | | | | | | | |
| 100-300 m | ... | ... | ... | ... | ... | ... | ... | ... | ... | 0 |
| 300-500 m | ... | + | 0 | ... | 9 (4) | ... | + | 0 | ... | 1 (1) |
| 500-700 m | + | 4 (1) | 0 | ... | 8 (2) | ... | 11 (11) | 13 (4) | 0 | 2 (2) |
| 700-900 m | 11 (3) | 11 (2) | 0 | ... | 6 (1) | ... | 34 (23) | 42 (7) | 13 (6) | 6 (2) |
| 900-1100 m | 63 (8) | 36 (3) | 0 | ... | 21 (2) | ... | 82 (13) | 57 (6) | 21 (8) | 20 (4) |
| 1100-1300 m | 82 (6) | 82 (3) | 4 (3) | 0 | 32 (3) | ... | 74 (12) | 69 (6) | 49 (10) | 89 (6) |
| 1300-1500 m | 91 (6) | 93 (5) | ... | 0 | 26 (3) | ... | 126 (17) | 102 (7) | 38 (10) | 77 (12) |
| 1500-1700 m | 56 (7) | 118 (6) | ... | 30 (8) | 10 (2) | ... | 199 (20) | 106 (8) | 21 (8) | ... |
| 1700-1900 m | 24 (5) | 99 (9) | ... | 13 (6) | 14 (2) | ... | ... | 101 (9) | 46 (12) | ... |
| 1900-2100 m | 2 (2) | 16 (8) | ... | + | 16 (3) | ... | ... | 81 (10) | ... | ... |
| 2100-2300 m | 0 | 4 (4) | ... | 0 | 7 (2) | 48 (11) | ... | 11 (5) | ... | ... |
| 2300-2500 m | ... | ... | ... | + | + | 21 (6) | ... | 3 (1) | ... | ... |
| 2500-2700 m | ... | ... | ... | ... | ... | 11 (5) | ... | 1 (1) | ... | ... |
| 2700-2900 m | ... | ... | ... | ... | ... | 4 (2) | ... | 3 (+) | ... | ... |
| 2900-3100 m | ... | ... | ... | ... | ... | 4 (3) | ... | ... | ... | ... |
| | ... | ... | ... | ... | ... | + | ... | ... | ... | ... |
| <i>Habitat</i> | | | | | | | | | | |
| Ohia | 48 (3) | 61 (2) | 4 (3) | 4 (1) | 14 (1) | ... | 88 (8) | 78 (4) | 34 (4) | 42 (3) |
| Koa-ohia | 83 (6) | 78 (4) | ... | 66 (18) | 22 (2) | ... | ... | 100 (7) | ... | ... |
| Koa-mamane | ... | 3 (3) | ... | 5 (2) | 17 (3) | ... | ... | ... | ... | ... |
| Mamane-naio | ... | ... | ... | ... | 12 (12) | 25 (4) | ... | ... | ... | ... |
| Mamane | ... | ... | ... | ... | 22 (3) | 1 (1) | ... | 4 (4) | ... | ... |
| Other natives | ... | 31 (10) | ... | 7 (7) | 15 (5) | ... | ... | 31 (4) | ... | + |
| Intro. trees | ... | 27 (8) | ... | ... | 8 (2) | ... | 171 (12) | 100 (13) | 0 | + |
| Treelless | 0 | 1 (1) | 0 | 15 (15) | + | ... | ... | 8 (1) | + | + |

^a Densities are given in birds/km²; + indicates stratum was in the species range but density < 0.3 birds/km²; 0 indicates stratum was outside range but was sampled; ... indicates stratum was not sampled in study area.

RED-BILLED LEIOTHRIX

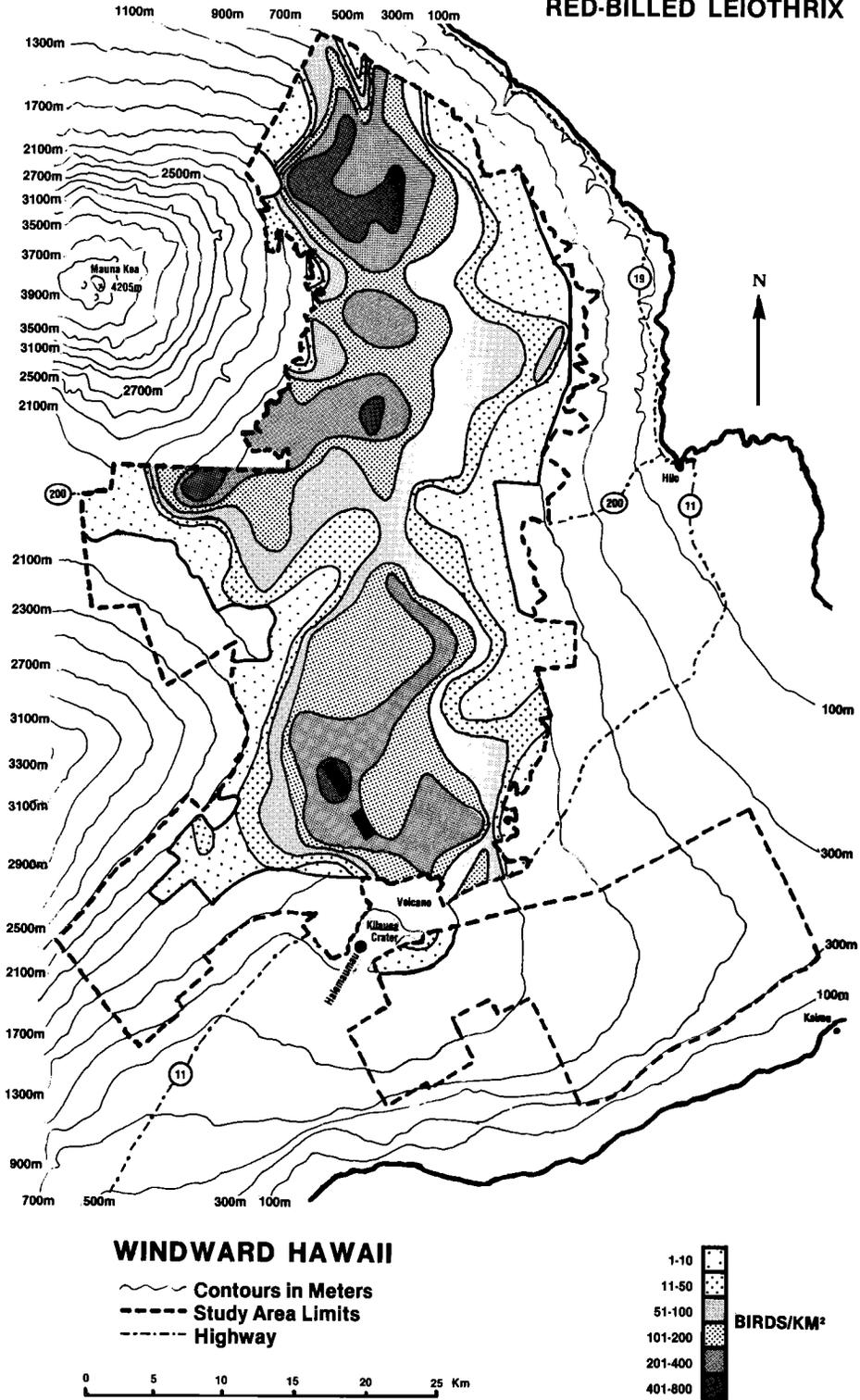


FIGURE 242. Distribution and abundance of the Red-billed Leiothrix in the windward Hawaii study areas.

RED-BILLED LEIOTHRIX

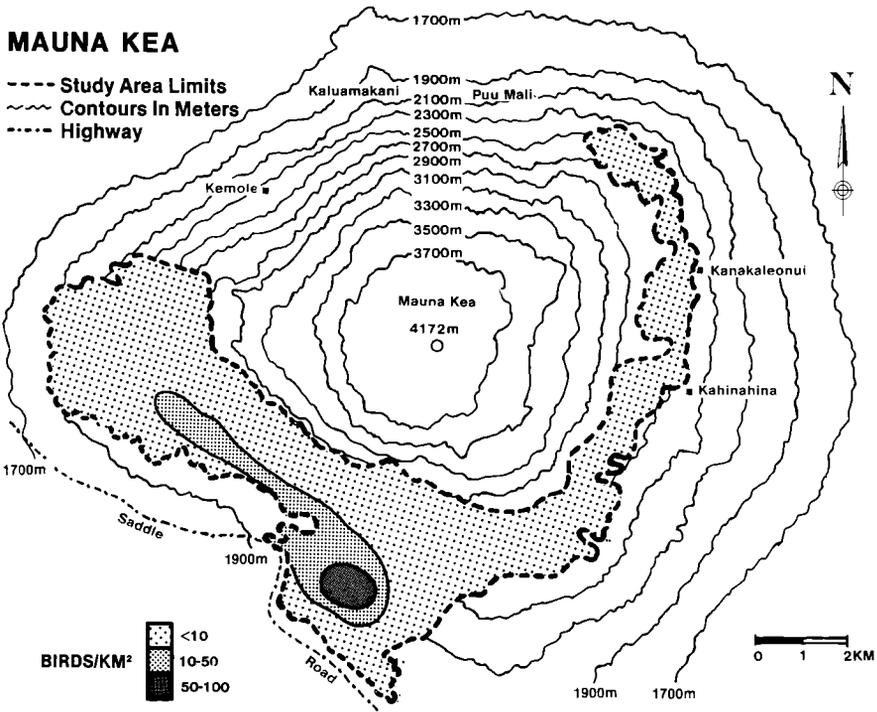


FIGURE 244. Distribution and abundance of the Red-billed Leiothrix in the Mauna Kea study area.

RED-BILLED LEIOTHRIX

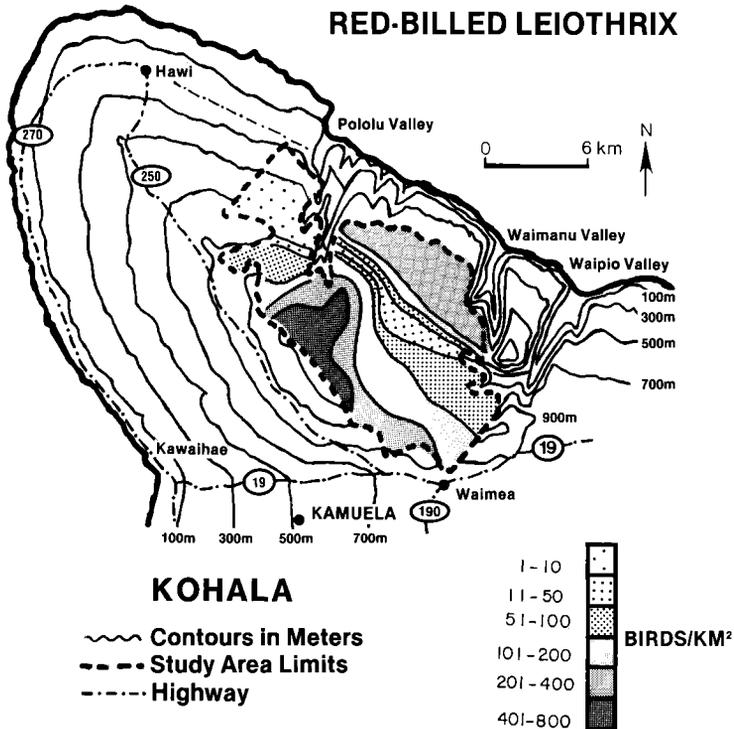


FIGURE 245. Distribution and abundance of the Red-billed Leiothrix in the Kohala study area.

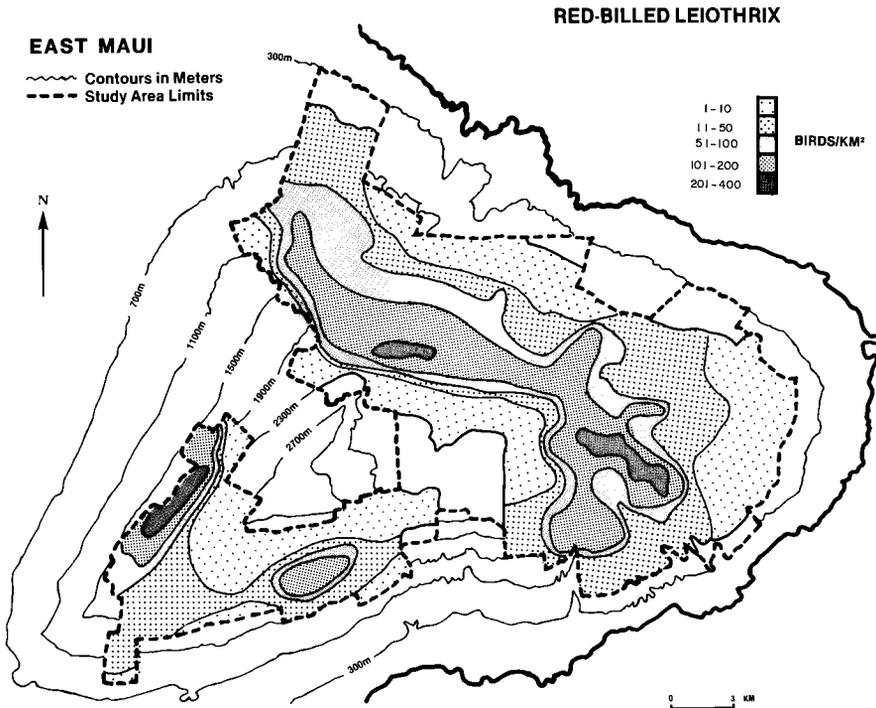


FIGURE 246. Distribution and abundance of the Red-billed Leiothrix in the East Maui study area.

waii Volcanoes National Park, densities appear to have declined sharply in the 1940–1975 interval (Conant 1975, Banko and Banko 1980). S. Conant (1980) noted their absence in the Puna study area. They are also absent from deforested areas at the north edge of the Hamakua study area and on the Kapapala Tract. Birds are well distributed in Kau and Kona, except for open pasturelands. The species was well established in Kohala during our survey and the 1970–1972 study by van Riper (1982).

On East Maui an estimated $19,000 \pm 1200$ (95% CI) birds are widespread and common in areas with adequate water, although densities tend to be lower below 1000 m elevation on the windward side. Since 1977 birds have expanded greatly in range and numbers on northwest Haleakala in Kula as the expanding black wattle (*Acacia decurrens*) forest developed and provided suitable habitat (C. B. Kepler, pers. observ.). Densities are substantially lower on West Maui than on East Maui (Table 54), and there the population totals 800 ± 200 birds.

On Molokai 1800 ± 200 (95% CI) birds occur chiefly above 1000 m elevation on the Olokui Plateau, Puu Ohelo, Ohialele Plateau, and in the Kamakou Preserve. Scott et al. (1977) found this species common on Molokai above 1200 m elevation.

On Kauai we failed to find this species. For 1968–1973, Sincoc et al. (1984) estimated 16 ± 30 (95% CI) birds for our study area and 2400 ± 2200 birds in native forests. Richardson and Bowles (1964) found this species restricted to areas above 1000 m elevation.

We found the Red-billed Leiothrix from 300 to 2900 m elevation on Hawaii, from 500 to 2900 m on Maui, and from 300 to 1500 m on Molokai; highest densities occurred at 900–1900 m on Hawaii, at 1100–1500 m on Molokai, and at 1300–2100 m on Maui. Fisher and Baldwin (1947) concluded that the upper distribution limit of 2400–2700 m elevation was determined by temperature. Our data suggest that the upper limit is not determined by thermoregulation, but by water requirements, as the distribution of densities > 10 birds/km² above 2500 m elevation on Mauna Kea closely corresponds with naio berries and gamebird watering sites.

Also intriguing is the lower elevational limit of about 1000 m in the Hawaiian Islands. In Burma, the Red-billed Leiothrix is distributed chiefly above 1500 m (Smythies 1953). We hypothesize that long-term survival of lowland populations is impeded by high temperatures, such as in the steamy lowlands of Burma or the more temperate lowlands of the Hawaiian Islands. This hypothesis would explain the absence

WEST MAUI

RED-BILLED LEIOTHRIX

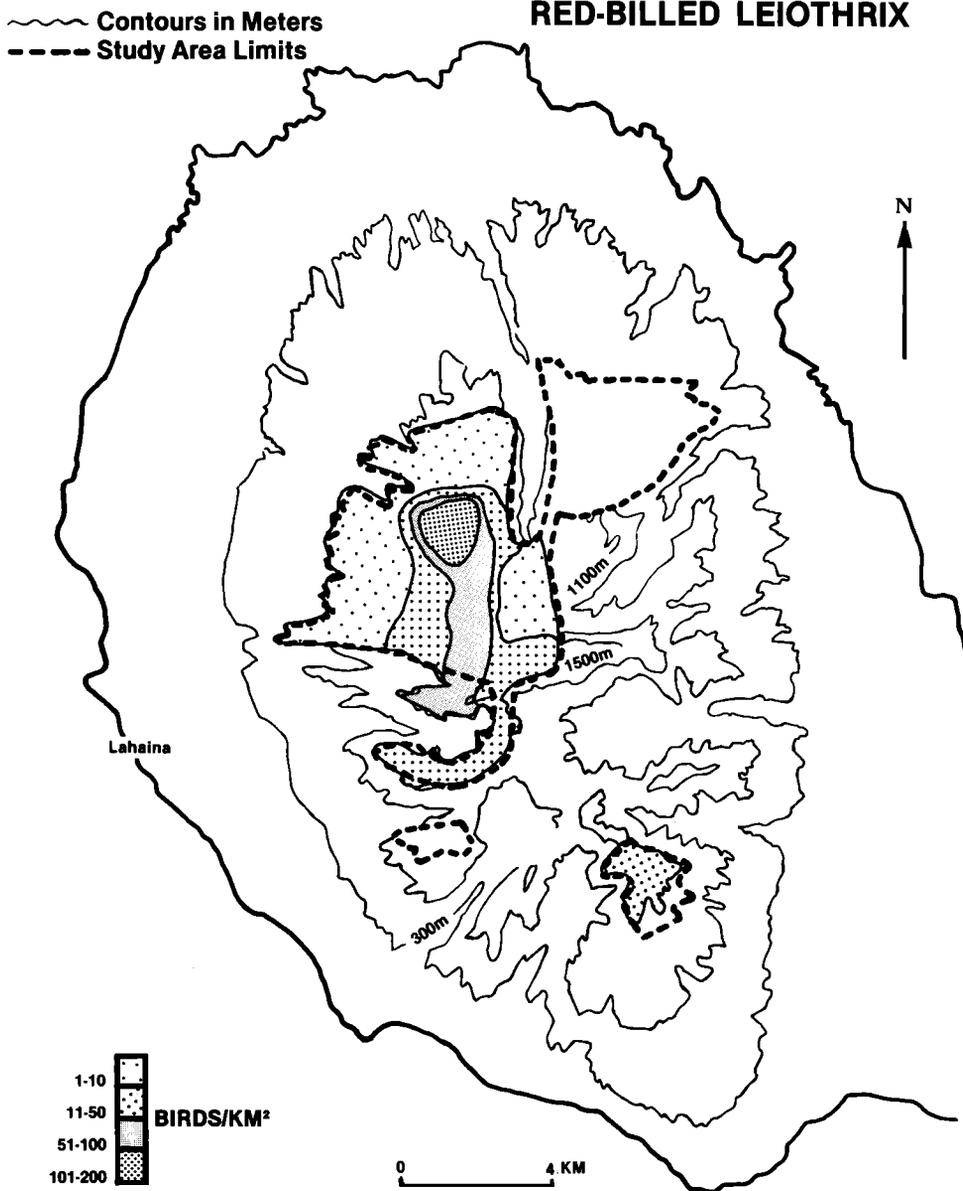


FIGURE 247. Distribution and abundance of the Red-billed Leiothrix in the West Maui study area.

or rarity of birds at lower elevations, and may also impart insight into the disappearance of birds on Oahu. As illustrated by annual Christmas Bird Counts, the Red-billed Leiothrix exhibited a drastic decline from about 100 birds per count before 1968 to 0–1 birds after 1969 (Anonymous 1974). Although birds were introduced and initially established large populations in lowland

areas, they may have died off during periods of unfavorable climate. If they are in fact limited by climate to areas above 1000 m elevation in the Hawaiian Islands, then self-sustaining populations will occur only on islands with substantial areas above 1000 m such as Hawaii and Maui, and will eventually decline to sparse distributions on other islands such as Oahu and Kauai.

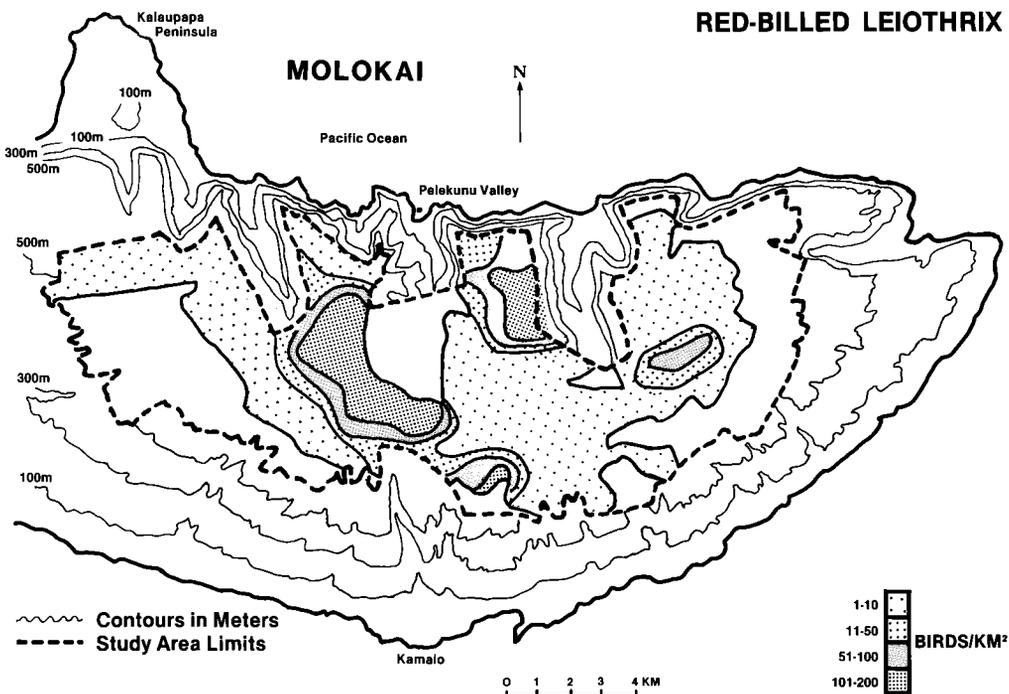


FIGURE 248. Distribution and abundance of the Red-billed Leiothrix in the Molokai study area.

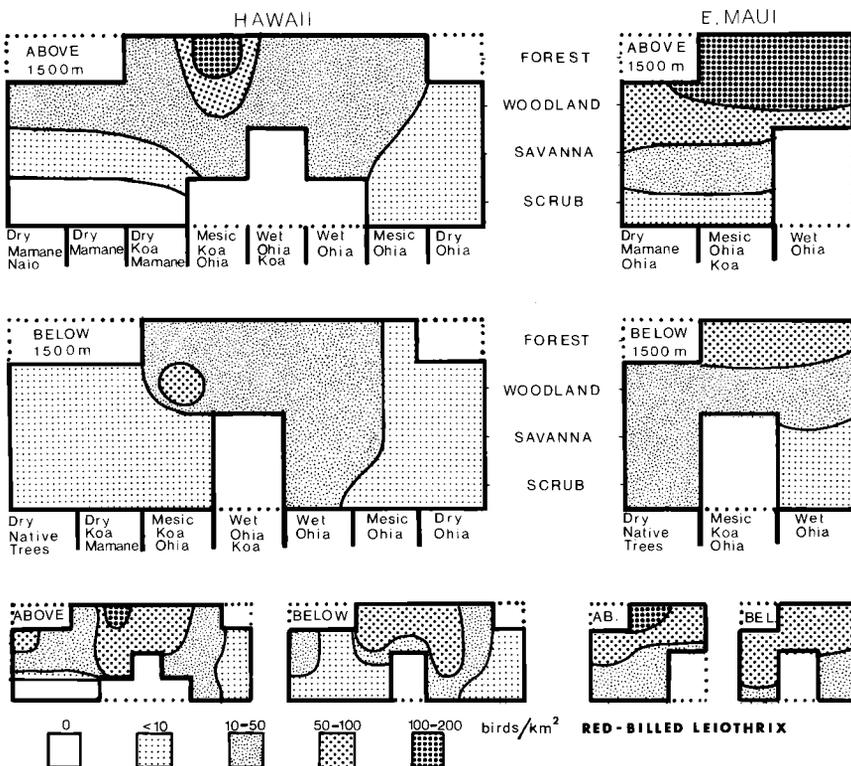


FIGURE 249. Habitat response graphs of the Red-billed Leiothrix. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

TABLE 55
REGRESSION MODELS FOR HABITAT RESPONSE OF THE RED-BILLED LEIOTHRIX^a

| | Kau | Hamakua | Kipukas | Kona | Mauna Kea | Kohala | Maui | Molokai |
|-----------------------------|--------|---------|---------|-------|-----------|--------|--------|---------|
| <i>R</i> ² | 0.32* | 0.45* | 0.09* | 0.34* | 0.24* | 0.35* | 0.51* | 0.62* |
| Moisture | ... | 8.8* | ... | 9.3* | X | X | ... | ... |
| Elevation | 10.3* | 13.2* | ... | 3.4* | -3.0 | 9.4* | 14.4* | -7.4* |
| (Elevation) ² | -10.7* | -9.0* | ... | ... | 2.6 | ... | -10.7* | 10.6* |
| Tree biomass | 5.5* | 2.9 | ... | ... | ... | ... | 2.4 | ... |
| (Tree biomass) ² | ... | ... | 4.7* | ... | ... | ... | 6.1* | ... |
| Crown cover | -5.8* | -3.6* | ... | 3.7* | ... | ... | ... | ... |
| Canopy height | -5.0* | 3.7* | ... | 2.3 | ... | ... | -3.0 | 3.6* |
| Koa | ... | 3.6* | ... | 3.5* | X | X | ... | X |
| Ohia | ... | ... | -3.7* | -9.1* | X | ... | -3.2 | ... |
| Naio | X | X | ... | 4.6* | 3.2 | X | X | X |
| Mamane | X | -3.0 | ... | ... | ... | X | -4.3* | X |
| Intro. trees | X | ... | X | ... | X | ... | ... | -2.5 |
| Shrub cover | ... | -4.8* | ... | ... | 3.7* | ... | ... | ... |
| Ground cover | -6.3* | ... | ... | ... | ... | ... | ... | ... |
| Native shrubs | ... | 6.7* | ... | 11.0* | X | ... | ... | ... |
| Intro. shrubs | X | 6.6* | ... | ... | X | ... | ... | ... |
| Ground ferns | X | X | ... | 3.1 | X | ... | ... | 5.5* |
| Matted ferns | -2.7 | -6.8* | ... | -3.0 | X | ... | ... | ... |
| Tree ferns | ... | X | X | 8.2* | X | 3.1 | ... | 4.1* |
| Ieie | X | X | X | -8.2* | X | X | ... | X |
| Passiflora | X | 6.7* | X | 6.0* | X | ... | ... | X |
| Native herbs | X | X | 2.3 | -3.3* | X | ... | ... | ... |
| Intro. herbs | X | X | ... | 5.0* | ... | ... | 3.9* | ... |
| Native grasses | ... | ... | ... | -5.9* | ... | ... | ... | 2.8 |
| Intro. grasses | ... | ... | ... | ... | 2.3 | ... | ... | ... |
| Ohia flowers | ... | 2.8 | -3.6* | ... | X | ... | ... | -3.4* |
| Olapa fruit | ... | 5.3* | ... | 8.6* | X | ... | 4.1* | 3.7* |
| Mamane flowers | X | X | ... | ... | ... | X | ... | X |
| Mamane fruit | X | X | X | X | ... | X | X | X |
| Naio fruit | X | X | X | X | ... | X | X | X |

^a *R*² is the variance accounted for by the model. Entries are *t* statistics and all are significant at *P* < 0.05; * indicates *P* < 0.001; ... indicates variable not significant (*P* > 0.05); X indicates variable not available for inclusion in model.

The habitat response graphs show a widespread, well-established species that is more abundant in mesic forests and woodlands (Fig. 249). Tree biomass, crown cover, and canopy height terms tend to balance one another in most regression models (Table 55), indicating that some trees are essential, but that birds occur from open woodland to dense forests. Birds are virtually limited to areas of naio on Mauna Kea. The low density of fleshy fruits in mamane stands is reflected in the negative mamane terms. The association with koa probably reflects the occurrence of birds in open rather mesic forests at intermediate elevations. Relative to the response to other tree species, the negative terms for ohia may be due to lack of fleshy fruit on ohia.

Response to total ground or shrub cover is weak and indicates a wide range of occurrence. Fisher and Baldwin (1947) concluded that "a cover of dense vegetation near the ground is the major characteristic of the habitat" in order to explain the absence of this species in ironwood (*Casuarina equisetifolia*) and eucalyptus groves

having barren understories. The models indicate that occupied habitat has the average understory of the study area. The average understory is considerably more dense than the understories of ironwood and eucalyptus groves. Positive responses to understory components occur for native shrubs, ground ferns, and introduced herbs. Matted ferns yield negative responses, probably because at high cover values they choke out other understory species, including berry plants. The association with passiflora indicates that the Red-billed Leiothrix is a potential dispersal agent for banana poka (Warshauer et al. 1983). The positive response to olapa fruit, reflecting occurrence in wet forest interiors, suggests local concentration at food sources. The association with fruit reflects the considerable quantity of fruit and berries in the diet (Fisher and Baldwin 1947).

NORTHERN MOCKINGBIRD (*Mimus polyglottos*)

Native to North America, Northern Mockingbirds are largely insectivorous but also feed on

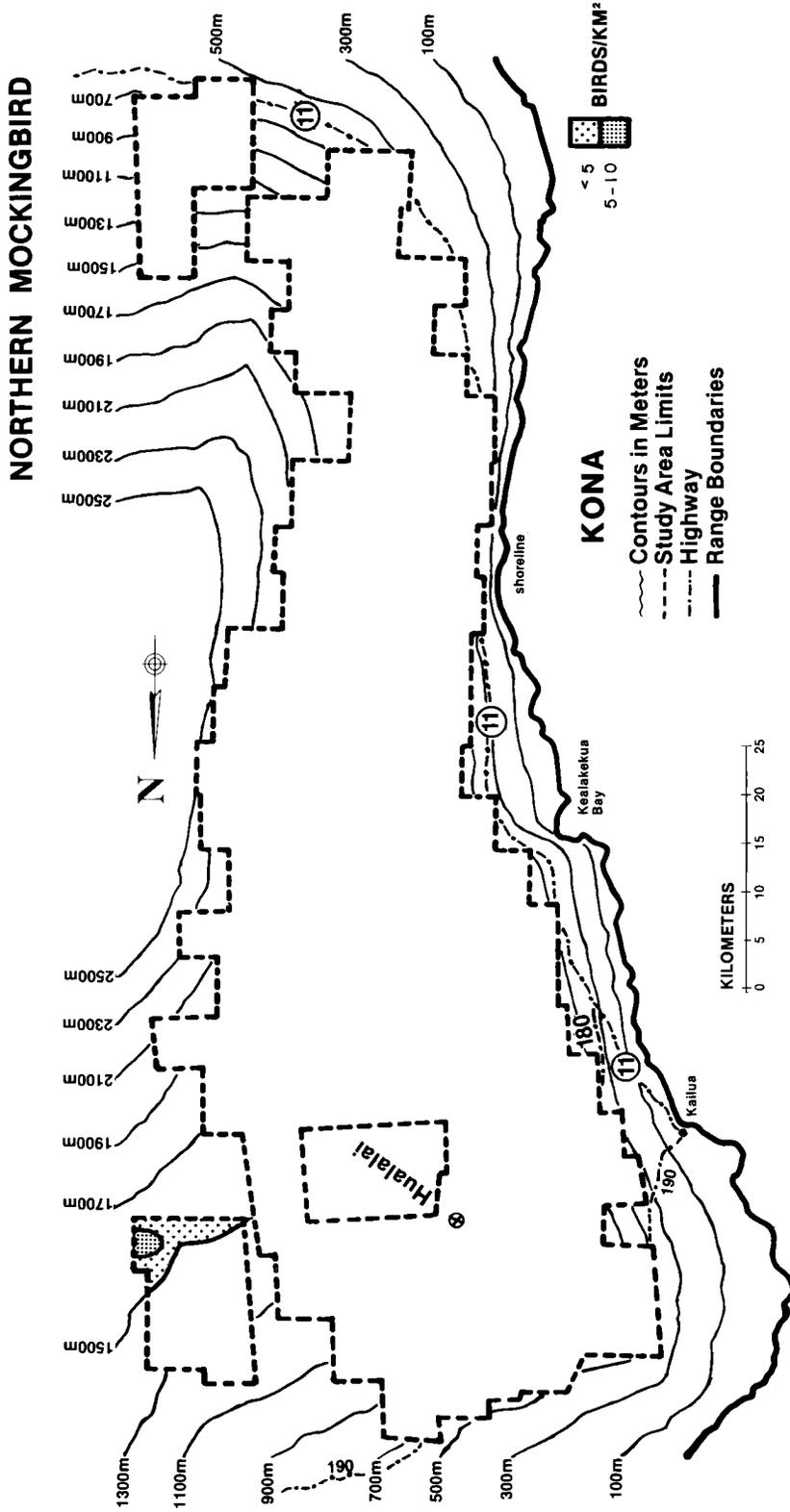


FIGURE 250. Distribution and abundance of the Northern Mockingbird in the Kona study area.

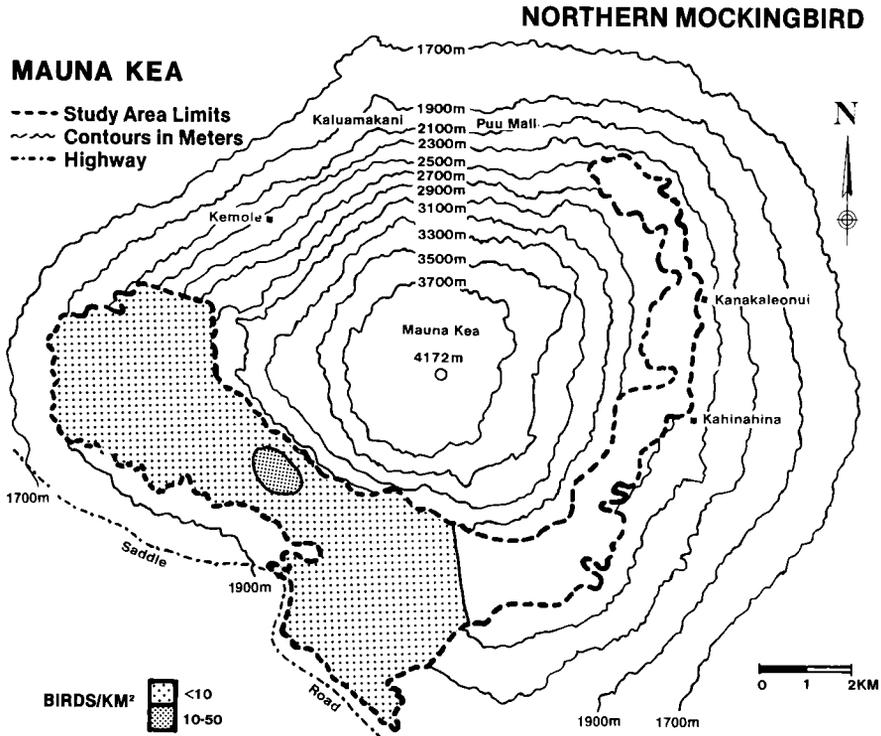


FIGURE 251. Distribution and abundance of the Northern Mockingbird in the Mauna Kea study area.

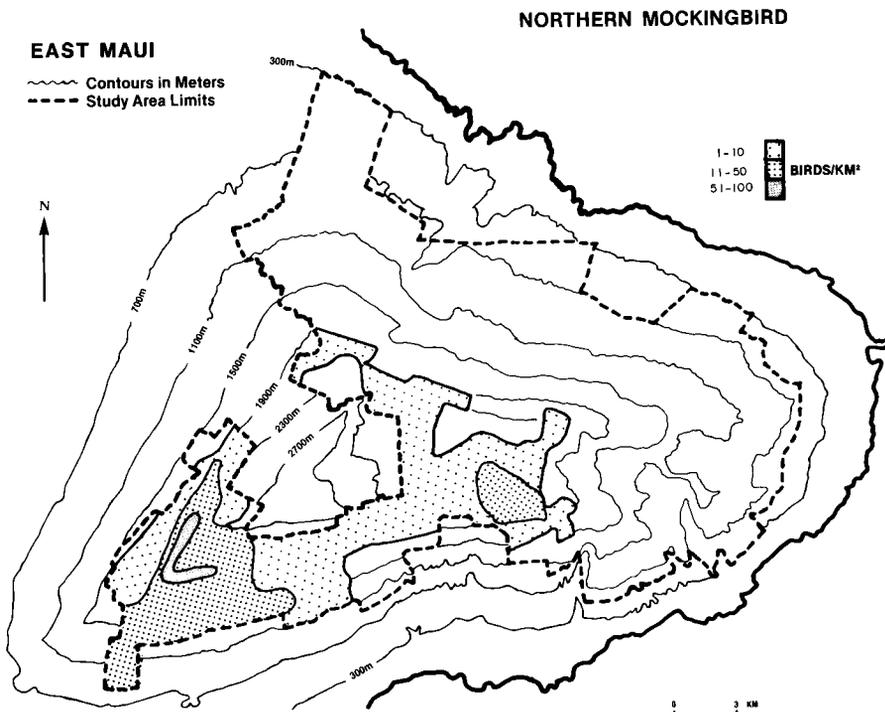


FIGURE 252. Distribution and abundance of the Northern Mockingbird in the East Maui study area.

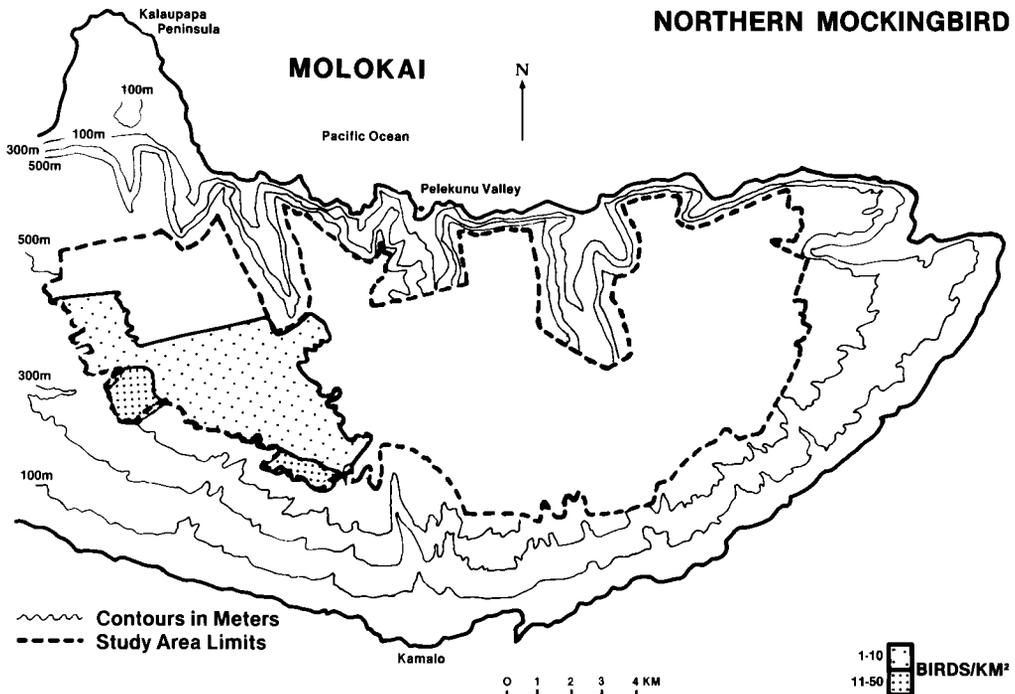


FIGURE 253. Distribution and abundance of the Northern Mockingbird in the Molokai study area.

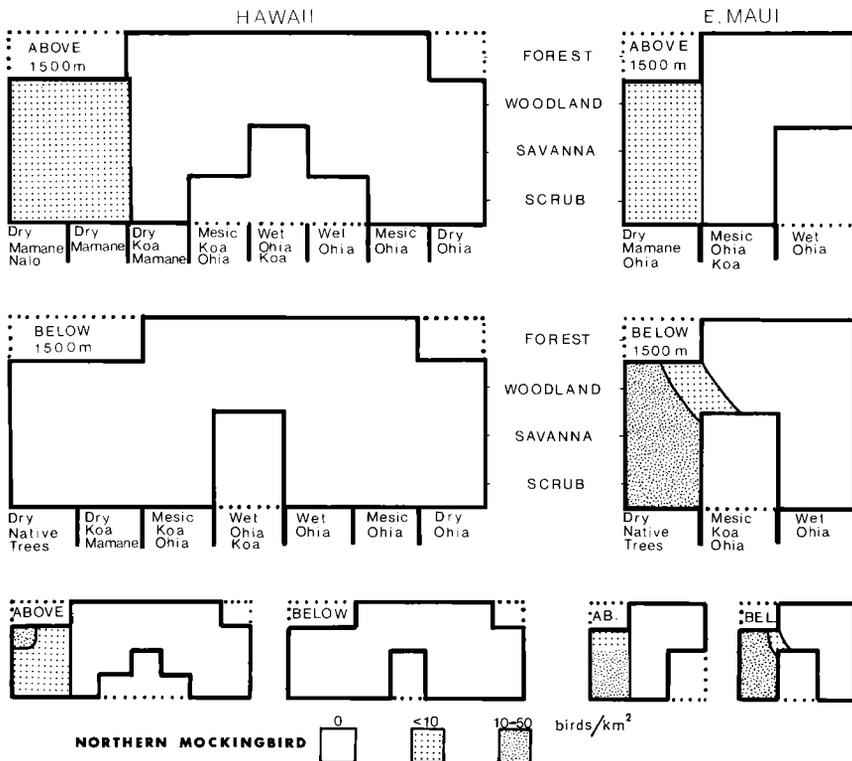


FIGURE 254. Habitat response graphs of the Northern Mockingbird. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

TABLE 56
DENSITY [MEAN (SE)] OF THE COMMON MYNA BY ELEVATION, HABITAT, AND STUDY AREA^a

| | Kau | Hamakua | Puna | Kipukas | Kona | Mauna
Kea | East Maui | Molokai | Lanai |
|------------------|-------|---------|--------|---------|--------|--------------|-----------|---------|-------|
| <i>Elevation</i> | | | | | | | | | |
| 100–300 m | ... | ... | ... | ... | ... | ... | ... | 7 (5) | ... |
| 300–500 m | ... | 0 | 0 | ... | + (+) | ... | 0 | + (+) | ... |
| 500–700 m | + (+) | 0 | 0 | ... | 6 (2) | ... | 0 | 30 (17) | 3 (2) |
| 700–900 m | 9 (6) | 7 (6) | 22 (5) | ... | 14 (2) | ... | 8 (5) | 1 (1) | + (+) |
| 900–1100 m | 0 | + (+) | 8 (7) | ... | 11 (3) | ... | 15 (3) | 1 (1) | + (+) |
| 1100–1300 m | 0 | 15 (3) | + (+) | 6 (2) | 9 (2) | ... | 5 (3) | 0 | ... |
| 1300–1500 m | 0 | 15 (5) | ... | 6 (2) | 7 (1) | ... | 13 (7) | 0 | ... |
| 1500–1700 m | 0 | 6 (2) | ... | 2 (1) | 5 (1) | ... | 10 (5) | ... | ... |
| 1700–1900 m | 0 | 7 (2) | ... | + (+) | + (+) | ... | + (+) | ... | ... |
| 1900–2100 m | 0 | 11 (2) | ... | 1 (+) | + (+) | 5 (4) | * | ... | ... |
| 2100–2300 m | 0 | 3 (2) | ... | + (+) | + (+) | 0 | 12 (12) | ... | ... |
| 2300–2500 m | ... | ... | ... | ... | + (+) | 0 | 0 | ... | ... |
| 2500–2700 m | ... | ... | ... | ... | ... | 0 | 0 | ... | ... |
| 2700–2900 m | ... | ... | ... | ... | ... | 0 | 0 | ... | ... |
| 2900–3100 m | ... | ... | ... | ... | ... | 0 | ... | ... | ... |
| <i>Habitat</i> | | | | | | | | | |
| Ohia | 9 (6) | 9 (2) | 12 (3) | 4 (1) | 5 (1) | ... | 0 | 0 | ... |
| Koa-ohia | 0 | 9 (3) | ... | 2 (1) | 14 (2) | ... | 21 (8) | ... | ... |
| Koa-mamane | ... | 11 (2) | ... | 2 (1) | 11 (2) | ... | ... | ... | ... |
| Mamane-naio | ... | ... | ... | ... | + (+) | 1 (1) | ... | ... | ... |
| Mamane | ... | ... | ... | ... | 2 (1) | + (+) | 0 | ... | ... |
| Other natives | ... | 13 (2) | ... | 2 (1) | 5 (1) | ... | 10 (2) | 5 (5) | + (+) |
| Intro. trees | ... | 2 (2) | ... | ... | 8 (3) | ... | 5 (2) | 14 (9) | 1 (+) |
| Treeless | 0 | + (+) | + (+) | + (+) | + (+) | ... | 0 | + (+) | + (+) |

^a Densities are given in birds/km²; + indicates stratum was in the species range but density <0.5 birds/km²; 0 indicates stratum was outside range but was sampled; ... indicates stratum was not sampled in study area; * indicates stratum was not sampled in range but was sampled elsewhere in study area.

fruits, especially during winter (Sprunt 1948). They occur in open forest, woodland, and scrub habitats throughout the southern United States and into Mexico (Grinnell and Miller 1944, Sprunt 1948).

Northern Mockingbirds were first released on Oahu in 1931 and on Maui in 1933 (Anonymous 1961). Berger (1981) found them well established in dry woodland areas on Hawaii, Maui, Molokai, Lanai, Oahu, and Kauai. Details of the distribution on Maui were given by Udvardy (1961), on Lanai by Hirai (1978), and on Kauai by Richardson and Bowles (1964). Birds were first reported on Hawaii in 1959 (Dunmire 1961), and have become well established in dry areas along the leeward coast.

We found Northern Mockingbirds in five study areas (Tables 33, 34, 51, Figs. 250–253), with highest densities on the crater and leeward slopes of Haleakala. The population on Mauna Kea became established after 1978, when birds were noted at Mauna Kea State Park. Occurrence in the Kona and West Maui study areas appears to be marginal. Birds occur on the dry southwest side of the Molokai study area, but are more abundant in the lowlands (Berger 1981).

Northern Mockingbirds occur over a wide

range of elevations and vegetation types (Table 51). The habitat response graphs show a strong association with dry habitat types on Hawaii and Maui (Fig. 254). Only the populations on Mauna Kea and Maui were sufficiently sampled to construct regression models. Those models (Table 50) show that highest densities occur in naio forest on Mauna Kea and in dry open mamane forest on Maui.

Udvardy (1961) found this species to be very common on Maui from sea level to 1000 m in dry mesquite woodlands. The negative tree biomass and positive crown cover terms in the Maui model indicate occurrence in sparse, open woodland, a physiognomy characteristic of both mamane and mesquite woodlands. The negative terms for other tree species indicate that birds did not occur with these trees in the study area.

Among understory components, the only strong response is towards passiflora. In North America wild fruit totals 43% of the diet (Beal et al. 1916). Northern Mockingbirds are potential dispersal agents for banana poka (Warshauer et al. 1983), particularly as the population expands on Hawaii.

The habitat response of Northern Mockingbirds in the Hawaiian Islands is similar to that

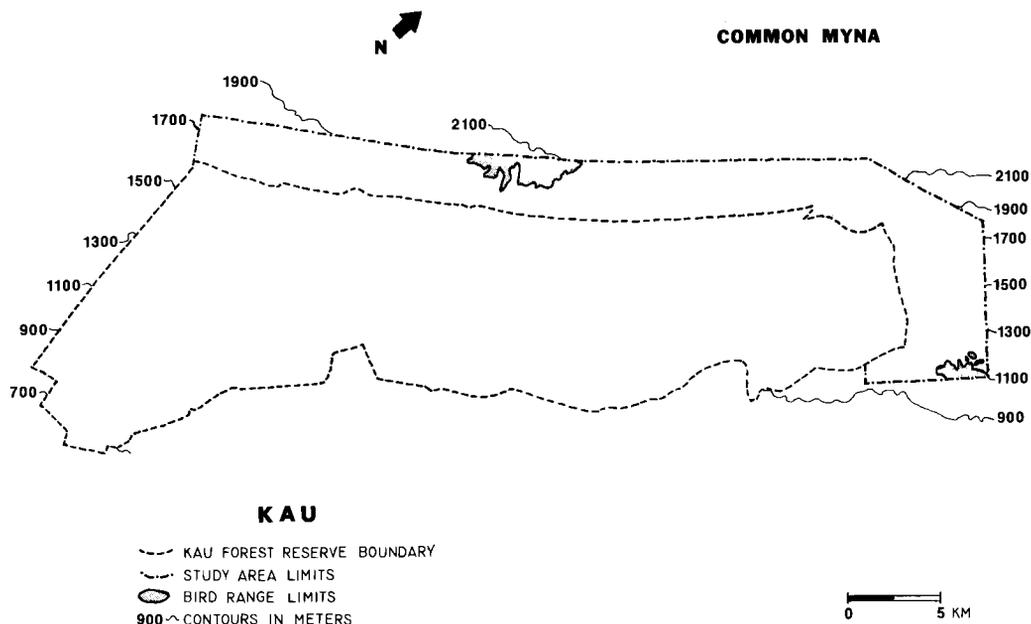


FIGURE 255. Distribution and abundance of the Common Myna in the Kau study area. (Density within range is less than 10 birds/km².)

shown by populations in the western United States, where high densities occur in scattered brush or very open woodland with variety of plants yielding fruits and berries (Grinnell and Miller 1944). Populations in the eastern United States tend to favor open woodland edges, pastures, and open brushland, as well as the more closed forests of "moss-bannered live oaks and towering magnolias" (Sprunt 1948).

COMMON MYNA (*Acridotheres tristis*)

Common Mynas, introduced from India in 1865 (Caum 1933), are common to abundant in most lowland areas except forest interiors. They are common residents of drier open forests from sea level to 1500 m in India (Ali and Ripley 1972), and are primarily terrestrial omnivores (Caum 1933, Berger 1981).

In the 1890s Common Mynas were widespread and common even in the deepest forests (W. A. Bryan and Seale 1901, Perkins 1903). This was a temporary situation, as E. H. Bryan (1940) later indicated that they seldom came into contact with native birds. Common Mynas occur in nine study areas (Tables 33, 34, 56, Figs. 255–259), always in association with forest edges, pastures, and other disturbed areas. On Hawaii 4500 ± 400 (95% CI) birds occur in the study areas; on Maui, 180 ± 90 ; on Molokai, 140 ± 150 ; and on Lanai, 20 ± 20 . Although neither we nor Sincov et al. (1984) found birds in the

Alakai Swamp, birds occurred on the summit of Waialeale in 1900 (Bryan and Seale 1901).

Common Mynas occur from sea level to 2300 m. Broad habitat preferences are seen in the habitat response graphs for Hawaii (Fig. 260), but occurrence in a habitat usually depends on the presence of water troughs or domestic stock. We found no birds in closed canopy forests. The regression models (Table 57) show that birds are most common in dry woodlands and partly open forests with low shrub cover at low elevations. There were too few sightings in the Maui, Molokai, and Lanai study areas to construct models; however, Common Mynas are common in dry open forest at low elevations in those areas.

Birds were associated with drier areas in every regression model. Bird density in three of the four models is associated with lower elevations, higher tree biomass, or lower shrub cover. The response to canopy height is positive and to crown cover negative, indicating association with open to scattered canopies of tall trees. Perhaps because of its height and open foliage, koa tends to generate positive responses, but ohia, which usually attains greatest biomass in wet forest interiors, generates negative ones. Common Mynas are not attracted to passiflora infestations, which mainly occur at higher elevations, nor to fern understories, which are probably too dense for foraging and are usually characteristic of wet forest interiors. In Hamakua the negative response

COMMON MYNA

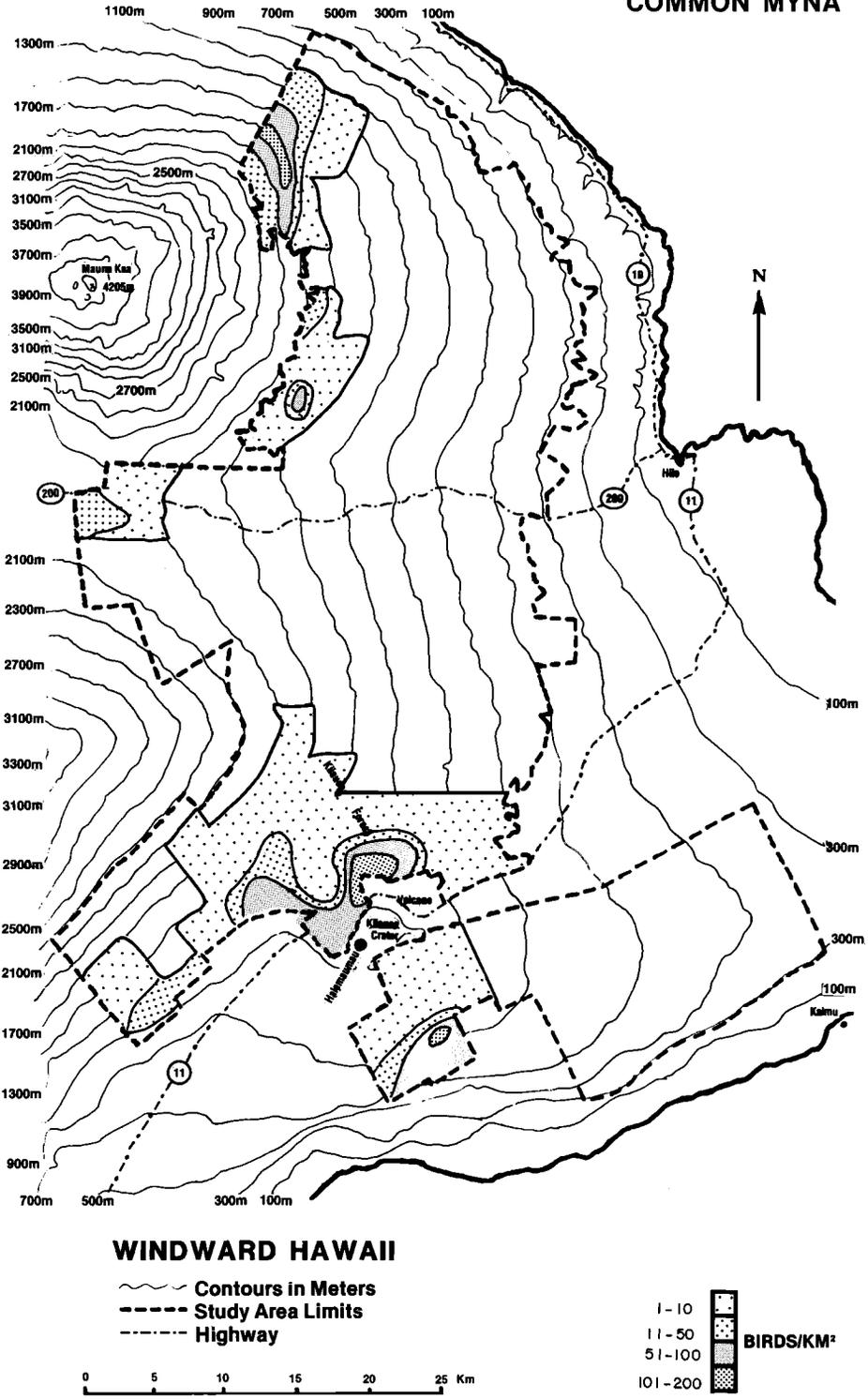


FIGURE 256. Distribution and abundance of the Common Myna in the windward Hawaii study areas.

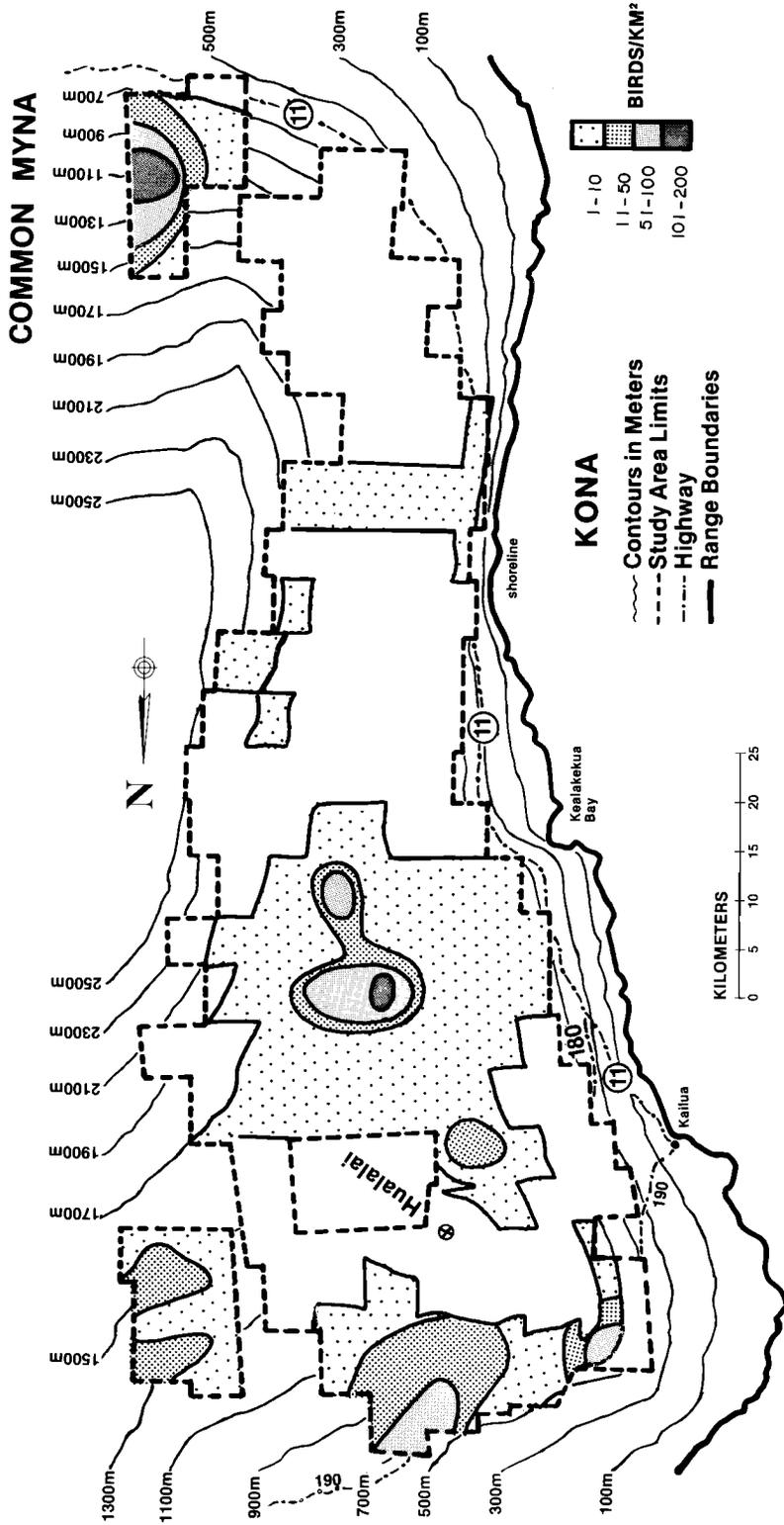


FIGURE 257. Distribution and abundance of the Common Myna in the Kona study area.

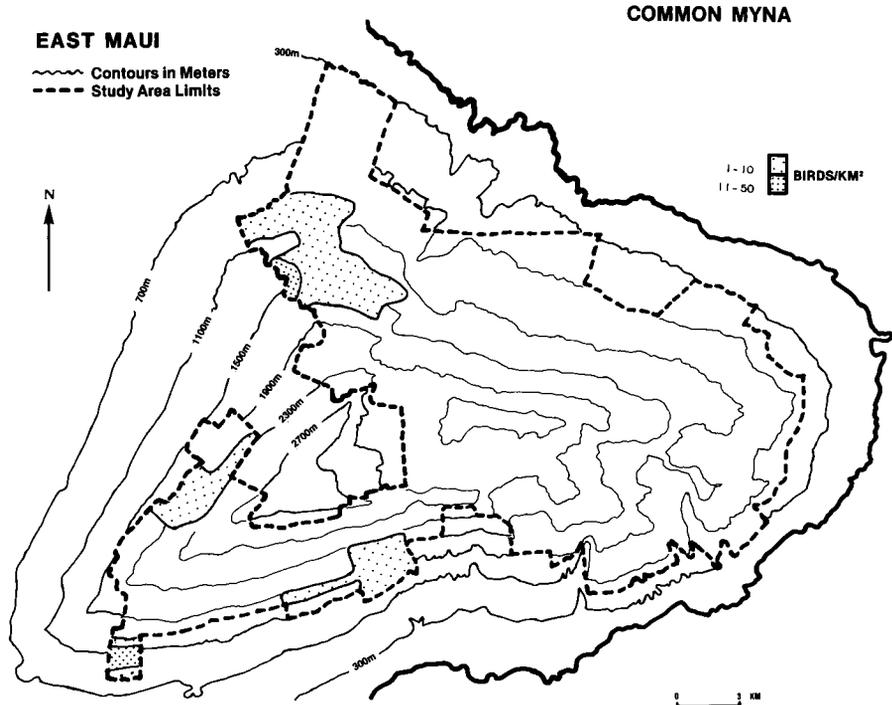


FIGURE 258. Distribution and abundance of the Common Myna in the East Maui study area.

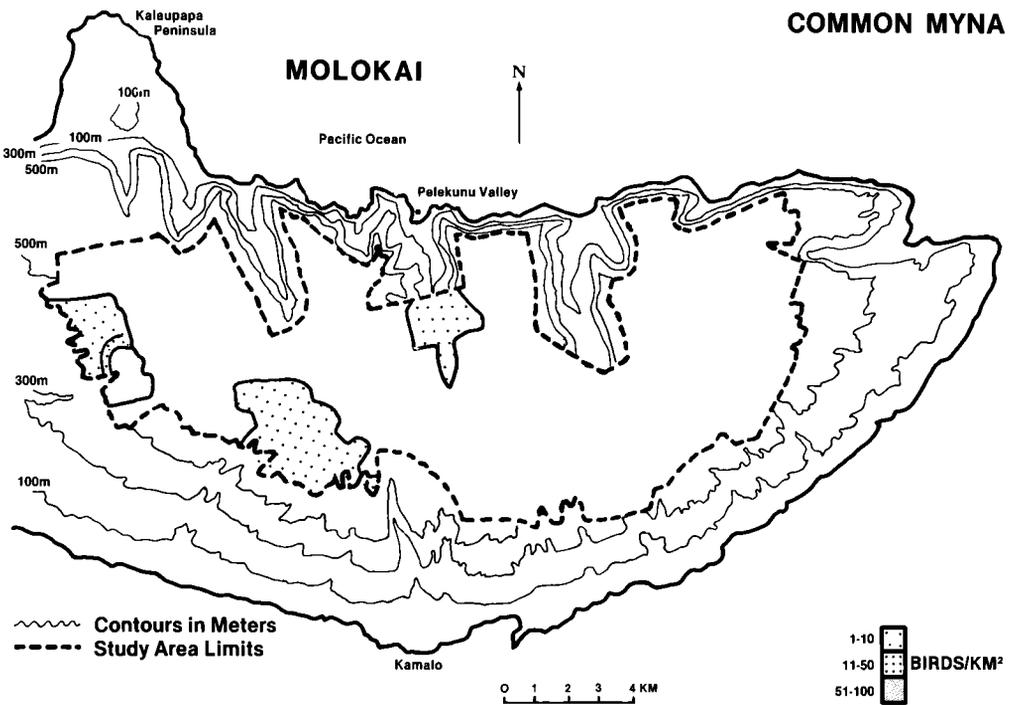


FIGURE 259. Distribution and abundance of the Common Myna in the Molokai study area.

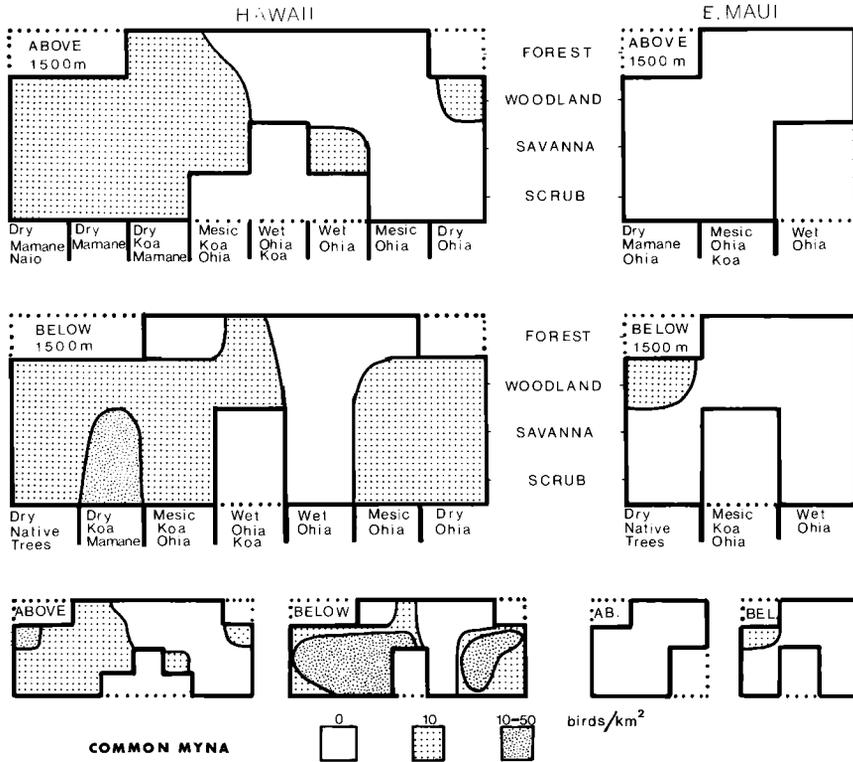


FIGURE 260. Habitat response graphs of the Common Myna. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

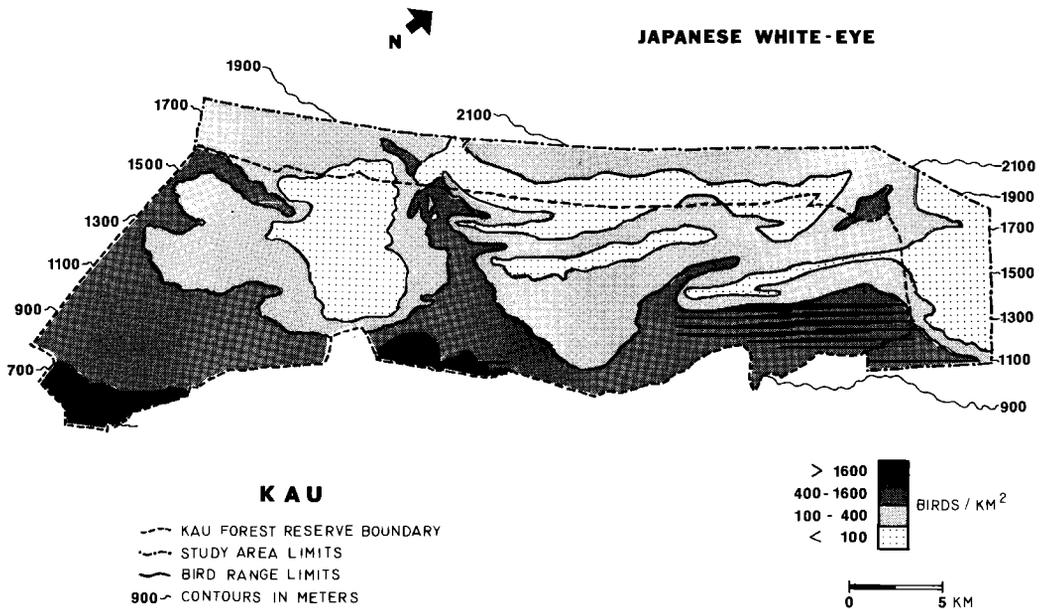


FIGURE 261. Distribution and abundance of the Japanese White-eye in the Kau study area.

TABLE 57
REGRESSION MODELS FOR HABITAT RESPONSE OF THE COMMON MYNA, SAFFRON FINCH, AND YELLOW-FRONTED CANARY^a

| | Common Myna | | | | Saffron Finch | Yellow-fronted Canary |
|-----------------------------|-------------|-------|---------|--------|---------------|-----------------------|
| | Hamakua | Puna | Kīpukas | Kona | Kona | Kona |
| <i>R</i> ² | 0.51* | 0.26* | 0.39* | 0.23* | 0.17* | 0.13* |
| Moisture | -6.1* | -3.5* | -5.0* | -5.7* | -3.4* | -9.7* |
| Elevation | ... | 4.5* | -7.3* | ... | -8.8* | -6.1* |
| (Elevation) ² | ... | -4.8* | 6.7* | -9.1* | ... | 3.5* |
| Tree biomass | 3.6* | 5.8* | ... | 6.2* | ... | ... |
| (Tree biomass) ² | ... | ... | ... | ... | -6.1* | -3.2 |
| Crown cover | ... | -5.1* | ... | -6.7* | ... | ... |
| Canopy height | 4.2* | ... | 2.7 | ... | 4.2* | ... |
| Koa | -2.2 | X | 3.7* | 8.3* | ... | ... |
| Ohia | -8.5* | ... | ... | -4.6* | ... | 6.0* |
| Naio | X | X | ... | -6.1* | -3.9* | ... |
| Mamane | ... | 4.7* | ... | ... | 4.4* | 5.3* |
| Intro. trees | -6.4* | ... | X | 2.6 | 13.7* | 5.7* |
| Shrub cover | -7.7* | ... | -4.3* | -4.1* | -4.0* | ... |
| Ground cover | -9.8* | ... | 4.8* | 8.2* | 4.2* | 7.0* |
| Native shrubs | -2.7 | 2.9 | -3.6* | ... | ... | -2.5 |
| Intro. shrubs | ... | ... | -2.7 | -2.7 | -3.6* | -3.9* |
| Ground ferns | X | ... | ... | -10.8* | ... | ... |
| Matted ferns | -3.1 | ... | ... | -2.5 | ... | ... |
| Tree ferns | X | -3.0 | X | ... | ... | ... |
| Ieie | X | ... | X | ... | ... | ... |
| Passiflora | -3.0 | X | X | ... | ... | 3.3 |
| Native herbs | X | ... | ... | ... | ... | ... |
| Intro. herbs | X | ... | ... | ... | ... | -3.6* |
| Native grasses | ... | ... | -2.6 | -2.3 | ... | ... |
| Intro. grasses | ... | ... | -3.5* | -4.2* | ... | ... |
| Ohia flowers | -2.4 | ... | ... | 2.5 | ... | ... |
| Olapa fruit | ... | ... | ... | 3.7* | ... | ... |
| Mamane flowers | X | X | ... | X | X | X |
| Mamane fruit | X | X | X | X | X | X |
| Naio fruit | X | X | X | X | X | X |

^a *R*² is the variance accounted for by the model. Entries are *t* statistics and all are significant at *P* < 0.05; * indicates *P* < 0.001; ... indicates variable not significant (*P* > 0.05); X indicates variable not available for inclusion in model.

to ground cover mainly represents low numbers in high elevation pastures.

Although common and widespread in many communities, Common Mynas seldom enter the higher-elevation forests where native bird densities are greatest. This suggests support for the hypothesis that Common Mynas had little involvement in the drastic decline of native birds at the turn of the century (Caum 1933, Munro 1944, Berger 1981); however, mynas are cavity-nesters and during their tenure in the montane forests in the 1890s, they may have been competitors with the Hawaii Oo, Kauai Oo, and other native cavity-nesters that began to decline in numbers thereafter. Common Mynas may also have been sources and reservoirs for avian diseases in remote areas during that era.

JAPANESE WHITE-EYE (*Zosterops japonicus*)

Japanese White-eyes, also known as Mejiro, are the most abundant land birds in the Hawaiian Islands. They were first introduced from Japan in 1929 to Oahu (Caum 1933), with an introduction to Hawaii in 1937 (Berger 1981). They occur from sea level to tree line, in very dry to very wet habitat on all the islands (Berger 1981). They are omnivores, feeding mostly on fruit, nectar, and insects from understory sites (Guest 1973, Conant 1975). In Hawaii Volcanoes National Park, Baldwin (1953) noted that the average frequency of this species on his plots increased from 23% in 1940–1944 to 50% in 1948–1949; by the 1970s, Conant (1975) and Banko

TABLE 58
DENSITY [MEAN (SE)] OF THE JAPANESE WHITE-EYE BY ELEVATION, HABITAT, AND STUDY AREA^a

| | Kau | Hamakua | Puna | Kipukas | Kona | Mauna Kea | Kohala | East Maui | West Maui | Molokai | Lana'i | Kauai |
|------------------|------------|----------|----------|----------|----------|-----------|------------|-----------|-----------|------------|-----------|----------|
| <i>Elevation</i> | | | | | | | | | | | | |
| 100-300 m | ... | ... | ... | ... | ... | ... | ... | ... | ... | 1386 (174) | ... | ... |
| 300-500 m | ... | 603 (55) | 719 (26) | ... | 526 (51) | ... | 174 (174) | 187 (64) | ... | 1269 (120) | ... | ... |
| 500-700 m | 1608 (92) | 716 (30) | 671 (26) | ... | 344 (24) | ... | 1157 (156) | 386 (51) | 473 (107) | 1147 (95) | 741 (280) | ... |
| 700-900 m | 1384 (124) | 770 (22) | 542 (23) | ... | 431 (17) | ... | 1289 (147) | 389 (41) | 658 (87) | 820 (70) | 491 (58) | ... |
| 900-1100 m | 768 (45) | 816 (24) | 671 (31) | ... | 431 (16) | ... | 675 (72) | 480 (34) | 366 (58) | 884 (66) | 641 (103) | ... |
| 1100-1300 m | 523 (43) | 682 (24) | 357 (58) | 608 (72) | 385 (16) | ... | 296 (39) | 426 (34) | 406 (52) | 759 (52) | ... | 707 (38) |
| 1300-1500 m | 163 (16) | 489 (22) | ... | 195 (33) | 233 (9) | ... | 176 (31) | 426 (34) | 338 (61) | 522 (140) | ... | 356 (33) |
| 1500-1700 m | 213 (24) | 408 (24) | ... | 137 (17) | 148 (7) | ... | 163 (77) | 338 (24) | 348 (61) | ... | ... | ... |
| 1700-1900 m | 137 (20) | 436 (36) | ... | 49 (8) | 100 (8) | ... | ... | 321 (31) | 442 (79) | ... | ... | ... |
| 1900-2100 m | 108 (23) | 177 (29) | ... | 35 (9) | 62 (7) | 291 (48) | ... | 214 (26) | ... | ... | ... | ... |
| 2100-2300 m | 119 (119) | 372 (90) | ... | 45 (16) | 17 (3) | 280 (42) | ... | 91 (14) | ... | ... | ... | ... |
| 2300-2500 m | ... | ... | ... | ... | + | 326 (41) | ... | 41 (12) | ... | ... | ... | ... |
| 2500-2700 m | ... | ... | ... | ... | ... | 171 (28) | ... | 16 (10) | ... | ... | ... | ... |
| 2700-2900 m | ... | ... | ... | ... | ... | 240 (53) | ... | + | ... | ... | ... | ... |
| 2900-3100 m | ... | ... | ... | ... | ... | 410 (200) | ... | ... | ... | ... | ... | ... |
| <i>Habitat</i> | | | | | | | | | | | | |
| Ohia | 469 (26) | 555 (12) | 654 (13) | 56 (6) | 259 (7) | ... | 459 (36) | 360 (15) | 473 (33) | 816 (36) | ... | 547 (29) |
| Koa-ohia | 319 (25) | 774 (17) | ... | 388 (50) | 344 (11) | ... | ... | 555 (37) | ... | ... | ... | ... |
| Koa-mamane | ... | 341 (53) | ... | 124 (20) | 186 (11) | ... | ... | ... | ... | ... | ... | ... |
| Mamane-naio | ... | ... | ... | ... | 95 (18) | 396 (27) | ... | ... | ... | ... | ... | ... |
| Mamane | ... | ... | ... | ... | 116 (11) | 115 (24) | ... | 59 (35) | ... | ... | ... | ... |
| Other natives | ... | 301 (31) | ... | 133 (32) | 195 (22) | ... | ... | 296 (26) | ... | 711 (87) | 660 (172) | ... |
| Intro. trees | ... | 523 (32) | ... | ... | 398 (40) | ... | 809 (285) | 352 (38) | 845 (846) | 1471 (96) | 571 (70) | ... |
| Treelless | 107 (71) | 101 (22) | 138 (55) | 20 (14) | 25 (6) | ... | ... | 99 (15) | 292 (70) | 477 (131) | 400 (175) | + (+) |

^a Densities are given in birds/km²; + indicates stratum was in the species range but density <0.5 birds/km²; 0 indicates stratum was outside range but was sampled; ... indicates stratum was not sampled in study area.

JAPANESE WHITE-EYE

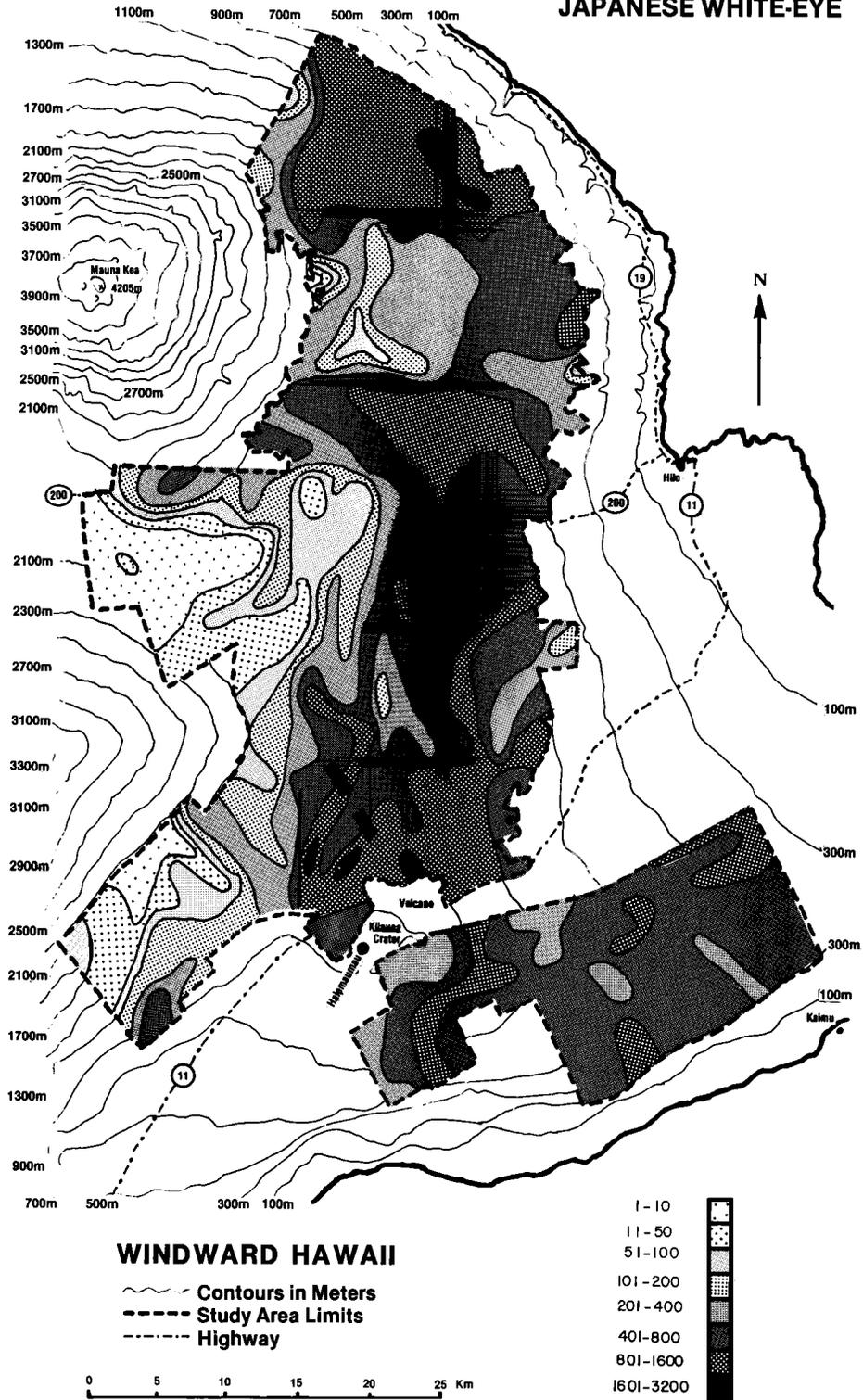


FIGURE 262. Distribution and abundance of the Japanese White-eye in the windward Hawaii study areas.

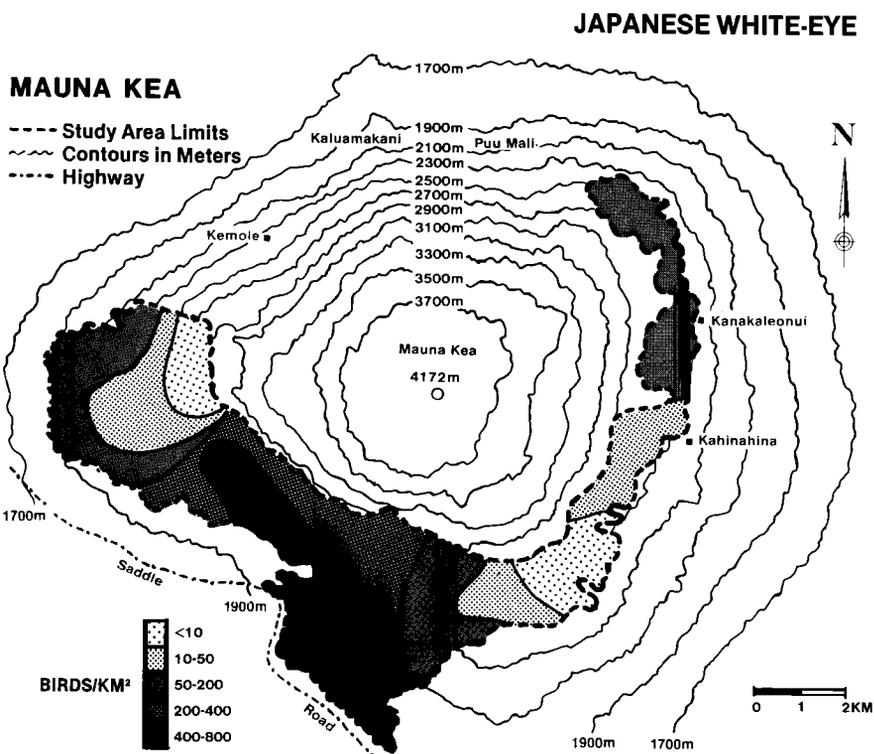


FIGURE 264. Distribution and abundance of the Japanese White-eye in the Mauna Kea study area.

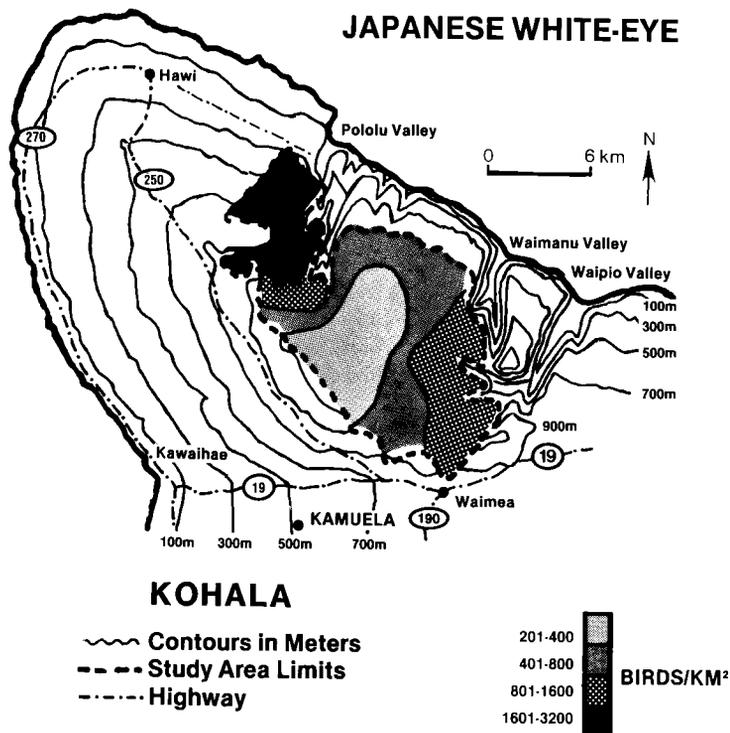


FIGURE 265. Distribution and abundance of the Japanese White-eye in the Kohala study area.

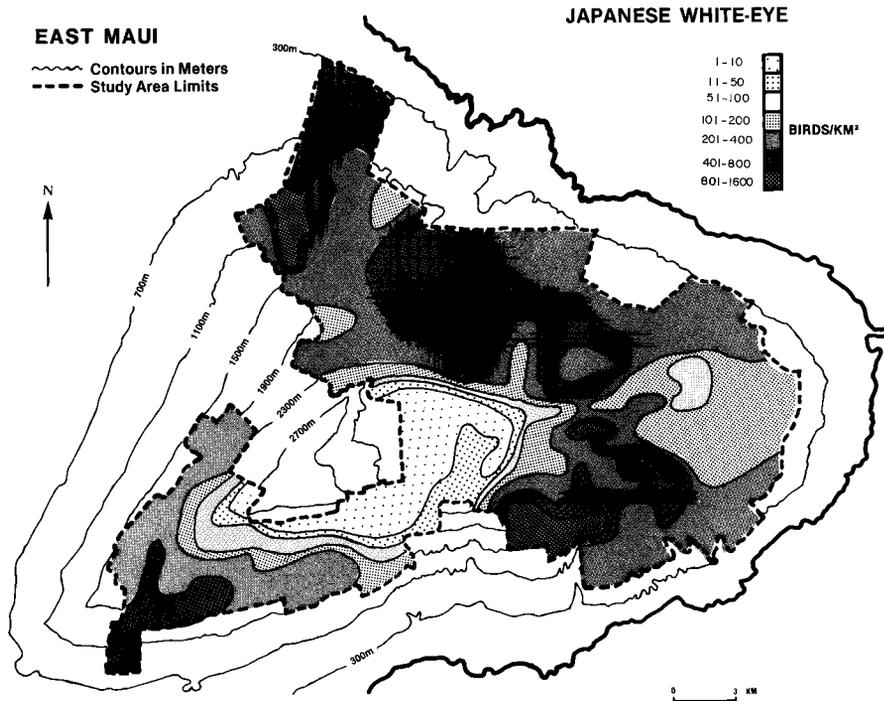


FIGURE 266. Distribution and abundance of the Japanese White-eye in the East Maui study area.

and Banko (1980) found frequencies approaching 100%.

Japanese White-eyes are ubiquitous in our study areas (Tables 33, 34, 58, Figs. 261–270). An estimated $1,300,000 \pm 25,000$ (95% CI) birds occupy the seven study areas on Hawaii, with the largest percentage (48%) in the Hamakua study area. Within our study areas we estimated $114,000 \pm 7000$ birds on East Maui, $19,000 \pm 2000$ on West Maui, $120,000 \pm 9000$ on Molokai, $11,000 \pm 4000$ on Lanai, and $15,000 \pm 1400$ on Kauai. For 1968–1973 Sincock et al. (1984) estimated $12,000 \pm 6000$ birds in our study area and a total of $256,000 \pm 37,000$ in native forests on Kauai.

Japanese White-eyes occur from sea level to 3100 m on Hawaii and 2700 m on Maui. Densities above 500 birds/km² occur below 1300 m on Hawaii and Kauai, and at all elevations sampled on Molokai and Lanai. Densities on Maui are lower than in other study areas, and reach 500 birds/km² only in one elevational stratum on West Maui. Distributional patterns on Hawaii, Maui, Molokai, and Kauai suggest the advance of lowland populations into montane forests. Japanese White-eyes tend to be more common along broad forest edges than within forest interiors, although habitat responses obscure this pattern somewhat. On Mauna Kea (Fig.

264) densities are lower in the middle of the mamane forest at Puu Laau than along the lower edges of the study area that border on pasture. In Kona (Fig. 263) densities are greater in the broken koa and mamane forest at Puu Lehua (25 km southeast of Kailua) than in the unbroken koa forests on north Hualalai (5 km north of the summit) and in central Kona (20 km east of Kealahou Bay). Densities in Kohala (Fig. 265) are greater along the forests of the northwest margins than in the forest interior. Windward Hawaii densities (Fig. 262) are much greater in koa-ohia and ohia forests in the northernmost sixth of the Hamakua study area lying along rangeland than in the forest interior of the next sixth south. Densities on East Maui (Fig. 266) are much greater along the northwest edge of the wet forest than at the same elevation in the forest interior. Japanese White-eye are widespread and common on West Maui. On Molokai (Fig. 268) densities are lowest in the interior Olokui plateau that is well buffered from forest edges. On Lanai, Japanese White-eyes are abundant throughout the study area. On Kauai (Fig. 270) densities decline towards the interior of the Alakai Swamp. Forest edges seem to act as avenues along which Japanese White-eyes disperse toward more remote areas.

The habitat response graphs indicate well-es-

WEST MAUI

JAPANESE WHITE-EYE

~~~~~ Contours in Meters  
 - - - - Study Area Limits

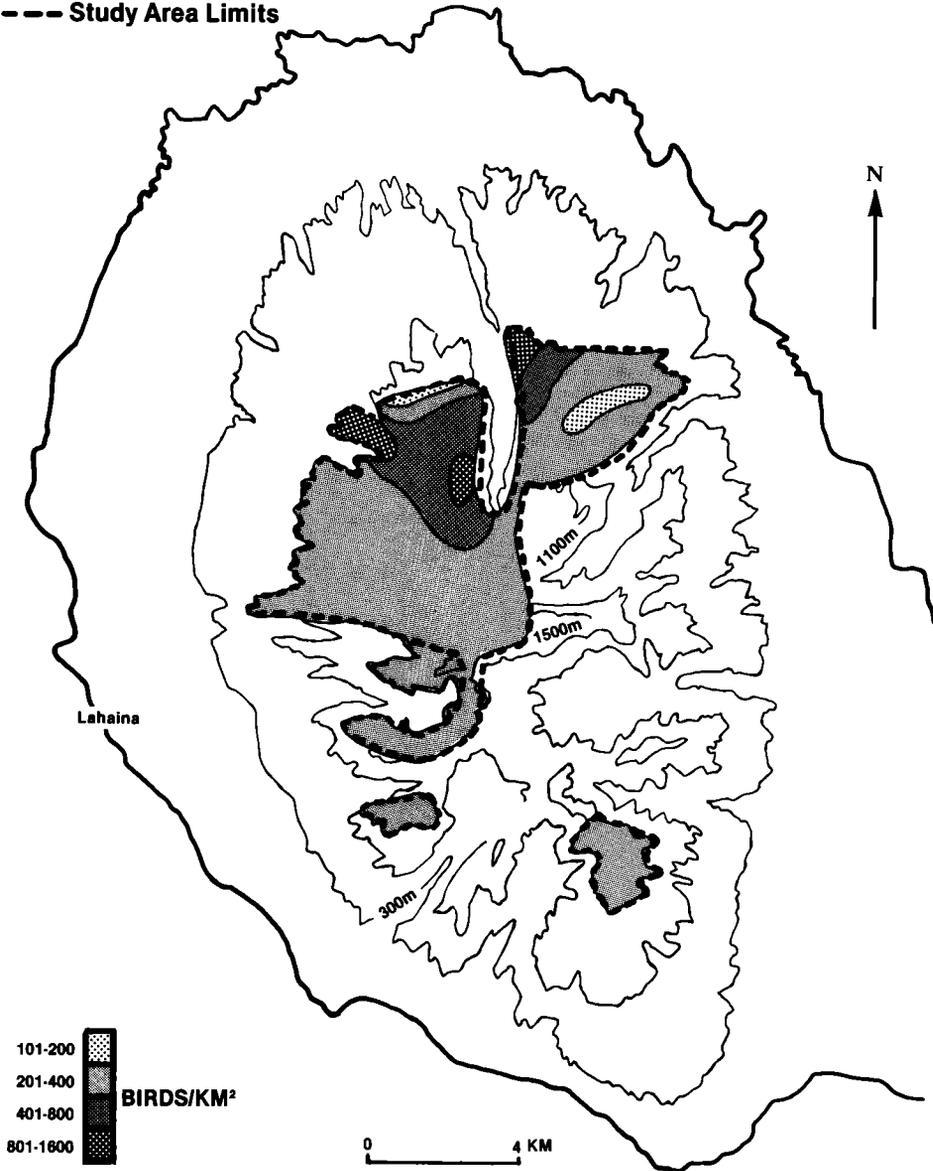


FIGURE 267. Distribution and abundance of the Japanese White-eye in the West Maui study area.

established populations with greatest densities in mesic koa-ohia forests (Fig. 271). Unlike most native and many introduced passerines, Japanese White-eyes maintain densities above 200 birds/km<sup>2</sup> in woodland, savanna, and even some scrub habitats. Rainforest interiors above 1500 m elevation have lower densities.

Compared with the regression models of other

common species, Japanese White-eyes (Table 59) have fewer significant variables than the norm, indicating a habitat generalist. They are most common at low-elevation sites with some trees and introduced ground cover.

Japanese White-eyes occur across a broad range of moisture regimes and in most regression models show no response to moisture. Koa, naio,

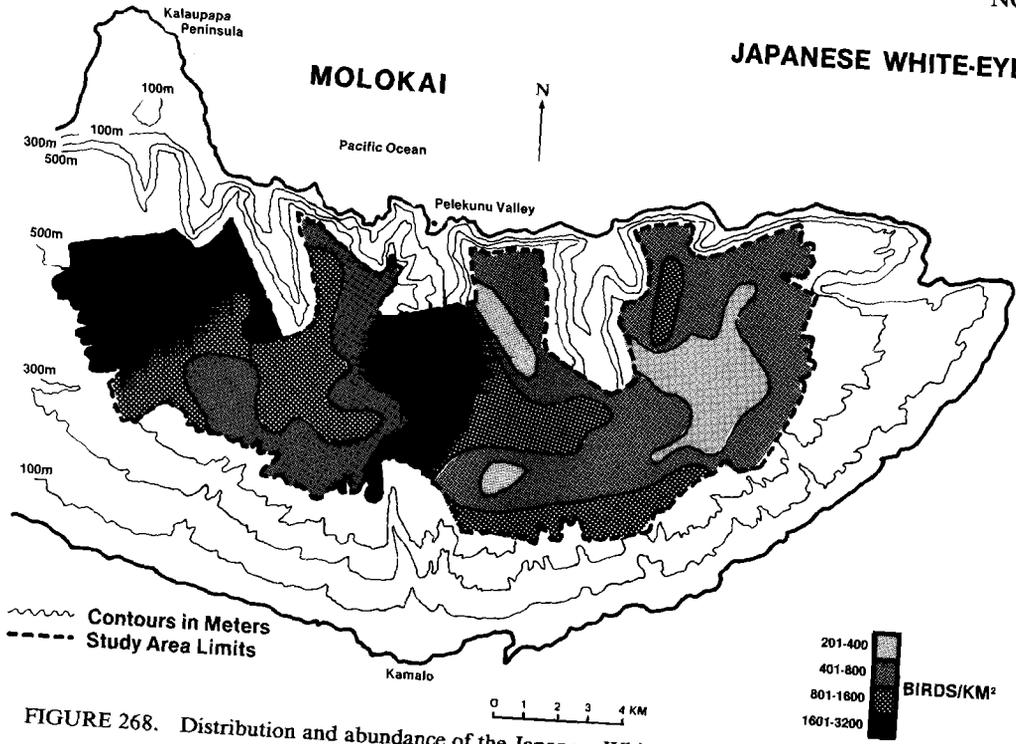


FIGURE 268. Distribution and abundance of the Japanese White-eye in the Molokai study area.

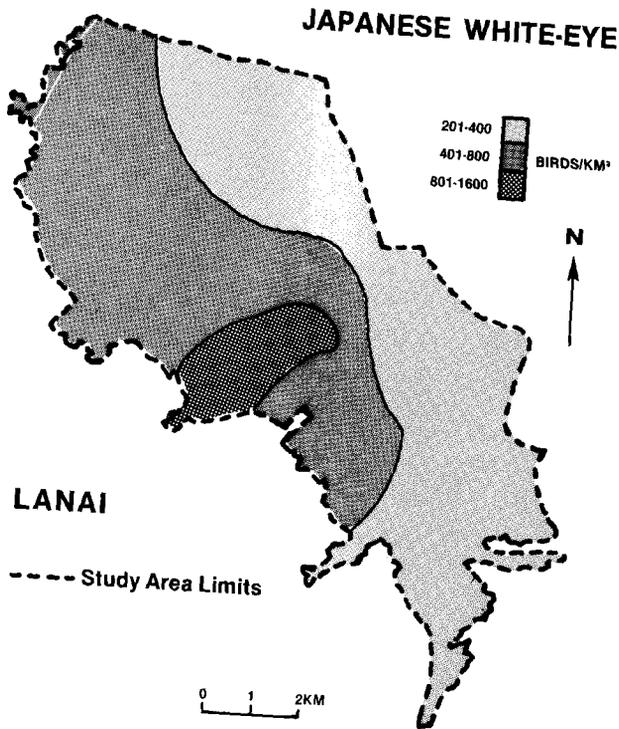


FIGURE 269. Distribution and abundance of the Japanese White-eye in the Lanai study area.

## JAPANESE WHITE-EYE

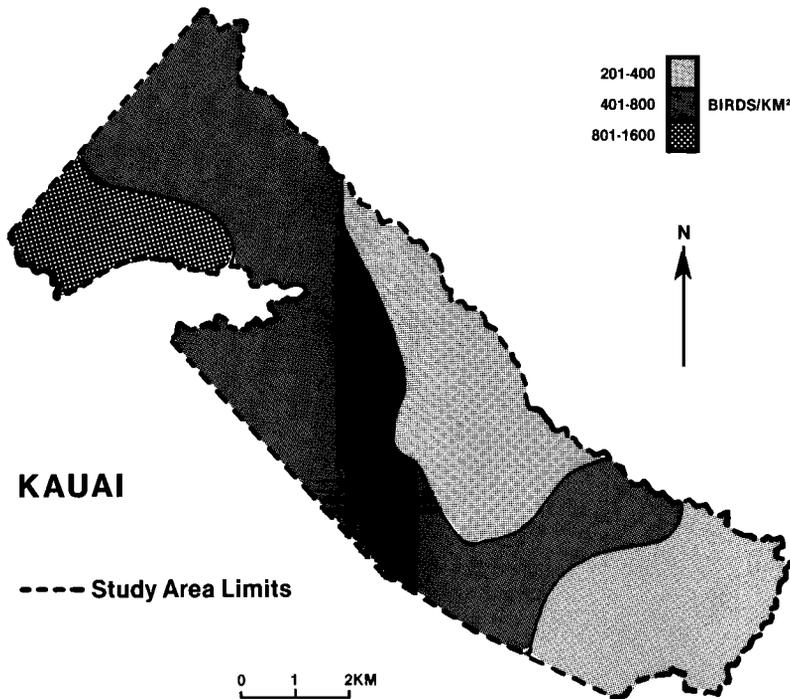


FIGURE 270. Distribution and abundance of the Japanese White-eye in the Kauai study area.

and mamane generate positive terms; ohia, usually negative terms. The two models with positive ohia terms are anomalous: Puna has a negative tree biomass correction term (here ohia is the main forest species and indexes forest development), and Molokai has a negative moisture term (indicating that ohia rainforest interiors are avoided). Responses to introduced trees, shrubs, and ferns are undistinguished.

Japanese White-eyes tend to occupy sites with introduced species dominating the ground cover. Response is positive to introduced herbs in four models and to passiflora and introduced grasses in one each. Native grasses have negative terms in two models. In the case of passiflora, birds are attracted to the nectar and fruit of banana poka (Warshauer et al. 1983). Introduced ground covers often indicate disturbance by grazing cattle or feral animals, and birds may enter forest interiors more rapidly via disturbed areas rather than through unbroken native forests. This is to be expected in view of the white-eye's recent introduction and its understory foraging zone, and was supported by anecdotal literature references. Dunmire (1962) noted that Japanese White-eye numbers "exploded" in Hawaii Volcanoes National Park in the 1940–1961 period, representing the arriving wave of a highly suc-

cessful, booming population. Scott and Sincok (1977) noted very few Japanese White-eyes in the upper Koolau Forest Reserve on Maui in 1975, and the 1967 Kipahulu Valley expedition found few birds at upper elevations (Warner 1967). During our 1980 survey on Maui, however, fairly high densities were found in these areas, suggesting a recent (around 1975–1980), substantial increase in numbers on windward Maui above 1500 m elevation. Since the habitat and regional distribution of Japanese White-eyes have not yet stabilized, the response to disturbed ground cover may indicate the "route of least resistance" for range expansion. Our analysis of interspecific competition suggests that Japanese White-eyes have negative impacts on native passerines, particularly on species that feed on similar foods, such as Elepaio, Common Amakihi, and Hawaii Creeper (Mountainspring and Scott 1985). This species also appears to have a negative impact on other introduced birds in lowland areas (Moulton and Pimm 1983).

NORTHERN CARDINAL  
(*Cardinalis cardinalis*)

Northern Cardinals were introduced to the Hawaiian Islands in 1929 (Caum 1933) and are well established in introduced and disturbed na-

TABLE 59  
REGRESSION MODELS FOR HABITAT RESPONSE OF THE JAPANESE WHITE-EYE<sup>a</sup>

|                             | Kau   | Hamakua | Puna  | Kipukas | Kona   | Mauna Kea | Kohala | Maui  | Molokai | Lanai | Kauai |
|-----------------------------|-------|---------|-------|---------|--------|-----------|--------|-------|---------|-------|-------|
| R <sup>2</sup>              | 0.34* | 0.25*   | 0.12* | 0.44*   | 0.39*  | 0.24*     | 0.43*  | 0.31* | 0.33*   | 0.18* | 0.20* |
| Moisture                    | ...   | ...     | ...   | ...     | 9.0*   | X         | X      | ...   | -8.1*   | ...   | X     |
| Elevation                   | -6.3* | ...     | -5.5* | -7.2*   | 5.3*   | ...       | ...    | 4.3*  | 3.2     | ...   | -5.9* |
| (Elevation) <sup>2</sup>    | 4.1*  | -19.5*  | ...   | 6.0*    | -10.0* | ...       | -6.6*  | -4.9* | -4.0*   | ...   | ...   |
| Tree biomass                | -2.2  | ...     | ...   | ...     | 6.4*   | ...       | ...    | 7.4*  | 9.9*    | 3.9*  | ...   |
| (Tree biomass) <sup>2</sup> | ...   | ...     | -2.9  | ...     | -3.8*  | ...       | ...    | -3.5* | ...     | ...   | ...   |
| Crown cover                 | ...   | ...     | ...   | ...     | ...    | ...       | ...    | ...   | ...     | ...   | ...   |
| Canopy height               | ...   | 4.3*    | ...   | ...     | ...    | ...       | ...    | ...   | ...     | ...   | ...   |
| Koa                         | ...   | 4.2*    | X     | ...     | ...    | X         | X      | ...   | X       | X     | X     |
| Ohia                        | X     | -5.5*   | 5.3*  | ...     | -3.9*  | X         | ...    | -3.2  | 5.3*    | ...   | X     |
| Naio                        | X     | X       | X     | 2.3     | 3.5*   | 8.9*      | X      | X     | X       | X     | X     |
| Mamane                      | X     | 2.3     | ...   | 4.8*    | ...    | ...       | X      | ...   | X       | X     | X     |
| Intro. trees                | X     | -2.8    | ...   | X       | ...    | X         | ...    | ...   | ...     | ...   | X     |
| Shrub cover                 | ...   | ...     | ...   | ...     | ...    | ...       | ...    | 6.5*  | ...     | ...   | ...   |
| Ground cover                | ...   | 3.4*    | ...   | ...     | ...    | ...       | ...    | -3.6* | ...     | ...   | ...   |
| Native shrubs               | ...   | ...     | ...   | ...     | -2.2   | X         | ...    | ...   | ...     | ...   | ...   |
| Intro. shrubs               | X     | ...     | ...   | ...     | ...    | X         | ...    | ...   | ...     | ...   | ...   |
| Ground ferns                | X     | X       | ...   | ...     | -2.8   | X         | ...    | ...   | -2.5    | X     | ...   |
| Matted ferns                | ...   | ...     | ...   | ...     | -6.0*  | X         | ...    | ...   | ...     | ...   | ...   |
| Tree ferns                  | 2.3   | X       | ...   | X       | ...    | X         | ...    | -2.3  | ...     | X     | ...   |
| Ieie                        | X     | X       | ...   | X       | ...    | X         | X      | ...   | X       | X     | ...   |
| Passiflora                  | X     | 6.5*    | X     | X       | ...    | X         | ...    | 4.4*  | X       | X     | X     |
| Native herbs                | X     | X       | ...   | ...     | ...    | X         | ...    | ...   | ...     | X     | ...   |
| Intro. herbs                | X     | X       | ...   | ...     | 3.8*   | 2.8       | 4.6*   | 4.9*  | ...     | X     | ...   |
| Native grasses              | ...   | -5.0*   | ...   | ...     | -5.0*  | ...       | ...    | ...   | ...     | X     | ...   |
| Intro. grasses              | ...   | ...     | ...   | ...     | ...    | ...       | 3.5*   | ...   | ...     | ...   | ...   |
| Ohia flowers                | 5.8*  | 10.6*   | ...   | ...     | 6.3*   | X         | ...    | 2.4   | ...     | ...   | ...   |
| Olapa fruit                 | ...   | 4.3*    | ...   | ...     | ...    | X         | ...    | ...   | ...     | ...   | ...   |
| Mamane flowers              | X     | X       | X     | ...     | X      | ...       | X      | -3.6* | X       | X     | X     |
| Mamane fruit                | X     | X       | X     | X       | X      | ...       | X      | X     | X       | X     | X     |
| Naio fruit                  | X     | X       | X     | X       | X      | ...       | X      | X     | X       | X     | X     |

<sup>a</sup> R<sup>2</sup> is the variance accounted for by the model. Entries are *t* statistics and all are significant at *P* < 0.05; \* indicates *P* < 0.001; ... indicates variable not significant (*P* > 0.05); X indicates variable not available for inclusion in model.

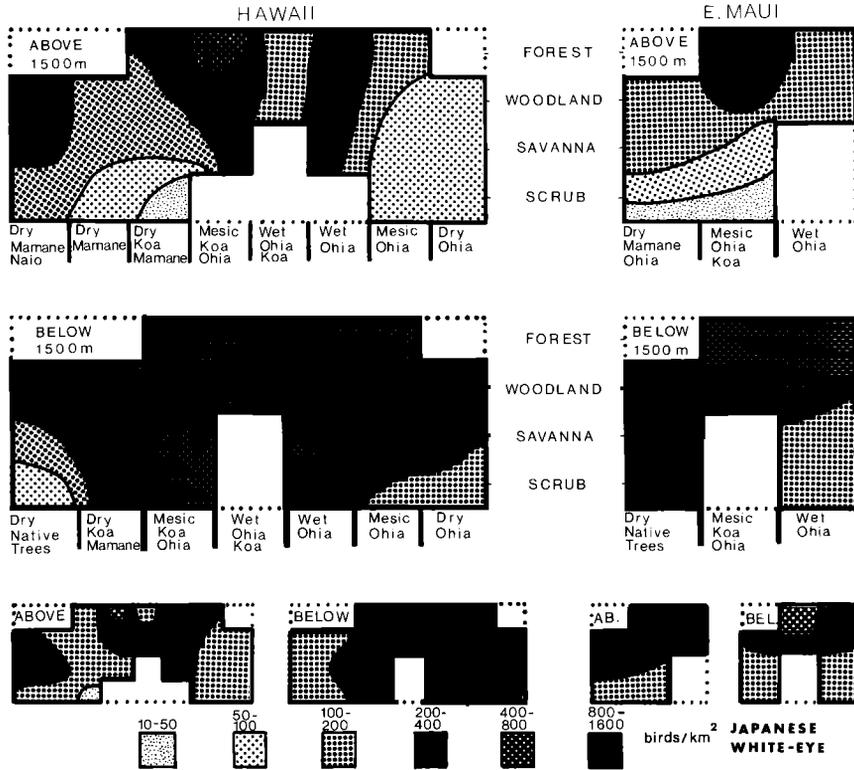


FIGURE 271. Habitat response graphs of the Japanese White-eye. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

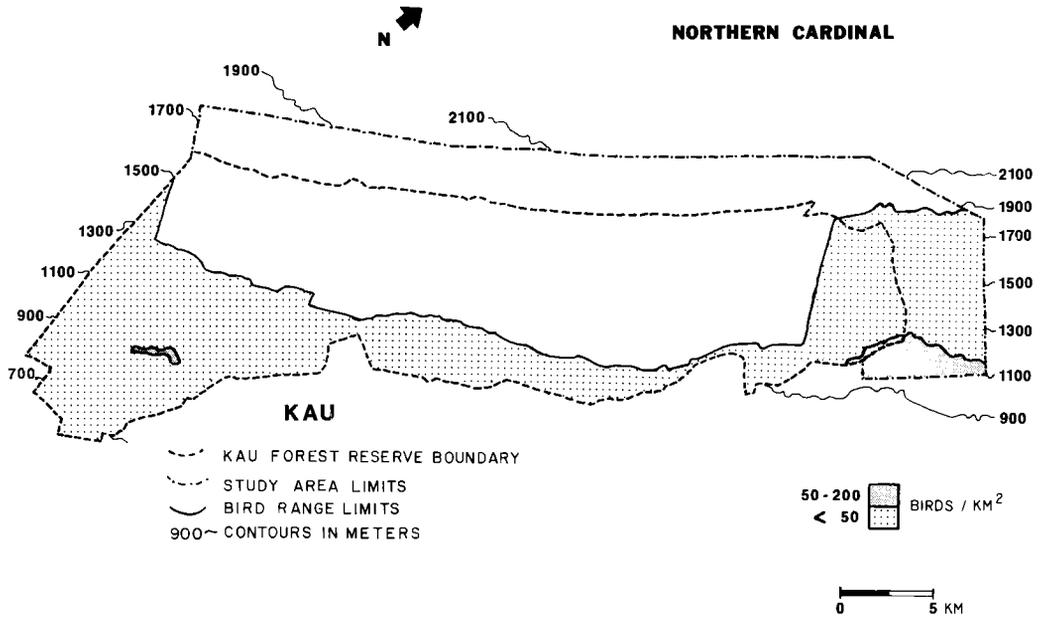


FIGURE 272. Distribution and abundance of the Northern Cardinal in the Kau study area.





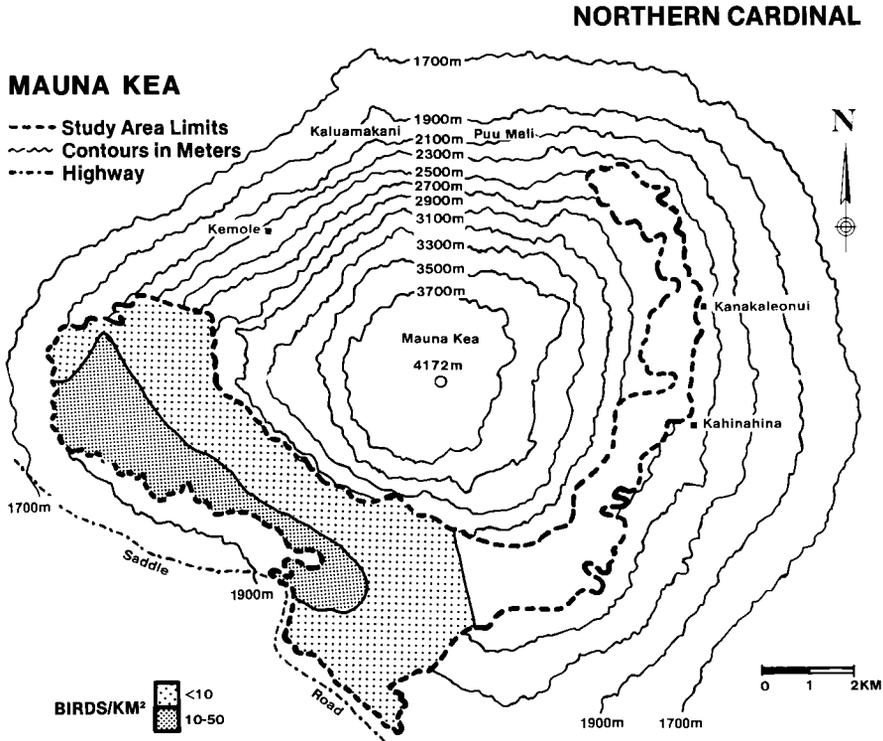


FIGURE 275. Distribution and abundance of the Northern Cardinal in the Mauna Kea study area.

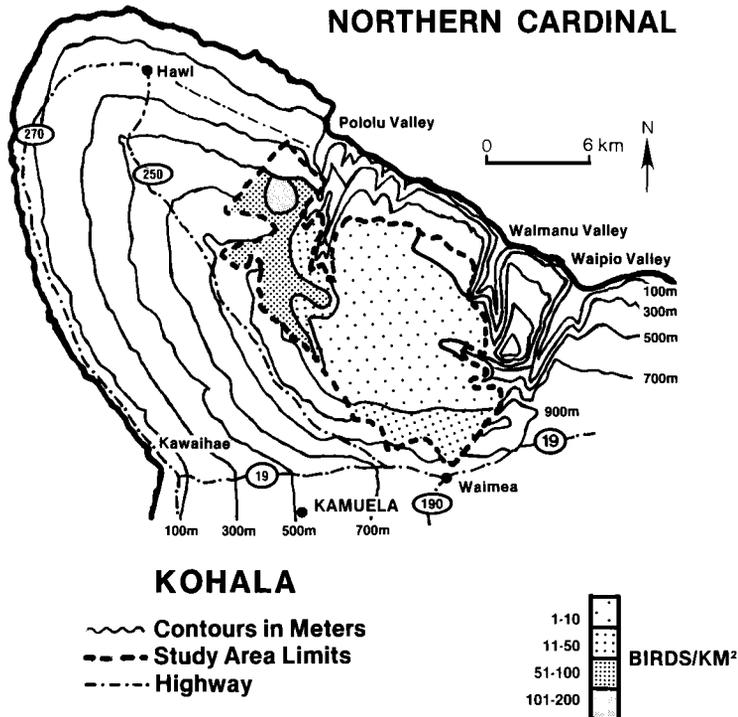


FIGURE 276. Distribution and abundance of the Northern Cardinal in the Kohala study area.

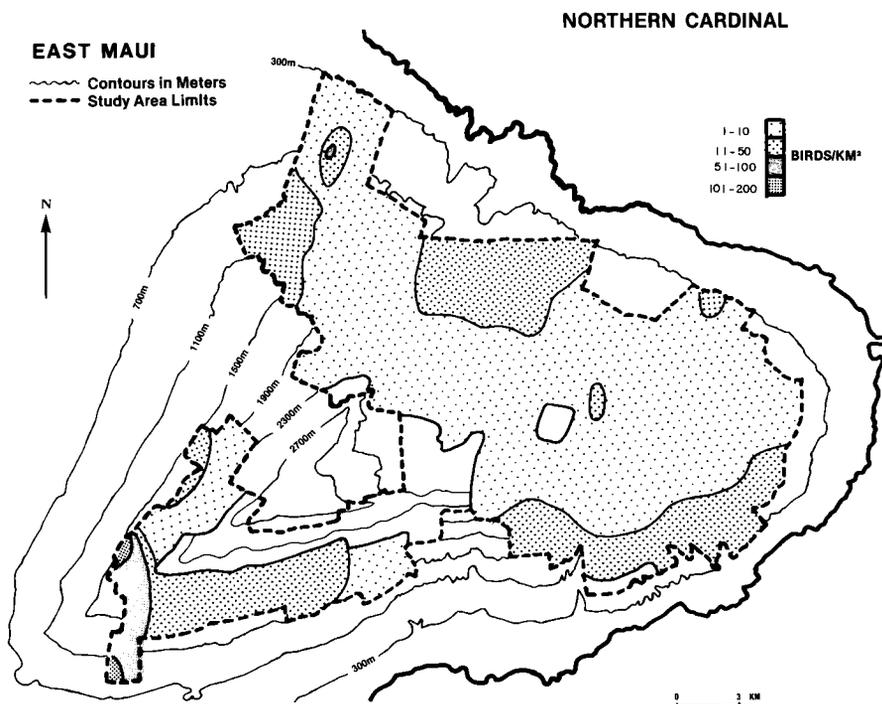


FIGURE 277. Distribution and abundance of the Northern Cardinal in the East Maui study area.

tive forests throughout the islands (Berger 1981). They are natives of North America that frequent hedges, thickets, and open woodlands and feed on seeds, fruits, and insects (Bent 1968). They are also known as Cardinals, Red Cardinals, American Cardinals, and Kentucky Cardinals, in contrast to the Red-crested or Brazilian Cardinal (*Paroaria coronata*) and the Yellow-billed Cardinal (*P. capitata*) of dry lowland areas, which were introduced from South America.

Northern Cardinals occur in all study areas (Figs. 272–281), but nowhere do they reach the densities of Japanese White-eyes (Tables 33, 34, 60). On Hawaii, 48,000 ± 1500 (95% CI) birds occur in the study areas. The distributional patterns for Hamakua and Kona indicate they inhabit forest edges and broken habitats rather than forest interiors. Their absence on the eastern Mauna Kea study area may be due to low food diversity, as this area has mamane trees but very little understory and no naio trees. Northern Cardinals feed on naio berries and may depend on them for water on Mauna Kea. Birds infiltrate most of the closed forest in the Puna study area. This is facilitated by three factors. First, the Puna forest has extensive edges with disturbed habitat along its north, east, and south boundaries. Second, an active volcanic rift zone runs through

the middle of the forest and supports disturbed habitat. And third, widespread localized marijuana (*Cannabis sativa* and *indica*) cultivation by feral man throughout the forest interior creates numerous canopy openings and provides seeds for the diet. In Hawaii Volcanoes National Park, Northern Cardinals were very rare in the 1940s (Baldwin 1953), but by the 1970s they were abundant at Kipuka Puaulu (Conant 1975, Banko and Banko 1980) and widespread elsewhere.

An estimated 3000 ± 400 (95% CI) birds occupy our study areas on Maui, 1700 ± 300 on Molokai, 1100 ± 300 on Lanai, and 110 ± 40 on Kauai. On these islands, forests are less extensive geographically than on Hawaii, and Northern Cardinals penetrate deeper into the forest as a result of the increased edge. On Molokai the only areas lacking birds are the high interior forest plateaux and the devastated habitat of east Molokai. On Kauai, birds are rare in the Alakai Swamp, and showed no statistical difference from the 50 ± 55 birds estimated for that area by Sincock et al. (1984). Richardson and Bowles (1964) found birds sparse at the edges of the Alakai, as our survey suggested, and more common elsewhere. Sincock et al. (1984) estimated a total of 8500 ± 2900 birds for native forests on Kauai.

## WEST MAUI

## NORTHERN CARDINAL

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 - - - - Study Area Limits

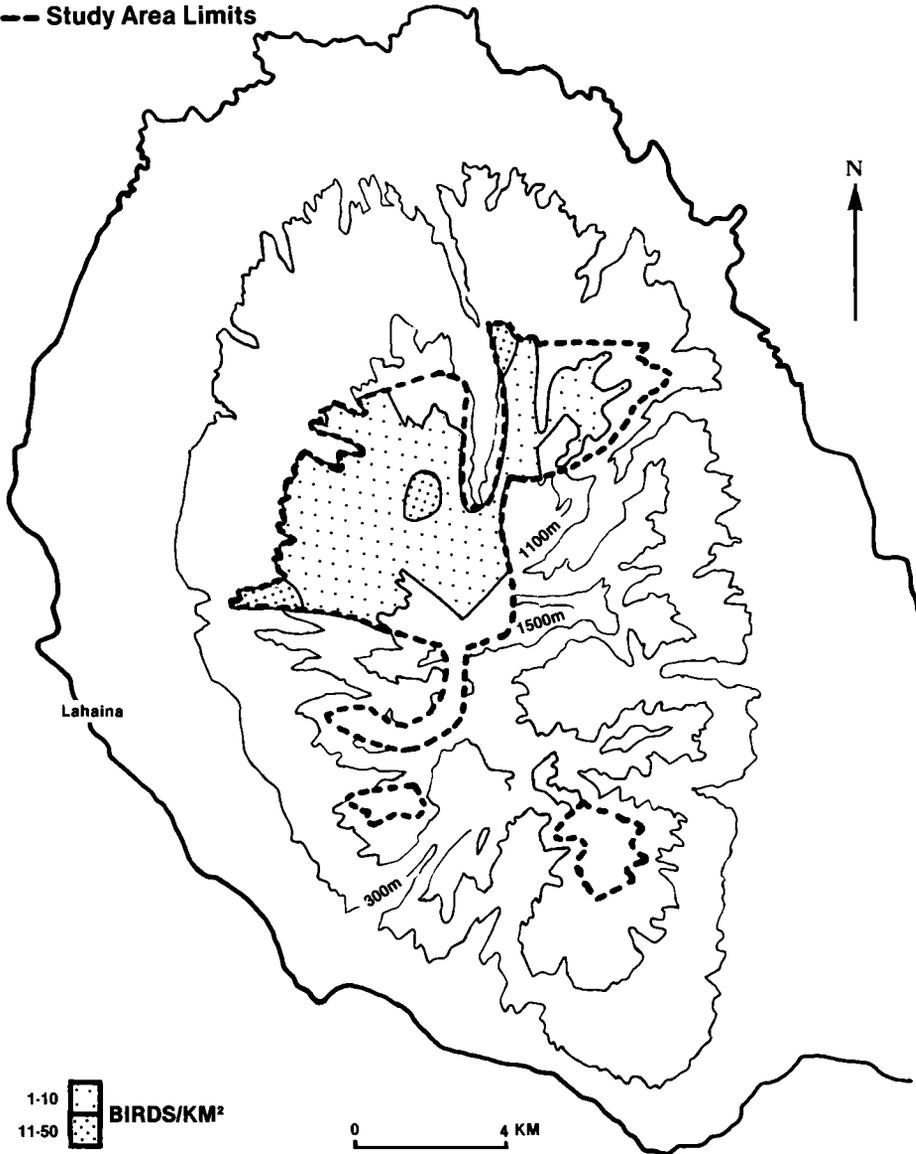


FIGURE 278. Distribution and abundance of the Northern Cardinal in the West Maui study area.

Northern Cardinals show remarkably uniform densities across all habitats, especially at lower elevations on Hawaii (Fig. 282). The regression models indicate that they are generally associated with dry, open forests at low elevations with understories of introduced shrubs and introduced grasses (Table 61). Although densities increase with tree biomass, crown cover, or canopy height in most models, the modest significance

of these terms and the frequency of negative correction terms indicates avoidance of dense forest and preference for more open and brushy situations. Response is positive to introduced shrubs in four models, to passiflora in two, and to introduced grasses in five. Negative responses appear for matted ferns and usually native grasses. The low significance and inconsistency between models for other understory components sug-

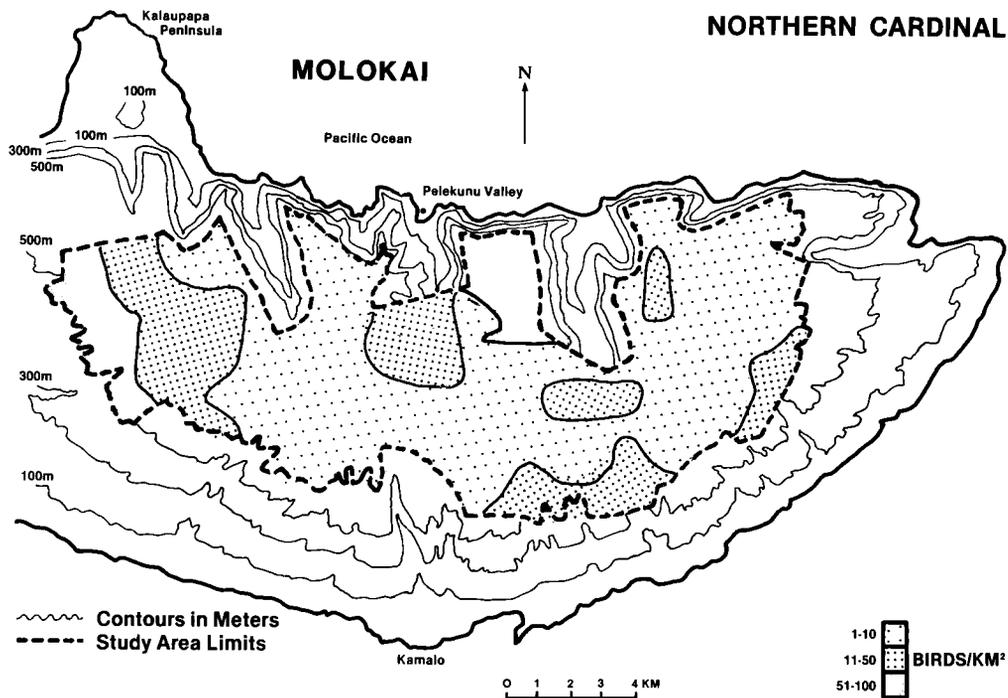


FIGURE 279. Distribution and abundance of the Northern Cardinal in the Molokai study area.

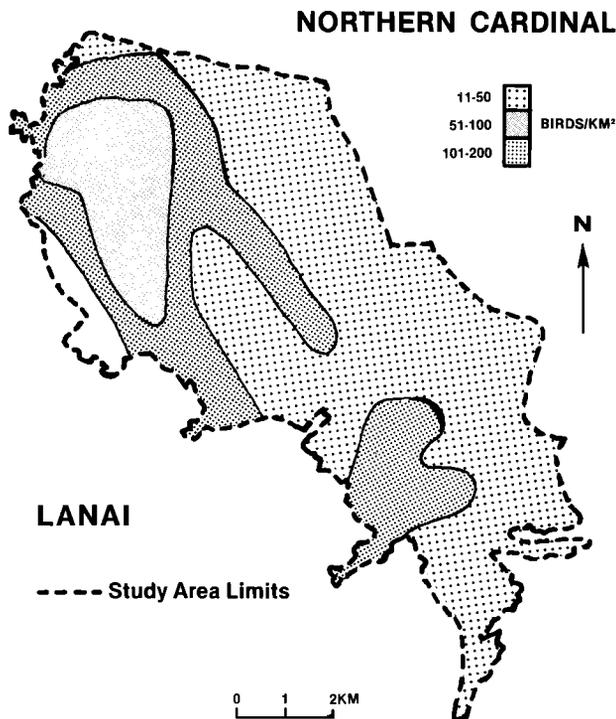


FIGURE 280. Distribution and abundance of the Northern Cardinal in the Lanai study area.

NORTHERN CARDINAL

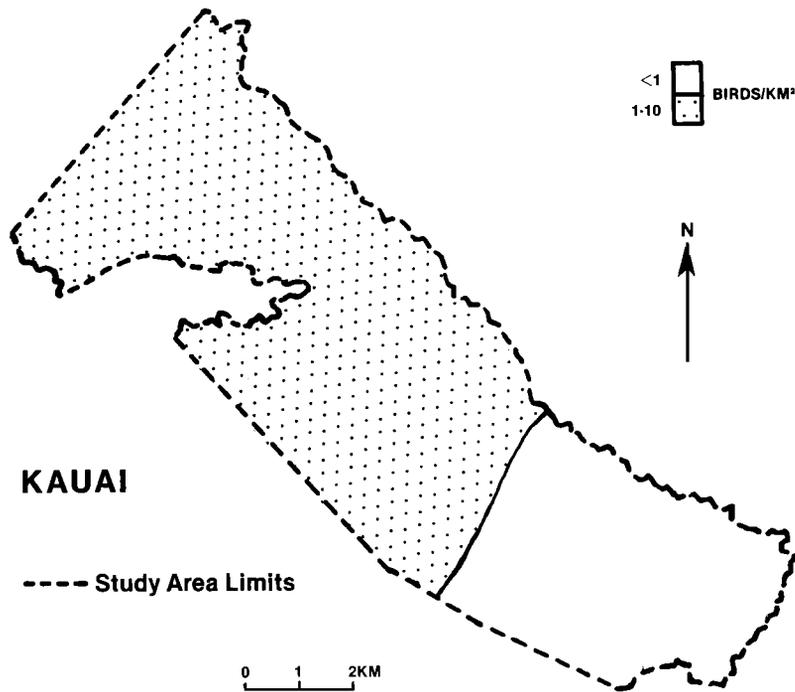


FIGURE 281. Distribution and abundance of the Northern Cardinal in the Kauai study area.

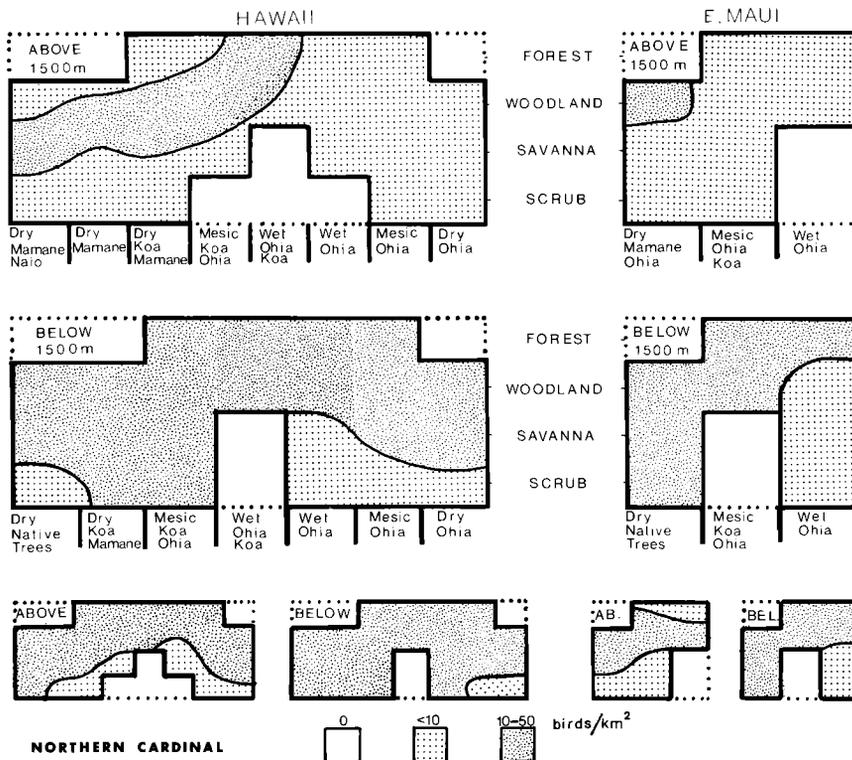


FIGURE 282. Habitat response graphs of the Northern Cardinal. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

TABLE 60
DENSITY [MEAN (SE)] OF THE NORTHERN CARDINAL BY ELEVATION, HABITAT, AND STUDY AREA^a

| | Kau | Hamakua | Puna | Kipukas | Kona | Mauna Kea | Kohala | East Maui | West Maui | Molokai | Lanai | Kauai |
|------------------|---------|---------|--------|---------|--------|-----------|---------|-----------|-----------|---------|----------|-------|
| <i>Elevation</i> | | | | | | | | | | | | |
| 100–300 m | ... | ... | ... | ... | ... | ... | ... | ... | ... | 29 (9) | ... | ... |
| 300–500 m | ... | 28 (6) | 37 (2) | ... | 25 (5) | ... | ... | 11 (6) | ... | 25 (4) | ... | ... |
| 500–700 m | 13 (8) | 25 (3) | 42 (3) | ... | 30 (2) | ... | 44 (9) | 15 (3) | 20 (20) | 26 (4) | ... | ... |
| 700–900 m | 8 (3) | 18 (2) | 12 (2) | ... | 32 (2) | ... | 16 (10) | 11 (2) | 8 (3) | 9 (2) | 104 (22) | ... |
| 900–1100 m | 23 (4) | 10 (1) | 2 (1) | ... | 22 (1) | ... | 10 (3) | 18 (3) | 1 (1) | 11 (3) | 38 (6) | ... |
| 1100–1300 m | 7 (2) | 7 (1) | + | 32 (6) | 25 (1) | ... | 8 (2) | 7 (1) | 4 (2) | 1 (+) | 63 (11) | 6 (1) |
| 1300–1500 m | 4 (2) | 6 (1) | ... | 14 (1) | 24 (1) | ... | 1 (1) | 8 (2) | + | + | ... | 1 (1) |
| 1500–1700 m | 3 (2) | 12 (2) | ... | 11 (2) | 27 (1) | ... | + | 9 (2) | + | ... | ... | ... |
| 1700–1900 m | 2 (2) | 13 (2) | ... | 5 (1) | 26 (1) | ... | ... | 11 (2) | + | ... | ... | ... |
| 1900–2100 m | 21 (21) | + | ... | 1 (1) | 18 (1) | 13 (4) | ... | 7 (2) | ... | ... | ... | ... |
| 2100–2300 m | 0 | 0 | ... | + | 9 (1) | 9 (3) | ... | 4 (2) | ... | ... | ... | ... |
| 2300–2500 m | ... | ... | ... | ... | 4 (1) | 4 (2) | ... | 1 (1) | ... | ... | ... | ... |
| 2500–2700 m | ... | ... | ... | ... | ... | ... | ... | + | ... | ... | ... | ... |
| 2700–2900 m | ... | ... | ... | ... | ... | + | ... | 0 | ... | ... | ... | ... |
| 2900–3100 m | ... | ... | ... | ... | ... | + | ... | ... | ... | ... | ... | ... |
| <i>Habitat</i> | | | | | | | | | | | | |
| Ohia | 11 (2) | 5 (+) | 24 (1) | 4 (1) | 20 (1) | ... | 8 (2) | 6 (1) | 4 (1) | 6 (1) | ... | 4 (1) |
| Koa-ohia | 16 (4) | 20 (1) | ... | 23 (1) | 32 (1) | ... | ... | 15 (2) | ... | ... | ... | ... |
| Koa-mamane | ... | + | ... | 10 (2) | 38 (2) | ... | ... | ... | ... | ... | ... | ... |
| Mamane-naio | ... | ... | ... | ... | 16 (3) | 6 (1) | ... | ... | ... | ... | ... | ... |
| Mamane | ... | ... | ... | ... | 23 (2) | 2 (1) | ... | 4 (4) | ... | ... | ... | ... |
| Other natives | ... | 6 (2) | ... | 19 (4) | 22 (2) | ... | ... | 19 (3) | ... | 7 (2) | 46 (13) | ... |
| Intro. trees | ... | 22 (2) | ... | ... | 39 (4) | ... | 30 (11) | 22 (3) | 20 (20) | 42 (5) | 61 (7) | ... |
| Treeless | 0 | + | + | 1 (+) | 5 (1) | ... | ... | 7 (2) | + | 5 (3) | 31 (19) | + |

^a Densities are given in birds/km²; + indicates stratum was in the species range but density <0.5 birds/km²; 0 indicates stratum was outside range but was sampled; ... indicates stratum was not sampled in study area.

TABLE 61
REGRESSION MODELS FOR HABITAT RESPONSE OF THE NORTHERN CARDINAL^a

| | Kau | Hamakua | Puna | Kipukas | Kona | Mauna Kea | Kohala | Maui | Molokai | Lanai | Kauai |
|-----------------------------|-------|---------|--------|---------|-------|-----------|--------|-------|---------|-------|-------|
| R ² | 0.27* | 0.34* | 0.53* | 0.60* | 0.23* | 0.17* | 0.31* | 0.23* | 0.41* | 0.23* | 0.10* |
| Moisture | -6.0* | -2.2 | ... | ... | ... | X | X | -9.3* | -12.4* | ... | X |
| Elevation | ... | -14.3* | ... | -3.8* | ... | ... | -3.1 | -5.2* | -12.0* | ... | -3.9* |
| (Elevation) ² | -9.8* | ... | -20.4* | 2.9 | ... | ... | ... | ... | ... | ... | ... |
| Tree biomass | 2.6 | -3.5* | ... | 4.8* | ... | ... | ... | ... | 9.0* | ... | ... |
| (Tree biomass) ² | ... | ... | ... | ... | ... | ... | ... | ... | ... | 4.4* | ... |
| Canopy cover | ... | 3.0 | ... | ... | 8.4* | ... | ... | 9.6* | ... | ... | ... |
| Canopy height | ... | 3.5* | ... | ... | ... | ... | 3.5* | ... | ... | ... | ... |
| Koa | ... | 4.9* | X | ... | 7.1* | X | X | ... | X | X | X |
| Ohia | ... | ... | ... | -5.8* | ... | X | -2.6 | ... | ... | ... | X |
| Naio | X | X | X | -4.0* | ... | ... | X | X | X | X | X |
| Mamane | X | ... | ... | ... | 5.0* | ... | X | ... | X | X | X |
| Intro. trees | X | ... | ... | X | ... | X | ... | 5.5* | ... | ... | X |
| Shrub cover | ... | 4.2* | 2.3 | ... | ... | -3.7* | ... | ... | ... | ... | ... |
| Ground cover | -5.0* | -3.9* | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| Native shrubs | ... | ... | ... | ... | ... | X | -2.5 | ... | ... | ... | ... |
| Intro. shrubs | X | 14.2* | 5.8* | ... | 9.8* | X | 3.6* | ... | ... | ... | ... |
| Ground ferns | X | X | ... | ... | -5.0* | X | ... | ... | ... | X | ... |
| Matted ferns | ... | -2.0 | ... | ... | -4.9* | X | ... | -2.8 | ... | ... | ... |
| Tree ferns | ... | X | ... | X | ... | X | ... | ... | ... | X | ... |
| Ieie | X | X | ... | X | ... | X | X | ... | X | X | ... |
| Passiflora | X | 15.6* | X | X | 2.8 | X | ... | ... | X | X | X |
| Native herbs | X | X | ... | ... | ... | X | ... | -2.2 | ... | X | ... |
| Intro. herbs | X | X | -3.2 | 3.1 | 4.3* | ... | ... | ... | ... | X | ... |
| Native grasses | ... | 3.7* | -4.4* | ... | -4.5* | ... | ... | -2.1 | ... | X | ... |
| Intro. grasses | 5.4* | 4.0* | ... | 4.5* | 7.8* | ... | ... | 2.3 | ... | ... | ... |
| Ohia flowers | ... | 5.5* | ... | ... | -4.8* | X | ... | ... | ... | ... | ... |
| Olapa fruit | ... | ... | ... | ... | 3.1 | X | ... | ... | ... | ... | ... |
| Mamane flowers | X | X | X | ... | X | ... | X | ... | X | X | X |
| Mamane fruit | X | X | X | X | 2.2 | X | X | X | X | X | X |
| Naio fruit | X | X | X | X | X | 5.4* | X | X | X | X | X |

^a R² is the variance accounted for by the model. Entries are *t* statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ... indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

TABLE 62
DENSITY [MEAN (SE)] OF THE SAFFRON FINCH, YELLOW-FRONTED CANARY, RED-CHEEKED CORDONBLEU,
LAVENDER WAXBILL, AND WARBLING SILVERBILL BY ELEVATION, HABITAT, AND STUDY AREA^a

| | Saffron Finch | Yellow-fronted
Canary | Red-cheeked
Cordonbleu | Lavender Waxbill | Warbling Silverbill | |
|------------------|---------------|--------------------------|---------------------------|------------------|---------------------|-----------|
| | Kona | Kona | Kona | Kona | Kona | Mauna Kea |
| <i>Elevation</i> | | | | | | |
| 100–300 m | ... | ... | ... | ... | ... | ... |
| 300–500 m | 0 | 0 | 0 | 0 | 0 | ... |
| 500–700 m | 27 (9) | 121 (41) | 2 (2) | 3 (3) | 51 (15) | ... |
| 700–900 m | 58 (11) | 131 (30) | 6 (6) | 15 (9) | 12 (7) | ... |
| 900–1100 m | 44 (11) | 44 (11) | 0 | 31 (31) | + | + |
| 1100–1300 m | 16 (5) | 23 (8) | + | + | + | + |
| 1300–1500 m | 2 (1) | 3 (2) | 0 | 0 | 0 | ... |
| 1500–1700 m | + | + | 0 | 0 | 0 | ... |
| 1700–1900 m | 0 | + | 0 | 0 | 0 | ... |
| 1900–2100 m | 0 | 0 | 0 | 0 | 0 | + |
| 2100–2300 m | 0 | 0 | 0 | 0 | 0 | + |
| 2300–2500 m | 0 | 0 | 0 | 0 | 0 | 14 (14) |
| 2500–2700 m | ... | ... | ... | ... | ... | + |
| 2700–2900 m | ... | ... | ... | ... | ... | + |
| 2900–3100 m | ... | ... | ... | ... | ... | + |
| <i>Habitat</i> | | | | | | |
| Ohia | 22 (4) | 84 (16) | 4 (4) | 6 (4) | 15 (3) | ... |
| Koa-ohia | 14 (7) | 48 (16) | 0 | 0 | 2 (1) | ... |
| Koa-mamane | 0 | 0 | 0 | 0 | 0 | ... |
| Mamane-naio | + | + | 0 | 0 | 15 (15) | 7 (7) |
| Mamane | 30 (7) | 5 (2) | 0 | 0 | 7 (4) | + |
| Other natives | 13 (6) | 12 (4) | 2 (2) | 3 (3) | 47 (12) | ... |
| Intro. trees | 89 (25) | 30 (15) | + | 103 (51) | 38 (26) | ... |
| Treeless | + | + | + | + | + | ... |

^a Densities are given in birds/km²; + indicates stratum was in the species range but density <0.5 birds/km²; 0 indicates stratum was outside range but was sampled; ... indicates stratum was not sampled in study area.

gests a minor role in determining habitat response.

Northern Cardinals occupy a diversity of habitats in North America and the Hawaiian Islands. On Kauai, Richardson and Bowles (1964) found them from arid scrub near sea level to wet montane forest in the Alakai Swamp. In eastern North America they are usually found in dense thickets and tangles near open areas, field edges, woodland borders, and swamps (Pough 1949), and in Arizona, in tall dense brush (Phillips et al. 1964). Dow (1968) found that Northern Cardinals are associated with dense shrubs and vines in Tennessee. The habitat response patterns we found in this study are in remarkable agreement, particularly the preferences for introduced shrub and passiflora understories that form dense tangled thickets.

The bill of this species is well adapted to feeding on large seeds. To a certain degree cardinals occupy the seed-eating niche left vacant by extinct finch-billed honeycreepers. Northern Cardinals regularly feed on koa, naio, and mamane seeds; at one site near Puu Lehua in Kona, 40–60% of the nearly mature sandalwood fruit had

been cut in half and the seed removed by cardinals (F. R. Warshauer, pers. observ.). In an extensive study of the food habits of this species, McAtee (1908) found that they feed primarily on almost all kinds of wild fruit and weed seed. The occurrence of birds in introduced grasslands and introduced shrub understories (often dominated by two prolific fruit-bearers, guava and Christmas-berry), probably reflects high food levels. Birds may have low densities in native grasslands because the seeds of the dominant native grass *D. australis* are too tiny to serve as a staple in the diet. On Mauna Kea, food resources may explain the association with mamane pods and naio berries in the regression model.

SAFFRON FINCH (*Sicalis flaveola*)

Saffron Finches were first recorded in the Hawaiian Islands on Oahu in 1965 and on Hawaii in 1966 (Berger 1981). These emberizine finches are native to South America.

In our study areas this species occurs only in the Puu Waawaa area of leeward Hawaii, where 2400 ± 600 (95% CI) birds occupy eight general habitat types (Tables 33, 62, Fig. 283). The range

TABLE 63
DENSITY [MEAN (SE)] OF THE HOUSE FINCH BY ELEVATION, HABITAT, AND STUDY AREA^a

| | Kau | Hamakua | Puna | Kipukas | Kona | Mauna Kea | Kohala | East Maui | West Maui | Molokai | Lanai | Kauai |
|------------------|---------|----------|----------|---------|----------|-----------|---------|-----------|-----------|----------|---------|-------|
| <i>Elevation</i> | | | | | | | | | | | | |
| 100-300 m | ... | ... | ... | ... | ... | ... | ... | ... | ... | 119 (45) | ... | ... |
| 300-500 m | ... | 19 (19) | 10 (3) | ... | 45 (18) | ... | 10 (10) | 0 | ... | 97 (29) | ... | ... |
| 500-700 m | + | 16 (8) | 6 (2) | ... | 63 (7) | ... | + | 0 | 13 (8) | 72 (13) | ... | ... |
| 700-900 m | 11 (11) | 0 | 33 (8) | ... | 75 (8) | ... | 19 (8) | 19 (11) | 5 (3) | 30 (11) | 90 (29) | ... |
| 900-1100 m | 0 | 0 | 120 (13) | ... | 53 (5) | ... | + | 67 (18) | 1 (1) | 38 (7) | + | ... |
| 1100-1300 m | 0 | 34 (11) | 150 (36) | 94 (15) | 71 (4) | ... | 1 (1) | 175 (29) | 5 (3) | 14 (4) | ... | 1 (1) |
| 1300-1500 m | 0 | 68 (11) | ... | 51 (7) | 84 (4) | ... | 3 (2) | 96 (29) | + | 5 (5) | ... | + |
| 1500-1700 m | 0 | 40 (7) | ... | 41 (6) | 59 (4) | ... | 8 (8) | 118 (37) | + | ... | ... | + |
| 1700-1900 m | + | 99 (15) | ... | 27 (7) | 35 (3) | ... | ... | 74 (18) | + | ... | ... | ... |
| 1900-2100 m | + | 102 (30) | ... | 41 (5) | 24 (3) | 246 (32) | ... | 33 (9) | ... | ... | ... | ... |
| 2100-2300 m | 0 | 157 (54) | ... | 1 (1) | 15 (2) | 140 (22) | ... | 19 (6) | ... | ... | ... | ... |
| 2300-2500 m | ... | ... | ... | ... | 7 (2) | 158 (16) | ... | + | ... | ... | ... | ... |
| 2500-2700 m | ... | ... | ... | ... | ... | 102 (17) | ... | + | ... | ... | ... | ... |
| 2700-2900 m | ... | ... | ... | ... | ... | 200 (48) | ... | 0 | ... | ... | ... | ... |
| 2900-3100 m | ... | ... | ... | ... | ... | 611 (362) | ... | ... | ... | ... | ... | ... |
| <i>Habitat</i> | | | | | | | | | | | | |
| Ohia | 3 (3) | 15 (3) | 30 (3) | 30 (3) | 60 (2) | ... | 4 (1) | 1 (1) | 4 (2) | 26 (5) | ... | 1 (1) |
| Koa-ohia | 0 | 73 (9) | ... | 83 (12) | 52 (4) | ... | ... | 103 (34) | ... | ... | ... | ... |
| Koa-mamane | ... | 118 (14) | ... | 30 (5) | 54 (4) | ... | ... | ... | ... | ... | ... | ... |
| Mamane-naio | ... | ... | ... | ... | 61 (11) | 217 (29) | ... | ... | ... | ... | ... | ... |
| Mamane | ... | ... | ... | ... | 74 (7) | 135 (21) | ... | 11 (11) | ... | ... | ... | ... |
| Other natives | ... | 208 (30) | ... | 70 (11) | 139 (10) | ... | ... | 77 (8) | ... | 55 (10) | 8 (8) | ... |
| Intro. trees | ... | 142 (38) | ... | ... | 75 (15) | ... | 15 (15) | 209 (33) | 27 (27) | 112 (19) | 12 (6) | ... |
| Treelss | 0 | + | + | 4 (4) | 12 (4) | ... | ... | 4 (1) | 9 (9) | 13 (8) | 42 (34) | + |

^a Densities are given in birds/km²; + indicates stratum was in the species range but density <0.5 birds/km²; 0 indicates stratum was outside range but was sampled; ... indicates stratum was not sampled in study area.

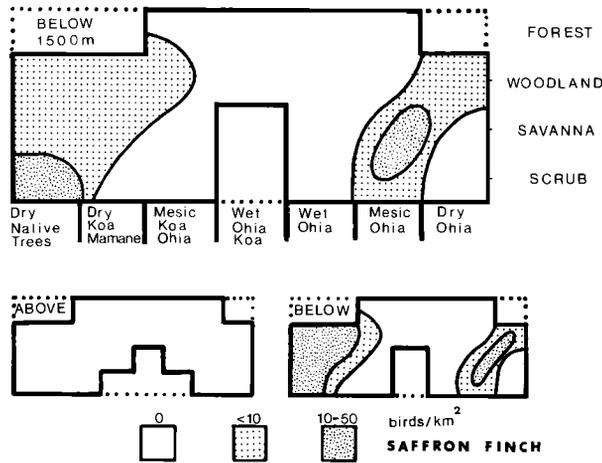


FIGURE 284. Habitat response graphs of the Saffron Finch. (Graphs give mean density below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

was fairly limited in 1978 but since then has expanded along the Kona coast (J. M. Scott, S. Mountainspring, pers. observ.).

Saffron Finches occur in dry to mesic areas at lower elevations with scattered trees and little shrub cover (Table 57, Fig. 284). Highest densities occur in habitats dominated by introduced trees, but most of the population is in ohia. The negative quadratic term for tree biomass in the regression model indicates fairly high densities over a range of very scattered to very open hab-

itats. Birds tend to be more common in mamane than in naio.

In South America, Saffron Finches inhabit gardens, shrublands, palm groves, savanna-like grasslands, open woodland, and second growth forests (Meyer de Schauensee 1976, Meyer de Schauensee and Phelps 1978). Their habitat response in Kona is similar, and they occur in coconut groves at Hapuna Bay and Kailua Bay along the Kona coast (S. Mountainspring, pers. observ.).

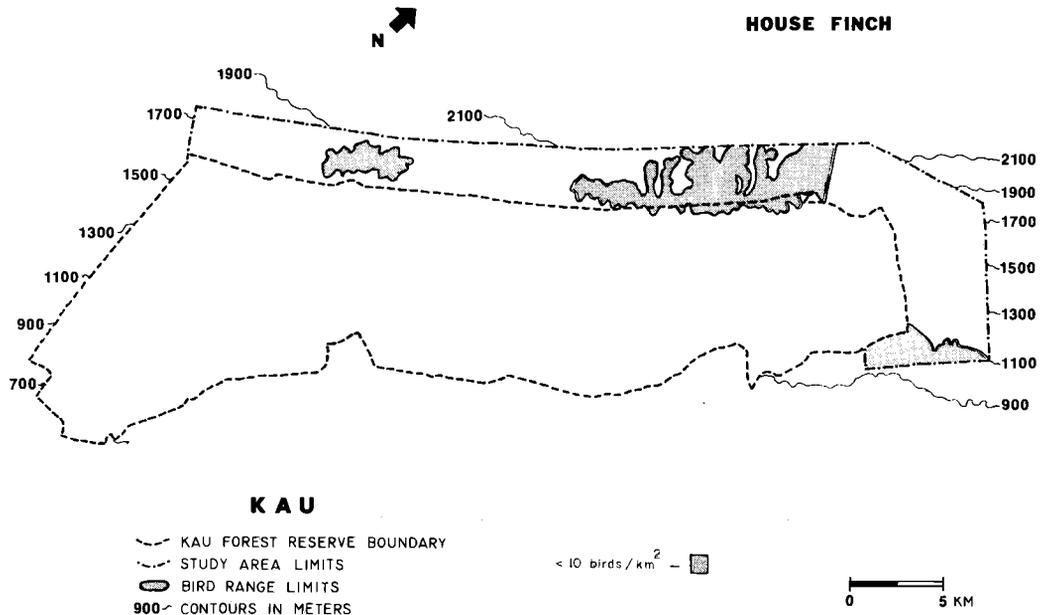


FIGURE 285. Distribution and abundance of the House Finch in the Kau study area.

HOUSE FINCH

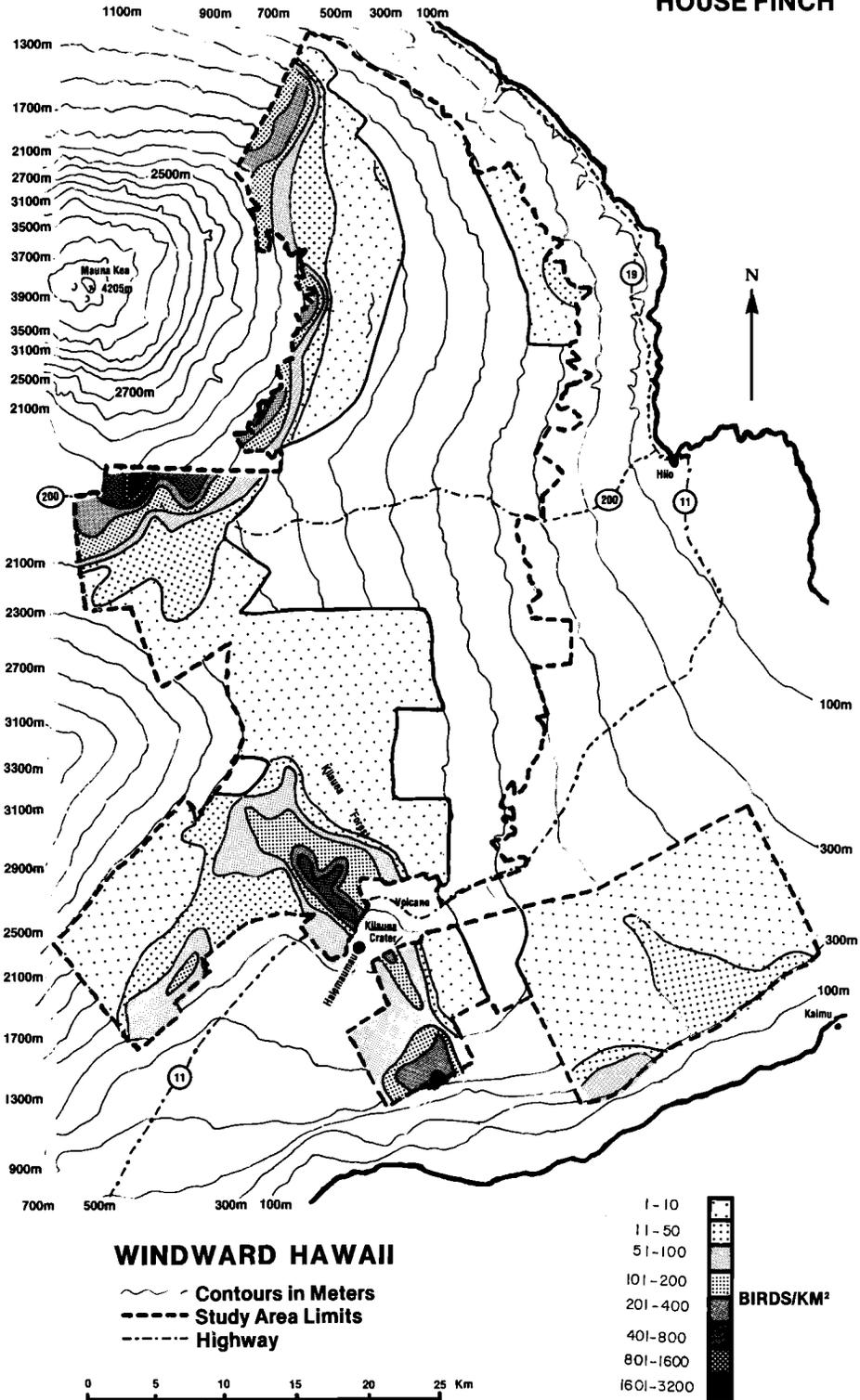


FIGURE 286. Distribution and abundance of the House Finch in the windward Hawaii study areas.

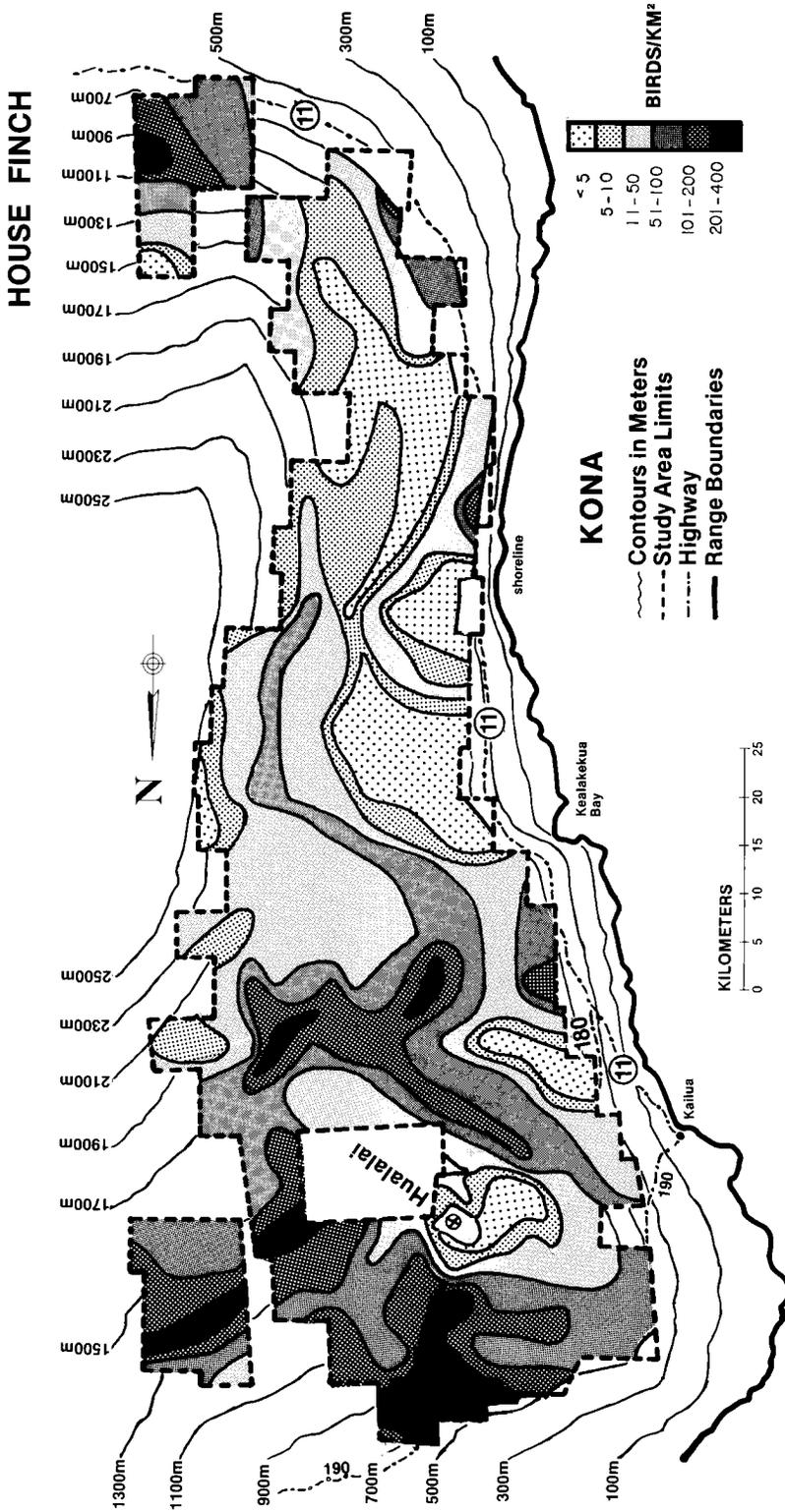


FIGURE 287. Distribution and abundance of the House Finch in the Kona study area.

HOUSE FINCH

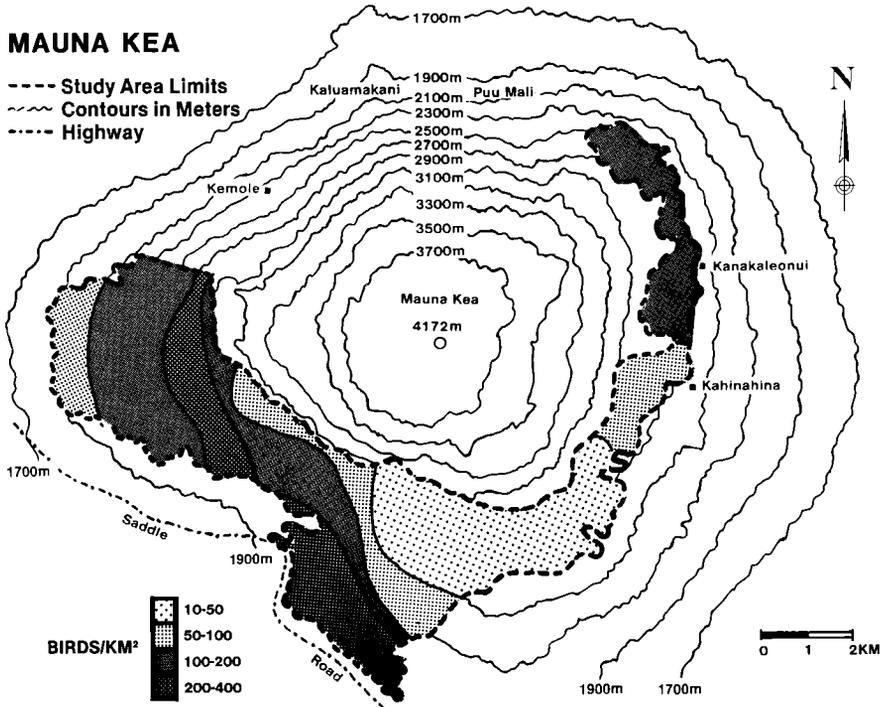


FIGURE 288. Distribution and abundance of the House Finch in the Mauna Kea study area.

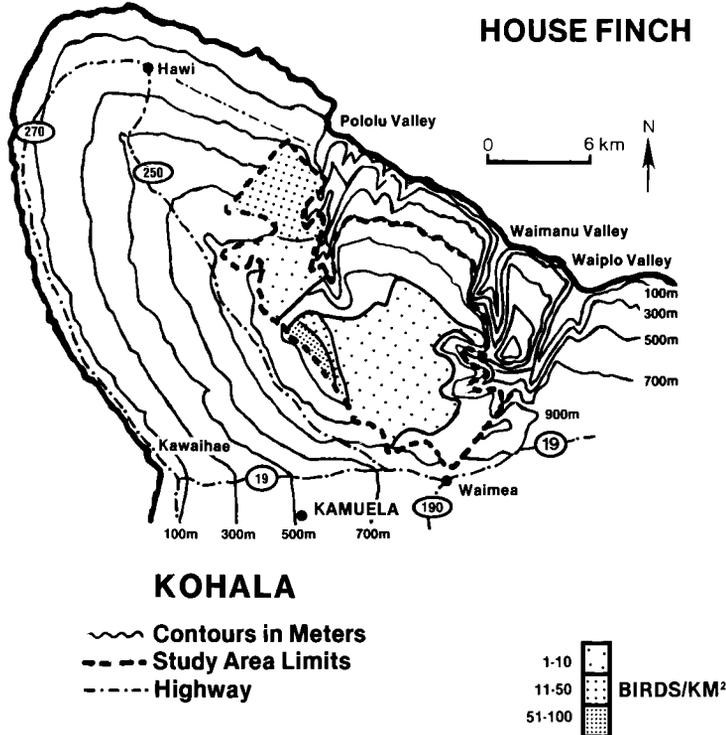


FIGURE 289. Distribution and abundance of the House Finch in the Kohala study area.

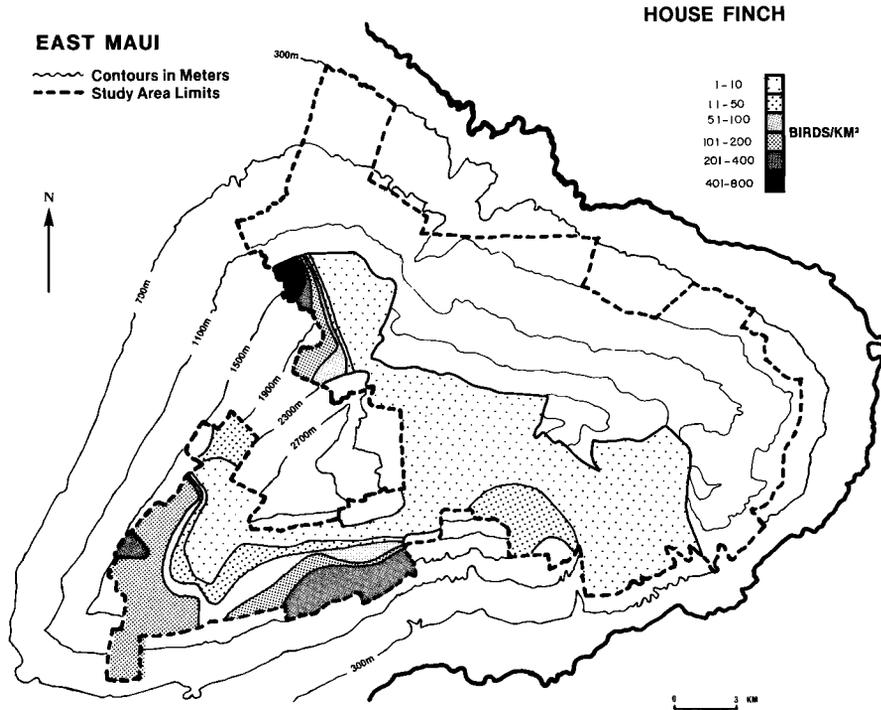


FIGURE 290. Distribution and abundance of the House Finch in the East Maui study area.

Apparently suitable habitat for this species is abundant in leeward Hawaii. It seems likely that Saffron Finches will expand in range north and south of Hualalai and up the drier slopes of Mauna Loa and Mauna Kea. Observers should be alert for possible range expansions to windward Hawaii and Maui.

HOUSE FINCH (*Carpodacus mexicanus*)

House Finches were introduced to the Hawaiian Islands before 1870, probably from San Francisco (Caum 1933, Berger 1975a). Munro (1944) found them well established on all the islands. This species is native to North America and widely distributed over the western half of the continent (Bent 1968). Known locally as papaya birds from the habit of feeding on papaya fruit, House Finches are omnivorous and feed extensively on seed, buds, and fruit. In the Hawaiian Islands, they are common in cities, towns, wet and dry agricultural areas, high-elevation ranchlands, mamane-naio woodland on Mauna Kea, and cutover wet forest (Berger 1981).

We found House Finches in all the study areas (Tables 33, 34, 63, Figs. 285–293). On Hawaii, $127,000 \pm 7000$ (95% CI) birds occur in the study areas; on Maui, 8000 ± 1000 ; on Molokai, 5300 ± 1300 ; on Lanai, 600 ± 400 ; and on Kauai, 20 ± 40 . They occur in low densities at

upper elevations in Kau and Hamakua, but are more uniformly distributed in Puna. In Hawaii Volcanoes National Park a general increase in frequency occurred over the 1940–1975 interval from 32% of plot counts to 51% (Baldwin 1953, Banko and Banko 1980). On Mauna Kea, House Finches have low densities in the Hale Pohaku area and reach greatest numbers in naio woodlands and areas with available water. In our study areas House Finches chiefly inhabit forest edges, pastures, open woodland, and scrub. They are widespread and abundant on Molokai, absent only on the heavily forested Olokui Plateau. One straggler occurred on a drier ridge top in the Alakai Swamp, where they are also generally absent. The fragmented forests of Kona appear to constitute ideal habitat.

This species occupies a broad range of habitats and is most common over a range of elevations in dry woodlands and savannas (Fig. 294). In most regression models an association appears with open woodlands having introduced grass and herb understories (Table 64). The models for Kohala and Lanai have no significant response to any variable. Response to elevation tends to be bell-shaped. The negative relation to elevation in the Kipukas reflects the high elevation of the area, and the positive relation in Hamakua reflects the absence of dry habitat at

WEST MAUI

HOUSE FINCH

~~~~~ Contours in Meters  
 - - - - Study Area Limits

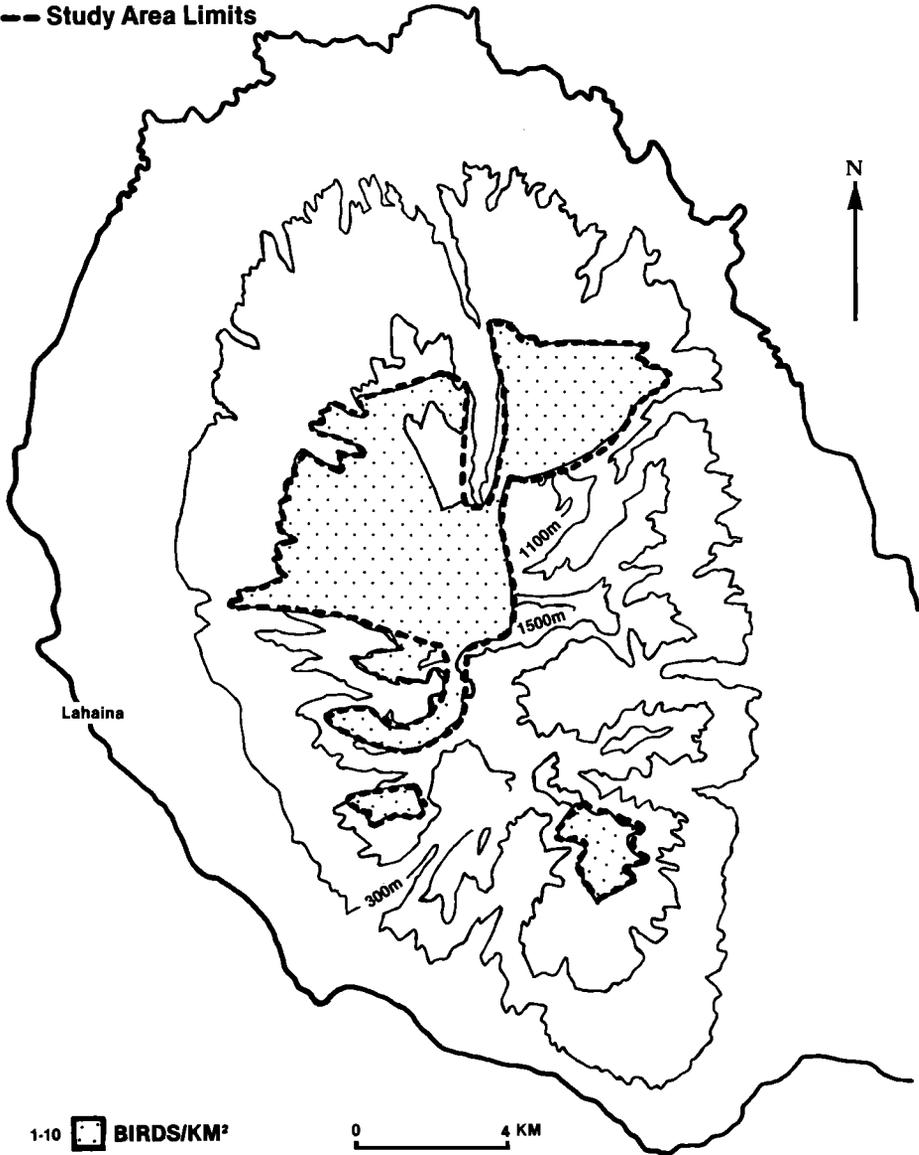


FIGURE 291. Distribution and abundance of the House Finch in the West Maui study area.

low elevations. Use of fruits and berries is reflected in the association with passiflora, and House Finches may actively disperse banana poka (Warshauer et al. 1983).

Grinnell and Miller (1944) found that the habitat requirements of House Finches include water in some form within a fairly wide cruising radius, open ground for growth of low stature seed-pro-

ducing plants, fruits and berries during part of the year, and cliffs or other structures for nesting and roosting. Water from cattle troughs on ranches and gamebird waterers on game management areas is readily available in most dry areas where House Finches occur in the Hawaiian Islands, but lack of water may limit populations on lava flows and above timberline on

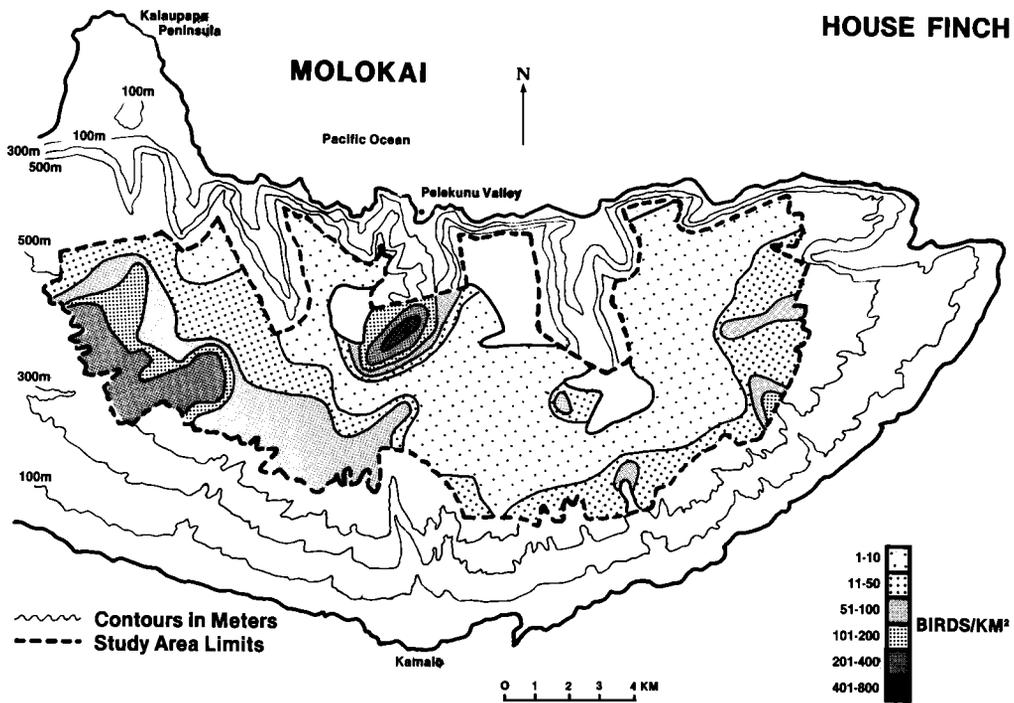


FIGURE 292. Distribution and abundance of the House Finch in the Molokai study area.

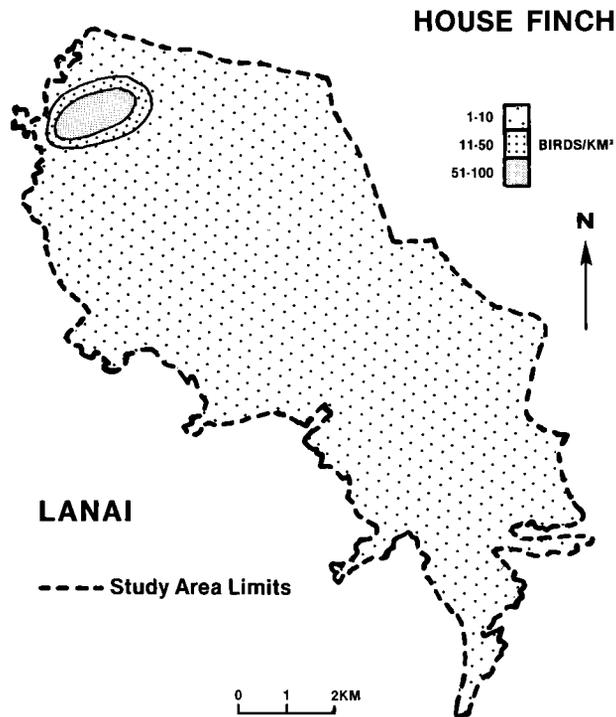


FIGURE 293. Distribution and abundance of the House Finch in the Lanai study area.

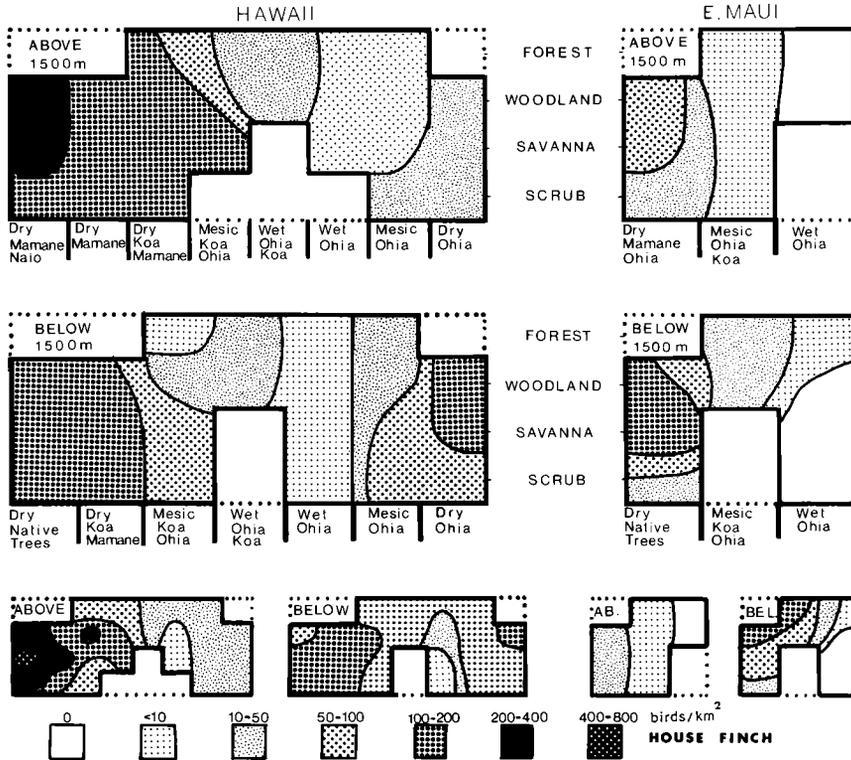


FIGURE 294. Habitat response graphs of the House Finch. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

Hawaii and in native grasslands and the crater desert on Maui. The abundance of this species on Hawaii was largely due to the spread of ranching (van Riper 1976). The highest densities on Mauna Kea are associated with water seeps at timberline. In dry woodland and open scrub, the fruit requirement is met by *Styphelia*, *Coprosma*, *Vaccinium*, lama, and naio.

**YELLOW-FRONTED CANARY**  
(*Serinus mozambicus*)

Yellow-fronted Canaries were first reported from the Hawaiian Islands on Oahu in June 1964, where they have since become frequent breeders (Berger 1977). They were first recorded from Hawaii in December 1977 on the upper slopes of Mauna Kea by van Riper (1978b), who speculated that they were released at Puu Waawaa, without documenting their occurrence there.

We found Yellow-fronted Canaries only on leeward Hawaii, concentrated in the Puu Waawaa area (Tables 33, 62, Fig. 295). They occur in five of eight general habitat types, most commonly in ohia forests below 1500 m elevation, although during winter, numbers occur in mamane and naio woodlands as high as 2800 m

(van Riper 1978b). An estimated  $4500 \pm 800$  (95% CI) birds occur in the Kona study area.

In the habitat analysis, Yellow-fronted Canaries are associated with dry woodland savannas (Fig. 296) with a light cover of ohia, mamane, or introduced trees (Table 57). The negative term for tree biomass in the regression model balances positive terms of three tree species, indicating fairly open forests.

Yellow-fronted Canaries feed mainly on seeds (Berger 1981) and in Africa occur in lightly wooded country, savanna, brush, and cultivated areas (Williams 1963). The woodlands on the north slopes of Hualalai and at higher elevations on Mauna Kea are fairly close to this description. The distribution and abundance of this species in Kona and recent observations well outside that area (Paton 1981) suggest that the range is expanding.

**HOUSE SPARROW** (*Passer domesticus*)

House Sparrows were first introduced to Oahu in 1871 and quickly became established (Caum 1933). They are presently found on all the islands, especially in urban and agricultural areas (Berger 1981). We found them in the Hamakua,

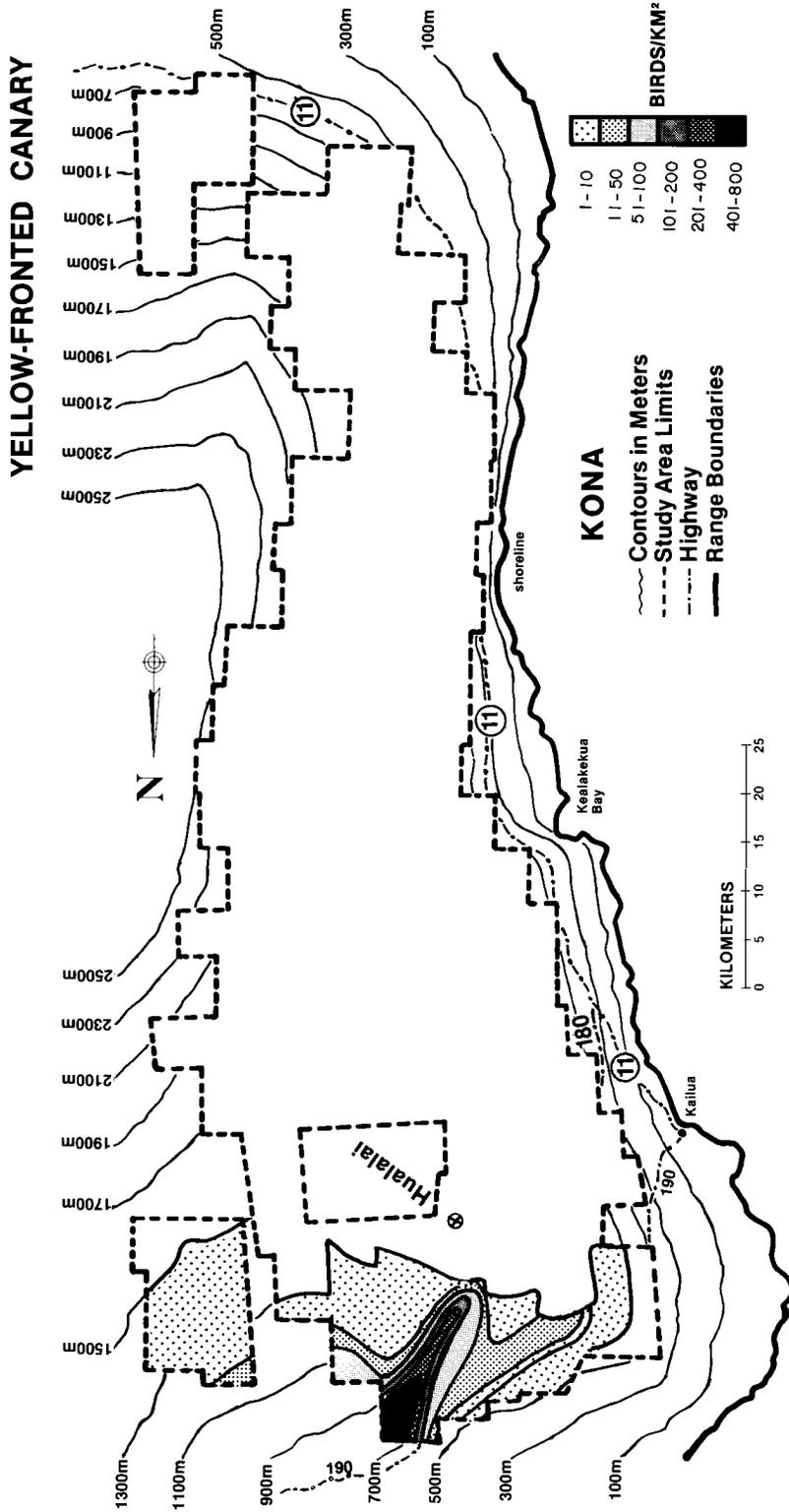


FIGURE 295. Distribution and abundance of the Yellow-fronted Canary in the Kona study area.

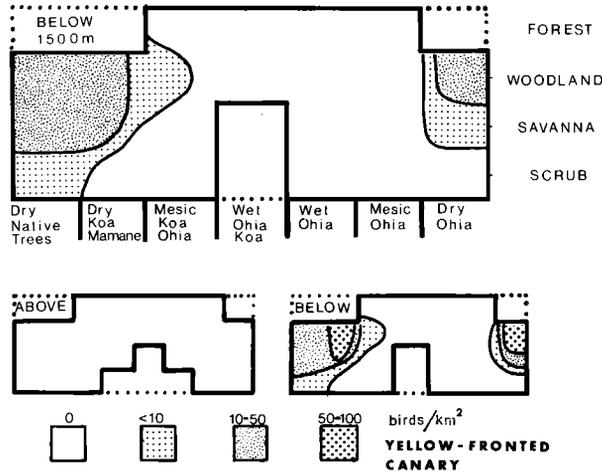


FIGURE 296. Habitat response graphs of the Yellow-fronted Canary. (Graphs give mean density below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

TABLE 64  
REGRESSION MODELS FOR HABITAT RESPONSE OF THE HOUSE FINCH<sup>a</sup>

|                             | Hamakua | Puna   | Kipukas | Kona   | Mauna Kea | Maui   | Molokai |
|-----------------------------|---------|--------|---------|--------|-----------|--------|---------|
| <i>R</i> <sup>2</sup>       | 0.52*   | 0.64*  | 0.44*   | 0.39*  | 0.13*     | 0.54*  | 0.30*   |
| Moisture                    | -8.5*   | -12.0* | -4.4*   | -18.8* | X         | -14.1* | -6.8*   |
| Elevation                   | ...     | ...    | -6.8*   | 9.4*   | ...       | 10.5*  | -3.1    |
| (Elevation) <sup>2</sup>    | 5.9*    | ...    | ...     | -12.9* | ...       | -10.4* | 2.2     |
| Tree biomass                | 6.2*    | 5.7*   | ...     | 6.8*   | ...       | 5.4*   | ...     |
| (Tree biomass) <sup>2</sup> | -3.1    | ...    | ...     | -3.3*  | ...       | -2.7   | ...     |
| Crown cover                 | -3.4*   | -5.8*  | ...     | -6.7*  | ...       | ...    | ...     |
| Canopy height               | ...     | -2.5   | 5.2*    | ...    | 6.9*      | ...    | ...     |
| Koa                         | ...     | X      | ...     | -3.6*  | X         | ...    | X       |
| Ohia                        | -12.6*  | ...    | ...     | 3.2    | X         | -2.8   | ...     |
| Naio                        | X       | X      | ...     | ...    | ...       | X      | X       |
| Mamane                      | ...     | ...    | ...     | 4.8*   | ...       | 3.5*   | X       |
| Intro. trees                | -4.5*   | ...    | X       | ...    | X         | 4.2*   | ...     |
| Shrub cover                 | ...     | ...    | ...     | -5.4*  | ...       | -6.2*  | ...     |
| Ground cover                | -7.8*   | ...    | ...     | ...    | ...       | 6.3*   | ...     |
| Native shrubs               | -8.0*   | ...    | ...     | ...    | X         | ...    | ...     |
| Intro. shrubs               | ...     | ...    | ...     | ...    | X         | ...    | ...     |
| Ground ferns                | X       | ...    | ...     | -5.1*  | X         | -3.1   | ...     |
| Matted ferns                | ...     | -4.8*  | ...     | -5.1*  | X         | ...    | ...     |
| Tree ferns                  | X       | -3.1   | X       | ...    | X         | ...    | -3.1    |
| Ieie                        | X       | ...    | X       | ...    | X         | ...    | X       |
| Passiflora                  | ...     | X      | X       | 2.3    | X         | 3.3    | X       |
| Native herbs                | X       | ...    | 3.9*    | ...    | X         | -3.1   | ...     |
| Intro. herbs                | X       | ...    | 4.4*    | 5.0*   | ...       | -3.4*  | ...     |
| Native grasses              | ...     | -4.6*  | -8.1*   | ...    | ...       | -6.7*  | ...     |
| Intro. grasses              | 8.0*    | ...    | ...     | 4.3*   | ...       | 4.6*   | ...     |
| Ohia flowers                | ...     | ...    | 4.8*    | ...    | X         | ...    | ...     |
| Olapa fruit                 | ...     | ...    | ...     | ...    | X         | ...    | ...     |
| Mamane flowers              | X       | X      | 2.9     | X      | ...       | -3.7*  | X       |
| Mamane fruit                | X       | X      | X       | X      | ...       | X      | X       |
| Naio fruit                  | X       | X      | X       | X      | ...       | X      | X       |

<sup>a</sup> *R*<sup>2</sup> is the variance accounted for by the model. Entries are *t* statistics and all are significant at *P* < 0.05; \* indicates *P* < 0.001; ... indicates variable not significant (*P* > 0.05); X indicates variable not available for inclusion in model.

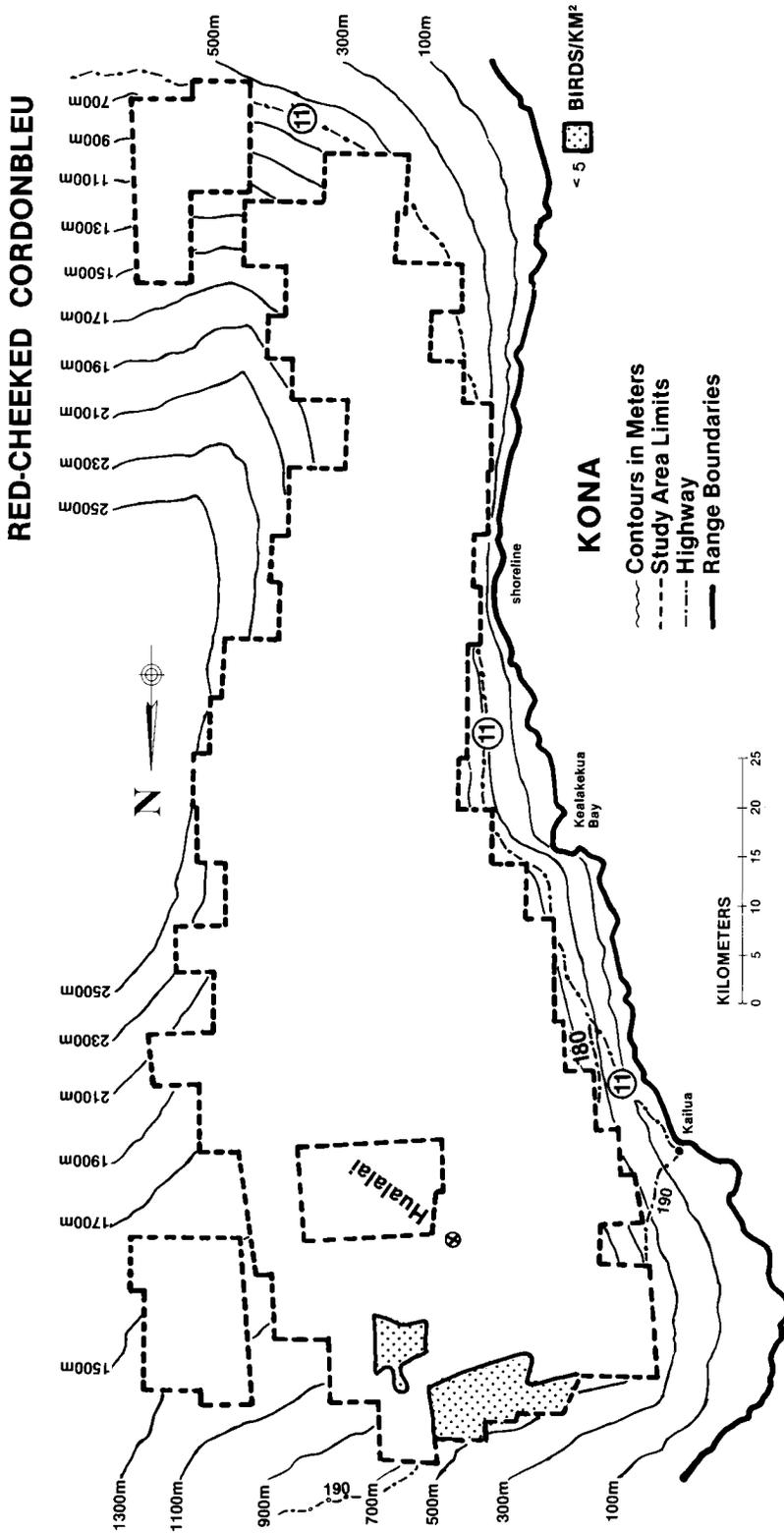


FIGURE 297. Distribution and abundance of the Red-cheeked Cordonbleu in the Kona study area.

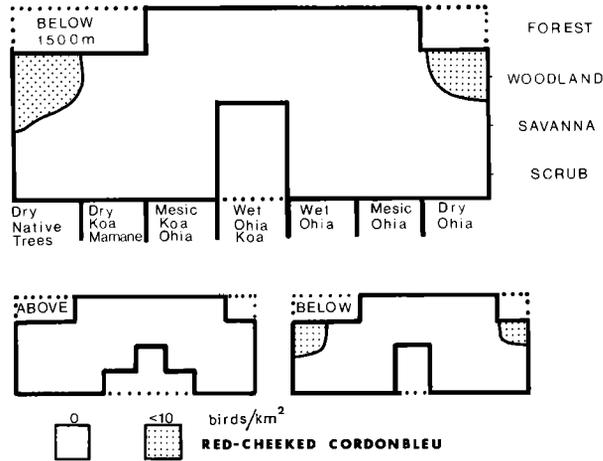


FIGURE 298. Habitat response graphs of the Red-cheeked Cordonbleu. (Graphs give mean density below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

Kona, Mauna Kea, Kipukas, and East Maui study areas (Tables 33, 34), always in association with human disturbance (inhabitations, ranch paddocks, feedlots, campgrounds). A large concentration occurs at Mauna Kea State Park in the Mauna Kea study area. Because of their close association with man, limited distribution, and small numbers, we did not calculate the distribution.

#### RED-CHEEKED CORDONBLEU (*Uraeginthus bengalus*)

The Red-cheeked Cordonbleu is native to tropical Africa, where it inhabits thorn shrub, savanna, dry woodland, and cultivated areas, and feeds on grass seeds and small invertebrates (Goodwin 1982).

The species was first introduced to the Hawaiian Islands in the 1960s on Oahu, and later released on the north slopes of Hualalai on Hawaii (Berger 1981). We found very low densities (Tables 33, 62, Fig. 297) on Puu Waawaa Ranch below 1100 m elevation. An estimated  $30 \pm 50$  (95% CI) birds occur in the study area, mostly in dry lama-ohia woodlands with introduced grass understories (Fig. 298). It remains to be seen whether this species will become established on Hawaii. Observers should be alert for range expansion.

#### LAVENDER WAXBILL (*Estrilda caerulea*)

Lavender Waxbills are native to tropical western Africa where they inhabit semi-arid savannas, woodlands, and brushlands, as well as gardens and cultivated areas. They feed on seeds, small fruits, and insects (Goodwin 1982). Lav-

ender Waxbills were first reported from the Hawaiian Islands on Oahu in 1965 (Berger 1981). During the HFBS, birds were discovered on Hawaii, the only other island of known occurrence (Ashman and Pyle 1979).

We found Lavender Waxbills only on the northern slopes of Hualalai on leeward Hawaii (Fig. 299) where they are uncommon below 1100 m elevation in dry lama-ohia woodlands and savannas (Tables 33, 62, Fig. 300). An estimated  $230 \pm 120$  (95% CI) birds occur in the study area.

The range of the Lavender Waxbill is centered on Puu Waawaa Ranch, an area where large numbers of introduced species have been released (Lewin 1971; van Riper 1973a, 1978b). This species may have been introduced there along with other estrildid finches. Unlike Saffron Finches and Yellow-fronted Canaries, Lavender Waxbills have not expanded their range to other parts of the island.

#### WARBLING SILVERBILL (*Lonchura malabrica*)

Warbling Silverbills are drab estrildid finches from Africa that were first collected from the Hawaiian Islands in 1972 on Hawaii (Berger 1975a) and have since spread to dry low habitat on Maui (Walters 1979), Lanai (Hirai 1980), Kahoolawe (Conant 1983), and Oahu (Conant 1984). Below our study areas on Hawaii and Maui, they are common in coastal mesquite woodlands with introduced grass and shrub understories.

An estimated  $4000 \pm 1700$  (95% CI) birds occupy our study areas (Tables 33, 62, Fig. 301). Flocks of over 200 birds occur on Puu Waawaa Ranch north of Hualalai in Kona and smaller

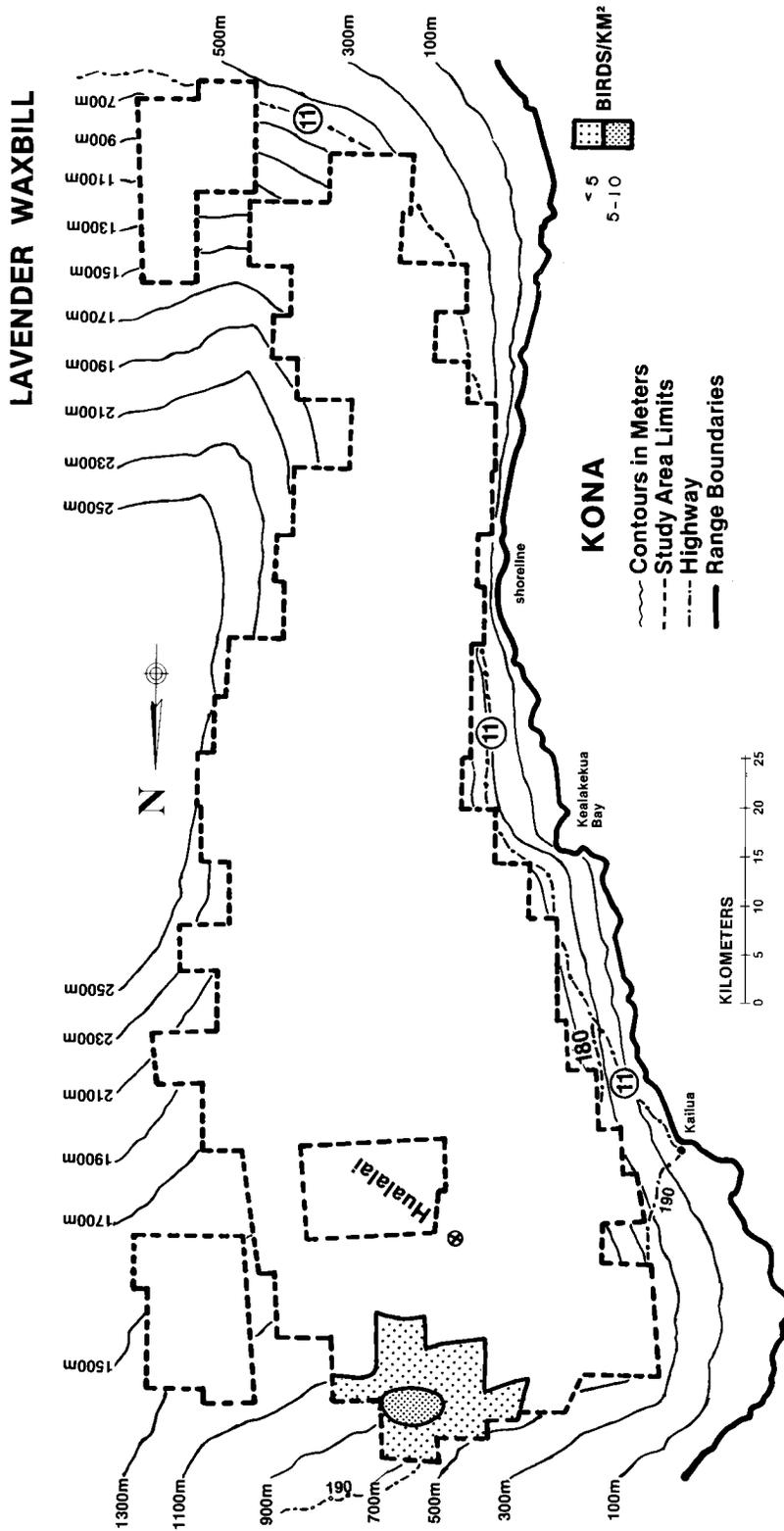


FIGURE 299. Distribution and abundance of the Lavender Waxbill in the Kona study area.

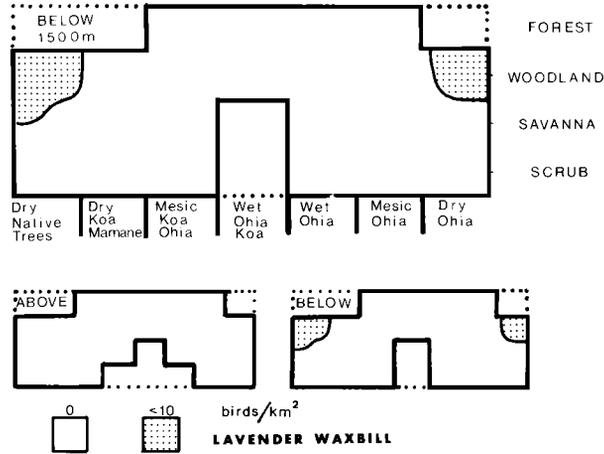


FIGURE 300. Habitat response graphs of the Lavender Waxbill. (Graphs give mean density below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

TABLE 65  
REGRESSION MODELS FOR HABITAT RESPONSE OF THE WARBLING SILVERBILL AND NUTMEG MANNIKIN<sup>a</sup>

|                             | Warbling Silverbill |         | Nutmeg Mannikin |         |       |        |       |         |
|-----------------------------|---------------------|---------|-----------------|---------|-------|--------|-------|---------|
|                             | Kona                | Hamakua | Puna            | Kipukas | Kona  | Kohala | Mau   | Molokai |
| <i>R</i> <sup>2</sup>       | 0.10*               | 0.06*   | 0.09*           | 0.11*   | 0.08* | 0.34*  | 0.23* | 0.23*   |
| Moisture                    | -10.4*              | ...     | ...             | ...     | ...   | X      | -3.9* | -5.5*   |
| Elevation                   | ...                 | -4.3*   | -2.9            | -5.8*   | -9.1* | -5.6*  | -7.7* | -2.6    |
| (Elevation) <sup>2</sup>    | -8.1*               | 3.5*    | ...             | ...     | ...   | 5.0*   | 5.8*  | 2.0     |
| Tree biomass                | 2.5                 | ...     | ...             | ...     | 2.2   | -3.5*  | 4.6*  | 3.6*    |
| (Tree biomass) <sup>2</sup> | ...                 | ...     | -2.8            | 5.4*    | -3.9* | 3.2    | -4.0* | -6.1*   |
| Crown cover                 | ...                 | ...     | ...             | ...     | ...   | ...    | ...   | 2.4     |
| Canopy height               | 4.0*                | ...     | ...             | ...     | ...   | ...    | ...   | ...     |
| Koa                         | -3.4*               | -2.3    | X               | ...     | ...   | X      | ...   | X       |
| Ohia                        | -4.8*               | ...     | 2.4             | ...     | ...   | ...    | ...   | ...     |
| Naio                        | -3.6*               | X       | X               | ...     | ...   | X      | X     | X       |
| Mamane                      | -5.0*               | ...     | 2.8             | ...     | ...   | X      | -4.1* | X       |
| Intro. trees                | -2.3                | 6.4*    | ...             | X       | 6.9*  | ...    | ...   | ...     |
| Shrub cover                 | ...                 | ...     | ...             | ...     | -3.5* | ...    | -2.7  | ...     |
| Ground cover                | 5.7*                | ...     | ...             | ...     | 4.1*  | ...    | 2.8   | ...     |
| Native shrubs               | ...                 | ...     | ...             | ...     | ...   | -2.5   | ...   | ...     |
| Intro. shrubs               | -3.6*               | ...     | ...             | ...     | ...   | -2.3   | ...   | ...     |
| Ground ferns                | ...                 | X       | ...             | ...     | ...   | ...    | ...   | ...     |
| Matted ferns                | ...                 | ...     | ...             | ...     | ...   | ...    | ...   | ...     |
| Tree ferns                  | ...                 | X       | -2.7            | X       | ...   | ...    | -3.0  | -2.4    |
| Ieie                        | ...                 | X       | ...             | X       | ...   | X      | ...   | X       |
| Passiflora                  | ...                 | ...     | X               | X       | ...   | ...    | 4.4*  | X       |
| Native herbs                | ...                 | X       | ...             | ...     | ...   | ...    | ...   | ...     |
| Intro. herbs                | 3.9*                | X       | ...             | ...     | -2.3  | ...    | ...   | ...     |
| Native grasses              | 2.8                 | ...     | ...             | ...     | ...   | ...    | ...   | ...     |
| Intro. grasses              | ...                 | ...     | ...             | ...     | ...   | ...    | 3.9*  | ...     |
| Ohia flowers                | ...                 | ...     | ...             | ...     | ...   | ...    | ...   | ...     |
| Olapa fruit                 | ...                 | ...     | ...             | ...     | ...   | ...    | -2.4  | ...     |
| Mamane flowers              | X                   | X       | X               | ...     | X     | X      | ...   | X       |
| Mamane fruit                | X                   | X       | X               | X       | X     | X      | X     | X       |
| Naio fruit                  | X                   | X       | X               | X       | X     | X      | X     | X       |

<sup>a</sup> *R*<sup>2</sup> is the variance accounted for by the model. Entries are *t* statistics and all are significant at *P* < 0.05; \* indicates *P* < 0.001; ... indicates variable not significant (*P* > 0.05); X indicates variable not available for inclusion in model.

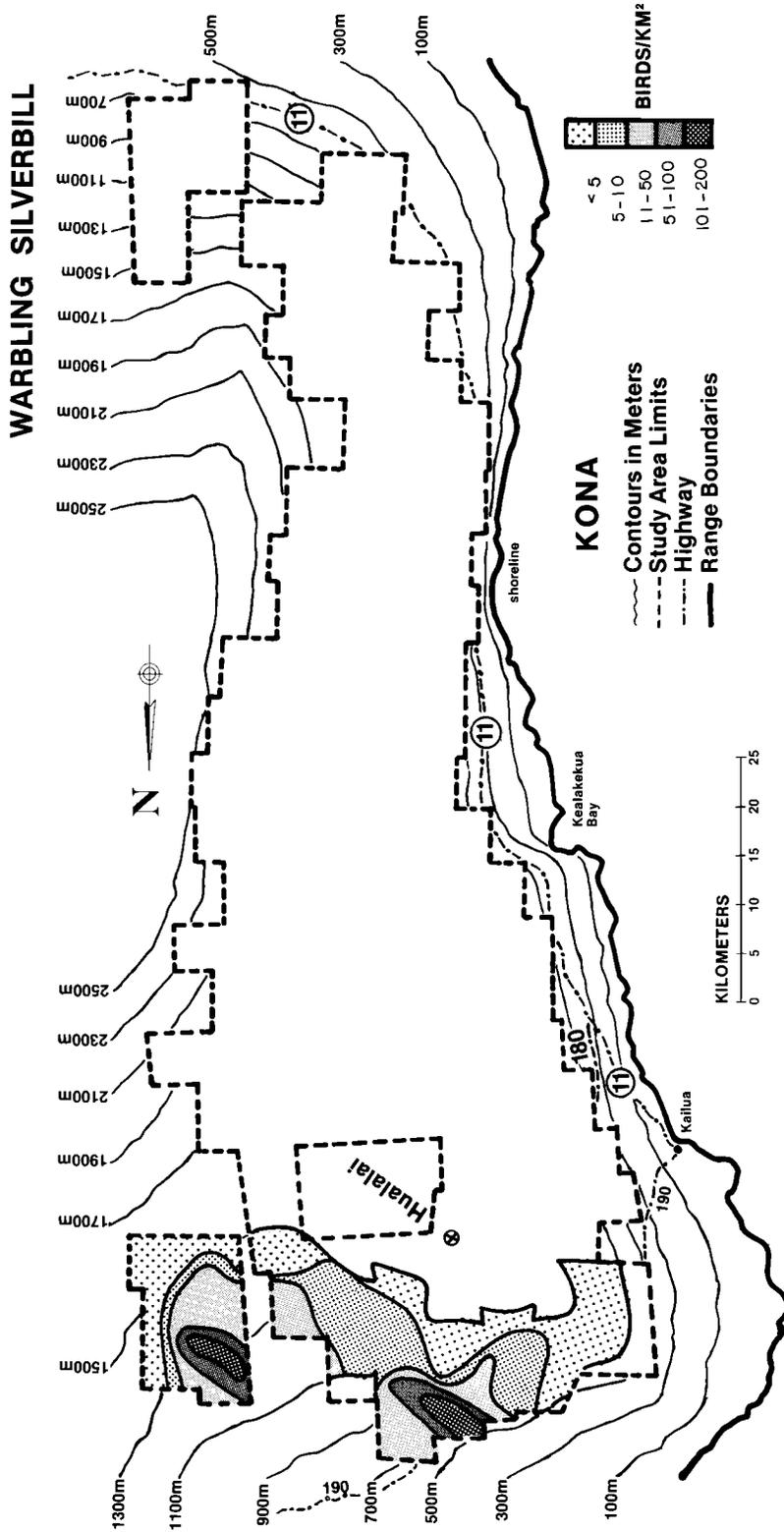


FIGURE 301. Distribution and abundance of the Warbling Silverbill in the Kona study area.

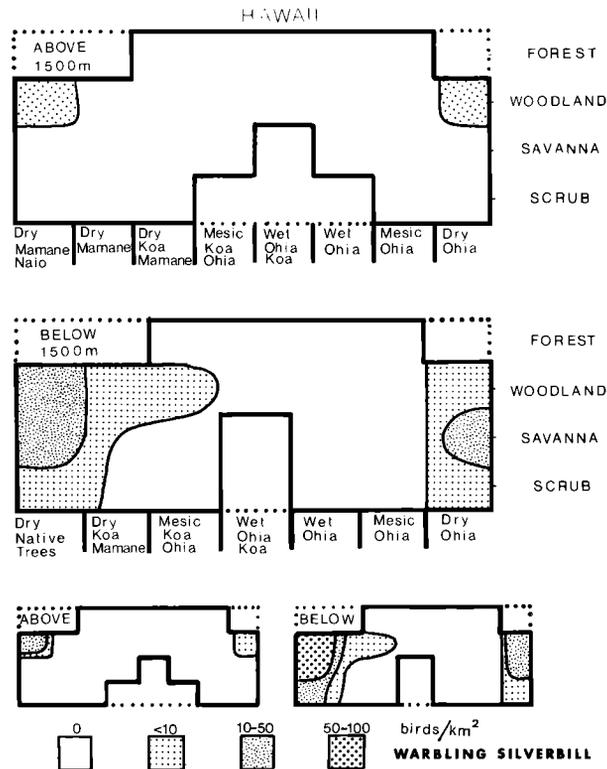


FIGURE 302. Habitat response graphs of the Warbling Silverbill. (Graphs give mean density above and below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

flocks occur on Mauna Kea and in the Mauna Kea-Mauna Loa saddle. They range to 1300 m elevation in their restricted range on Hualalai and occur to 3100 m on Mauna Kea.

Highest densities occur in our study areas in a very dry native tree association at low elevations (Fig. 302). The negative quadratic elevation term in the regression model (Table 65) reflects increasingly higher densities at lower elevations. The negative terms for all five tree species reflect association with dry open lama-ohia woodlands at Puu Waawaa.

In Africa, Warbling Silverbills occupy dry savannas, thorn-scrub, grasslands, and desert areas near water; they feed almost exclusively on seeds (Goodwin 1982). The niche and habitat of Warbling Silverbills in Hawaii appear to be quite similar to those in Africa.

**NUTMEG MANNIKIN (*Lonchura punctulata*)**

In the Hawaiian Islands, Nutmeg Mannikins are widely known as Ricebirds or Spotted Munias. They increased rapidly following introduction about 1865 (Caum 1933) and became pests in rice fields (Munro 1944). Berger (1981) found them well established and widely distributed on

all the islands, but no longer agricultural pests. Nutmeg Mannikins are highly nomadic and occasionally appear on most sites.

We found this species in all but two study areas, usually in very open or disturbed sites or on the edge of forests (Tables 33, 34, 66, Figs. 303-309). On Hawaii an estimated  $25,000 \pm 5000$  (95% CI) birds occur in the study areas, with most in Hamakua (42% of the total) and Kona (26%). In Hawaii Volcanoes National Park, numbers appeared to increase over the 1940-1975 interval (Conant 1975, Banko and Banko 1980). We estimated  $8000 \pm 3000$  birds on East Maui,  $3000 \pm 2000$  on West Maui, and  $11,000 \pm 4000$  on Molokai. Highest densities were recorded on Molokai. We failed to find them on Lanai in early May 1979, but Hirai (1978) noted that they were abundant in the mountain forests from August to November. We also failed to find them on Kauai in May 1981, but Sincock et al. (1984) estimated populations of  $2100 \pm 1100$  birds for our study area and  $109,000 \pm 38,000$  birds in native forests on Kauai.

Nutmeg Mannikins occupy a wider variety of habitat types below 1500 m than above on Hawaii and Maui, although they are very infrequent

TABLE 66  
DENSITY [MEAN (SE)] OF THE NUTMEG MANNIKIN BY ELEVATION, HABITAT, AND STUDY AREA\*

| Elevation      | Hamakua   | Puna    | Kipukas | Kona    | Mauna Kea | Kohala  | East Maui | West Maui | Molokai    | Kauai |
|----------------|-----------|---------|---------|---------|-----------|---------|-----------|-----------|------------|-------|
| 100-300 m      | ...       | 21 (5)  | ...     | ...     | ...       | ...     | ...       | ...       | 138 (77)   | ...   |
| 300-500 m      | 308 (120) | 15 (9)  | ...     | 0       | ...       | 71 (71) | 233 (177) | ...       | 367 (155)  | ...   |
| 500-700 m      | 58 (19)   | 64 (37) | ...     | 43 (12) | ...       | 89 (47) | 104 (30)  | 302 (107) | 122 (39)   | ...   |
| 700-900 m      | 30 (10)   | 14 (8)  | ...     | 41 (14) | ...       | 61 (28) | 37 (10)   | 178 (76)  | 128 (42)   | ...   |
| 900-1100 m     | 22 (8)    | 4 (4)   | ...     | 22 (6)  | ...       | 11 (11) | 56 (27)   | 18 (18)   | 61 (17)    | ...   |
| 1100-1300 m    | 17 (8)    | ...     | 40 (17) | 17 (4)  | ...       | 12 (8)  | 63 (24)   | +         | 47 (24)    | 7 (1) |
| 1300-1500 m    | 9 (5)     | ...     | 62 (32) | 1 (1)   | ...       | +       | 104 (70)  | +         | 0          | +     |
| 1500-1700 m    | 3 (3)     | ...     | 0       | 3 (3)   | ...       | 0       | 38 (20)   | +         | ...        | ...   |
| 1700-1900 m    | +         | ...     | 0       | +       | ...       | ...     | 55 (23)   | +         | ...        | ...   |
| 1900-2100 m    | +         | ...     | 11 (8)  | +       | ...       | ...     | +         | ...       | ...        | ...   |
| 2100-2300 m    | 0         | ...     | 0       | +       | ...       | ...     | 6 (6)     | ...       | ...        | ...   |
| 2300-2500 m    | ...       | ...     | ...     | +       | ...       | ...     | +         | ...       | ...        | ...   |
| 2500-2700 m    | ...       | ...     | ...     | +       | ...       | ...     | +         | ...       | ...        | ...   |
| 2700-2900 m    | ...       | ...     | ...     | ...     | 82 (56)   | ...     | 0         | ...       | ...        | ...   |
| 2900-3100 m    | ...       | ...     | ...     | ...     | 27 (27)   | ...     | ...       | ...       | ...        | ...   |
|                |           |         |         |         | +         | ...     | ...       | ...       | ...        | ...   |
| <i>Habitat</i> |           |         |         |         |           |         |           |           |            |       |
| Ohia           | 13 (3)    | 18 (4)  | +       | 27 (7)  | ...       | 30 (9)  | 29 (9)    | 116 (35)  | 49 (10)    | 4 (4) |
| Koa-ohia       | 28 (7)    | ...     | 52 (18) | 10 (2)  | ...       | ...     | 99 (30)   | ...       | ...        | ...   |
| Koa-mamane     | 0         | ...     | +       | 0       | ...       | ...     | ...       | ...       | ...        | ...   |
| Mamane-naio    | ...       | ...     | ...     | 0       | 48 (31)   | ...     | ...       | ...       | ...        | ...   |
| Mamane         | ...       | ...     | ...     | 26 (8)  | 6 (6)     | ...     | 0         | ...       | ...        | ...   |
| Other natives  | 51 (51)   | ...     | 15 (10) | 19 (7)  | ...       | ...     | 136 (38)  | ...       | 169 (43)   | ...   |
| Intro. trees   | 89 (17)   | ...     | ...     | 42 (15) | ...       | +       | 52 (19)   | 0         | 251 (67)   | ...   |
| Treeless       | 0         | +       | +       | +       | ...       | ...     | 3 (3)     | +         | 1628 (998) | +     |

\* Densities are given in birds/km<sup>2</sup>; + indicates stratum was in the species range but density <0.5 birds/km<sup>2</sup>; 0 indicates stratum was outside range but was sampled; ... indicates stratum was not sampled in study area.

**NUTMEG MANNIKIN**

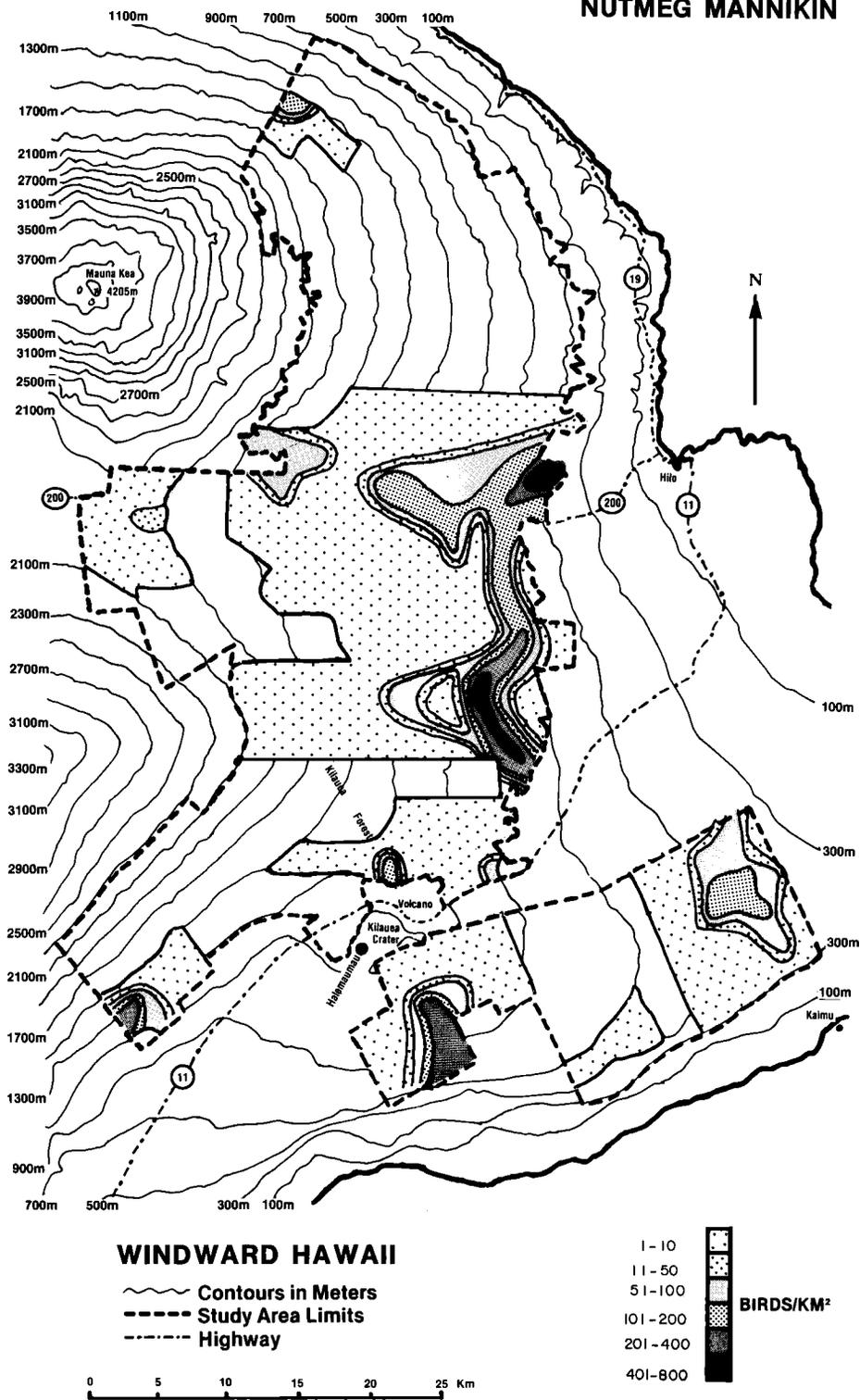


FIGURE 303. Distribution and abundance of the Nutmeg Mannikin in the windward Hawaii study areas.



**NUTMEG MANNIKIN**

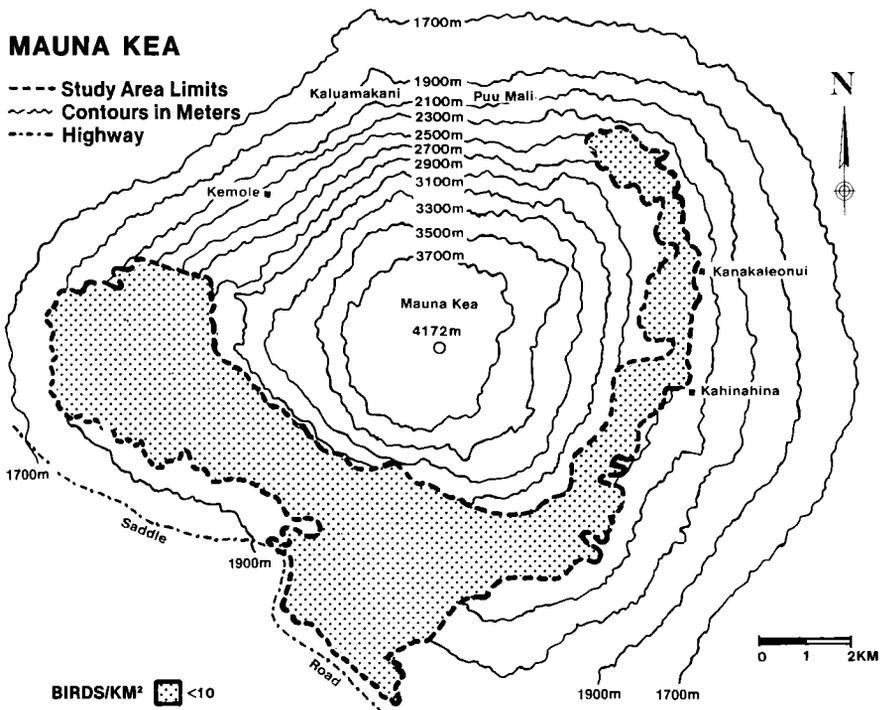


FIGURE 305. Distribution and abundance of the Nutmeg Mannikin in the Mauna Kea study area.

**NUTMEG MANNIKIN**

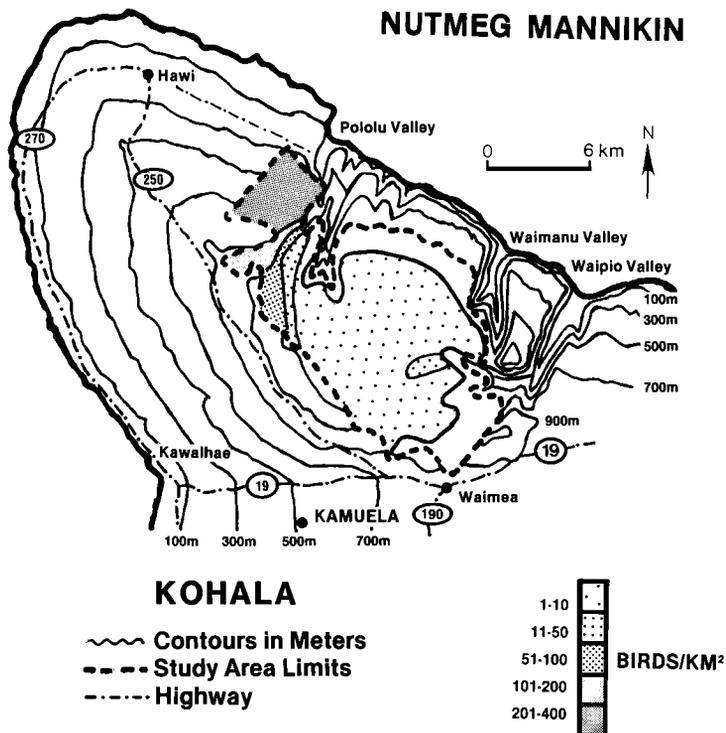


FIGURE 306. Distribution and abundance of the Nutmeg Mannikin in the Kohala study area.

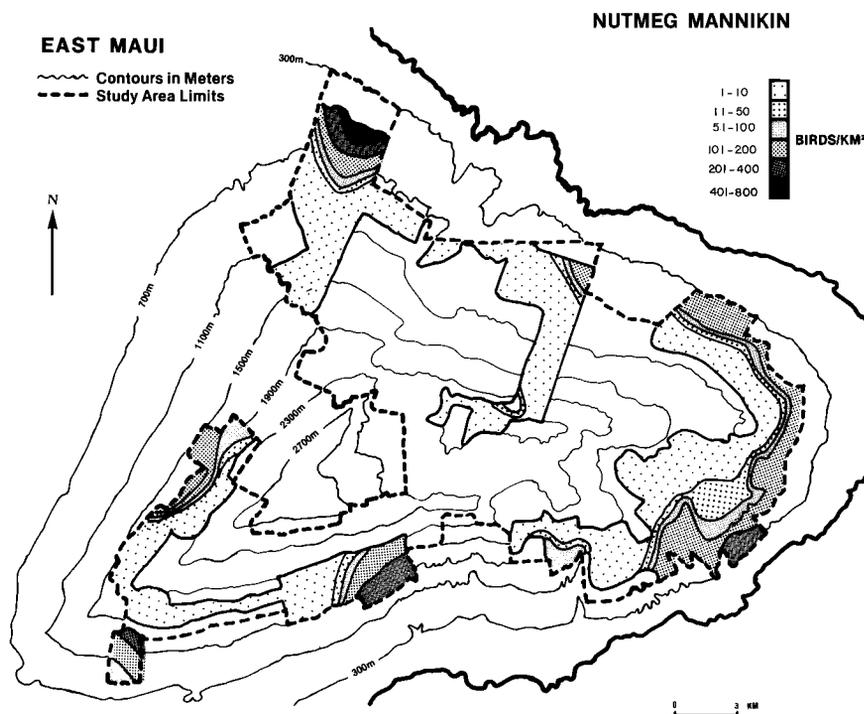


FIGURE 307. Distribution and abundance of the Nutmeg Mannikin in the East Maui study area.

in rainforest interiors (Fig. 310). The regression models (Table 65) show an association with introduced trees in low elevation areas. Other than these trends, the habitat response pattern appears to comprise a scattered, erratic series of relations to other variables. This is also seen in the high variance of the habitat response graphs, and reflects the flocking habit and highly erratic variation in seasonal and annual distribution across a broad span of habitats (see Berger 1981). Richardson and Bowles (1964) found that Nutmeg Mannikins occupy a diverse range of habitats on Kauai, from dry lowland to fairly wet montane sites.

In southeast Asia, Nutmeg Mannikins primarily occur at lower elevations in a range of open and semi-open habitats (Goodwin 1982). They feed almost entirely on seeds, and the positive response to introduced grasses in the Maui regression model may reflect attraction to grass seeds.

## COMMUNITY ECOLOGY

### SPECIES-AREA RELATIONSHIPS

Island area is a critical component of biogeographic theory (MacArthur and Wilson 1967; Diamond 1973, 1975; Slud 1976; Diamond and Mayr 1976). Distinctive habitats often have island-like relationships between their area and

species composition, as noted for birds in deciduous forests surrounded by agricultural land (Bond 1957), in primary versus secondary tropical forest (Terborgh and Weske 1969), and in páramo habitats in the Andes (Vuilleumier 1970, Vuilleumier and Simberloff 1980). On the main Hawaiian Islands, rainforests tend to form distinctive habitat islands surrounded by agricultural land, introduced vegetation, and unforested areas. Although in a few cases boundaries are inexact (e.g., in windward and leeward Hawaii), 20 major rainforest islands may be distinguished (Fig. 311). The data from the HFBS and work on Oahu (Shallenberger and Vaughn 1978) and Kauai (Sincock et al. 1984) allowed us to examine the relationships between the area of these habitat islands, their maximum elevation, and the number of native land bird species present.

The classic species relationship,  $S = cA^z$ , where  $S$  = number of extant native species and  $A$  = area in  $\text{km}^2$  (MacArthur and Wilson 1967), fits our data. The best fit ( $R^2 = 0.41$ ,  $P < 0.01$ ) is obtained when  $z = 0.20$ , a value toward the low end but within the range of typical examples for birds (MacArthur and Wilson 1967). A significantly better fit ( $R^2 = 0.71$ ,  $P < 10^{-4}$ ) occurs when elevation ( $E$ , in km) is included in the regression equation

$$S = -1.84 + 0.37E + 0.76 \log_e A;$$