of the time and cost constraints inherent in analyzing large data sets. For example, although nonparametric techniques are preferable to parametric ones (Bradley 1968), for our data set parametric methods were far more cost-efficient. The analysis chosen met our needs and was applied uniformly to all species to facilitate objective comparison. If one or two species were of special interest, a model (and the study itself) could be tailored to reflect current knowledge of habitat requirements.

The vocalizations of some species, such as Red Junglefowl, Ring-necked Pheasant, Common Peafowl, California Quail, Spotted Dove, Hawaiian Crow, Kauai Oo, and Ou, carry long distances. Such birds were sometimes in a different habitat than the observer and could mislead efforts to determine habitat requirements (e.g., gamebirds calling at water), but the usual effect of including these birds in the analysis is to inflate the estimate of variance in habitat response. A solution to the problem would be to instruct the observers to note birds they believed were calling from a different habitat type, and then exclude these records from the analysis of habitat response.

### Interspecific Competition

The analysis of interspecific competition presented here is a condensed summary of a treatment presented elsewhere (Mountainspring and Scott 1985). We tested for prima facie evidence that competition modified the distribution of the species by statistically removing the effect of the habitat variables on bird distributions and then evaluating the association (negative, neutral, or positive) between each species pair by using partial correlation analysis (see development by Schoener 1974, Crowell and Pimm 1976, and Hallett and Pimm 1979).

### Species-Area Relationships

To approach in a general way the relationship between the number of extant native species and habitat area, we assembled a sample set of 20 major "habitat islands" of montane rainforest. These habitat islands were relatively isolated from one another by degraded and non-rainforest habitat. Data from the HFBS, Sincock's 1968–1973 Kauai survey, Shallenberger's 1977–1978 Oahu surveys, and the open literature were used to tabulate for each area: (1) the probable number of extant native passerine species, (2) the maximum elevation of rainforest, and (3) the approximate area of the habitat island. Multiple regression was used to quantify the statistical relationships among these variables.

### Comparisons with Earlier Surveys

The Hawaiian avifauna has been surveyed with varying intensities a number of times in the past, most notably by Wilson and Evans (1890–1899), Palmer (in Rothschild 1893–1900), Henshaw (1902), Munro (1944), Baldwin (1953), Richardson and Bowles (1964), Berger (1972, 1981), and Conant (1975, 1980, 1981), by Caum (1933) and Schwartz and Schwartz (1949) for introduced species, and by Olson and James (1982b) for fossils. In the species accounts we attempt to compare the present distribution, abundance, and habitat response of native birds with their status as indicated in earlier accounts in order to document historical trends and gain further insight on limiting factors.

A particularly useful study for these purposes was J. L. Sincock's 1968–1973 survey of Kauai. Because the results of this survey were partly unpublished, not widely available (Sincock et al. 1984), and Sincock has kindly granted us access to them, we briefly outline his research to give an idea of the techniques and magnitude of that survey. J. L. Sincock (pers. comm.) recorded all birds seen within a constant distance along a transect of known length that he slowly walked during a 30 min period. He censused 866 transects at 50 sites that were randomly located within seven strata that represented all native forests above 300 m elevation on Kauai. Densities were estimated for each stratum from the transect data and extrapolated to population sizes based on the stratum area. Ranges were calculated from transect data and incidental observations. To facilitate comparison between his study and ours, we sampled an area in 1981 for which Sincock estimated bird population sizes during 1968–1973.

### Survey Limitations

In the studies of Perkins (1903), Munro (1944), Baldwin (1953), MacMillen and Carpenter (1980), and van Riper (1984), attention was drawn to mass movements of nectarivorous species (Iiwi, Apapane) and more localized movements of Common Amakihi. Conant (1981) documented a similar distributional shift of Crested Honeycreeper to lower elevations in winter in Kipahulu Valley. Because the nectarivores in particular fly long distances to patchily distributed, locally abundant nectar sources, their distributions and areas of high density shift markedly throughout the year. Population sizes of Hawaiian birds have wide annual variations (Ely and Clapp 1973, Clapp et al. 1977, Scott et al. 1984), even though non-nectarivorous species tend to have the same distribution and habitat response patterns from year to year (Scott et al. 1984). These phenomena should serve to note that our survey represented a "snapshot" of bird distribution at a moment in time: densities, population sizes, habitat response, and, to a lesser extent, distributions can be expected to change in the seasons and years that follow this survey.

## NATIVE SPECIES ACCOUNTS

Our discussion of the distribution, abundance, and habitat response of Hawaiian forest birds focuses on individual species in order to facilitate comparisons between the populations of different forests and islands, and to infer historical and contemporary limiting factors for native species. Native and introduced birds are treated in separate sections; phylogenetic order within each section follows the A.O.U. *Check-list* (1983) and its 35th supplement (1985). Established Hawaiian names not used by the A.O.U. are given in parentheses in the headings for the species accounts, while other frequently used alternate names are given at the beginning of the accounts.

*(Continued on page 68)*

TABLE 10
SUMMARY STATISTICS FOR NATIVE BIRDS IN THE STUDY AREAS ON HAWAII

| | Kau | Hamakua | Puna | Kipukas | Kona | Mauna Kea | Kohala |
|---|---|---|---|---|---|---|---|
| Hawaiian Goose (Nene) | | | | | | | |
| Range (km²) | 64 | 148 | ... | 111 | 91 | ... | ... |
| Stations in range | 95 | 224 | ... | 178 | 146 | ... | ... |
| Stations occupied | 8 | 19 | ... | 26 | 16 | ... | ... |
| Birds recorded | 24 | 52 | ... | 82 | 41 | ... | ... |
| % pop. above 1500 m | 100 | 100 | ... | 100 | 87 | ... | ... |
| Total population | 59 | 93 | ... | 112 | 76 | ... | ... |
| SE | 25 | 25 | ... | 38 | 28 | ... | ... |
| Pop. by habitat type | | | | | | | |
| Ohia | 59 | 87 | ... | 105 | 53 | ... | ... |
| Koa-ohia | ... | 6 | ... | 1 | 11 | ... | ... |
| Koa-mamane | ... | ... | ... | 2 | 3 | ... | ... |
| Mamane | ... | ... | ... | ... | 9 | ... | ... |
| Other natives | ... | ... | ... | 4 | ... | ... | ... |
| Hawaiian Hawk (Io) | | | | | | | |
| Stations occupied | 7 | 36 | 1 | 2 | 56 | 1 | ... |
| Birds recorded | 7 | 52 | 1 | 5 | 78 | 1 | ... |
| Lesser Golden-Plover (Kolea) | | | | | | | |
| Stations occupied | ... | 8 | ... | 10 | 4 | 2 | 1 |
| Birds recorded | ... | 10 | ... | 18 | 2 | 4 | 1 |
| Short-eared Owl (Pueo) | | | | | | | |
| Stations occupied | 11 | 4 | ... | 4 | 21 | 3 | ... |
| Birds recorded | 11 | 5 | ... | 4 | 23 | 3 | ... |
| Hawaiian Crow (Alala) | | | | | | | |
| Range (km²) | ... | ... | ... | ... | 253 | ... | ... |
| Stations in range | ... | ... | ... | ... | 613 | ... | ... |
| Stations occupied | ... | ... | ... | ... | 103 | ... | ... |
| Birds recorded | ... | ... | ... | ... | 259 | ... | ... |
| % pop. above 1500 m | ... | ... | ... | ... | 20 | ... | ... |
| Total population | ... | ... | ... | ... | 76 | ... | ... |
| SE | ... | ... | ... | ... | 9 | ... | ... |
| Pop. by habitat type | | | | | | | |
| Ohia | ... | ... | ... | ... | 23 | ... | ... |
| Koa-ohia | ... | ... | ... | ... | 52 | ... | ... |
| Elepaio | | | | | | | |
| Range (km²) | 252 | 1014 | 219 | 100 | 988 | 97 | 79 |
| Stations in range | 706 | 2226 | 547 | 233 | 2313 | 234 | 159 |
| Stations occupied | 250 | 1201 | 168 | 68 | 1239 | 38 | 121 |
| Birds recorded | 404 | 3513 | 380 | 163 | 4187 | 64 | 372 |
| % pop. above 1500 m | 15 | 36 | 0 | 78 | 49 | 100 | 9 |
| Total population | 12,181 | 112,570 | 857 | 2737 | 62,782 | 2501 | 13,642 |
| SE | 846 | 3054 | 689 | 202 | 1698 | 443 | 1030 |
| Pop. by habitat type | | | | | | | |
| Ohia | 4474 | 62,028 | 8576 | 365 | 24,673 | ... | 13,098 |
| Koa-ohia | 7708 | 49,536 | ... | 786 | 20,075 | ... | ... |
| Koa-mamane | ... | 408 | ... | 512 | 9474 | ... | ... |
| Mamane-naio | ... | ... | ... | ... | 33 | 1792 | ... |
| Mamane | ... | ... | ... | ... | 5353 | 709 | ... |
| Other natives | ... | 219 | ... | 747 | 29 | ... | ... |
| Intro. trees | ... | 378 | ... | ... | 2765 | ... | 544 |
| Treeless | ... | ... | ... | 327 | 378 | ... | ... |
| Omao | | | | | | | |
| Range (km²) | 327 | 978 | 227 | 204 | 19 | ... | ... |
| Stations in range | 863 | 2134 | 558 | 361 | 57 | ... | ... |
| Stations occupied | 752 | 1678 | 429 | 132 | 34 | ... | ... |
| Birds recorded | 3436 | 8116 | 1987 | 554 | 151 | ... | ... |
| % pop. above 1500 m | 31 | 34 | 0 | 98 | 16 | ... | ... |

TABLE 10
CONTINUED

| | Kau | Hamakua | Puna | Kipukas | Kona | Mauna Kea | Kohala |
|---|---|---|---|---|---|---|---|
| Total population | 56,443 | 95,662 | 15,509 | 2106 | 732 | ... | ... |
| SE | 1342 | 1488 | 503 | 111 | 55 | ... | ... |
| Pop. by habitat type | | | | | | | |
| Ohia | 38,716 | 65,391 | 15,508 | 1268 | 68 | ... | ... |
| Koa-ohia | 17,728 | 28,984 | ... | 301 | 664 | ... | ... |
| Koa-mamane | ... | 138 | ... | 110 | ... | ... | ... |
| Other natives | ... | 204 | ... | 11 | ... | ... | ... |
| Intro. trees | ... | 827 | ... | ... | ... | ... | ... |
| Treeless | ... | 119 | 1 | 417 | ... | ... | ... |
| Ou | | | | | | | |
| Range (km²) | ... | 92 | 53 | ... | ... | ... | ... |
| Stations in range | ... | 212 | 145 | ... | ... | ... | ... |
| Stations occupied | ... | 10 | 1 | ... | ... | ... | ... |
| Birds recorded | ... | 32 | 1 | ... | ... | ... | ... |
| % pop. above 1500 m | ... | 0 | 0 | ... | ... | ... | ... |
| Total population | ... | 385 | 9 | ... | ... | ... | ... |
| SE | ... | 157 | 9 | ... | ... | ... | ... |
| Pop. by habitat type | | | | | | | |
| Ohia | ... | 385 | 9 | ... | ... | ... | ... |
| Palila | | | | | | | |
| Range (km²) | ... | ... | ... | ... | ... | 139 | ... |
| Stations in range | ... | ... | ... | ... | ... | 317 | ... |
| Stations occupied | ... | ... | ... | ... | ... | 51 | ... |
| Birds recorded | ... | ... | ... | ... | ... | 97 | ... |
| % pop. above 1500 m | ... | ... | ... | ... | ... | 100 | ... |
| Total population | ... | ... | ... | ... | ... | 2268 | ... |
| SE | ... | ... | ... | ... | ... | 342 | ... |
| Pop. by habitat type | | | | | | | |
| Mamane-naio | ... | ... | ... | ... | ... | 1669 | ... |
| Mamane | ... | ... | ... | ... | ... | 599 | ... |
| Common Amakihi | | | | | | | |
| Range (km²) | 329 | 870 | 245 | 268 | 1133 | 139 | 107 |
| Stations in range | 868 | 1876 | 618 | 469 | 2665 | 317 | 202 |
| Stations occupied | 604 | 1050 | 144 | 413 | 2233 | 272 | 158 |
| Birds recorded | 2587 | 3878 | 1034 | 3298 | 20,350 | 1378 | 645 |
| % pop. above 1500 m | 74 | 57 | 0 | 89 | 48 | 100 | 18 |
| Total population | 157,408 | 172,741 | 32,465 | 41,556 | 348,879 | 87,624 | 29,175 |
| SE | 7377 | 4920 | 2461 | 1280 | 5324 | 3777 | 1632 |
| Pop. by habitat type | | | | | | | |
| Ohia | 111,098 | 59,321 | 32,253 | 26,274 | 210,118 | ... | 27,730 |
| Koa-ohia | 155,896 | 104,429 | ... | 7032 | 77,019 | ... | ... |
| Koa-mamane | ... | 2490 | ... | 5063 | 30,391 | ... | ... |
| Mamane-naio | ... | ... | ... | ... | 1983 | 37,057 | ... |
| Mamane | ... | ... | ... | ... | 19,497 | 50,567 | ... |
| Other natives | ... | 2645 | ... | 1229 | 2076 | ... | ... |
| Intro. trees | ... | 3831 | ... | ... | 2895 | ... | 1445 |
| Treeless | 1589 | 24 | 212 | 1957 | 4901 | ... | ... |
| Akiapolaau | | | | | | | |
| Range (km²) | 60 | 314 | ... | 5 | 61 | 139 | ... |
| Stations in range | 199 | 669 | ... | 12 | 129 | 317 | ... |
| Stations occupied | 19 | 70 | ... | 1 | 6 | 3 | ... |
| Birds recorded | 30 | 126 | ... | 1 | 7 | 3 | ... |
| % pop. above 1500 m | 53 | 69 | ... | 100 | 73 | 100 | ... |
| Total population | 533 | 891 | ... | 2 | 22 | 46 | ... |
| SE | 163 | 118 | ... | 2 | 9 | 26 | ... |
| Pop. by habitat type | | | | | | | |
| Ohia | 2 | 180 | ... | ... | 2 | ... | ... |
| Koa-ohia | 531 | 711 | ... | 2 | 20 | ... | ... |
| Mamane | ... | ... | ... | ... | ... | 46 | ... |

TABLE 10
CONTINUED

| | Kau | Hamakua | Puna | Kipukas | Kona | Mauna Kea | Kohala |
|---|---|---|---|---|---|---|---|
| Hawaii Creeper | | | | | | | |
| Range (km²) | 189 | 439 | ... | ... | 102 | ... | ... |
| Stations in range | 582 | 898 | ... | ... | 246 | ... | ... |
| Stations occupied | 31 | 166 | ... | ... | 20 | ... | ... |
| Birds recorded | 40 | 393 | ... | ... | 33 | ... | ... |
| % pop. above 1500 m | 78 | 77 | ... | ... | 81 | ... | ... |
| Total population | 2102 | 10,102 | ... | ... | 297 | ... | ... |
| SE | 540 | 827 | ... | ... | 73 | ... | ... |
| Pop. by habitat type | | | | | | | |
| Ohia | 1472 | 2792 | ... | ... | ... | ... | ... |
| Koa-ohia | 630 | 7299 | ... | ... | 289 | ... | ... |
| Koa-mamane | ... | 11 | ... | ... | 8 | ... | ... |
| Akepa | | | | | | | |
| Range (km²) | 180 | 268 | ... | ... | 32 | ... | ... |
| Stations in range | 503 | 489 | ... | ... | 69 | ... | ... |
| Stations occupied | 63 | 93 | ... | ... | 24 | ... | ... |
| Birds recorded | 108 | 195 | ... | ... | 43 | ... | ... |
| % pop. above 1500 m | 81 | 83 | ... | ... | 86 | ... | ... |
| Total population | 5293 | 7938 | ... | ... | 661 | ... | ... |
| SE | 780 | 919 | ... | ... | 126 | ... | ... |
| Pop. by habitat type | | | | | | | |
| Ohia | 4160 | 1908 | ... | ... | ... | ... | ... |
| Koa-ohia | 1134 | 6030 | ... | ... | 661 | ... | ... |
| Iiwi | | | | | | | |
| Range (km²) | 280 | 792 | 109 | 126 | 753 | 42 | 56 |
| Stations in range | 770 | 1681 | 347 | 283 | 1748 | 83 | 131 |
| Stations occupied | 451 | 1096 | 8 | 63 | 789 | 5 | 12 |
| Birds recorded | 1623 | 6133 | 10 | 151 | 2902 | 7 | 23 |
| % pop. above 1500 m | 74 | 59 | 0 | 99 | 42 | 100 | 16 |
| Total population | 56,561 | 228,034 | 191 | 2339 | 52,008 | 482 | 802 |
| SE | 1968 | 5460 | 70 | 427 | 1875 | 219 | 286 |
| Pop. by habitat type | | | | | | | |
| Ohia | 31,979 | 90,058 | 191 | 682 | 21,672 | ... | 780 |
| Koa-ohia | 24,581 | 129,599 | ... | 540 | 24,640 | ... | ... |
| Koa-mamane | ... | 1936 | ... | 714 | 2465 | ... | ... |
| Mamane-naio | ... | ... | ... | ... | 65 | ... | ... |
| Mamane | ... | ... | ... | ... | 550 | 483 | ... |
| Other natives | ... | 252 | ... | 279 | ... | ... | ... |
| Intro. trees | ... | 6188 | ... | ... | 2367 | ... | 22 |
| Treeless | ... | ... | ... | 125 | 248 | ... | ... |
| Apapane | | | | | | | |
| Range (km²) | 329 | 1050 | 264 | 278 | 1132 | 42 | 108 |
| Stations in range | 869 | 2316 | 652 | 482 | 2637 | 83 | 207 |
| Stations occupied | 789 | 1750 | 529 | 422 | 1912 | 3 | 136 |
| Birds recorded | 6376 | 11,905 | 5469 | 3468 | 12,741 | 3 | 517 |
| % pop. above 1500 m | 65 | 34 | 0 | 74 | 28 | 100 | 12 |
| Total population | 273,477 | 408,852 | 132,023 | 37,665 | 225,338 | 219 | 20,374 |
| SE | 6514 | 8881 | 3452 | 1526 | 5125 | 123 | 1737 |
| Pop. by habitat type | | | | | | | |
| Ohia | 180,892 | 214,254 | 129,782 | 19,288 | 129,351 | ... | 20,052 |
| Koa-ohia | 92,585 | 188,554 | ... | 10,427 | 69,871 | ... | ... |
| Koa-mamane | ... | 705 | ... | 5581 | 6183 | ... | ... |
| Mamane-naio | ... | ... | ... | ... | 90 | ... | ... |
| Mamane | ... | ... | ... | ... | 3047 | 219 | ... |
| Other natives | ... | 2058 | ... | 1320 | 33 | ... | ... |
| Intro. trees | ... | 3201 | ... | ... | 11,585 | ... | 322 |
| Treeless | ... | 81 | 2241 | 1048 | 5178 | ... | ... |

TABLE 11
SUMMARY STATISTICS FOR NATIVE BIRDS IN THE STUDY AREAS ON MAUI, MOLOKAI, LANAI, AND KAUAI

| | East Maui | West Maui | Molokai | Lanai | Kauai |
|---|---|---|---|---|---|
| Hawaiian Goose (Nene) | | | | | |
| Range (km²) | 35 | ... | ... | ... | ... |
| Stations in range | 138 | ... | ... | ... | ... |
| Stations occupied | 20 | ... | ... | ... | ... |
| Birds recorded | 62 | ... | ... | ... | ... |
| % pop. above 1500 m | 90 | ... | ... | ... | ... |
| Total population | 49 | ... | ... | ... | ... |
| SE | 12 | ... | ... | ... | ... |
| Pop. by habitat type | | | | | |
| Ohia | 7 | ... | ... | ... | ... |
| Mamane | 2 | ... | ... | ... | ... |
| Other natives | 7 | ... | ... | ... | ... |
| Treeless | 33 | ... | ... | ... | ... |
| Lesser Golden-Plover (Kolea) | | | | | |
| Stations occupied | 4 | 8 | 1 | ... | ... |
| Birds recorded | 6 | 14 | 1 | ... | ... |
| Short-eared Owl (Pueo) | | | | | |
| Stations occupied | 12 | ... | ... | 3 | 8 |
| Birds recorded | 27 | ... | ... | 4 | 12 |
| Elepaio | | | | | |
| Range (km²) | ... | ... | ... | ... | 25 |
| Stations in range | ... | ... | ... | ... | 140 |
| Stations occupied | ... | ... | ... | ... | 139 |
| Birds recorded | ... | ... | ... | ... | 1332 |
| % pop. above 1500 m | ... | ... | ... | ... | 0 |
| Total population | ... | ... | ... | ... | 5929 |
| SE | ... | ... | ... | ... | 250 |
| Pop. by habitat type | | | | | |
| Ohia | ... | ... | ... | ... | 5928 |
| Treeless | ... | ... | ... | ... | 1 |
| Kamao | | | | | |
| Range (km²) | ... | ... | ... | ... | 25 |
| Stations in range | ... | ... | ... | ... | 140 |
| Stations occupied | ... | ... | ... | ... | 9 |
| Birds recorded | ... | ... | ... | ... | 23 |
| % pop. above 1500 m | ... | ... | ... | ... | 0 |
| Total population | ... | ... | ... | ... | 24 |
| SE | ... | ... | ... | ... | 10 |
| Pop. by habitat type | | | | | |
| Ohia | ... | ... | ... | ... | 24 |
| Olomao | | | | | |
| Range (km²) | ... | ... | 16 | ... | ... |
| Stations in range | ... | ... | 120 | ... | ... |
| Stations occupied | ... | ... | 1 | ... | ... |
| Birds recorded | ... | ... | 1 | ... | ... |
| % pop. above 1500 m | ... | ... | 0 | ... | ... |
| Total population | ... | ... | 19 | ... | ... |
| SE | ... | ... | 19 | ... | ... |
| Pop. by habitat type | | | | | |
| Ohia | ... | ... | 19 | ... | ... |
| Puaiohi | | | | | |
| Range (km²) | ... | ... | ... | ... | 25 |
| Stations in range | ... | ... | ... | ... | 140 |
| Stations occupied | ... | ... | ... | ... | 3 |
| Birds recorded | ... | ... | ... | ... | 13 |

TABLE 11
CONTINUED

| | East Maui | West Maui | Molokai | Lanai | Kauai |
|---|---|---|---|---|---|
| % pop. above 1500 m | ... | ... | ... | ... | 0 |
| Total population | ... | ... | ... | ... | 20 |
| SE | ... | ... | ... | ... | 17 |
| Pop. by habitat type | | | | | |
| Ohia | ... | ... | ... | ... | 20 |
| Kauai Oo (Ooaa) | | | | | |
| Range ($km^2$) | ... | ... | ... | ... | 25 |
| Stations in range | ... | ... | ... | ... | 140 |
| Stations occupied | ... | ... | ... | ... | 3 |
| Birds recorded | ... | ... | ... | ... | 6 |
| % pop. above 1500 m | ... | ... | ... | ... | 0 |
| Total population | ... | ... | ... | ... | 2 |
| SE | ... | ... | ... | ... | 1 |
| Pop. by habitat type | | | | | |
| Ohia | ... | ... | ... | ... | 2 |
| Ou | | | | | |
| Range ($km^2$) | ... | ... | ... | ... | 25 |
| Stations in range | ... | ... | ... | ... | 140 |
| Stations occupied | ... | ... | ... | ... | 1 |
| Birds recorded | ... | ... | ... | ... | 1 |
| % pop. above 1500 m | ... | ... | ... | ... | 0 |
| Total population | ... | ... | ... | ... | 3 |
| SE | ... | ... | ... | ... | 3 |
| Pop. by habitat type | | | | | |
| Ohia | ... | ... | ... | ... | 3 |
| Maui Parrotbill | | | | | |
| Range ($km^2$) | 50 | ... | ... | ... | ... |
| Stations in range | 193 | ... | ... | ... | ... |
| Stations occupied | 26 | ... | ... | ... | ... |
| Birds recorded | 57 | ... | ... | ... | ... |
| % pop. above 1500 m | 71 | ... | ... | ... | ... |
| Total population | 502 | ... | ... | ... | ... |
| SE | 116 | ... | ... | ... | ... |
| Pop. by habitat type | | | | | |
| Ohia | 502 | ... | ... | ... | ... |
| Common Amakihi | | | | | |
| Range ($km^2$) | 340 | 36 | 37 | ... | 25 |
| Stations in range | 1001 | 177 | 178 | ... | 140 |
| Stations occupied | 601 | 58 | 48 | ... | 101 |
| Birds recorded | 2077 | 138 | 95 | ... | 381 |
| % pop. above 1500 m | 39 | 0.4 | 0 | ... | 0 |
| Total population | 43,930 | 2762 | 1834 | ... | 2257 |
| SE | 1725 | 421 | 363 | ... | 217 |
| Pop. by habitat type | | | | | |
| Ohia | 28,549 | 2762 | 922 | ... | 2257 |
| Koa-ohia | 4104 | ... | ... | ... | ... |
| Mamane | 27 | ... | ... | ... | ... |
| Other natives | 6287 | ... | ... | ... | ... |
| Intro. trees | 3638 | ... | 912 | ... | ... |
| Treeless | 1323 | ... | ... | ... | ... |
| Anianiau | | | | | |
| Range ($km^2$) | ... | ... | ... | ... | 25 |
| Stations in range | ... | ... | ... | ... | 140 |
| Stations occupied | ... | ... | ... | ... | 134 |
| Birds recorded | ... | ... | ... | ... | 1546 |

TABLE 11
CONTINUED

| | East Maui | West Maui | Molokai | Lanai | Kauai |
|---|---|---|---|---|---|
| % pop. above 1500 m | ... | ... | ... | ... | 0 |
| Total population | ... | ... | ... | ... | 6077 |
| SE | ... | ... | ... | ... | 277 |
| Pop. by habitat type | | | | | |
| Ohia | ... | ... | ... | ... | 6072 |
| Treeless | ... | ... | ... | ... | 5 |
| Nukupuu | | | | | |
| Range (km²) | 7 | ... | ... | ... | 25 |
| Stations in range | 35 | ... | ... | ... | 140 |
| Stations occupied | 1 | ... | ... | ... | 0 |
| Birds recorded | 2 | ... | ... | ... | 0 |
| % pop. above 1500 m | 38 | ... | ... | ... | 0 |
| Total population | 28 | ... | ... | ... | ? |
| SE | 28 | ... | ... | ... | ... |
| Pop. by habitat type | | | | | |
| Ohia | 28 | ... | ... | ... | ... |
| Kauai Creeper | | | | | |
| Range (km²) | ... | ... | ... | ... | 25 |
| Stations in range | ... | ... | ... | ... | 140 |
| Stations occupied | ... | ... | ... | ... | 65 |
| Birds recorded | ... | ... | ... | ... | 341 |
| % pop. above 1500 m | ... | ... | ... | ... | 0 |
| Total population | ... | ... | ... | ... | 1649 |
| SE | ... | ... | ... | ... | 214 |
| Pop. by habitat type | | | | | |
| Ohia | ... | ... | ... | ... | 1649 |
| Maui Creeper | | | | | |
| Range (km²) | 135 | ... | ... | ... | ... |
| Stations in range | 462 | ... | ... | ... | ... |
| Stations occupied | 221 | ... | ... | ... | ... |
| Birds recorded | 990 | ... | ... | ... | ... |
| % pop. above 1500 m | 76 | ... | ... | ... | ... |
| Total population | 34,839 | ... | ... | ... | ... |
| SE | 2723 | ... | ... | ... | ... |
| Pop. by habitat type | | | | | |
| Ohia | 30,484 | ... | ... | ... | ... |
| Koa-ohia | 1096 | ... | ... | ... | ... |
| Intro. trees | 2324 | ... | ... | ... | ... |
| Treeless | 934 | ... | ... | ... | ... |
| Akepa | | | | | |
| Range (km²) | 23 | ... | ... | ... | 25 |
| Stations in range | 84 | ... | ... | ... | 140 |
| Stations occupied | 4 | ... | ... | ... | 92 |
| Birds recorded | 8 | ... | ... | ... | 349 |
| % pop. above 1500 m | 88 | ... | ... | ... | 0 |
| Total population | 227 | ... | ... | ... | 1674 |
| SE | 146 | ... | ... | ... | 168 |
| Pop. by habitat type | | | | | |
| Ohia | 199 | ... | ... | ... | 1674 |
| Koa-ohia | 28 | ... | ... | ... | ... |
| Iiwi | | | | | |
| Range (km²) | 207 | 16 | 18 | ... | 25 |
| Stations in range | 654 | 81 | 120 | ... | 140 |
| Stations occupied | 336 | 6 | 7 | ... | 139 |

TABLE 11
CONTINUED

| | East Maui | West Maui | Molokai | Lanai | Kauai |
|---|---|---|---|---|---|
| Birds recorded | 1488 | 9 | 12 | ... | 1214 |
| % pop. above 1500 m | 38 | 1 | 0 | ... | 0 |
| Total population | 18,812 | 176 | 80 | ... | 5400 |
| SE | 1006 | 74 | 33 | ... | 264 |
| Pop. by habitat type | | | | | |
| Ohia | 16,392 | 176 | 80 | ... | 5397 |
| Koa-ohia | 2156 | ... | ... | ... | ... |
| Other natives | 79 | ... | ... | ... | ... |
| Intro. trees | 93 | ... | ... | ... | ... |
| Treeless | 93 | ... | ... | ... | 3 |
| Crested Honeycreeper (Akohekohe) | | | | | |
| Range (km²) | 58 | ... | ... | ... | ... |
| Stations in range | 215 | ... | ... | ... | ... |
| Stations occupied | 102 | ... | ... | ... | ... |
| Birds recorded | 415 | ... | ... | ... | ... |
| % pop. above 1500 m | 99 | ... | ... | ... | ... |
| Total population | 3753 | ... | ... | ... | ... |
| SE | 373 | ... | ... | ... | ... |
| Pop. by habitat type | | | | | |
| Ohia | 3551 | ... | ... | ... | ... |
| Koa-ohia | 86 | ... | ... | ... | ... |
| Treeless | 117 | ... | ... | ... | ... |
| Apapane | | | | | |
| Range (km²) | 370 | 41 | 118 | 20 | 25 |
| Stations in range | 1069 | 184 | 565 | 77 | 140 |
| Stations occupied | 772 | 160 | 404 | 21 | 140 |
| Birds recorded | 4422 | 973 | 2362 | 47 | 5781 |
| % pop. above 1500 m | 40 | 3 | 0 | 0 | 0 |
| Total population | 93,818 | 15,825 | 38,643 | 540 | 30,327 |
| SE | 3511 | 1129 | 2360 | 213 | 716 |
| Pop. by habitat type | | | | | |
| Ohia | 70,106 | 15,684 | 27,868 | ... | 30,303 |
| Koa-ohia | 9825 | ... | ... | ... | ... |
| Mamane | 32 | ... | ... | ... | ... |
| Other natives | 5562 | ... | 717 | 68 | ... |
| Intro. trees | 3802 | ... | 10,055 | 472 | ... |
| Treeless | 4491 | 141 | 3 | ... | 24 |
| Poo-uli | | | | | |
| Range (km²) | 13 | ... | ... | ... | ... |
| Stations in range | 53 | ... | ... | ... | ... |
| Stations occupied | 1 | ... | ... | ... | ... |
| Birds recorded | 3 | ... | ... | ... | ... |
| % pop. above 1500 m | 73 | ... | ... | ... | ... |
| Total population | 141 | ... | ... | ... | ... |
| SE | 141 | ... | ... | ... | ... |
| Pop. by habitat type | | | | | |
| Ohia | 141 | ... | ... | ... | ... |

(*Continued from page 61*)
Population estimates have been rounded to an appropriate number of significant digits in the text; exact computed values may be found in Tables 10 and 11. After each estimate the 95% confidence interval (abbreviated as "95% CI") is given in text; approximate values of these may be obtained by doubling the standard errors (SE) given in Tables 10 and 11. For unrecorded endemic species we estimated the probability of having detected at least one bird during our survey (Table 12).

TABLE 12
PROBABILITY OF DETECTING AT LEAST ONE BIRD OF SPECIES UNRECORDED DURING THE HFBS

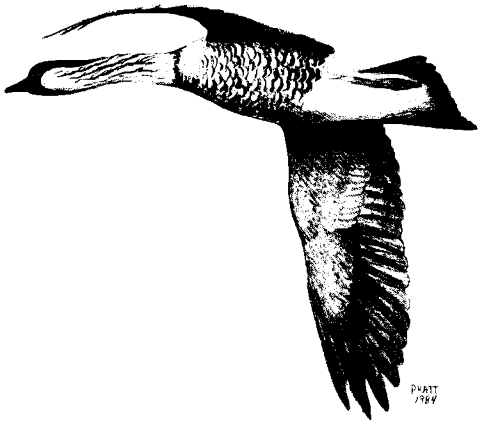
| | | Probability of detection | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Study areas | | | | | | | | | | | |
| Species | Population | Kau | Hamakua | Puna | Kipukas | Kona | Mauna Kea | Kohala | East Maui | West Maui | Molokai | Lanai | Kauai |
| Hawaiian Rail | 10 | 0.074 | 0.056 | 0.086 | 0.048 | 0.066 | | 0.064 | | | | | |
| | 50 | 0.318 | 0.252 | 0.364 | 0.218 | 0.288 | | 0.288 | | | | | |
| | 100 | 0.535 | 0.440 | 0.595 | 0.388 | 0.494 | | 0.494 | | | | | |
| Omao | 10 | | | | | | | 0.235 | | | | | |
| | 50 | | | | | | | 0.731 | | | | | |
| | 100 | | | | | | | 0.931 | | | | | |
| Olomao | 10 | | | | | | | | 0.348 | 0.445 | | 0.359 | |
| | 50 | | | | | | | | 0.882 | 0.948 | | 0.892 | |
| | 100 | | | | | | | | 0.986 | 0.997 | | 0.988 | |
| Bishop's Oo | 10 | | | | | | | | 0.492 | 0.608 | 0.759 | | |
| | 50 | | | | | | | | 0.966 | 0.991 | 0.999 | | |
| | 100 | | | | | | | | 0.999 | 0.999 | 0.999 | | |
| Hawaii Oo | 10 | 0.387 | 0.308 | 0.440 | 0.267 | 0.351 | 0.337 | 0.344 | | | | | |
| | 50 | 0.913 | 0.841 | 0.945 | 0.789 | 0.885 | 0.872 | 0.879 | | | | | |
| | 100 | 0.992 | 0.975 | 0.996 | 0.955 | 0.987 | 0.984 | 0.985 | | | | | |
| Kioea | 10 | 0.387 | 0.308 | 0.440 | 0.267 | 0.351 | | 0.344 | | | | | |
| | 50 | 0.913 | 0.841 | 0.945 | 0.789 | 0.885 | | 0.879 | | | | | |
| | 100 | 0.992 | 0.975 | 0.996 | 0.955 | 0.987 | | 0.985 | | | | | |
| Ou | 10 | 0.314 | | | | 0.284 | | 0.278 | 0.406 | 0.512 | 0.661 | 0.418 | |
| | 50 | 0.848 | | | | 0.811 | | 0.803 | 0.926 | 0.972 | 0.996 | 0.933 | |
| | 100 | 0.977 | | | | 0.964 | | 0.961 | 0.995 | 0.999 | 0.999 | 0.996 | |
| Palila | 10 | | | | | 0.240 | | | | | | | |
| | 50 | | | | | 0.747 | | | | | | | |
| | 100 | | | | | 0.936 | | | | | | | |
| Lesser Koa-Finch | 10 | | 0.059 | | 0.007 | 0.058 | | | | | | | |
| | 50 | | 0.261 | | 0.033 | 0.260 | | | | | | | |
| | 100 | | 0.454 | | 0.066 | 0.453 | | | | | | | |
| Greater Koa-Finch | 10 | | 0.059 | | 0.007 | 0.058 | | | | | | | |
| | 50 | | 0.261 | | 0.033 | 0.260 | | | | | | | |
| | 100 | | 0.454 | | 0.066 | 0.453 | | | | | | | |
| Kona Grosbeak | 10 | | | | | 0.058 | | | | | | | |
| | 50 | | | | | 0.260 | | | | | | | |
| | 100 | | | | | 0.453 | | | | | | | |

TABLE 12
CONTINUED

| | | Probability of detection | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Study areas | | | | | | | | | | | |
| Species | Population | Kau | Hamakua | Puna | Kipukas | Kona | Mauna Kea | Kohala | East Maui | West Maui | Molokai | Lanai | Kauai |
| Maui Parrotbill | 10 | | | | | | | | | 0.334 | | | |
| | 50 | | | | | | | | | 0.868 | | | |
| | 100 | | | | | | | | | 0.983 | | | |
| Common Amakihi | 10 | | | | | | | | | | | 0.117 | |
| | 50 | | | | | | | | | | | 0.464 | |
| | 100 | | | | | | | | | | | 0.712 | |
| Greater Amakihi | 10 | | 0.064 | | | | | | | | | | |
| | 50 | | 0.281 | | | | | | | | | | |
| | 100 | | 0.483 | | | | | | | | | | |
| Hawaiian Akialoa | 10 | 0.074 | 0.056 | 0.086 | 0.007 | 0.066 | | 0.064 | | | | 0.104 | |
| | 50 | 0.318 | 0.252 | 0.364 | 0.033 | 0.288 | | 0.282 | | | | 0.421 | |
| | 100 | 0.535 | 0.440 | 0.595 | 0.066 | 0.494 | | 0.485 | | | | 0.665 | |
| Kauai Akialoa | 10 | | | | | | | | | | | | 0.148 |
| | 50 | | | | | | | | | | | | 0.550 |
| | 100 | | | | | | | | | | | | 0.797 |
| Nukupuu | 10 | | | | | | | | | 0.217 | | | 0.238 |
| | 50 | | | | | | | | | 0.706 | | | 0.742 |
| | 100 | | | | | | | | | 0.914 | | | 0.934 |
| Akiapolaau | 10 | | | 0.484 | | | | 0.382 | | | | | |
| | 50 | | | 0.964 | | | | 0.910 | | | | | |
| | 100 | | | 0.999 | | | | 0.992 | | | | | |
| Hawaii Creeper | 10 | | | 0.178 | 0.015 | | | 0.134 | | | | | |
| | 50 | | | 0.624 | 0.070 | | | 0.511 | | | | | |
| | 100 | | | 0.858 | 0.136 | | | 0.761 | | | | | |
| Maui Creeper | 10 | | | | | | | | | 0.118 | | 0.091 | |
| | 50 | | | | | | | | | 0.466 | | 0.379 | |
| | 100 | | | | | | | | | 0.715 | | 0.614 | |
| Molokai Creeper | 10 | | | | | | | | | | 0.170 | | |
| | 50 | | | | | | | | | | 0.606 | | |
| | 100 | | | | | | | | | | 0.845 | | |
| Akepa | 10 | | | 0.110 | 0.009 | | | 0.082 | | 0.169 | | | |
| | 50 | | | 0.441 | 0.043 | | | 0.347 | | 0.605 | | | |
| | 100 | | | 0.687 | 0.083 | | | 0.547 | | 0.844 | | | |

TABLE 12
CONTINUED

| Species | Population | Kau | Hamakua | Puna | Kipukas | Kona | Mauna Kea | Kohala | East Maui | West Maui | Molokai | Lanai | Kauai |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Probability of detection | | | | | | | | | | | |
| | | Study areas | | | | | | | | | | | |
| Ula-ai-hawane | 10 | | 0.056 | 0.086 | | 0.066 | | 0.064 | | | | | |
| | 50 | | 0.252 | 0.364 | | 0.288 | | 0.282 | | | | | |
| | 100 | | 0.440 | 0.595 | | 0.494 | | 0.485 | | | | | |
| Iiwi | 10 | | | | | | | | | | | 0.146 | |
| | 50 | | | | | | | | | | | 0.546 | |
| | 100 | | | | | | | | | | | 0.794 | |
| Hawaii Mamo | 10 | 0.128 | 0.098 | 0.149 | 0.012 | 0.114 | 0.109 | 0.112 | | | | | |
| | 50 | 0.495 | 0.404 | 0.554 | 0.059 | 0.455 | 0.438 | 0.446 | | | | | |
| | 100 | 0.745 | 0.644 | 0.801 | 0.114 | 0.703 | 0.684 | 0.694 | | | | | |
| Black Mamo | 10 | | | | | | | | | | 0.319 | | |
| | 50 | | | | | | | | | | 0.854 | | |
| | 100 | | | | | | | | | | 0.979 | | |
| Crested Honeycreeper | 10 | | | | | | | | | 0.290 | 0.400 | | |
| | 50 | | | | | | | | | 0.819 | 0.922 | | |
| | 100 | | | | | | | | | 0.967 | 0.994 | | |
| Poo-uli | 10 | | | | | | | | | 0.081 | | | |
| | 50 | | | | | | | | | 0.345 | | | |
| | 100 | | | | | | | | | 0.570 | | | |




# HAWAIIAN GOOSE
*Nesochen sandvicensis*

HAWAIIAN GOOSE [NENE]
(*Nesochen sandvicensis*)

Hawaiian Geese, or Nene, have unique anatomical adaptations for living on rugged arid lava flows (Miller 1937), where they feed on the leaves, buds, flowers, and seeds of *Hypocharis radicata*, grasses, and other herbs, and on the fruits of *Vaccinium* spp., *Coprosma ernodeoides*, and other plants (Baldwin 1947b, Kear and Berger 1980).

Fossil remains suggest that Hawaiian Geese originally occurred on all the main islands (Olson and James 1982b). Historically they occurred on Hawaii from near sea level to 2400 m elevation in the subalpine scrublands of Mauna Loa, and probably on Maui in the subalpine zone (Baldwin 1945a). Presently they are restricted to upland areas on Hawaii and Maui; the Maui population is the result of a translocation effort begun in 1962 (Kear 1975, Kear and Berger 1980). The lowlands, however, may have been the most important breeding area (Perkins 1903).

Prior to the 20th century, Hawaiian Geese were common on Hawaii (Baldwin 1945a). The numbers decreased significantly as a result of hunting, habitat modification, introduced predators, diseases, and competitors (Baldwin 1945a), so that by 1951 the wild population was estimated at no more than 30 birds (Smith 1952). Since then, a captive propagation and release program by state, federal, and private agencies has resulted in increased numbers (Walker 1966, Kear and Berger 1980).

Surveys conducted by the Hawaii Division of Fish and Game suggest that the number of Hawaiian Geese in the wild began to decline when the number of captive-reared birds released to the wild was sharply reduced (Devick 1981a, 1981b). The population estimates for our study areas (Tables 10, 11) were less than the number released in sanctuaries during the seven years prior to our survey (Kear and Berger 1980), suggesting a population maintained mostly by captive-reared birds (Banko and Manuwal 1982).

Hawaiian Geese occur in the Hamakua, Kipukas, Kona, and Kau study areas on Hawaii and on East Maui (Table 13). The highest densities on Hawaii are on the upper slopes of Hualalai, the upper Kau study area, and the saddle area of Mauna Loa. Hawaiian Geese do not occur in the mamane and mamane-naio woodlands of Mauna Kea. They occur at middle elevations in Hawaii Volcanoes National Park as a result of captive releases (Banko and Manuwal 1982) and are frequently seen on the Volcano Golf Course (HFBS data). Areas near 2400 m elevation, the upper limit for this species, were not fully surveyed on Hawaii; in Kau and Kona, birds undoubtedly occur higher than we found them (maximum elevation 2100 m). The lower limits, about 1300 m, are usually bounded by closed canopy forest.

The 390 ± 120 (95% CI) Hawaiian Geese estimated to live in the wild (Tables 10, 11) comprise three distinct populations. Above 260 ± 100 (95% CI) birds occur at upper elevations in Kau (Fig. 64) and windward Hawaii (Fig. 65). Birds occasionally fly across the Kapapala Tract (transects 82–86) between the upper Hamakua and Kau areas, but Hawaiian Geese do not breed there. A second population of 75 ± 55 (95% CI) birds occurs on the south to southwest slopes of Hualalai (Fig. 66). The two Hawaii populations use pastures opened by ranching and some birds are attracted to stock ponds. The third population consists of 50 ± 25 (95% CI) birds confined to scrub and grasslands on the crater and upper slopes of Haleakala (Fig. 67). Vagrant birds occasionally occur at low elevations on both islands.

TABLE 13
DENSITY [MEAN (SE)] OF THE HAWAIIAN GOOSE (NENE) AND HAWAIIAN CROW (ALALA) BY ELEVATION, HABITAT, AND STUDY AREA[a]

| | Hawaiian Goose | | | | | Hawaiian Crow |
|---|---|---|---|---|---|---|
| | Kau | Hamakua | Kipukas | Kona | E. Maui | Kona |
| *Elevation* | | | | | | |
| 100–300 m | ··· | ··· | ··· | ··· | ··· | ··· |
| 300–500 m | ··· | 0 | ··· | 0 | 0 | 0 |
| 500–700 m | 0 | 0 | ··· | 0 | 0 | 0 |
| 700–900 m | 0 | 0 | ··· | 0 | 0 | 0 |
| 900–1100 m | 0 | 0 | ··· | 0 | 0 | + (+) |
| 1100–1300 m | 0 | 0 | 0 | + (+) | 0 | + (1) |
| 1300–1500 m | 0 | 0 | 0 | 1 (1) | 1 (1) | + (+) |
| 1500–1700 m | 1 (1) | + (+) | + (+) | 1 (+) | * | + (+) |
| 1700–1900 m | + (+) | 1 (1) | 1 (+) | + (+) | 2 (1) | + (+) |
| 1900–2100 m | 1 (1) | 5 (2) | 1 (+) | + (+) | 3 (1) | 0 |
| 2100–2300 m | + (+) | 0 | + (+) | 0 | 2 (1) | 0 |
| 2300–2500 m | ··· | ··· | ··· | 0 | + (+) | 0 |
| 2500–2700 m | ··· | ··· | ··· | ··· | 1 (1) | ··· |
| 2700–2900 m | ··· | ··· | ··· | ··· | + (+) | ··· |
| 2900–3100 m | ··· | ··· | ··· | ··· | ··· | ··· |
| *Habitat* | | | | | | |
| Ohia | 1 (+) | 1 (+) | 1 (+) | 1 (+) | 2 (1) | + (+) |
| Koa-ohia | + (+) | 1 (+) | + (+) | 1 (+) | + (+) | 1 (+) |
| Koa-mamane | ··· | 0 | 1 (+) | + (+) | ··· | + (+) |
| Mamane-naio | ··· | ··· | ··· | 0 | ··· | + (+) |
| Mamane | ··· | ··· | ··· | 1 (1) | 2 (1) | 0 |
| Other natives | ··· | 0 | 6 (3) | 0 | 1 (1) | 0 |
| Intro. trees | ··· | 0 | ··· | 0 | 0 | 0 |
| Treeless | ··· | 0 | 0 | 0 | 2 (1) | 0 |

[a] Densities are given in birds/km$^2$; + indicates stratum was in the species range but density <0.5 birds/km$^2$; 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.

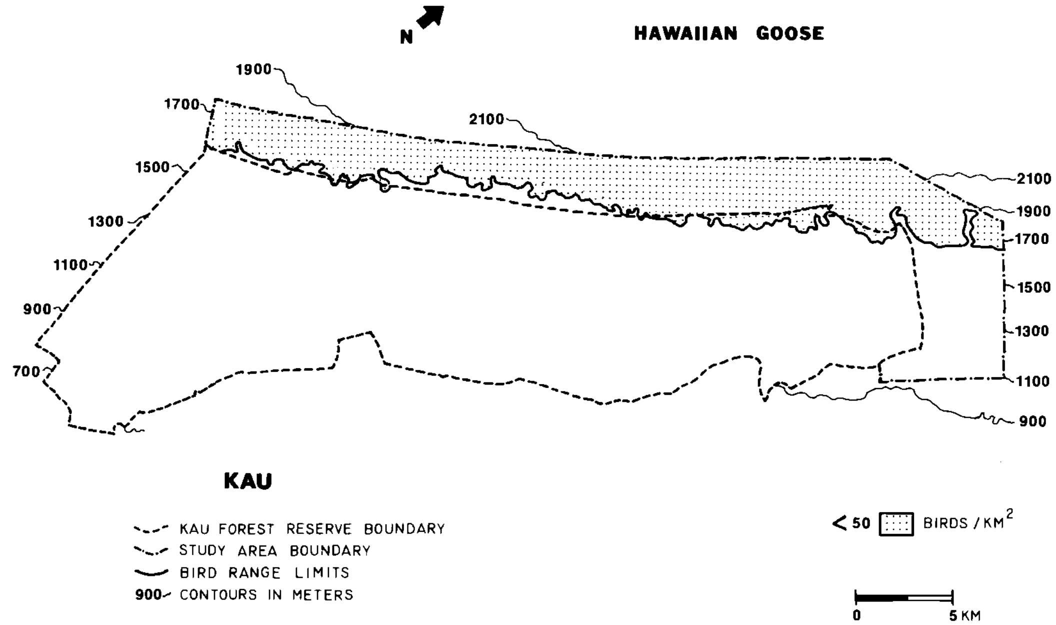



FIGURE 64. Distribution and abundance of the Hawaiian Goose (Nene) in the Kau study area.

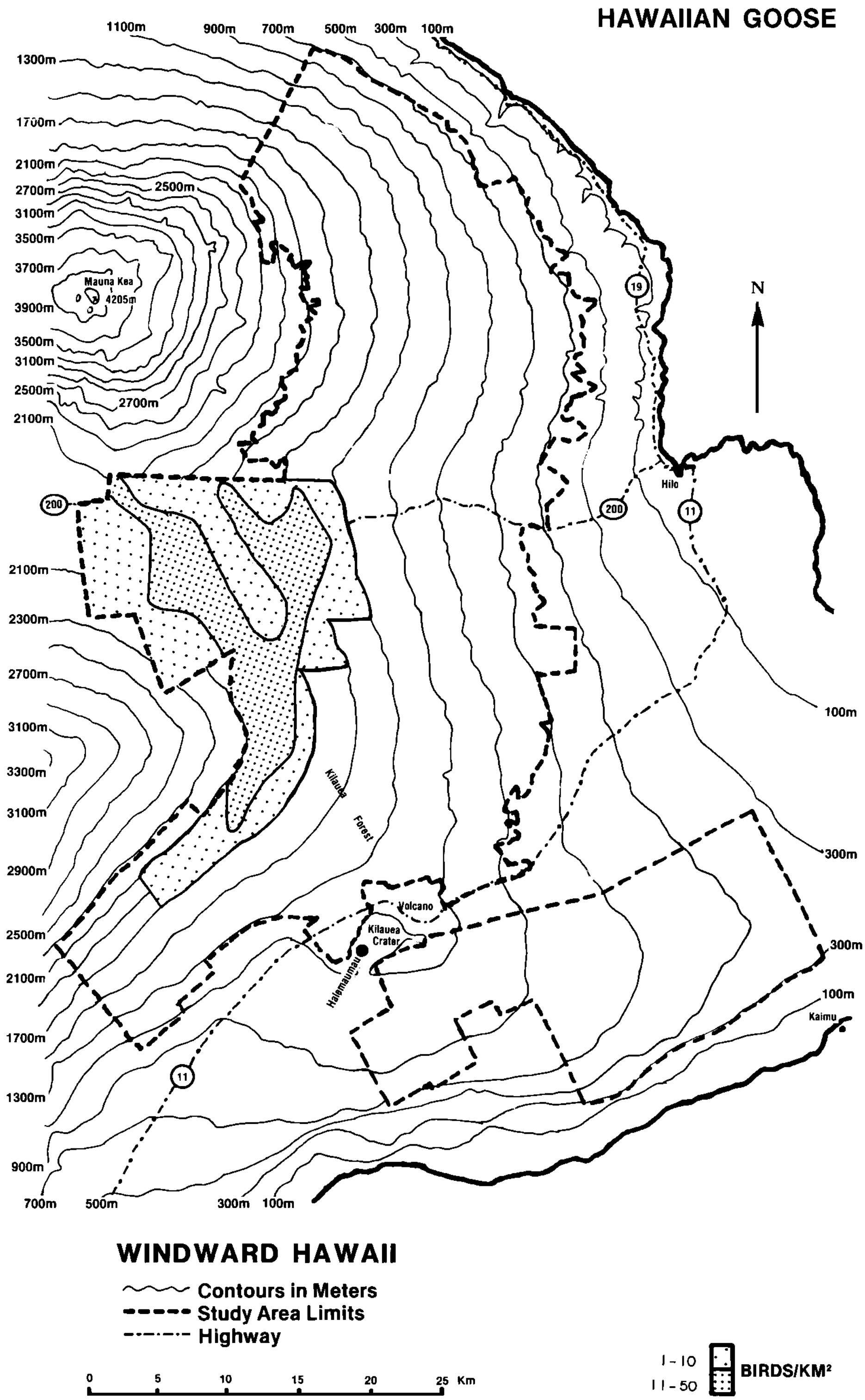



FIGURE 65. Distribution and abundance of the Hawaiian Goose (Nene) in the windward Hawaii study areas.

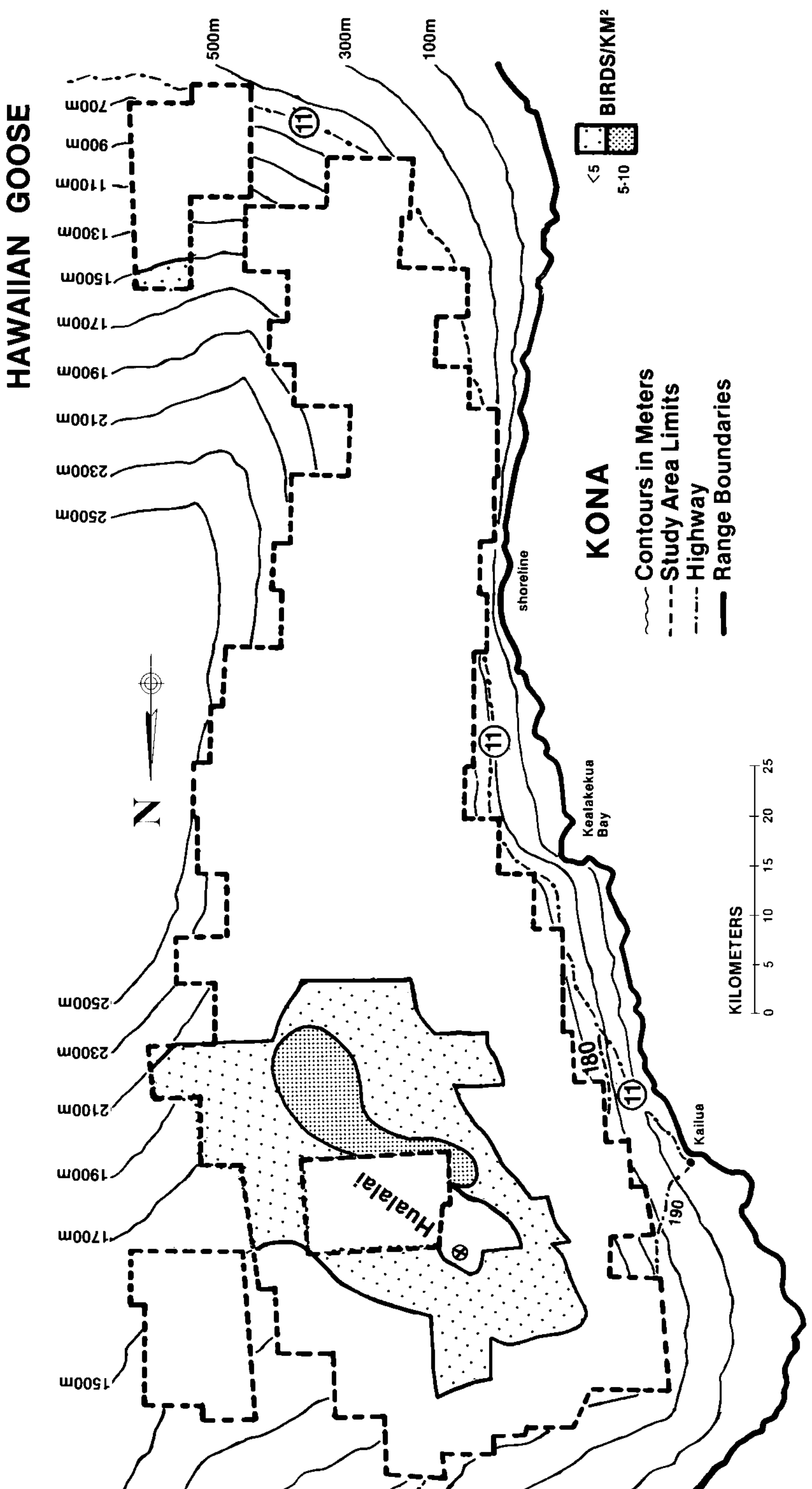



FIGURE 66. Distribution and abundance of the Hawaiian Goose (Nene) in the Kona study area.

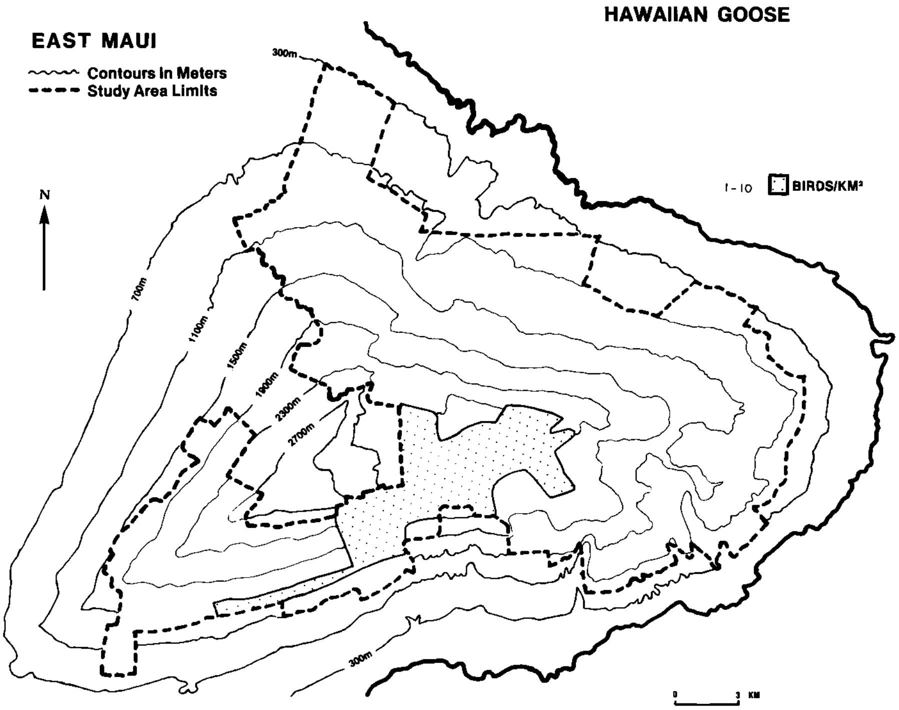



FIGURE 67. Distribution and abundance of the Hawaiian Goose (Nene) in the East Maui study area.

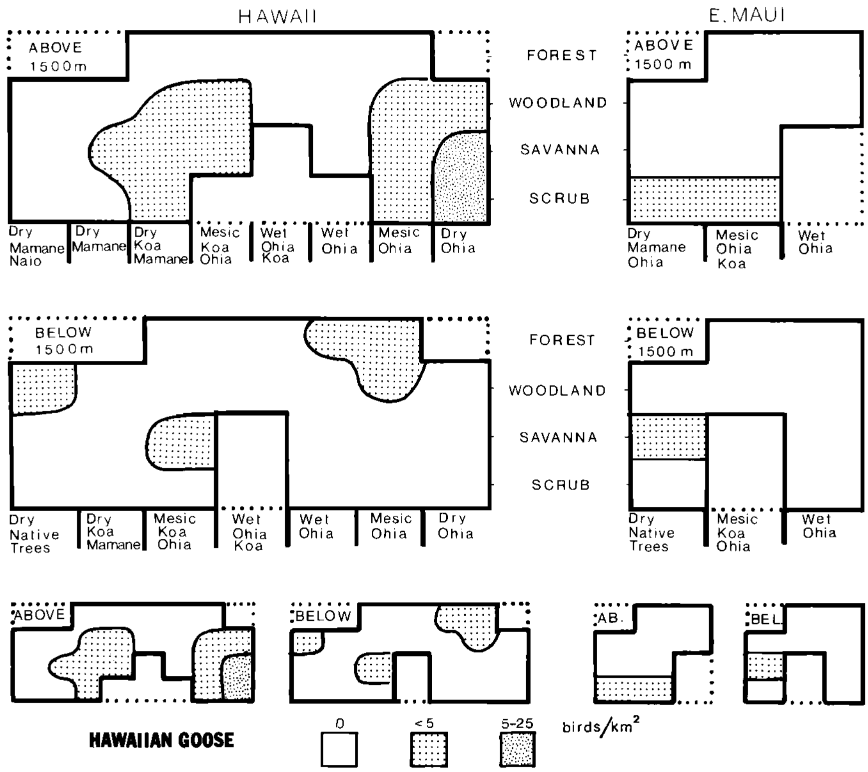


TABLE 14
REGRESSION MODELS FOR HABITAT RESPONSE OF THE HAWAIIAN GOOSE (NENE) AND HAWAIIAN CROW (ALALA)[a]

| | Hawaiian Goose | | | | | Hawaiian Crow |
|---|---|---|---|---|---|---|
| | Kau | Hamakua | Kipukas | Kona | Maui | Kona |
| $R^2$ | 0.41* | 0.11* | 0.41* | 0.02* | 0.03* | 0.11* |
| Moisture | ... | −3.7* | −2.6 | ... | ... | 2.4 |
| Elevation | ... | −5.4* | ... | 2.6 | 2.3 | 3.0 |
| (Elevation)$^2$ | ... | 5.9* | ... | ... | ... | −2.8 |
| Tree biomass | −2.3 | ... | ... | −4.5* | 2.2 | ... |
| (Tree biomass)$^2$ | 15.1* | ... | ... | 2.9 | ... | ... |
| Crown cover | −3.2 | 2.7 | ... | ... | −2.9 | ... |
| Canopy height | −2.2 | −2.8 | ... | ... | ... | ... |
| Koa | ... | −6.1* | ... | ... | ... | 5.4* |
| Ohia | 2.8 | 4.8* | ... | ... | ... | ... |
| Naio | X | X | ... | ... | X | ... |
| Mamane | X | ... | ... | ... | ... | ... |
| Intro. trees | X | ... | X | ... | ... | ... |
| Shrub cover | ... | ... | ... | ... | ... | ... |
| Ground cover | ... | −3.3* | ... | ... | ... | ... |
| Native shrubs | ... | ... | −3.1 | ... | ... | ... |
| Intro. shrubs | X | ... | ... | ... | ... | ... |
| Ground ferns | X | X | ... | ... | ... | 6.4* |
| Matted ferns | ... | ... | ... | ... | ... | −2.8 |
| Tree ferns | ... | X | X | ... | ... | 3.4* |
| Ieie | X | X | X | ... | ... | −5.6* |
| Passiflora | X | ... | X | ... | ... | ... |
| Native herbs | X | X | 6.2* | ... | ... | ... |
| Intro. herbs | X | X | −2.7 | ... | ... | ... |
| Native grasses | 7.0* | 3.6* | ... | ... | ... | ... |
| Intro. grasses | ... | 3.2 | ... | ... | ... | −3.3 |
| Ohia flowers | X | X | X | X | X | ... |
| Olapa fruit | X | X | X | X | X | 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.

Hawaiian Goose densities are highest in dry subalpine ohia scrub and savanna on the island of Hawaii (Fig. 68). Occasional birds representing flyovers also occur in mesic and woodland habitat. A few pairs breed in the edges of mesic to wet forest kipukas surrounded by barren lava flows (N. Santos, R. Bachman, pers. comm.), but most nests are placed in areas of sparse vegetation (Elder and Woodside 1958). Hawaiian Geese have lower populations and densities on Maui than on Hawaii (Table 13), and occupy a narrower range of habitats. The regression models for habitat response (Table 14) indicate that Hawaiian Geese are most commonly associated with dry high elevation areas. Strong positive terms (i.e., $t$-statistics for the regression coefficients) for native herbs and native grasses in the three windward Hawaii models (Kau, Hamakua, Kipukas) reflect the diet of browse and seeds, suggesting that habitat response is partly determined by availability of suitable forage.

Stone et al. (1983) noted that all wild Hawaiian Goose populations require continual captive releases to sustain stable numbers. Some wild-hatched goslings continuously lost weight, suggesting insufficient quantity or quality of food (Banko 1982, Banko and Manuwal 1982). Habitat modification and predation are probable causes for the present failure to maintain self-sustaining populations. Suitable lowland habitat may also be critical to long-term survival (Stone et al. 1983).

←

FIGURE 68. Habitat response graphs of the Hawaiian Goose (Nene) differentiated along gradients of general vegetation type (horizontal axis) and forest development (vertical axis). (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

# HAWAIIAN HAWK
*Buteo solitarius*

HAWAIIAN HAWK [IO] (*Buteo solitarius*)

Hawaiian Hawks, or Io, breed only on Hawaii, although vagrant birds have been recorded from Maui, Oahu, and Kauai (Banko 1980–1984). Recent fossil finds indicate that birds originally occurred on Molokai (Olson and James 1982b). This species is very adaptable and feeds on introduced and native birds, mammals, insects, and spiders (Perkins 1903, Tomich 1971a).

Perkins (1903) characterized Hawaiian Hawks as widely distributed and moderately common from sea level to at least 1500 m elevation. Munro (1944) stated that they were "well distributed over the island from about [600 to 1500 m] elevation," and that the numbers appeared to have declined from the 1890s. Morrison (1969) recorded 0.05 birds per observer hour in Hawaii Volcanoes National Park, leading Baldwin (1969a) to state that the numbers and range had increased in the national park from the 1940s.

TABLE 15
INCIDENTAL OBSERVATIONS OF THE HAWAIIAN HAWK

| Study area | Dark phase | Light phase | Unidentified | Total |
|---|---|---|---|---|
| Kau | 11 | 7 | 9 | 27 |
| Hamakua | 67 | 32 | 49 | 148 |
| Kipukas | 4 | 3 | 10 | 17 |
| Kohala | 0 | 0 | 2 | 2 |
| Kona | 29 | 14 | 37 | 80 |
| Dark/light ratio | | | | |
| Windward | 1.95/1.00 | | | |
| Leeward | 2.07/1.00 | | | |
| Total | 111 | 56 | 107 | 274 |

Hawaiian Hawks occur in distinct light and dark color phases. We found that dark phase birds outnumber light phase birds 1.98:1, with no significant differences in this ratio between leeward and windward forests ($P = 0.88$, $X^2 = 0.02$, $df = 1$, Table 15). This contrasts with earlier statements that dark phase birds were relatively more common on the windward coast (Henshaw 1902).

Hawaiian Hawks occupy a broad range of habitats from papaya and macadamia orchards through virtually all types of forest including ohia rainforest and subalpine mamane-naio woodland (Fig. 69). They are virtually absent from areas with few or no trees. This species has probably adapted better than any other native bird to the introduced flora and fauna that dominate lowland areas. Illegal shooting and harassment of nest sites are probably the most significant factors affecting the species at present (Griffin 1984).

We found Hawaiian Hawks in all study areas on Hawaii. They are widely distributed outside

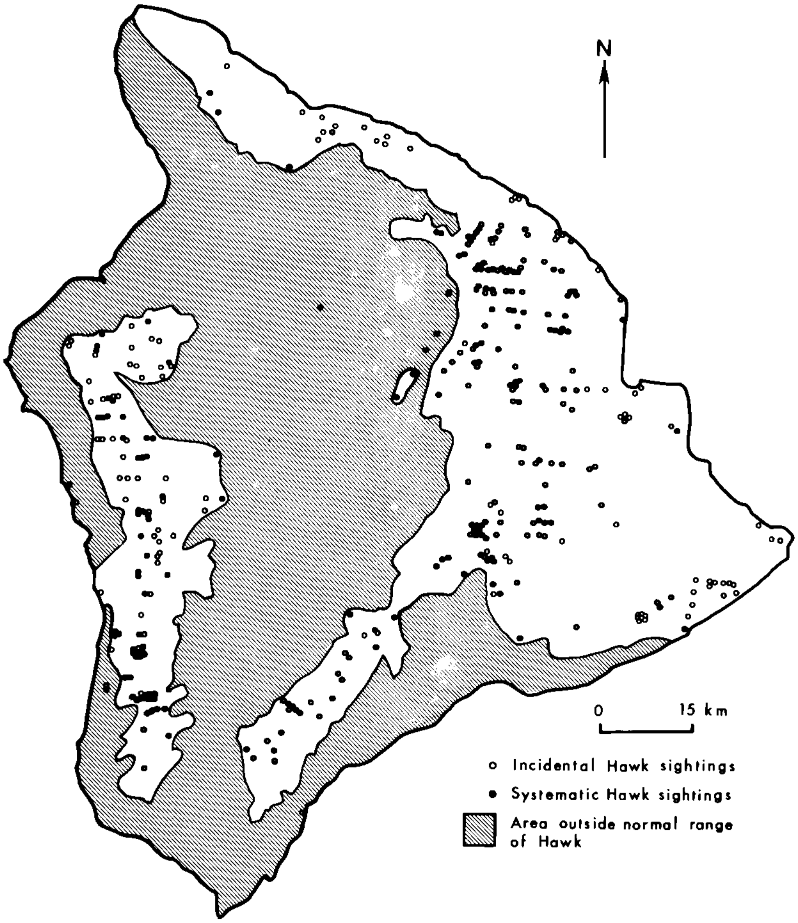



FIGURE 69. Distribution of the Hawaiian Hawk (Io) on the island of Hawaii.

our study areas, but are absent from the arid grasslands on the northwest side of the island, the Kau Desert, the dry scrublands of the Kapapala Tract, and the open savanna of the Kahuku tract. The species occurs from sea level to 2600 m elevation in favorable habitat. We did not estimate population size because the Hawaiian Hawk, like many other raptors, failed to meet many of the assumptions that underlie our density estimates. Griffin (1984) estimated the population to be 1400–2500 birds.

HAWAIIAN RAIL [MOHO]
(*Porzana sandwichensis*)

The Hawaiian Rail, or Moho, was definitely known only from the island of Hawaii, but it or a similar species probably occurred on Molokai in historic times (Perkins 1903; Olson and James 1982a, 1982b). Last seen about 1884, Hawaiian Rails were reported to live in open scrub near continuous forest (Perkins 1903). Rats, dogs, and cats probably played a major role in their extinction (Berger 1981). Olson and James (1982b) found that at least eight flightless rail species originally occurred in the main Hawaiian Islands, with only one surviving into the 19th century. One of the fossil species, the very small Molokai rail, appears to be the smallest known rail.

Very little is known of the behavior of the Hawaiian Rail. Based on descriptions of the vocalizations and behavior of the closely related extinct Laysan Rail, we estimated the effective detection distance to be 30 m. Although the probability of detecting an extant population of 100 birds is among the lowest for all species (Table 12), we believe this value to be very conservative and the chance of this species still existing to be quite small.

Small flightless black birds reported in 1977 by hunters in scrub ohia forest on Hawaii, upon investigation turned out to be juvenile Kalij Pheasants (J. M. Scott, pers. observ.).

# LESSER GOLDEN-PLOVER
## *Pluvialis dominica*

LESSER GOLDEN-PLOVER [KOLEA]
(*Pluvialis dominica*)

Lesser Golden-Plovers, or Kolea, occur as winter visitors in the Hawaiian Islands from sea level to over 3000 m elevation; a few birds stay through summer (Berger 1981). This species inhabits pastures, roadsides, golf courses, and other open areas. It is omnivorous, feeding extensively on insects, other invertebrates, and various plants (Okimoto 1975). Conversion of forest areas to pasturelands have probably resulted in a larger population than was present at Western contact.

We found birds in open areas, pasture lands, and bogs on Hawaii and Maui in several vegetation types (Tables 10, 11); they were most abundant in the bogs of West Maui. These birds were probably early arriving migrants. The occasional plovers found in other areas probably represent birds that failed to migrate to the Arctic breeding grounds.

# SHORT-EARED OWL
## *Asio flammeus sandwichensis*

SHORT-EARED OWL [PUEO]
(*Asio flammeus sandwichensis*)

The Short-eared Owl, or Pueo, is an endemic subspecies found on all the main islands, with records for many of the Northwestern Hawaiian Islands as well (Berger 1981). It is one of two extant raptors native to the Hawaiian Islands. Recent excavations have documented the occurrence of several other owls and hawks in the islands antedating Polynesian contact (Olson and James 1982b).

This species was widespread on all the main islands in the 1890s, although Perkins (1903) felt that numbers had declined since Western contact due to the increased area of land under cultivation (especially sugar cane) and possibly shooting. Their ground-nesting habit makes them vulnerable to cat and mongoose predation.

Short-eared Owls feed extensively on house mice (*Mus musculus*) and Polynesian rats (*Rattus exulans*) (Tomich 1971a). Fossil evidence suggests that they failed to become established in the Hawaiian Islands until Polynesians introduced *R. exulans* (Olson and James 1982b), but it is possible that flightless rails and other birds provide a sufficient prey base prior to rodent introductions.

We found Short-eared Owls on all the islands, more frequently as incidental observations than during count periods. Birds most often occur in grasslands, shrublands, and montane parklands. Less frequently they are seen quartering low over closed forest canopies. Short-eared Owls occur in almost all the study areas (Tables 10, 11) and are known from sea level to tree line outside these areas (Berger 1981). Because of the birds' behavior and our few observations, we did not estimate the population size or density. Because of the ubiquitous distribution, range maps were not constructed.

# HAWAIIAN CROW
## *Corvus hawaiiensis*

HAWAIIAN CROW [ALALA]
(*Corvus hawaiiensis*)

Hawaiian Crows, or Alala, are the largest passerines in the islands and feed primarily on fruit and to a lesser degree on arthropods, nestling birds, carrion, and nectar (Sakai and Ralph 1980, Giffin 1983). Olson and James (1982b) reported two fossil crow species from Oahu and Molokai, but found no evidence that Alala ever occurred on any island except Hawaii.

Hawaiian Crows have experienced a drastic decline in numbers and marked contraction in range since the early 1890s (Banko 1980–1984; J. G. Giffin, pers. comm.). Perkins (1893, 1903) found them common in wet forest and in koa and ohia parkland in Kona in 1892, but by 1894–1896 the population began to decline. Henshaw (1902) collected numerous specimens below 1000 m elevation in the Kau District from 1899 to 1902. A shooting campaign was waged against Hawaiian Crows by farmers in Kona in the early 1890s and by 1937 the numbers were greatly reduced in both Kau and Kona (Munro 1944). Unconfirmed reports of birds being shot continue to appear. Populations continued to decline from 1938 to 1949 (Baldwin 1969b). Banko (1980–1984) estimated that about 50 birds remained in 1976, occurring only in the North and South Kona Districts. Although Berger (1981) felt that the reasons for the great decline in numbers during the 20th century were inconclusive, J. G. Giffin (pers. comm.) suggested that loss and modification of suitable breeding habitat was one factor in the decline.

We recorded Hawaiian Crows during count periods only in the Kona study area (Fig. 70, Table 10), where they were rare within the 253 km² range. The average density was 0.35 birds/km² with significant differences between general vegetation types (Table 13). The population was estimated to be 76 ± 18 (95% CI) birds with 68% of those in koa-ohia forests and 30% in ohia.

The Hawaiian Crow appeared to have two major and two minor populations during our 1978 survey. One major population of about 24 birds occupied the north and west slopes of Hualalai;

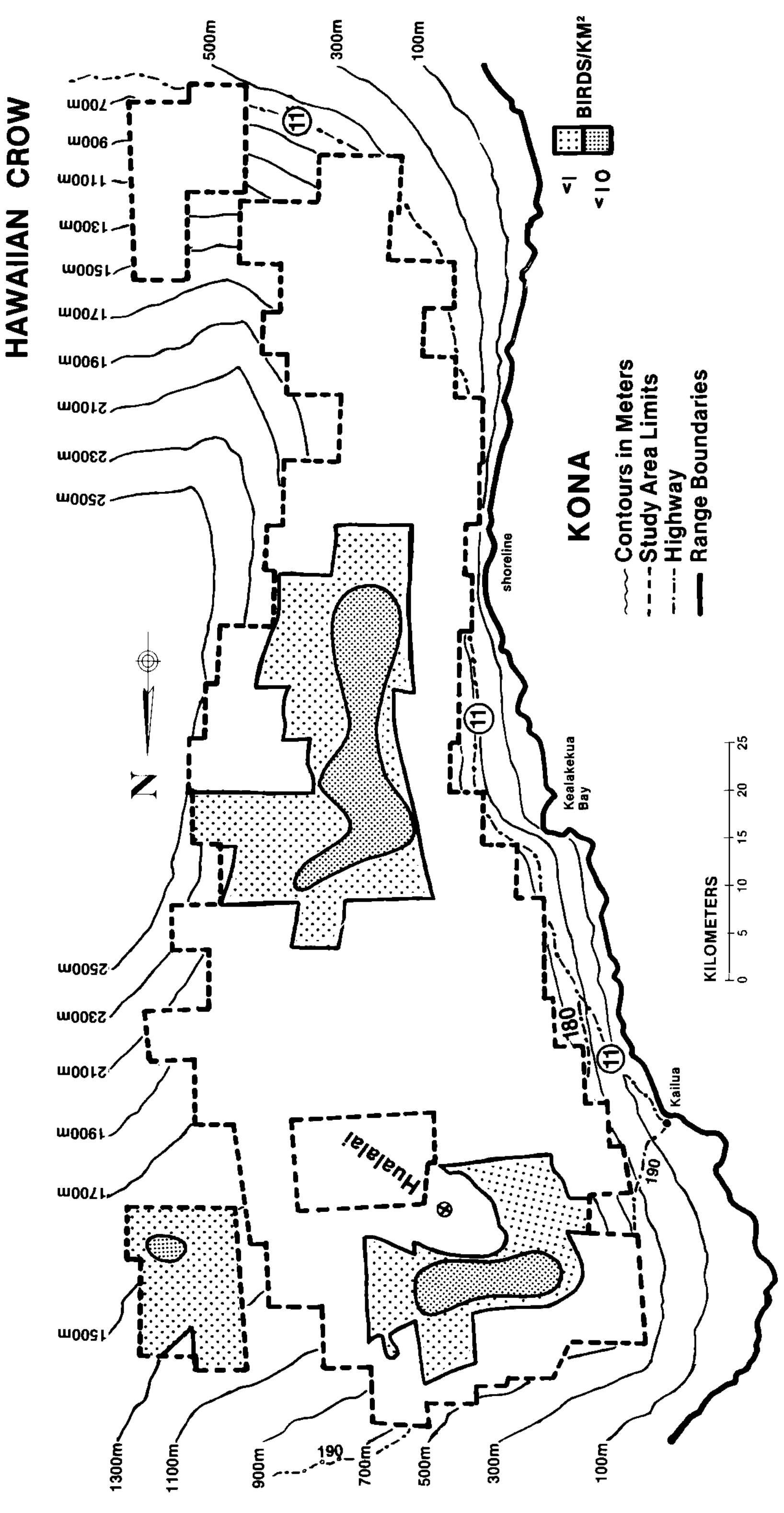



FIGURE 70. Distribution and abundance of the Hawaiian Crow (Alala) in the Kona study area.

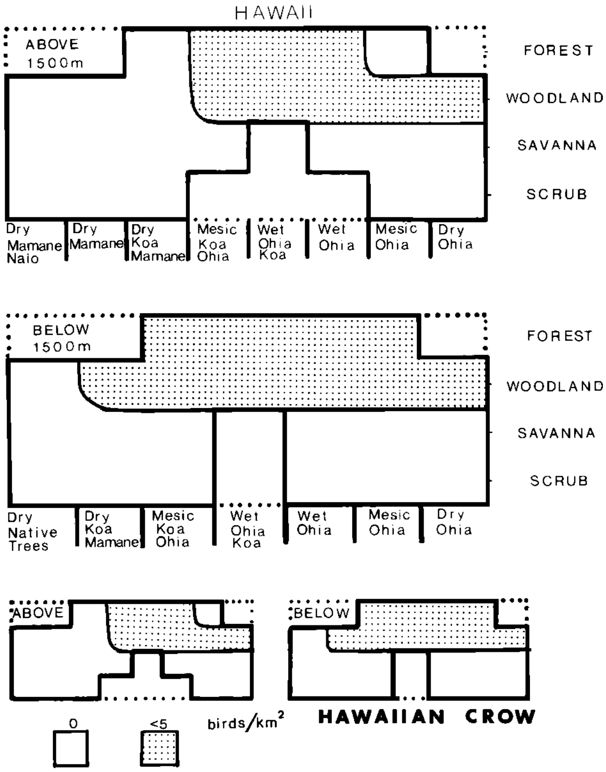



FIGURE 71. Habitat response graphs of the Hawaiian Crow (Alala). (Graphs give mean density above and below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

the other of about 51 birds occupied the central Kona slopes of Mauna Loa above Kealakekua Bay. A 25-km gap of deforested ranchland and recent lava flows separates the two populations. Since our study, the Hualalai population has drastically declined to two birds, partly because of disturbance, unlawful logging, and illegal shooting, while the central Kona birds appear to have declined to probably fewer than 10 pairs on McCandless Ranch (J. G. Giffin, pers. comm.). The minor populations comprised one pair in south Kona on the Honomalino Tract that was not detected by us (the nest site was midway between transects and in 1984 only one bird remained [J. G. Giffin, pers. comm.]) and two detections northeast of Hualalai near Kipuka Alala. These latter observations were corroborated by ranchers who reported a few birds in this remote and rugged area.

We found three birds in the Kau study area, but none during a count period. Two were heard on 4 July 1976 at 1460 m elevation near transect 2 in an open-canopy ohia forest with a mixed native shrub understory. A single bird was heard on 6 June 1976 in a tall open ohia-koa forest with native shrub understory at 1340 m near transect 4.

Assuming an effective detection distance of 282 m, there is a 0.02 probability that 20 crows resided in the Kau study area without having been detected on a single station. Assuming clustered distributions of two (most likely), three, or four individuals, then the probabilities of no detection are 0.15, 0.28, and 0.38, respectively. In view of of the large amount of time we spent in Kau and our failure to locate the Kau birds earlier that year or since then, we suspect that they were postbreeding dispersants from the Kona populations.

The habitat response graphs for the Hawaiian Crow indicate a broad association with woodlands and forests; more habitat types are occupied below 1500 m than above (Fig. 71). The regression model (Table 14) shows that Hawaiian Crows are positively associated with mesic open to relatively closed forests. The habitat with highest breeding densities during the 1970–1982 period was relatively undisturbed koa-ohia forest (J. G. Giffin, pers. comm.); this is reflected in the regression model by the positive terms for koa and ground ferns, and negative terms for introduced grasses. J. G. Giffin (pers. comm.) found that Hawaiian Crows occupied virtually all of the undisturbed and none of the heavily disturbed koa-ohia forests in Kona, suggesting that habitat modification by cattle grazing and lumbering is a major limiting factor. The preference for undisturbed habitat is related to the diet, which consists chiefly of the fruit and nectar of subcanopy trees and understory shrubs sensitive to ungulate activity (Perkins 1903, Rock 1913, Munro 1944, Sakai and Ralph 1980, Giffin 1983). The positive term for olapa fruit in the regression model may also represent this. The diet changed to include carrion and fruit of introduced plants as the countryside was settled. Although the term for ieie in the regression model is negative, Hawaiian Crows feed on ieie in winter when they move to lower elevations where ieie is common.

Munro (1944) found that Hawaiian Crows occurred from 300 to 2400 m elevation; the range in 1978 was from 900 to 1900 m. We found the highest densities at 1300–1500 m near the lower elevational boundary of the range (Table 13; J. G. Giffin, pers. comm.). Only 20% of the present population occurs above 1500 m. In Kona the upper level of mosquitoes is usually 1400–1600 m elevation (HFBS data). Berger (1981) and D. Jenkins (in Giffin 1983) reported several cases of avian malaria and pox infections in Hawaiian Crows. The wide-cruising range and seasonal movement of Hawaiian Crows (Giffin 1983) may increase their vulnerability to disease by increasing the frequency with which individual birds enter disease-infested areas. Although habitat quality has dramatically improved in the Honaunau Forest Reserve due to natural reforestation since 1960 (R. Bachman, pers. comm.) and Hawaiian Crows were once common there, few birds have been seen there since 1982 (J. G. Giffin, pers. comm.). The parallel near-absence of Akiapolaau, Hawaii Creeper, and Akepa there and elsewhere in central Kona where the habitat appears to be suitable, is significant because avian disease is suspected to be a limiting factor for these species.

In some areas fire has destroyed Hawaiian Crow habitat. Tomich (1971b) pointed out the threat of fountain grass to dry native forest where Hawaiian Crows formerly nested. This aggressive and fire-adapted African tussock grass dies back annually and survives wildfires that result from the accumulation of dead material. In 1960 and 1969 fires decimated areas of mature dry forests north of Puu Waawaa where Hawaiian Crows nested because fountain grass had invaded the understory (Tomich 1971b).

Unlike most passerines, fledgling Hawaiian Crows are unable to fly when they leave the nest (Giffin 1983). Mongoose predation on fledglings has been documented (Giffin 1983), and feral cats are presumably another problem.

Intensive management of the Hawaiian Crow has begun through the Hawaii Division of Forestry and Wildlife. At the Pohakuloa Endangered Species Breeding Facility on Hawaii, a small captive flock has bred successfully and it is hoped that the flock will produce birds that can be used in restocking wild populations. In 1984 the Hawaii Board of Land and Natural Resources established a wildlife sanctuary in the koa-ohia forest on the north slopes of Hualalai to protect the remnant populations of Hawaiian Crows, Hawaii Creepers, and Akepa.

The distributional pattern of the Hawaiian Crow (Fig. 70) suggests a relict population contracting to the best remaining habitat (Diamond 1975). We suspect that because of avian disease these areas lie at higher elevations than the optimum historical habitats, which may have centered on mature dry and mesic forests (Tomich 1971b), such as those characterized by the remnant woodlands at Puu Waawaa (see Table 2). At present a viable wild population may survive only in central Kona (transects 60–65). Clearly the Hawaiian Crow is on the verge of extinction. Management actions needed to restore this species have been discussed in the recovery and restoration plans (Burr et al. 1982, Burr 1984). Without prompt action, the outlook for the Hawaiian Crow is not optimistic.

# ELEPAIO
## *Chasiempis sandwichensis*

ELEPAIO (*Chasiempis sandwichensis*)

The Elepaio, a monarchine flycatcher endemic to the islands, feeds on insects and other invertebrates, often capturing them in the air by sallying from a perch (Conant 1977). Separate subspecies occur on Hawaii, Oahu, and Kauai. There is no fossil evidence that Elepaio ever occurred on Maui, Molokai, or Lanai (Olson and James 1982b).

Local plumage variation between habitats led Pratt (1980) to recognize three subspecies on Hawaii: *ridgwayi* on the wet windward slopes, *bryani* in the arid mamane-naio woodland on Mauna Kea, and *sandwichensis* on the mesic Kona slopes. The sedentary nature of the species and local difference in rainfall probably facilitated this phenomenon (Pratt 1980). Intra-island subspecific differentiation may also indicate substantial ability of Elepaio to adapt genetically to prevailing local conditions, and help explain how the bird came to occupy a wide variety of habitats.

In the 19th century, Elepaio were described as extremely common to abundant and widely distributed on Oahu, Kauai, and Hawaii (Wilson and Evans 1890–1899, Perkins 1903). Munro (1944) indicated that birds were holding their own on all three islands. On Kauai, Richardson and Bowles (1964) considered them to be common and widespread chiefly in native forests.

We found Elepaio widespread on Hawaii (Tables 10, 11, Figs. 72–76), occurring in every study area, frequently at high densities and low elevations (Table 16). Highest Elepaio densities were recorded on Kohala Mountain and the koa-ohia forests of Kau. The distributional patterns and numbers of Elepaio on Hawaii and Kauai indicate a healthy population at the species level.

The Mauna Kea subspecies *bryani* may have a precarious future. Isolated from the other subspecies, it occupies only a fraction of the potential range (Pratt 1980), and has a population of 2500 ± 900 (95% CI) birds centered in a dry woodland that is highly susceptible to wildfire. On Mauna Kea, populations of Elepaio, Palila, Common Amakihi, and Akiapolaau are most common at Puu Laau. A 7-km gap of apparently unsuitable habitat (disturbed scrub and grassland) separates the Mauna Kea and Kona subspecies of Elepaio.

The leeward Hawaii subspecies *sandwichensis* has a population of 63,000 ± 3000 (95% CI) birds in the Kona study area. Elepaio drop out at low elevations north of Hualalai at the beginning of the Keamuku flow. Low densities south of Hualalai correspond to deforested ranchland. The Kona population is tenuously connected to Kau across the open pastures, residential subdivisions, and recent flows of the Kahuku Tract.

The subspecies *ridgwayi* is divided into three populations. The 12,000 ± 1500 (95% CI) birds in Kau reach highest densities in koa-ohia forest. Few birds occupy the lower elevations of the south corner of the study area or the very wet central forest. The Kau population drops out sharply in the deforested rangeland of the Kapapala Tract. The windward Hawaii population of 124,000 ± 6000 (95% CI) birds also shows marked avoidance of disturbed understories in the upper northwest corner of the Hamakua study area, and in the dry scrubland of Puna and Kapapala. In Hawaii Volcanoes National Park, population studies by Baldwin (1953), Conant (1975), and Banko and Banko (1980) suggest that Elepaio abundance changed little in most habitats in the 1940–1975 period, except for greater abundance in koa-ohia parkland at 1800 m elevation along the Mauna Loa Strip Road, where habitat regeneration is probably a factor. The third population of *ridgwayi* comprises 14,000 ± 2000 birds in the Kohala study area. Low densities occur in the northeast and at the edges of

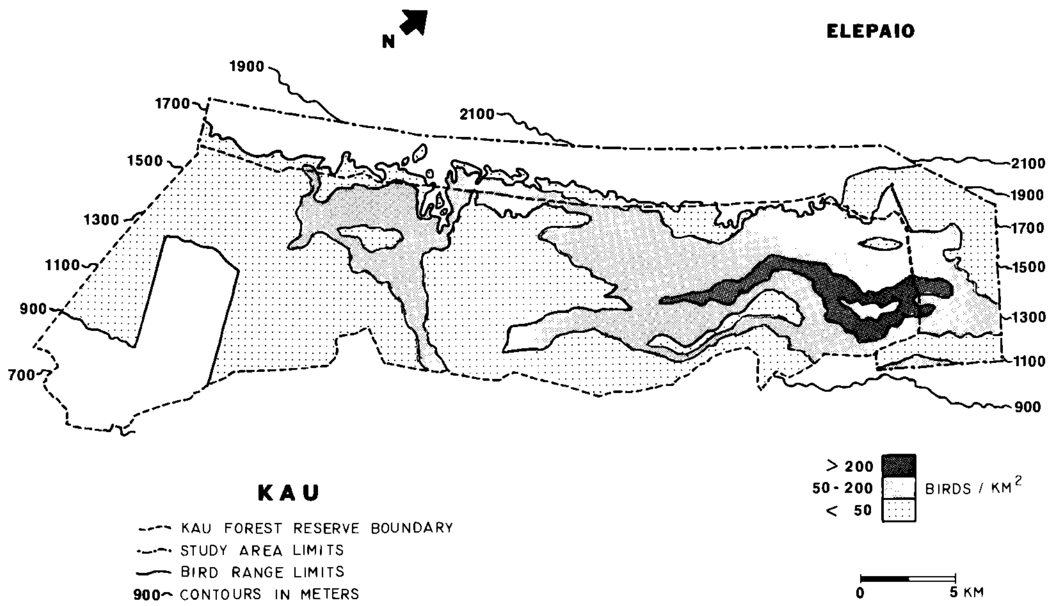



FIGURE 72. Distribution and abundance of the Elepaio in the Kau study area.

TABLE 16
DENSITY [MEAN (SE)] OF THE ELEPAIO BY ELEVATION, HABITAT, AND STUDY AREA[a]

| | Kau | Hamakua | Puna | Kipukas | Kona | Mauna Kea | Kohala | Kauai |
|---|---|---|---|---|---|---|---|---|
| *Elevation* | | | | | | | | |
| 100–300 m | ··· | ··· | ··· | ··· | ··· | ··· | ··· | ··· |
| 300–500 m | ··· | 23 (11) | 22 (4) | ··· | 78 (23) | ··· | 0 | ··· |
| 500–700 m | 0 | 32 (5) | 52 (7) | ··· | 85 (11) | ··· | 0 | ··· |
| 700–900 m | 24 (13) | 46 (5) | 87 (11) | ··· | 57 (6) | ··· | 0 | ··· |
| 900–1100 m | 47 (9) | 91 (8) | 10 (4) | ··· | 61 (5) | ··· | 78 (21) | ··· |
| 1100–1300 m | 47 (8) | 107 (7) | 9 (6) | 88 (18) | 55 (5) | ··· | 183 (28) | ··· |
| 1300–1500 m | 73 (9) | 196 (10) | ··· | 32 (10) | 47 (4) | ··· | 254 (23) | 267 (14) |
| 1500–1700 m | 67 (8) | 226 (14) | ··· | 63 (11) | 98 (5) | ··· | 241 (37) | 230 (13) |
| 1700–1900 m | 55 (8) | 160 (13) | ··· | 16 (6) | 96 (7) | ··· | ··· | ··· |
| 1900–2100 m | 42 (14) | 30 (8) | ··· | 8 (6) | 59 (6) | 47 (17) | ··· | ··· |
| 2100–2300 m | 0 | 47 (21) | ··· | 0 | 38 (6) | 39 (10) | ··· | ··· |
| 2300–2500 m | ··· | ··· | ··· | ··· | 17 (7) | 32 (9) | ··· | ··· |
| 2500–2700 m | ··· | ··· | ··· | ··· | ··· | 17 (10) | ··· | ··· |
| 2700–2900 m | ··· | ··· | ··· | ··· | ··· | + (+) | ··· | ··· |
| 2900–3100 m | ··· | ··· | ··· | ··· | ··· | + (+) | ··· | ··· |
| *Habitat* | | | | | | | | |
| Ohia | 29 (3) | 124 (5) | 47 (4) | 9 (3) | 48 (2) | ··· | 198 (16) | 249 (9) |
| Koa-ohia | 104 (7) | 132 (6) | ··· | 83 (14) | 101 (5) | ··· | ··· | ··· |
| Koa-mamane | ··· | 47 (12) | ··· | 27 (6) | 99 (6) | ··· | ··· | ··· |
| Mamane-naio | ··· | ··· | ··· | ··· | 12 (7) | 26 (5) | ··· | ··· |
| Mamane | ··· | ··· | ··· | ··· | 101 (8) | 25 (9) | ··· | ··· |
| Other natives | ··· | 48 (13) | ··· | 56 (31) | 12 (5) | ··· | ··· | ··· |
| Intro. trees | ··· | 13 (4) | ··· | ··· | 38 (10) | ··· | 153 (54) | ··· |
| Treeless | 0 | | 0 | 26 (26) | 14 (7) | ··· | ··· | 13 (13) |

[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.

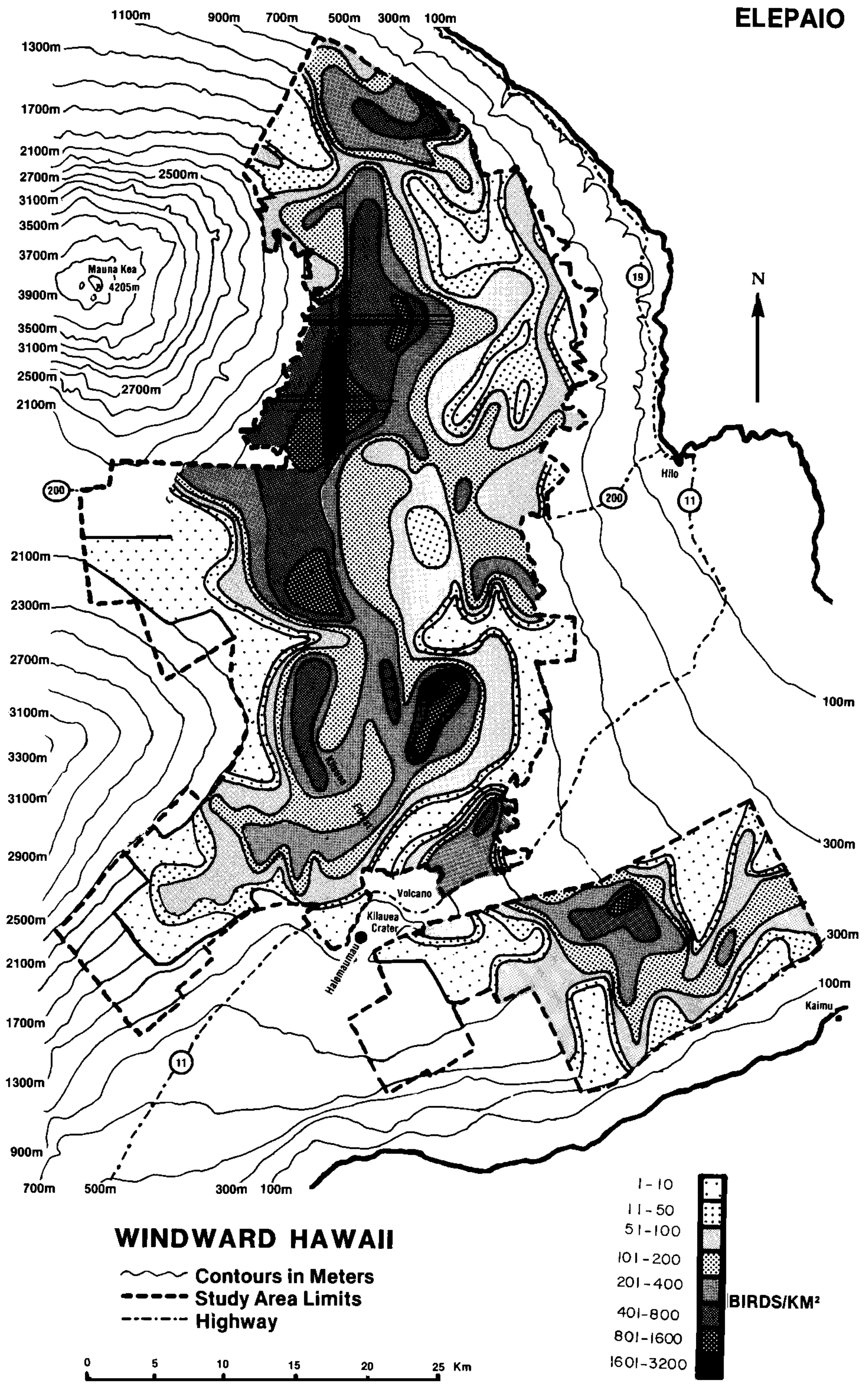



FIGURE 73. Distribution and abundance of the Elepaio in the windward Hawaii study areas.

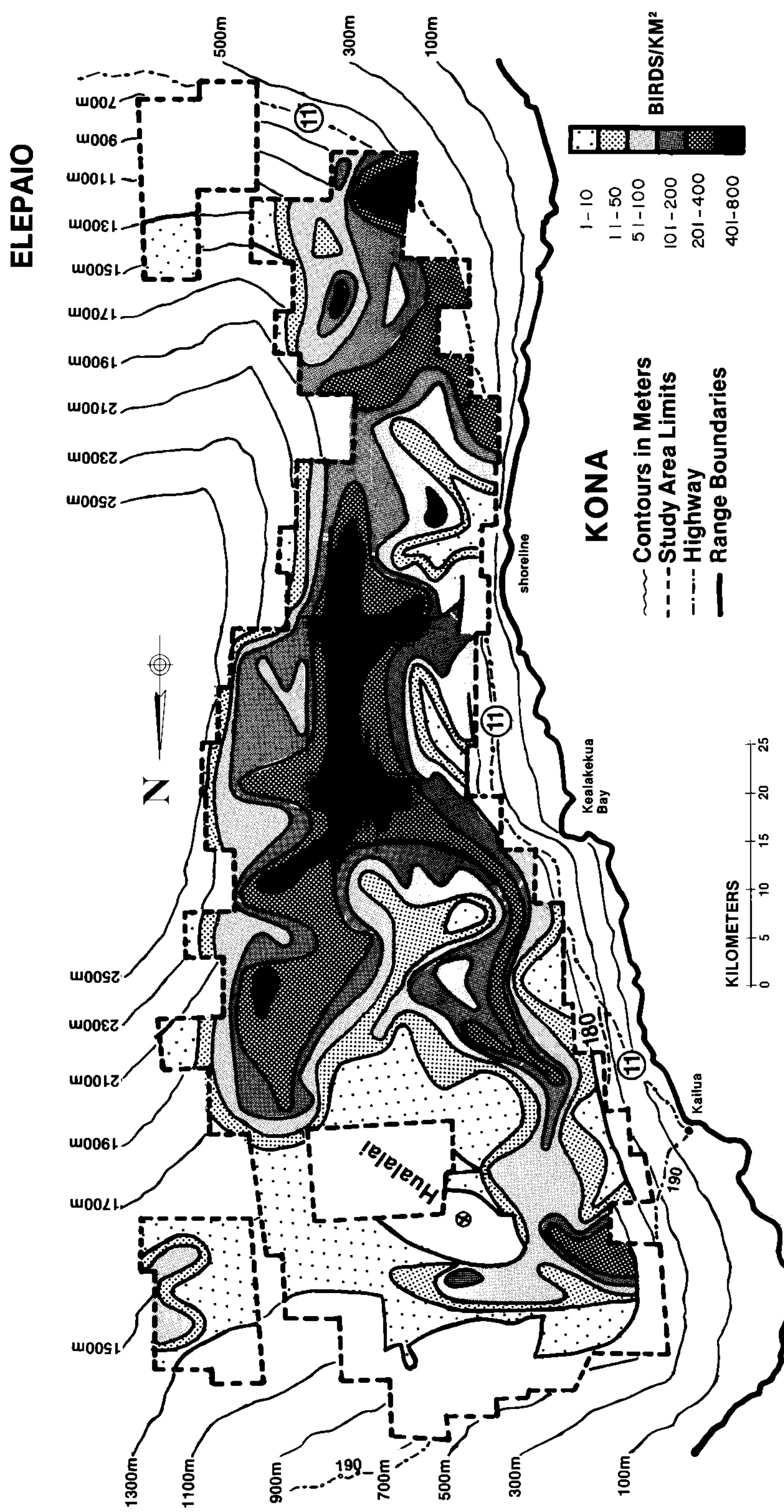



FIGURE 74. Distribution and abundance of the Elepaio in the Kona study area.

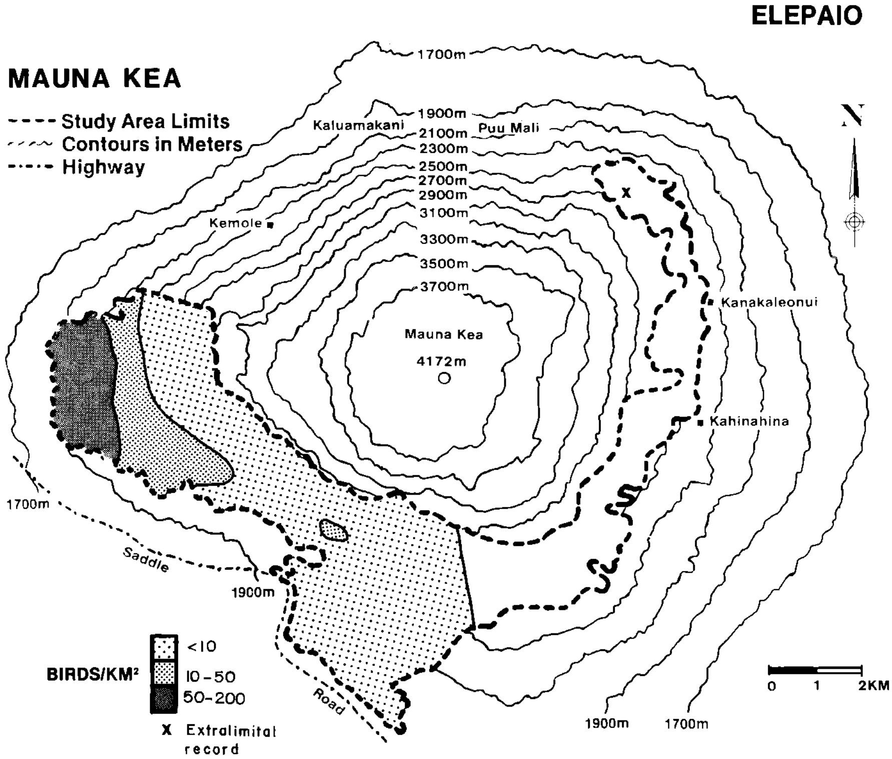



FIGURE 75. Distribution and abundance of the Elepaio in the Mauna Kea study area.

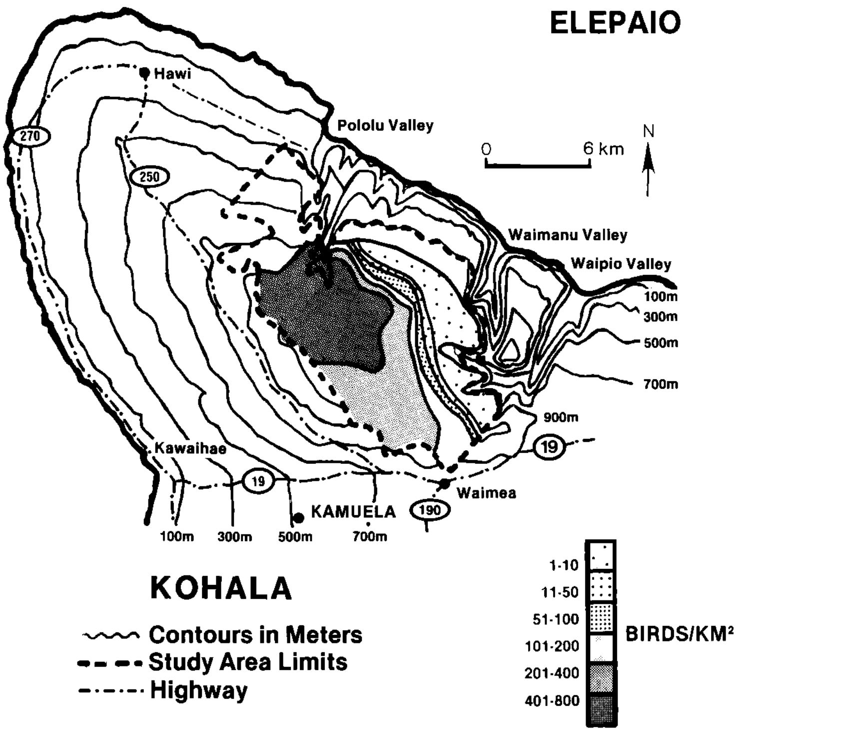



FIGURE 76. Distribution and abundance of the Elepaio in the Kohala study area of Hawaii.

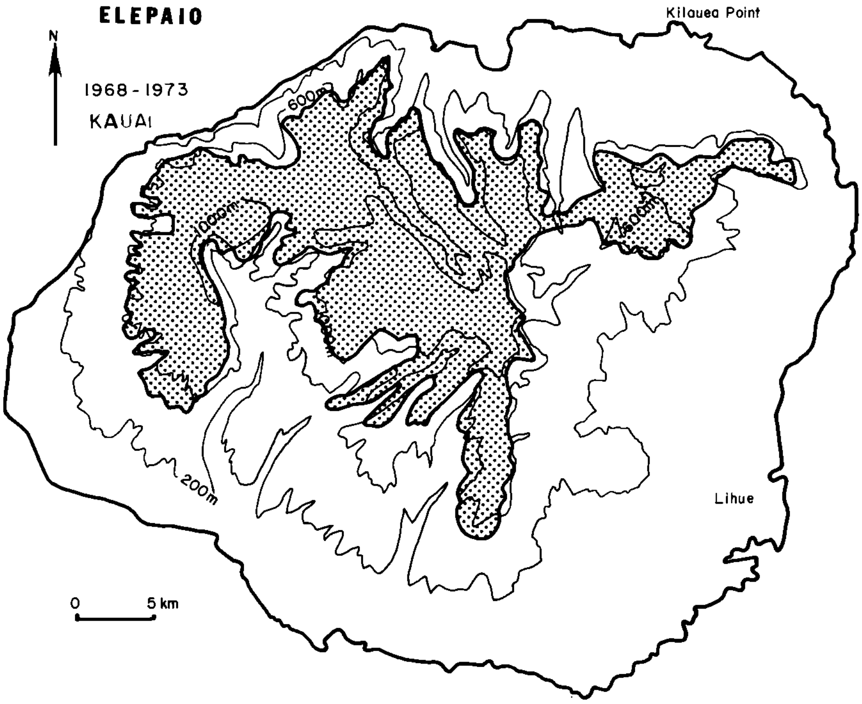



FIGURE 77. Range of the Elepaio on Kauai, based on 1968–1973 survey (J. L. Sincock, unpub. data).

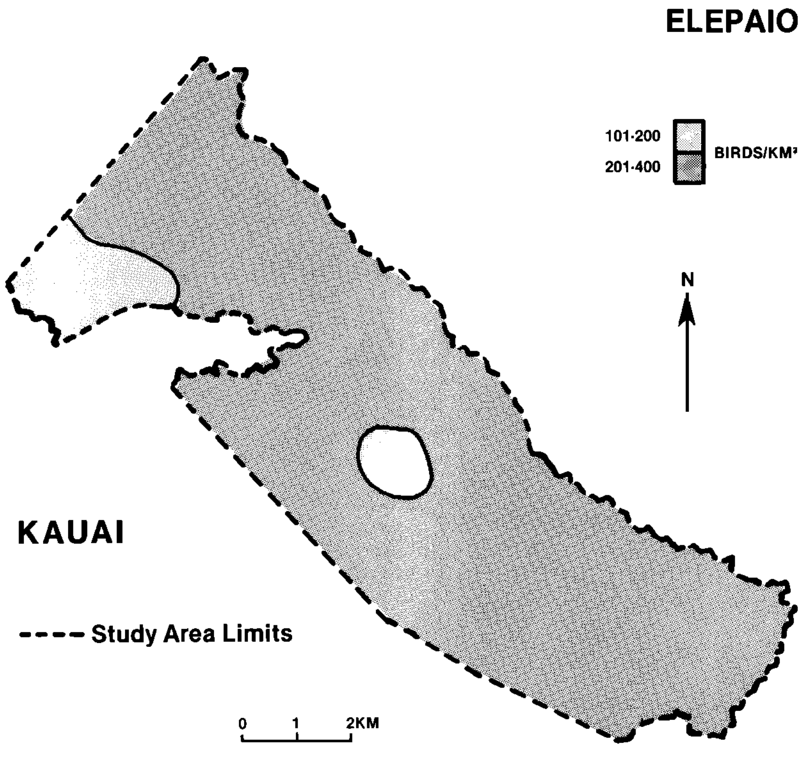



FIGURE 78. Distribution and abundance of the Elepaio in the Kauai study area.

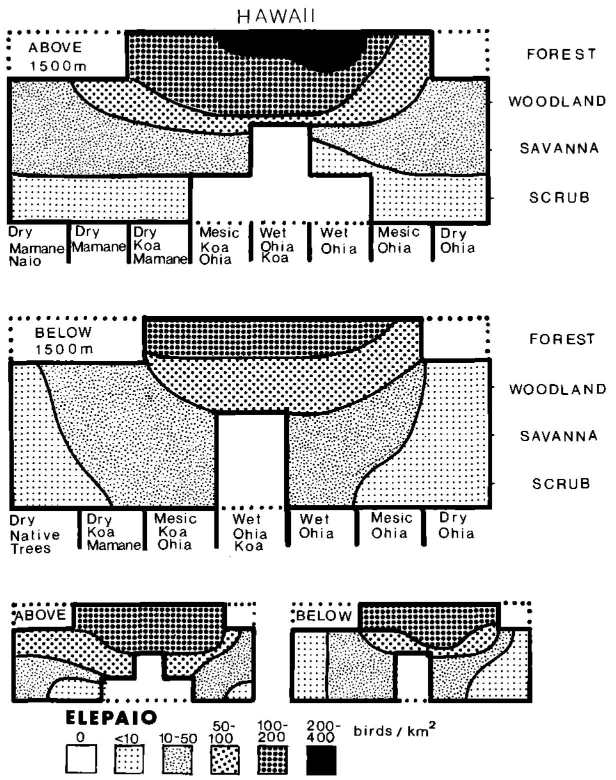



FIGURE 79. Habitat response graphs of the Elepaio. (Graphs give mean density above and below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

the study area where understories were opened by cattle.

Elepaio are widely distributed in the native forests of Kauai, inhabiting the west rim and slopes of Waimea Canyon, the Na Pali plateaux, Kokee State Park, the Alakai Swamp, Kahili Peak and the Kapalaoa Ridge, Laau Ridge, Namolokama Mountain, the Makaleha Mountains, and Anahola Mountain (Sincock et al. 1984, Fig. 77). Sincock et al. (1984) estimated a total population of 40,000 ± 7000 birds for all of Kauai. In the Kauai study area, Elepaio have a wide distribution (Fig. 78, Table 11) and a population of 5900 ± 500 (95% CI). The 1968–1973 survey by J. L. Sincock (pers. comm.) showed 5000 ± 1000 birds for the same area. The difference in results between his survey and ours is statistically insignificant, well within expected annual variation for a passerine population, and suggests a stable population in that area.

The habitat response graph (Fig. 79) shows that Elepaio occupy virtually every major habitat type above and below 1500 m elevation. Like many native passerines, Elepaio attain highest densities in wet to mesic forests above 1500 m (Fig. 79). Densities are lower in woodland, savanna, scrub, and drier habitats. The regression models (Table 17) show that they are most common in wet forests at higher elevations. The weak response of Elepaio to flower or fruit variables in the models may reflect the insectivorous diet.

Little response is seen in the regression models toward total shrub or ground cover; however, there are strong responses to individual understory components. Elepaio are negatively associated with matted ferns in five models and with passiflora and grasses in two models. Little response to native shrubs and conflicting response to introduced shrubs is seen in Hamakua and Puna. This may represent a bell-shaped response to introduced shrubs, since Puna has the highest introduced shrub cover of the eight study areas occupied by Elepaio. Elepaio may also respond negatively to fire tree, which frequently dominates the understory in Puna but not elsewhere.

Elepaio appear to be the most successful native passerine in adapting to introduced vegetation, although highest densities occur in native forests.

TABLE 17
REGRESSION MODELS FOR HABITAT RESPONSE OF THE ELEPAIO[a]

| | Kau | Hamakua | Puna | Kipukas | Kona | Mauna Kea | Kohala | Kauai |
|---|---|---|---|---|---|---|---|---|
| $R^2$ | 0.23* | 0.30* | 0.26* | 0.43* | 0.37* | 0.31* | 0.60* | 0.21* |
| Moisture | ··· | ··· | 5.0* | ··· | 8.3* | X | X | X |
| Elevation | 2.6 | 12.2* | ··· | 3.3 | −3.7* | ··· | 13.0* | 2.6 |
| (Elevation)² | −2.2 | −8.9* | ··· | −3.5* | 6.7* | −3.5* | ··· | ··· |
| Tree biomass | ··· | −4.0* | −4.3* | 5.6* | −8.5* | 5.8* | 3.4* | 3.5* |
| (Tree biomass)² | 5.0* | 7.6* | ··· | ··· | 12.8* | ··· | ··· | −3.0 |
| Crown cover | ··· | ··· | 5.1* | ··· | ··· | ··· | ··· | ··· |
| Canopy height | ··· | ··· | 2.7 | ··· | ··· | ··· | 2.7 | ··· |
| Koa | 9.8* | ··· | X | ··· | 7.2* | X | X | X |
| Ohia | ··· | 4.9* | ··· | −5.4* | ··· | X | ··· | X |
| Naio | X | X | X | 4.3* | 4.3* | ··· | X | X |
| Mamane | X | ··· | ··· | 2.1 | 8.6* | −4.8* | X | X |
| Intro. trees | X | −3.8* | ··· | X | ··· | X | ··· | X |
| Shrub cover | ··· | ··· | ··· | ··· | ··· | −10.3* | ··· | ··· |
| Ground cover | ··· | ··· | ··· | ··· | ··· | ··· | ··· | ··· |
| Native shrubs | ··· | ··· | ··· | −5.3* | ··· | X | ··· | ··· |
| Intro. shrubs | X | 7.4* | −4.9* | ··· | ··· | X | ··· | ··· |
| Ground ferns | X | X | ··· | ··· | 7.0* | X | ··· | ··· |
| Matted ferns | ··· | −2.5 | −5.9* | ··· | −4.1* | X | −2.6 | −2.5 |
| Tree ferns | ··· | X | ··· | X | ··· | X | ··· | ··· |
| Ieie | X | X | ··· | X | ··· | X | X | ··· |
| Passiflora | X | −11.9* | X | X | −10.1* | X | ··· | X |
| Native herbs | X | X | ··· | ··· | −2.8 | X | ··· | ··· |
| Intro. herbs | X | X | ··· | ··· | ··· | ··· | −4.7* | ··· |
| Native grasses | ··· | ··· | −4.1* | ··· | −8.1* | ··· | ··· | ··· |
| Intro. grasses | ··· | ··· | −4.4* | ··· | ··· | ··· | ··· | ··· |
| Ohia flowers | ··· | ··· | −2.3 | ··· | −2.6 | X | ··· | ··· |
| Olapa fruit | ··· | −3.8* | ··· | −5.4* | ··· | X | ··· | ··· |
| Mamane flowers | X | X | 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 $P < 0.01$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

On Oahu, Elepaio occupy a wide variety of native and introduced forests (Berger 1981), and nest in dense introduced shrub understory (Conant 1977). On Kauai, Elepaio frequent lowland forests of introduced trees (Richardson and Bowles 1964).

### KAMAO (*Myadestes myadestinus*)

Pratt (1982) offered convincing evidence that *Phaeornis* should be merged with the solitaire genus *Myadestes,* and that some Hawaiian thrushes formerly treated as subspecies are sufficiently distinct to merit full species status. Pratt recognized the Kauai race as *M. myadestina,* the Lanai, Molokai, and presumably Maui races as *M. lanaiensis,* and the Hawaii race as *M. obscurus.* Our field experience with the Hawaiian thrushes corroborates Pratt's conclusions that these appear to be biologically distinct species.

The Kamao is sometimes referred to as the Large Kauai Thrush. Kamao feed opportunistically on fruit and to a lesser extent on insects and land snails (Henshaw 1902, Perkins 1903).

Kamao were the most common forest birds in 1891 on Kauai, but by 1928 they were gone from the lower forests (Munro 1944). Richardson and Bowles (1964) found them mostly restricted to the Alakai, and guessed the population was "some hundreds, if not a few thousands." For 1968–1973 Sincock et al. (1984) estimated a population of 337 ± 243 (95% CI) birds with 173 ± 116 in our study area. During the 1981 survey, only 24 ± 20 birds remained, located at the remote south portion of the Alakai (Table 18, Fig. 80). Sincock et al. (1984) found the species primarily distributed in the upper (south) Alakai Swamp, with one isolated occurrence in Kokee State Park (Fig. 81). This pattern is also reflected by the positive term for elevation in the regression model for habitat response (Table 19). Abundant suit-

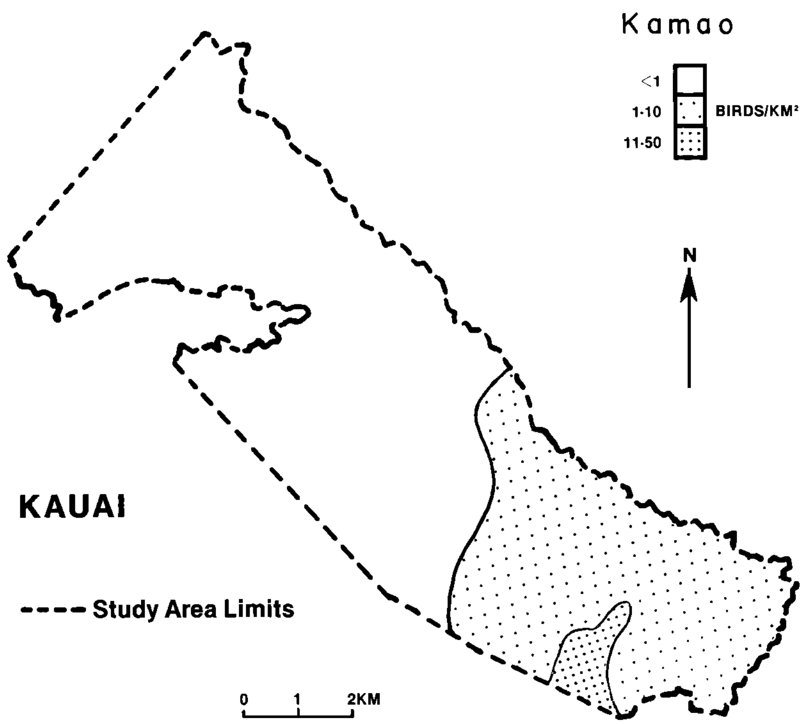



FIGURE 80. Distribution and abundance of the Kamao in the Kauai study area.

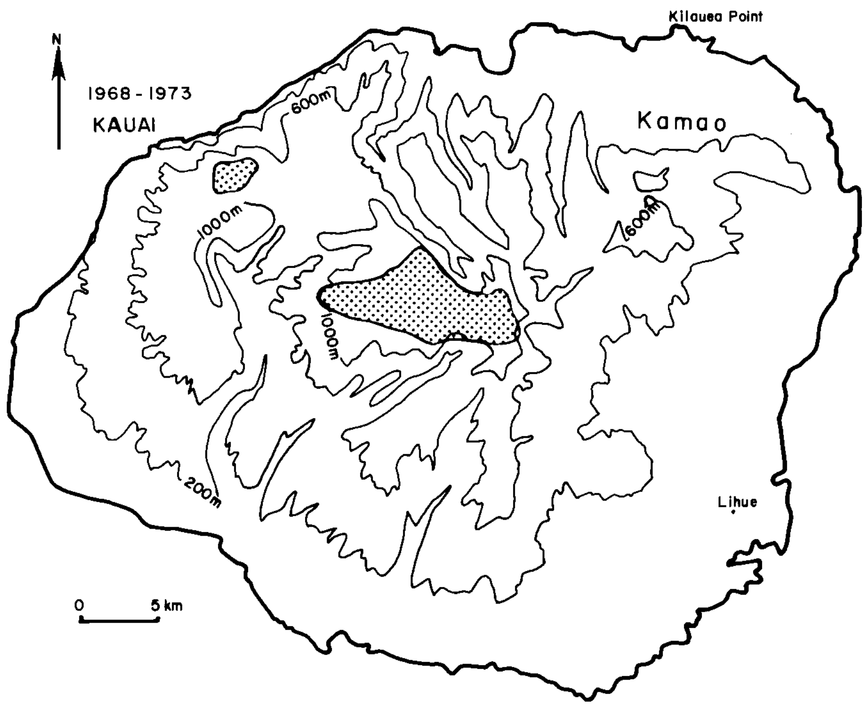



FIGURE 81. Range of the Kamao on Kauai, based on 1968–1973 survey (J. L. Sincock, unpub. data).

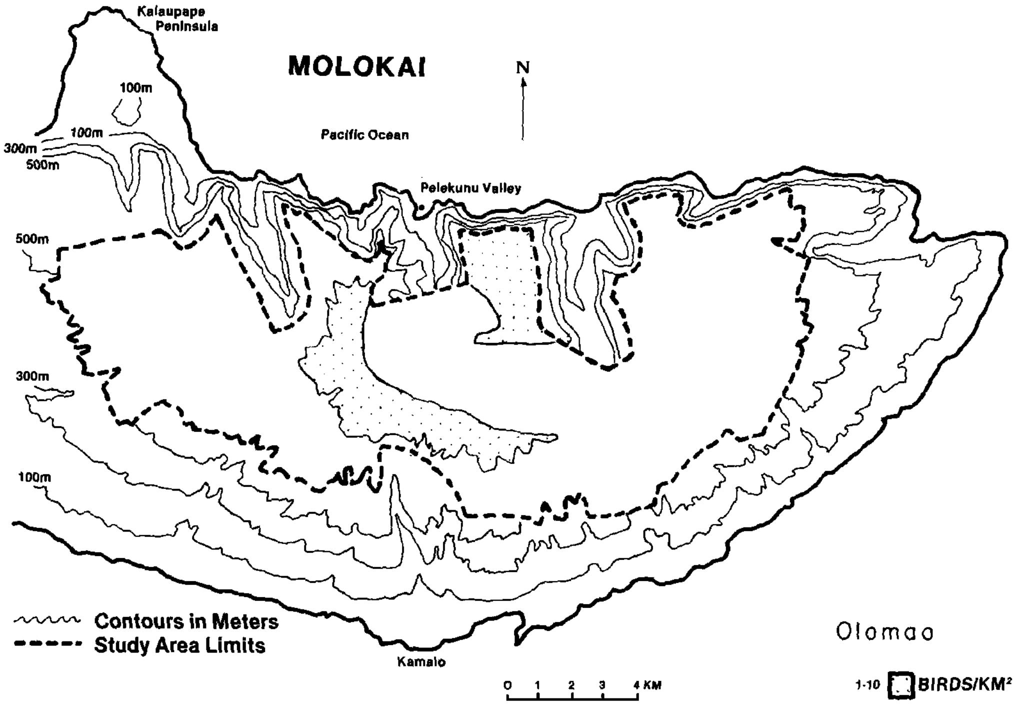



FIGURE 82. Distribution and abundance of the Olomao in the Molokai study area.

TABLE 18
DENSITY [MEAN (SE)] OF THE KAMAO, OLOMAO, OMAO, AND PUAIOHI BY ELEVATION, HABITAT, AND STUDY AREA[a]

| | Kamao | Olomao | Omao | | | | | Puaiohi |
|---|---|---|---|---|---|---|---|---|
| | Kauai | Molokai | Kau | Hamakua | Puna | Kipukas | Kona | Kauai |
| *Elevation* | | | | | | | | |
| 100–300 m | ... | 0 | ... | ... | ... | ... | ... | ... |
| 300–500 m | ... | 0 | ... | 24 (24) | 20 (3) | ... | 0 | ... |
| 500–700 m | ... | 0 | 0 | 17 (4) | 84 (5) | ... | 0 | ... |
| 700–900 m | ... | 0 | 174 (18) | 47 (4) | 117 (6) | ... | 0 | ... |
| 900–1100 m | ... | 3 (3) | 191 (13) | 90 (5) | 173 (14) | ... | 0 | ... |
| 1100–1300 m | + (+) | + (+) | 211 (11) | 96 (3) | 56 (10) | 1 (1) | 15 (8) | 1 (1) |
| 1300–1500 m | 4 (2) | + (+) | 236 (9) | 149 (5) | ... | 5 (2) | 81 (7) | + (+) |
| 1500–1700 m | ... | ... | 202 (12) | 153 (6) | ... | 14 (3) | 52 (10) | ... |
| 1700–1900 m | ... | ... | 185 (13) | 129 (7) | ... | 44 (4) | 3 (2) | ... |
| 1900–2100 m | ... | ... | 44 (8) | 52 (7) | ... | 4 (1) | 0 | ... |
| 2100–2300 m | ... | ... | 0 | 0 | ... | 9 (3) | 1 (1) | ... |
| 2300–2500 m | ... | ... | ... | ... | ... | ... | 0 | ... |
| 2500–2700 m | ... | ... | ... | ... | ... | ... | ... | ... |
| 2700–2900 m | ... | ... | ... | ... | ... | ... | ... | ... |
| 2900–3100 m | ... | ... | ... | ... | ... | ... | ... | ... |
| *Habitat* | | | | | | | | |
| Ohia | 2 (1) | 1 (1) | 178 (6) | 118 (3) | 88 (4) | 15 (2) | 10 (4) | 1 (+) |
| Koa-ohia | ... | ... | 222 (8) | 92 (3) | ... | 34 (6) | 51 (7) | ... |
| Koa-mamane | ... | ... | ... | 28 (13) | ... | 8 (3) | 0 | ... |
| Mamane-naio | ... | ... | ... | ... | ... | ... | 0 | ... |
| Mamane | ... | ... | ... | ... | ... | ... | 0 | ... |
| Other natives | ... | 0 | ... | 38 (6) | ... | 39 (20) | 0 | ... |
| Intro. trees | ... | 0 | ... | 41 (7) | ... | ... | 0 | ... |
| Treeless | 0 | 0 | 40 (28) | 35 (4) | 12 (12) | 14 (11) | 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.

able habitat appears to occur outside the present range. The contraction of the range of the Kamao into the Alakai occurred approximately simultaneously with similar contractions by several other native species.

OLOMAO (*Myadestes lanaiensis*)

Olomao were almost ubiquitous in the forests of Molokai and Lanai in the 1890s (Perkins 1903), but the decline in numbers and reduction in range occurred before the 1930s (Munro 1944). Aside from a secondhand report for West Maui (Perkins 1903), there was no evidence that this species ever occurred on Maui until S. L. Olson and H. F. James (pers. comm.) unearthed fossils at Ulupalakua in 1982. The chances of our having missed a population of 100 birds in the Maui study areas are quite low (Table 12). Olomao feed opportunistically on fruit and to a lesser extent on insects and land snails (Henshaw 1902, Perkins 1903).

The population on Molokai (Fig. 82), estimated at 19 ± 38 (95% CI), is a small remnant and appears to have a low probability of long-term survival. Suitable habitat appears to be abundant. We found birds on Olokui Plateau (3 HFBS sightings), and in Kamakou Preserve and adjacent areas (2 sightings by Scott et al. [1977] and 3 HFBS sightings). Olomao generally occur above 1000 m elevation (Table 18).

# OMAO
## *Myadestes obscurus*

OMAO (*Myadestes obscurus*)

Omao were abundant and widespread in the denser forests on Hawaii above 300 m elevation (Henshaw 1902, Perkins 1903). They now occupy only about 30% of their former range on Hawaii (van Riper and Scott 1979). Omao feed opportunistically on fruit and to a lesser extent on insects and land snails (Henshaw 1902, Perkins 1903, van Riper and Scott 1979, Berger 1981). Perkins (1903) reported that birds migrated in the forests to caterpillar outbreaks, although we have noted only relatively localized movement. Most Omao nests have been found in cavities and on protected platforms (van Riper and Scott 1979). This may be a bioenergetic adaptation for the cold wet environment of montane rainforests, reflecting the close relationship with other *Myadestes* solitaires.

Omao are widespread and common in the forests of windward Hawaii, but are absent from Kohala and most of Kona (Tables 10, 18, Figs. 83–85). Two well-established populations

TABLE 19
REGRESSION MODELS FOR HABITAT RESPONSE OF THE KAMAO, OMAO, AND PUAIOHI[a]

| | Kamao | Omao | | | | Puaiohi |
|---|---|---|---|---|---|---|
| | Kauai | Kau | Hamakua | Puna | Kipukas | Kauai |
| $R^2$ | 0.12* | 0.36* | 0.57* | 0.64* | 0.32* | 0.04 |
| Moisture | X | 3.6* | ... | 7.4* | ... | X |
| Elevation | 3.9* | 6.4* | 20.7* | 5.9* | 3.2 | ... |
| (Elevation)$^2$ | ... | −5.8* | −16.4* | −4.8* | −3.6* | ... |
| Tree biomass | 2.2 | −2.0 | ... | ... | ... | ... |
| (Tree biomass)$^2$ | ... | 4.5* | 3.1 | −2.4 | 5.6* | ... |
| Crown cover | ... | ... | −5.9* | 3.8* | ... | ... |
| Canopy height | ... | ... | ... | ... | ... | ... |
| Koa | X | ... | −7.8* | X | ... | X |
| Ohia | X | ... | 7.4* | ... | ... | X |
| Naio | X | X | X | X | ... | X |
| Mamane | X | X | ... | ... | ... | X |
| Intro. trees | X | X | −3.9* | ... | X | X |
| Shrub cover | ... | 3.1 | 3.2 | ... | ... | ... |
| Ground cover | ... | ... | −7.5* | ... | ... | ... |
| Native shrubs | ... | ... | 2.3 | ... | ... | ... |
| Intro. shrubs | ... | X | 9.4* | −2.9 | ... | ... |
| Ground ferns | ... | X | X | ... | 2.4 | ... |
| Matted ferns | ... | ... | ... | ... | ... | ... |
| Tree ferns | ... | ... | X | 6.0* | X | ... |
| Ieie | ... | X | X | ... | X | ... |
| Passiflora | X | X | −8.3* | X | X | X |
| Native herbs | ... | X | X | ... | 2.3 | ... |
| Intro. herbs | ... | X | X | −6.3* | −4.0* | ... |
| Native grasses | ... | ... | 6.7* | 4.8* | ... | ... |
| Intro. grasses | ... | ... | 7.5* | −3.8* | −3.8* | ... |
| Ohia flowers | ... | ... | 4.1* | ... | −5.1* | ... |
| Olapa fruit | ... | ... | ... | ... | ... | 2.5 |
| Mamane flowers | 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.

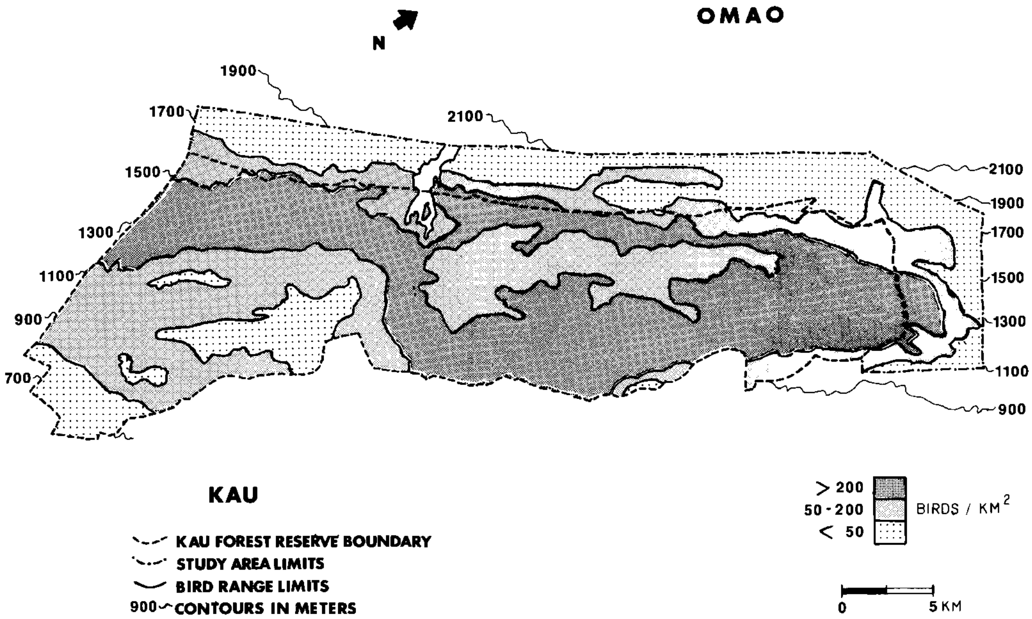



FIGURE 83. Distribution and abundance of the Omao in the Kau study area.

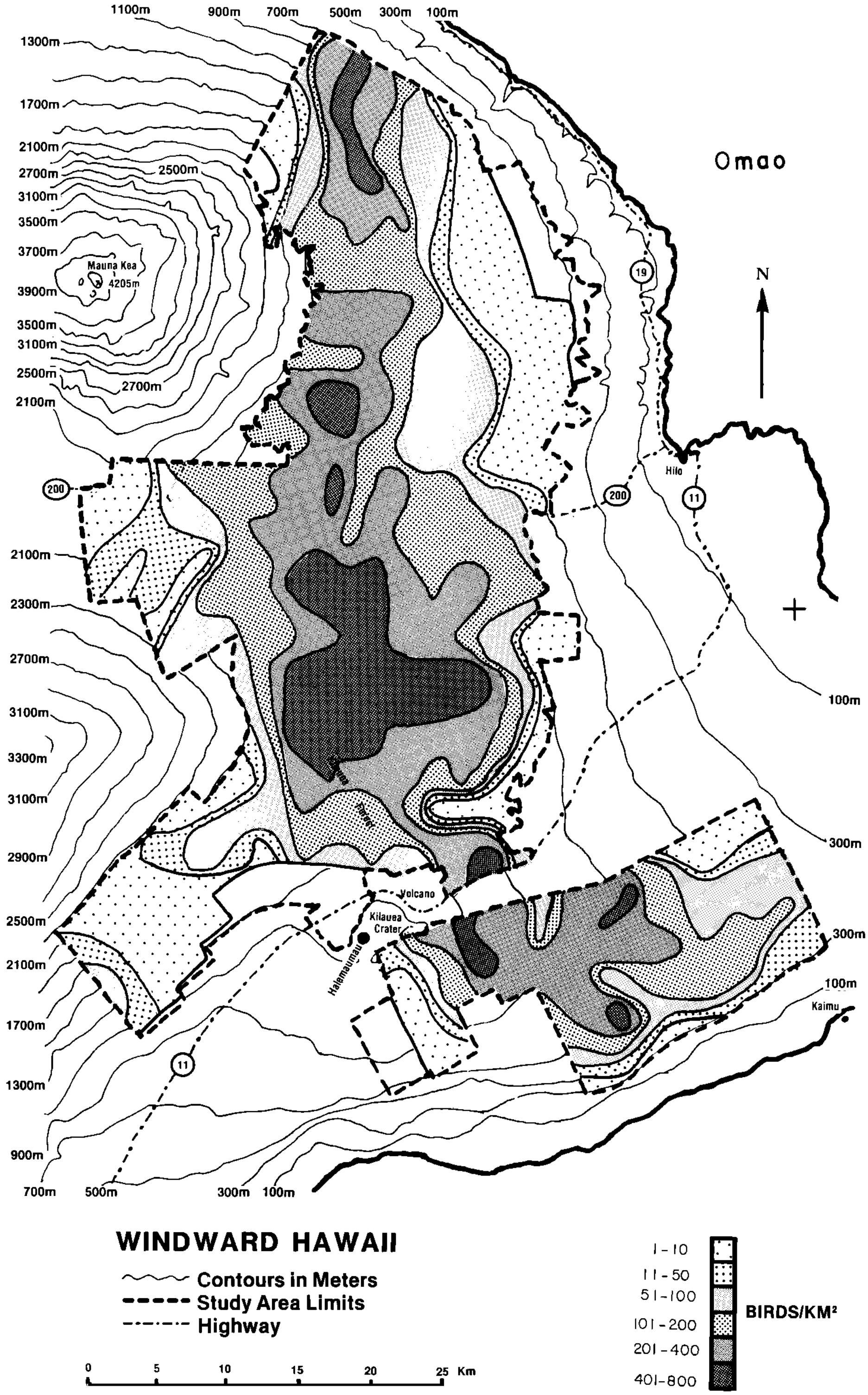



FIGURE 84. Distribution and abundance of the Omao in the windward Hawaii study areas.

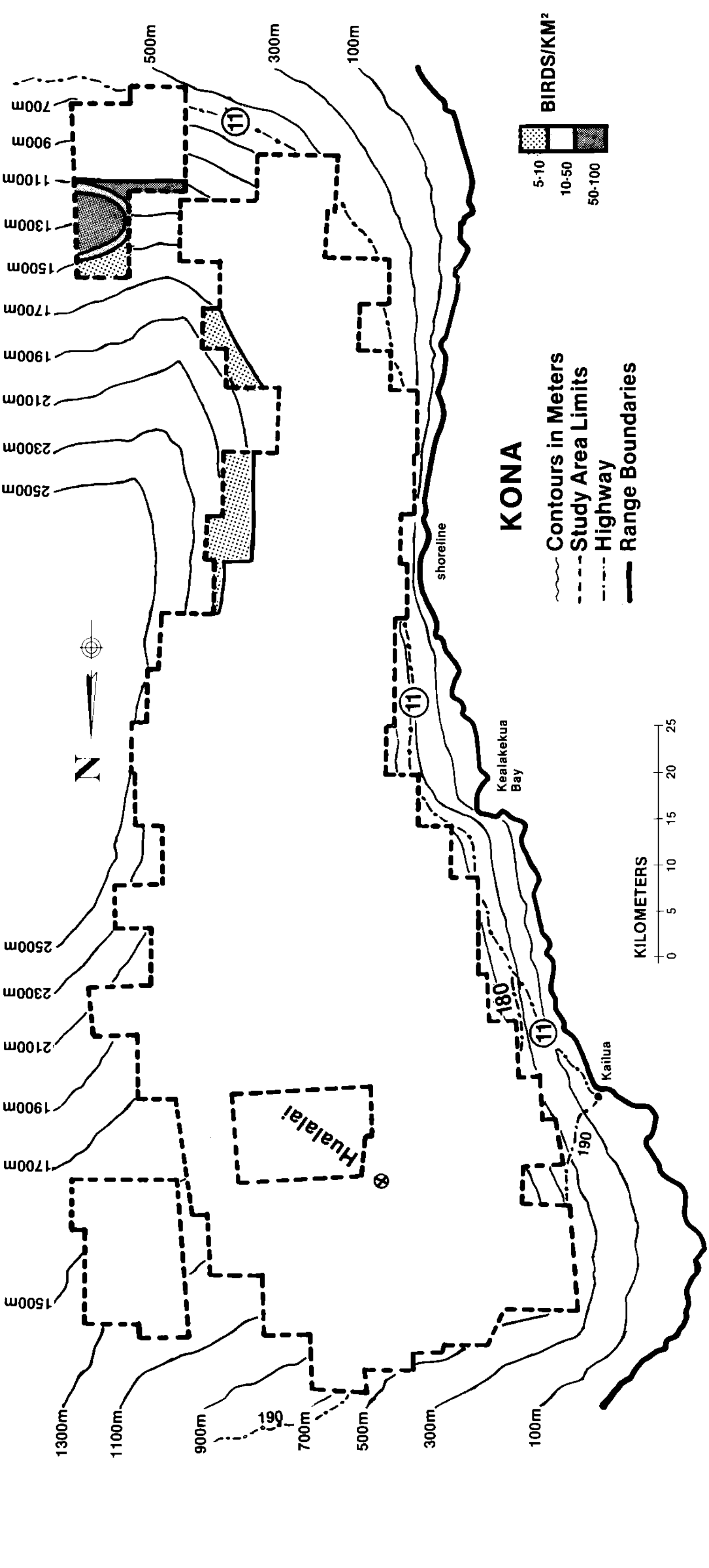



FIGURE 85. Distribution and abundance of the Omao in the Kona study area.

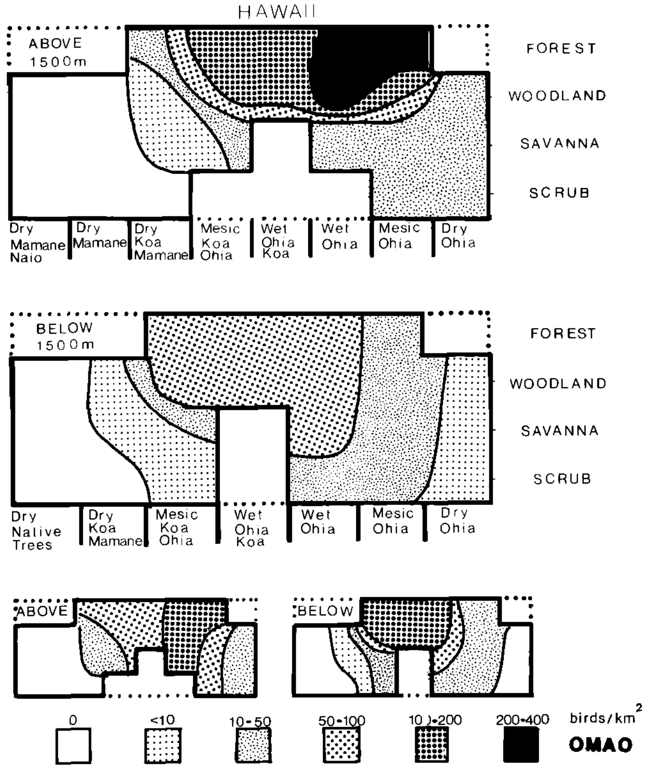



FIGURE 86. Habitat response graphs of the Omao. (Graphs give mean density above and below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

occur on Hawaii, the 56,000 ± 3000 (95% CI) Kau birds weakly separated from the 113,000 ± 3000 Hamakua and Puna birds by deforested rangeland on the Kapapala Tract. A third population may exist above the areas we sampled in the alpine scrub on Mauna Loa from 2000 to 3000 m elevation (Dunmire 1961, van Riper and Scott 1979, Conant 1981). The few birds observed in Kona seemed to represent birds from the margins of the Kau and alpine populations, and not remnants of the original Kona forest population.

Highest observed densities of Omao occur in the Kau study area. Fairly high numbers at lower elevations in Kau and Puna indicate a robust population not threatened by extinction. The absence from low elevations in north Hamakua appears to be a distributional anomaly of unknown origin. Population studies in Hawaii Volcanoes National Park suggest that bird densities increased during 1940–1975 in ohia rainforest near Kilauea Crater and in koa-ohia parkland along the Mauna Loa Strip Road (Baldwin 1953, Conant 1975, Banko and Banko 1980).

The habitat response graph (Fig. 86) shows that Omao are common in mesic and wet ohia forests above 1500 m elevation. Omao are much less common in shrub and savanna, and do not occur in low rainfall habitats (left end of response graphs). A strong negative response to passiflora (banana poka in this case) is seen in the regression model for the Hamakua area (Table 19). Habitat response to introduced shrubs and introduced grasses appears to differ between the Hamakua and Puna areas.

If reported correctly, the habit of migrating to local areas of food abundance would have made birds especially likely to contract avian disease. Malaria or pox susceptibility combined with seasonal movement may explain the early extinction over most of Kona.

# PUAIOHI
## *Myadestes palmeri*

PUAIOHI [SMALL KAUAI THRUSH]
(*Myadestes palmeri*)

Puaiohi are very rare birds of the high-elevation ohia forests in the Alakai Swamp (Richardson and Bowles 1964, Sincock et al. 1984). They were always rare historically (Perkins 1903), and their biology is little known. Puaiohi feed primarily on fruit and insects (Richardson and Bowles 1964, Sincock et al. 1984).

The first known nest was found during the HFBS (Kepler and Kepler 1983); it was constructed on a shelf in a cliff face adjacent to a stream and was similar in appearance, construction, and placement to nests of Townsend's Solitaire (*Myadestes townsendi*). The similarity of the nests of these two species supports the placement of *Phaeornis* in *Myadestes* (Pratt 1982). A second nest similar to the first was found in 1983 (Ashman et al. 1984). Like Omao (van Riper and Scott 1979), Puaiohi seem to be cavity and platform nesters. Although this behavior may be bioenergetically adaptive to the cold wet environment of montane rainforests, it is probably retained from the putative mainland ancestors; Townsend's Solitaire was suggested as the closest living relative (Pratt 1982).

We detected 13 Puaiohi during our intensive surveys of the Alakai Swamp (Table 11, Fig. 87). Five more were recorded outside the count periods. We estimated the population at 20 ± 34 (95% CI) birds (Tables 11 and 18). This compares with an estimate of 176 ± 192 birds for all of Kauai in 1968–1973 and 97 ± 129 for our study area by Sincock et al. (1984). Sincock et al. (1984) found that this species occurred through all but the southwest portion of the Alakai Swamp, and on Laau Ridge, with an isolated occurrence at Kokee State park (Fig. 88).

In the 1890s Kamao were 100 times more numerous than Puaiohi (Perkins 1903). They are now about equally common on Kauai, and both taxa apparently experienced a tenfold drop in populations during the 1970s. Both our data and Sincock's indicate that Puaiohi are more common than Kamao in the north half of the Alakai, and that Kamao are more common in the south Alakai. Sincock et al. (1984) found that Puaiohi had retreated from the Kokee State Park area, along with the other endangered passerines. Puaiohi are most frequently encountered near stream banks covered with ferns, sedges, and mosses (Sincock et al. 1984). Future efforts to determine population size should consider this in allocating sampling effort.

The regression model (Table 19) shows that Puaiohi are associated with olapa fruit. Although small sample sizes are involved, this result is probably accurate, because olapa fruit constitute a chief dietary item (Richardson and Bowles 1964).

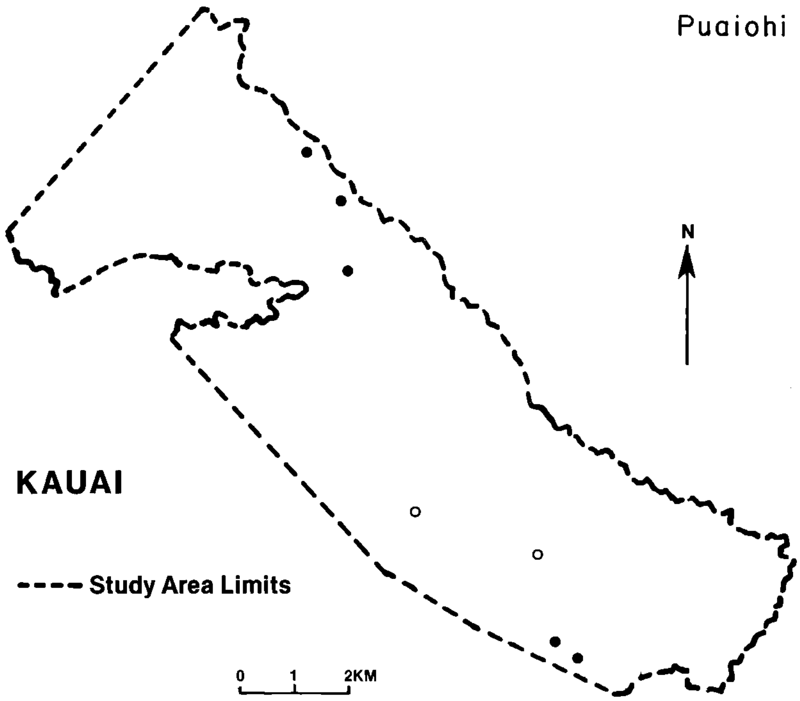



FIGURE 87. Distribution and abundance of the Puaiohi (Small Kauai Thrush) in the Kauai study area. (Solid circles mark count records; open circles mark incidental observations during the survey period.)

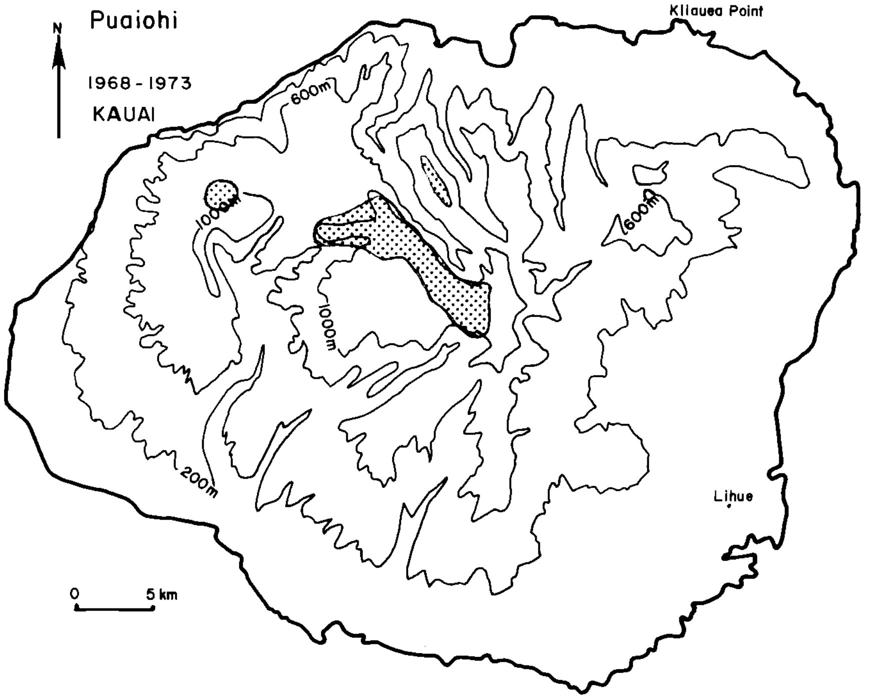



FIGURE 88. Range of the Puaiohi (Small Kauai Thrush) on Kauai, based on 1968–1973 survey (J. L. Sincock, unpub. data).

# KAUAI OO
## *Moho braccatus*

KAUAI OO [OOAA] (*Moho braccatus*)

Also known as the Ooaa, the Kauai Oo is the smallest of the four oo species found in the Hawaiian Islands, and is endemic to Kauai. In the 1890s, they were common forest birds from near sea level to the highest elevations (Munro 1944). Fossils have been found in former dry lowland forest areas (Olson and James 1982b). Kauai Oo apparently suffered a drastic decline in numbers shortly after 1900, as Munro (1944) was unable to locate them in the 1920s and 1930s. They were sighted in 1936 and 1940 (Donaghho 1941), rediscovered in 1960 (Richardson and Bowles 1961), and have been recorded regularly since (Sincock et al. 1984). Sincock located the first nest in 1971 in a tree cavity and found similar nests in 1972 and 1973. Kauai Oo feed primarily on invertebrates but also take olapa fruit and nectar from ohia and other plants (Perkins 1903, Richardson and Bowles 1964).

We estimated a total population of only 2 ± 2 (95% CI) Kauai Oo; we found one pair, recorded six times during our 1981 survey (Tables 11, 20, Fig. 89). They were carrying nesting material and giving the "beep beep" call of nesting birds. There may be little hope for the continued survival of this species. Because of the loud, easily identified call during the breeding season, it seems unlikely that we missed any breeding pairs in the study area, although possibly a few nonbreeding birds were overlooked, and additional birds may occur outside the area. The pair we found was in a stream valley in the south Alakai Swamp in dense, closed ohia-olapa forest with a closed, native understory typical of that region. Richardson and Bowles (1964) described the habitat of the species as thick forest, with the birds preferring high elevation canyons instead of forested ridges.

In 1960 Richardson and Bowles (1964) found a small population near the head of Koaie Stream. Sincock et al. (1984) estimated a total of 36 ± 29 (95% CI) birds for 1968–1973, with only 12 ± 17 occurring in our study area. Sincock found the species only within the southeast and southwest areas of the Alakai Swamp (Fig. 90), except possibly for one unidentified large dark bird fleetingly sighted on Namolokama Mountain in 1968. This species has steadily declined in numbers since 1968 and retreated from the Koaie Stream area; the last known birds are located in a very remote area of the Alakai (Sincock et al. 1984). Because this area has torrential rainfall and Richardson and Bowles (1964) found no Kauai Oo in this area, the habitat may be marginal. In 1983 J. L. Sincock and P. W. Sykes, Jr., found one remaining bird at a nest site in the central Alakai Swamp; no evidence of its mate was found over a three-day period. In 1984 U.S.F.W.S. biologists saw one bird and heard a possible second in the same area in May, and saw a single bird in September.

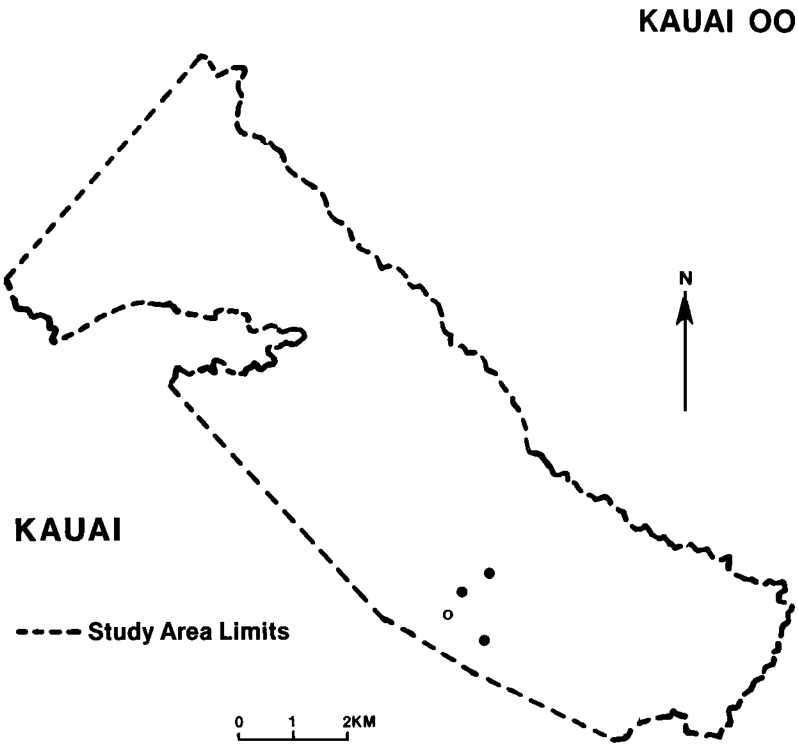



FIGURE 89. Distribution and abundance of the Kauai Oo (Ooaa) in the Kauai study area. (Circles mark count records.)

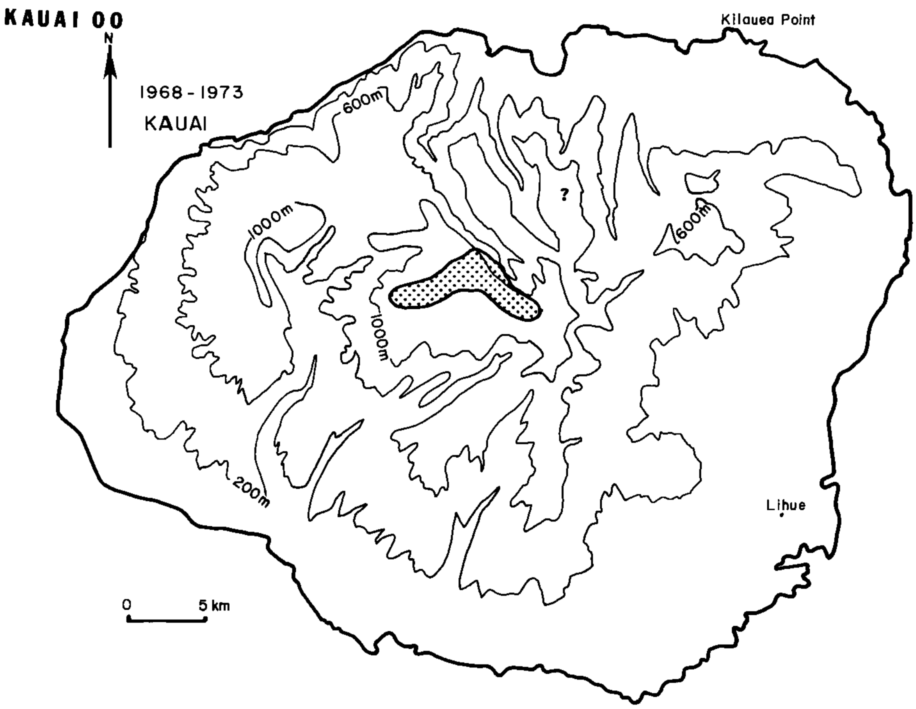



FIGURE 90. Range of the Kauai Oo (Ooaa) on Kauai, based on 1968–1973 survey (J. L. Sincock, unpub. data).

TABLE 20
DENSITY [MEAN (SE)] OF THE KAUAI OO, OU, PALILA, MAUI PARROTBILL, ANIANIAU, AND NUKUPUU BY ELEVATION, HABITAT, AND STUDY AREA[a]

| | Kauai Oo | Ou | | | Palila | Maui Parrotbill | Anianiau | Nukupuu |
|---|---|---|---|---|---|---|---|---|
| | Kauai | Hamakua | Puna | Kauai | Mauna Kea | E. Maui | Kauai | E. Maui |
| *Elevation* | | | | | | | | |
| 100–300 m | ··· | ··· | ··· | ··· | ··· | ··· | ··· | ··· |
| 300–500 m | ··· | 0 | 0 | ··· | ··· | 0 | ··· | 0 |
| 500–700 m | ··· | 0 | 0 | ··· | ··· | 0 | ··· | 0 |
| 700–900 m | ··· | 0 | + (+) | ··· | ··· | 0 | ··· | 0 |
| 900–1100 m | ··· | + (+) | 0 | ··· | ··· | 0 | ··· | 0 |
| 1100–1300 m | + (+) | 1 (1) | 0 | ··· | ··· | 3 (3) | 235 (14) | 0 |
| 1300–1500 m | + (+) | 8 (3) | ··· | 0 | ··· | 9 (5) | 276 (18) | 7 (7) |
| 1500–1700 m | ··· | + (+) | ··· | + (+) | ··· | 7 (3) | ··· | + (+) |
| 1700–1900 m | ··· | + (+) | ··· | ··· | ··· | 15 (5) | ··· | + (+) |
| 1900–2100 m | ··· | 0 | ··· | ··· | 10 (5) | 21 (17) | ··· | + (+) |
| 2100–2300 m | ··· | 0 | ··· | ··· | 37 (12) | + (+) | ··· | + (+) |
| 2300–2500 m | ··· | ··· | ··· | ··· | 18 (4) | 0 | ··· | 0 |
| 2500–2700 m | ··· | ··· | ··· | ··· | 18 (5) | 0 | ··· | 0 |
| 2700–2900 m | ··· | ··· | ··· | ··· | 9 (5) | 0 | ··· | 0 |
| 2900–3100 m | ··· | ··· | ··· | ··· | + (+) | ··· | ··· | ··· |
| *Habitat* | | | | | | | | |
| Ohia | + (+) | 4 (2) | + (+) | + (+) | ··· | 12 (3) | 255 (11) | 4 (4) |
| Koa-ohia | ··· | 0 | ··· | ··· | ··· | + (+) | ··· | + (+) |
| Koa-mamane | ··· | 0 | ··· | ··· | ··· | ··· | ··· | ··· |
| Mamane-naio | ··· | ··· | ··· | ··· | 24 (4) | ··· | ··· | ··· |
| Mamane | ··· | ··· | ··· | ··· | 9 (3) | 0 | ··· | 0 |
| Other natives | ··· | 0 | ··· | ··· | ··· | 0 | ··· | 0 |
| Intro. trees | ··· | 0 | ··· | ··· | ··· | 0 | ··· | 0 |
| Treeless | 0 | 0 | 0 | 0 | ··· | 0 | 44 (44) | 0 |

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

# BISHOP'S OO
*Moho bishopi*

BISHOP'S OO (*Moho bishopi*)

This species has been collected only from Molokai where birds were last seen in 1904 (Munro 1944), and where more recent searches have failed to find them (Richardson 1949; Pekelo 1963a, 1963b, 1967; Pratt 1974; Scott et al. 1977; HFBS data).

Munro (1944:86) described Bishop's Oo as "active birds in the low trees on the gulch wall. They were inquisitive and though they approached me closely, they were timid and continually on the alert; never still an instant, chattering continuously. They stayed for some time before taking fright and leaving." Perkins (1903: 442) stated that they were "easily called by imitating [the] cry, though [they] will not infrequently come and inspect the intruder uncalled . . . [they] rarely expose [themselves] to more than a momentary view, diving beneath the foliage of the bushes at the slightest alarm." Perkins noted that the call was sometimes audible at a distance of 1000 m.

Based on these descriptions, we used an effective detection distance of 75 m in determining the probability of our finding Bishop's Oo or a similar species on Molokai and Maui (Table 12). We estimated the probability of detecting an extant population of 10, 50, and 100 birds on Maui at 0.49, 0.97, and 0.99, respectively. Probabilites are lower for Molokai.

Oo have been reported from Maui since 1828 (Banko 1980–1984), the most notable sightings being by Henshaw (1902) and Sabo (1982). In these two sightings the observers were convinced that the bird was an adult oo, possibly Bishop's Oo from the field marks; these records have been accepted by Pyle and Ralph (1982) and the A.O.U. (1983). Until a specimen or photograph is obtained, however, the specific identity of the "Maui Oo" remains debatable. The most recent sightings were from ohia rainforests on the northeast slopes of Haleakala, in the Hanawi watershed at 1600–2000 m elevation. There was one incidental sighting of an unidentified black bird with an oo silhouette from that area during the 1980 HFBS and another by D. Boynton (pers. comm.) in 1983. Fossils of *Moho* sp. occur on Maui (S. L. Olson, pers. comm.).

Bishop's Oo are primarily nectarivorous and were said to especially prefer lobeliad nectar (Perkins 1903). Lobeliads are particularly sensitive to habitat degradation by pigs, indicating that pigs posed an indirect threat to the species.

HAWAII OO (*Moho nobilis*)

Hawaii Oo were one of the most spectacular native birds. They were aggressive birds at the top of the dominance hierarchy of nectarivores and displaced Iiwi, Hawaii Mamo, and Apapane from nectar sources (Perkins 1903).

Once widely distributed throughout the forests on Hawaii, Hawaii Oo were commonly found from 400 to 1200 m elevation (Wilson and Evans 1890–1899), with seasonal movements to 1800 m (Rothschild 1893–1900). Perkins (1893) noted that they occurred mostly from 500 to 900 m elevation, inhabited ohia and koa-ohia forests, but deserted forests opened up by cattle. Hawaii Oo had disappeared by 1896 from the Puu Lehua area in Kona (Banko 1980–1984).

Records of this species occurring seasonally in the mamane forests of the Mauna Kea-Mauna

Loa saddle (Wilson and Evans 1890–1899) suggest that they may have exploited the rich nectar sources in that forest by daily movements up the mountain, similar to the mass movements still seen for Iiwi and Apapane (Baldwin 1953; MacMillen and Carpenter 1980; C. B. Kepler and J. M. Scott, pers. observ.).

Hawaii Oo were very common during the 1800s, and as late as 1898 more than 1000 were collected for the feather trade above Hilo (Henshaw 1902). By the turn of the century, they had decreased drastically (Perkins 1903). There have been numerous unverified records during the 1900s with several reports even into the 1970s on windward Mauna Kea, but none by trained biologists (Banko 1980–1984). We failed to sight Hawaii Oo or other unidentified black birds on Hawaii.

Hawaii Oo apparently seldom sang (Perkins 1903) but had a very loud and distinctive call uttered frequently before 09:00 that could be heard at great distances. Perkins (1903) heard the call from 800 m away and described it as "unlike that of any native bird and no one who has once heard it and identified it can ever again be in doubt as to the bird." This species was very active, "constantly on the move from tree to tree, hardly ever at a less height than [30 m] from the ground" (Wilson and Evans 1890–1899).

These descriptions of the behavior contrast with others that these were the most timid and wary of forest birds and flew off as soon as a human was sighted (Munro 1944:87). Based on the descriptions in the literature and our experience with Kauai Oo, we estimated the effective detection distance for Hawaii Oo to be 75 m. The chances of our having overlooked a population of 100 birds in the study areas on Hawaii are small (Table 12).

KIOEA (*Chaetoptila angustipluma*)

Kioea were the largest historically known Hawaiian meliphagids, and were lively nectarivores (Munro 1944). Only four specimens of this poorly known species were collected, all in the 19th century from the island of Hawaii (Banko 1979). The areas mentioned in discussions of the range were the eastern slopes of Mauna Loa northwest of Kilauea Crater and the saddle area between Mauna Loa and Mauna Kea, corresponding to our Hamakua and Kipukas study areas. Recent findings of Olson and James (1982b, pers. comm.) indicate that similar species occurred on Oahu and East Maui. From the fossil records and fragmentary natural history notes, it appears that Kioea occurred primarily in dry woodlands or scrublands below 1500 m elevation.

The only descriptions of Kioea vocalizations were by Peale (1848) who found them "disposed to be musical," and Pickering (in Cassin 1858) who saw them land in the tops of trees and utter a loud "chuck." We thus have little information on which to base our estimates of area surveyed for this species. Based on the limited data, we assumed they would be about as detectable as Hawaii Oo. The chances of this species still existing are remote (Table 12). We know of no records since Mills collected specimens about 1859.

## OU
## *Psittirostra psittacea*

OU (*Psittirostra psittacea*)

Ou feed principally on fruit and, to a lesser degree, on insects and nectar (Perkins 1903, Munro 1944). Perkins (1903) observed that the fruit and flowers of ieie were a chief food of Ou, and suggested that their peculiar bill may have

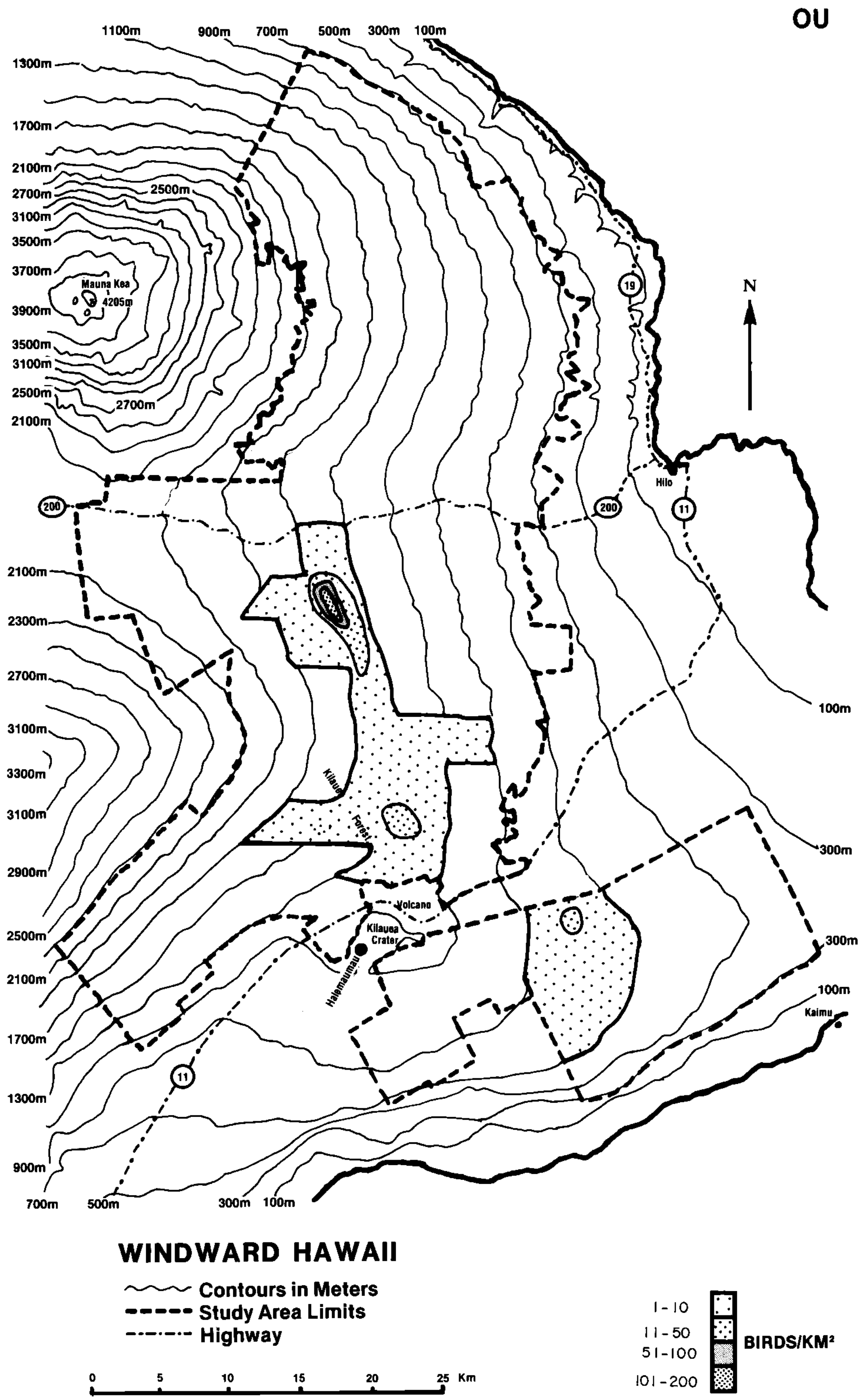



FIGURE 91. Distribution and abundance of the Ou in windward Hawaii study areas.

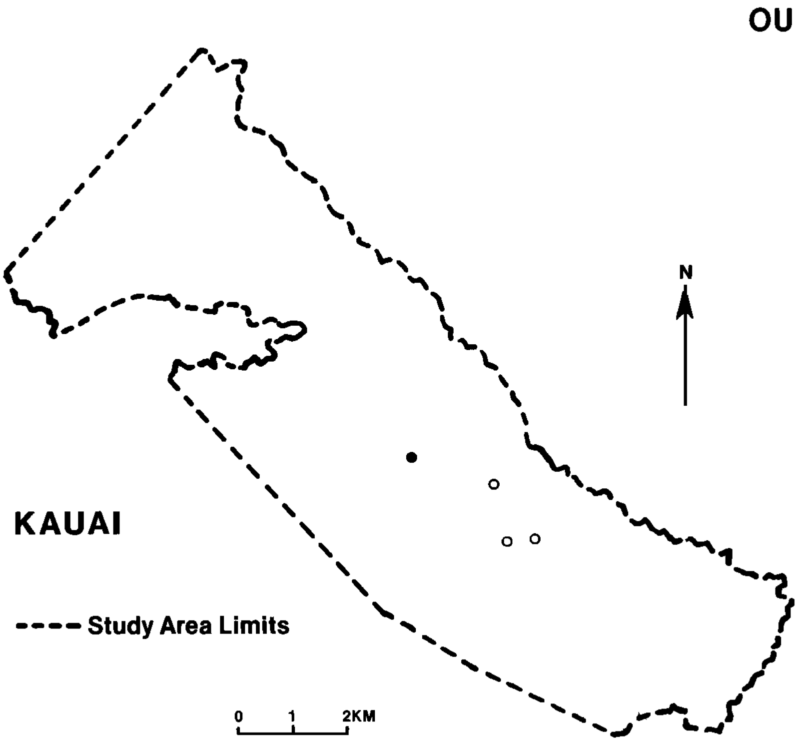



FIGURE 92. Distribution and abundance of the Ou in the Kauai study area. (Open circle marks count record; closed circles mark incidental observations during study period.)

been adapted originally for feeding on ieie. Ou also feed on other fruit, including lobliads, *Ilex, Pelea, Pipturus,* the introduced mountain apple (*Eugenia malaccensis*), guavas, and formerly banana and peach (Henshaw 1902, Perkins 1903). Ou used to wander down to lower elevations (Perkins 1893), particularly to feed on guava, and Munro (1944) suggested that this habit rendered them vulnerable to mosquito-borne diseases. The early disappearance of Ou from Kona may have been due to this habit and to the high elevational range of mosquitoes in that area.

Ou were extremely rare and localized on Hawaii and Kauai (Table 20, Figs. 91 and 92) during our survey. They were limited to two small populations, one of 400 ± 300 (95% CI) birds in the Hamakua and Puna study areas on Hawaii, the other of 3 ± 6 birds in the Alakai Swamp on Kauai.

Ou were formerly common on Hawaii, Maui, Molokai, Lanai, Oahu, and Kauai (Perkins 1903, Wilson and Evans 1890–1899). In the 1890s Ou were abundant at certain times of the year at Kilauea Crater (Perkins *in* Banko and Banko 1980). During 1936–1951, Ou appeared to be uncommon in Hawaii Volcanoes National Park from 800 to 1200 m elevation (Richards and Baldwin 1953), although areas in range from 1200 to 1500 m may have been rarely visited. Baldwin (1953) recorded Ou on 5 of 23 plot counts at Napau Crater (870 m elevation), with as many as six in one day; Richards found 15 in one day on the Olaa Tract. Location concentrations were found during our survey on the Olaa Tract and in the kipukas below Powerline Road in Upper Waiakea Forest Reserve, where as many as 12 birds were counted on one station. Ou have been infrequently seen in ohia rainforest near Kilauea Crater (van Riper 1978a) and east of Napau Crater (D. Reeser, pers. comm.), in mesic ohia woodland near Kilauea Iki, and mixed mesophytic forest at Kipuka Puaulu (S. Mountainspring, pers. observ.). One incidental record was made during our survey north of Saddle Road in the Mauna Kea forests of the Hamakua study area, but the historical record for Ou in this area is poor. A resurvey of the Ou's range in 1984 suggested that populations had declined in the Hamakua study area since 1977 (U.S.F.W.S. data).

Sincock et al. (1984) estimated a population of 62 ± 82 (95% CI) Ou on Kauai for the 1968–

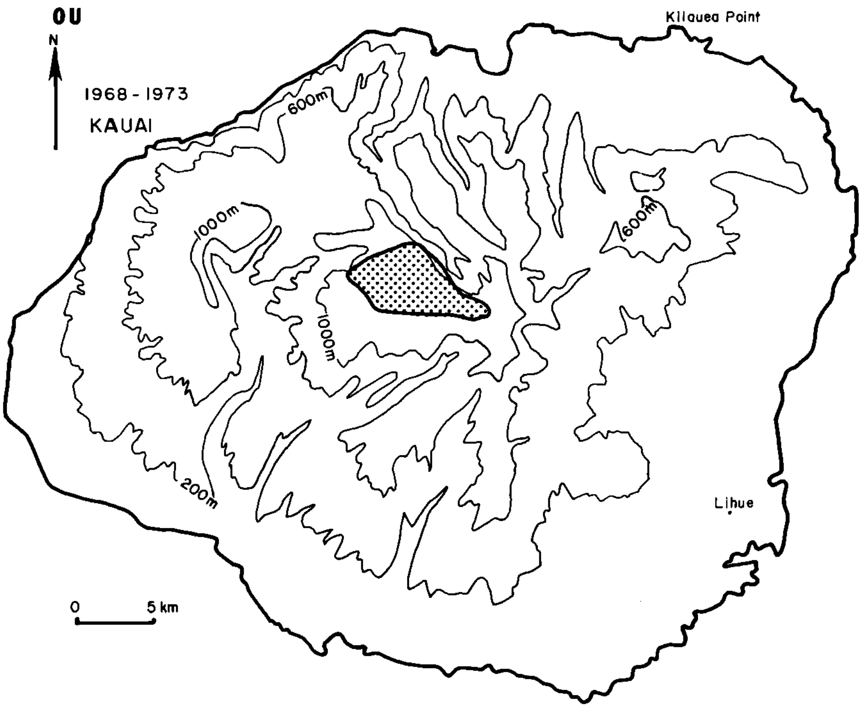



FIGURE 93. Range of the Ou on Kauai, based on 1968–1973 survey (J. L. Sincock, unpub. data).

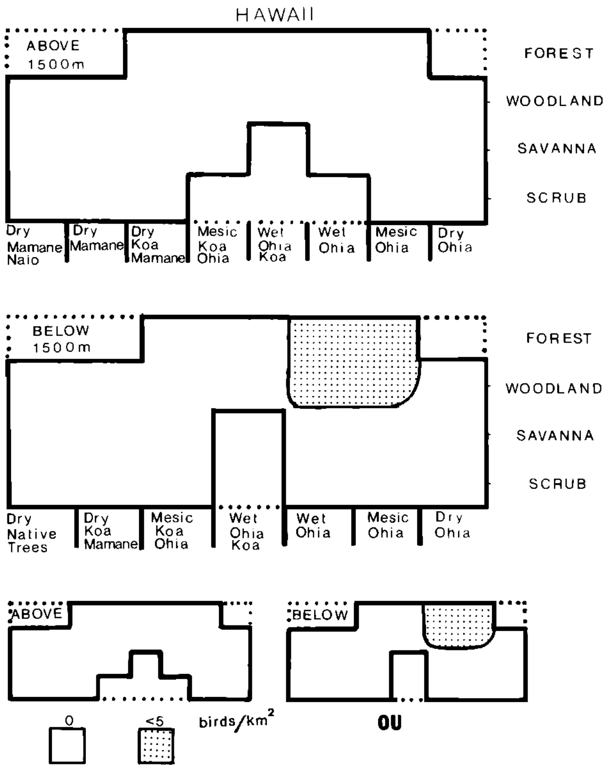



FIGURE 94. Habitat response graphs of the Ou. (Graphs give mean density above and below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

1973 period, including 34 ± 40 in our study area. His incidental observations suggest that the population increased in the mid 1970s, but by 1981 had grown quite scarce. Our data suggest a population of fewer than ten birds. A small number of birds may have occurred outside our study area. Five birds were seen flying in the same direction over a five-minute period in an incidental observation during the 1981 survey, but some of these possibly were duplicate sightings. In 1968–1973 Ou occurred chiefly in the central and southeast areas of the Alakai Swamp (Fig. 93). Like other endangered Kauai passerines, Ou are retreating to the core of the Alakai Swamp.

During our survey Ou were most abundant on Hawaii from 1300 to 1500 m elevation and were recorded as low as 900 m in Puna. The habitat response graphs show that Ou occupy mesic to wet ohia forests and woodlands, but are absent from koa forests and parkland (Fig. 94). The absence in koa is also reflected in the regression model for habitat response (Table 21). Ou appear to occupy a restricted range of habitats compared to the range recorded in historical accounts; Perkins (1903), for example, noted seasonal occurrences in koa forests and dry montane woodlands on Hawaii. Baldwin (1953) found Ou in tree ferns and the upper parts of trees; our survey found them in similar areas, often in the vicinity of *Tetraplasandra* trees, whose fruit they probably feed upon (see also Mull and Mull 1971).

Because of the Ou's vocal nature, the probability is low that we failed to detect a population as large as 100 birds in those areas where they are widely regarded as extinct (Table 12).

The absence of Ou in the Kau study area may reflect the lack of extensive tracts of wet forest at low elevations in this area. Low elevation forests may have provided food or shelter during seasonal periods of resource shortage or inclement weather at higher elevations. In Kona we speculate that Ou became extinct because of (1) extensive conversion of low elevation forest to agriculture by 1900, (2) habitat fragmentation at mid and upper elevations, and (3) early spread of disease in leeward Hawaii. That Ou were much more common at lower elevations on Hawaii as recently as the 1940s (Richards and Baldwin 1953) suggests that additional limiting factors may have come into play.

# PALILA
## *Loxioides bailleui*

Palila (*Loxioides bailleui*)

Palila occurred historically in the mamane-naio forests on west and southwest Mauna Loa and on Mauna Kea. They presently occur only on the upper slopes of Mauna Kea. The population has fluctuated between 1600 and 6400 birds since 1975, and has been studied to a greater extent than most other endangered species (Berger 1970, van Riper et al. 1978, van Riper 1980, Scott et al. 1984). Fossil records reveal that Palila

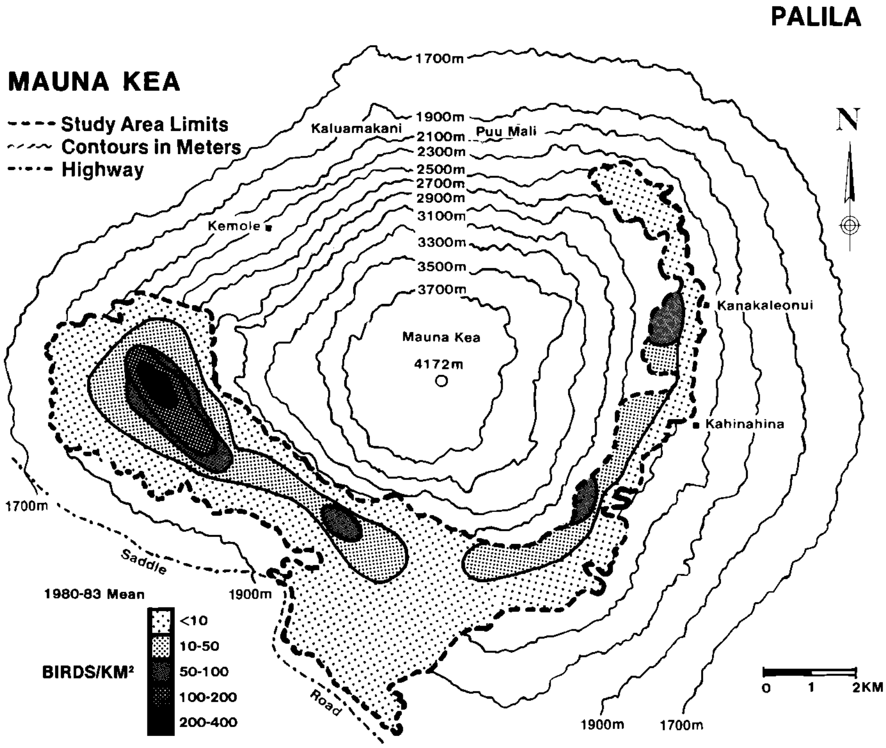



FIGURE 95. Distribution and abundance of the Palila in the Mauna Kea study area.

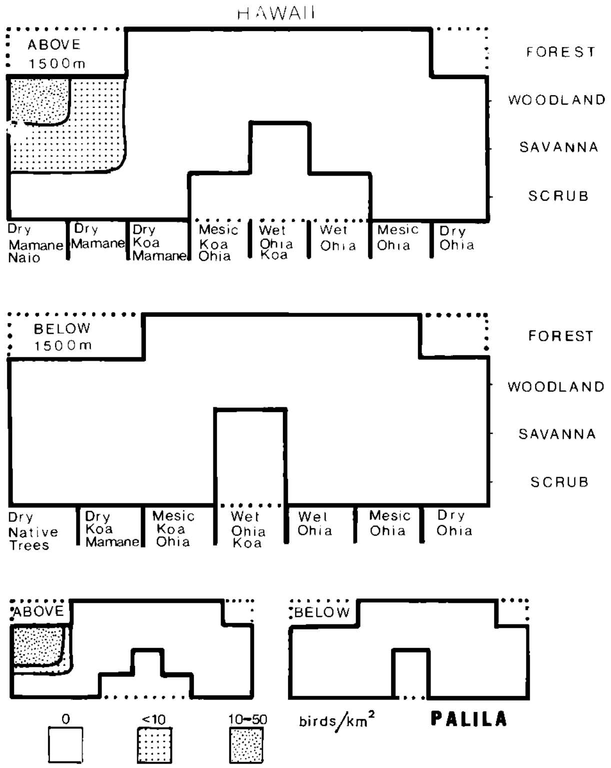


TABLE 21
REGRESSION MODELS FOR HABITAT RESPONSE OF THE OU, PALILA, MAUI PARROTBILL, ANIANIAU, AND AKIAPOLAAU[a]

| | Ou | Palila | Maui Parrotbill | Anianiau | Akiapolaau | | | |
|---|---|---|---|---|---|---|---|---|
| | Hamakua | Mauna Kea | Maui | Kauai | Kau | Hamakua | Kona | Mauna Kea |
| $R^2$ | 0.01 | 0.12* | 0.06* | 0.20* | 0.06* | 0.09* | 0.01* | 0.01 |
| Moisture | ... | X | 4.7* | X | ... | ... | ... | X |
| Elevation | ... | ... | 4.9* | ... | ... | 10.3* | ... | ... |
| (Elevation)$^2$ | ... | ... | ... | ... | ... | ... | ... | ... |
| Tree biomass | ... | 4.3* | 2.8 | ... | ... | ... | ... | ... |
| (Tree biomass)$^2$ | ... | ... | ... | ... | ... | ... | ... | ... |
| Crown cover | ... | ... | ... | ... | ... | ... | ... | ... |
| Canopy height | ... | ... | ... | ... | ... | ... | ... | ... |
| Koa | −2.4 | X | ... | X | 6.3* | 8.6* | 3.9* | X |
| Ohia | ... | X | ... | X | ... | ... | ... | X |
| Naio | X | ... | X | X | X | X | ... | ... |
| Mamane | ... | −3.2 | ... | X | X | −3.9* | ... | 2.1 |
| Intro. trees | ... | X | ... | X | X | ... | ... | X |
| Shrub cover | ... | ... | ... | ... | ... | ... | ... | ... |
| Ground cover | ... | ... | ... | ... | ... | 4.0* | ... | ... |
| Native shrubs | ... | X | ... | ... | ... | 6.2* | ... | X |
| Intro. shrubs | ... | X | ... | −5.7* | X | 3.0 | ... | X |
| Ground ferns | X | X | ... | 2.3 | X | X | ... | X |
| Matted ferns | ... | X | ... | ... | ... | ... | ... | X |
| Tree ferns | X | X | ... | ... | ... | X | ... | X |
| Ieie | X | X | ... | ... | X | X | ... | X |
| Passiflora | ... | X | ... | X | X | −4.5* | ... | X |
| Native herbs | X | X | ... | ... | X | X | ... | X |
| Intro. herbs | X | ... | ... | ... | X | X | ... | ... |
| Native grasses | ... | ... | 2.6 | ... | 3.6* | −4.3* | ... | ... |
| Intro. grasses | ... | ... | ... | ... | ... | −4.0* | ... | ... |
| Ohia flowers | ... | X | ... | ... | ... | −3.1 | ... | X |
| Olapa fruit | ... | X | −2.4 | ... | ... | ... | ... | X |
| Mamane flowers | X | −2.6 | ... | X | X | X | X | ... |
| Mamane fruit | X | 3.5* | 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.

originally occurred down to sea level on Oahu, thus providing "a striking example of how the distribution of native birds has been artificially modified in the Hawaiian archipelago" (Olson and James 1982b:39). Palila feed chiefly on the green pods of the mamane tree but also take naio berries and insects, especially caterpillars.

We found this species only on Mauna Kea in dry mamane and mamane-naio savanna and woodlands (Tables 10, 20, Fig. 95). Palila reach highest densities in mixed woodland near Puu Laau. Secondary population centers are located northeast of Mauna Kea State Park (Pohakuloa Gulch area) in well-developed mamane-naio woodland, on the southeast slope at timberline, and near Kanakaleonui on the east slope in a relict stand of mamane. The overall Palila distribution suggests a very tenuous connection between the eastern and western halves of the population in the vicinity of the Hale Pohaku development.

Palila range from 2000 to 3000 m elevation, reaching highest densities at 2100–2300 m (Table 20). These bounds are much higher than its 1200 to 1800 m range in Kona in 1892 (Perkins 1903). Scott et al. (1984) showed that the dis-

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FIGURE 96. Habitat response graphs of the Palila. (Graphs give mean density above and below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

tance from the upper to the lower elevational limit of mamane-naio woodland is the most important variable in determining habitat response. Palila are more common in areas with greater crown cover, taller trees, and higher proportion of native plants in the understory. Annual variation of Palila density within a habitat type is related to the levels of their staple food, mamane pods. Scott et al. (1984) suggested that the population is limited by the width of the mamane-naio zone and the abundance of mamane pods.

The habitat response graph (Fig. 96) underscores the dependence on mamane and mamane-naio woodlands, and shows lower densities in deforested areas. In some years Palila were more common in mamane than in mamane-naio. The regression model (Table 21) emphasizes tree biomass and mamane fruit; the negative mamane term reflects the low levels of mamane fruit in pure mamane areas in 1983 (Scott et al. 1984).

The probability of our having missed a population of 100 birds of this species in Kona is low (Table 12). Extensive searches of the mamane forests on Hualalai and Mauna Loa subsequent to our survey also failed to locate this species (J. L. Giffin, pers. comm.). The extinction in Kona was probably related to the contemporaneous disappearance of the other finch-billed honeycreepers, but is puzzling because of the well-developed mamane forests extant on Mauna Loa.

### Lesser Koa-Finch (*Rhodacanthis flaviceps*)

One of five large finch-billed species extant on Hawaii when Cook arrived in 1778, Lesser Koa-Finches were known only from the koa forests of the upper leeward slopes of Mauna Loa (Munro 1944). They fed on koa pods in flocks with Greater Koa-Finches, and nothing else is known of their behavior. The range was restricted to the environs of Puu Lehua, about 15 km SSE of Hualalai (Rothschild 1893–1900), and the species was probably on the verge of extinction when discovered. Originally, birds were apparently widespread in dry lowland habitat, as fossils have been found at Barber's Point on Oahu (Olson and James 1982b).

Our assumptions of effective detection distance (30 m) were based on descriptions of the very similar Greater Koa-Finch and our knowledge of Palila behavior. In assessing the possible distribution pattern, we assumed that they most likely inhabited upper elevation koa forests. There have been no records of this species since Munro and Palmer collected their specimens in 1891, and it is generally regarded as extinct (Table 12, Berger 1981).

### Greater Koa-Finch (*Rhodacanthis palmeri*)

The largest of the historically known Hawaiian honeycreepers was the Greater Koa-Finch. These birds sometimes flocked with Lesser Koa-Finches, and like them fed extensively on the seeds of the koa tree, also taking other seeds and lepidoptera larvae (Perkins 1903). Greater Koa-Finches were most numerous in koa forests at 1200 m elevation and occurred from 900 m probably to 1800 m (based on vegetation and H. Palmer's diary in Rothschild 1893–1900); they ranged in Kona from Puu Lehua (15 km SSE of Hualalai) south at least to the Honaunau Tract, and also occurred in the koa forests north of Kilauea Crater (Rothschild 1893–1900, Perkins 1903).

Munro (1944) described the song or call as "several whistled flute-like notes, the last ones prolonged" and found birds by their whistles "loud from the tops of the koas." We assumed that the calls of this species would be detectable at least to the distances (30 m) we have documented for Palila (Scott et al. 1984). In assessing the distribution, we assumed that birds would be found throughout the koa forests of Kona and Kau above 1500 m elevation.

Munro (1944) reported two unverified records for Greater Koa-Finches, one as late as 1937 at Kipuka Puaulu in Hawaii Volcanoes National Park by Donaghho (1951). We know of no substantiated recent records and there appears to be little chance that this species survives (Table 12).

### Kona Grosbeak (*Chloridops kona*)

Kona Grosbeaks, also known as Grosbeak Finches, fed almost exclusively on the hard dried fruit of naio, which their powerful jaws were well adapted to crack (Perkins 1903). Until recently, Kona Grosbeaks stood as an extreme example of adaptive radiation in the Hawaiian honeycreepers. At least eight additional species of finch-billed honeycreepers are now known to have formerly inhabited Hawaiian forests, however, including the giant Oahu grosbeak finch, whose "massive mandible rivals in size that [of] the largest finchlike bills in the world" (Olson and James 1982b:40).

Kona Grosbeaks frequented naio stands on rough aa flows from 1050 to 1650 m elevation in a small area in Kona from Puu Lehua south to the Honaunau Tract (Rothschild 1893–1900). Kona Grosbeaks were apparently rare when Wilson (1888) first collected them. Perkins (1903) also collected in the same area and described them as rare and patchy in distribution over a 10-km² area, although Palmer found them over a distance of 20–30 km (Rothschild 1893–1900).

Kona Grosbeaks were apparently silent for longer intervals than the other finches, and their call was weak (Perkins 1903). The birds were also sluggish, solitary, and inconspicuous (Perkins 1903). Thus we assumed an effective detection distance of 30 m. In determining the probability of overlooking this species, we considered all dry and mesic forests above 1500 m elevation with naio to have been within the range (Table 12).

# MAUI PARROTBILL
## *Pseudonestor xanthophrys*

MAUI PARROTBILL
(*Pseudonestor xanthophrys*)

Maui Parrotbills, or Pseudonestor, are relatively rare birds of the upper montane rainforest of East Maui. They were considered rare in the 1890s, and Munro (1944) failed to find them in 1928. Early workers thought the birds were restricted "to a small portion of the forest on the northwest slope of Haleakala, at an elevation of [1200–1500 m]" (Perkins 1903).

Perkins (1903) and Henshaw (1902) associated Maui Parrotbills with koa forests, where they feed chiefly on the boring larvae and pupae of native longhorn beetles (Cerambycidae). Most koa forests above 1300 m elevation have been destroyed since the 1890s, and the distribution has mostly contracted to areas of ohia rainforest (Richards and Baldwin 1953, Banko 1968, Scott and Sincock 1977, Conant 1981). In rainforests the birds excavate for borers as observed on koa, the prey also including the larvae and pupae of microlepidopteran moths (S. Mountainspring, pers. observ.).

Maui Parrotbills have an apparently continuous distribution from the upper Waikamoi watershed southeast to upper Kipahulu Valley. Highest densities are reached in the Hanawi watershed area. Although we did not find birds between Kipahulu Valley and Kaupo Gap (Fig. 97), a likely place for them would be the koa-ohia forest at 1500–1900 m elevation between Manawainui Valley and Kuiki Peak. Maui Parrotbills also occur in the koa-ohia forests of Waikamoi Preserve (U.S.F.W.S., unpub. data).

The total population is about 500 ± 230 (95% CI) birds (Table 11). Maui Parrotbills occur from 1200 to 2150 m elevation with highest densities at 1700–2100 m (Table 20). The habitat response graphs (Fig. 98) show that highest densities are in wet ohia forests above 1500 m elevation. Maui Parrotbills are rare in all other forests above or below 1500 m. The regression model (Table 21) explains 6% of the variance, and emphasizes wet high elevation forests. Maui Parrotbills usually forage in subcanopy trees and understory shrubs (Carothers et al. 1983). These plants are more sensitive to pig disturbance than canopy trees, indicating that pigs may have a negative effect on this species.

Subfossils associated with dry lowland habitat near Ilio Point, Molokai (Olson and James 1982b), and near Kaupo, East Maui (S. L. Olson, pers. comm.), suggest that Maui Parrotbills originally occupied a wider range of habitats. Populations in dry forests may have perished during early Hawaiian clearing and burning. Maui Par-

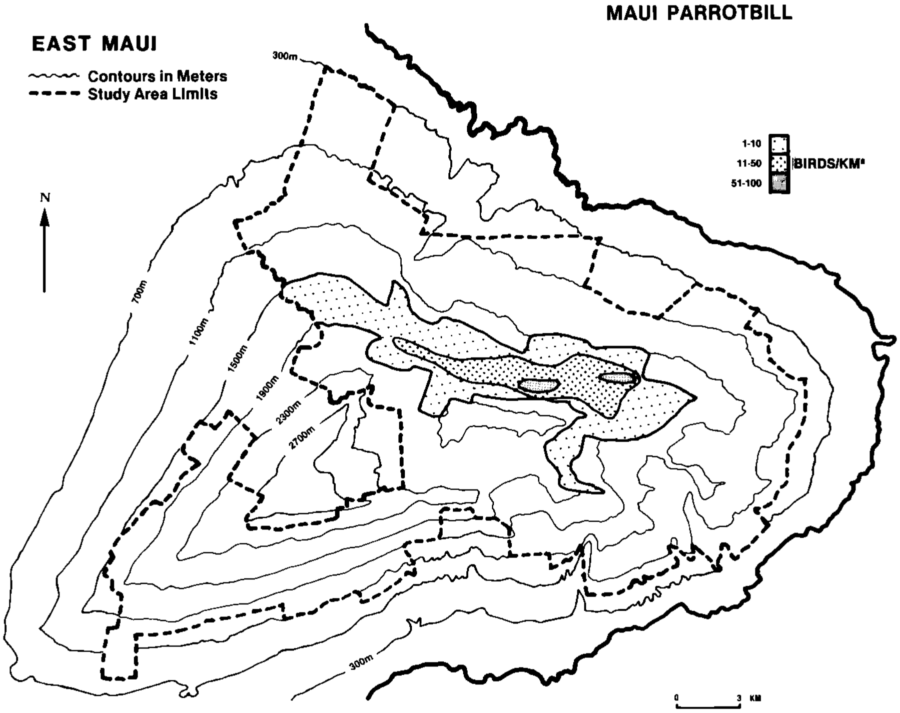
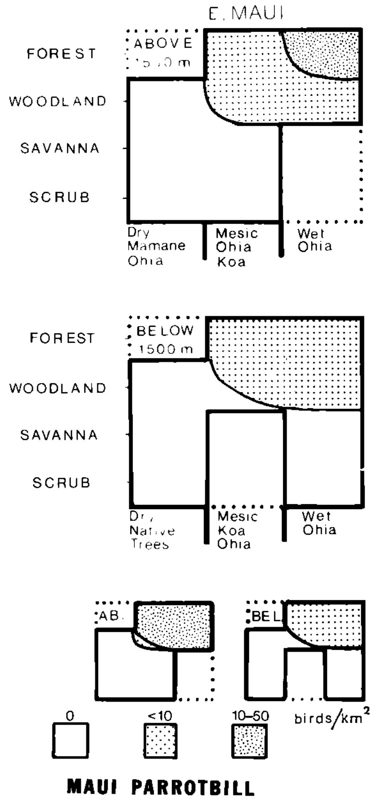



FIGURE 97. Distribution and abundance of the Maui Parrotbill in the East Maui study area.



rotbills were not known historically from Molokai, a relatively well-collected island; moreover, Hawaiians apparently had no name for this distinctive species and did not recognize it (Perkins 1903, Munro 1944). By the time early ornithologists explored Maui and Molokai, the range had probably long since contracted to remote forests because of habitat modification and early release of mosquitoes on Maui (Warner 1968, Pratt 1979).

# COMMON AMAKIHI
## *Hemignathus virens*

COMMON AMAKIHI (*Hemignathus virens*)

This species, widely known as the Amakihi, was common and generally distributed on all the main islands except Niihau and Kahoolawe during the 19th century (Perkins 1903). Munro (1944) found the species common everywhere but on Lanai, where the population declined in the 1920s and 1930s. Numbers on Kauai appeared to diminish after 1891 (Palmer in Rothschild 1893–1900; Perkins 1893, 1903). In Hawaii Volcanoes National Park, birds were fairly common from 700 to 2300 m elevation in the 1940s and 1970s, and the frequency of occurrence increased over this period in dry ohia woodland at 700 m (Baldwin 1953, Conant 1975, Banko and Banko 1980). Birds were considered rare on Molokai in 1975 (Scott et al. 1977). Fossils are known from Kauai and Oahu, but are surprisingly absent from Molokai (Olson and James 1982b). Seasonal movements between areas have been noted (Baldwin 1953), and may explain some of the patterns we observed. Common Amakihi feed on nectar, insects, other invertebrates, and fruit (Perkins 1903, Baldwin 1953, Pimm and Pimm 1982). Nectar levels affect local population densities, breeding success, and individual movements on Mauna Kea (van Riper 1984). The breeding biology has been studied extensively in dry (van Riper 1978c) and wet forests (Eddinger 1970).

Common Amakihi are among the most common of native birds. They are abundant on Hawaii, Maui, and Kauai, locally common on Molokai (Tables 10, 11, Figs. 99–108), uncommon on Oahu (M. Morin, pers. comm., *contra* Berger 1981), but have not been found on Lanai since 1976 (Hirai 1978) and may be extinct there.

On Hawaii they occur in all study areas and locally attain densities of 1600 birds/km$^2$ in the mamane and mamane-naio forests near Puu Laau on Mauna Kea and in the subalpine ohia forests of Kau (Figs. 99 and 102). An estimated 870,000 ± 11,000 (95% CI) birds inhabit the study areas on Hawaii, with the largest proportions of that population in the Kona (40%), Hamakua (20%), and Kau (18%) study areas. The species has a strong association with dry and mesic forests. Unlike other native passerines, Common Amakihi have fairly high densities at low elevations in Puna and along the margins of the Kau Desert. Low-elevation wet forests typically support low Com-

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FIGURE 98. Habitat response graphs of the Maui Parrotbill. (Graphs give mean density above and below 1500 m elevation for East Maui; half-size graphs give standard deviation.)

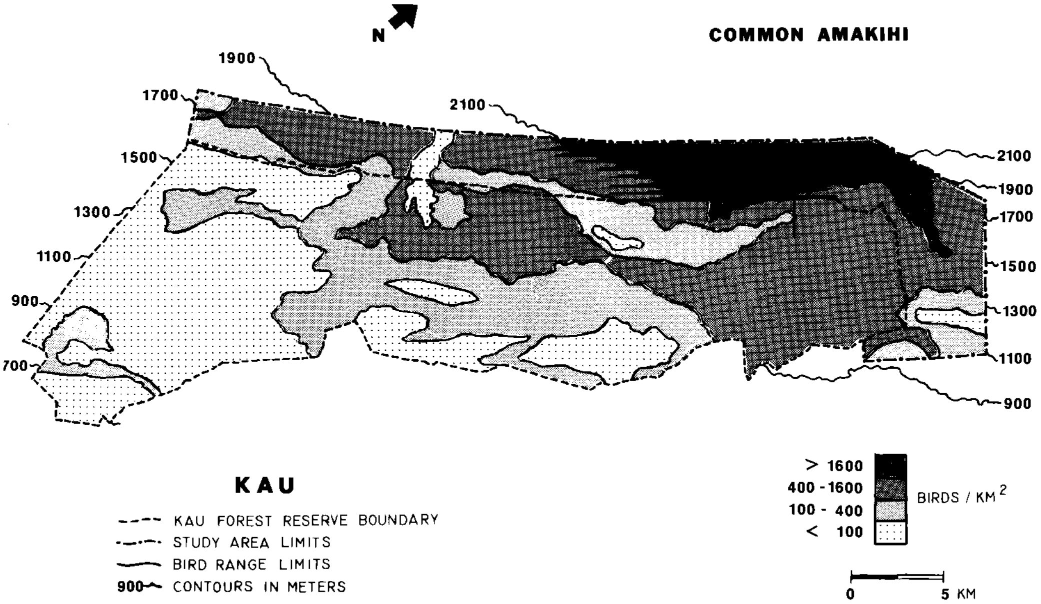


FIGURE 99. Distribution and abundance of the Common Amakihi in the Kau study area.

mon Amakihi densities, notably in Hamakua and Kohala. Deforestation due to lava flows, residential development, and grazing is the probable cause for the low densities between the Kau and Kona populations, and for the loss of birds at lower elevations in Kona east of Kailua and northeast of Kealakekua Bay.

Although densities were lower on Maui than on Hawaii, large populations of 44,000 ± 3500 (95% CI) and 3000 ± 800 birds occur on East and West Maui, respectively (Figs. 104 and 105). The low densities in dry forests on Maui contrast with high ones on Hawaii (Fig. 109), and reflect extensive habitat degradation by feral ungulates. Common Amakihi and Apapane are the only remaining native passerines on the largely deforested dry south slope of East Maui. Common Amakihi are seasonally attracted to mamane flowers in the sparse vegetation of Haleakala Crater. On windward East Maui, they are uncommon at lower elevations. Near absence at low elevations west of Waikamoi Stream marks the mesic/wet habitat transition, but seems anomalous and may reflect seasonal movement out of the area (see Baldwin 1953). On West Maui, abundance varies predictably with habitat, from high densities in dry to mesic montane forests, to virtual absence in very wet forests, bogs, and grasslands.

Common Amakihi have a limited range on Molokai and a total population of only 1800 ± 700 (95% CI) birds. Densities of 100 birds/km² occur locally in the north central part of the study area (Fig. 106), in Waikolu, Pelekunu, and Wailau Valleys, and on the Olokui and Ohialele Plateaux.

The densities on Kauai appear to be one-half to one-third those found in similar habitats on Hawaii and East Maui (Fig. 107). High densities of Anianiau and Kauai Creeper in the Alakai possibly depress Common Amakihi densities via competition for food resources. The 2300 ± 400 (95% CI) birds in the Alakai Swamp study area suggest a substantial increase over the 600 ± 250 birds in the same area for the 1968–1973 period (Sincock et al. 1984), but may reflect seasonal movement into the area during our survey. On Kauai, Common Amakihi are more abundant in the drier koa-ohia forests west of the Alakai, and Sincock et al. (1984) estimated a population of 11,000 ± 2000 birds for all of Kauai. During 1968–1973 birds occurred on the slopes above Waimea Canyon, the Na Pali plateaux, the Alakai Swamp, and the Makaleha Mountains (Fig. 108).

Common Amakihi occur in a wide variety of habitat types (Table 22). They reach highest densities on the island of Hawaii above 1500 m in drier woodlands and forests, as seen in the habitat response graphs (Fig. 109) and regression models (Table 23). In similar habitat types, densities are lower on Maui than on Hawaii. Densities are lower in dry ohia savannas than in dry ohia scrub, although this may reflect a seasonal

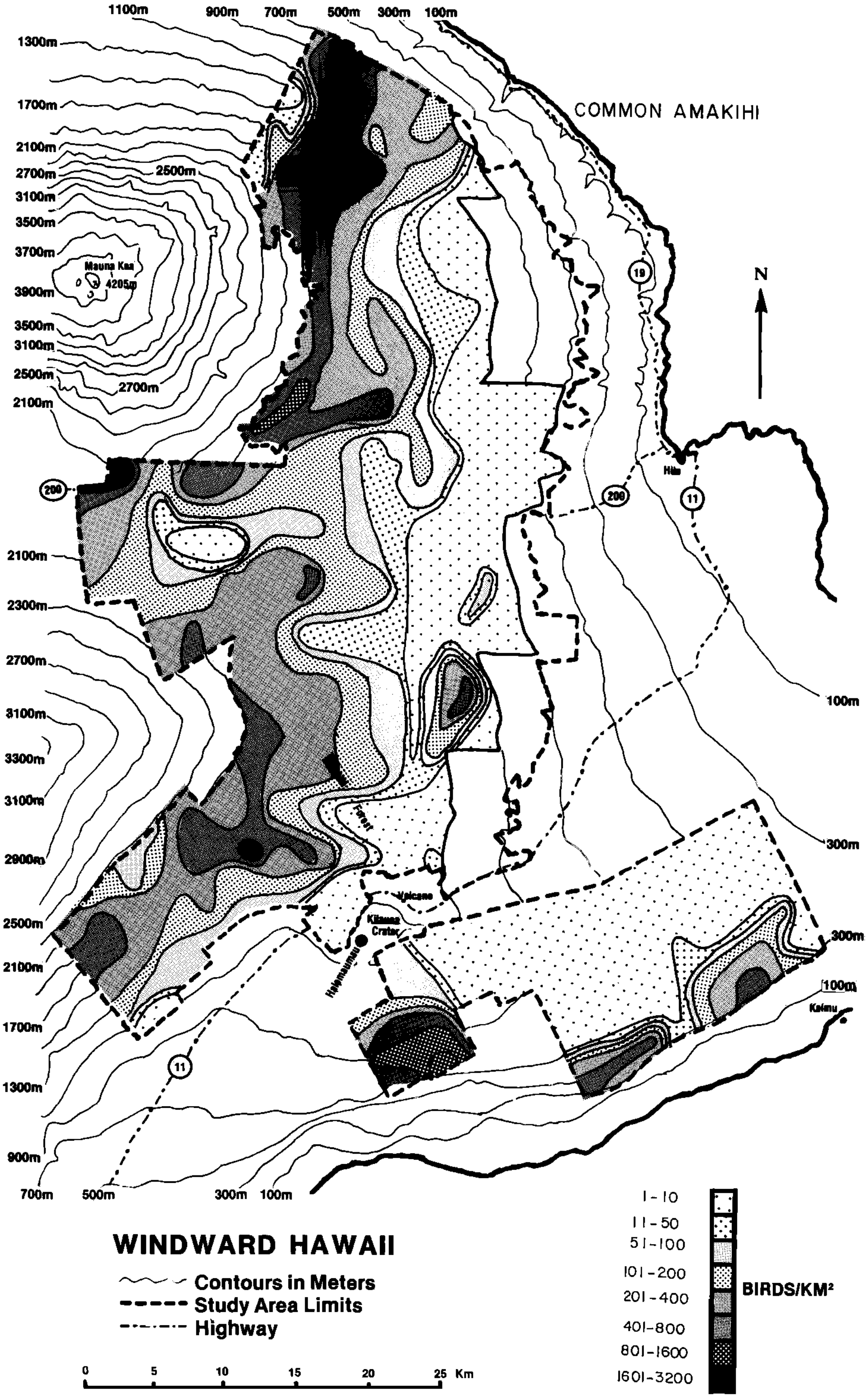


FIGURE 100. Distribution and abundance of the Common Amakihi in the windward Hawaii study areas.

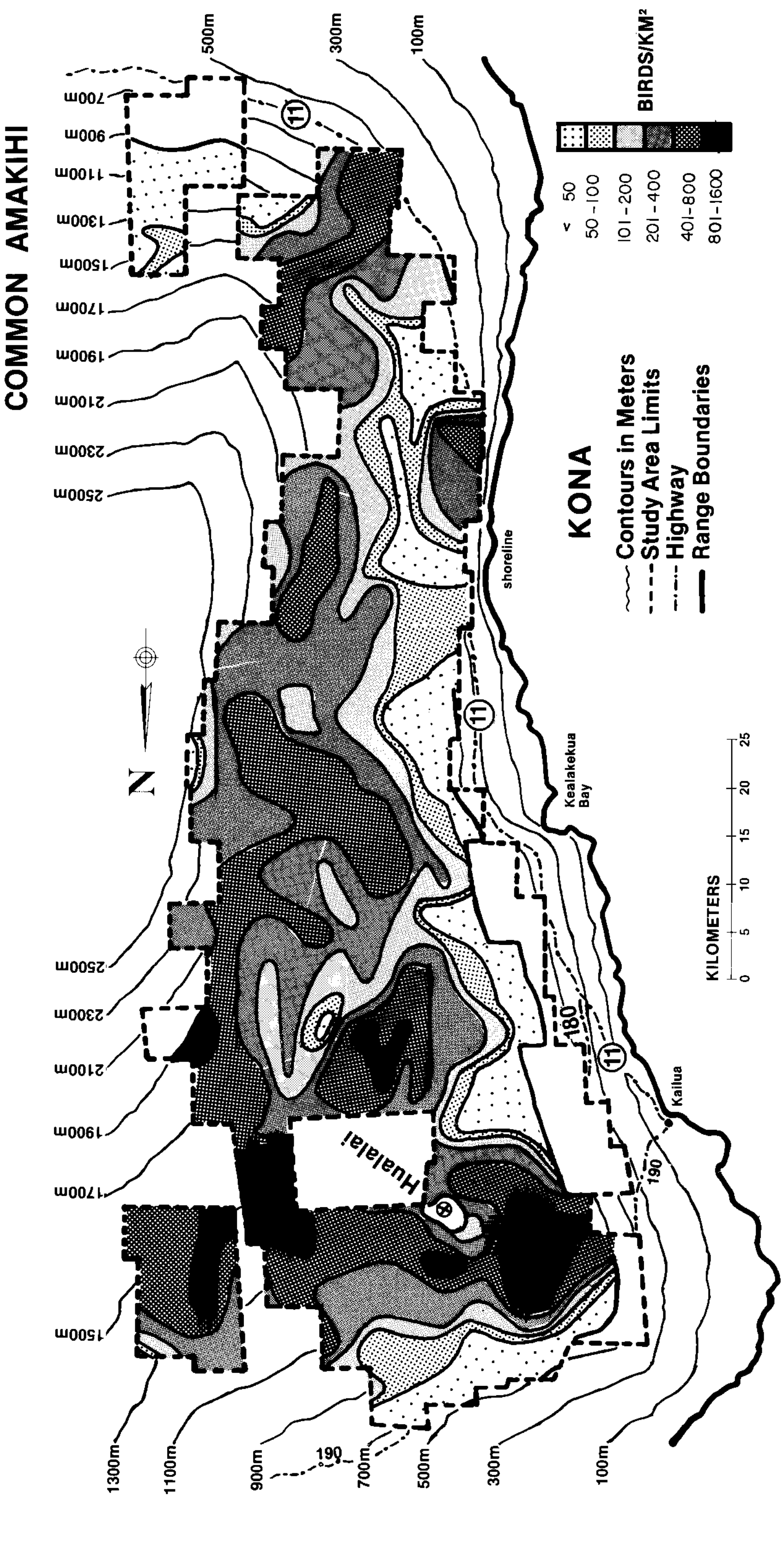


FIGURE 101. Distribution and abundance of the Common Amakihi in the Kona study area.

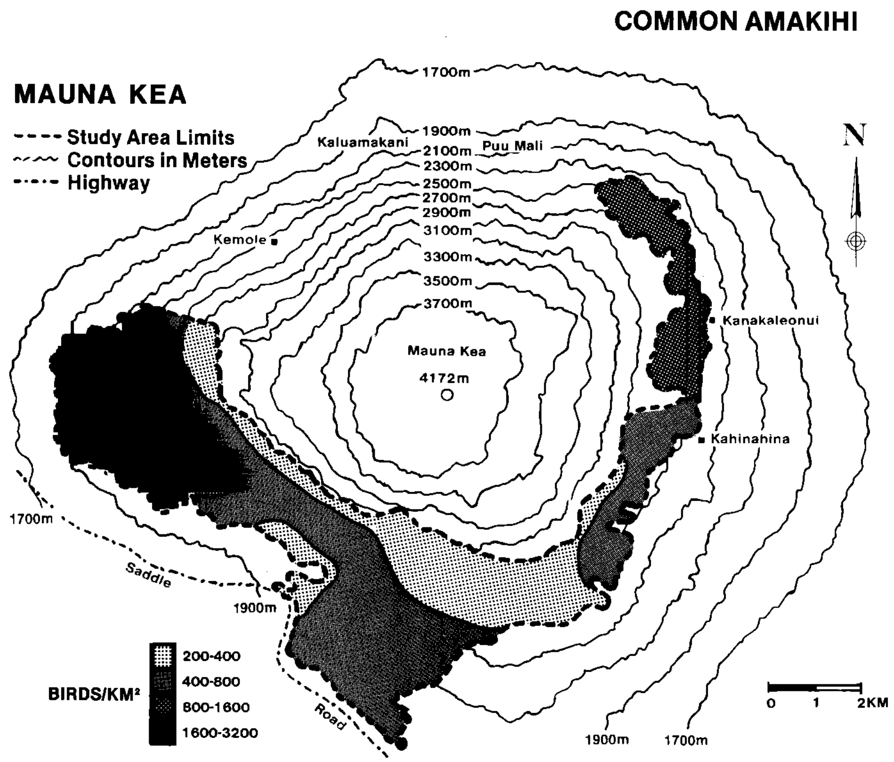


FIGURE 102. Distribution and abundance of the Common Amakihi in the Mauna Kea study area.

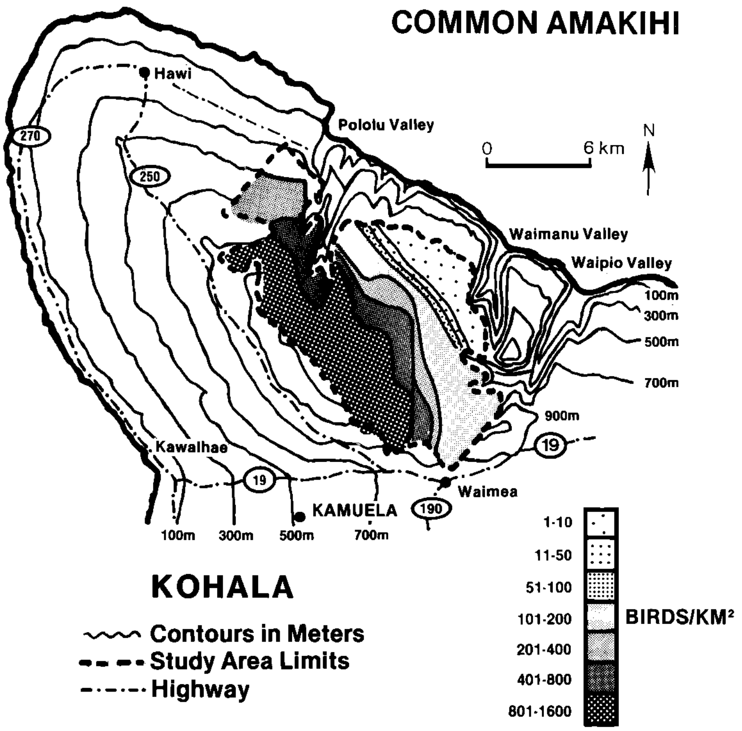


FIGURE 103. Distribution and abundance of the Common Amakihi in the Kohala study area.

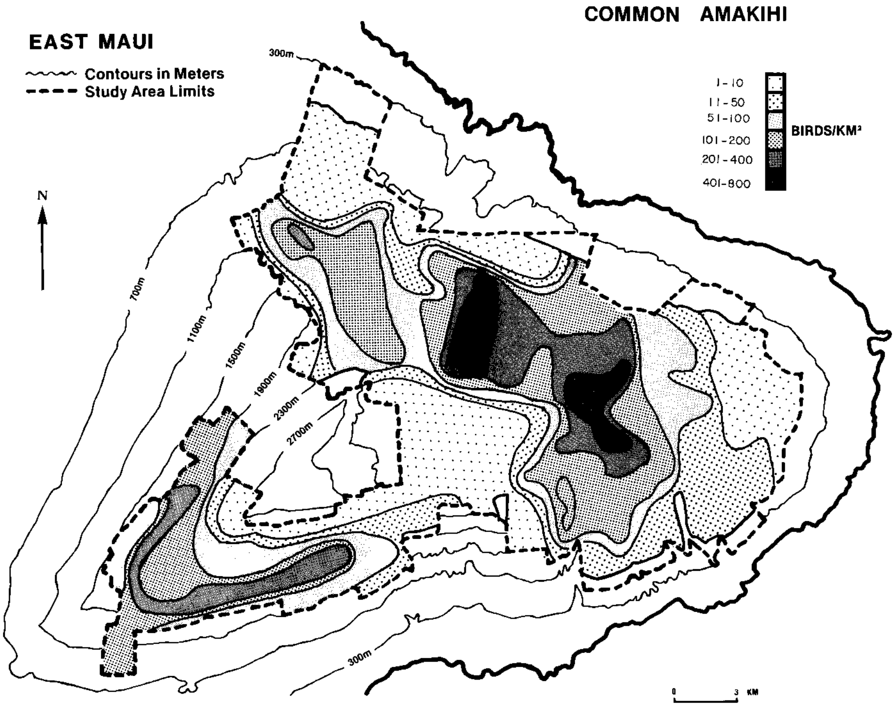


FIGURE 104. Distribution and abundance of the Common Amakihi in the East Maui study area.

pattern or sampling error. Negative moisture terms occur in six of nine regression models. No terms enter the Kauai model, indicating uniform response within the rather homogeneous study area. Common Amakihi have a negative response in three models to matted ferns; the positive term in the Maui model reflects fairly high densities in some ohia dieback areas. Birds are attracted to banana poka infestations for the copious nectar, reflected in the positive terms for passiflora. Native herbs, typical of forest interiors and alpine grasslands, have negative terms in three models. Variables indicating open disturbed forest (introduced herbs, introduced grasses) have positive responses in seven models. Ohia flowers have positive terms in five models, probably reflecting the nectarivorous diet (Baldwin 1953). On Maui, the negative term for mamane flowers reflects low densities in the cinder desert in Haleakala Crater.

Common Amakihi are usually quite uncommon below 500 m elevation, perhaps reflecting a negative response to introduced vegetation, high levels of mosquito infestation, or, less likely, intense competition for food with introduced birds. Exceptions occur where higher densities correspond with dry to mesic native forest at low elevations on Hawaii and Molokai. These patterns are the reverse of the elevational responses shown by other native forest birds. On Hawaii, such areas occur in the Puna study area and below the Kona study area on the Kapua Tract (Table 2). On Molokai, the low-elevation populations occur near the bases of valley headwalls, in a narrow band of mesic to dry forests on precipitous slopes. Common Amakihi thrive in these low-elevation native forests despite the dense populations of mosquitoes and introduced birds. In Pelekunu Valley, Molokai, Common Amakihi move in numbers to low elevations (100 m) during the winter months, but are absent during summer (C. Soares, pers. comm.).

MacMillan (1974) studied the bioenergetics of Common Amakihi from wet montane forest on Kauai and dry subalpine woodland on Hawaii. As with Anianiau, he found that they had thermoregulatory adaptations to the low nocturnal temperatures typical of their environment. Such adaptations to cold montane climates may impede population movement and dispersal between lowland and montane habitats.

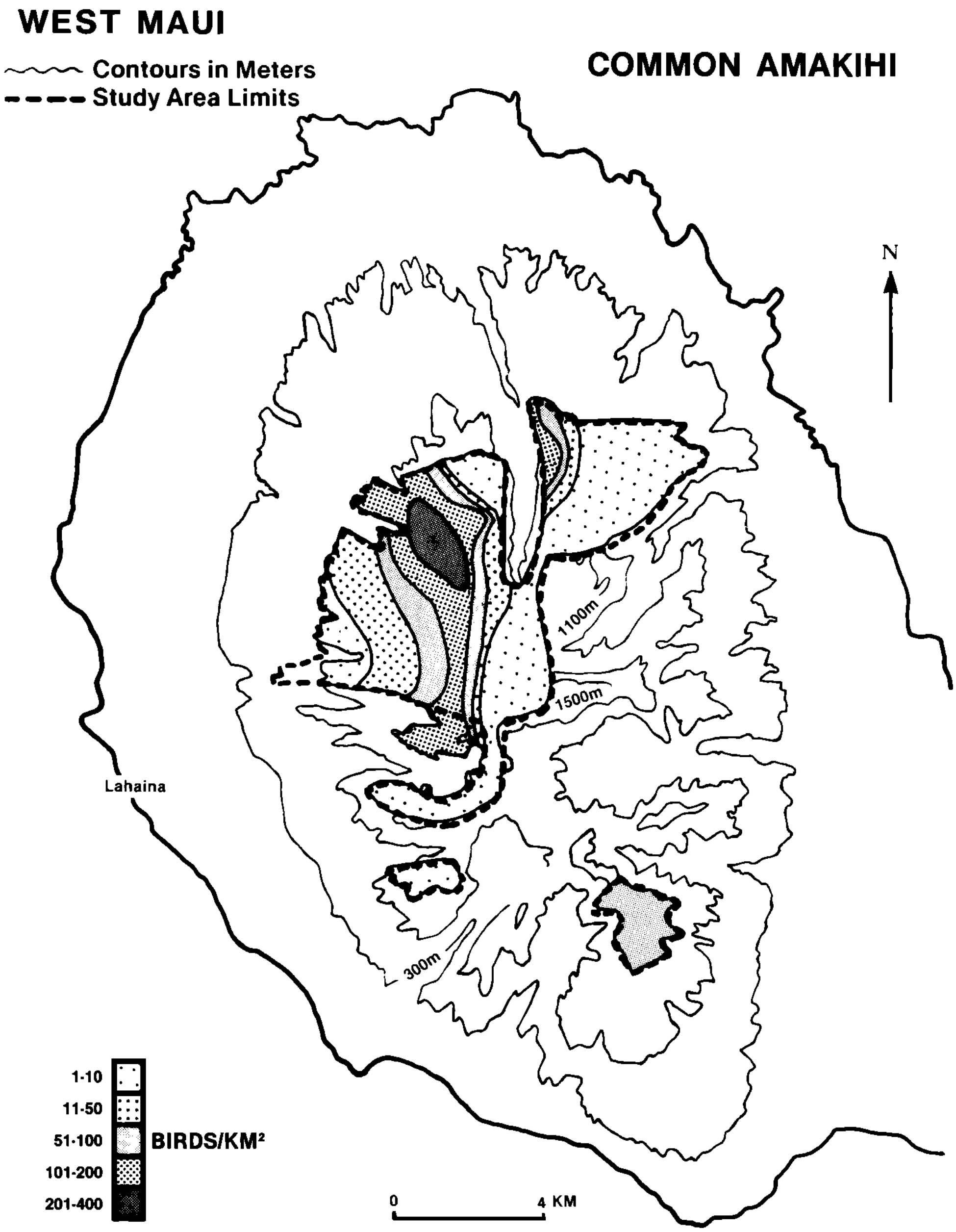


FIGURE 105. Distribution and abundance of the Common Amakihi in the West Maui study area.

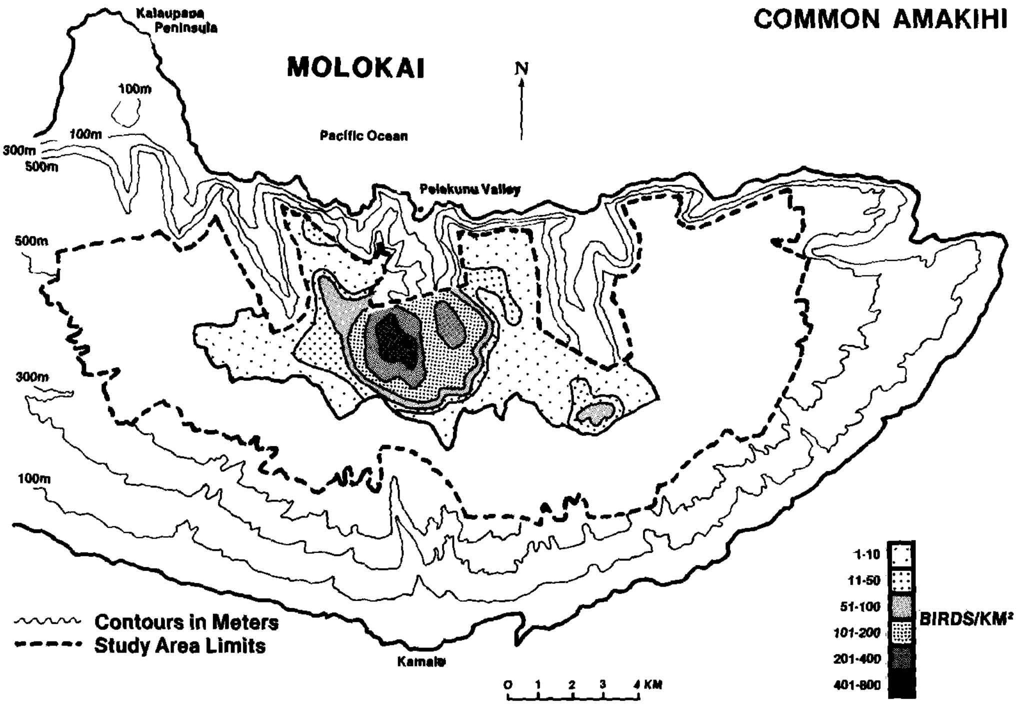


FIGURE 106. Distribution and abundance of the Common Amakihi in the Molokai study area.

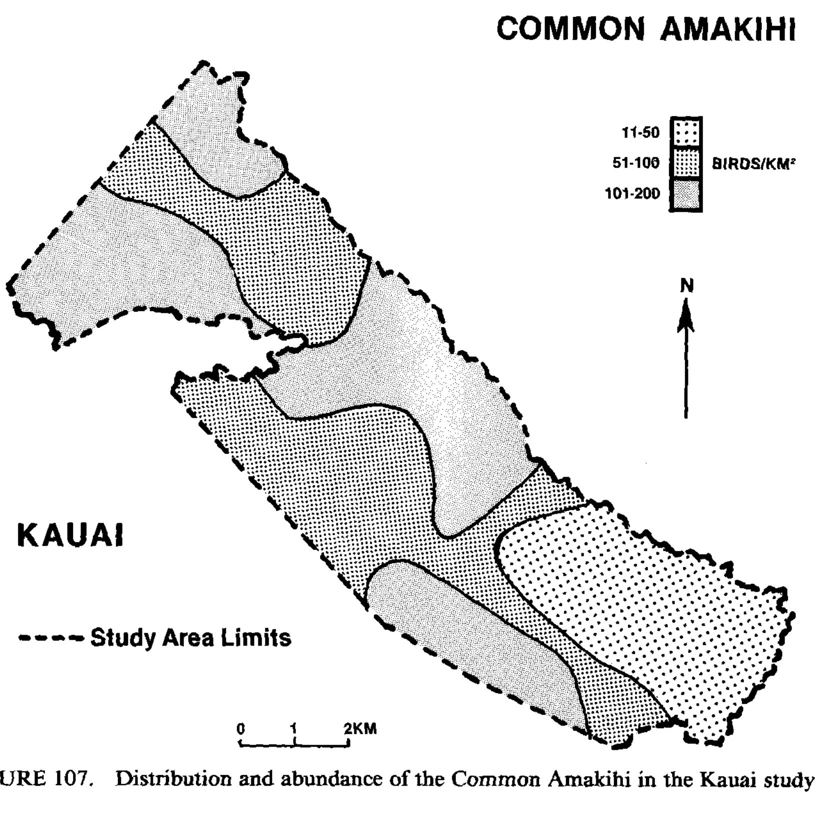


FIGURE 107. Distribution and abundance of the Common Amakihi in the Kauai study area.

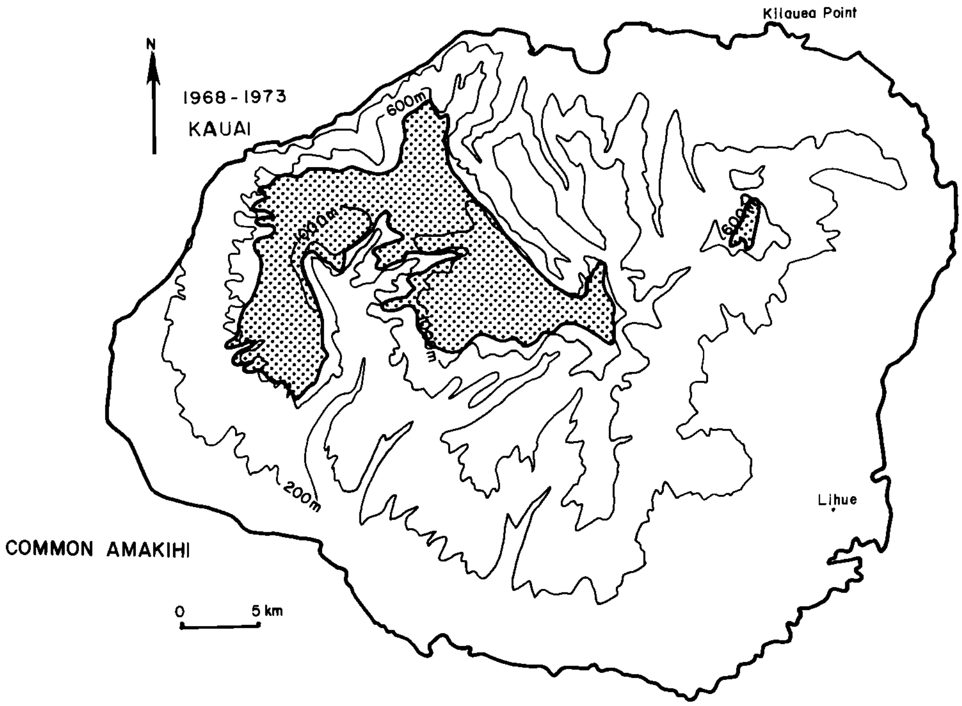


FIGURE 108. Range of the Common Amakihi on Kauai, based on 1968–1973 survey (J. L. Sincock, unpub. data).

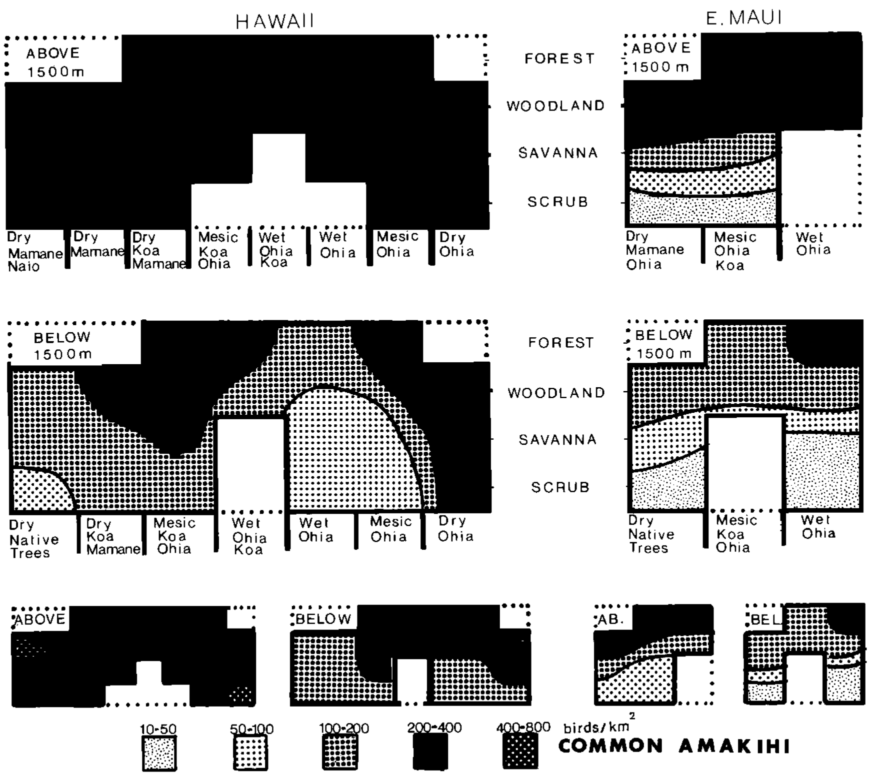


FIGURE 109. Habitat response graphs of the Common Amakihi. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

TABLE 22
DENSITY [MEAN (SE)] OF THE COMMON AMAKIHI BY ELEVATION, HABITAT, AND STUDY AREA[a]

| | Kau | Hamakua | Puna | Kipukas | Kona | Mauna Kea | Kohala | East Maui | West Maui | Molokai | Kauai |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Elevation* | | | | | | | | | | | |
| 100–300 m | ··· | ··· | ··· | ··· | ··· | ··· | ··· | ··· | ··· | 138 (47) | ··· |
| 300–500 m | ··· | 0 | 47 (11) | ··· | 387 (74) | ··· | 0 | 0 | ··· | 222 (60) | ··· |
| 500–700 m | 133 (64) | 2 (2) | 41 (13) | ··· | 152 (20) | ··· | 59 (43) | 91 (23) | 62 (62) | 83 (35) | ··· |
| 700–900 m | 63 (15) | 89 (15) | 175 (44) | ··· | 103 (10) | ··· | 215 (61) | 53 (10) | 69 (18) | * | ··· |
| 900–1100 m | 171 (23) | 129 (16) | 330 (45) | ··· | 131 (12) | ··· | 198 (34) | 138 (15) | 140 (42) | 10 (5) | ··· |
| 1100–1300 m | 217 (27) | 102 (9) | 15 (8) | 25 (11) | 281 (16) | ··· | 296 (36) | 189 (19) | 85 (15) | 16 (4) | 97 (11) |
| 1300–1500 m | 440 (30) | 211 (15) | ··· | 141 (16) | 479 (16) | ··· | 472 (41) | 203 (20) | 48 (9) | 31 (26) | 74 (10) |
| 1500–1700 m | 483 (40) | 377 (23) | ··· | 316 (22) | 424 (14) | ··· | 684 (56) | 221 (19) | 4 (4) | ··· | ··· |
| 1700–1900 m | 597 (41) | 469 (34) | ··· | 259 (20) | 480 (19) | ··· | ··· | 220 (23) | + (+) | ··· | ··· |
| 1900–2100 m | 1428 (102) | 381 (31) | ··· | 234 (13) | 448 (21) | 826 (77) | ··· | 160 (19) | ··· | ··· | ··· |
| 2100–2300 m | 1662 (291) | 334 (57) | ··· | 265 (31) | 290 (16) | 940 (106) | ··· | 56 (11) | ··· | ··· | ··· |
| 2300–2500 m | ··· | ··· | ··· | ··· | 139 (27) | 709 (68) | ··· | 27 (12) | ··· | ··· | ··· |
| 2500–2700 m | ··· | ··· | ··· | ··· | ··· | 618 (47) | ··· | 2 (2) | ··· | ··· | ··· |
| 2700–2900 m | ··· | ··· | ··· | ··· | ··· | 369 (37) | ··· | + (+) | ··· | ··· | ··· |
| 2900–3100 m | ··· | ··· | ··· | ··· | ··· | 239 (79) | ··· | ··· | ··· | ··· | ··· |
| *Habitat* | | | | | | | | | | | |
| Ohia | 341 (22) | 116 (5) | 136 (16) | 257 (11) | 375 (9) | ··· | 323 (22) | 201 (10) | 79 (12) | 51 (13) | 87 (8) |
| Koa-ohia | 655 (30) | 351 (16) | ··· | 192 (22) | 343 (13) | ··· | ··· | 143 (12) | ··· | ··· | ··· |
| Koa-mamane | ··· | 271 (40) | ··· | 274 (23) | 326 (13) | ··· | ··· | ··· | ··· | ··· | ··· |
| Mamane-naio | ··· | ··· | ··· | ··· | 346 (38) | 747 (39) | ··· | ··· | ··· | ··· | ··· |
| Mamane | ··· | ··· | ··· | ··· | 255 (15) | 532 (43) | ··· | 30 (21) | ··· | ··· | ··· |
| Other natives | ··· | 231 (37) | ··· | 97 (25) | 118 (19) | ··· | ··· | 123 (12) | ··· | 0 | ··· |
| Intro. trees | ··· | 161 (72) | ··· | ··· | 183 (37) | ··· | 486 (102) | 139 (15) | 0 | 123 (33) | ··· |
| Treeless | 1512 (174) | 4 (3) | 31 (13) | 67 (24) | 112 (18) | ··· | ··· | 32 (2) | + (+) | + (+) | 0 |

[a] Densities are given in birds/km$^2$; + indicates stratum was in the species range but density <0.5 birds/km$^2$, 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.

TABLE 23
REGRESSION MODELS FOR HABITAT RESPONSE OF THE COMMON AMAKIHI[a]

| | Kau | Hamakua | Puna | Kipukas | Kona | Mauna Kea | Kohala | Maui | Molokai |
|---|---|---|---|---|---|---|---|---|---|
| $R^2$ | 0.42* | 0.48* | 0.65* | 0.60* | 0.46* | 0.26* | 0.43* | 0.31* | 0.24* |
| Moisture | −4.5* | ··· | −10.8* | −2.1 | −8.3* | X | X | −2.3 | −3.0 |
| Elevation | ··· | 8.6* | ··· | 14.3* | 11.7* | ··· | 9.2* | 6.5* | −5.3* |
| (Elevation)$^2$ | 12.1* | −4.0* | ··· | −12.9* | −7.2* | ··· | ··· | −4.1* | 4.8* |
| Tree biomass | ··· | −3.2 | ··· | 4.5* | ··· | 2.9 | 3.0 | 11.5* | ··· |
| (Tree biomass)$^2$ | ··· | ··· | 7.4* | ··· | 9.7* | ··· | ··· | ··· | ··· |
| Crown cover | ··· | 4.5* | ··· | ··· | −5.2* | ··· | ··· | ··· | ··· |
| Canopy height | ··· | ··· | ··· | ··· | 2.4 | 5.2* | ··· | ··· | ··· |
| Koa | 13.1* | 6.8* | X | ··· | −5.2* | X | X | ··· | X |
| Ohia | ··· | ··· | ··· | 4.4* | 3.8* | X | ··· | 2.0 | 2.9 |
| Naio | X | X | X | 4.6* | 2.1 | ··· | X | X | X |
| Mamane | X | ··· | ··· | ··· | 4.0* | ··· | X | ··· | X |
| Intro. trees | X | ··· | ··· | X | −2.6 | X | ··· | ··· | ··· |
| Shrub cover | ··· | 6.7* | 3.5* | ··· | ··· | −3.1 | ··· | ··· | ··· |
| Ground cover | ··· | −2.1 | ··· | ··· | −3.6* | ··· | ··· | ··· | ··· |
| Native shrubs | ··· | ··· | ··· | ··· | 3.0 | X | 2.4 | ··· | ··· |
| Intro. shrubs | X | 4.2* | ··· | −2.7 | −4.7* | X | ··· | ··· | ··· |
| Ground ferns | X | X | ··· | ··· | 8.7* | X | ··· | ··· | 4.0* |
| Matted ferns | ··· | −4.8* | −5.9* | ··· | ··· | X | −3.3 | 3.8* | ··· |
| Tree ferns | 4.3* | X | −5.3* | X | −3.5* | X | −3.4* | ··· | ··· |
| Ieie | X | X | ··· | X | −5.1* | X | X | 4.2* | X |
| Passiflora | X | 4.2* | X | X | 3.9* | X | ··· | 4.2* | X |
| Native herbs | X | X | −2.9 | −4.3* | −3.1 | X | ··· | ··· | ··· |
| Intro. herbs | X | X | ··· | ··· | 5.5* | ··· | 2.5 | ··· | 2.7 |
| Native grasses | ··· | ··· | −4.2* | 3.4* | ··· | ··· | ··· | 2.8 | ··· |
| Intro. grasses | 2.6 | 2.6 | ··· | 6.1* | ··· | ··· | ··· | 3.8* | ··· |
| Ohia flowers | ··· | 8.6* | 3.2 | ··· | 3.7* | X | ··· | 4.2* | 2.8 |
| Olapa fruit | ··· | −2.3 | ··· | ··· | −2.7 | X | ··· | ··· | ··· |
| Mamane flowers | X | 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 |

[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.

# ANIANIAU
## *Hemignathus parvus*

ANIANIAU (*Hemignathus parvus*)

Anianiau, also known as Lesser Amakihi, inhabit the ohia rainforests of Kauai (Berger 1981). They were extremely numerous in all Kauai forests in the 19th century (Perkins 1903, Munro 1944) and were still common over a smaller area 40–50 years later (Munro 1944). Richardson and Bowles (1964) considered them moderately common residents of native forest areas above 450 m elevation. Fossils of this species have been found only on Kauai (Olson and James 1982b). Anianiau feed on insects and nectar (Richardson and Bowles 1964, Berger 1981). Their nesting biology has been studied by Berger et al. (1969) and Eddinger (1970).

We found Anianiau widespread and abundant throughout the Alakai Swamp study area (Tables 11, 20, Fig. 110). Densities are somewhat higher towards the interior of the area. The 6100 ± 600 (95% CI) birds in the area compare closely to the 5500 ± 900 birds estimated for the same area in 1968–1973 (J. L. Sincock, pers. comm.) and suggest a healthy population. Sincock et al. (1984) estimated a total of 24,000 ± 3000 birds for Kauai, and found them in Kokee State Park, the Na Pali plateaux, the Alakai Swamp, Laau Ridge, Namolokama Mountain, Kapalaoa Ridge, and Makaleha Mountains (Fig. 111). Anianiau occur in ohia and koa-ohia forests from near sea level at Nualolo Kai State Park to 1550 m elevation near the summit of Waialeale (Sincock et al. 1984).

The regression model (Table 21) shows that higher Anianiau densities are associated with ground ferns and lower ones with introduced shrubs, but otherwise little habitat response is seen. This generally reflects sampling within fairly homogeneous habitat.

GREATER AMAKIHI
(*Hemignathus sagittirostris*)

Greater Amakihi were poorly known birds from Hawaii. The Hawaiians apparently had no name for them, but early collectors called them Green Solitaires. Greater Amakihi were mostly insectivorous but also fed occasionally on nectar (Perkins 1903). Perkins (1903) indicated that they gleaned insects from ieie and the loose bark of ohia trees in lowland koa-ohia forests. This species was found from 150 to 1200 m elevation along the Wailuku River and in adjacent forests above Hilo, Hawaii. The restriction of this species to the low-elevation forests was unusual among historically known forest birds. No close ecological equivalent was known from higher elevations.

The call of this species was distinctive but rather similar to that of Common Amakihi (Perkins 1903). We therefore assumed that the effective detection distances of the two species were identical. In assessing the historical range, we assumed the Greater Amakihi occurred from transects 12 through 26 as high as 1300 m. The probability that an extant population went un-

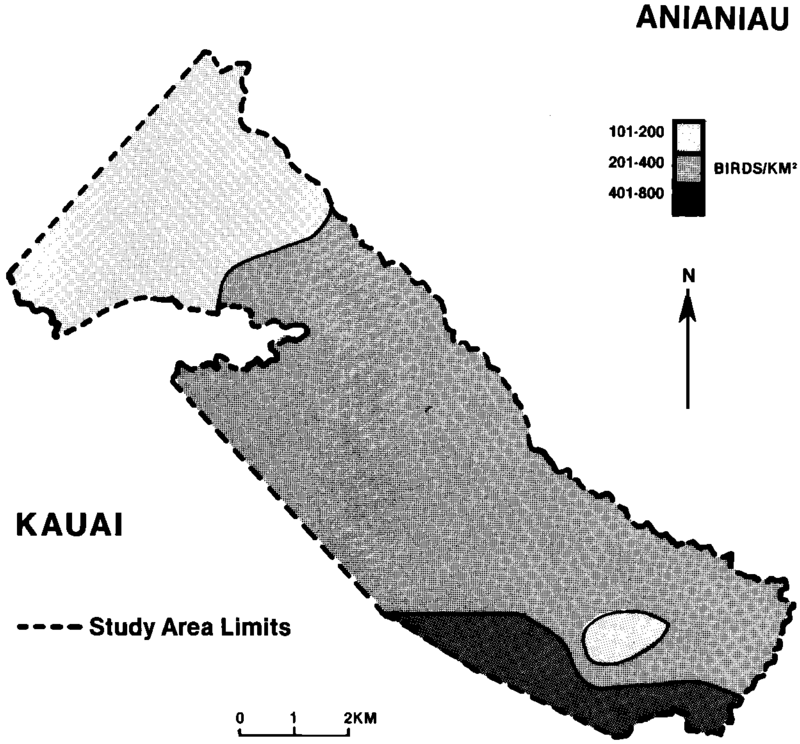


FIGURE 110. Distribution and abundance of the Anianiau in the Kauai study area.

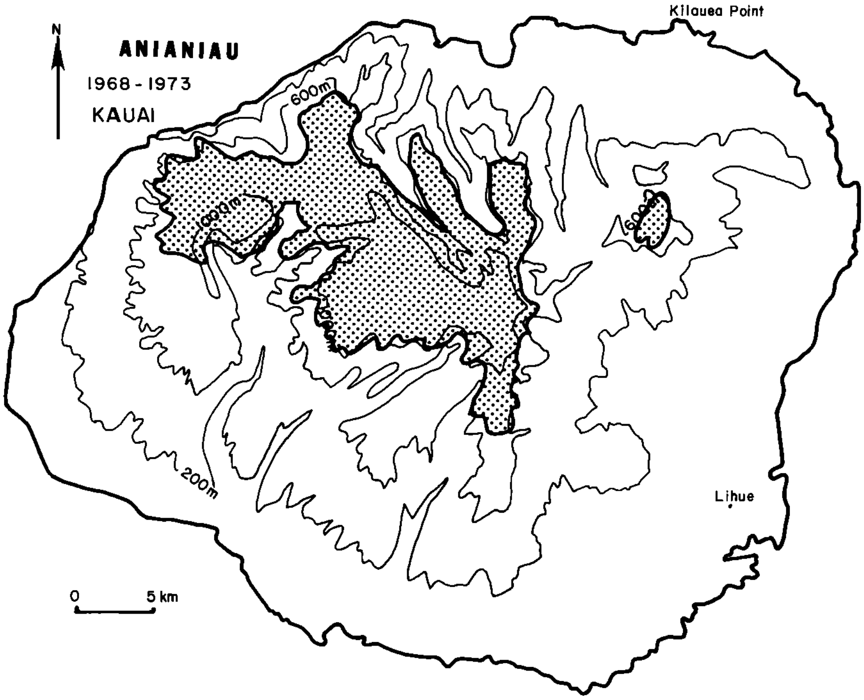


FIGURE 111. Range of the Anianiau on Kauai, based on 1968–1973 survey (J. L. Sincock, unpub. data).

detected during the HFBS is moderate (Table 12), but we believe the species is extinct. There have been no records since the last collection in 1901, and virtually all of the habitat in the historical range has been replaced by introduced plant species.

HAWAIIAN AKIALOA (*Hemignathus obscurus*)

Hawaiian Akialoa, also known as Akialoa, were first collected in 1779 during Cook's stay at Kealakekua Bay, Hawaii (Stresemann 1950). They were historically found on Hawaii, Lanai, and Oahu; fossils are also known from Molokai (Olson and James 1982b). Wilson and Evans (1890–1899) reported them as scarce and restricted to forests from 350 to 750 m elevation, and failed to find them in the higher forests of Kona. Perkins (1903) and Munro (1944), however, found them to be "not uncommon" in many localities and to occur throughout Hawaii above 150 m elevation. In the 1890s they were abundant in koa-ohia forests 5 km from Kilauea Crater (Perkins *in* Banko and Banko 1980). Data on specimen labels indicate that Hawaiian Akialoa occurred in several areas on Hawaii as high as 1800 m (Banko 1979). Munro (1944) and Baldwin (1953) failed to find Hawaiian Akialoa in the 1930s and 1940s. The Lanai subspecies was apparently rare even when first collected in 1892 (Rothschild 1893–1900).

Hawaiian Akialoa fed with their enormous sickle-shaped bill on the nectar of ohia and lobeliads (Perkins 1903). They also frequently fed on insects and spiders by gleaning and probing in the bark of trees, under lichens, and in the bases of ieie leaves (Munro 1944).

The call note of this species was easily recognized and birds could be traced by the audible tapping made by the bill against bark (Perkins 1903). This same sound helps present-day observers identify Akiapolaau. The song was described as a short vigorous trill similar to that of Akiapolaau and Common Amakihi; the call note was louder than that of Common Amakihi (Perkins 1903).

Based on these descriptions, we assumed that the effective detection distance for Hawaiian Akialoa (39 m) would be intermediate to those of Common Amakihi and Akiapolaau. We further assumed a distribution similar to that described by Perkins (1903), except that they would now be absent below 1500 m elevation. There have been no documented records for this species since the turn of the century, except for one possible sighting in 1940 high on the windward side of Hawaii (Greenway 1958). It seems unlikely that this species is still extant (Table 12).

KAUAI AKIALOA (*Hemignathus procerus*)

The Kauai Akialoa may best be considered a subspecies of the Hawaiian Akialoa (Pratt 1979). It is abundant in the Kauai fossil record (Olson and James 1982b). This species was numerous on Kauai in the 1890s but apparently declined in numbers shortly after 1900. Munro (1944) knew of only one record since 1920. Richardson and Bowles (1964) rediscovered the species in 1960. They described it as a "rare resident of the undisturbed native forest of the Alakai Swamp." The last well-documented bird was seen in 1965 (Huber 1966). Despite intensive searches and rumors that Kauai Akialoa still exist, no further convincing sightings have been made (Sincock et al. 1984).

Munro (1944) reported that these birds frequently came to the forest edge and to low elevations. He suggested that this habit exposed them to introduced diseases to which they were susceptible, and Perkins (1903) described several birds incapacitated by parasites and apparent pox lesions.

The feeding habits were similar to those described for Hawaiian Akialoa. We assumed the effective detection distance to be the same as well (Table 12). In assessing the probability of missing this species during our survey, we assumed that it would have occurred throughout the survey area. The Kauai Akialoa is on the verge of extinction, if not already gone.

# NUKUPUU
## *Hemignathus lucidus*

NUKUPUU (*Hemignathus lucidus*)

Nukupuu are one of the rarest honeycreepers, although they were not uncommon in the 1890s (Perkins 1903, Wilson and Evans 1890–1899). On Maui, all recent sightings have been on the northeast slopes of Haleakala or in Kipahulu Valley from 1450 to 2000 m elevation in wet ohia and koa-ohia forests with well-developed native understories (Banko 1968, Conant 1981). There are no recent records west of Koolau Gap. Perkins (1903) found Nukupuu from 1200 to 1400 m elevation in the koa forests that formerly covered the northwest slopes of Haleakala. On Kauai, Perkins (1903) found birds as low as 600 m and in the Alakai Swamp. Perkins noted that Nukupuu on Kauai were especially associated with koa trees, and inferred from earlier reports and vegetation remnants that they had been associated with koa on Oahu prior to extinction. Like Akiapolaau, Nukupuu probably prefer to foraage on koa instead of ohia because of the greater abundance of borers on koa (Gressitt and Samuelson 1981).

We saw one Nukupuu on Maui during the HFBS (Fig. 112). This bird was sighted on transect 8 at 1600 m elevation in wet ohia forest with about 60% canopy cover and a closed native understory dominated by shrubs. From recent sightings on Maui we infer that Nukupuu inhabit wet ohia forest and woodlands and the upper portions of mesic koa-ohia forests (Table 20). Perkins (1903) remarked that Maui Parrotbills had a wider elevational range than Nukupuu, suggesting that Maui Parrotbills may tolerate a wider range of habitat, as supported by recent data in the wider range of elevation and habitat types that Maui Parrotbills occupy. This inference, if correct, may explain why Maui Parrotbills are more common than Nukupuu.

We estimated a population of 28 ± 56 (95% CI) Nukupuu on Maui. An immature bird, significant as an indication of successful breeding, was observed in July 1983 in the Hanawi watershed (S. Mountainspring, pers. observ.). An undetected Nukupuu population may inhabit the koa-ohia forest from 1500 to 1900 m elevation above Manawainui Valley, east of Kaupo Gap.

Most records of Nukupuu on Kauai since 1960 fall within 1 km of the Wainiha Pali in the Alakai Swamp (Fig. 113), with the most recent record in 1975 (Sincock et al. 1984). We failed to locate the species during our survey of the Alakai and any remaining population must be very small (Table 12). During 17 years of field work, J. L. Sincock (pers. comm.) saw only two Nukupuu.

Van Riper (1982) reported observing a Nukupuu in 1971 on Kohala Mountain; however, he originally reported the bird as an Akiapolaau (van Riper 1973a). On biogeographical grounds, the Akiapolaau or Common Amakihi appear more plausible from this area, but one Nukupuu specimen in the U.S. National Museum was collected by Titian Peale between 1838 and 1842 from the island of Hawaii (S. L. Olson, pers. comm.).

Nukupuu feed on boring larvae, spiders, and weevils, although they excavate less than Akiapolaau (Perkins 1903). Unlike Akiapolaau, Nukupuu occasionally feed on or among ohia flowers (Perkins 1903; J. L. Sincock, pers. comm.), indicating that ohia forests have resources available for this species. Nukupuu also formerly fed from the flowers of banana and orange on Oahu and Kauai (Perkins 1903); the birds are adapted for facultative nectarivory because their tongue can roll into a tube for sucking and both mandibles are slender and decurved (Amadon 1950).

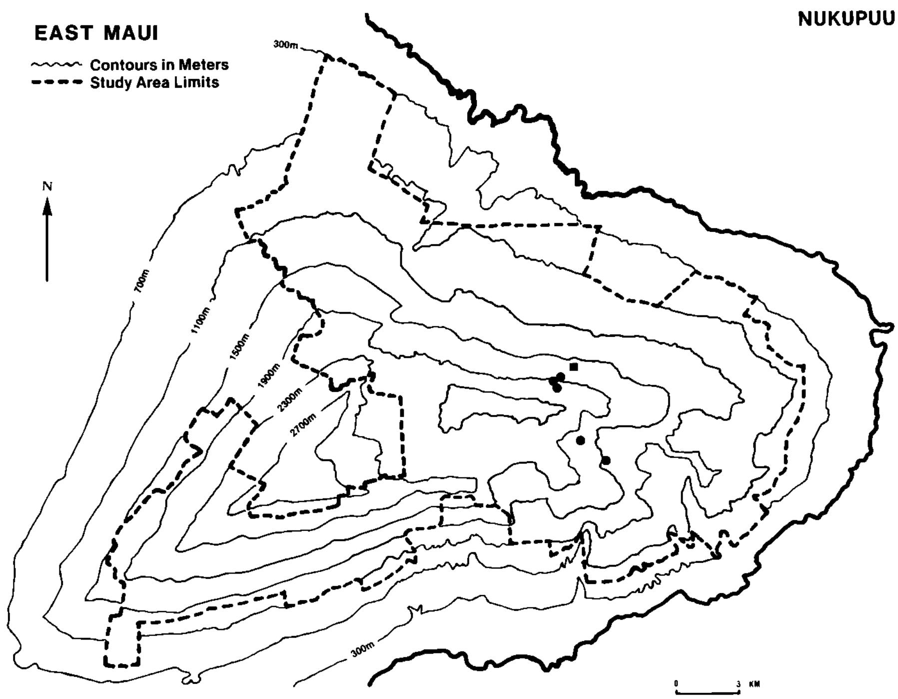


FIGURE 112. Distribution and abundance of the Nukupuu in the East Maui study area. (Square indicates location of birds observed during the HFBS; circles indicate location of other recent records.)

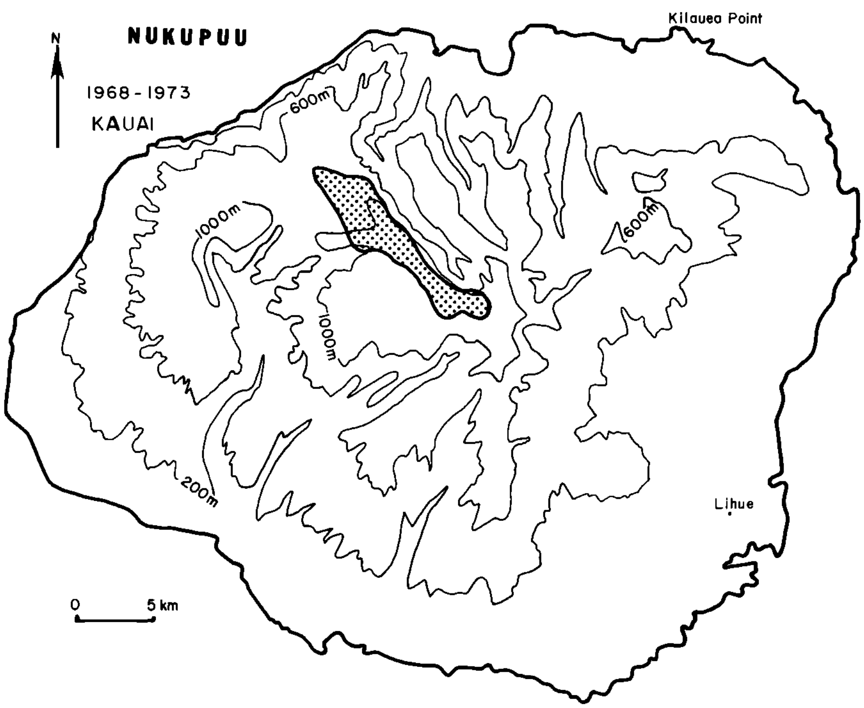


FIGURE 113. Range of the Nukupuu on Kauai, based on 1968–1973 survey and incidental sightings (J. L. Sincock, unpub. data).

# AKIAPOLAAU
## *Hemignathus munroi*

AKIAPOLAAU (*Hemignathus munroi*)

Akiapolaau are bizarre honeycreepers with a stout, woodpecker-like lower bill, and a slender, decurved, sickle-like upper bill. Akiapolaau use their lower bill in woodpecker fashion to excavate burrowing insect larvae and their upper bill to probe and pry in surface deformities (Perkins 1903). They also capture invertebrates by gleaning (C. J. Ralph, pers. comm.).

Akiapolaau are rare to uncommon inhabitants of mesic to wet koa-ohia forest and dry mamane-naio woodland on Hawaii. In the 1890s Akiapolaau had a wide distribution and were fairly abundant on Hawaii (Perkins 1903). In central Kona, Perkins found them abundant above 1100 m elevation in mixed koa-mamane-naio forest, but not at lower elevations in wet koa forest lacking naio. In koa forests near Hilo, Perkins found Akiapolaau as low as 500 m; he also noted birds in koa in Kau and in mamane on Mauna Kea. This implies that Akiapolaau had a wider and more continuous distribution then than today. Originally the mesic and dry forests were continuous, particularly from the mamane woodland on east Mauna Kea to the upper montane forests of koa, mamane, and naio in Hamakua. A series of dry forest communities bridged the gap from the mamane-naio forest on the west side of Mauna Kea to the north slopes of Hualalai and the Mauna Loa-Hualalai saddle, connecting with the koa-mamane-naio forests of Kona (Rock 1913). Goat, cattle, and sheep activity in the 19th century (Tomich 1969, Kramer 1971) and sandalwood harvest in the early 19th century (Rock 1913, Judd 1927) fragmented and deforested this extensive upper-elevation dry forest. Akiapolaau were probably once found throughout the mesic and dry forests, but the populations occurring in mamane-naio on Mauna Kea, in koa in Hamakua, Kau, and Kona have been separated by deforestation. Whether individual birds attempt to move from one area to another is unknown.

In the 1890s, Perkins (*in* Banko and Banko 1980) considered Akiapolaau to be common around Kilauea Crater, finding as many as 12 birds in one day. Munro (1944) indicated that they still occurred in fair numbers in the 1930s near Hawaii Volcanoes National Park, and Richards and Baldwin (1953) reported them as "rather common locally above 1200 m on the eastern slope of Mauna Loa and the northeastern slope of Mauna Kea." During the 1940s, Baldwin (1953) found this species on 48 of 110 plot-counts in koa-ohia parkland at 1700 m elevation along the Mauna Loa Strip Road in the national park; extensive searches in the 1970s failed to find the species in the park (Conant 1975, Banko and Banko 1980, HFBS data). The most recent survey of ornithological records prior to the HFBS concluded that Akiapolaau occurred only at Puu Laau on Mauna Kea and in the Keauhou-Kilauea area north of the national park (Berger 1972).

Akiapolaau presently have four disjunct populations totalling 1500 ± 400 (95% CI) birds (Tables 10, 24, Figs. 114–117). The Hamakua population of 900 ± 200 birds is five times more abundant in koa-ohia forest than in ohia forest. These birds are separated from the Mauna Kea population by 3 km of open pasture and from the Kau population by 25 km of scrub and deforested rangeland. The 500 ± 300 birds in Kau are virtually confined to koa-ohia forest, where the species achieves its highest density of 12 birds/km$^2$. The 50 ± 50 birds on Mauna Kea have two population nuclei—the main one at Puu Laau, and a secondary one in a relict mamane woodland near Kanakaleonui. A small popula-

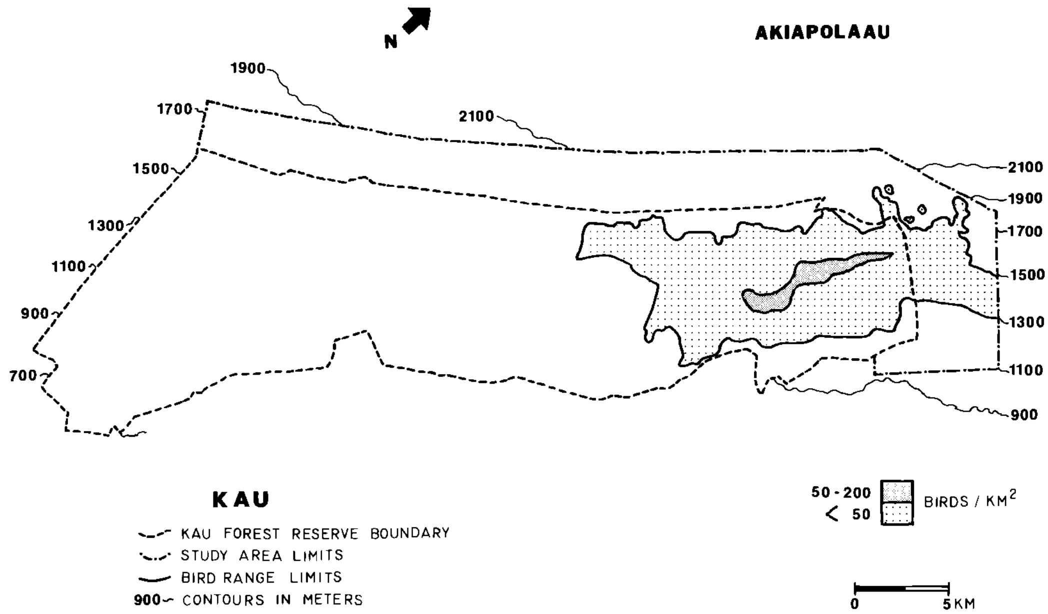


FIGURE 114. Distribution and abundance of the Akiapolaau in the Kau study area.

TABLE 24
DENSITY [MEAN (SE)] OF THE AKIAPOLAAU AND POO-ULI BY ELEVATION, HABITAT, AND STUDY AREA[a]

| | Akiapolaau | | | | | Poo-uli |
|---|---|---|---|---|---|---|
| | Kau | Hamakua | Kipukas | Kona | Mauna Kea | E. Maui |
| *Elevation* | | | | | | |
| 100–300 m | ··· | ··· | ··· | ··· | ··· | ··· |
| 300–500 m | ··· | 0 | ··· | 0 | ··· | 0 |
| 500–700 m | 0 | 0 | ··· | 0 | ··· | 0 |
| 700–900 m | 0 | 0 | ··· | 0 | ··· | 0 |
| 900–1100 m | + (+) | 0 | ··· | 0 | ··· | 0 |
| 1100–1300 m | 2 (2) | 1 (1) | 0 | 0 | ··· | 0 |
| 1300–1500 m | 20 (9) | 3 (1) | 0 | 1 (1) | ··· | 63 (63) |
| 1500–1700 m | 16 (6) | 5 (1) | 0 | + (+) | ··· | + (+) |
| 1700–1900 m | 5 (3) | 2 (1) | 1 (1) | 1 (+) | ··· | + (+) |
| 1900–2100 m | 14 (14) | + (+) | 0 | 0 | + (+) | + (+) |
| 2100–2300 m | 0 | 0 | 0 | 0 | + (+) | + (+) |
| 2300–2500 m | ··· | ··· | ··· | 0 | 1 (1) | 0 |
| 2500–2700 m | ··· | ··· | ··· | ··· | + (+) | 0 |
| 2700–2900 m | ··· | ··· | ··· | ··· | + (+) | 0 |
| 2900–3100 m | ··· | ··· | ··· | ··· | + (+) | ··· |
| *Habitat* | | | | | | |
| Ohia | + (+) | 1 (+) | + (+) | + (+) | ··· | 12 (12) |
| Koa-ohia | 12 (3) | 5 (1) | 2 (2) | + (+) | ··· | 0 |
| Koa-mamane | ··· | 0 | 0 | 0 | ··· | ··· |
| Mamane-naio | ··· | ··· | ··· | 0 | + (+) | ··· |
| Mamane | ··· | ··· | ··· | 0 | 1 (+) | 0 |
| Other natives | ··· | 0 | 0 | 0 | ··· | 0 |
| Intro. trees | ··· | 0 | ··· | 0 | ··· | 0 |
| Treeless | 0 | 0 | 0 | 0 | ··· | 0 |

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

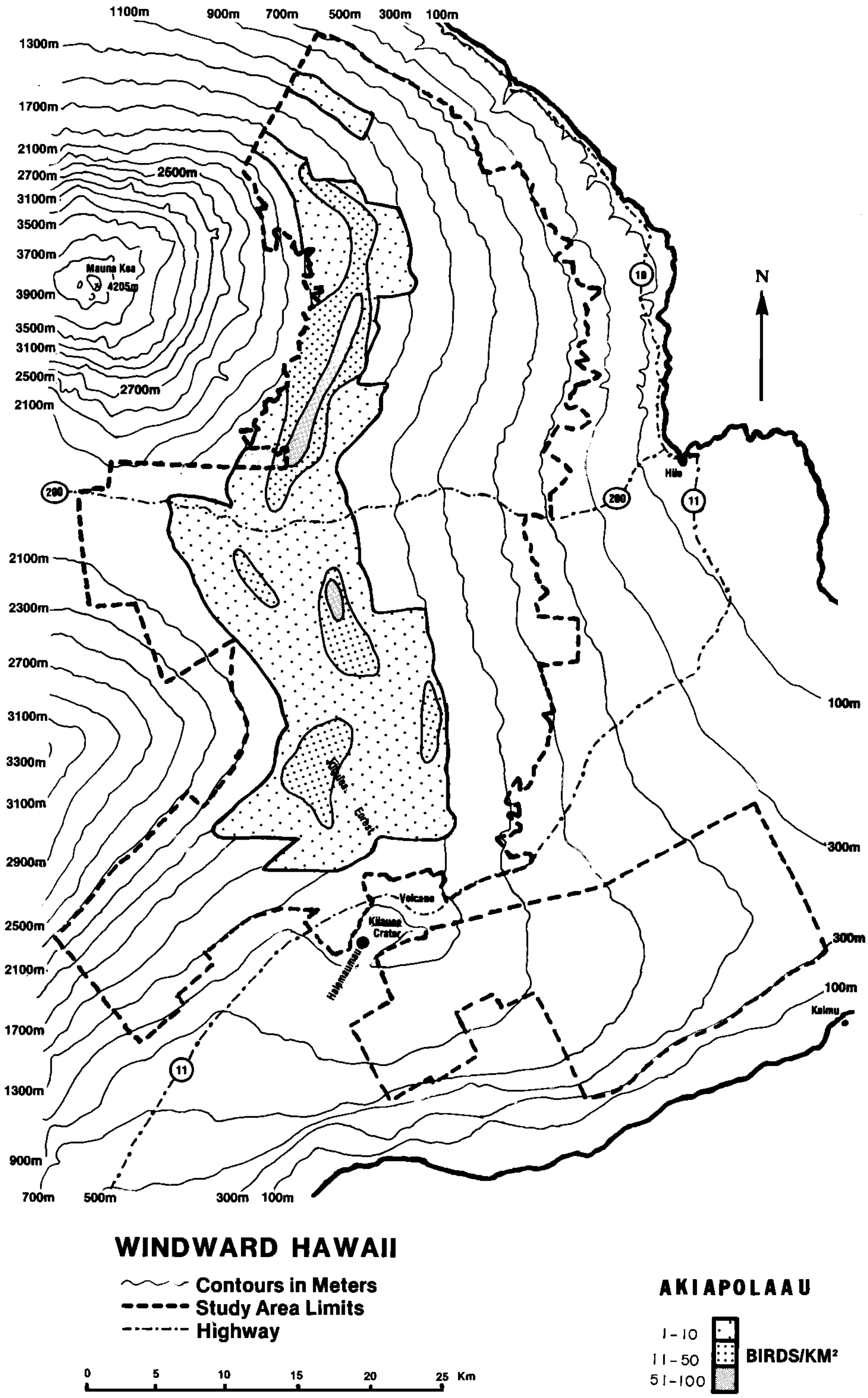


FIGURE 115. Distribution and abundance of the Akiapolaau in the windward Hawaii study areas.

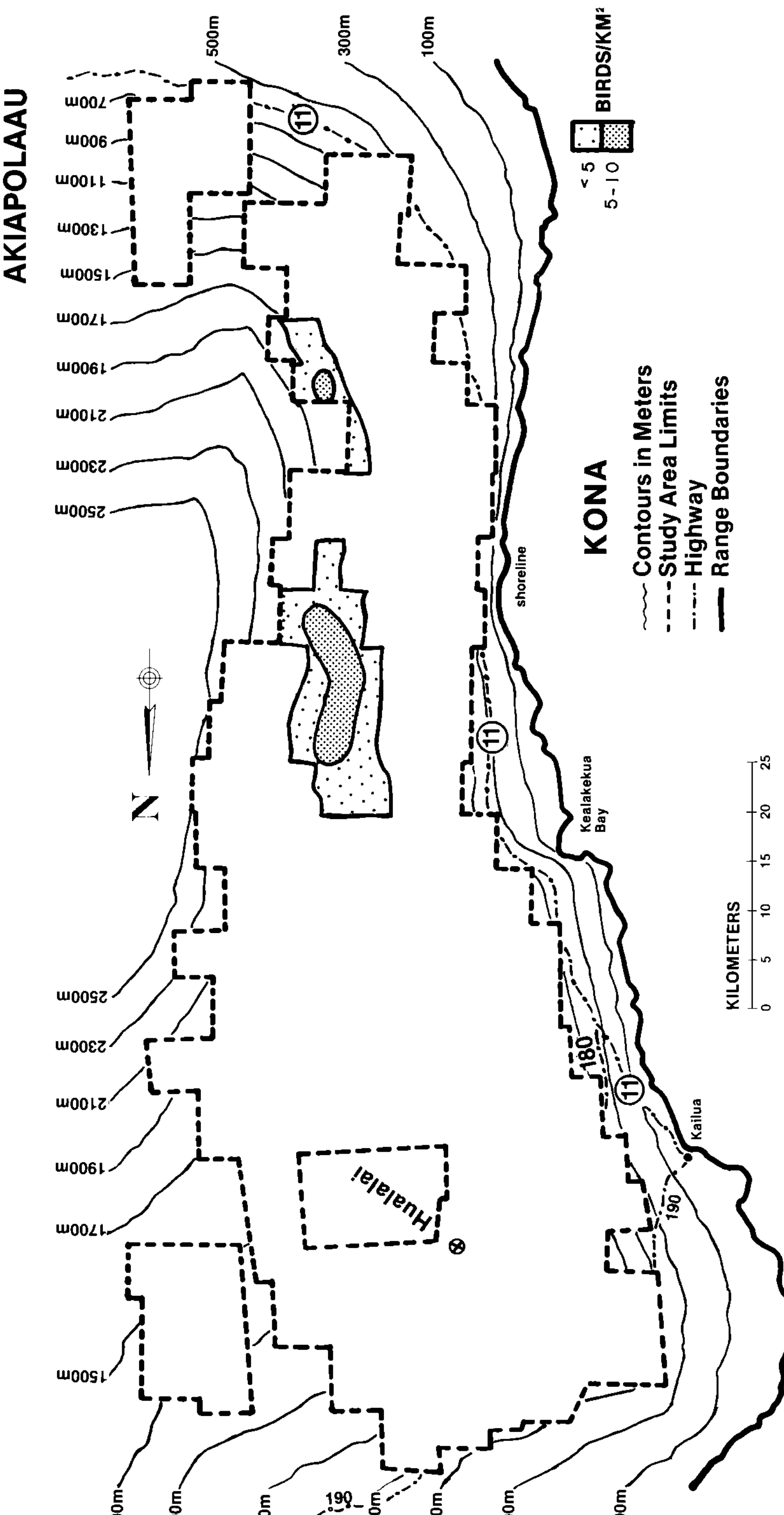


FIGURE 116. Distribution and abundance of the Akiapolaau in the Kona study area.

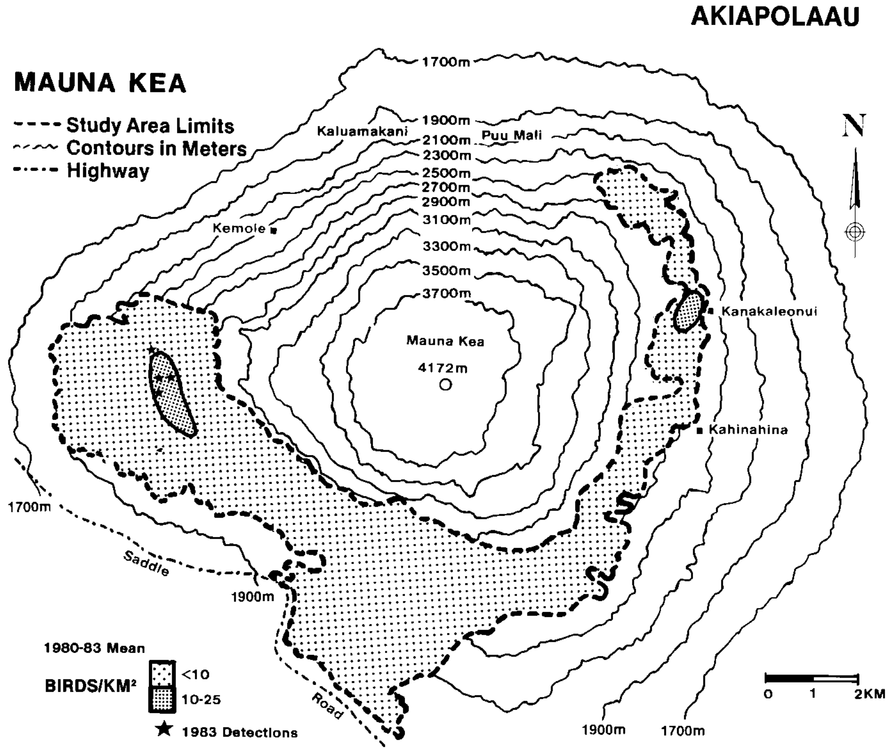


FIGURE 117. Distribution and abundance of the Akiapolaau in the Mauna Kea study area.

tion of about 20 ± 5 birds is on the verge of extinction in central Kona, with one additional record from south Kona (Sakai and Ralph 1980). The absence of birds from the 16 km$^2$ koa-ohia forest on north Hualalai where Akepa and Hawaii Creeper occur implies that that "habitat island" is too small to sustain a viable population. Based on Akiapolaau densities in similar habitat (koa-ohia forest with introduced understory) in windward Hawaii, we predict that the Hualalai area could support 5 birds/km$^2$, or a total population of about 80 birds. The only recent record on Hualalai was of a single bird in 1971 at 1700 m elevation on the western slopes (van Riper 1973a); this bird was probably a vagrant.

Annual surveys of the Mauna Kea area show significant fluctuations in Akaipolaau population between years. Populations in 1980 and 1981 were 345 ± 196 (95% CI) and 803 ± 462 birds, significantly higher than the 31 ± 42 and 46 ± 52 birds of 1982 and 1983; 1984 was intermediate with 169 ± 75 birds (HFBS data). Ongoing monitoring will determine whether such fluctuations are normal for this population, part of a trend toward extinction, or a result of migration between isolated populations.

The fragmented relictual nature of Akiapolaau populations increases their jeopardy of extinction. Linking the populations would improve the prospect for long-term survival. A vigorous reforestation effort in the upland pastures of Keauhou and Kapapala would reestablish the historical link between the Kau and Hamakua populations, and reforestation of upland koa-mamane and koa-ohia forests would link the Mauna Kea and Hamakua populations. Koa forest along the Mauna Loa Strip Road in Hawaii Volcanoes National Park regenerated naturally after the area was fenced and the goats and cattle removed, and will provide potential transplant locations as the habitat matures.

Akiapolaau range from 1000 to 2100 m elevation in Kau, Hamakua, and Kona, with greatest densities at 1300–2100 m in Kau and at 1300–1900 m in Hamakua. The upper limit is lower in Hamakua because of deforestation at higher elevations. On Mauna Kea, Akiapolaau range from 1900 to 2900 m elevation.

The habitat response graph shows that Akiapolaau reach greatest densities in mesic koa-ohia woodland and forest (Fig. 118). Because of low densities and irregular occurrence, relatively few patterns appear in the regression models (Table 21), but the positive association with koa is quite

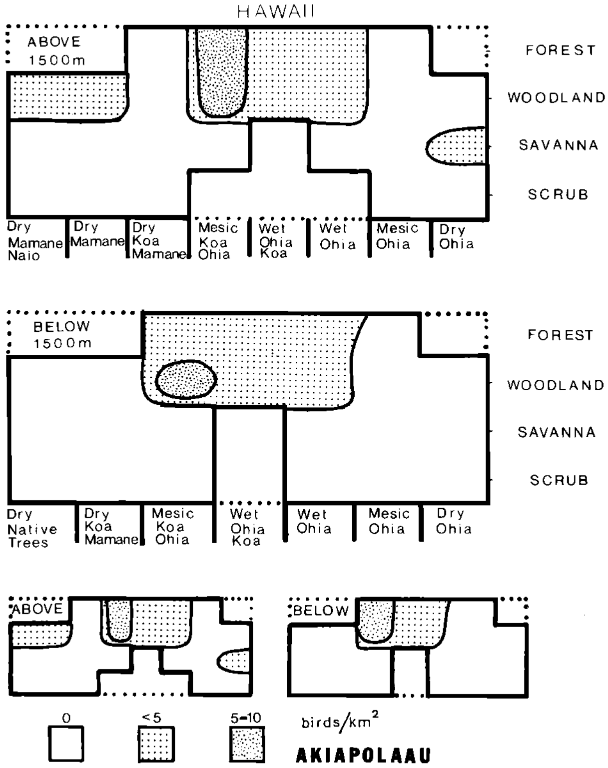


FIGURE 118. Habitat response graphs of the Akiapolaau. (Graphs give mean density above and below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

clear in every model. The invasion of passiflora coincides with depressed Akiapolaau numbers. A number of other variables enter only one model, usually at low levels of significance, or enter no models at all, and thus may be of minor or only local importance in determining habitat response.

The association of Akiapolaau with koa forests probably reflects exploitation of koa for foraging substrates. In a mixed koa-ohia-naio forest, C. J. Ralph (pers. comm.) found that Akiapolaau spend 63–83% of their time in koa trees, a significant difference from the 15–36% of bark surface area constituted by koa. He also found that Akiapolaau seldom use ohia (6–16% of the time vs. 59–71% of bark surface area) and use naio in proportion to its availability. In the Mauna Kea woodland, Ralph found that Akiapolaau feed on both mamane and naio in proportion to their abundance. The underlying cause for these tree preferences is probably related to the abundance of prey, particularly cerambycid borers. In rainforest near Kilauea Crater, Gressitt and Samuelson (1981) found that cerambycid borer larvae are virtually absent in ohia, relatively common in koa, moderately common in naio, and rather sparse overall. This suggests that the distribution of food resources plays a major role in shaping the habitat response of Akiapolaau.

# KAUAI CREEPER
## *Oreomystis bairdi*

KAUAI CREEPER (*Oreomystis bairdi*)

Kauai Creepers, or Akikiki, were common and widely distributed in the 1890s from low to high elevation forests on Kauai (Perkins 1903). They are similar in habits to Hawaii Creepers, and until recently all five Hawaiian creeper species were considered conspecific (Pratt 1979). This species forages for insects and other invertebrates by moving slowly along branches and trunks, probing and prying in cracks and beneath the bark, and gleaning from foliage.

Munro (1944) found Kauai Creepers on the "wet mountain tops above [900 m], being common above [1200 m]." Richardson and Bowles (1964) found them abundant in some regions of native forest in or near the Alakai Swamp area, almost always in loose flocks.

We found Kauai Creepers common through-

TABLE 25
DENSITY [MEAN (SE)] OF THE KAUAI CREEPER, HAWAII CREEPER, AND MAUI CREEPER BY ELEVATION, HABITAT, AND STUDY AREA[a]

| | Kauai Creeper | Hawaii Creeper | | | Maui Creeper |
|---|---|---|---|---|---|
| | Kauai | Kau | Hamakua | Kona | E. Maui |
| *Elevation* | | | | | |
| 100–300 m | ... | ... | ... | ... | ... |
| 300–500 m | ... | ... | 0 | 0 | 0 |
| 500–700 m | ... | + (+) | 0 | 0 | 0 |
| 700–900 m | ... | 6 (6) | 4 (3) | 0 | 0 |
| 900–1100 m | ... | + (+) | 10 (4) | 0 | 20 (15) |
| 1100–1300 m | 57 (11) | 4 (3) | 3 (1) | 11 (11) | 104 (24) |
| 1300–1500 m | 93 (14) | 3 (2) | 14 (2) | 2 (1) | 247 (45) |
| 1500–1700 m | ... | 20 (6) | 48 (7) | 4 (1) | 511 (88) |
| 1700–1900 m | ... | 39 (11) | 61 (11) | 5 (2) | 495 (60) |
| 1900–2100 m | ... | 10 (10) | 3 (2) | 0 | 374 (48) |
| 2100–2300 m | ... | 0 | + (+) | 0 | 35 (23) |
| 2300–2500 m | ... | ... | ... | 0 | + (+) |
| 2500–2700 m | ... | ... | ... | ... | + (+) |
| 2700–2900 m | ... | ... | ... | ... | 0 |
| 2900–3100 m | ... | ... | ... | ... | ... |
| *Habitat* | | | | | |
| Ohia | 74 (9) | 15 (3) | 11 (2) | 0 | 380 (34) |
| Koa-ohia | ... | 12 (4) | 50 (6) | 4 (1) | 110 (32) |
| Koa-mamane | ... | ... | 2 (2) | 5 (5) | ... |
| Mamane-naio | ... | ... | ... | 0 | ... |
| Mamane | ... | ... | ... | 0 | 0 |
| Other natives | ... | ... | 0 | 0 | 0 |
| Intro. trees | ... | ... | 0 | 0 | 141 (34) |
| Treeless | + (+) | 0 | 0 | 0 | 77 (34) |

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

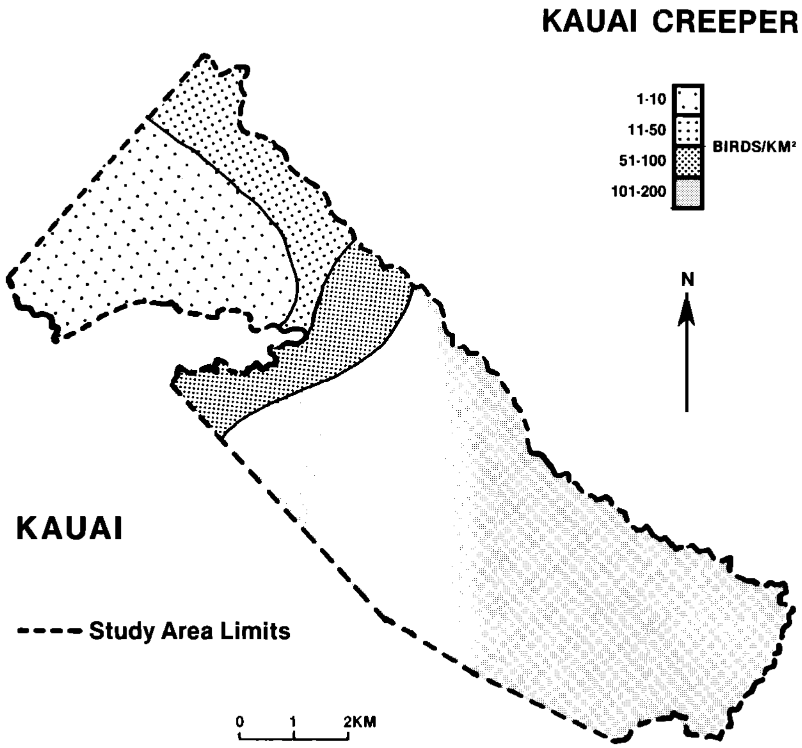


FIGURE 119. Distribution and abundance of the Kauai Creeper in the Kauai study area.

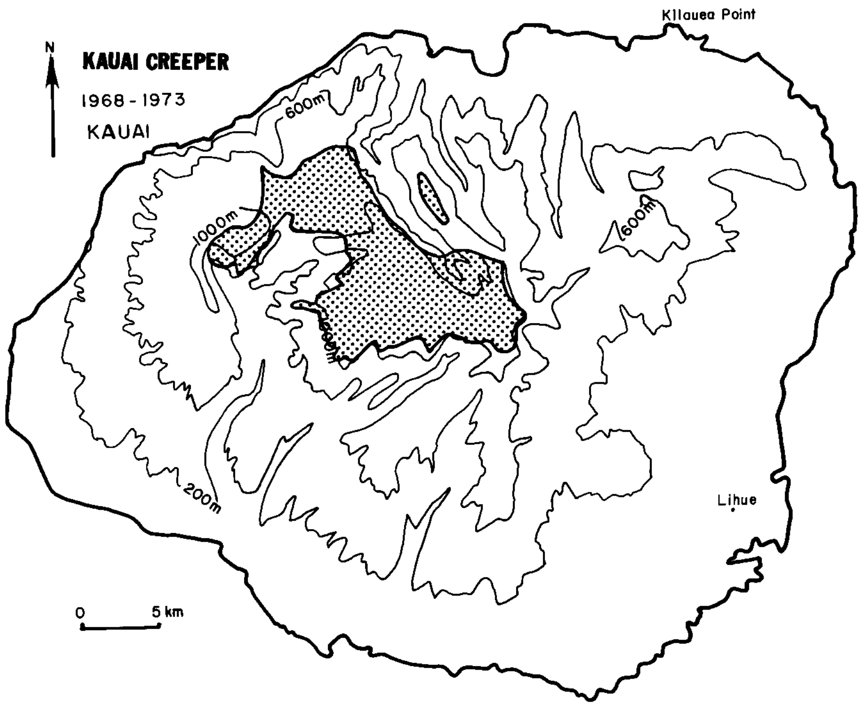


FIGURE 120. Range of the Kauai Creeper on Kauai, based on 1968–1973 survey (J. L. Sincock, unpub. data).

TABLE 26
REGRESSION MODELS FOR HABITAT RESPONSE OF THE KAUAI CREEPER, HAWAII CREEPER, AND MAUI CREEPER[a]

| | Kauai Creeper | Hawaii Creeper | | | Mau Creeper |
|---|---|---|---|---|---|
| | Kauai | Kau | Hamakua | Kona | Maui |
| $R^2$ | 0.08 | 0.05* | 0.19* | 0.07* | 0.44* |
| Moisture | X | ... | 5.3* | ... | 6.4* |
| Elevation | 2.4 | 5.7* | ... | ... | 13.2* |
| (Elevation)$^2$ | ... | ... | 16.5* | ... | ... |
| Tree biomass | ... | 5.1* | ... | ... | ... |
| (Tree biomass)$^2$ | ... | ... | 3.2 | ... | 13.3* |
| Crown cover | ... | ... | ... | ... | ... |
| Canopy height | ... | −2.7 | −2.6 | ... | ... |
| Koa | X | −2.5 | 5.1* | 5.8* | −6.6* |
| Ohia | X | ... | ... | ... | ... |
| Naio | X | X | X | 8.6* | X |
| Mamane | X | X | −5.4* | −6.5* | −3.8* |
| Intro. trees | X | X | ... | ... | ... |
| Shrub cover | ... | ... | 5.0* | ... | −3.4* |
| Ground cover | ... | ... | 4.3* | ... | 4.1* |
| Native shrubs | ... | ... | ... | ... | ... |
| Intro. shrubs | ... | X | ... | ... | ... |
| Ground ferns | ... | X | X | 2.2 | ... |
| Matted ferns | ... | ... | ... | ... | ... |
| Tree ferns | 2.6 | ... | X | ... | −6.1* |
| Ieie | ... | X | X | ... | 3.1 |
| Passiflora | X | X | −4.5* | 6.2* | ... |
| Native herbs | ... | X | X | ... | ... |
| Intro. herbs | ... | X | X | ... | −2.1 |
| Native grasses | ... | ... | −4.7* | 3.2 | 5.5* |
| Intro. grasses | ... | ... | −4.3* | ... | ... |
| Ohia flowers | ... | ... | −4.7* | ... | 3.7* |
| Olapa fruit | ... | ... | −2.7 | ... | ... |
| Mamane flowers | 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.

out the more remote sections of the Alakai Swamp (Tables 11, 25, Fig. 119), but the distribution indicates that the interior of the Alakai may be the last refuge for the species. It has definitely declined in numbers since the Richardson and Bowles (1964) survey. They indicated that Kauai Creepers were three times more common than either Anianiau or Common Amakihi, but we found that creepers are rarer than those species. The 1968–1973 (Sincock et al. 1984) survey also showed that creepers were rarer than those species over all of Kauai, but were more common than Common Amakihi within the Alakai. Sincock et al. (1984) estimated a total population of 6800 ± 1900 (95% CI) birds, with the range limited to the upper elevation forested slopes of Waimea Canyon, Kokee State Park, the Alakai Swamp, and Laau Ridge (Fig. 120). The species has retreated from the Kokee region since 1973 (J. L. Sincock, pers. comm.). The 1650 ± 450 birds we found were similar to the 2300 ± 700 birds found in the same part of the Alakai ten years earlier (J. L. Sincock, pers. comm.). This species fits into the pattern of population decline and retreat to the remote Alakai interior seen among the endangered Kauai passerines.

The regression model for the Kauai Creeper (Table 26) shows that they tend to be more common in the upper reaches of the Alakai and in areas with tree fern understories.

# HAWAII CREEPER
## *Oreomystis mana*

HAWAII CREEPER (*Oreomystis mana*)

Hawaii Creepers are uncommon in wet montane forests on Hawaii, where they feed on insects, spiders, and invertebrates gleaned from trunks and larger branches. In the 1890s they occupied a wide range of habitats from dry upper forests in Kona to rainforests in Hamakua, occurring above 1000 m elevation in Kona and at lower elevations near Hilo (Perkins 1903). Perkins noted that they were very abundant and generally distributed but had puzzling gaps in distribution, especially at lower elevations. Henshaw (1902) indicated that they were common in some districts but rare in others and generally found above 600 m elevation. The historical status is clouded by the difficulty of identification and uncertainty of field marks (Scott et al. 1979). Berger (1972) stated that "so little is known about the present distribution of the Hawaii Creeper that we do not know whether it is uncommon or so rare that it is on the verge of extinction."

In the 1890s Hawaii Creepers were common in the vicinity of Kilauea Crater (Perkins *in* Banko and Banko 1980). A dramatic decline in numbers apparently occurred in that area during the late 1930s to early 1940s. In the 1940s Baldwin (1953) found birds to be rare from 1100 to 1700 m elevation in the national park, but reports virtually ceased after the 1950s (Banko and Banko 1980). Because both this species and the Japanese White-eye are arboreal insectivores, the decline may have been due to interspecific competition (Dunmire 1961). In the Christmas bird counts for this area, the number of Hawaii Creep-

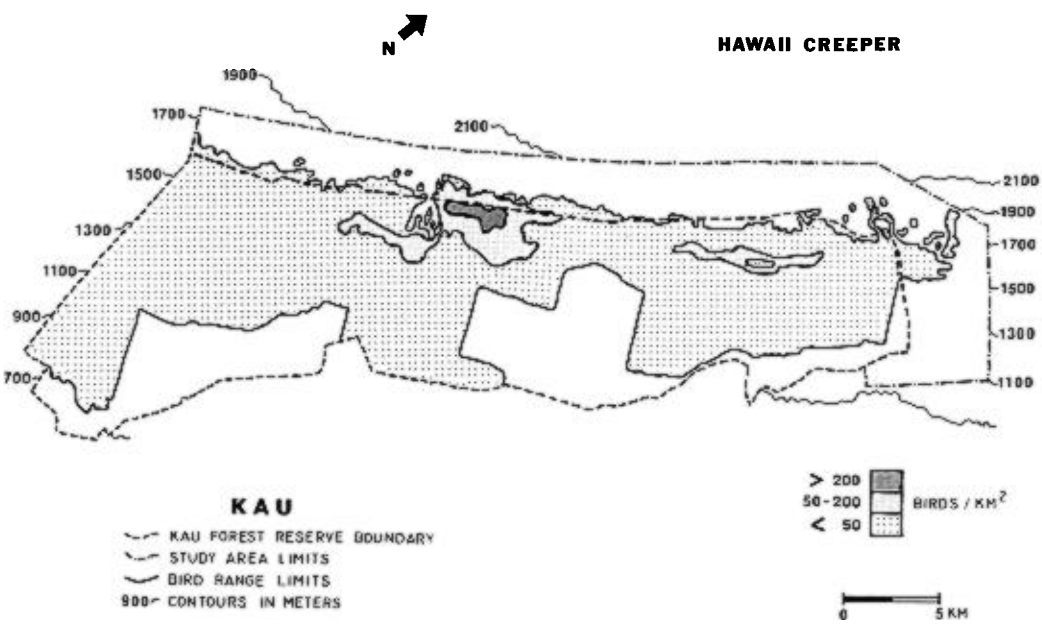


FIGURE 121. Distribution and abundance of the Hawaii Creeper in the Kau study area.

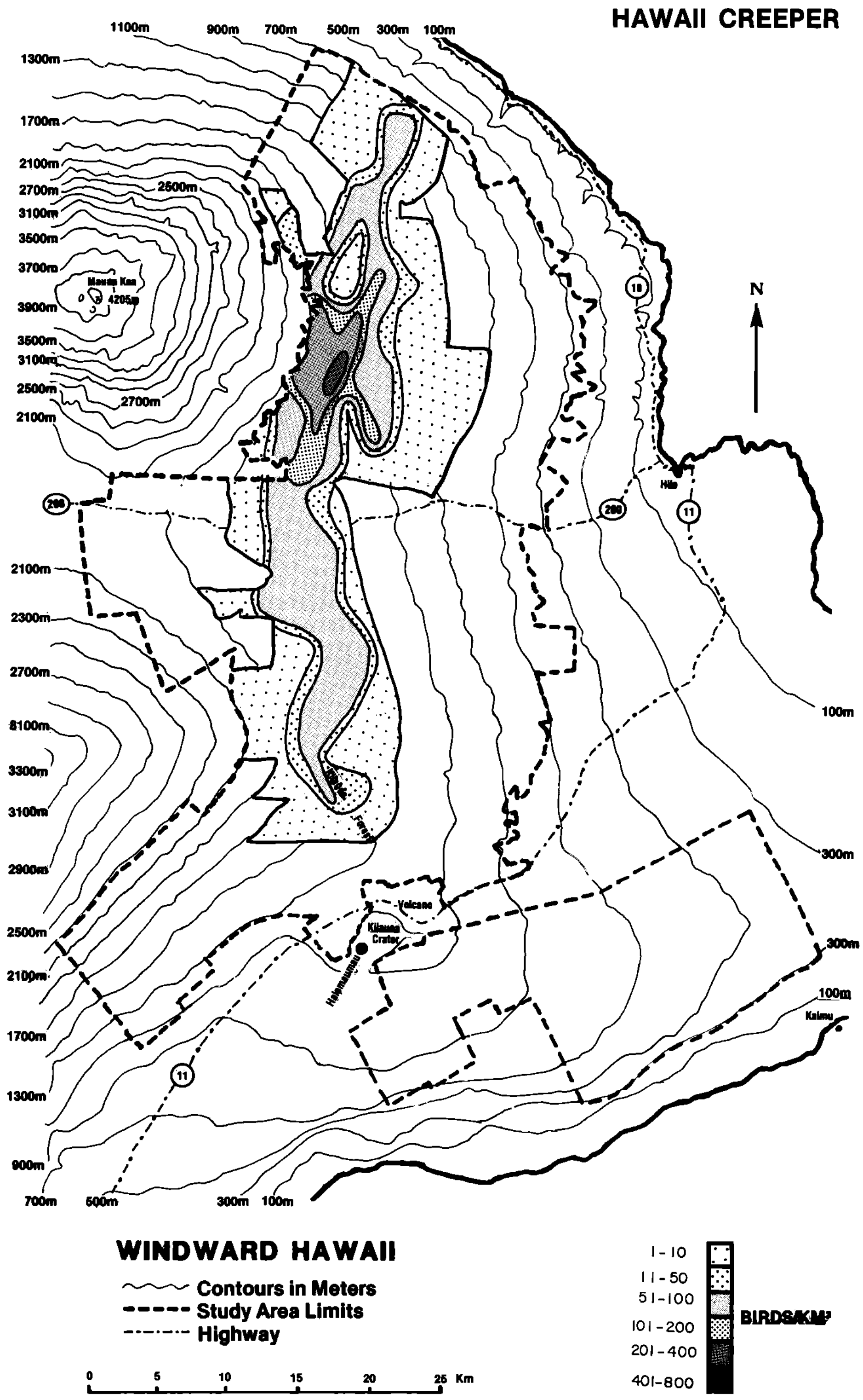


FIGURE 122. Distribution and abundance of the Hawaii Creeper in the windward Hawaii study areas.

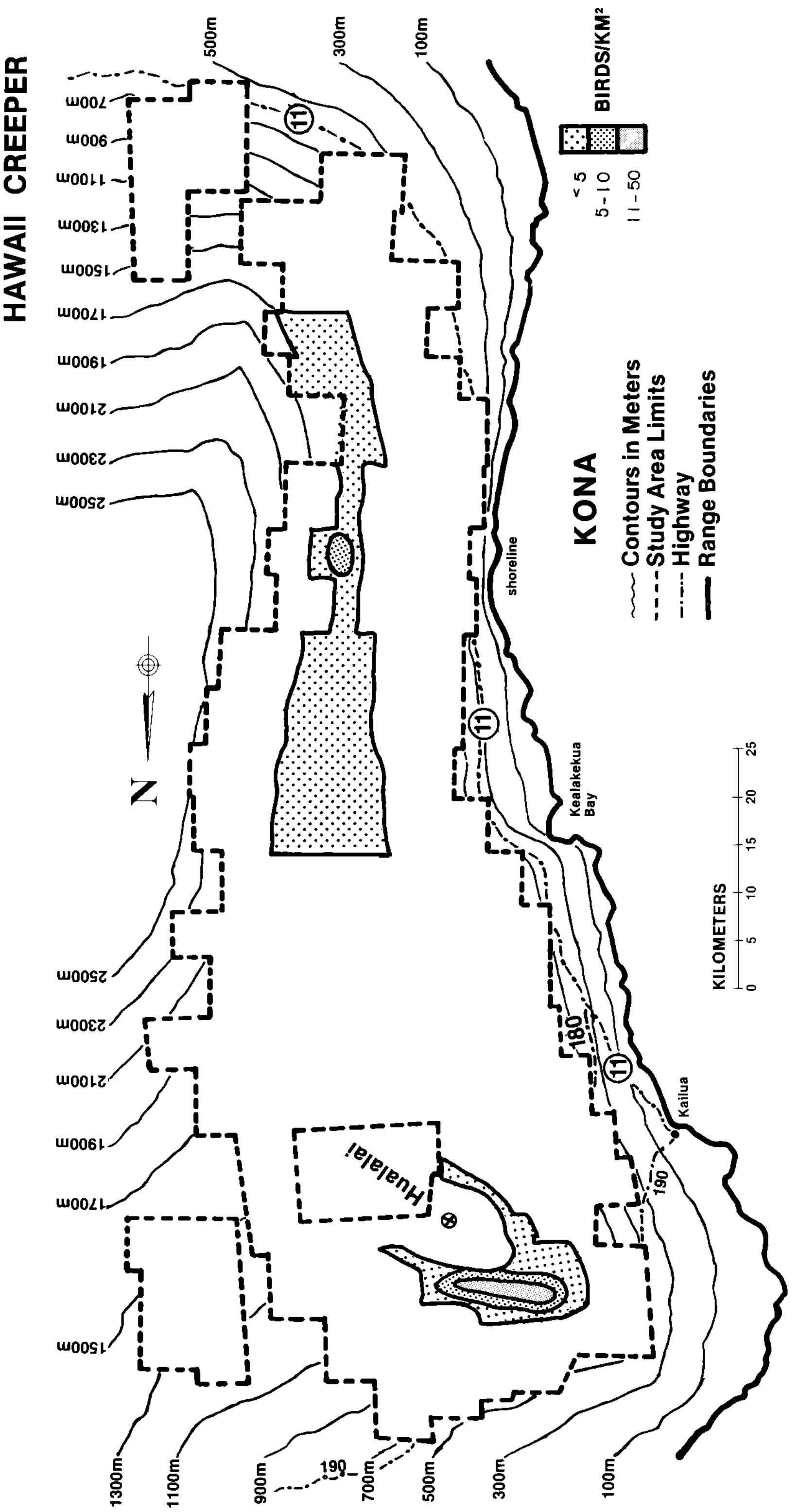


FIGURE 123. Distribution and abundance of the Hawaii Creeper in the Kona study area.

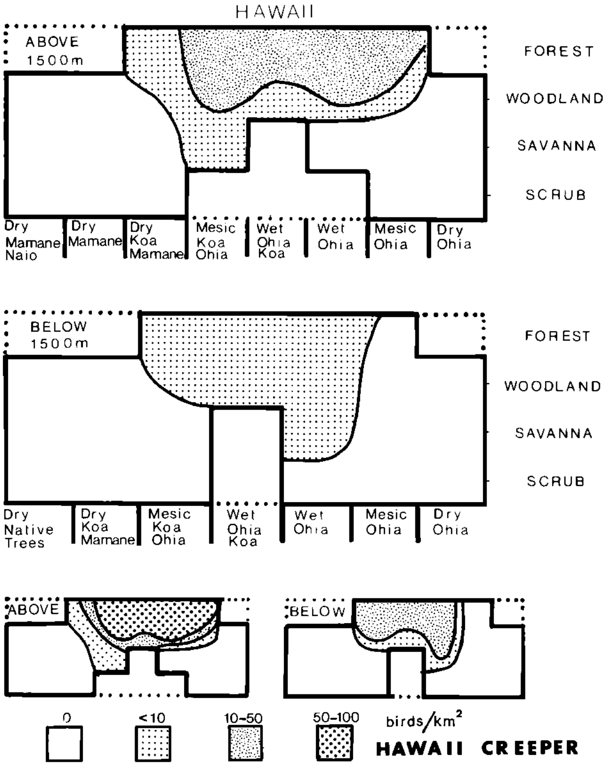


FIGURE 124. Habitat response graphs of the Hawaii Creeper. (Graphs give mean density above and below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

ers dropped from 26 in 1937 to 0 in 1939 and 1940, but no Japanese White-eyes were recorded during these years. If these data were typical for the year round, then other factors probably caused the decline of the species in this area. On the other hand, the results of our competition analysis (Mountainspring and Scott 1985) showed that densities of Hawaii Creepers and Japanese White-eyes were negatively related in the Hamakua study area, possibly reflecting gradual displacement of Hawaii Creepers through interspecific competition for food. An alternate explanation for these patterns is that the spread of avian disease caused the declines, and may be correlated with the spread of Japanese White-eyes.

Hawaii Creepers have four disjunct populations totalling 12,500 ± 2000 (95% CI) birds (Tables 10, 25, Figs. 121–123). About 2100 ± 1100 birds occur over nearly the whole length of Kau in both ohia and koa-ohia forests, and extend below 700 m elevation. A 27-km gap between the Kau population and the 10,000 ± 1600 birds in the Hamakua study area coincides with deforested habitat on the Kapapala Tract. In Hamakua, Hawaii Creepers are, overall, nearly five times more common in koa-ohia than in ohia. As in Kau, creepers extend to low elevations in Hamakua, particularly in stands with large old koa trees.

Two populations totalling 300 ± 150 (95% CI) birds inhabit Kona, primarily in koa-ohia forests. About 220 birds live in the koa-ohia forests on north Hualalai and extend down to 1100 m elevation. The central Kona population of only 75 birds is restricted to areas above 1500 m elevation. The two populations are separated by 35 km of open pasture.

Van Riper (1982) reported 11 Hawaii Creepers during 47 counts on Kohala Mountain in 1972, although these may have represented multiple records of as few as two birds (C. van Riper III, pers. comm.). We failed to find this species during our Kohala survey despite thorough familiarity with it. The probability of our missing a population of 100 birds is small (Table 12). Other recent observers have also failed to find the species in that area.

Hawaii Creepers occur from 700 to 2200 m elevation, but only in the wet forest of Kau and Hamakua are they found below 1100 m. Highest densities occur at 1500–1900 m in Kau and Hamakua. The habitat response graph shows that Hawaii Creepers are most common in the mesic and wet forests above 1500 m elevation (Fig. 124).

The regression models (Table 26) indicate that Hawaii Creepers are most common in wet, dense forests at higher elevations with more koa and less tree fern than average. Hawaii Creepers are positively associated with wetter areas in the Hamakua model. Elevation has positive terms in two models. The low significance of tree biomass, crown cover, and canopy height reflects the range of forest types occupied, although densities are higher in dense forests than in savannas or scrublands. Response to koa is positive in two models and negative in one. Response to understory and phenology variables is generally unimpressive. Passiflora has a negative response in Hamakua, but in Kona passiflora occurs in the north Hualalai refugium and yields a positive response. (A parallel case is seen with Akepa.)

Further insight into Hawaii Creeper habitat requirements is suggested by nest sites. In a five-year study involving nearly 20 person-years of field effort, Sakai and Johanos (1983) reported finding eight nests, or 1.62 nests/person-year, in an unlogged, ungrazed, closed canopy, mature koa-ohia forest, but only one nest, or 0.07 nests/person-year, in an adjacent open canopy koa-ohia forest that was grazed by cattle and logged for koa for many years. Their study suggests that the species prefers relatively undisturbed koa-ohia forests, and our data show that highest densities occur in areas least modified by logging and grazing.

# MAUI CREEPER
## *Paroreomyza montana*

MAUI CREEPER (*Paroreomyza montana*)

Maui Creepers, or Alauwahio, are aberrant honeycreepers bearing little similarity to the Hawaii or Kauai species (Pratt 1979, Berger 1981). They were originally present on East Maui, West Maui, and Lanai. Fossil records suggest that they once occurred on Molokai (Olson and James 1982b).

In the 1890s this species was ubiquitous in Lanai forests above 600 m elevation, abundant in the West Maui mountains even into guava scrub, and extremely abundant in the forests of East Maui (Perkins 1903). Munro (1944) saw a pair on Lanai in 1937, but that population is now extinct (Hirai 1978). The West Maui population was last reported at the turn of the century (Perkins 1903) and is now extinct. The probability of even small populations still occurring

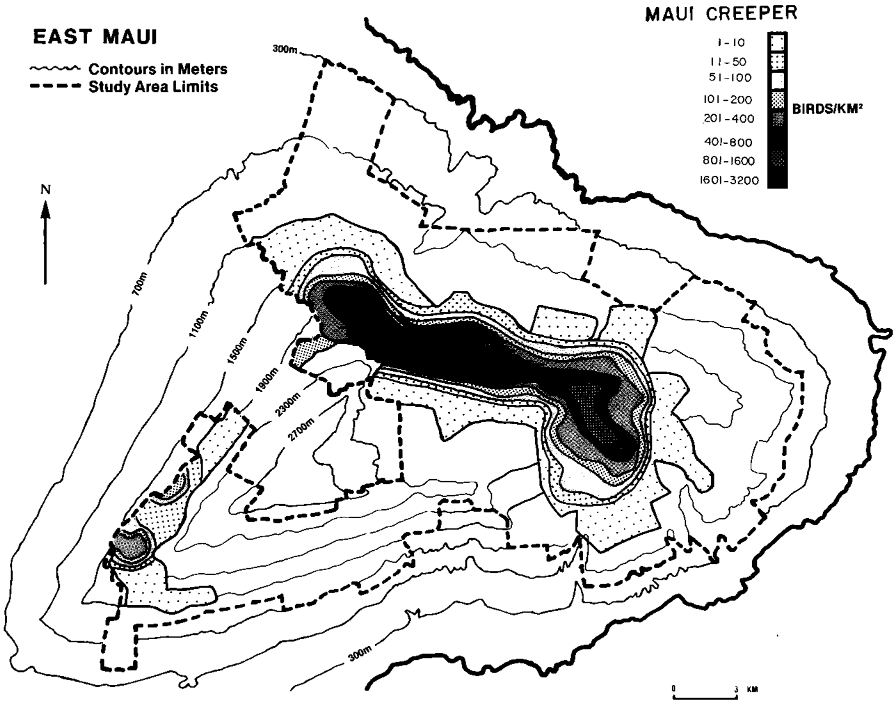


FIGURE 125. Distribution and abundance of the Maui Creeper in the East Maui study area.

on West Maui is small (Table 12). On East Maui, birds were considered "not uncommon" in 1928 (Munro 1944). In the 1960s they were common in upper elevation forests (Berger 1972). Scott and Sincock (1977) found them abundant in the Koolau Forest Reserve in 1975.

Maui Creepers feed on insects and nectar (Berger 1981) and use a wider variety of foraging substrates and maneuvers than Hawaii Creepers (Scott and Sincock 1977). They frequently glean insects from foliage and occasionally take nectar from understory plants (Carothers 1982). Their behavior resembles more nearly that of warblers (Parulinae) than that of creepers (Certhiidae) or nuthatches (Sittidae). Pratt (1979) noted the behavioral similarity to the Black-and-white Warbler (*Mniotilta varia*).

We found Maui Creepers abundant on East Maui, especially at higher elevations in the wet forests, with an estimated population of 35,000 ± 5000 (95% CI) (Tables 11, 25, Fig. 125). Birds are fairly common in high elevation areas of pine, eucalyptus, and other introduced trees at Hosmer Grove and Polipoli State Park. The Polipoli birds are confined entirely to a forest of introduced trees more than 15 km from suitable native habitat. The disjunct distribution reflects the unsuitability of most dry deforested habitats on Maui for this species.

In contrast to Hawaii Creepers, Maui Creepers occur in some savannas and scrublands (Fig. 126). Above 1500 m elevation, they occupy all habitats on the response graph, but are most common in mesic and wet ohia forests. Densities are much higher than those of Hawaii Creepers in similar vegetation types. Maui Creepers occur from 900 to 2500 m elevation and reach highest densities at 1500–2100 m.

The regression model (Table 26) shows that Maui Creepers are most common in dense, wet, high-elevation forests with few tree ferns. Densities are lower in areas with koa or mamane. The positive terms for ground cover and native grasses and the negative term for introduced herbs indicate association with forest interiors that are less damaged by feral pigs.

Maui Creepers are most often found in small flocks. Such flocks are of particular interest in management, because individual birds of three endangered species, Maui Parrotbills, Nukupuu, and Poo-uli, often join these flocks and feed together. On the western dry side of East Maui, far from the main range, we found widely scattered individual birds or family groups, indicating considerable ability of this rainforest species to disperse across extensive areas of dry scrub, grassland, and barren desert. It seems highly probable that if the habitat quality on leeward East Maui

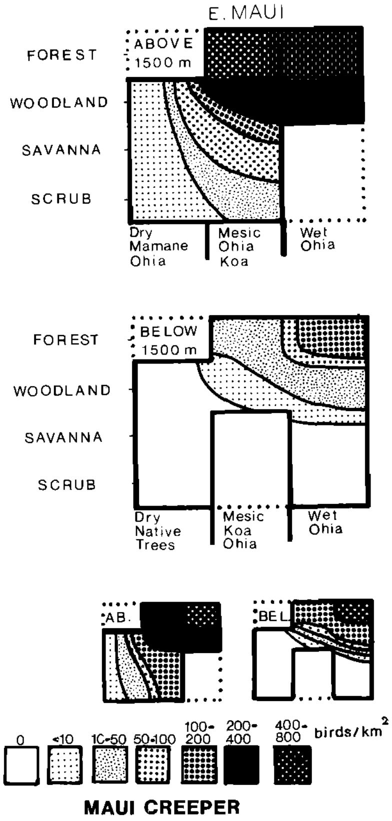


FIGURE 126. Habitat response graphs of the Maui Creeper. (Graphs give mean density above and below 1500 m elevation for East Maui; half-size graphs give standard deviation.)

were improved, Maui Creepers would repopulate these areas.

The numbers and distribution of Maui Creepers suggest that they may be among the first birds to disappear if whatever factor limiting the distribution to upland forests becomes operational at higher elevations. The sharp drop-off of densities at lower elevations is quite striking and suggests that the species is very sensitive to a limiting factor with a mirror image distribution, possibly avian disease. Below 1400 m elevation densities decline drastically west of Waikamoi Stream. Densities on windward East Maui sharply delimit the refugium where the endangered passerines occur. The sharp drop-off of densities at 1600 m elevation in the Hana Forest Reserve parallels the range limits of the Maui Parrotbill and Crested Honeycreeper, suggesting a common limiting factor.

## Molokai Creeper (*Paroreomyza flammea*)

This is the only species of creeper that shows marked sexual dimorphism in plumage. Males of this species are various shades of scarlet, and females are brown with some scarlet markings. Like other creeper species, they glean insects and other invertebrates from trunks and limbs of trees (Bryan 1908). Molokai Creepers are considerably larger than the other creepers.

Perkins (1903) characterized Molokai Creepers as widely distributed and common in the 1890s. Birds were common in 1907 but by the 1930s they were in danger of extinction (Munro 1944). Many have unsuccessfully searched for them since Munro's survey (Richardson 1949, Pratt 1974, Scott et al. 1977). Pekelo (1963a) reported several sightings from the rainforest on the west rim of Pelekunu Valley on the Ohialele Plateau (transect 4 area).

The Hawaiian name for this species, Kakawahie, meant "woodchopping" and was said to describe their chipping call. They were also said to be attracted to observers (Munro 1944). We assumed that the area surveyed at a station for this species was identical to that of the Maui Creeper and that if Molokai Creepers still existed, they would have occurred in any of the native forests we sampled. We failed to find this species, and it may now be extinct (Table 12).

# AKEPA
## *Loxops coccineus*

AKEPA (*Loxops coccineus*)

Akepa were known from Hawaii, Maui, Oahu, and Kauai. The Kauai subspecies, also known as Ou-holowai, is particularly distinct and possibly a separate species (Pratt 1979, A.O.U. 1983). No fossils have been found yet (Olson and James 1982b). One desiccated specimen found in 1943 at the edge of Lake Waiau, elevation 3968 m, near the summit of Mauna Kea, probably represents a bird carried in a wind storm (Munro 1944). Akepa use their unusual asymmetric bill and jaw musculature (Richards and Bock 1973) to capture insects on koa and ohia by twisting apart ohia leaf buds, prying into woven-together koa phyllodes, and foraging among terminal leaf clusters (Perkins 1903).

On Hawaii in the 1890s, Akepa were "rare in most districts" but "comparatively common in the mixed ohia and koa forests on the north side of the Wailuku river at an altitude of [550 m] upwards; and in the koa forest of Kau" (Henshaw 1902). An elevation of 600 m was specified for 12 of 23 elevations recorded on specimen tags (Banko 1979). Perkins (1903) considered Akepa

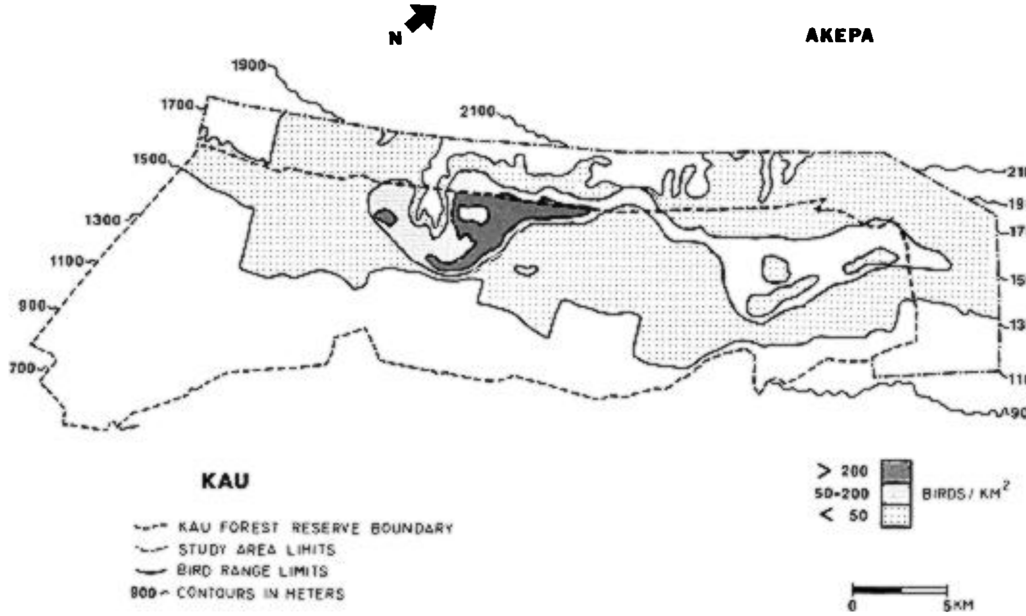


FIGURE 127. Distribution and abundance of the Akepa in the Kau study area.

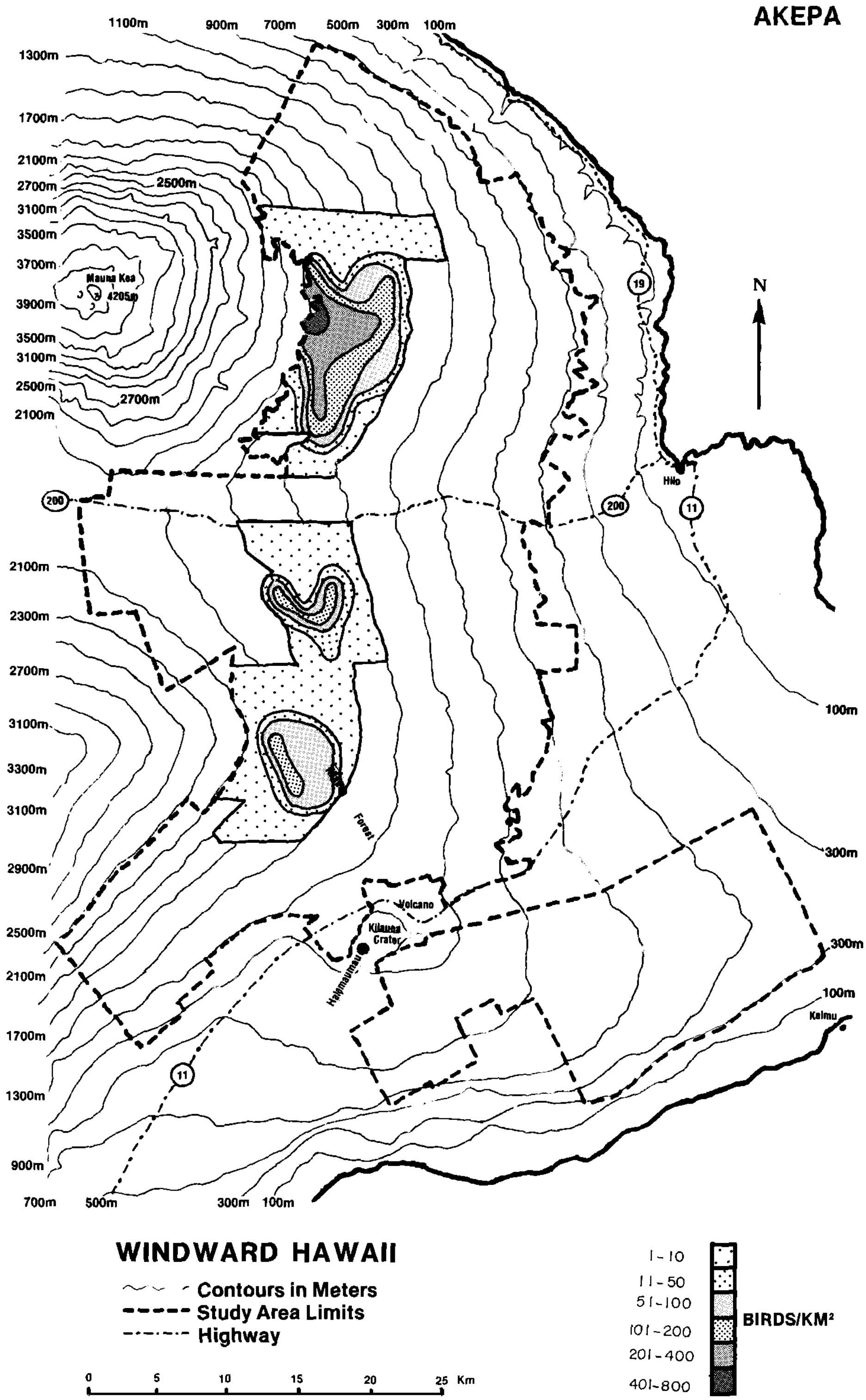


FIGURE 128. Distribution and abundance of the Akepa in the windward Hawaii study areas.

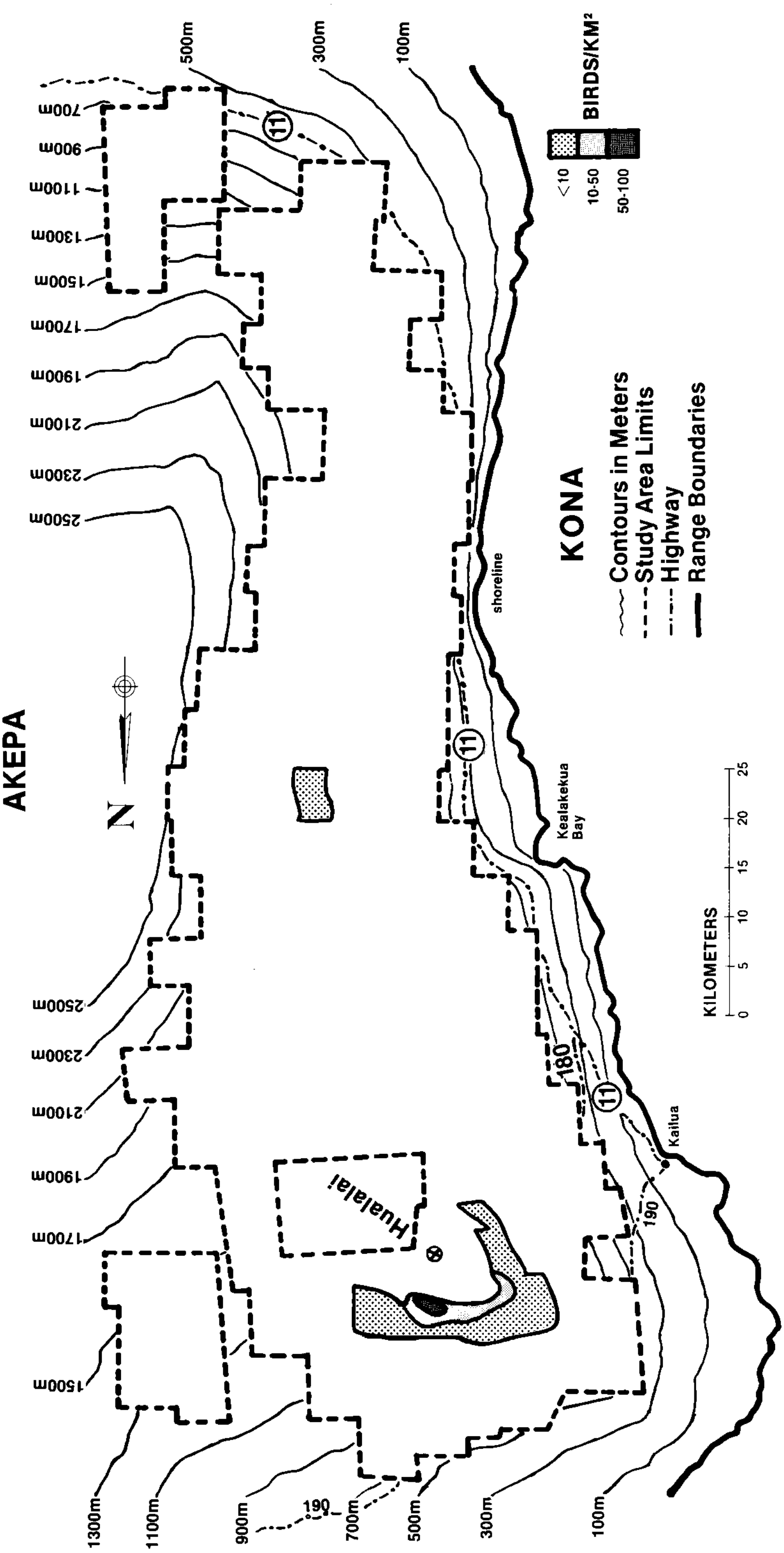


FIGURE 129. Distribution and abundance of the Akepa in the Kona study area.

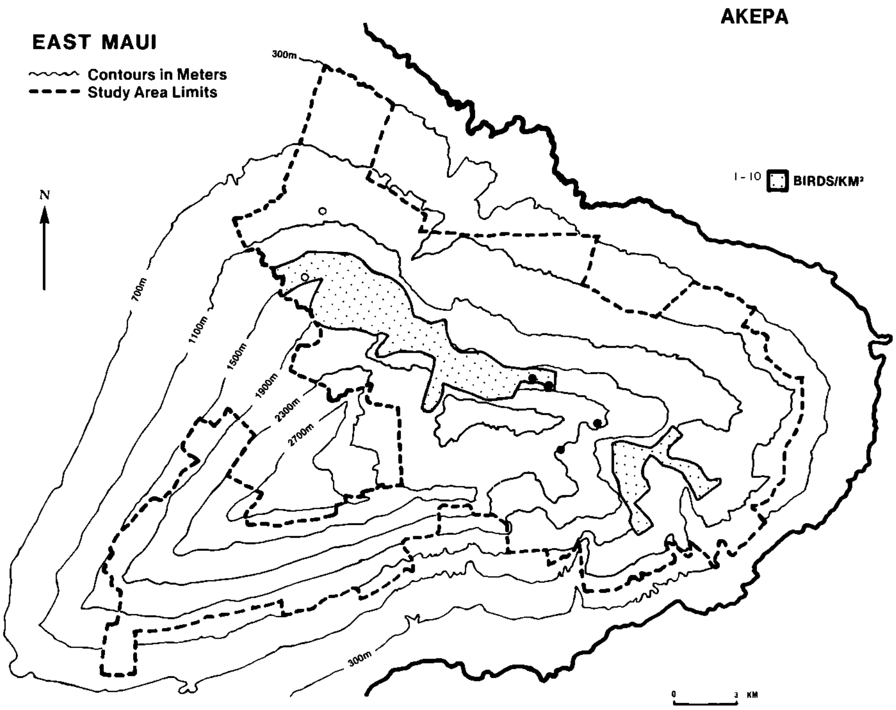


FIGURE 130. Distribution of Akepa in East Maui study area. (Birds recorded as incidentals during the HFBS are indicated by open circles; recent records by other observers are indicated by closed circles.)

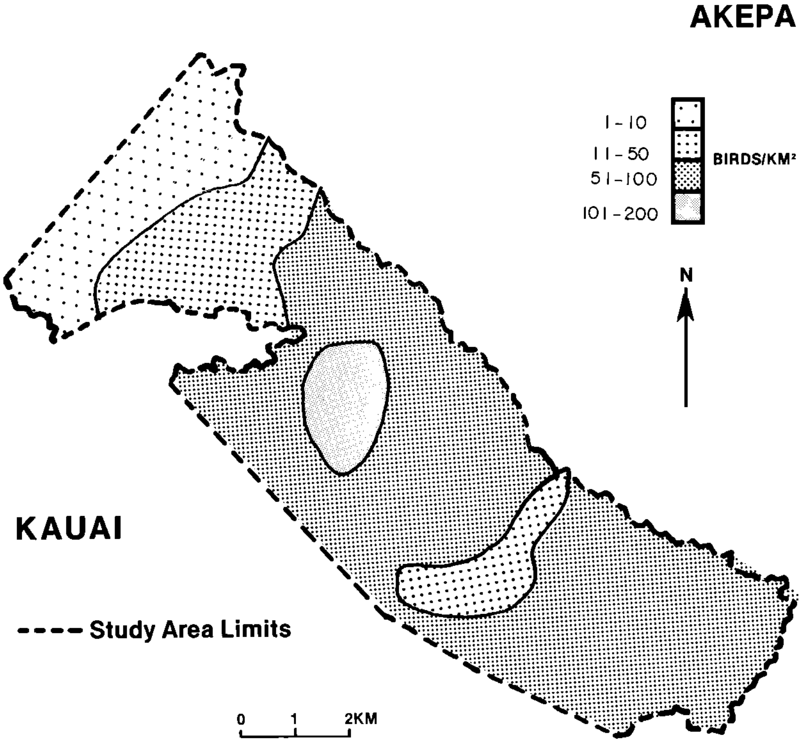


FIGURE 131. Distribution and abundance of the Akepa in the Kauai study area.

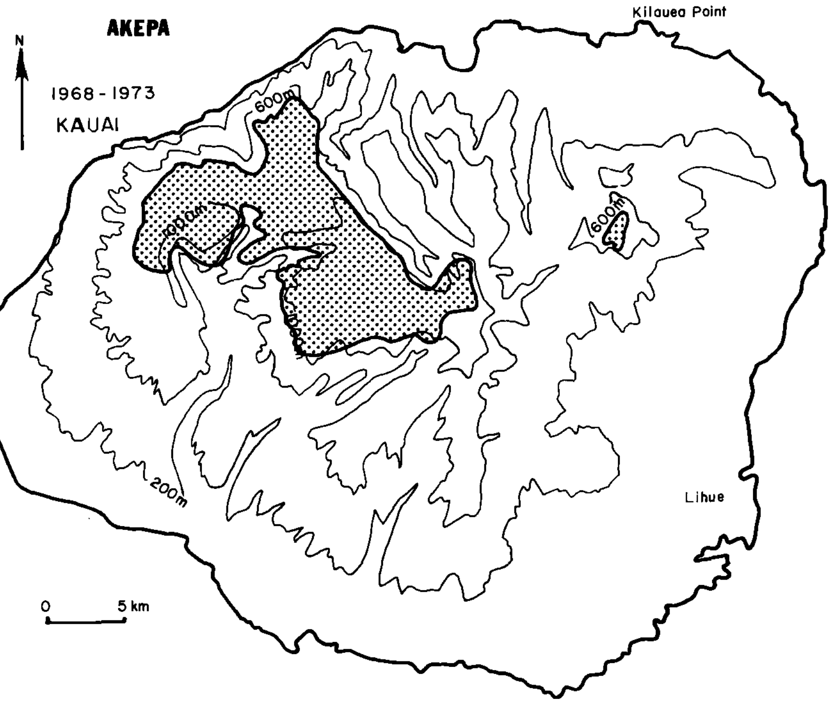


FIGURE 132. Range of the Akepa on Kauai, based on 1968–1973 survey (J. L. Sincock, unpub. data).

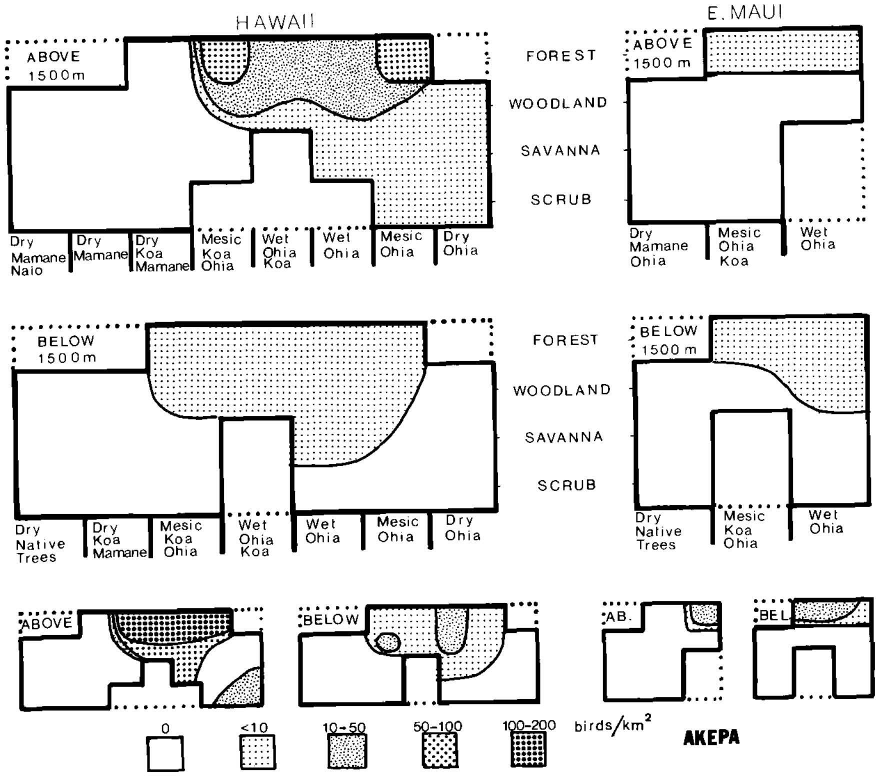


FIGURE 133. Habitat response graphs of the Akepa. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

TABLE 27
DENSITY [MEAN (SE)] OF THE AKEPA AND CRESTED HONEYCREEPER (AKOHEKOHE) BY ELEVATION, HABITAT, AND STUDY AREA[a]

| | Akepa | | | | | Crested Honeycreeper |
|---|---|---|---|---|---|---|
| | Kau | Hamakua | Kona | E. Maui | Kauai | E. Maui |
| *Elevation* | | | | | | |
| 100–300 m | ··· | ··· | ··· | ··· | ··· | ··· |
| 300–500 m | ··· | 0 | 0 | 0 | ··· | 0 |
| 500–700 m | 0 | 0 | 0 | 0 | ··· | 0 |
| 700–900 m | 0 | 0 | 0 | 0 | ··· | 0 |
| 900–1100 m | 0 | 0 | 0 | 0 | ··· | 0 |
| 1100–1300 m | 11 (8) | 0 | 0 | 14 (14) | 68 (9) | 0 |
| 1300–1500 m | 14 (6) | 17 (5) | 19 (8) | 8 (8) | 66 (9) | 31 (31) |
| 1500–1700 m | 30 (7) | 32 (6) | 44 (11) | 15 (14) | ··· | 64 (12) |
| 1700–1900 m | 77 (17) | 83 (19) | 41 (16) | + (+) | ··· | 116 (17) |
| 1900–2100 m | 24 (11) | 77 (33) | 0 | + (+) | ··· | 80 (16) |
| 2100–2300 m | + (+) | 0 | 0 | 0 | ··· | 6 (5) |
| 2300–2500 m | ··· | ··· | 0 | 0 | ··· | + (+) |
| 2500–2700 m | ··· | ··· | ··· | 0 | ··· | 0 |
| 2700–2900 m | ··· | ··· | ··· | 0 | ··· | 0 |
| 2900–3100 m | ··· | ··· | ··· | ··· | ··· | ··· |
| *Habitat* | | | | | | |
| Ohia | 50 (9) | 15 (4) | 0 | 10 (7) | 68 (6) | 92 (9) |
| Koa-ohia | 17 (4) | 67 (10) | 40 (8) | 14 (14) | ··· | 25 (15) |
| Koa-mamane | ··· | 0 | 0 | ··· | ··· | ··· |
| Mamane-naio | ··· | ··· | 0 | ··· | ··· | ··· |
| Mamane | ··· | ··· | 0 | 0 | ··· | 0 |
| Other natives | ··· | 0 | 0 | 0 | ··· | 0 |
| Intro. trees | ··· | + (+) | 0 | 0 | ··· | 0 |
| Treeless | 0 | 0 | 0 | 0 | 0 | 10 (5) |

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

very widely distributed and abundant in the Kau, Hilo, Kohala, and parts of the Kona districts. Richards and Baldwin (1953) reported them locally common at higher elevations on eastern slopes of Mauna Loa and scattered as low as 600 m. Berger (1972) stated that Hawaii Akepa were rare. In Hawaii Volcanoes National Park, Perkins (*in* Banko and Banko 1980) found as many as 12 birds in one koa tree in the vicinity of Kilauea Crater in the 1890s. By the 1940s, Akepa were rare in the national park and occurred only in the Ainahou area in dry ohia woodland at 800 m elevation (Baldwin 1953), and by the 1970s they were gone from the national park (Conant 1975, Banko and Banko 1980).

We found Akepa on Hawaii, Maui, and Kauai (Figs. 127–131). The three Hawaii populations are widely separated and total 14,000 ± 2500 (95% CI) birds (Tables 10, 27). Highest densities of 300 birds/km$^2$ occur in subalpine ohia woodland in Kau. The 5300 ± 1500 birds of that population are well distributed over the study area, except for the south portion. The 7900 ± 1800 birds in Hamakua show an incipient patchy distribution, with a hiatus in the Saddle Road area. Akepa are also absent from the northern fifth of the Hamakua study area. In Kona, 99% of the 660 ± 250 birds inhabit the koa-ohia forests on north Hualalai; there was one incidental observation of a bird in central Kona. Akepa occur from 1100 to 2100 m elevation on Hawaii, with highest densities at 1500–1900 m in Kau and Kona, and at 1500–2100 m in Hamakua. We failed to find Akepa in the Kohala study area (Table 12), as did van Riper (1982).

Akepa were locally abundant on East Maui in the 1890s (Perkins 1903). Munro failed to find them in 1928 and again in 1936. Maui Akepa have been rarely reported since the turn of the century (Richards and Baldwin 1953, Casey 1973, Scott and Sincock 1977). All observers prior to our survey considered it to be very rare (Berger 1972). Perkins (1903) did not find Akepa in the West Maui Mountains. We estimated the Maui population at 230 ± 290 (95% CI) birds with a patchy, relict distribution. Maui Akepa occur from 1100 to 2100 m elevation in ohia and koa-ohia forests, with several records in and west of Waikamoi watershed. An undetected Akepa population may occur above 1500 m elevation

TABLE 28
REGRESSION MODELS FOR HABITAT RESPONSE OF THE AKEPA AND CRESTED HONEYCREEPER (AKOHEKOHE)[a]

| | Akepa | | | | Crested Honeycreeper |
|---|---|---|---|---|---|
| | Kau | Hamakua | Kona | Kauai | Maui |
| $R^2$ | 0.11* | 0.16* | 0.11* | 0.08 | 0.34* |
| Moisture | ··· | 5.7* | ··· | X | 8.9* |
| Elevation | ··· | −3.7* | 2.5 | ··· | ··· |
| (Elevation)$^2$ | 10.0* | 6.0* | ··· | ··· | 11.7* |
| Tree biomass | ··· | −3.0 | ··· | ··· | 8.1* |
| (Tree biomass)$^2$ | ··· | 3.3 | ··· | ··· | ··· |
| Crown cover | ··· | ··· | ··· | ··· | ··· |
| Canopy height | 6.7* | ··· | ··· | ··· | ··· |
| Koa | −2.7 | 3.4* | 2.4 | X | −4.5* |
| Ohia | ··· | ··· | 2.6 | X | ··· |
| Naio | X | X | 5.4* | X | X |
| Mamane | X | −5.8* | −2.8 | X | −4.6* |
| Intro. trees | X | ··· | ··· | X | −4.2* |
| Shrub cover | ··· | ··· | −2.6 | −2.4 | ··· |
| Ground cover | ··· | 2.7 | ··· | ··· | ··· |
| Native shrubs | ··· | 7.2* | ··· | ··· | −2.2 |
| Intro. shrubs | X | 2.5 | ··· | ··· | ··· |
| Ground ferns | X | X | 7.2* | ··· | ··· |
| Matted ferns | ··· | ··· | ··· | −2.4 | −6.7* |
| Tree ferns | ··· | X | −4.5* | ··· | −4.3* |
| Ieie | X | X | ··· | ··· | ··· |
| Passiflora | X | −6.0* | 10.5* | X | ··· |
| Native herbs | X | X | ··· | ··· | −4.8* |
| Intro. herbs | X | X | −3.3 | ··· | ··· |
| Native grasses | ··· | −3.0* | ··· | ··· | 3.4* |
| Intro. grasses | ··· | −2.7* | ··· | ··· | ··· |
| Ohia flowers | ··· | ··· | ··· | ··· | 4.8* |
| Olapa fruit | ··· | ··· | ··· | ··· | 2.7 |
| Mamane flowers | 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.

in the koa-ohia forest above Manawainui Valley. Our survey failed to find Akepa in the area of the putative 1950 record on the dry south side of East Maui, 3 km east of Lualailua Hills (Richards and Baldwin 1953).

Kauai Akepa were common in the 1890s "over a large part of the high plateau" (Perkins 1903). Richardson and Bowles (1964) noted that they were fairly common in higher elevation forests. We estimated 1700 ± 300 (95% CI) Akepa in the Alakai Swamp study area, with far higher densities in the remote interior than towards Kokee State Park. Sincock et al. (1984) estimated a population of 5100 ± 1700 for Kauai, with 600 ± 200 birds in our study area. Population levels should be monitored to determine whether a long-term decline is occurring as for Kauai Creeper, although the data suggest otherwise. During the 1968–1973 survey Akepa occurred on the northwest slopes of Waimea Canyon, Kokee State Park, the Na Pali plateaux, the Alakai Swamp, and the Makaleha Mountains (Fig. 132).

Oahu Akepa were apparently rare and locally distributed in the 1890s (Perkins 1903). They were considered extinct by Berger (1981), but in 1976 Shallenberger and Vaughn (1978) reported a probable sighting of a female Akepa in the central Koolau range near the headwaters of Kaukonahua Stream.

Akepa are most common on Hawaii above 1500 m elevation in tall, mesic to wet forests, and are absent from mamane woodland (Tables 27, 28, Fig. 133). The Kauai regression model indicates little response within the fairly uniform Alakai study area. There are too few Maui Akepa sightings to construct a regression model.

Akepa response to understory elements varies between study areas (Table 28). The Kona population is associated with ground ferns and passiflora, but the passiflora infestation in Hamakua is associated with lower Akepa numbers. This difference appears to be due to the fortuitous occurrence of passiflora in the north Hualalai refugium. Native shrubs have a strong positive response in the Hamakua regression model, but the Kau model has no response to any understory element. The absence of ohia flowers and olapa fruit in the models probably reflects the mainly insectivorous diet.

Perkins (1903) found Akepa widespread in koa and ohia forests on Hawaii and Maui, and Sincock et al. (1984) found them in these forest types on Kauai. This is reflected by the positive terms for koa in the Hamakua and Kona models, and by the location of a majority of Maui records in koa habitat. In Kau, however, Akepa have higher densities in ohia than in koa. The Hawaii subspecies nests in cavities; mature trees and snags may be an essential habitat component (Sincock and Scott 1980, Collins 1984).

ULA-AI-HAWANE (*Ciridops anna*)

Ula-ai-hawane are among the least known historically of the Hawaiian forest birds, and only five specimens were collected. This species is known to have occurred only on the island of Hawaii in the Kona, Hilo, and Kohala districts (Perkins 1903). Fossil records show that congeners formerly occurred on Kauai, Molokai, and Oahu (Olson and James 1982b). This species fed on the blossoms and unripe fruit of loulu palms (*Pritchardia* spp.), according to secondhand reports (Perkins 1903); however, the stomach of the sole alcoholic specimen was filled with foliage insects (S. L. Olson, pers. comm.). Nothing more is known of the behavior. The hind limb has a peculiar stout morphology (Olson and James 1982b), and conceivably these birds were adapted to foraging for insects among the foliage of *Pritchardia* palms, much like the palm creeper *Berlepschia rikeri* in the Amazon Basin forages on *Mauritia* palms (Vaurie 1980).

Ula-ai-hawane were quite rare even when first collected in 1859; they have not been seen since 1892 and are probably extinct. Munro (1944) had a possible sighting on Kohala Mountain in 1937. Extensive searches of the Kohala area by us and others (van Riper 1973a, 1982) have failed to yield any evidence that they still exist. We assumed that the effective detection distances for this species (30 m) and the Apapane were similar (Table 12).

# IIWI
## *Vestiaria coccinea*

IIWI (*Vestiaria coccinea*)

The vermilion plumage and sharply decurved, orange bill of Iiwi are spectacular. In the 1890s Iiwi were one of the most abundant and widespread of the native birds (Wilson and Evans 1890–1899, Henshaw 1902, Perkins 1903). Fossils are known only from Oahu (Olson and James 1982b).

Munro (1944) stated that Iiwi, formerly very numerous, were greatly reduced by the 1940s and were absent on Molokai and Lanai. They became extinct on Lanai by 1929 (Munro 1944) and are currently very rare on Oahu (Shallenberger and Vaughn 1978) and Molokai (Pratt 1974, Scott et al. 1977). In Hawaii Volcanoes National Park, Iiwi were fairly common in ohia rainforest and koa-ohia parkland in the 1940s (Baldwin 1953); by the 1970s, occurrences were less frequent below 1300 m elevation but more frequent in koa-ohia parkland at 1700 m (possibly reflecting habitat regeneration since the halt of grazing in the 1940s) (Conant 1975, Banko and Banko 1980).

We found Iiwi in all study areas except Lanai (Tables 10, 11, 29, Figs. 134–142). On Hawaii, Iiwi comprise one or perhaps two populations, depending on the degree to which birds travel across the Waimea Plains. The main population of 340,000 ± 12,000 (95% CI) birds forms a virtually continuous band from the Mauna Kea, Hamakua, and Kipukas study areas to the Kau and Kona study areas; 88% of these birds occur in Hamakua. In the Kapapala Tract, the Kahuku Tract, and around Puu Lehua, deforested areas have low densities and incipient hiatuses.

Iiwi occur at greatly reduced densities below 1000 m elevation, except in Kona where moderate densities occur as low as 300 m. Iiwi occur as low as 700 m in Hamakua at the north end of the study area in old growth koa-ohia forest and areas with exceptional ohia bloom. About 200 Iiwi occur in the Puna study area. Although Iiwi breed on Kohala Mountain (van Riper 1982) and the satellite population of 800 ± 600 (95% CI) birds there may be a deme separate from the main population, it is also possible that all low elevation Iiwi populations on Hawaii and Maui

TABLE 29

DENSITY [MEAN (SE)] OF THE IIWI BY ELEVATION, HABITAT, AND STUDY AREA[a]

| | Kau | Hamakua | Puna | Kipukas | Kona | Mauna Kea | Kohala | East Maui | West Maui | Molokai | Kauai |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Elevation* | | | | | | | | | | | |
| 100–300 m | ··· | ··· | ··· | ··· | ··· | ··· | ··· | ··· | ··· | 0 | ··· |
| 300–500 m | ··· | 0 | 0 | ··· | 82 (24) | ··· | 0 | 0 | ··· | 0 | ··· |
| 500–700 m | 0 | 0 | 0 | ··· | 46 (10) | ··· | 0 | 56 (19) | 0 | 0 | ··· |
| 700–900 m | 26 (14) | 35 (9) | 1 (1) | ··· | 49 (8) | ··· | 0 | 50 (11) | + (+) | 0 | ··· |
| 900–1100 m | 46 (14) | 99 (17) | 2 (2) | ··· | 56 (6) | ··· | 0 | 54 (9) | 5 (5) | 7 (4) | ··· |
| 1100–1300 m | 68 (11) | 119 (7) | 4 (4) | 0 | 68 (7) | ··· | 9 (4) | 111 (15) | 28 (14) | 2 (1) | 202 (13) |
| 1300–1500 m | 199 (14) | 365 (17) | ··· | 13 (7) | 84 (8) | ··· | 21 (11) | 155 (18) | 6 (6) | 10 (10) | 264 (15) |
| 1500–1700 m | 414 (25) | 638 (34) | ··· | 49 (11) | 153 (11) | ··· | 24 (24) | 151 (18) | + (+) | ··· | ··· |
| 1700–1900 m | 495 (36) | 612 (44) | ··· | 32 (8) | 81 (10) | ··· | ··· | 176 (22) | + (+) | ··· | ··· |
| 1900–2100 m | 155 (28) | 332 (39) | ··· | 7 (4) | 34 (7) | 0 | ··· | 143 (28) | ··· | ··· | ··· |
| 2100–2300 m | 25 (25) | 57 (30) | ··· | + (+) | 7 (2) | 0 | ··· | 11 (7) | ··· | ··· | ··· |
| 2300–2500 m | ··· | ··· | ··· | ··· | + (+) | + (+) | ··· | + (+) | ··· | ··· | ··· |
| 2500–2700 m | ··· | ··· | ··· | ··· | ··· | 25 (11) | ··· | + (+) | ··· | ··· | ··· |
| 2700–2900 m | ··· | ··· | ··· | ··· | ··· | + (+) | ··· | 0 | ··· | ··· | ··· |
| 2900–3100 m | ··· | ··· | ··· | ··· | ··· | 0 | ··· | ··· | ··· | ··· | ··· |
| *Habitat* | | | | | | | | | | | |
| Ohia | 190 (13) | 197 (7) | 2 (1) | 10 (4) | 54 (3) | ··· | 15 (6) | 128 (8) | 13 (6) | 4 (2) | 232 (10) |
| Koa-ohia | 328 (20) | 518 (24) | ··· | 120 (28) | 125 (7) | ··· | ··· | 82 (12) | ··· | ··· | ··· |
| Koa-mamane | ··· | 283 (61) | ··· | 41 (8) | 40 (8) | ··· | ··· | ··· | ··· | ··· | ··· |
| Mamane-naio | ··· | ··· | ··· | ··· | 178 (178) | 0 | ··· | ··· | ··· | ··· | ··· |
| Mamane | ··· | ··· | ··· | ··· | 20 (4) | 11 (5) | ··· | 0 | ··· | ··· | ··· |
| Other natives | ··· | 42 (11) | ··· | 78 (78) | 0 | ··· | ··· | 26 (26) | ··· | 0 | ··· |
| Intro. trees | ··· | 338 (127) | ··· | ··· | 226 (42) | ··· | 31 (31) | 24 (11) | 0 | 0 | ··· |
| Treeless | 0 | 0 | 0 | 10 (1) | 5 (2) | ··· | ··· | 7 (3) | + (+) | 0 | + (+) |

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

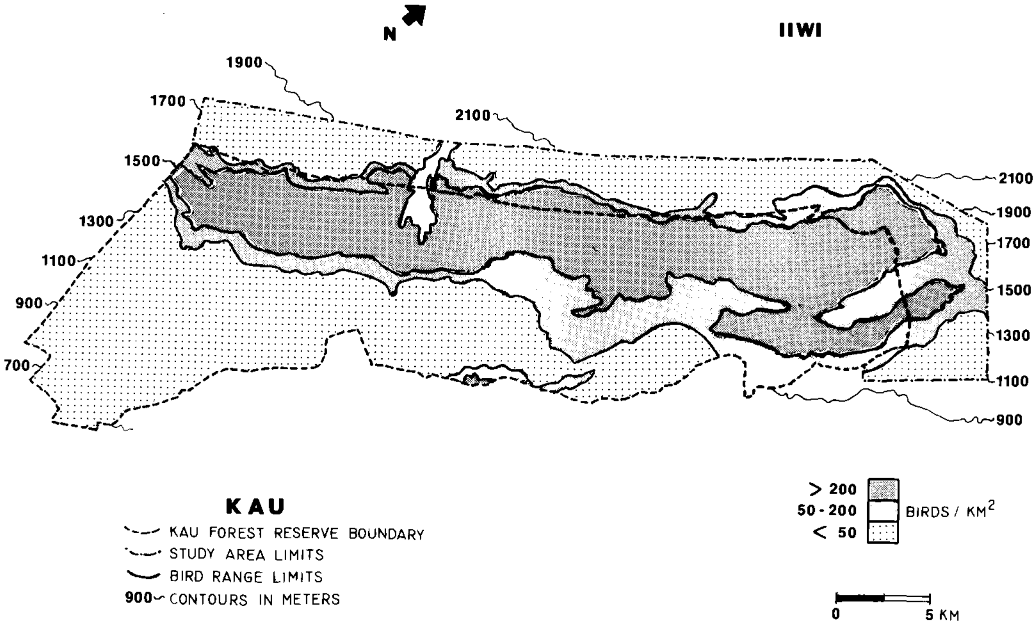


FIGURE 134. Distribution and abundance of the Iiwi in the Kau study area.

are sustained primarily by recruitment of migrants from higher elevations. On Hawaii, Iiwi range from 300 to 2900 m elevation and attain greatest densities at 1300–1900 m.

Mass movements between areas are undertaken by Iiwi in search of flowering plants such as ohia, mamane, and mountain apple (Henshaw 1902, Perkins 1903, Baldwin 1953). Birds on Mauna Kea probably make daily excursions from lower elevations to feed on nectar. In January 1979 hundreds of migrants ("bombers") were seen moving up at dawn from mid-elevation koa-ohia forests in the Hamakua study area to mamane woodland in bloom on Mauna Kea (C. B. Kepler and J. M. Scott, pers. observ.). Although Iiwi were rare on the southwest slopes of Mauna Kea during our 1983 survey, in good flowering years they invade these areas too (J. M. Scott, pers. observ.). Iiwi in the Kipukas study area also seem to move opportunistically into areas with mamane or ohia bloom (see Baldwin 1953, Pimm and Pimm 1982).

The 19,000 ± 2000 (95% CI) birds on East Maui show a sharp drop-off below 1100 m elevation. Mass movements are less pronounced on Maui than on Hawaii, but local concentrations of Iiwi and Apapane are associated with eucalyptus bloom in Hosmer Grove and Polipoli State Park, and with mamane bloom in Hosmer Grove and Haleakala Crater near Paliku. On West Maui 180 ± 150 Iiwi represent a localized, relict population in the vicinity of the Kaulalewelewe Ridge. Incidental observations by many observers over the past 20 years suggest that this population is relatively stable.

On Molokai a population of 80 ± 65 (95% CI) Iiwi has a relict distribution in two areas, Olokui Plateau and Kamakou Preserve. Iiwi are absent from the valleys and confined to ridges and cliffs.

On Kauai our estimate of 5400 ± 500 (95% CI) Iiwi in the Alakai study area suggests a fair-sized population that has perhaps declined from the 7800 ± 2300 birds estimated for that area in 1968–1973 (J. L. Sincock, pers. comm.). Sincock et al. (1984) estimated a total population of 26,000 ± 6000 birds on Kauai. The 1968–1973 range included the area west of Waimea Canyon, Kokee State Park, the Na Pali plateaux, the Alakai Swamp, Kapalaoa Ridge, and Namolokama Mountain (Fig. 143).

Iiwi feed primarily on flower nectar and foliage insects (Henshaw 1902, Perkins 1903, Baldwin 1953, Ralph et al. 1980, Carothers 1982, Pimm and Pimm 1982). The markedly decurved bill perfectly fits the decurved flowers of several lobeliads. Perkins (1903), later corroborated by Spieth (1966), reported that Iiwi feed frequently on lobeliads such as *Clermontia arborescens.* Although lobeliads are not obligately fertilized by honeycreepers (Rock 1919, Spieth 1966), the morphological adaptation of Iiwi points to a long-term association that may have been important when lobeliads were dominant understory elements, before the impact of feral ungulates. This rela-

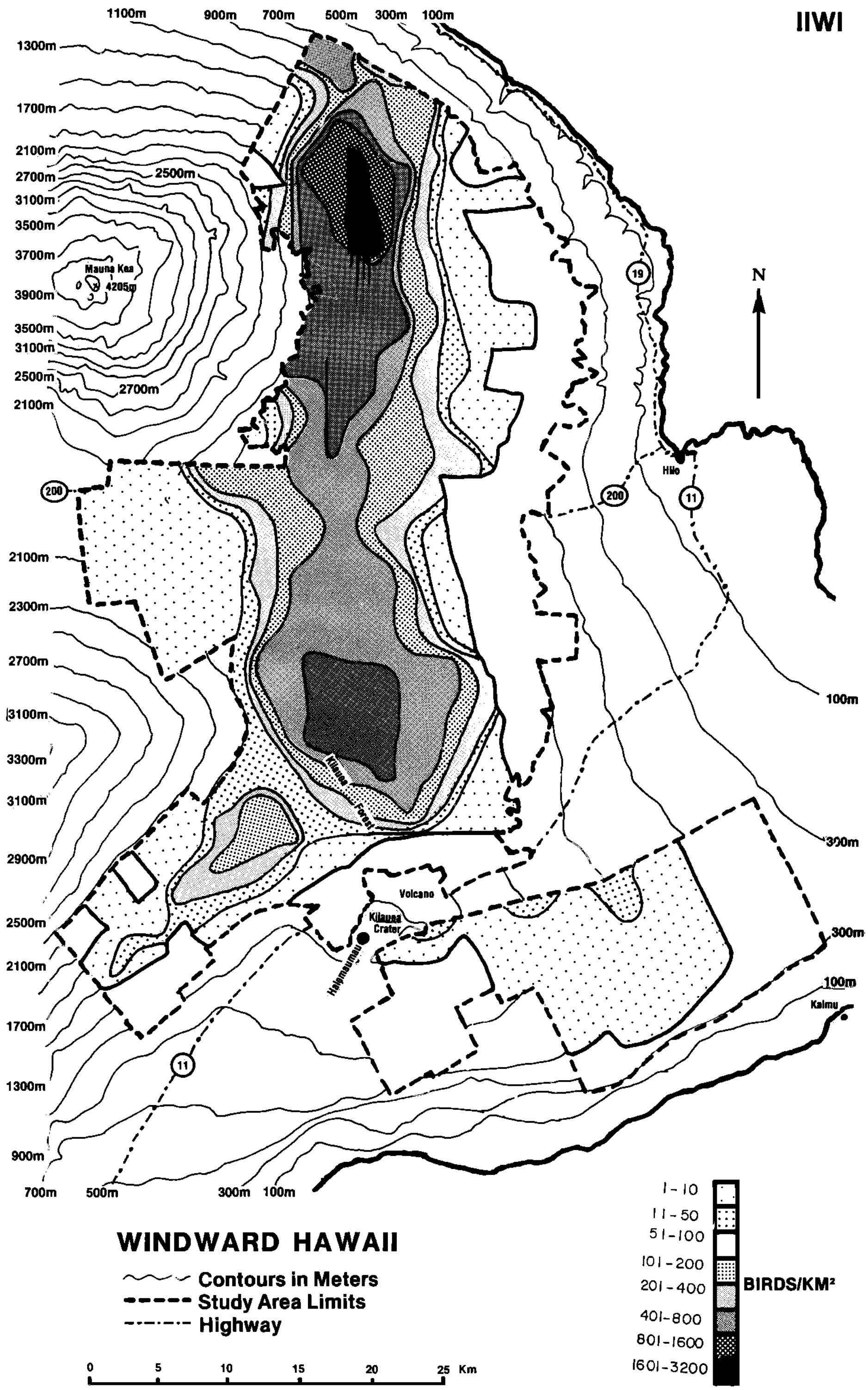


FIGURE 135. Distribution and abundance of the Iiwi in the windward Hawaii study areas.

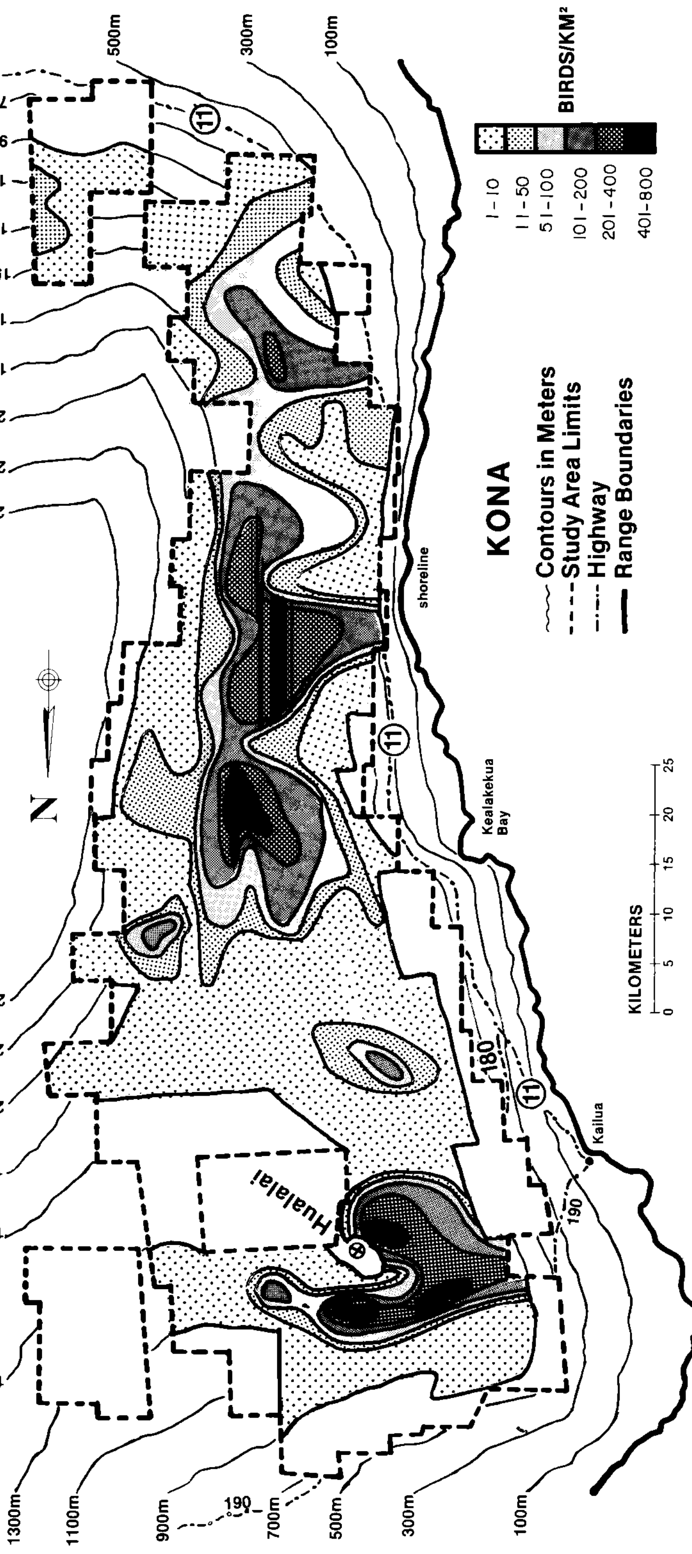


FIGURE 136. Distribution and abundance of the Iiwi in the Kona study area.

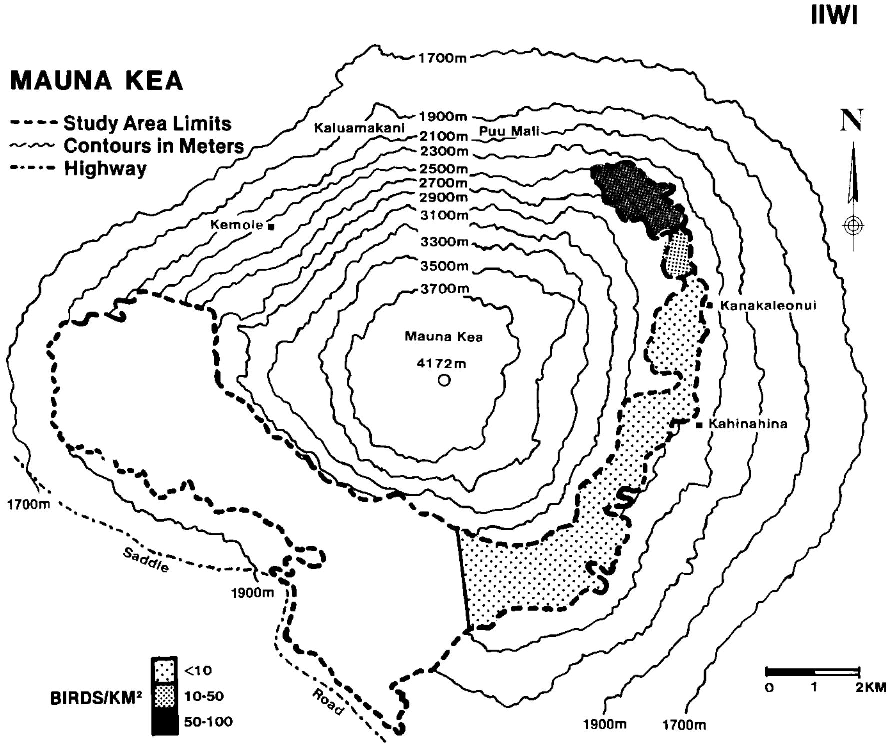


FIGURE 137. Distribution and abundance of the Iiwi in the Mauna Kea study area.

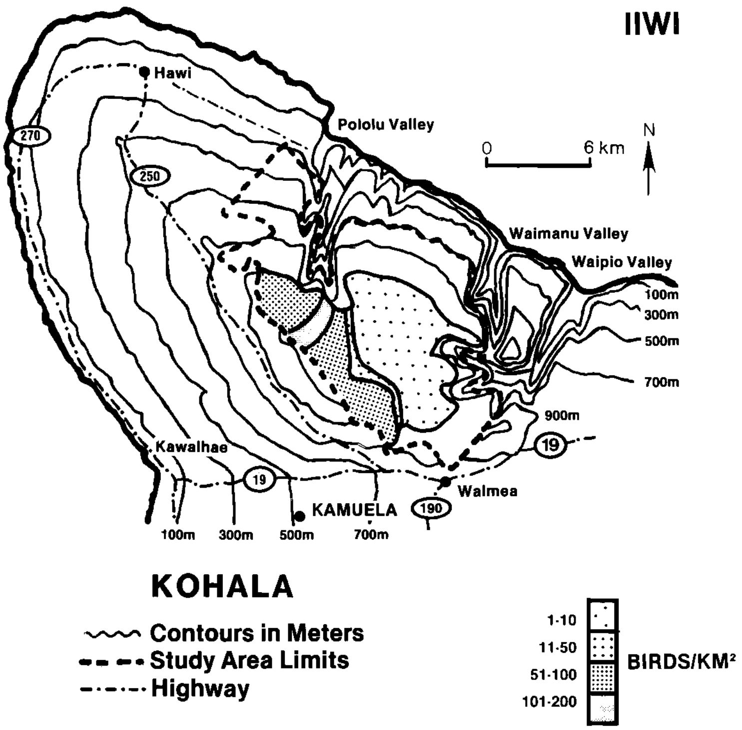


FIGURE 138. Distribution and abundance of the Iiwi in the Kohala study area.

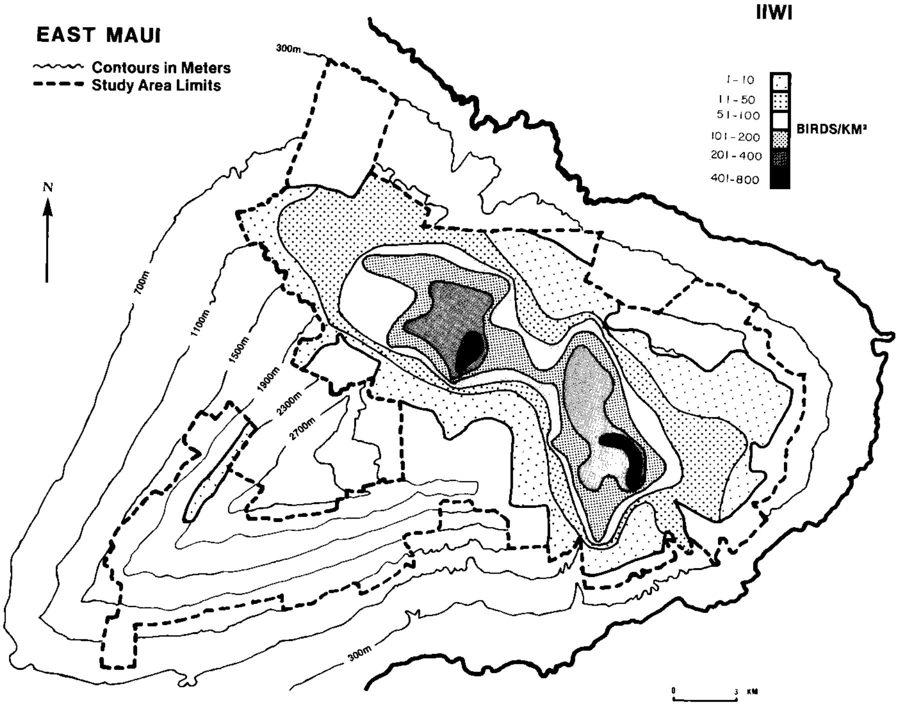


FIGURE 139. Distribution and abundance of the Iiwi in the East Maui study area.

tionship may predate the rise of ohia as a dominant tree, given the putatively greater antiquity of Hawaiian lobeliads (Perkins 1903:403).

The habitat response graphs show that Iiwi are widely distributed on Hawaii and absent only in areas with low rainfall (left end of response graphs, Fig. 144). Iiwi utilize dry mamane and mamane-naio woodlands when they are in bloom. Similar use may be made of other xerophytic native trees (e.g., wiliwili), but only extensive sampling on a seasonal basis would reveal this. Densities are lower below 1500 m elevation on both Maui and Hawaii. Densities on Maui are generally lower than in similar vegetation types on Hawaii. Iiwi are most abundant in mesic to wet forests at higher elevations.

Higher densities are associated with wetter habitat in four regression models (Table 30). In most models a strong response to elevation is evident. The poor fit of the Kauai regression model appears to indicate sampling within a homogeneous cluster. Iiwi generally respond positively to forest development. Iiwi are strikingly associated with passiflora, particularly banana poka. They also respond positively to such other diet items as ohia flowers, olapa fruit, and mamane flowers.

The regression models show that Iiwi have a much weaker response to ohia flowers than do Apapane. This may reflect that Iiwi are less adapted morphologically than Apapane to feed on ohia, although territorial spacing may partly obscure the response. Carpenter and MacMillen (1976) noted that Iiwi are more dependent on nectar than Apapane, and establish feeding territories in the forest interior at moderate densities of ohia flowers. Flocks of Iiwi and Apapane occasionally make towering flights to 100 m or higher, which may help to identify areas with high bloom intensity, as the flowering crowns of ohia and mamane are conspicuous from several kilometers (Perkins 1903).

### Hawaii Mamo (*Drepanis pacifica*)

Hawaii Mamo were magnificent, mostly black birds whose yellow feathers were avidly sought by Hawaiians for the construction of feathered war cloaks (ahuula) for ruling chiefs (Brigham 1899). Kamehameha I had a cloak of pure mamo feathers, but cloaks made after Western contact for lesser royalty used oo feathers (Brigham 1899).

Restricted to the island of Hawaii, Hawaii Mamo were first collected in 1778 or 1779 (Stresemann 1950) and last reported in 1899 (Henshaw 1902). Following the great lava flow of 1880 above Hilo, a considerable number were shot for their feathers, but by the 1890s they were extremely rare (Perkins 1903). Hawaii Mamo had a wide range including most leeward and wind-

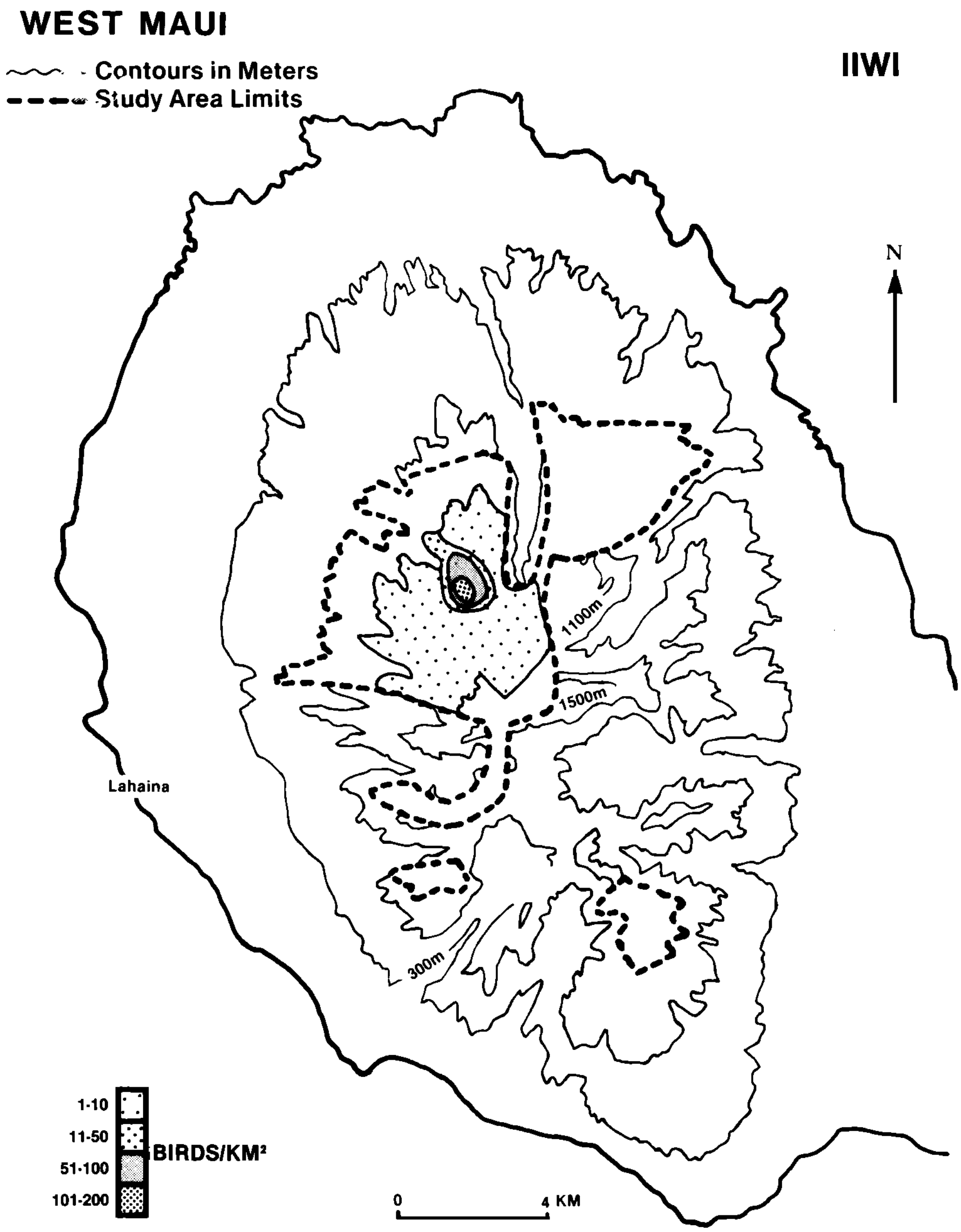


FIGURE 140. Distribution and abundance of the Iiwi in the West Maui study area.

ward forests and Kohala Mountain (Perkins 1903).

Hawaii Mamo used their long decurved bill to feed extensively on the nectar of lobeliads, mamane, ohia, and loulu palms (Perkins 1903), and on insects (Henshaw 1902). They were aggressive, frequently displacing other nectarivores.

The call was described as a single rather long and plaintive note. Henshaw (1902) said he watched birds for more than two hours without hearing them call or sing. We assumed that Hawaii Mamo were less conspicuous than Hawaii Oo (effective detection distance of 40 m), thus the lower probability of detecting this species during our survey (Table 12). Nevertheless, it is extremely doubtful that this species still survives.

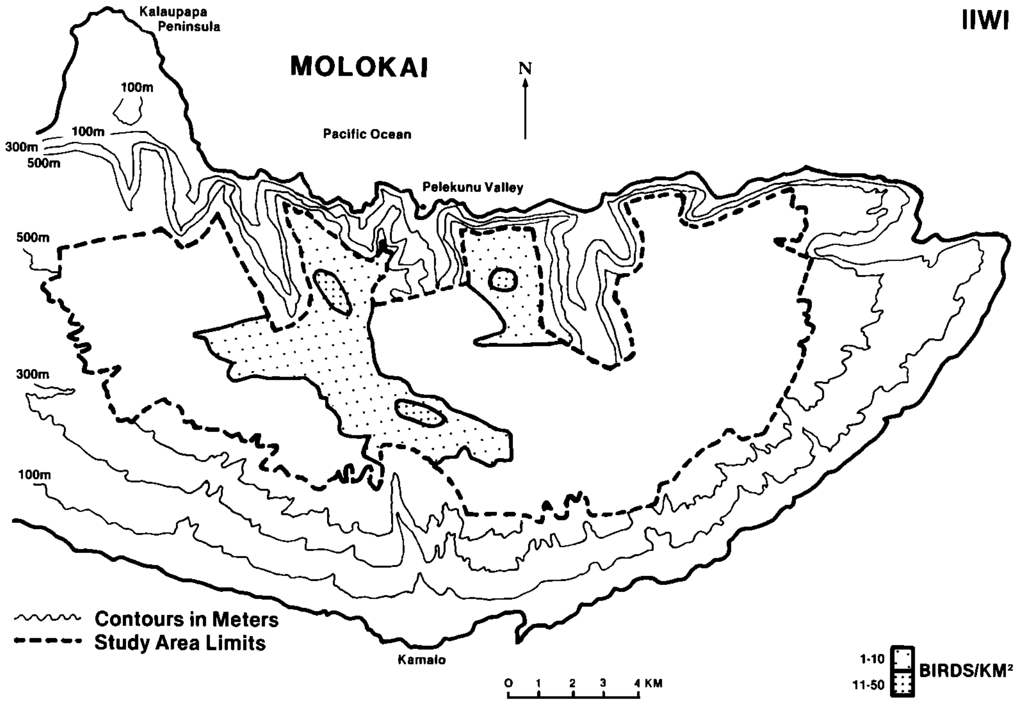


FIGURE 141. Distribution and abundance of the Iiwi in the Molokai study area.

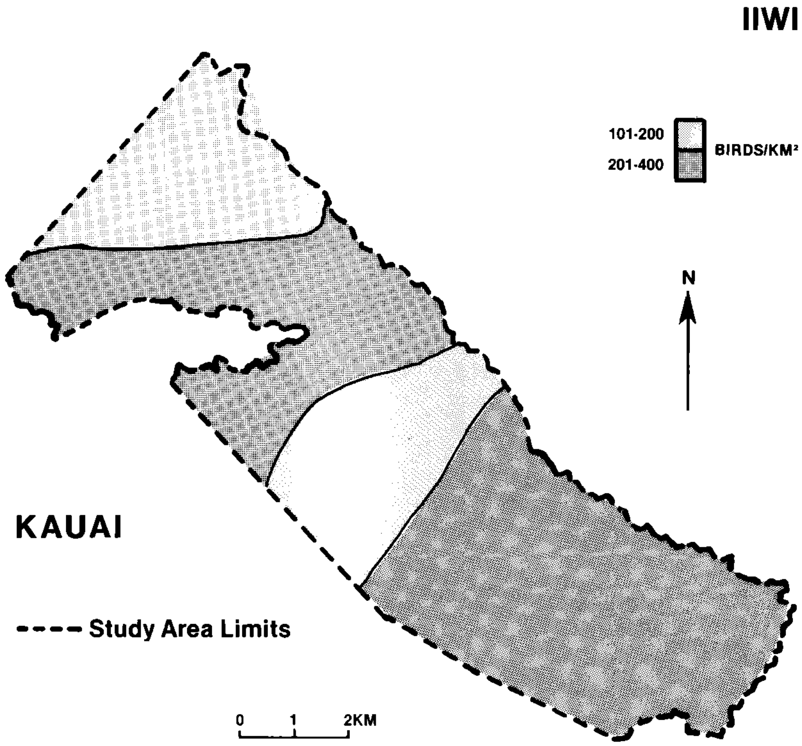


FIGURE 142. Distribution and abundance of the Iiwi in the Kauai study area.

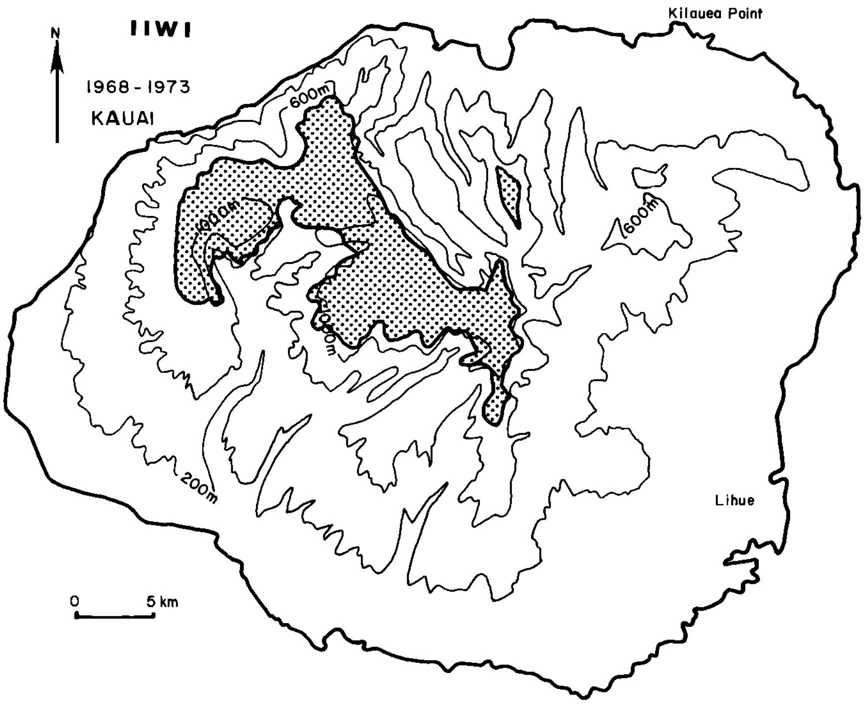


FIGURE 143. Range of the Iiwi on Kauai, based on 1968–1973 survey (J. L. Sincock, unpub. data).

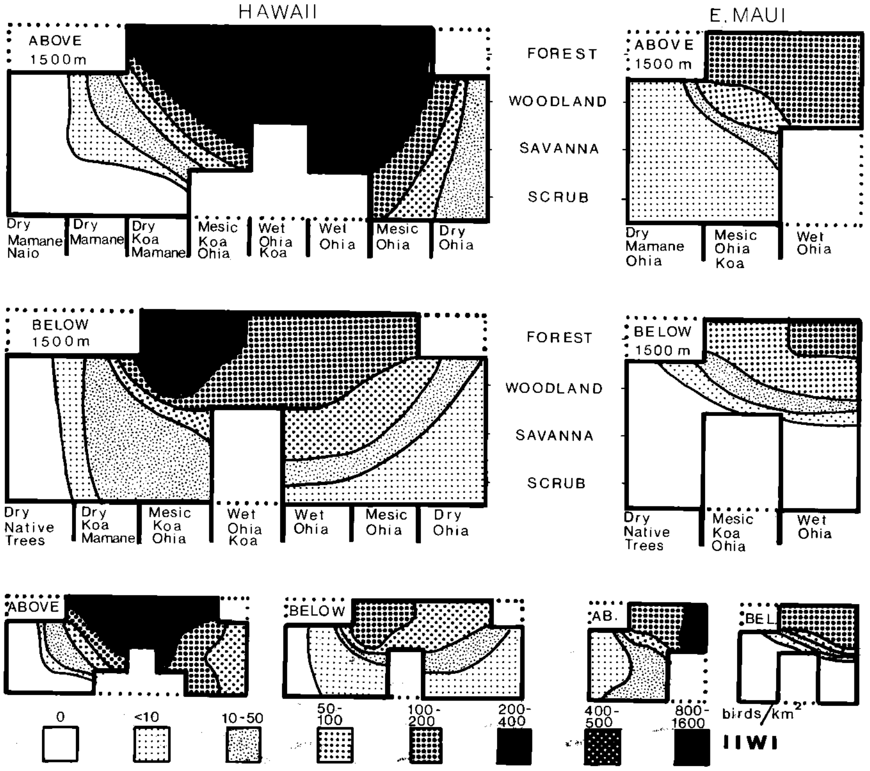


FIGURE 144. Habitat response graphs of the Iiwi. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

TABLE 30
REGRESSION MODELS FOR HABITAT RESPONSE OF THE IIWI[a]

| | Kau | Hamakua | Kipukas | Kona | Kohala | Maui | Kauai |
|---|---|---|---|---|---|---|---|
| $R^2$ | 0.55* | 0.65* | 0.22* | 0.42* | 0.15* | 0.40* | 0.05 |
| Moisture | 5.3* | 11.5* | ... | 8.6* | X | 6.1* | X |
| Elevation | 6.4* | 12.2* | ... | ... | 2.3 | 6.5* | 2.6 |
| (Elevation)$^2$ | −2.6 | −3.6* | ... | 10.0* | ... | ... | ... |
| Tree biomass | ... | −2.9 | ... | −8.0* | ... | −5.0* | ... |
| (Tree biomass)$^2$ | 16.1* | 3.8* | 6.0* | 11.1* | ... | 8.2* | ... |
| Crown cover | ... | ... | ... | ... | ... | ... | ... |
| Canopy height | ... | ... | ... | ... | 2.2 | ... | ... |
| Koa | ... | 5.6* | ... | 4.8* | X | −2.4 | X |
| Ohia | ... | 4.0* | −3.9* | ... | ... | 2.4 | X |
| Naio | X | X | ... | ... | X | X | X |
| Mamane | X | ... | 5.8* | −2.8 | X | ... | X |
| Intro. trees | X | 3.4* | X | ... | ... | −2.7 | X |
| Shrub cover | ... | ... | ... | 8.6* | ... | ... | ... |
| Ground cover | 2.3 | ... | ... | 7.8* | ... | ... | ... |
| Native shrubs | ... | 9.4* | ... | −6.0* | ... | ... | ... |
| Intro. shrubs | X | 6.7* | −2.8 | −9.6* | ... | ... | ... |
| Ground ferns | X | X | ... | 7.1* | ... | ... | ... |
| Matted ferns | ... | −7.2* | ... | ... | ... | ... | ... |
| Tree ferns | ... | X | X | ... | ... | −5.2* | ... |
| Ieie | X | X | X | −9.1* | X | ... | ... |
| Passiflora | X | 5.2* | X | 5.7* | 2.8 | ... | X |
| Native herbs | X | X | ... | −3.7* | ... | ... | ... |
| Intro. herbs | X | X | ... | −5.5* | ... | ... | ... |
| Native grasses | ... | ... | ... | ... | ... | 4.0* | ... |
| Intro. grasses | ... | ... | ... | ... | ... | ... | ... |
| Ohia flowers | ... | 6.8* | ... | ... | ... | ... | ... |
| Olapa fruit | ... | ... | ... | ... | 2.5 | 3.8* | ... |
| Mamane flowers | X | X | 4.1* | 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.

BLACK MAMO (*Drepanis funerea*)

Known only from Molokai, Black Mamo were known as Oo-nuku-umu or Hoa, and were discovered in 1893 by Perkins (Berger 1981). The last Black Mamo recorded was a specimen taken in 1907 (Bryan 1908). Numerous surveys from 1936 to the present have failed to find the species (Munro 1944, Richardson 1949, Pratt 1974, Scott et al. 1977, HFBS). Black Mamo were originally known from wet forests in Kamakou Preserve (Perkins 1903), the transect 15 area (Bryan 1908), and Wailau Valley (Munro 1944). Neither mamo species is known from the fossil record (Olson and James 1982b), but since both species were nectarivores of higher elevation wet ohia forests, mamo species could have occurred on Maui, Oahu, and Kauai and been unrepresented in the dry area fossil sites at lower elevations. The ecologically similar and still widespread Iiwi is also poorly represented by fossils.

Black Mamo have a long decurved bill and take nectar from the large tubular flowers of lobeliads and sometimes from ohia. Perkins (1903) characterized them as very tame birds of the underbrush. Like their congener on Hawaii, Black Mamo were very aggressive and displaced all other nectarivores except oo from flowers (Perkins 1903).

The call of this species was characterized by Bryan (1908) as a rising, whistled "hoa." Perkins (1903) stated that they uttered a loud call of extraordinary clarity repeatedly at short intervals. We estimated the effective detection distance to be 40 m. The probability of detecting a population of 50 birds on Molokai was 85% (Table 12).

# CRESTED HONEYCREEPER *Palmeria dolei*

CRESTED HONEYCREEPER [AKOHEKOHE] (*Palmeria dolei*)

Crested Honeycreepers, also known as Akohekohe, originally occurred on Molokai and East Maui, and were locally abundant in the 1890s (Perkins 1903). On Molokai they were last seen in 1907 (Bryan 1908) and were considered extinct by 1944 (Richardson 1949), but reports of unidentified black birds in montane rainforests persisted through the 1960s (Pekelo 1967). Recent efforts to find the species on Molokai have been unsuccessful (Pratt 1974, Scott et al. 1977, HFBS). It seems highly unlikely that a population of 50 survives on Molokai or West Maui (Table 12).

Munro (1944) failed to find Crested Honeycreepers on Maui during the 1920s and 1930s. Richards and Baldwin (1953) reported them rare on the north slopes of Haleakala above 1750 m elevation. Greenway (1958) concluded that they were reduced to a small population or perhaps extinct on Maui. Scott and Sincock (1977) reported them very common in the upper Hanawi watershed. Conant (1981) considered them locally common and widespread above Manawainui Valley, in Kipahulu Valley, and from Wai Anapanapa to the upper Hanawi. W. E. Banko (pers. comm.) found this species common at higher elevations in Kipahulu Valley during 1967. This differs from the formal account of the Kipahulu Valley Expedition (Warner 1967), which reported only one or two sightings per person day in the upper valley. Our survey found that they are moderately common in the upper valley, with as many as eight sightings per person day.

We found Crested Honeycreepers only at upper elevations on East Maui (Tables 11, 27, Fig. 145). The population numbers 3800 ± 700 (95% CI) birds. In three areas above 1500 m elevation densities exceed 200 birds/km$^2$ and the species appears well established: west of Koolau Gap to Waikamoi Stream, east of Koolau Gap to Wai Anapanapa and Kipahulu Valley, and Kuiki Peak to Manawainui Valley. We found birds from 1300 to 2300 m elevation, with highest densities at 1500–2100 m. The densities, distributional patterns, and historical records indicate that the population is more secure than previously thought.

Like Apapane and Iiwi, Crested Honeycreepers feed primarily on the nectar of ohia flowers. Crested Honeycreepers are aggressively dominant over Apapane and Iiwi in the crowns of flowering ohia trees (Perkins 1903). Crested Honeycreepers also feed on foliage insects and fruit, particularly when nectar is scarce (J. H. Carothers, S. Mountainspring, pers. observ.).

The habitat response graphs for Crested Honeycreepers indicate that they are restricted almost entirely to habitats above 1500 m elevation

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FIGURE 146. Habitat response graphs of the Crested Honeycreeper (Akohekohe). (Graphs give mean density above and below 1500 m elevation for East Maui; half-size graphs give standard deviation.)

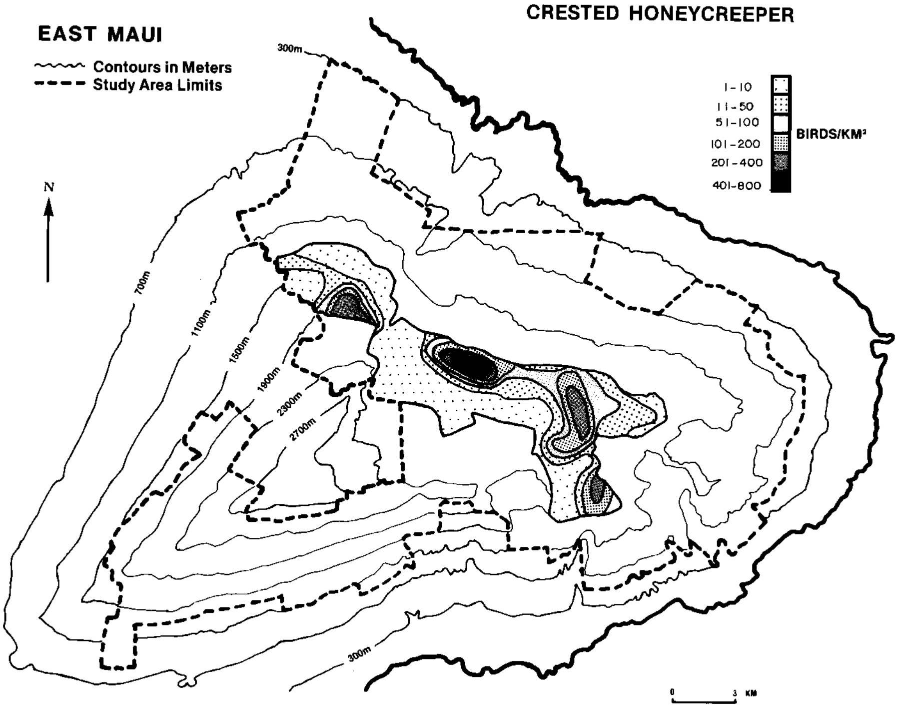
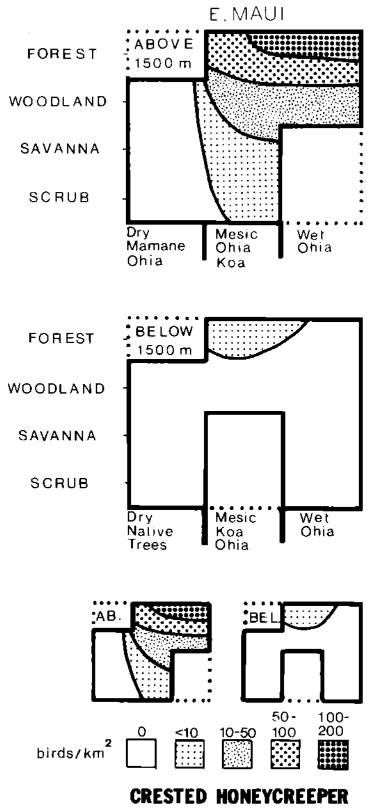



FIGURE 145. Distribution and abundance of the Crested Honeycreeper (Akohekohe) in the East Maui study area.



and are most abundant in mesic ohia-koa and wet ohia forests (Fig. 146). They are completely absent from dry ohia and mamane forests, plantations of introduced trees, and ohia dieback areas (Table 27). Densities are positively associated with forest biomass. Negative responses in the regression models (Table 28) to mamane and introduced trees mainly reflect absence in dry montane forests. Because this species feeds on understory flowers and fruit when ohia is not flowering, the tendency of matted ferns to choke out flowering plants probably lowers habitat quality. The regression model also shows a weak association with ohia flowers and olapa fruit.

Conant (1981) noted seasonal movement in the Kipahulu Valley area. In March, Crested Honeycreepers are found only at higher elevations (1700–2100 m), whereas in June and August, they occur as low as 1100 m elevation. This may represent range contraction during the breeding season followed by postbreeding dispersal. Apapane and Iiwi breed in January–May on Hawaii, with birds more widespread during the non-breeding season (Baldwin 1953); Palila have a similar seasonal cycle (van Riper et al. 1978, van Riper 1980). During July 1980 all Crested Honeycreepers we found at the range periphery were immature birds.

# APAPANE
## *Himatione sanguinea*

APAPANE (*Himatione sanguinea*)

Apapane are the most abundant honeycreepers. Early writers noted their abundance on the six principal islands (Perkins 1903). Munro (1944) characterized them as "occurring in fair numbers on Hawaii, Maui, Oahu and Kauai, a few on Lanai and but one seen on Molokai." Baldwin (1953) found Apapane were the most common native birds in Hawaii Volcanoes National Park and documented seasonal movements in response to changes in available food. Apapane appear to have increased slightly in abundance in the national park over the 1940–1975 period (Conant 1975, Banko and Banko 1980).

Apapane feed primarily on the nectar of ohia flowers and on foliage insects (Baldwin 1953). They occasionally visit other flowers (Perkins 1903, Berger 1981) and immature birds sometimes feed on berries when nectar is scarce, but Apapane appear to be less opportunistic than Iiwi in feeding on other flowers. Baldwin (1953) thought their bill was best adapted for probing the cuplike receptacles of ohia flowers. Pollination of ohia by honeycreepers, especially Apapane, is essential for high levels of fruit-set and outbreeding, a possible result of co-evolved mutualism (Carpenter 1976).

Apapane are usually gregarious, with recognition of individuals probably facilitated by their complex vocal repertoire (Ward 1964). An in-

TABLE 31
DENSITY [MEAN (SE)] OF THE APAPANE BY ELEVATION, HABITAT, AND STUDY AREA[a]

| | Kau | Hamakua | Puna | Kipukas | Kona | Mauna Kea | Kohala | E. Maui | W. Maui | Molokai | Lanai | Kauai |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Elevation* | | | | | | | | | | | | |
| 100–300 m | ··· | ··· | ··· | ··· | ··· | ··· | ··· | ··· | ··· | 488 (178) | ··· | ··· |
| 300–500 m | ··· | 0 | 104 (14) | ··· | 604 (96) | ··· | + (+) | 34 (18) | ··· | 687 (129) | ··· | ··· |
| 500–700 m | 208 (85) | 66 (11) | 362 (24) | ··· | 516 (48) | ··· | 51 (28) | 116 (23) | 125 (81) | 229 (37) | + (+) | ··· |
| 700–900 m | 662 (93) | 129 (13) | 863 (32) | ··· | 187 (16) | ··· | 143 (42) | 183 (22) | 306 (40) | 153 (25) | 51 (18) | ··· |
| 900–1100 m | 568 (64) | 310 (23) | 1000 (67) | ··· | 238 (14) | ··· | 357 (80) | 354 (34) | 668 (112) | 337 (32) | 46 (18) | ··· |
| 1100–1300 m | 477 (37) | 500 (24) | 473 (47) | 252 (47) | 225 (14) | ··· | 144 (26) | 339 (28) | 595 (89) | 445 (34) | ··· | 1256 (45) |
| 1300–1500 m | 711 (39) | 623 (29) | ··· | 204 (23) | 179 (10) | ··· | 203 (26) | 397 (32) | 521 (69) | 362 (104) | ··· | 1139 (36) |
| 1500–1700 m | 1292 (51) | 588 (30) | ··· | 310 (29) | 196 (11) | ··· | 443 (55) | 586 (56) | 213 (40) | ··· | ··· | ··· |
| 1700–1900 m | 1524 (77) | 577 (42) | ··· | 214 (20) | 188 (14) | ··· | ··· | 455 (59) | 302 (55) | ··· | ··· | ··· |
| 1900–2100 m | 1286 (101) | 576 (68) | ··· | 153 (16) | 122 (12) | 0 | ··· | 291 (37) | ··· | ··· | ··· | ··· |
| 2100–2300 m | 1891 (350) | 87 (30) | ··· | 192 (47) | 88 (11) | 0 | ··· | 81 (18) | ··· | ··· | ··· | ··· |
| 2300–2500 m | ··· | ··· | ··· | ··· | 14 (6) | + (+) | ··· | 7 (3) | ··· | ··· | ··· | ··· |
| 2500–2700 m | ··· | ··· | ··· | ··· | ··· | 4 (4) | ··· | 1 (1) | ··· | ··· | ··· | ··· |
| 2700–2900 m | ··· | ··· | ··· | ··· | ··· | 12 (8) | ··· | + (+) | ··· | ··· | ··· | ··· |
| 2900–3100 m | ··· | ··· | ··· | ··· | ··· | 0 | ··· | ··· | ··· | ··· | ··· | ··· |
| *Habitat* | | | | | | | | | | | | |
| Ohia | 751 (30) | 391 (12) | 573 (23) | 187 (13) | 209 (7) | ··· | 216 (22) | 452 (22) | 479 (39) | 324 (21) | ··· | 1209 (28) |
| Koa-ohia | 1294 (48) | 525 (21) | ··· | 263 (26) | 288 (10) | ··· | ··· | 328 (23) | ··· | ··· | ··· | ··· |
| Koa-mamane | ··· | 81 (21) | ··· | 309 (30) | 68 (6) | ··· | ··· | ··· | ··· | ··· | ··· | ··· |
| Mamane-naio | ··· | ··· | ··· | ··· | 21 (7) | 0 | ··· | ··· | ··· | ··· | ··· | ··· |
| Mamane | ··· | ··· | ··· | ··· | 50 (7) | 5 (3) | ··· | 21 (12) | ··· | ··· | ··· | ··· |
| Other natives | ··· | 128 (31) | ··· | 100 (26) | 6 (4) | ··· | ··· | 116 (20) | ··· | 54 (13) | 17 (13) | ··· |
| Intro. trees | ··· | 81 (18) | ··· | ··· | 371 (90) | ··· | 128 (42) | 111 (20) | * | 447 (58) | 56 (15) | ··· |
| Treeless | 814 (156) | 19 (6) | 326 (115) | 39 (20) | 86 (16) | ··· | ··· | 96 (16) | 199 (50) | 18 (8) | + (+) | 227 (227) |

[a] Densities are given in birds/$km^2$; + indicates stratum was in the species range but density <0.5 birds/$km^2$; 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.

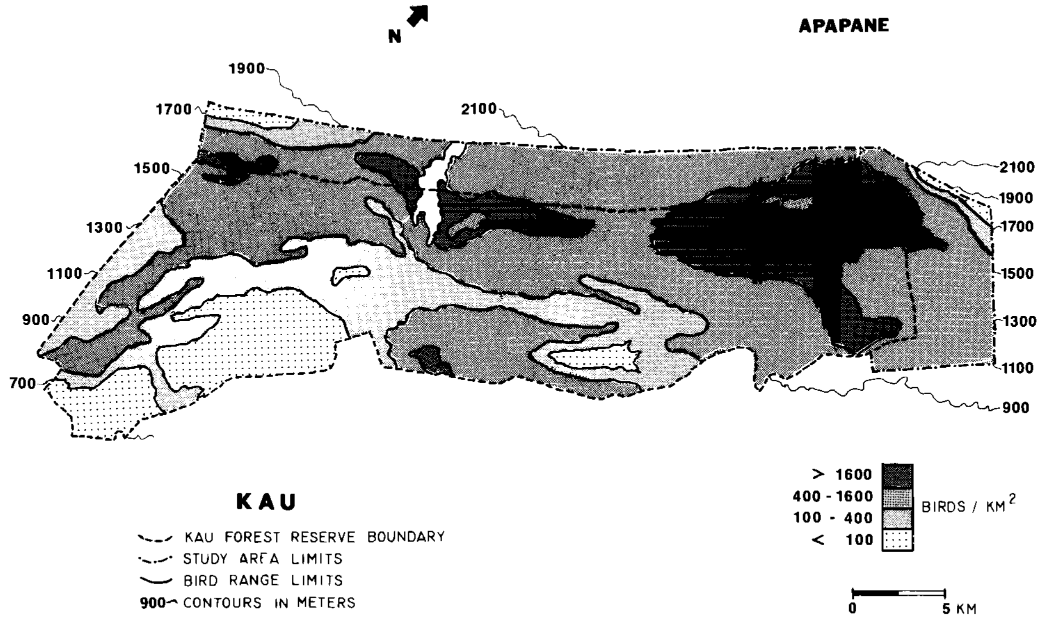



FIGURE 147. Distribution and abundance of the Apapane in the Kau study area.

terspecific social dominance hierarchy of nectarivores is maintained at flowering trees by aggressive interactions. At the base of this hierarchy are Apapane, followed above by Iiwi, then by Crested Honeycreepers on Maui and formerly Molokai (Perkins 1903, Pimm and Pimm 1982). Flocking by Apapane may thwart defense of flowering trees by Iiwi and Crested Honeycreepers. Flocking is also related to large scale mass movements between widely separated (>7 km) roosting and feeding sites (MacMillen and Carpenter 1980). On 26 July 1974 these observers estimated 42,000 Apapane and Iiwi in an evening flight of 1.5 hr duration, presumably gaining an overnight energy savings as a result of thermal protection in mature forest and escape from a nocturnal fog belt. Perhaps because of sharper topographic contrast, smaller land area, and smaller populations, mass flights are less apparent on Maui and the smaller islands than on Hawaii (C. B. Kepler and J. M. Scott, pers. observ.).

We found Apapane in all study areas. They are the most abundant native bird in all areas but Mauna Kea (Tables 10, 11, 31, Figs. 147–156). More than 1,000,000 birds inhabit our study areas on Hawaii, forming two populations that probably exchange individuals.

On Hawaii the main population of 1,080,000 ± 25,000 (95% CI) birds forms a continuous band from Hamakua through Puna and Kau to Kona. Low densities below 2000 m elevation correspond to deforested habitat, particularly in Kona. As with Iiwi, the 200 Apapane in the mamane woodland on Mauna Kea are migrants to areas of high bloom (C. B. Kepler and J. M. Scott, unpub. data). In some years Apapane also occur on the west slopes of Mauna Kea. Apapane are well established throughout Hamakua and Puna, these two areas possessing 50% of the main population. The absence of birds at low elevations north of Hilo and in the northeast corner of the Puna study area corresponded closely to areas lacking ohia bloom. Kau has 25% of the main population. Low densities in the extreme south of the study area again corresponded to areas with low ohia bloom. Bird densities in Kona are also strongly affected by the distribution of ohia bloom, and deforestation accounts for low densities around Puu Waawaa north of Hualalai and around Puu Lehua south of Hualalai (Fig. 149). Apapane occur from sea level below the Puna and Kona study areas to 2900 m elevation on Mauna Kea. Densities exceeding 500 birds/km$^2$ occur at 300–700 m elevation in Kona, at 700–1100 m in Puna, at 1100–2100 m in Hamakua, and at 700–2300 m in Kau. Similar patterns were found in Hawaii Volcanoes National Park by Conant (1975, 1980). Maximum densities of 2000 birds/km$^2$ occur in the Kau area and are among the highest bird densities recorded for a noncolonial species (Udvardy 1957). A population of 20,000 ± 3000 (95% CI) birds on Kohala Mountain are separated by 30 km of pastures from the

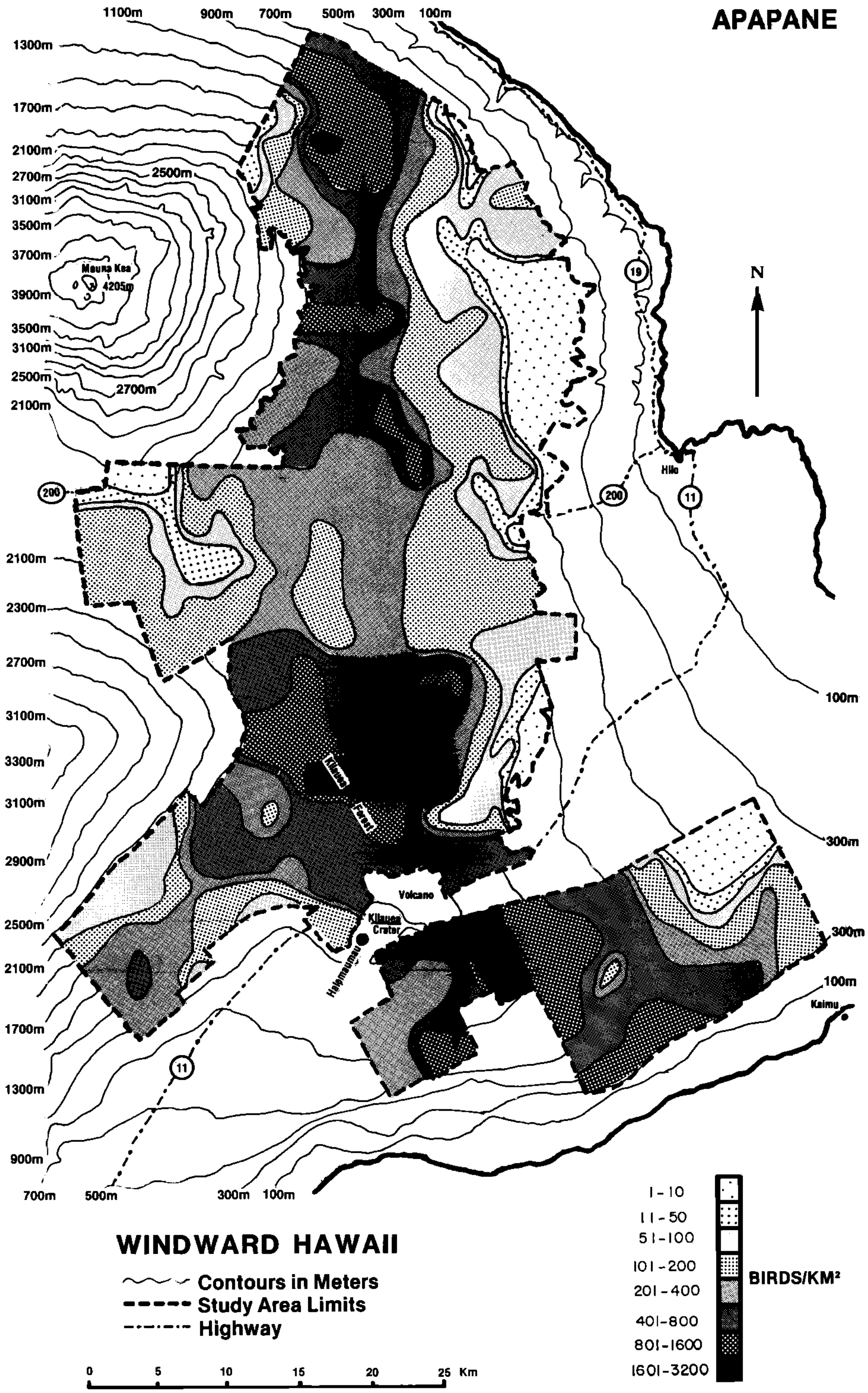



FIGURE 148. Distribution and abundance of the Apapane in the windward Hawaii study areas.

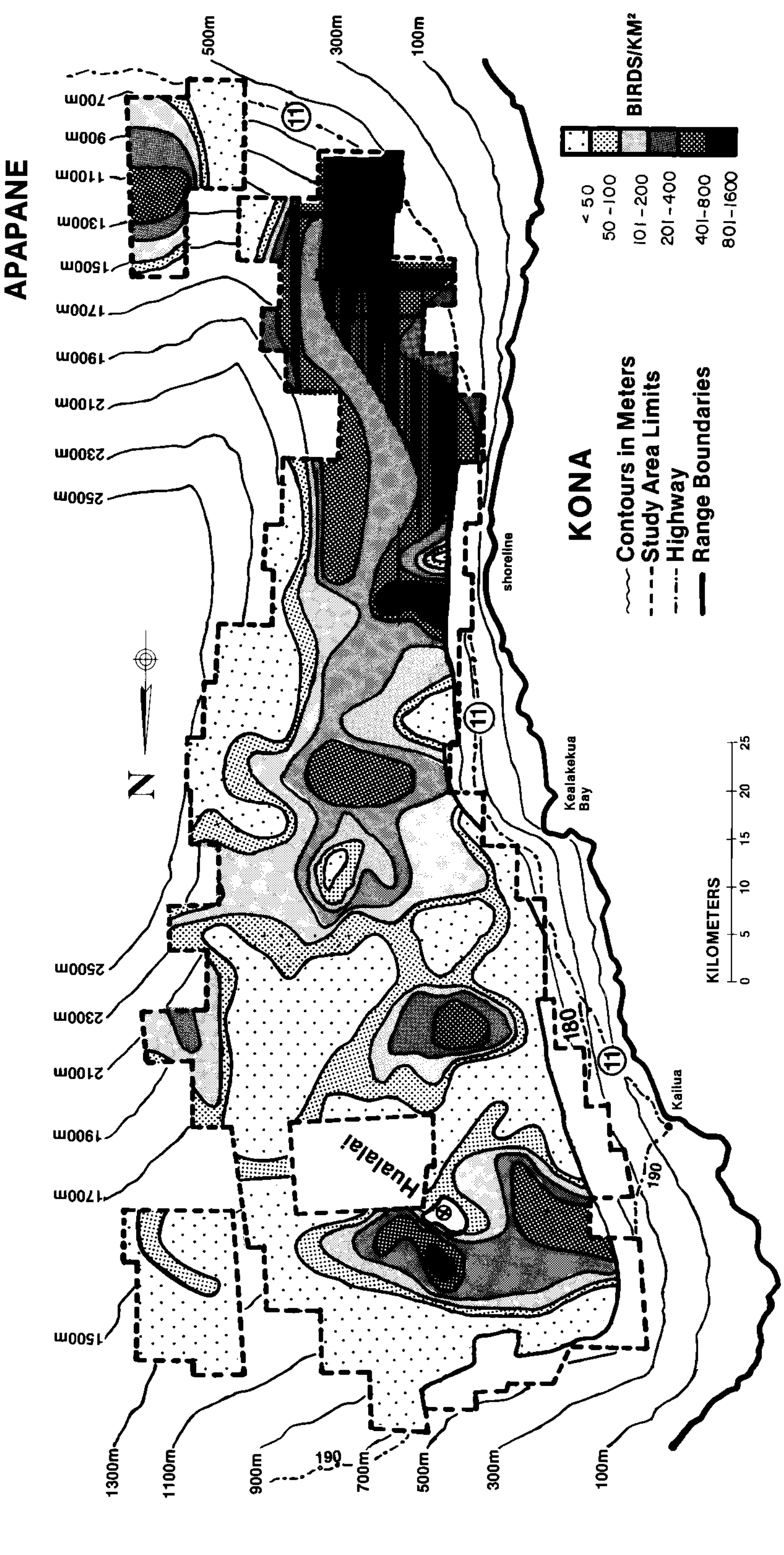



FIGURE 149. Distribution and abundance of the Apapane in the Kona study area.

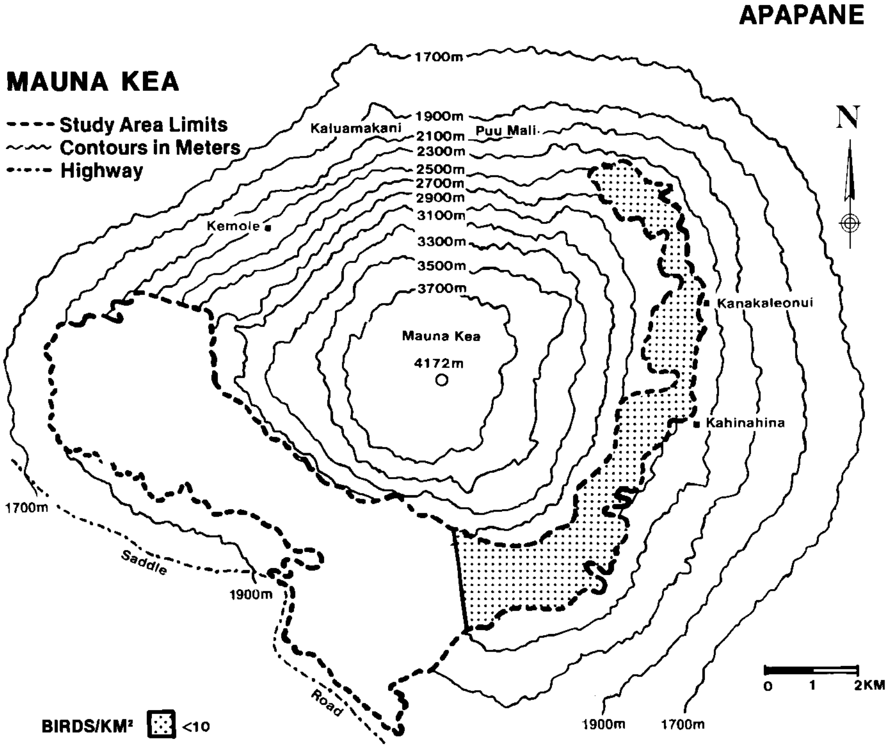



FIGURE 150. Distribution and abundance of the Apapane in the Mauna Kea study area.

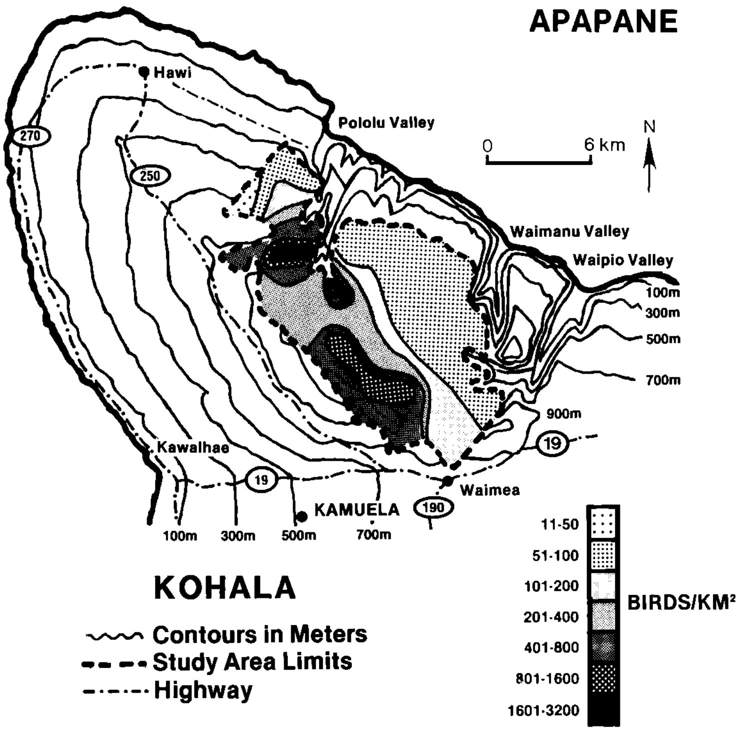



FIGURE 151. Distribution and abundance of the Apapane in the Kohala study area.

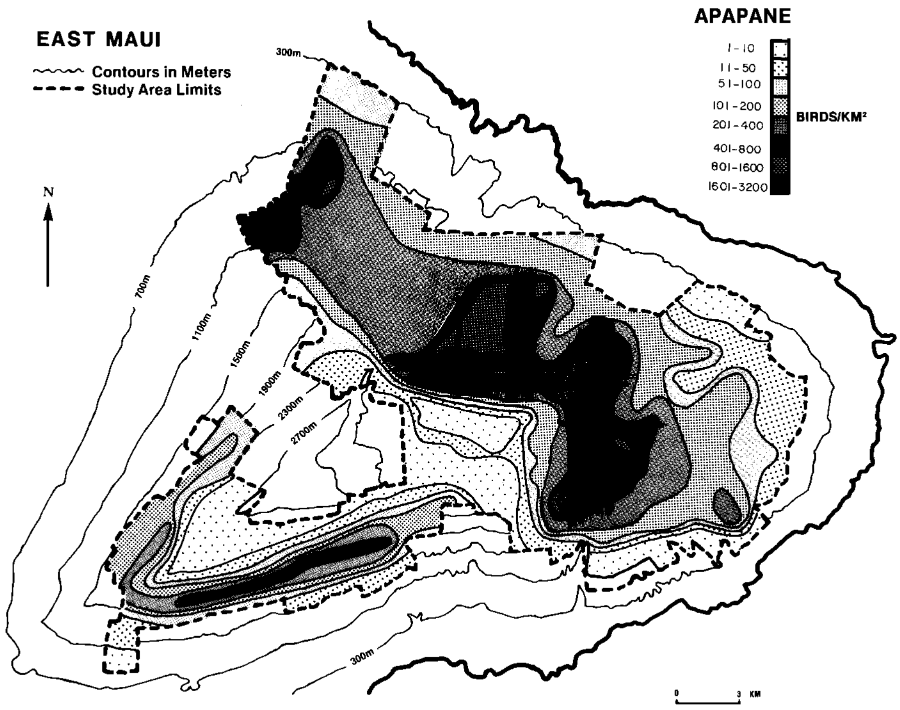



FIGURE 152. Distribution and abundance of the Apapane in the East Maui study area.

main population and are more common at higher elevations.

On East Maui 94,000 ± 7000 (95% CI) Apapane are distributed over the entire study area, with far higher densities in wet ohia forests than in degraded dry woodlands. In Kahikinui, birds are associated with remnant habitat patches. On windward East Maui, densities are lower at lower elevations. Apapane range from 300 to 2700 m elevation on East Maui, reaching highest densities at 1500–1900 m.

West Maui supports a robust population of 16,000 ± 2000 (95% CI) Apapane centered around Puu Kukui and its subsidiary ridges. The near absence of birds on Keahikauo Ridge reflects the presence of bogs and lack of forest in the area.

On Molokai 39,000 ± 5000 (95% CI) Apapane have low densities or are absent due to deforestation on the eastern part of the study area by axis deer, pigs, and cattle, and on the southwest study area margin by deer and goats. Highest densities occur in Pelekunu Valley down to 100 m elevation and in Kamakou Preserve at 900–1500 m.

Only 540 ± 420 (95% CI) Apapane survive on Lanai and have low densities in the remaining native forests. The Lanai population appears to be threatened with extinction, but may be sustained by occasional immigrants from Molokai or Maui.

Apapane are widespread and abundant throughout the Alakai Swamp study area on Kauai. We estimated a population of 30,000 ± 1500 (95% CI) birds that did not differ beyond normal annual variation from the 43,000 ± 9000 birds that J. L. Sincock (unpub. data) estimated for that area for 1968–1973. Sincock et al. (1984) estimated a total of 163,000 ± 23,000 birds for Kauai. The 1968–1973 range showed a virtually continuous population through most areas of native forest on Kauai, with occasional occurrences on the isolated Hoary Head Range (Fig. 157).

Apapane are more abundant above 1500 m elevation on Hawaii than on Maui (Fig. 158). Densities are comparable below 1500 m on the two islands. On all four habitat response graphs, birds occupy every available habitat, but are most common in mesic to wet ohia and koa-ohia forests.

The regression models show that Apapane are especially common in wet, fairly dense, ohia forest at mid to high elevations with good ohia bloom (Table 32). Densities generally increase with tree biomass. In Puna, crown cover and canopy height index the positive response to forest development. Among tree species, ohia have positive terms in four models. Ohia flowers generate pos-

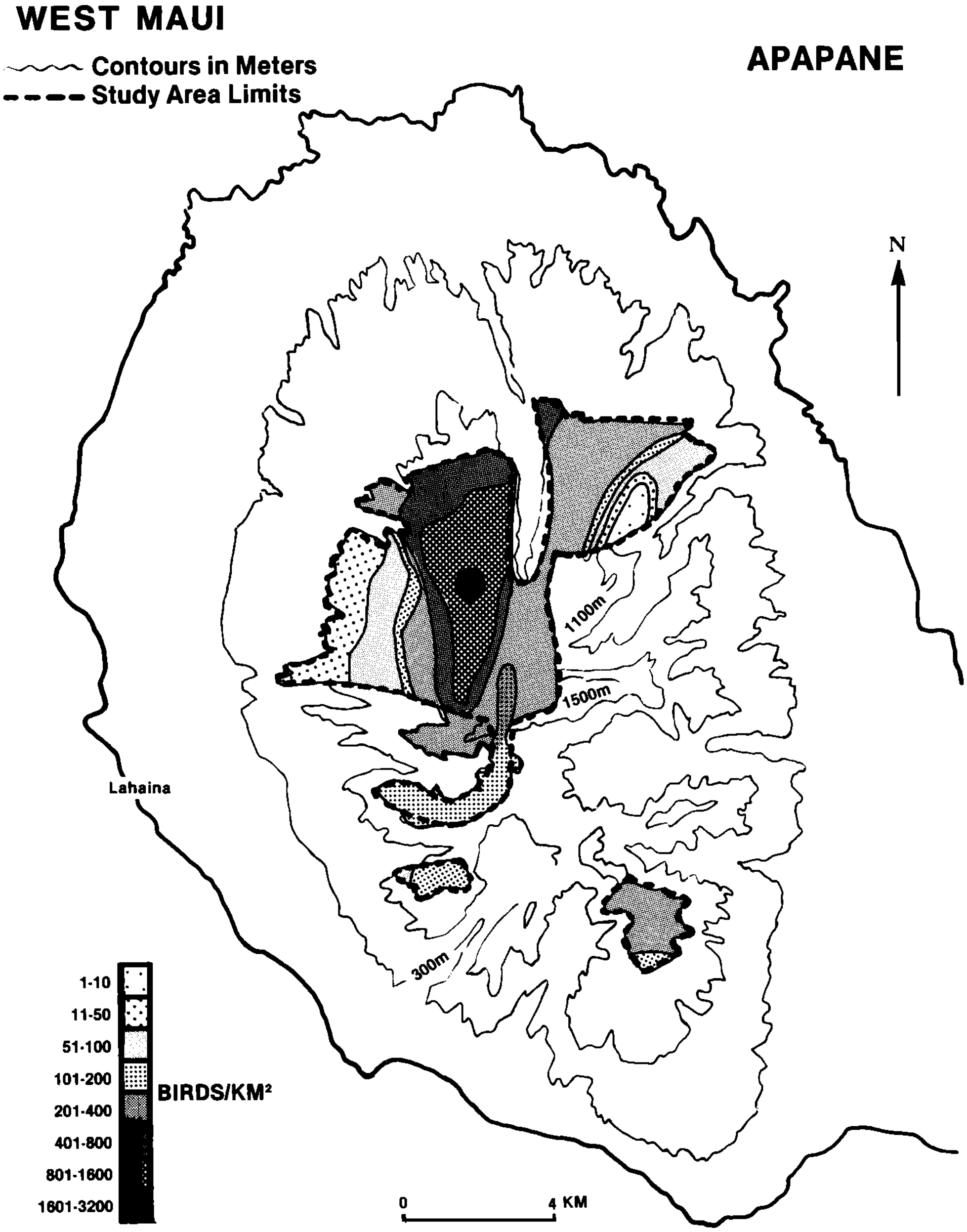



FIGURE 153. Distribution and abundance of the Apapane in the West Maui study area.

itive response in six models and would enter the Puna model at the 0.06 significance level. Responses to other tree species suggest that many combinations provide acceptable habitat. Weak negative responses to introduced trees occur in two models, but densities above 200 birds/km$^2$ occasionally occur in eucalyptus forests. With few exceptions, Apapane do not respond strongly to understory components, and some of the weaker responses are contradictory between forests. Birds are often associated with native graminoids, an indicator of undisturbed communities and forest interiors.

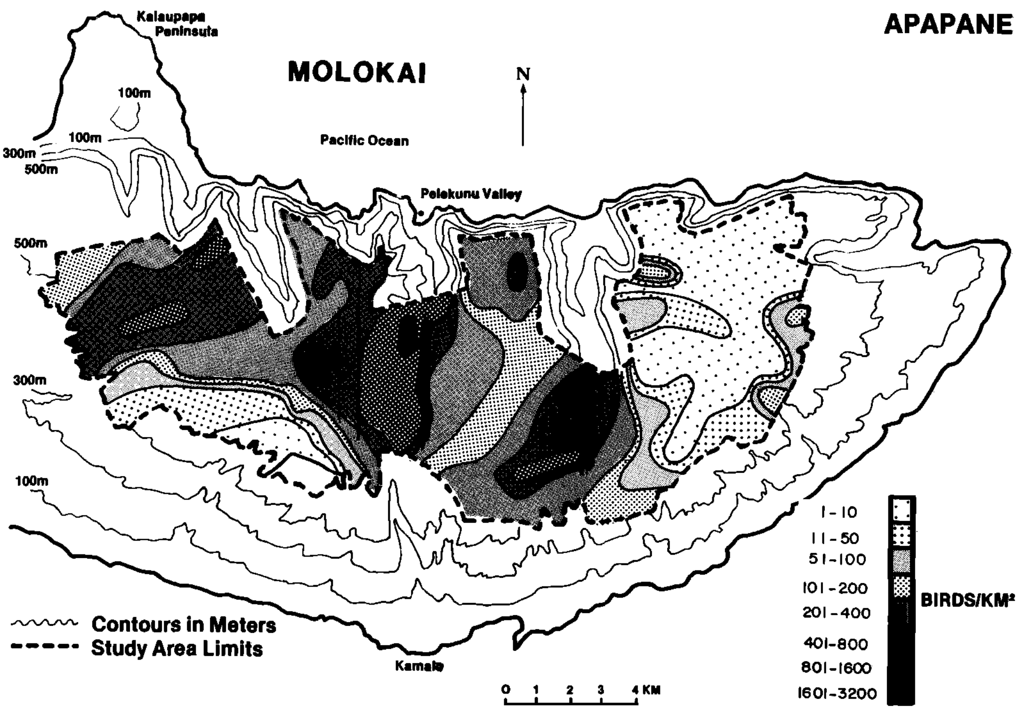



FIGURE 154. Distribution and abundance of the Apapane in the Molokai study area.

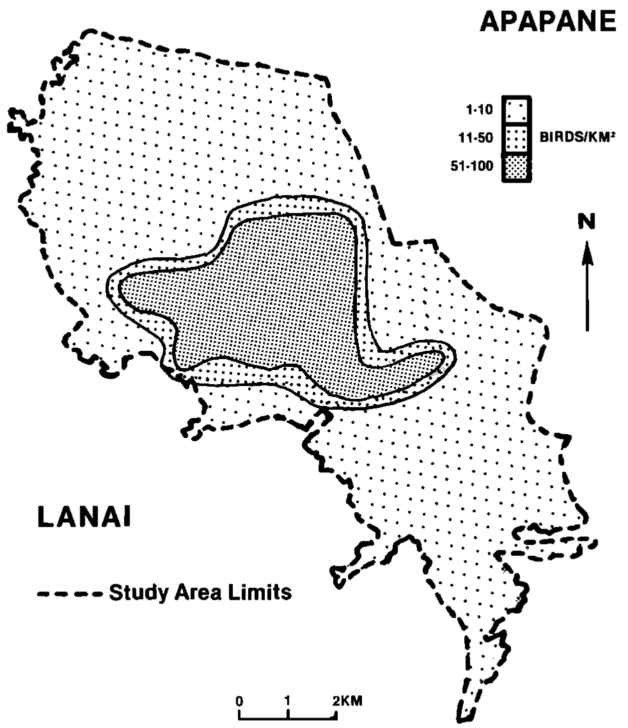



FIGURE 155. Distribution and abundance of the Apapane in the Lanai study area.

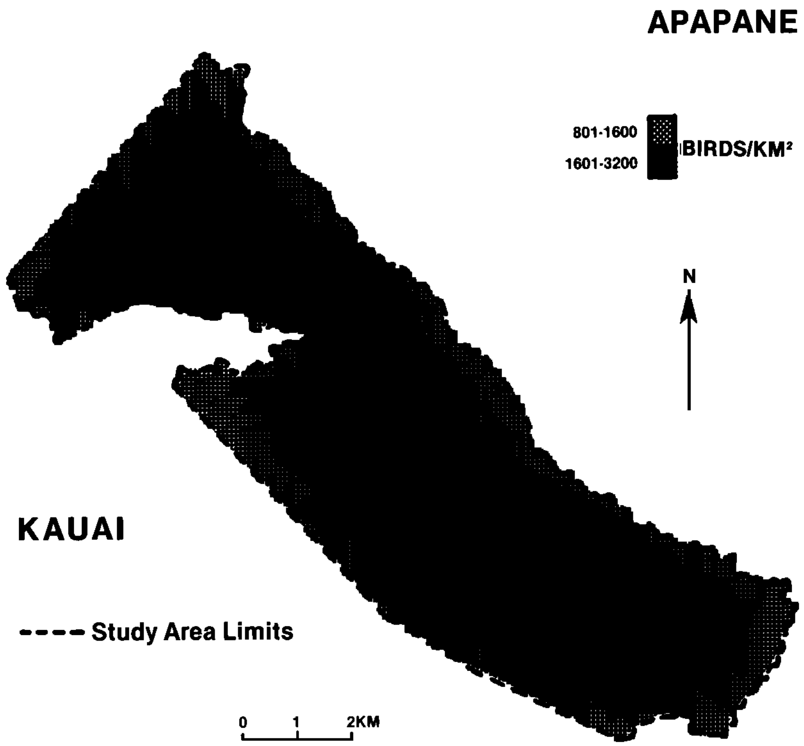



FIGURE 156. Distribution and abundance of the Apapane in the Kauai study area.

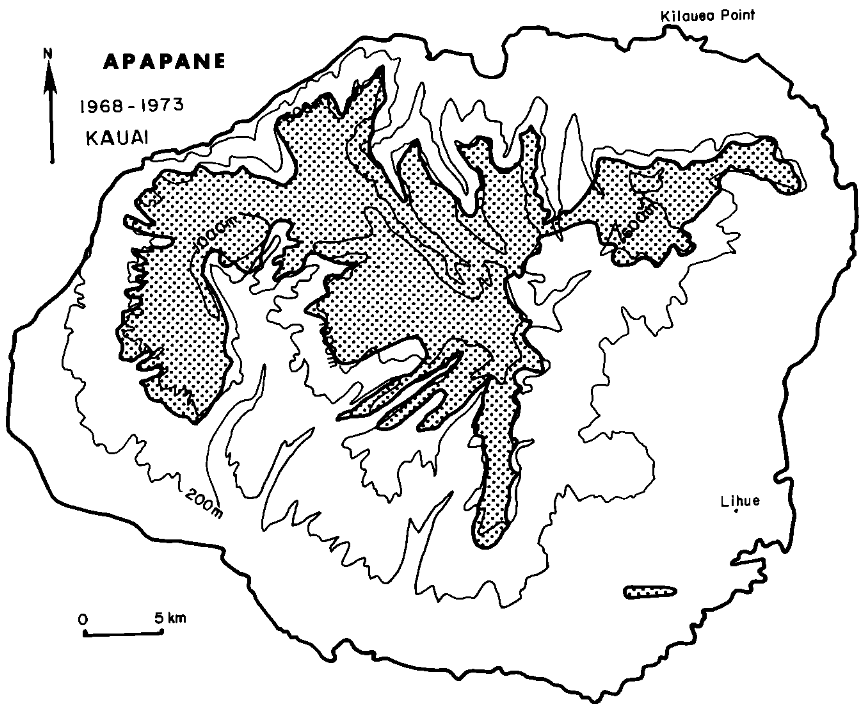



FIGURE 157. Range of the Apapane on Kauai, based on 1968–1973 survey (J. L. Sincock, unpub. data).

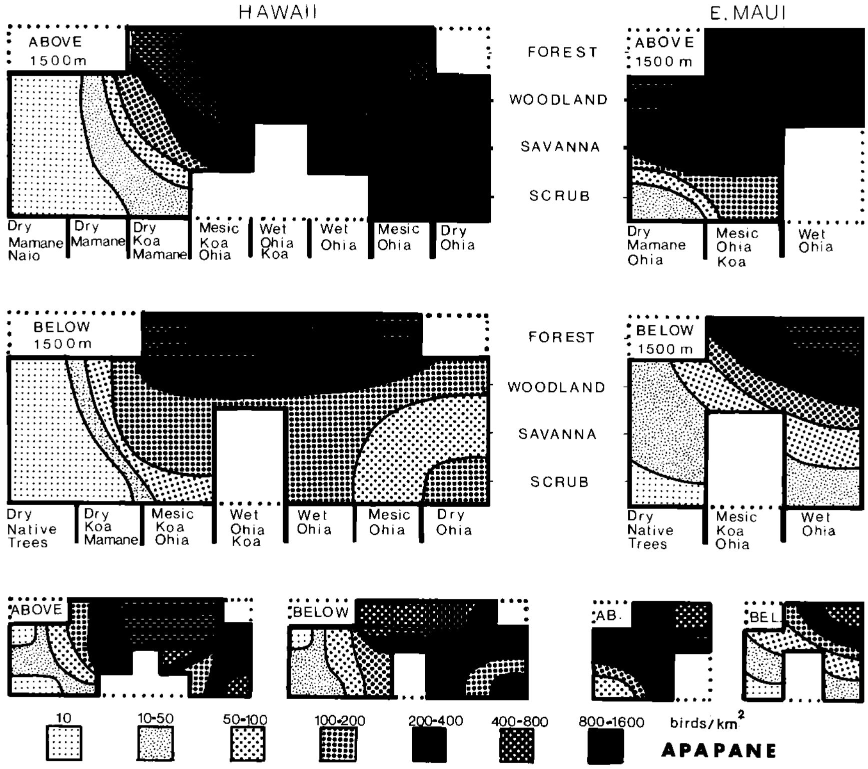



FIGURE 158. Habitat response graphs of the Apapane. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

TABLE 32
REGRESSION MODELS FOR HABITAT RESPONSE OF THE APAPANE[a]

| | Kau | Hamakua | Puna | Kipukas | Kona | Kohala | Maui | Molokai | Lanai | Kauai |
|---|---|---|---|---|---|---|---|---|---|---|
| $R^2$ | 0.33* | 0.51* | 0.56* | 0.36* | 0.43* | 0.23* | 0.50* | 0.50* | 0.07 | 0.23* |
| Moisture | 2.5 | ... | −3.2 | ... | 12.5* | X | 3.0 | ... | ... | X |
| Elevation | 12.0* | 17.7* | 8.5* | ... | ... | 5.4* | 7.8* | ... | ... | ... |
| (Elevation)$^2$ | ... | −13.2* | −6.6* | ... | 14.7* | ... | −6.1* | 3.4* | ... | ... |
| Tree biomass | ... | ... | ... | ... | −7.7* | ... | 5.7* | −2.3 | 2.2 | 4.8* |
| (Tree biomass)$^2$ | 8.1* | ... | ... | 3.3 | 10.3* | ... | ... | 5.6* | ... | −4.1* |
| Crown cover | ... | ... | 4.4* | 2.3 | ... | ... | ... | ... | ... | ... |
| Canopy height | −3.8* | ... | 4.4* | ... | ... | ... | ... | ... | ... | ... |
| Koa | 2.7 | ... | X | ... | 3.3 | X | ... | X | X | X |
| Ohia | ... | 4.3* | ... | ... | 5.6* | ... | 8.3* | 2.7 | ... | X |
| Naio | X | X | X | ... | ... | X | X | X | X | X |
| Mamane | X | ... | ... | ... | ... | X | −3.7* | X | X | X |
| Intro. trees | X | −2.1 | ... | X | −2.8 | ... | ... | ... | ... | X |
| Shrub cover | ... | 6.3* | ... | ... | −3.4* | ... | ... | ... | ... | ... |
| Ground cover | 2.6 | −4.1* | ... | ... | ... | ... | ... | ... | ... | ... |
| Native shrubs | ... | ... | ... | ... | 5.6* | ... | 4.2* | ... | ... | ... |
| Intro. shrubs | X | 5.3* | ... | ... | ... | ... | −3.0 | ... | ... | ... |
| Ground ferns | X | X | ... | ... | 3.0 | ... | ... | ... | X | ... |
| Matted ferns | ... | −4.6* | −4.5* | ... | 2.7 | ... | ... | 3.1 | ... | ... |
| Tree ferns | ... | X | 2.3 | X | ... | ... | ... | −4.4* | X | ... |
| Ieie | X | X | −3.2 | X | −6.3* | X | 4.8* | X | X | ... |
| Passiflora | X | −2.8 | X | X | ... | ... | ... | X | X | ... |
| Native herbs | X | X | ... | −4.8* | −4.3* | ... | ... | ... | X | ... |
| Intro. herbs | X | X | −2.9 | 5.3* | ... | 2.9 | 4.7* | ... | X | ... |
| Native grasses | ... | 3.8* | 6.6* | 5.4* | 5.8* | ... | ... | ... | X | ... |
| Intro. grasses | ... | 4.1* | −6.5* | ... | −2.5 | ... | ... | −3.9* | ... | ... |
| Ohia flowers | 3.0 | 15.8* | ... | ... | 9.9* | 5.3* | 4.6* | 3.4* | ... | ... |
| Olapa fruit | −3.7* | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| Mamane flowers | X | 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.

# POO-ULI
## *Melamprosops phaeosoma*

POO-ULI (*Melamprosops phaeosoma*)

Poo-uli are rare, little-known birds discovered on East Maui in 1973 (Casey and Jacobi 1974). They feed on snails and insects gleaned from foliage and bark (Baldwin and Casey 1983). Two birds were recorded at a single station during our survey. This station was located at 1480 m elevation in wet ohia forest with about 60% crown

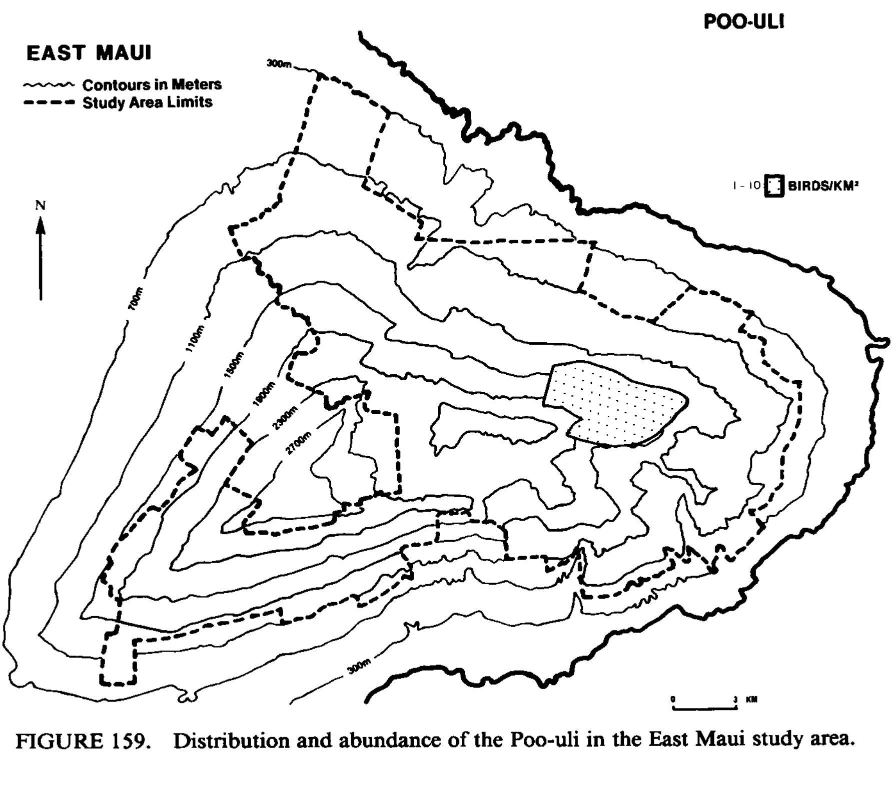



FIGURE 159. Distribution and abundance of the Poo-uli in the East Maui study area.

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 ± 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).