BIRD DISTRIBUTION AND ABUNDANCE ABOVE 3000 FEET IN HAWAII VOLCANOES NATIONAL PARK

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I conducted studies of bird distribution and abundance in Hawaii Volcanoes National Park as part of a subproject of the US International Biological Program (IBP) Island Ecosystems Integrated Research Program. The results of part of this work were published in the program's technical report series (Conant, 1975). This paper presents a brief summary of the work with emphasis on descriptions of spatial distribution patterns of the more abundant bird species found above 3000 ft in Hawaii Volcanoes National Park.

The objective of the study was to examine patterns of bird distribution and abundance on an altitudinal gradient from 3,000 to 10,000 ft on the east flank of Mauna Loa. A transect (called the Mauna Loa Transect) spanning the ecosystems along this gradient was established by IBP researchers, and individual IBP study sites identified at intervals along the transect (see Fig. 1 for site locations).

Eight one-mile bird census transects were established in seven different ecosystems that lay along the Mauna Loa Transect.

1. *Metrosideros* tree-line ecosystem at 7,500 to 8,500 ft

2. Open *Metrosideros-Sophora* subalpine scrub at 6,500 to 7,500 ft

3. *Acacia* mountain parkland in a matrix of grassland at 4,500 to 6,500 ft (2 transects)

4. *Acacia-Sapindus* savannah at 4,200 ft

5. Closed mesic, kīpuka forest at 4,000 ft

6. Open, dry *Metrosideros* forest at 4,000 ft.

7. Closed *Metrosideros-Cibotium* montane rain forest at 3,900 ft

Censi were conducted monthly from December 1972 to July 1973, and from August 1974 to March 1975. One ecosystem on the altitudinal gradient (open wet *Metrosideros-Gleichenia* forest) was not sampled because it did not cover a sufficiently large area in which to sample bird populations. No census transect was established between 8,500 and 10,000 ft (alpine stone desert). Rather, I visited the area four times to assess the status of the single bird species found there.

I used Emlen's (1971) "count x detectability" method for censusing. Values for bird species frequency and density for each site were calculated from the census data. Frequency and density data were subjected to two types of community ordinations to identify patterns of spatial distribution, and to determine if distributionally associated bird species groups existed.

The first type of ordination was a community ordination and was based on a qualitative similarity index. Results of this analysis allowed evaluation of the degree of similarity among census transects. The method was described by McCammon (1968) and adapted by Mueller-Dombois and Ellenberg (1974). Census sites were "lumped" into zones on the basis of similarity.

The second type of ordination was the two-way synthesis table technique (Mueller-Dombois and Bridges, 1975), for which I used the Ceska-Roemer (1971) computer program. This is a species ordination that allows recognition of distributionally associated species groups. It is based on presence-absence criteria for each bird species (Conant, 1975).

Similar analyses of plant communities were conducted previously (Mueller-Dombois and Bridges, 1975), and provides a basis for evaluating the influence of plant community structure on bird distribution.

Results

Community ordinations.

During censi on IBP study sites 22 bird species were recorded (Table 1). Community ordinations with these species resulted in the definition of six zones within the Mauna Loa Transect.

Zone I -- *Rhacomitrium*-moss desert (8,500-10,000 ft) and *Metrosideros* tree-line ecosystem

Zone II -- Open *Metrosideros-Sophora* subalpine scrub

Zone III -- *Acacia koa* mountain parkland

Zone IV -- *Acacia-Sapindus* savannah (including a closed mesic kīpuka forest)

Zone V -- Open dry *Metrosideros*-forest

Zone VI -- Closed *Metrosideros-Cibotium* montane rain forest

These zones are very similar to those derived from community ordinations of vegetation data (Mueller-Dombois and Bridges, 1975).

Species ordinations and distribution patterns. Figure 1 shows patterns of nine native birds and Figure 2 shows that of eight exotic birds. These 17 species were the most abundant, and it is possible to identify well-defined distribution trends for them. In the figures, bird species abundance (birds per 40 ha [100 acres]) is indicated by the height of the curves as explained in the captions. Species are grouped according to distributional similarities with high altitude species shown at the top, ubiquitous species at the bottom. The six transect zones established by community ordinations are shown at the top of the figure.

Two-way table analyses resulted in the definition of two distributionally associated species groups of native birds (3 and 4). Qualitative assessment of spatial distribution patterns allowed the establishment of two additional groups (1 and 2).

The 'Ōma'o (*Phaeornis obscurus obscurus*) was considered a single group (group 1) because of its distinct and unusual distribution. This bird occurred in low densities in the alpine stone desert, tree-line ecosystem and subalpine scrub (Zones I and II). It was observed very rarely in the upper reaches of mountain parkland (Zone III), and did not reappear on the transect again except in closed *Metrosideros-Cibotium* montane rain forest (Zone VI), where it occurred at its highest density.

Group 2, including Nēnē (*Branta sandvicensis*), Golden Plover (*Pluvialis dominica*) and Pueo (*Asio flammeus sandwichensis*), was found characteristically in open habitats. All three species occurred in the mountain parkland (Zone III). Only the Nēnē occurred at tree-line (Zone I) and in the subalpine scrub (Zone II), and of the three, only the Pueo was observed in the *Acacia-Sapindus* savannah (Zone IV). Neither Pueo nor Nēnē were observed in open dry *Metrosideros* forest (Zone V) where the Plover occurred.

TABLE 1. Summary of the means of bird species densities (birds/40 ha) in selected IBP sites on the Mauna Loa Transect. (P = present at a density of less than 1 bird per 40 ha.)

Species	IBP Census Site Number								Mean total no. of individuals
	1	3	16	4	5	7	9	12	
Nēnē	-	-	-	-	1	1	3	P	5
'Io	1	P	-	1	1	1	-	-	4
California Quail	-	P	8	P	1	69	23	-	101
Chukar	-	-	-	-	-	-	1	1	2
Erckel's Francolin	-	-	1	-	-	-	-	-	2
pheasants	-	1	2	2	2	2	1	-	11
Golden Plover	-	P	-	-	P	P	-	-	-
Spotted Dove	-	1	1	-	-	-	-	-	2
Barred Dove	-	-	-	-	-	P	-	-	-
Barn Owl	-	-	1	1	-	-	-	-	2
Pueo	-	-	1	1	1	-	-	-	3
Leiothrix	-	-	69	35	27	69	9	-	209
Hawai'i 'Ōma'o	61	-	-	-	-	P	P	7	68
Hawai'i 'Elepaio	17	-	46	28	41	51	1	-	184
Mynah	-	P	P	-	-	-	-	-	3
White-eye	254	123	466	316	210	150	81	1	1726
Hawai'i 'Amakihi	62	1	20	91	166	292	174	24	949

Table 1. (Continued)

Species	IBP Census Site Number 1	3	16	4	5	7	9	12	Mean total no. of individuals
'Apapane	511	65	267	335	88	243	112	19	1641
'I'iwi	16	-	40	15	28	127	13	-	239
House Finch	1	32	138	93	53	32	37	1	570
Spotted Munia	-	P	3	5	3	1	-	-	32
Cardinal	1	1	46	7	5	1	-	-	61
Mean number of individuals per site	924	229	1110	931	629	1041	455	53	
Total number of species[1] per site	9	12	16	14	16	15	12	6	
Total number of native species	6	4	5	6	8	8	6	3	
Total number of exotic species	3	8	11	8	8	7	6	3	

[1] The two pheasants are added as one species.

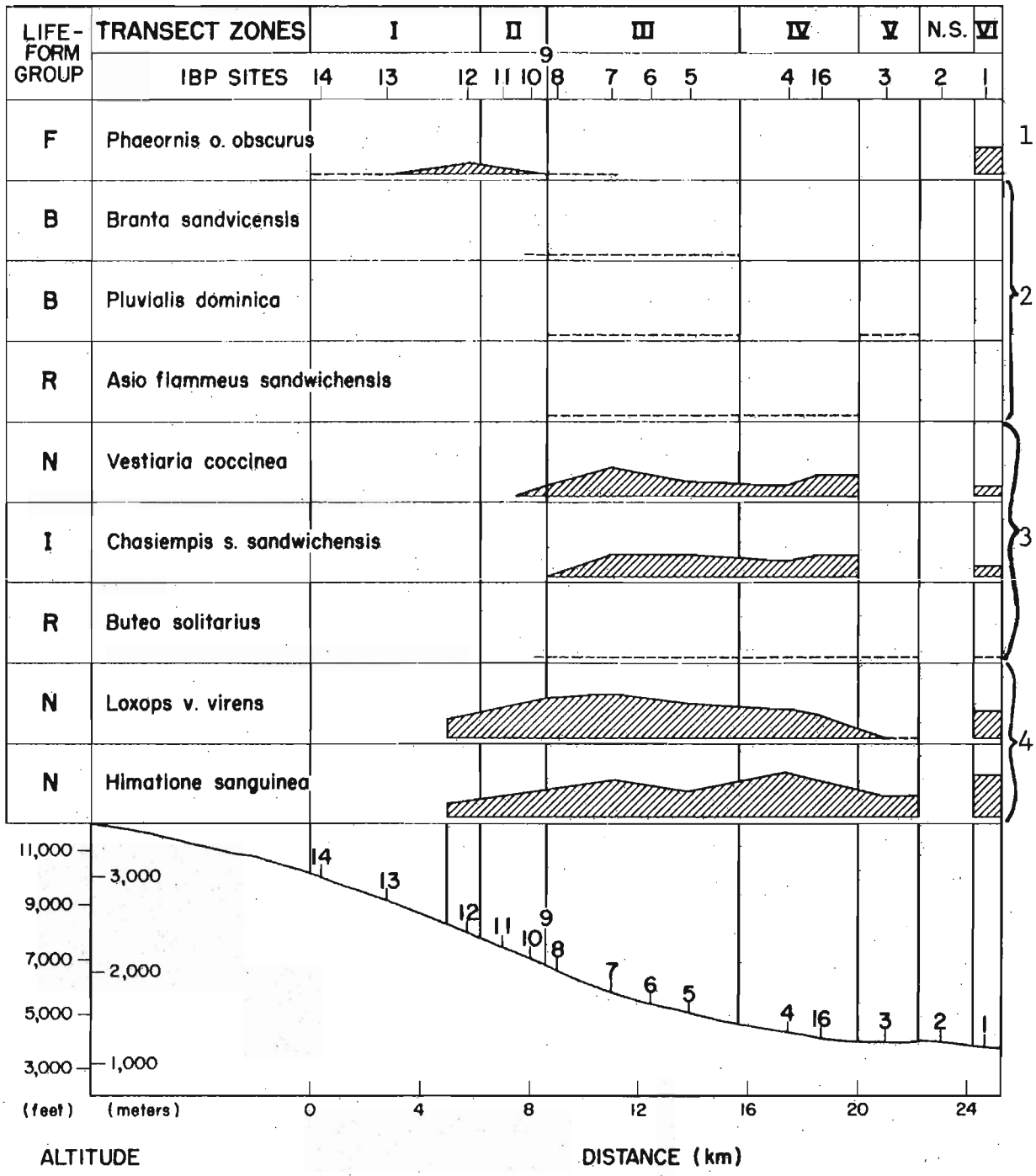

Figure 1. Spatial distribution of endemic bird species on the east flank of Mauna Loa. Transect zones are those generated by the presence/absence Sørensen similarity index. N.S. = not sampled.

Life-form groups:
F = fruit-insect eaters
B = browsers
R = raptorial predators
N = nectar-insect eaters
I = insect eaters

Amplitude scale:
(Birds/40 hectares [100 acres])
broken line ≤ 1
1 mm = 2- 5
2 mm = 6-15
3 mm = 16-30
4 mm = 31-70
5 mm = 71-120
6 mm = 121-160
7 mm = 161-300
8 mm ≥ 301

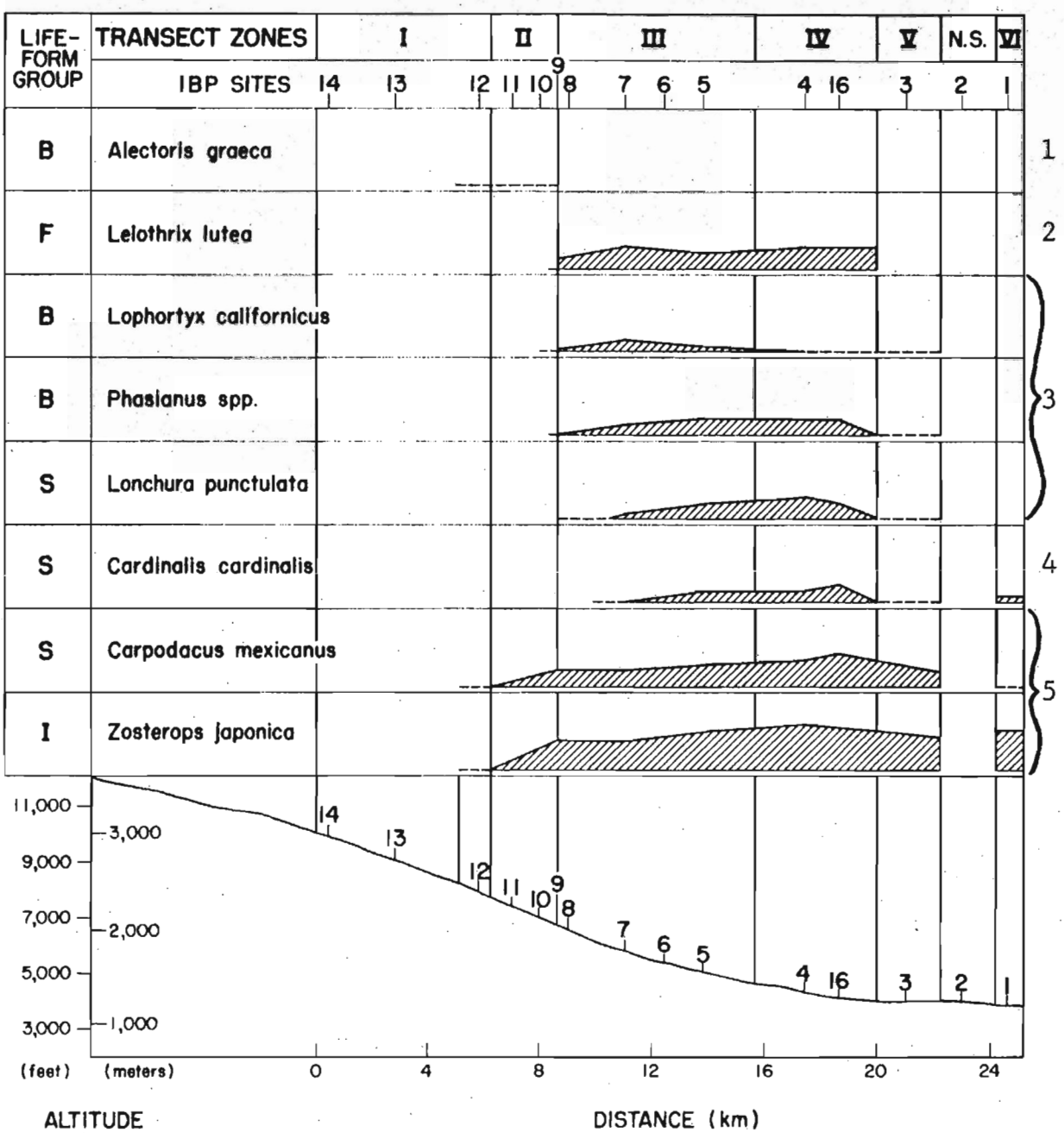

Figure 2. Spatial distribution of exotic bird species on the east flank of Mauna Loa. Transect zones are those generated by the presence/absence Sørensen similarity index. N.S. = not sampled.

Life-form groups:
B = browsers
F = fruit-insect eaters
S = seed eaters
I = insect eaters

Amplitude scale:
(birds/40 hectares [100 acres])
broken line ≤ 1

1 mm = 2- 5	5 mm = 71-120
2 mm = 6-15	6 mm = 121-160
3 mm = 16-30	7 mm = 161-300
4 mm = 31-70	8 mm ≥ 301

Group 3, a quantitatively defined group, had a wider distribution than group 2, occurring from the lower subalpine scrub (Zone II) to the rain forest (Zone IV). Although the 'Io (*Buteo solitarius*) was observed in open dry *Metrosideros* forest (Zone V), 'Elepaio (*Chasiempis sandwichensis sandwichensis*) and 'I'iwi (*Vestiaria coccinea*) were absent. This suggests that the latter two species are to some extent dependent on tree colonies, within which they were observed on censi.

Group 4 includes the 'Amakihi (*Loxops virens virens*) and the 'Apapane (*Himatione sanguinea*), the two most abundant native birds. The birds were almost ubiquitous on the transect. Although they share a common range, the 'Apapane appeared to be less dependent on closed tree colonies as suggested by its higher densities in open dry *Metrosideros* forest (Zone V).

Five spatial groups were established for the exotic birds, and two of these (3 and 5) were quantitatively defined. The Chukar (*Alectoris chukar*), in group 1, had the most restricted distribution of any species, being found only above the mountain parkland. The Red-billed Leiothrix (*Leiothrix lutea*) in group 2, had a rather unique distribution, although it was quite similar to that of the 'I'iwi, 'Elepaio, and 'Io, except that the Leiothrix was not observed in rain forest (Zone VI). However, Baldwin (1953) found this species in rain forest, so its disappearance from that zone is historically recent.

Group 3 consisted of California Quail (*Lophortyx californicus*), the pheasants (*Phasianus spp.*) and the Spotted Munia (*Lonchura punctulata*). These birds were found in the mountain parkland, savannah and open dry *Metrosideros* forest (Zones III, IV, and V), and can be considered "open area" birds. This group is distributionally similar, but not identical to, the group formed by Nēnē, Plover and Pueo.

The last three exotic birds extended into the closed rain forest (Zone VI). The Cardinal (*Cardinalis cardinalis*) was considered unique, but its distribution is almost identical to that of 'I'iwi, 'Elepaio, and 'Io. Thus, two exotic birds, Leiothrix and Cardinal, can be associated with group 3 or the native birds. These two exotics probably do not offer serious competition to the endemic birds because their food preferences are so different.

The last group (group 5) includes the House Finch (*Carpo dacus mexicanus frontalis*) and the Japanese White-eye (*Zosterops japonica*), which occupy the same range as the 'Amakihi and the 'Apapane. Although the House Finch is a seed eater, and thus does not compete with the two honeycreepers for food, the White-eye takes insects and nectar, just as the honeycreepers.

However, at the extremes of the transect gradient, neither exotic species is as common as the native honeycreepers. It appears that along most of the transect the White-eye may well compete with 'Amakihi and 'Apapane for some habitat resources.

Discussion

Censi conducted along the Mauna Loa Transect were important in an attempt to correlate the relationship of vegetation, elevation and climatic factors to bird distribution along the environmental gradients of the transect. Interpretation of distribution patterns can be made using Figures 1 and 2. Any species whose distributions began or ended abruptly in a sharp transition between different plant communities was considered to be limited by abrupt changes in vegetation structure. For example, densities of the Red-billed Leiothrix drop off abruptly at the lower limit of the *Acacia-Sapindus* savannah and at the upper limit of the mountain parkland, indicating that the species is limited by vegetation type rather than some physical environmental factor. Those species whose distributions did not terminate abruptly at a sharp boundary between plant communities were judged to be limited by environmental factors varying along the transect. For example, Spotted Munia densities gradually drop off at the upper and lower limits of its distribution, suggesting that altitude, temperature or rainfall are limiting factors for the species on the Mauna Loa Transect. In some cases, one end of a species' range appears to be limited by vegetation structure, while the other end appears to be limited by an environmental factor. The 'I'iwi is a good example of this because its density in Zone V (open dry *Metrosideros* forest) drops to zero from about 25 birds/40 ha (100 acres) in Zone IV (*Acacia-Sapindus* savannah), increasing again abruptly to about 16 birds/40 ha (100 acres) in Zone VI (closed *Metrosideros-Cibotium* rain forest). At the upper end of its range 'I'iwi density falls off gradually in Zones III and II (subalpine scrub and tree line ecosystems).

Using the above criteria, and considering upper and lower distribution limits of species separately, I judged that vegetation structure accounts for about 60 percent of the distributional limits of birds on Mauna Loa Transect, and continuously varying environmental factors for about 40 percent. The definition of six zones in the Mauna Loa Transect with distinct avian communities that closely correspond with vegetation transect zones lends further support to the conclusion that vegetation structure has a significant influence on the patterns of spatial distribution on this transect.

Other studies of avian communities (MacArthur and MacArthur, 1971; Karr and Roth, 1971; Terborgh, 1971; Willson, 1974; Terborgh and Weske, 1975) have also demonstrated that the structure of vegetation influences avian community structure in other parts of the world. In a study of the distribution of Peruvian forest birds along an environmental gradient (elevation) Terborgh and Weske (1975) found competition and continuously varying environmental factors (they included gradual changes in vegetation structure here), rather than sharp vegetation transitions to be the most important limiting factors for bird distribution. It is difficult to assess why abrupt changes in vegetation structure play a more important role in limiting species distributions on the Mauna Loa Transect than in Peruvian habitats, especially in the absence of comparative data on vegetation structure. Perhaps boundaries between plant communities are more distinct here than in the Peruvian study area because the Mauna Loa Transect crosses a number of rather drastic changes in substrate within an area that is geologically quite young (less than 1 million years).

Although it is not an important factor determining species distribution limits, diffuse competition (i.e., competition among species exploiting a common pool of resources) may influence species densities on the Mauna Loa Transect where competitors occur together. For example, the 'Apapane and the Hawai'i 'Amakihi compete for food (Conant, unpublished). Although these two species occur together all along the transect, the peak density of the 'Apapane occurs in Zone VI (closed *Metrosideros-Cibotium* rain forest), that of the Hawai'i 'Amakihi in Zone III (Mountain parkland). One interpretation of these differences in density is that 'Apapane obtain food more successfully where nectar is the principal resource, as it is in Zones IV (*Acacia-Sapindus* savannah), V (open dry *Metrosideros* forest), and VI (closed *Metrosideros-Cibotium* rain forest). 'Apapane densities exceed those of Hawai'i 'Amakihi in these zones. Another interpretation of the data is that areas of high rainfall provide optimum habitat for 'Apapane, and that Hawai'i 'Amakihi are more successful in drier areas. This interpretation is also supported by the data, which show that Hawai'i 'Amakihi densities exceed 'Apapane densities in the drier transect zones. The two interpretations are compatible, and both may be invoked to explain the distribution patterns of these species.

Perhaps the most interesting distribution pattern is that of the 'Ōma'o which is characteristically a rain forest species (Berger, 1972). Only on Mauna Loa has it been found in subalpine scrub and at tree line. Food and competition for food from the Red-billed Leiothrix, the only other frugivore on the transect, may be limiting factors in the distribution of the 'Ōma'o (Baldwin, 1953), and, at present, both species occur in rain forests elsewhere (Conant, 1975).

However, plant species with suitable fruit are more abundant in closed rain forests than they are in mountain parkland or *Acacia-Sapindus* savannah. The fact that Red-billed Leiothrix are present in dry forests where 'Ōma'o are absent (Conant, 1975; van Riper and Scott, in review) suggests that it is more tolerant of dry forest conditions than the 'Ōma'o. This hypothesis needs further investigation.

Compared to continental tropical ecosystems (Karr, 1971, 1975; Karr and Roth, 1971; Terborgh and Weske, 1975) the avian communities in this study area have very low species diversities. Recent extinctions have increased the number of "empty niches" that existed in the original avifauna, few, if any, of which are now occupied by exotic species. Competition among endemic species is thought to be minimized by differences in anatomy (Lack, 1971), diet, habitat segregation, foraging strategies or behavioral interactions (Conant, unpublished). Thus, one of the principal ways in which spatial distribution of birds on the Mauna Loa Transect differs from that in continental ecosystems is that competition apparently does not play an important role in determining distributional limits.

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