FIGURE 58. Remnant woodland on the Auwahi Tract, an area at 1200 m elevation on East Maui with an exceptionally rich assemblage of xerophytic species. Arborescent monocot in foreground is halapepe (*Dracaena aurea*). (Photograph by R. Hobdy)

vation at campsites were used to document the occurrence of *Culex quinquefasciatus* and other mosquito species. We used only casual observations at campsites in subsequent years.

DATA ANALYSIS

ESTIMATION OF EFFECTIVE AREA SURVEYED

Bird densities were determined from the field data using "plotless" or "variable area" survey procedures, where estimation of the area surveyed poses a statistical problem. The theory of variable area techniques originated with studies of line transect surveys (Emlen 1971, Seber 1973, Burnham and Anderson 1976, Ramsey 1979), and was extended to more general survey methods (Ramsey et al. 1979, Ramsey and Scott 1981a), including the variable circular-plot method (Reynolds et al. 1980). Ramsey and Scott (1979, 1981a) outlined the methods to obtain smoothed estimates.

Raw estimates of effective area

Each station was assigned to one of 13 detectability classes (Table 5) based on canopy and understory conditions that affected visibility. Twelve of these classes represented the factorial combinations of crown cover (closed, open, scattered), canopy height (tall, short), and understory (closed, open); class 13 designated treeless stations. Detections were grouped into data cells by species, observer, detectability class, and study area.

Detection distances D were converted to the area X that was searched to obtain that detection as $X = \pi D^2$. Detection areas in each cell were arranged in order of increasing magnitude from 1 to N and then used to construct a cumulative distribution curve (Fig. 61). A

line from any point P_1 at (x_1, y_1) to another point P_2 at (x_2, y_2) on the cumulative distribution function has slope equal to the density of detections in area (see Ramsey and Scott 1981a). We constructed the convex envelope of the cumulative distribution function by drawing a straight line from the origin (0, 0) to the point P_1 at (x_1, y_1) that gave the greatest slope of all

TABLE 5
ADJUSTMENT FACTORS FOR THE EFFECTS OF HABITAT CONFIGURATION ON EFFECTIVE AREA

Detectability class	Multiplicative factor
Closed canopy (>60% cover)	
Open understory, height >10 m	1.00
Open understory, height 2–10 m	1.46
Closed understory, height >10 m	0.87
Closed understory, height 2–10 m	0.98
Open canopy (20–60% cover)	
Open understory, height >10 m	1.24
Open understory, height 2–10 m	1.89
Closed understory, height >10 m	1.02
Closed understory, height 2–10 m	1.10
Scattered canopy (<20% cover)	
Open understory, height >10 m	1.84
Open understory, height 2–10 m	3.38
Closed understory, height >10 m	0.85
Closed understory, height 2–10 m	1.16
Treeless	6.79

FIGURE 59. Elfin woodland in Hana Forest Reserve at 1500 m elevation on East Maui. Note dense bryophyte and fern cover on all surfaces. (Photograph by C. B. Kepler)

points on the curve, and extending the envelope from P_1 to the point P_2 that gave the greatest slope beyond P_1, and so forth to P_3, P_4, etc.

The slope of the envelope curve is constant over sections and does not increase as the area searched increases. We used a likelihood ratio rule to decide when the decline in slope (density) from point P_r (x, y) to P_{r+1} (x', y') was significant. Letting M be the slope from the origin to P_r, M' the slope from the origin to P_{r+1}, and m the slope from P_r to P_{r+1}, we considered that the decline in slope from P_r to P_{r+1} was significant at (x^*, y^*), the first point with $y > \sqrt{n}$ (see Ramsey and Scott 1979), such that

$$y \cdot \ln(M) + (y' - y) \cdot \ln(m) - y' \cdot \ln(M') < -2.$$

The raw estimate of effective area surveyed A could then be found graphically by extending the line from the origin through (x^*, y^*) to intersect the line $y = n$, and dropping from there to the horizontal axis (Fig. 61). Therefore, $A = nx^*/y^*$ (see Wildman 1983).

Burnham et al. (1981) suggested that a cell size of $n \geq 30$ was desirable for nonparametric estimates of effective area. We used $n \geq 25$ as a limit with the HFBS

data. Even with this cutoff, the majority of cells had too few detections to produce raw estimates.

One potential source of error in estimating effective area was inaccurate estimation of detection distance. Rigorous observer training increased accuracy (Kepler and Scott 1981), and in field tests our observers estimated the distance to birds heard but not seen to within ±10% (range of observer averages, −9.1% to +6.3%) (Scott, Ramsey, and Kepler 1981). The error thus introduced into the area surveyed and the population estimates from inaccurate distance estimates varied from −17.4% to +13.0%, with an average absolute deviation of 9.2%.

Smoothed estimates

Missing cell values were estimated and available cell estimates were smoothed by fitting a model that represented the influence of species, observer, and detectability code on the effective area. Examination of the residuals from a preliminary model justified the inclusion of terrain dissection in the final model.

Let y_{fzod} be the natural logarithm of the raw estimate of effective area in the cell with study area f, species z,

FIGURE 60. Introduced strawberry guava forest typical of wet lowland habitat, 800 m elevation on windward East Maui. (Photograph by C. B. Kepler)

observer o, and detectability code d, and let n_{fzod} be the number of detections in that cell. The logarithmic transformation stabilized the variance, produced a scale in which factors had negligible interaction effects, but did not yield normally distributed residuals.

The expected effective area was given by:

$$\text{Exp}(y_{fzod}) = a_z + b_o + c_d + g_f, \qquad [1]$$

with a_z as the average log-transformed effective area of species z, b_o as the effect of observer o, c_d as the effect of detectability code d, and g_f as the effect of topography in study area f. The model was fit by weighted least squares, with the weights being the square roots of cell sample sizes. Sufficient data were collected on 1747 cells to estimate effects for 28 observers and 13 detectability classes on detecting the 20 most abundant species.

A full examination of all possible interactions was not possible. We fit models with the Kau, Hamakua, and Kona data that allowed for observer-by-detectability interactions and for different effects by seven abundant species (Elepaio, Omao, Red-billed Leio-thrix, Japanese White-eye, Common Amakihi, Iiwi, and Apapane). The effects of observers and detectability codes were remarkably consistent among species and were independent of each other. When this analysis was extended to Hawaii Creeper and Akepa, however, the data suggested that one observer was more efficient at locating rare birds than common ones (Scott and Ramsey 1981b). Several other anomalies were found and had rational explanations but they were rather unimportant in comparison with the major factor effects.

To illustrate the relative importance and consistency of effects, we fit separate models like model [1] within each study area (without g_f) and compared the results with the overall model in an analysis of variance (Table 6). The sums of squares and the degrees of freedom are not precisely additive because of the sparseness and imbalance of the cells used. Species differences account for about 37% of the total variation in the logarithms of effective area. Significant variation occurs among study areas in the effective areas for certain species. However, variation in observer adjustments among
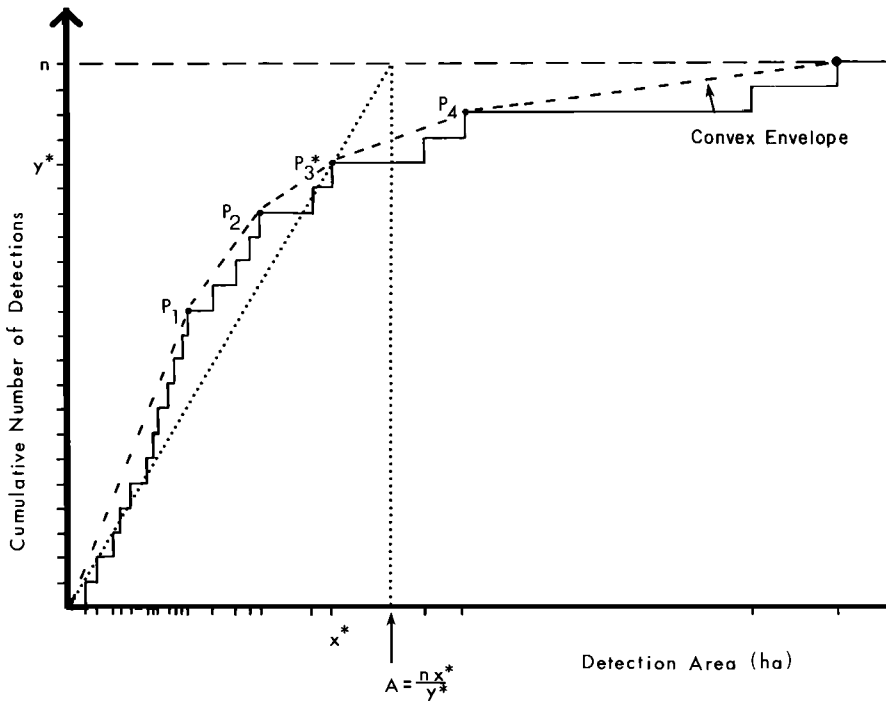
FIGURE 61. The cumulative detection curve and its envelope. In this example a significant decline in slope occurs at P_3. (See pages 48–49 for explanation.)

study areas is nonsignificant, and variation in habitat configuration effects among study areas has relatively minor significance.

The multiplicative factors for observer effects in the general model varied from 0.57 to 2.09 ($\bar{x} = 1.08$, SD = 0.44), suggesting that the best observer covered about four times as much area as the worst. The effects of detectability classes (Table 5) had greater statistical significance than those of observers. Detectability class effects were not satisfactorily explained in terms of a main-effect factorial model of canopy cover, canopy height, and understory cover. The effect of canopy cov-

er depended on the understory: with a closed understory the effective area surveyed was about the same for closed canopy and scattered trees. Where the understory was sparse, however, the increase in effective area surveyed from open canopy to scattered trees was dramatic. This suggested that a single index of visibility might serve as well as our detectability classes. With such an index, observers would classify detectability conditions according to how much total vegetation occurred within a certain distance.

After fitting the preliminary model, we calculated residuals for Japanese White-eye, Common Amakihi,

TABLE 6

ANALYSIS OF VARIANCE FOR THE EFFECT OF SPECIES, OBSERVER, AND HABITAT CONFIGURATION ON EFFECTIVE DETECTION DISTANCE

Source	df	Sum of squares	Mean square	F[a]
Species	19	792.67	41.72	157.49***
Obervers	27	15.49	0.57	2.17**
Habitat configuration	12	33.63	2.80	10.58***
Between study areas				
Species	60	830.14	13.84	52.23***
Observers	54	13.37	0.25	0.93
Habitat configuration	52	19.69	0.38	1.43*
Residual	1532	405.84	0.26	
Total	1746	2076.56	1.19	

[a] *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

TABLE 7
EFFECTIVE DETECTION DISTANCES FOR HAWAIIAN
BIRDS

Species	Effective detection distance (m)	Method of determination[a]
Hawaiian Goose	200	2
Black Francolin	186	2
Erckel's Francolin	163	2
Gray Francolin	136	2
Chukar	51	1
Japanese Quail	60	2
Kalij Pheasant	42	2
Red Junglefowl	557	2
Ring-necked Pheasant	269	2
Common Peafowl	434	2
Wild Turkey	183	2
California Quail	125	2
Lesser Golden-Plover	53	2
Spotted Dove	150	2
Zebra Dove	124	2
Mourning Dove	150	3
Eurasian Skylark	76	1
Hawaiian Crow	282	2
Japanese Bush-Warbler	73	2
Elepaio	37	1
White-rumped Shama	78	2
Omao	60	1
Kamao	60	1
Olomao	23	3
Puaiohi	50	3
Melodious Laughing-thrush	95	1
Red-billed Leiothrix	56	1
Northern Mockingbird	77	1
Common Myna	89	1
Kauai Oo	150	3
Japanese White-eye	27	1
Northern Cardinal	71	1
Saffron Finch	28	2
House Finch	43	1
Yellow-fronted Canary	31	2
Ou	66	2
Palila	60	2
Maui Parrotbill	50	2
Common Amakihi	32	1
Anianiau	38	1
Nukupuu	39	2
Akiapolaau	80	2
Kauai Creeper	29	1
Hawaii Creeper	44	2
Maui Creeper	28	1
Akepa	34	1
Iiwi	36	1
Crested Honeycreeper	46	1
Apapane	35	1
Poo-uli	23	3
House Sparrow	43	2
Red-cheeked Cordonbleu	28	3
Lavender Waxbill	28	3
Warbling Silverbill	32	2
Nutmeg Mannikin	23	1

[a] Method of determination: 1 = species used in fitting the full model; 2 = species means found by pooling data groups; 3 = distance estimate based on extrapolation from similar species.

Iiwi, and Apapane, and determined the percent of positive residuals within each forest. These ranged from a high of 90% in Kipukas to a low of 30% in Molokai. This wide variability was probably due to topography, particularly the degree of topographic dissection in each study area. A crude measure of the topographic dissection of each study area was strongly correlated with the percent of positive residuals ($r = 0.80$). Our results suggested that steep rugged terrain increased the observer-bird distances required to achieve the same horizontal distances as on flat areas and also concealed some birds in topographic relief. This resulted in reduced detectability and smaller effective areas surveyed. We incorporated this topographic effect into the model by introducing a single variable (g_f) to indicate three general levels of topographic dissection: $+1$ for Kona and Kipukas; -1 for Molokai, Kohala, and West Maui; and 0 for the other study areas. The estimate of the effect of different terrain translated to 49% higher effective areas in Kona and Kipukas and to 33% lower effective areas in Molokai, Kohala, and West Maui, compared to the other study areas.

Density estimates derived by our procedures may have been subject to other occasional sources of error: field mis-identifications, inaccurate distance estimates, movement of birds, and multiple sightings. Nonetheless, density estimates were preferable to raw numbers because the density estimates statistically accounted for the differential conspicuousness of different bird species, the effect of habitat structure on detectability, and observer variability.

The assumptions behind the density estimates were best met by the native passerines and non-flocking introduced passerines. For most Hawaiian forest passerines at least one and usually several vocal cues were given in an eight-minute period during the morning hours (Ralph 1981; J. M. Scott, unpub. data). We shortened the count period to six minutes on Mauna Kea because Palila gave several cues per six-minute count and such counts detected 95% of the individuals of other species that were detected during simultaneous eight-minute counts (J. M. Scott, S. Mountainspring, unpub. data).

BIRDS PER COUNT PERIOD

Researchers interested in comparing their results with ours may find it useful to convert the density values given in our tables to corresponding birds per eight-minute count period. This can be done by multiplying bird density by the effective area surveyed per count. The effective area surveyed per count is computed from the effective detection distance for a species (Table 7) and the mean multiplicative detectability factor for the appropriate stratum and study area (Table 8). As an example, the density of Elepaio at 1500–1700 m elevation in the Hamakua study area is 226 birds/km² (see Table 16). The effective detection distance for Elepaio from Table 7 is 37 m. The raw value of the effective area surveyed would be πr^2, or 4301 m². According to Table 8, stations in the 1500–1700-m stratum of the Hamakua study area have a mean multiplicative detectability factor of 1.02, i.e., the actual effective area that was surveyed during the HFBS averaged 1.02 times greater than the raw value due to habitat and observer effects. Thus the effective area surveyed per count would

TABLE 8
MULTIPLICATIVE FACTORS FOR EFFECTIVE AREAS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hama-kua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Elevational strata												
100–300 m	···[a]	···	···	···	···	···	···	···	···	0.90	···	···
300–500 m	···	1.03	1.79	···	1.91	···	0.81	0.66	···	1.17	···	···
500–700 m	2.15	1.20	1.16	···	1.42	···	1.07	1.15	1.43	1.19	1.29	···
700–900 m	0.88	1.15	1.06	···	1.66	···	1.07	1.19	1.38	1.30	2.04	···
900–1100 m	0.89	1.10	1.22	···	1.85	···	1.28	1.23	0.94	1.29	1.24	···
1100–1300 m	1.01	1.12	2.23	2.30	1.98	···	1.17	1.31	1.07	1.13	···	0.97
1300–1500 m	0.97	1.13	···	2.90	2.10	···	0.98	1.54	0.97	1.14	···	1.19
1500–1700 m	0.86	1.02	···	2.49	2.19	···	0.92	1.55	1.19	···	···	···
1700–1900 m	0.84	1.03	···	2.56	2.23	···	···	1.96	1.37	···	···	···
1900–2100 m	1.14	1.55	···	2.67	2.53	2.19	···	2.63	···	···	···	···
2100–2300 m	0.81	2.15	···	3.13	3.11	2.10	···	2.73	···	···	···	···
2300–2500 m	···	···	···	···	2.33	2.12	···	4.02	···	···	···	···
2500–2700 m	···	···	···	···	···	2.16	···	4.30	···	···	···	···
2700–2900 m	···	···	···	···	···	2.19	···	6.45	···	···	···	···
2900–3100 m	···	···	···	···	···	2.19	···					
Habitat types												
Ohia	1.00	1.12	1.31	2.81	1.98	···	1.09	1.31	1.10	1.24	···	1.05
Koa-ohia	0.79	0.96	···	2.24	1.85	···	···	1.09	···	···	···	···
Koa-mamane	···	1.95	···	2.31	2.27	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	2.95	2.19	···	···	···	···	···	···
Mamane	···	···	···	···	2.51	2.12	···	1.84	···	···	···	···
Other natives	···	1.95	···	2.65	2.67	···	···	2.23	···	1.72	2.28	···
Intro. trees	···	1.67	···	···	1.47	···	0.98	1.81	1.07	0.87	1.35	···
Treeless	···	3.22	1.41	5.91	5.29	···	···	3.44	1.79	2.58	2.76	4.30

[a] ··· indicates stratum not sampled in study area.

be 1.02 × 4301 m², or 0.0044 km². A density of 226 birds/km² surveyed over 0.0044 km² yields a value of 0.99 birds/count period for Elepaio in the indicated stratum. By an identical procedure, the standard error of 14 birds/km² converts to 0.06 birds/count period.

RANGE DETERMINATION

Bird populations and densities in a study area were calculated for those areas within the geographic range of a species. To determine the range, study areas were first divided into geographic cells using 200 m elevational contours and the midpoint lines between transects. We then determined the distributional area for each species using the following criteria.

1) If a bird species occurred in a given vegetation map unit along a transect, its range was interpreted as extending to the limits of that vegetation type within the geographic cell.
2) If a vegetation map unit was sampled within a geographic cell and the bird species did not occur in that vegetation type, then it was omitted from the range for that cell, unless it was adjacent to occupied range on at least three sides and occupied less than 20 ha.
3) If a vegetation map unit was not sampled within a geographic cell but the species occurred in that cell or in the same elevational stratum on an adjacent transect, then we included that vegetation type within the range, unless the species did not occur elsewhere in that vegetation type.

4) If a species was not found within a vegetation type that was sampled in a geographic cell, but was found in the same vegetation type at a lower elevation (for native birds), in the same elevation on an adjacent transect, or as a result of incidental observations, then we included that vegetation type within the range.

If a particular vegetation type was not surveyed in the study area, then density estimates were not determined and the area of that vegetation type was not used in determining population estimates. Density values were plotted by hand and smoothed by eye from seven-point moving averages for the Kau study area maps and from averages over 2–9 stations for other study areas, the exact numbers being a function of sampling intensity. Continuous declines and increases in density were assumed between widely scattered values.

POPULATION ESTIMATES

Determination of population estimates began with the weighted mean densities and the effective areas surveyed at each station. The effective area surveyed for the Kau study area was based on observations made only in that area. All other analyses used pooled samples for all years. Stations were stratified by the eight general habitat types and by 200-m elevational intervals. Within each stratum we calculated the average density and its variance for those stations that fell within the species range. The average densities were mul-

TABLE 9
HABITAT AND AREA IN ASSUMED ORIGINAL RANGE OF NATIVE BIRDS

Species	Habitat types occupied[a]									Original range (km²)[b]				
										Hawaii	Maui	Molo-kai	Lanai	Kauai
Hawaiian Goose	A	D₁	D₂					S	G	4084	809	410	332	336
Hawaiian Hawk	A	D₁	D₂	M₁	M₂	W₁	W₂			7720	...	...	...	...
Hawaiian Rail				M₁		W₁				2417	...	...	...	...
Short-eared Owl	A	D₁	D₂	M₁	M₂	W₁	W₂	S	G	9033	1824	672	365	1429
Hawaiian Crow	A	D₁	D₂	M₁	M₂					5028	...	...	...	...
Elepaio	A	D₁	D₂	M₁	M₂	W₁	W₂			7720	...	...	...	1429
Kamao	A		D₂	M₁	M₂	W₁	W₂			...	...	...	...	1429
Olomao	A	D₁	D₂	M₁	M₂	W₁	W₂			...	1805	672	365	...
Omao	A	D₁	D₂	M₁	M₂	W₁	W₂			9033	...	...	...	...
Puaiohi				M₁	M₂	W₁	W₂			...	...	...	...	1094
Kauai Oo	A	D₁		M₁	M₂	W₁	W₂			...	...	...	...	1429
Bishop's Oo	A	D₁	D₂	M₁	M₂	W₁	W₂			...	1805	672	...	...
Hawaii Oo	A	D₁	D₂	M₁	M₂	W₁	W₂			7720	...	...	...	...
Kioea				?						?	...	...	...	...
Ou		D₁	D₂	M₁	M₂	W₁	W₂			7043	1485	501	186	1368
Palila	A	D₁	D₂							2771	683	410	332	336
Lesser Koa-Finch	A	D₁	D₂	M₁	M₂					4543	...	...	...	...
Greater Koa-Finch	A	D₁	D₂	M₁	M₂					4543	...	...	...	...
Kona Grosbeak	A	D₁	D₂	M₁	M₂					4543	...	...	...	...
Maui Parrotbill	A	D₁	D₂	M₁	M₂	W₁	W₂			...	1805	672	365	...
Common Amakihi	A	D₁	D₂	M₁	M₂	W₁	W₂	S		9033	1815	672	365	1429
Anianiau		D₁		M₁	M₂	W₁	W₂			...	...	...	...	1368
Greater Amakihi						W₁	W₂			3178	...	...	...	...
Akialoa	A	D₁	D₂	M₁	M₂	W₁	W₂			7720	...	672	365	...
Kauai Akialoa	A	D₁		M₁	M₂	W₁	W₂			...	...	...	...	1429
Nukupuu	A	D₁	D₂	M₁	M₂	W₁	W₂			?	1805	672	365	1429
Akiapolaau	A	D₁	D₂	M₁	M₂	W₁	W₂			7720	...	...	...	...
Kauai Creeper	A	D₁		M₁	M₂	W₁	W₂			...	...	...	...	1429
Hawaii Creeper				M₁	M₂	W₁	W₂			4949	...	...	...	...
Maui Creeper	A	D₁	D₂	M₁	M₂	W₁	W₂			...	1805	513	365	...
Molokai Creeper				M₁	M₂	W₁	W₂			...	...	262	...	...
Akepa				M₁	M₂	W₁	W₂			4949	1015	...	...	1094
Ula-ai-hawane						W₁	W₂			3178	...	...	...	...
Iiwi			D₂	M₁	M₂	W₁	W₂			5730	1122	262	33	1094
Hawaii Mamo						W₁	W₂			3178	...	...	...	...
Black Mamo						W₁	W₂			...	...	159	...	...
Crested Honeycreeper				M₁	M₂	W₁	W₂			...	1015	262	...	...
Apapane		D₁	D₂	M₁	M₂	W₁	W₂			5730	1122	262	185	1094
Poo-uli				M₁	M₂	W₁	W₂			...	1015	...	...	...
15 species extinct honeycreepers	A	D₁								1990	683	410	332	336

[a] Habitat types: A = arid low elevation woodland, D₁ = dry lowland forest, D₂ = dry montane forest, M₁ = mesic lowland forest, M₂ = mesic montane forest, W₁ = wet lowland forest, W₂ = wet montane forest, S = alpine scrub, G = alpine grassland.
[b] ··· indicates species assumed not to have occurred originally on this island.

tiplied by the total areas of the strata within the species range, and these were added to obtain a population estimate. A confidence interval for the population estimate was computed from the pooled estimate of variance (Ramsey and Scott 1978, 1979, 1981a).

UNRECORDED SPECIES

The status of some native Hawaiian forest birds has been the subject of much speculation. Since 1950 several species believed extinct have been rediscovered (Richards and Baldwin 1953; Pekelo 1963a, 1963b; Richardson and Bowles 1961, 1964; Banko 1968; Shallenberger and Vaughn 1978; Sabo 1982).

It is possible that species that occur in areas we sur-

veyed were missed by our sampling efforts. We assumed that the effective detection distance for each of the possibly undetected species was similar to related extant species, and that the current range was similar to that of extant species with similar habitat preferences. These values were used to determine the probability of detecting at least one individual in randomly distributed populations of 10, 50, and 100 birds within the presumed range.

Using similar extant species, we estimated an effective area surveyed for the unrecorded species at each station, taking into account observer and detectability effects. The sum of effective area over all stations in the range gave a, the total area effectively surveyed for

the species. Given a total area A in the species range, the probability of recording at least one individual of a species with a population of N was approximated as

$$P = 1 - (1 - a/A)^N.$$

We considered the probability statements to be extremely conservative because they assumed each point was sampled only once (we sampled each one at least twice) and ignored the many hours spent by us and others looking for these species outside the eight-minute count periods.

ORIGINAL RANGES

In order to compare the present range of a species with the original range prior to Polynesian contact, we constructed maps (Figs. 4–8) that show in a general way the probable vegetation zonation before human disturbance, using maps modified from Ripperton and Hosaka (1942). We then turned to early historical accounts of ranges and habitat preferences (primarily Palmer in Rothschild 1893–1900, Henshaw 1902, Perkins 1903, and Munro 1944) and fossil records (Olson and James 1982b) to infer the vegetation zones and islands that we assumed species originally inhabited. We then computed the area of the species range on each island (Table 9). It should be realized that this procedure gave at best an approximation of the original ranges, because of the selective and incomplete nature of fossil deposits and of the areas studied by early workers (remote montane areas had few fossil deposits and were often neglected by workers; Hawaii had fewer lowland fossil deposits than other islands because of its comparative geological recency). Nonetheless, we felt the attempt to "reconstruct" original ranges provided valuable insights into the present status of a species.

ANALYSIS AND INTERPRETATION OF HABITAT RESPONSE

From the HFBS data base we developed a landscape perspective (Whittaker 1967, Whittaker et al. 1973) for habitat response patterns; that is, we attempted to describe the response of a species in terms of habitat elements that varied between the communities that constituted the landscape of the study area. Whenever the responses of several species have been compared across a range of habitats, they have been found to be individualistic, with their modal responses scattered along landscape gradients, and their distributions overlapping broadly (Whittaker 1972). The principle of species individuality, first articulated by Ramensky (1924, 1983) and later emphasized by Gleason (1926, 1939), prompted us to focus the analysis on individual species and then to infer the underlying limiting factors of a species from repeating themes in the habitat response patterns.

The study of habitat response required a multivariate approach because many components were involved in habitat structure (Green 1971). Beals (1960), James (1971), Shugart and Patten (1972), and Anderson and Shugart (1974) were among the first to apply to birds the classical multivariate techniques that are widely used in describing habitat response patterns. Equally important to interpreting habitat response patterns have been studies on physiological and morphological adaptations, reproductive biology, wintering habits, predation, food limitation and competition, plant-insect-bird interactions, historical factors, etc.

The objectives of habitat analysis were to (1) evaluate the strength of association of individual habitat variables with species habitat response, (2) compare variation in habitat response of a species across different study areas, (3) evaluate the effect of interspecific competition between ecologically similar species in modifying habitat response, and (4) analyze the habitat response of synthetic variables that describe community structure in terms of species richness (number of species), and bird species diversity.

Although the term "habitat selection" appears frequently in the literature of bird-habitat relationships, we preferred the more neutral term "habitat response," in the sense of a statistical association with an underlying stimulus factor.

Habitat variables

Each station was classified into one of three moisture classes on the basis of the field description of floristic components: dry, mesic, and wet. An extensive series of indicator species was used to determine the appropriate moisture class for a station. Initially we sought to include precipitation, as given by standard rainfall maps, to indicate moisture, but the maps were inaccurate in some areas and other factors interfered. The moisture classes that we used integrated precipitation with the water-holding capacity of the soil, fog drip, local drainage, relative humidity, and other factors. Dry forests pioneering recent lava flows, for example, lie adjacent to wet forests in areas of heavy rainfall.

Because of our on-going development of techniques for quantifying habitat structure, habitat structure was characterized differently in the Kau and Hamakua study areas (1976–1977) compared with later work. In Kau and Hamakua, individual understory components were not recorded unless present as substantial cover ($>20\%$), usually leading to an underestimate for sparse ground cover types. Although the difference did not affect analyses of habitat response within a study area, it affected comparisons of responses in Kau and Hamakua with responses in study areas surveyed later.

The habitat, or independent, variables that entered the habitat analysis as primary data for each station, together with comments on their measurement and justification for their inclusion, follow. (The mean and standard error for these variables, stratified by elevation, habitat type and study area, may be found in the Appendix).

Moisture.—A score of 2 was given to stations classified as dry, 4 to mesic, and 6 to wet. A small number ($<1\%$) of stations were classified as intermediate to the main groups. The use of a mid-value for the mesic group assumed that bird response to mesic habitat was about midway between habitat responses to dry and wet habitat. An initial analysis using two dummy variables (dry/not dry and wet/not wet) showed that this assumption was generally appropriate.

Elevation.—Elevation above mean sea level in meters was determined from the standard U.S. Geological Survey 1:24,000 topographic map series and from readings made at each station with an altimeter calibrated to control points on the U.S.G.S. topographic map.

Tree biomass.—An index of forest development was calculated as crown cover in percent times canopy height in meters. Tree biomass also indexed foliage volume. Vegetation and canopy volume were used in analyzing avian habitat response by Sturman (1968), Karr and Roth (1971), Sabo (1980), and Rice et al. (1983).

Crown cover.—Crown cover was entered as percent cover. Observers were trained to divide classes at 5%, 25%, 60%, and 80% cover values. In the analysis, cover was entered as the midpoint value for the cover class to which the station was assigned. In the field some stations were given cover values intermediate to the designated classes, and the analysis preserved such values. In some cases cover values summed to >100% due to multi-layering in dense canopies.

Canopy height.—Canopy height was entered as the height in meters of the highest canopy layer. Observers were trained to divide classes at 2, 5, 10, and 25 m heights. In the analysis, height was entered as the midpoint value for the height class to which the station was assigned. In the field some observers designated intermediate heights to the established classes, and the analysis preserved such data.

Dominant tree species.—Five dominant tree types were used as separate variables in the analysis: koa, ohia, naio, mamane, and introduced trees (mainly guavas, eucalyptus, and Christmas-berry). The values entered were the tree biomass for that tree type.

Understory summaries.—Shrub cover was computed as the total cover of plants with shrub-like habit above 50 cm height; ground cover as the total cover of plants with stature below 50 cm height.

Understory components.—Eleven understory types were entered as variables in the analysis as percent cover: native shrubs, introduced shrubs, ground ferns (sum of native and introduced species), matted ferns, tree ferns, ieie, passiflora, native herbs, introduced herbs, native grasses, and introduced grasses. Due to methodological differences mentioned earlier, ground fern, ieie, and native herbs were not recorded in Kau or Hamakua.

Flowers and fruit phenology.—The mean phenology scores for the 10 trees nearest to the station of ohia (flowers), olapa (fruit), mamane (flowers, fruit), and naio (fruit) were multiplied by the tree biomass variables; these variables indexed the total amount of flowers and fruit of those species in the area.

Community variables

For each station three variables were computed from the bird data to estimate properties of community structure and the relative role of native and introduced species. The variables used and their construction are given below.

Species richness.—Two variables, native species richness and introduced species richness, summarized the number of native and introduced bird species occurring at a station. Originally we also examined total species richness and bird densities for native, introduced, and all species. Our analysis of total species richness and total bird density indicated that these variables behaved like composites of their native and introduced components. This made comparisons between study areas difficult, because the study areas differed greatly in the relative dominance of native and

introduced elements. Separate analyses of the native and introduced components were more instructive. Similar questions were raised in our analysis of bird density. By its nature, density weighted individual species disproportionately. We found that composite density variables were strongly influenced by one or two dominant species. In every study area the habitat response of introduced bird density was almost identical to that of the extremely common Japanese White-eye. Where two or three species contributed 80–90% of the native bird density, it was almost impossible to make meaningful comparisons between study areas, because of the idiosyncratic effect of different proportions of the major species. This problem was especially severe in interpreting the effect of tree species and understory variables. Our preliminary analysis suggested that the complexity of community structure was more meaningfully indexed by species richness than by density because richness tended to maintain its integrity between study areas, whereas density was frequently overwhelmed by the responses specific to particular species.

Bird species diversity.—The reciprocal of Simpson's (1949) index of heterogeneity was taken as an estimate of the diversity and dominance of the bird populations at each station. This variable was computed as $1/\Sigma p_i^2$, where p_i was the density of species i divided by the total bird density at the station. This measure was interpreted as the number of equally common species required to produce the same heterogeneity as observed at the station (Peet 1974). Simpson's index was better suited to our data than the Shannon-Wiener information index ($-\Sigma p_i \log_e p_i$) because the latter was biased for samples with small (10 vs. 50–100) number of individuals (Routledge 1980) and was more sensitive to changes in rare species, which were more likely to be missed during eight-minute counts. The reciprocal Simpson index, however, was more sensitive to changes in the most abundant species (Peet 1974), and thus reflected the degree of dominance by the most common species.

Preliminary screening

Before we constructed habitat response models, the bird and habitat variables were carefully examined for a number of potential problems. Univariate distributions of each variable were examined for outliers and departures from the normal probability function. Each variable was mapped in geographic space to determine inconsistencies in measurement and to identify variables unsuitable for further analysis. Multiple regression was performed on random subsets of the data and the residuals examined for nonlinear trends and heteroscedasticity (variance of subsamples changing with the mean). These preliminary analyses were useful in focusing on key issues and in realizing the limitations of the analysis.

The variance tended to increase with the mean for many variables in the screening process, and therefore all bird densities and all habitat variables except elevation and moisture were transformed by $x' = \log_{10}(x + 1)$ to stabilize the variance. The log transformation brought most variables into reasonable conformance with the multivariate normal distribution and corrected many problems evident in the analysis of resid-

uals. Use of the log transformation has also been appropriate and customary for analyzing population fluctuations as percent changes (Whittaker 1975).

Another result of the preliminary screening was the determination that many bird species demonstrated a curvilinear response to two important variables, elevation and tree biomass. Quadratic (x^2) terms for these variables were therefore included in the analyses to represent curvilinearity. Nonlinear response to other variables occasionally appeared in the analysis of residuals but was relatively rare. Screening also showed that in many Hamakua and Kipukas models, the tree fern and moisture variables usually took on surrogate relations, where one variable served as a proxy for another presumably causal variable (see also the section on interpreting habitat response). Tree fern was eliminated from these models to facilitate interpretation.

Regression models

We sought to implement a multivariate model that (1) accounted for the intercorrelations among habitat variables in order to avoid confounding, (2) could be uniformly applied to all dependent variables in order to facilitate objective comparisons of species, and (3) could be interpreted by readers with a moderate statistical background.

Regression models were constructed from a multiple regression design. The predicted density y of a bird species took the form of

$$y = a_0 + \Sigma \, b_i x_i,$$

where a_0 was the constant term, x_i was the value and b_i the coefficient of habitat variable i. This multiple regression model was based on the analysis of variance (ANOVA) paradigm and permitted statistical significance tests of the overall equation and of individual effects (Draper and Smith 1981). The regression equation took into account not only the effect of the habitat variables on the birds, but also intercorrelations among the habitat variables. This reduced spurious and confounding relations due to surrogate effects. Community variables were subjected to the same analysis as bird densities. Multiple linear regression has been effective in analyzing the responses of individual species (Sturman 1968, Abbott et al. 1977, Dyer 1978, Westman 1981) and community variables (Glenn-Lewin 1976).

Multiple regression equations may be constructed in many different ways, depending on the criteria for entering or deleting variables. We developed a model design that could be implemented on standard statistical packages such as the Biomedical Computer Programs P-series (BMDP, Dixon and Brown 1979) or the Statistical Package for the Social Sciences (SPSS, Nie et al. 1975); an updated version of the latter was used for portions of this analysis.

The model design used was a structured stepwise procedure that worked down through a series of hierarchical levels, adding significant variables to the regression equation and deleting variables that became insignificant as others were added. The process ended at the bottom level when no more variables could significantly enter the model and only significant ones remained in the model; this was the "final model." The final model was therefore arrived at through a series of inclusion and deletion steps (as many as 36 steps were needed in fitting the final model). At each step, the only difference between our procedure and standard forward stepwise regression was that the variables at hierarchical levels below the current entry level were not available for inclusion. The criterion for entry of a variable to the model was a minimum F-to-enter value of 5.00, corresponding approximately to the 0.025 significance level. For variables in the model, deletion occurred when F-to-exit dipped below 3.84, the 0.05 significance level. The significance levels to enter were more stringent than those to exit to ensure that the model with the entering variable (often the pool of potential candidates was large) actually "explained" habitat response better than the model without the variable.

The key feature of this procedure was the organization of variables into hierarchical levels. The hierarchical organization we used (1) gave certain variables perceived as more important, or more extensive, the opportunity to enter the model before more localized variables that may have had trivially higher F values; (2) represented the notion that most birds responded more strongly to a gross habitat feature (e.g., tree biomass) than to a fine one (e.g., native herbs) if the final equation could have included only one of the two variables; (3) organized the entry of correlated variables so that specific interpretations could be made (e.g., tree biomass was entered first as an index of forest development, then canopy height as a particular forest feature, then ohia as one element of the forest, and then ohia flowers as a food resource); and (4) considered linear terms of elevation and tree biomass before quadratic ones.

Following fundamental considerations on the architecture and description of complexity (Simon 1962, Gauch 1982), the hierarchy worked from the general to the specific by proceeding from extensive abiotic variables to increasingly intensive and small-scale variables, down through this series of levels:

1) elevation and moisture—represent abiotic elements such as temperature, moisture, exposure, and precipitation;
2) [elevation]^2;
3) tree biomass—as a general index of forest development;
4) [tree biomass]^2;
5) crown cover and canopy height—specific aspects of forest structure after general forest development has been considered;
6) the five tree types: koa, ohia, etc.—specific dominant floristic elements of the forest;
7) shrub cover and ground cover—general aspect of the understory;
8) the eleven understory types: native shrubs, matted ferns, etc.—specific growth forms and taxa of the understory; and
9) the five flowers and fruit variables—included for passerines as potential food sources.

Habitat response models were computed for each bird species for which we had sufficient data, and for the three community variables in each study area. Because of the small size of the West Maui study area
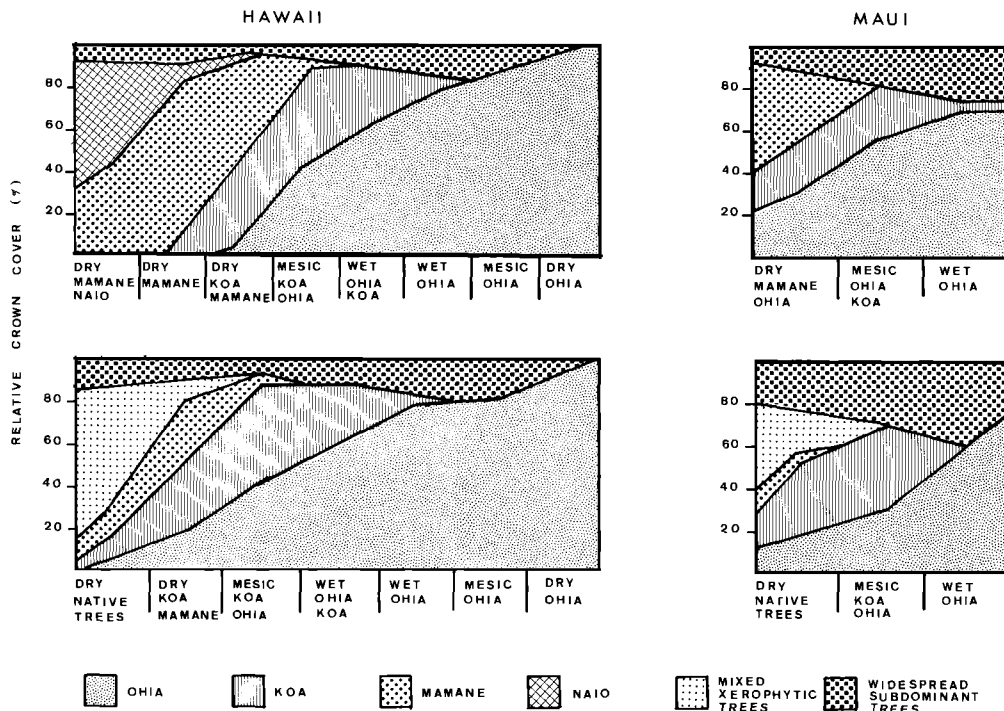
FIGURE 62. Relative abundance of dominant tree species in forest and woodland habitat types on Hawaii and Maui.

and the similarity of bird response patterns on East and West Maui, the two areas were combined in the regression analysis.

Habitat response graphs

Contour graphs of habitat response were used to complement the multiple regression models. Because habitat response graphs require a fairly large number of data points that are well distributed across the habitat space, we constructed contour graphs only for Hawaii and Maui (Figs. 62 and 63). Although the graphs are only two dimensional and thus could not display species response to every habitat component, contour graphs are more sensitive than regression models to nonlinear response and variable interaction, and are straightforward in interpretation once their design is grasped. Contour mapping of the population response to environmental gradients is a form of direct gradient analysis and is one of the best ordination techniques for giving detailed information on the distributions of species (Margalef 1963, Whittaker and Gauch 1978). The technique was pioneered by Whittaker (1952, 1956, 1960), and has been frequently applied to bird distributions in habitat space (Sabo 1980, Rotenberry and Wiens 1981, James and Wamer 1982).

The choice of axes for the contour graphs was based on the general results of the habitat response models. The axes represented (1) elevation and mosquito presence, (2) forest development, and (3) moisture and dominant tree composition. A summary of habitat re-

sponse models presented later (Table 70) showed that the habitat variables representing these axes had significant entries in over half the models.

To represent elevation and mosquito presence, we constructed separate contour graphs for areas above and below 1500 m elevation, the approximate upper limit of mosquitoes in the Hawaiian Islands (see Goff and van Riper 1980). Forest development was represented on the Y-axis by tree biomass (m-%), the product of crown cover (%) and canopy height (m) (as described in the *Habitat variables* section above). The Y-axis was labeled in physiognomic terms: forest (tree biomass > 500 m-%—, equivalent to > 10 m high, closed canopy); woodland (150–500 m-%— 5–10 m high, open canopy); savanna (50–150 m-%— < 5 m high, very open canopy, or 5–10 m high, scattered trees); and scrub (< 50 m-%— < 5 m high, scattered trees, shrubland, grassland, or barren).

Moisture was represented on the X-axis by a gradient from dry to wet. A detailed hierarchical classification of the vegetation types on Hawaii showed two parallel series of vegetation types along this axis that were differentiated mainly by substrate age. On the immature substrates of younger lava flows and ash deposits, ohia dominated dry, mesic, and wet moisture classes. On older lava and ash substrates, mamane, koa, and other native trees dominated dry and mesic areas; ohia dominated the wettest sites. To represent the complex effect of substrate age on vegetation along the X-axis, we pivoted the younger dry and mesic ohia sites away from dry and mesic sites on older substrates. Hence, the
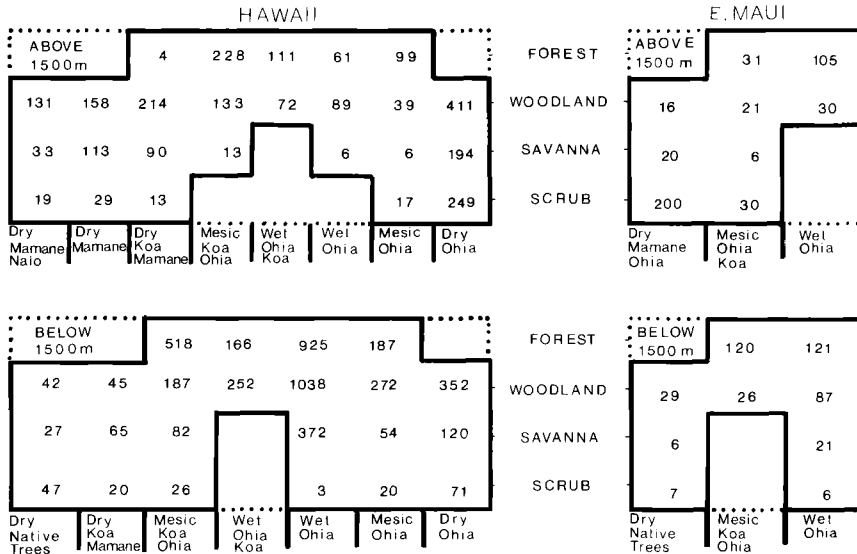
HAWAII — ABOVE 1500m

	Dry Mamane Naio	Dry Mamane	Dry Koa Mamane	Mesic Koa Ohia	Wet Ohia Koa	Wet Ohia	Mesic Ohia	Dry Ohia
FOREST		4	228	111		61		99
WOODLAND	131	158	214	133	72	89	39	411
SAVANNA	33	113	90	13		6	6	194
SCRUB	19	29	13				17	249

E. MAUI — ABOVE 1500m

	Dry Mamane Ohia	Mesic Ohia Koa	Wet Ohia
FOREST		31	105
WOODLAND	16	21	30
SAVANNA	20	6	
SCRUB	200	30	

HAWAII — BELOW 1500m

	Dry Native Trees	Dry Koa Mamane	Mesic Koa Ohia	Wet Ohia Koa	Wet Ohia	Mesic Ohia	Dry Ohia
FOREST		518	166		925		187
WOODLAND	42	45	187	252	1038	272	352
SAVANNA	27	65	82		372	54	120
SCRUB	47	20	26		3	20	71

E. MAUI — BELOW 1500m

	Dry Native Trees	Mesic Koa Ohia	Wet Ohia
FOREST		120	121
WOODLAND	29	26	87
SAVANNA	6		21
SCRUB	7		6

FIGURE 63. Sample sizes for cells on the habitat response graphs.

X-axis extended from drier mamane and koa-ohia sites, through wet ohia sites, to drier ohia sites (Fig. 62). On Maui, recent substrates covered a negligible portion of the study area and did not require differentiation. The X-axis on the Maui graphs thus corresponded to the left half on Hawaii graphs (Fig. 62).

Once the axes were defined, each vegetation type was positioned on the graph. Although some subjectivity was necessary in placing units along the X-axis, tree species composition for the units was recorded below the X-axis to permit objective comparisons. Some differences in tree species composition occurred along the X-axes between areas above and areas below 1500 m elevation, mainly reflecting the replacement of mamane and naio above by a dry native tree association dominated by lama and halapepe below 1500 m. Also notable was the rarity of dry closed forests (especially below 1500 m) and wet scattered forests. On Maui, the narrowness of the mesic zone and its widespread destruction resulted in few samples in mesic areas.

Contour graphs for habitat response were constructed as follows: (1) the location of each detailed vegetation type on the habitat graph was determined; (2) the mean and standard deviation of bird density for the stations in each vegetation type were computed; (3) the mean and standard deviation were plotted on the habitat graph; (4) incidental observations were used to determine the range limits of a species in habitat space; and (5) isopleths were drawn by hand and smoothed, taking sample sizes (Fig. 63) of the vegetation types into account.

Interpreting habitat response

Although multivariate analyses of habitat response frequently appear in the literature, rarely are the bases for interpreting analytical results explicitly described. Because regression models require care in their interpretation, this section describes the main procedures

for interpreting habitat response and may be useful to other investigators applying regression or discriminant function analysis to large data sets.

The final equation of the structured regression procedure, the regression model, is a major source of statements on bird response. Each of the 164 regression models has a suite of descriptive and ancillary statistics. The most useful statistics in interpreting these models are the signed t tests for the coefficients of the habitat variables in the final models. These t values usually give a fair indication of the habitat response of a species. The coefficients of the regression equation are useful but sensitive to transformations and the other variables in the model. Due to space limitations, the coefficients and other statistics are not included in the tables that follow but are available at the Mauna Loa Field Station. In addition to the above variables, the partial correlations of variables not in the model, the simple bivariate correlations, and the habitat response graphs were consulted in interpreting response patterns and comparing patterns between study areas.

Quadratic terms for elevation and tree biomass indicate response patterns modeled as parabolas (see also Meents et al. 1983). When the x^2 term is positive, the parabola opens upward (bimodal), and when negative, it opens downward to approximate a bell-shaped curve. The relation of the parabola's axis of symmetry to the actual range of values of the habitat variable is helpful in interpreting a model. The position of the axis is determined by the ratio of the linear coefficient to the quadratic coefficient. When the axis lies below the actual range of values, then the habitat response resembles a linear function (of the same sign from the x^2 term), but leveling off at high values. An axis within the actual range represents bimodal (rare) or bell-shaped response. We use the contour graphs and densities tabulated by elevation to interpret nonlinear habitat response to elevation and tree biomass.

Because of the high dimensional configuration of habitat space, our interpretation of bird response attempts to distinguish the most important effects among many interrelated factors acting simultaneously. In many models a gestalt-like response to several related variables is apparent. Surrogate relations appear among variables that are moderately to highly correlated and are a source of discord when comparing regression models across several study areas. We could not arrange orthogonal contrasts to avoid this as in classic ANOVA, because the distribution of vegetation types was unknown prior to sampling. In models where surrogate relations appear between variables such as tree biomass, crown cover, and canopy height, the relative magnitudes of the t tests and the regression coefficients are useful in interpreting the habitat response, as are bivariate correlations with the dependent variable and the habitat response graph.

Methodological differences between study areas in quantifying ground cover in the field may have caused discrepancies for these variables when Kau and Hamakua models are compared with other areas. Another problem is sampling error of the dependent variable when most stations have a value of zero. For rare species, unoccupied areas may still be suitable habitat (Wiens 1981), and the effect of this sort of sporadic rarity on regression analysis is usually a reduction in statistical significance. In many models R^2 values are less than 0.10, i.e., the model explains less than 10% of the total variance. Although such models have low predictive value, R^2 is not the appropriate criterion for judging the usefulness of the model in identifying factors that affect habitat response (Draper and Smith 1981). For this purpose we used the t statistics for the individual variables included in the model. As explained below, the importance of individual t statistics is interpreted by comparison with other t statistics in that model, in other models for the same species, and in models for other species. For rare species we therefore tended to place greater emphasis on the habitat effects identified in a model than the low R^2 values would otherwise seem to warrant.

In addition to the assumptions and mechanics of model construction, the relation of the study area to the geographic range of a species also affects interpretation. If only the periphery of a species range was sampled (e.g., many introduced birds common at low elevations), the patterns sometimes give a misleading impression of the species habitat preferences taken as a whole because the edge of the range represented marginal or sporadically occupied habitat. For some recently introduced species (e.g., Kalij Pheasant and Yellow-fronted Canary on Hawaii), range boundaries are still dynamic, and the regression models may better indicate the habitat currently occupied than the range of habitat that these birds may eventually find optimal.

Significant variation in habitat structure is necessary in the landscape sampled to determine habitat response patterns. The Kauai and Kohala study areas are rather homogeneous, and some models based on these areas show weak or no patterns of habitat response, i.e., not statistically different from sampling within a uniform cluster.

Our data did not exactly meet the assumptions underlying the statistical tests associated with the AN-OVA model. The significance levels for the F and t tests, although often astronomical, were interpreted as indicators of the relative importance of variables, not as exact tests, due to stepwise variable selection and deviation of the data from strict multivariate normality (Draper et al. 1971, Pope and Webster 1972, Johnson 1981a). Variables having large numbers of stations with a value of zero usually deviate from the normal distribution; in such cases the regression model still provides the best unbiased linear estimator (Draper and Smith 1981) even though the significance tests are inaccurate (Bradley 1968).

Comparison of the regression models for a given species across different study areas shows that each area has unique peculiarities that tend to reappear when examining the regression models for other bird species. It was therefore appropriate to interpret a particular habitat response model in a relativistic manner, i.e., the relation of species X to habitat variable Y in a given area was indicated not only by significance tests but also by X's response to other variables in that model, the nature of that model compared with other models for species X, and the patterns of the models for species X compared with the models for other species. Thus a t value of 5 (highly significant) was of great importance in some models (e.g., those for study areas with smaller sample sizes or for very rare species) and of relatively little importance in others (e.g., a model with large sample size that included six variables with $t > 10$). For each species we noted the principal effects along with the basis for their interpretation. We attempted to reconcile major discrepancies between study areas in each species account in terms of model mechanics, geographical pattern, and historical context.

In many habitat analyses, correlated variables "compete" as possible explanations for a habitat response pattern. In this analysis we impose an ordering from extensive geographic-scale variables (elevation, moisture) to more detailed-scale habitat components because the resulting explanation (1) reflects the role of large scale components as determinants of the small scale ones, (2) is of greater use in developing habitat management strategy, and (3) seems to parallel the conceptualizing faculty of the human mind (Simon 1962). A similar structured approach is found in the technique of path analysis (Turner and Stevens 1959, Overton and Florschutz 1962, Duncan 1966). Although in some instances the imposed ordering may not reflect the biological mechanisms determining the habitat response patterns, important lower level variables still have high significance values in the final model due to the least squares algorithm. When several highly correlated hypotheses compete to explain a particular pattern (e.g., whether a response is due to tree biomass, or to crown cover and canopy height, or to the sum of differentially preferred tree species), our approach is inadequate to distinguish the true "cause" behind the pattern, which in all probability is a complex, unmeasurable gestalt variable. The variable hierarchy then offers a pragmatic first approximation to understanding the pattern.

It must also be recognized that an indefinitely large number of appropriate analyses are possible for identifying habitat response patterns. We were prevented from examining a broader range of techniques because

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.