INTERSPECIFIC COMPETITION AMONG HAWAIIAN FOREST BIRDS[1]

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Abstract. The object of this study was to determine whether interspecific competition modified local geographic distribution, after taking into account the effect of habitat structure. The tendencies for 14 passerine birds to have positive or negative associations were examined, using 7861 sample points in seven native forests on the islands of Hawaii, Maui, and Kauai. All birds were at least partly insectivorous and were fairly common in forested areas, although some fed chiefly on nectar or fruit. Species-pairs were classified as primary or secondary potential competitors based on general dietary similarity.

To evaluate the association between species and to account for the effect of individual species' habitat preferences, partial correlations were computed for each species-pair in a study area from the simple correlations between the species and 26 habitat variables plus two quadratic terms to represent nonlinearity. The partial correlations represented a short-term ("instantaneous") assessment of the strength of competitive interactions, and did not reflect the accumulation of competitive displacement through time. Of 170 partial correlations in the analysis, only 10 indicated significant negative association. The general pattern was of positive association (76 significantly positive partials), which probably resulted from flocking and from attraction of birds to areas of resource superabundance. Two species-pairs showed consistent patterns of negative partial correlations over several adjacent study areas, the Japanese White-eye/Iiwi in montane Hawaii, and the Japanese White-eye/Elepaio in windward Hawaii; both patterns could be reasonably attributed to direct competition.

Species-pairs were grouped by the native or exotic status of the component species. Native/exotic pairs had a significantly greater proportion of negative partial correlations (37%) than either native/ native pairs (8%) or exotic/exotic pairs (0%). This pattern was consistent across the seven study areas and appeared to reflect the occurrence of interspecific competition along a broad and diffuse ecological "front" between a co-evolved native avifauna and recently introduced exotic species. The role of competition in the pattern was corroborated by the significantly higher proportion of negative partial correlations among species-pairs of primary potential competitors than among those of secondary potential competitors. Our results suggested that ≈47% of the primary potential competitors among native/exotic species-pairs may experience at least small depressions in local population density due to competition. Although the negative correlations were for the most part small (average negative $r = 0.06$), one species could eventually replace another as spatial displacement accumulated through time. The Japanese White-eye appeared to have a principal role in native/exotic interactions, with 62% of the partial correlations between it and native primary potential competitor species being negative.

Noteworthy implications were that (1) it was important to account for the habitat responses of individual species when studying the role of interspecific competition in modifying small-scale geographic distribution; (2) competition was frequently sporadic in its geographic occurrence and in the species affected, thus supporting Wiens' (1977) theory of competition; and (3) as a consequence, the role of interspecific competition in modifying distribution may be difficult to detect statistically with small data sets.

Key words: diffuse competition; exotic species; habitat response; Hawaiian Islands; interspecific competition; partial correlation; passerine birds; taxon cycle.

INTRODUCTION

The effect of interspecific competition on the geographic and landscape distribution of species has proved notoriously difficult to demonstrate in natural populations (Connell 1983, Strong 1983). Although some have regarded competition as pervasive (e.g., MacArthur 1972, Cody 1974), Andrewartha and Birch (1954) thought that it occurred rarely, with weather, predation, and spatial heterogeneity exerting a greater

influence on species response. Wiens (1977) also suggested that competition was uncommon in a varying environment because populations would seldom be at the carrying capacity, and resources would often be superabundant.

At first, the number of species on the islands of various archipelagoes seemed to offer good evidence for interspecific competition (Diamond 1975, Abbott et al. 1977, Juvik and Austring 1979, Faaborg 1982). This line of investigation became less promising, however, as workers disagreed on appropriate null hypotheses (Connor and Simberloff 1979, Strong et al. 1979, Alatalo 1982, Diamond and Gilpin 1982), and the effect of prehistoric human disturbance (Olson and James 1982*a, b*). Comparisons of communities on both
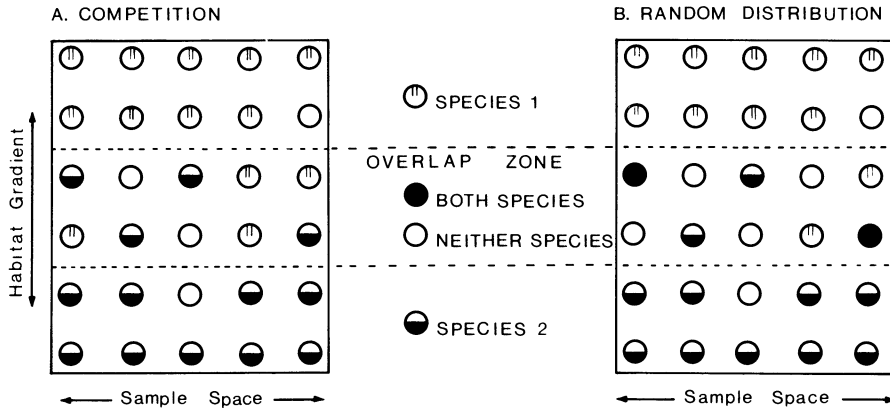
FIG. 1. Distribution of hypothetical species-pairs A and B in habitat space (e.g., elevation) and real space (equivalent to sampling space).

oceanic islands and continental habitat islands with their mainland counterparts suggested that competition was often less and niches broader on islands (Crowell 1962, MacArthur et al. 1972, Terborgh and Weske 1975, Morse 1976). Competition has also been inferred from the elevational limits of bird distributions on mountains (Terborgh 1971, Diamond 1973, 1978, Able and Noon 1976) and from extinction rates among exotic birds in the Hawaiian Islands (Moulton and Pimm 1983).

Although elevation gives a rough index of habitat-type, bird distributions respond strongly to finer levels of habitat detail, such as foliage height profile (MacArthur and MacArthur 1961, James 1971, Karr and Roth 1971, Willson 1974), dominant plant species (Balda 1969, Tomoff 1974, Sabo 1980, Noon 1981, Wiens and Rotenberry 1981), levels of flower and fruit resources (Snow and Snow 1971, Scott et al., *in press*), and temperature and moisture regime (Bond 1957, Smith 1977, Holmes et al. 1979, Sabo 1980, Weathers and van Riper 1982, Karr and Freemark 1983). Unless care is taken to ensure habitat uniformity between elevational belts, between mainland and island sites, or between the islands of an archipelago, the observed patterns may merely represent bird response to unrecorded habitat elements that differ between sites.

Consider the distribution of two pairs of species across a landscape (Fig. 1). In both pairs ranges overlap, with one species more common at the upper end of a habitat gradient, and the other species more common at the lower end. Does interspecific competition operate in the area of overlap? In Fig. 1, the species in pair A overlap in range, but at individual sites within the overlap zone, only one species occurs. Species in pair B have an equivalent overlap in range, but in the overlap zone co-occurrence is random.

By statistically removing the effect of the habitat gradient and then evaluating the association (negative or positive) between two species, we test for prima facie evidence that competition modifies the distribution of

the two species. This approach yields an "instantaneous" view of competitive displacement (i.e., the degree to which one species depresses densities of the other within a habitat during the study period), not representative of displacement that may have accumulated through time (e.g., exclusion from or uniformly depressed densities within a particular habitat), and thus tends to underestimate the true degree of competitive displacement. This statistical approach to quantifying competition was first suggested by Schoener (1974), and has been theoretically developed and tested using Monte Carlo techniques by Hallett and Pimm (1979). Crowell and Pimm (1976) estimated competitive interaction in an experimental manipulation using a modification of this technique, and Toft et al. (1982) applied a similar procedure to a study of taiga ducks.

The argument that competition for food resources is at least partly responsible for the negative associations would be supported if species-pairs with very similar dietary preferences show a greater incidence of negative association than species-pairs with rather dissimilar diets. By measuring most major features of habitat structure, particularly those to which species appear to respond, we attempt to ensure that the features most important to the habitat preferences of individual species are included in the analysis.

In this paper we examine the relationships of species-pairs across landscapes after removing the effect of habitat variables through partial correlation. We utilized the extensive data set of the Hawaiian Forest Bird Survey (HFBS), sponsored by the United States Fish and Wildlife Service. The relations of forest passerines were compared across seven native forest study areas that were intensively sampled over a 6-yr period. Habitat structure was described in detail and bird density was estimated at hundreds of points in each study area, thus allowing us to evaluate the effect of competition on distributions of species across landscapes by the procedure outlined above.

TABLE 1. Diet and average live mass of common Hawaiian birds in native forests. Codes in italics indicate exotic species.

Code	Species	Body mass (g)*	Food preferences†					
			Arthro-pods	Ohia nectar	Mamane nectar	Other nectar	Fleshy fruits	Seeds
MLTH	Melodious Laughing-thrush (*Garrulax canorus*)	55	1	. . .	. . .	. . .	1	. . .
RBLE	Red-billed Leiothrix (*Leiothrix lutea*)	22	1	. . .	. . .	. . .	1	. . .
HATH	Hawaiian Thrush (*Phaeornis obscurus*)	50	2	. . .	. . .	. . .	1	. . .
ELEP	Elepaio (*Chasiempis sandwichensis*)	14	1	. . .	. . .	. . .	. . .	. . .
JWEY	Japanese White-eye (*Zosterops japonicus*)	10	1	2	2	1	2	. . .
AMAK	Common Amakihi (*Hemignathus virens*)	13‡	1	2	1	2	2	. . .
ANIA	Anianiau (*Hemignathus parvus*)	9	1	2	. . .	2	. . .	. . .
KACR	Kauai Creeper (*Oreomystis bairdi*)	*14*	1	. . .	. . .	. . .	. . .	. . .
MACR	Maui Creeper (*Paroreomyza montana*)	*11*	1	. . .	. . .	2	. . .	. . .
AKEP	Akepa (*Loxops coccineus*)	*11*	1	. . .	. . .	. . .	. . .	. . .
APAP	Apapane (*Himatione sanguinea*)	15	2	1	2	2	. . .	. . .
CRHO	Crested Honeycreeper (*Palmeria dolei*)	*22*	2	1	. . .	. . .	. . .	. . .
IIWI	Iiwi (*Vestiaria coccinea*)	17	2	1	2	1	. . .	. . .
NOCA	Northern Cardinal (*Cardinalis cardinalis*)	42	2	. . .	. . .	. . .	1	1

* Body masses from the literature and personal communications from C. J. Ralph and C. van Riper III; masses in italics estimated from related species by regression on wing length.

† Diet: 1 = principal food all or most seasons; 2 = important secondary or seasonal diet item; . . . = item seldom taken.

‡ The Kauai subspecies, *H. v. stejnegeri*, weighs *17* g.

In reviewing the presumed causes of decline among rare birds, King (1978) estimated that competition affects 9% of the taxa worldwide, and was probably an important factor in the decline of the native Hawaiian avifauna. Berger (1981), too, suggested that exotic birds, particularly the Japanese White-eye (*Zosterops japonicus*), may have an adverse effect on native passerines and noted the need for studies on competition. By comparing the patterns of partial correlations within and between native and exotic species, we attempt to quantify the relationship between the native and exotic avifaunas in the Hawaiian Islands.

Our principal objectives are to examine (1) the correlations between species-pairs before and after removing the effects of habitat structure, (2) the relations between species more likely to compete and those less likely to compete for food resources, (3) the relations within and between the native and the exotic species, and (4) the relations of individual species-pairs across the seven study areas.

FOCAL SPECIES

The species selected for study (scientific names in Table 1) are small- to medium-sized arboreal forest passerines that feed frequently on insects, although other food items may be utilized even more frequently.

We examined the relations only among the more common (> 5–10 birds/km²) species, because this was where we expected competition to be operating most obviously, and because for most rare species small sample sizes led to statistically inconclusive results due to sampling error. Although rare species may be negatively affected by more common species, the impact of rare species was probably miniscule on focal species that were typically hundreds of times more abundant.

Food preferences (Table 1) were compiled from our personal observations, literature accounts, and personal communications from other field workers. The list indicates major foraging behaviors, and is by no means an exhaustive compilation; virtually every species occasionally feeds on every food type. From this list and our knowledge of each species' foraging behavior, we divided the species-pairs into two categories: primary potential competitors and secondary potential competitors. Admittedly these groups grade into one another, but we mainly sought to distinguish cases where dietary preferences are close enough that competition for food resources is quite plausible from those cases where we expected much less frequent, generally weaker, or even no competitive pressure. The major criteria for primary potential competitors were (1) primary dietary preferences in the same food category, and (2)

similar foraging sites as to understory/canopy, foliage/bark surfaces. Euryphagic species like the Japanese White-eye thus had more primary potential competitors than stenophagic ones like the Apapane. We now briefly characterize the foraging behavior, habitat response, and relevant natural history of the focal species. See Perkins (1903), Munro (1944), Berger (1981), and Scott et al. (*in press*) for additional details.

The Melodious Laughing-thrush is sedentary and most common below 1200 m elevation, occurs from very wet forests to dry scrub, prefers brushy understories with structural and florstic diversity, feeds at low heights on foliage insects and fruit, and has not yet colonized the Kau and most of the Kona study areas.

The Red-billed Leiothrix is most common in wet forests above 1200 m elevation, occurs in both woodlands and dense forests, feeds mostly in the understory on foliage insects and fruit, and disperses widely after breeding.

The Hawaiian Thrush is most common in partly open rain forests from 1000 m elevation to timberline, feeds opportunistically below the canopy on fruit and less frequently on insects (particularly caterpillars), and may migrate to insect outbreak areas (van Riper and Scott 1979). Populations in Kona and Kohala were extirpated around 1900, probably through contact with avian disease, but Puna birds may be resistant to malaria and pox.

The Elepaio is very sedentary and common in wet forests above 1200 m elevation, prefers sites with koa (*Acacia koa*) trees, is also common in dry woodlands of mamane (*Sophora chrysophylla*) and naio (*Myoporum sandwicense*), and feeds almost entirely in the understory and subcanopy on insects that it gleans from foliage, bark, and ground substrates or captures in flight. Aggressive interactions with the Japanese White-eye and Red-billed Leiothrix are frequent (Conant 1977).

The Japanese White-eye, the most abundant land bird in the Hawaiian Islands, occurs from sea level to tree line, in very dry to very wet habitat, in sparse low scrub to tall dense forests. It is most common at low elevations, and was introduced in 1929 (Berger 1981). Its tubular, brush-tipped tongue is adapted for nectarivory, but its catholic diet also includes understory and subcanopy fleshy fruit, and foliage and bark insects. Local movement occurs during the nonbreeding season, often in flocks with as many as 200 birds.

The Common Amakihi is sedentary, found in virtually all native scrubland and forest, and is most associated with drier native forests at higher elevations. Several populations appear to have developed resistance to avian disease (van Riper et al. 1982). In dry areas the Amakihi feeds mostly on mamane nectar, but in rain forests it feeds on foliage insects and less often on nectar from understory plants.

The Anianiau is sedentary, inhabits wet native forests on Kauai, and feeds on insects and nectar in the

mid and upper canopy (J. L. Sincock, *personal communication*). Character displacement in bill and body size between it and the Amakihi probably minimize competition for food resources (Bock 1970).

The Kauai Creeper, a sedentary and rather solitary species, is most common in the ohia (*Metrosideros polymorpha*) rain forests above 1000 m elevation. It feeds primarily by gleaning insects from bark and trunk surfaces in the mid canopy and understory (J. L. Sincock, *personal communication*).

The Maui Creeper, a sedentary species, is common in dense, wet, mosquito-free, native forests of East Maui. It feeds in the understory and subcanopy on foliage and bark insects, but takes nectar from understory plants seasonally (Carothers 1982).

The Akepa is a rather sedentary species still common in the Alakai Swamp on Kauai but too rare on Hawaii and Maui to include in the analysis. It is most common in wet areas with fairly well-developed high forests of ohia or koa. The Akepa feeds on canopy insects, using its asymmetric bill and jaw musculature to twist apart ohia leaf buds, pry into woven-together koa phyllodes, and force open koa seed pods (Richards and Bock 1973). It sometimes forms small loose flocks with the Kauai Creeper (J. L. Sincock, *personal communication*).

The Apapane, a vagile species that may fly 10 km between feeding and roosting areas, is most common in wet, fairly dense ohia forests above 1000 m elevation with good ohia bloom. Some populations are apparently resistant to avian disease, and fairly high densities occur in some low-elevation ohia forests. The Apapane is primarily adapted to feeding on ohia nectar (Baldwin 1953), but juveniles also feed on foliage insects and occasionally on fruit. Apapane are frequently displaced from ohia trees by Iiwi and Crested Honeycreeper.

The Crested Honeycreeper is a moderately vagile species confined to mosquito-free rain forests on East Maui. It feeds primarily on ohia nectar, but foliage insects and nectar from understory plants are also important in the diet. Crested Honeycreepers frequently chase Apapane and Iiwi from ohia trees in good bloom when flowers are scarce elsewhere. This behavior is very probably an example of interference competition (J. H. Carothers, S. Mountainspring, *personal observations*).

The Iiwi, a vagile species like the Apapane, reaches greatest abundance in dense, mosquito-free rain forests, and is rare in mosquito-infested areas. It feeds primarily on the nectar of ohia, mamane (in dry areas), and understory plants. Foliage insects and occasionally fruit are also taken. Iiwi are strongly territorial at certain times, and aggressively displace Apapane from ohia trees and Amakihi from mamane (Carpenter and MacMillen 1976, Pimm and Pimm 1982).

The Northern Cardinal was introduced to the Hawaiian Islands in 1929, and is most common in dry, open forests at low elevations with understories of ex-
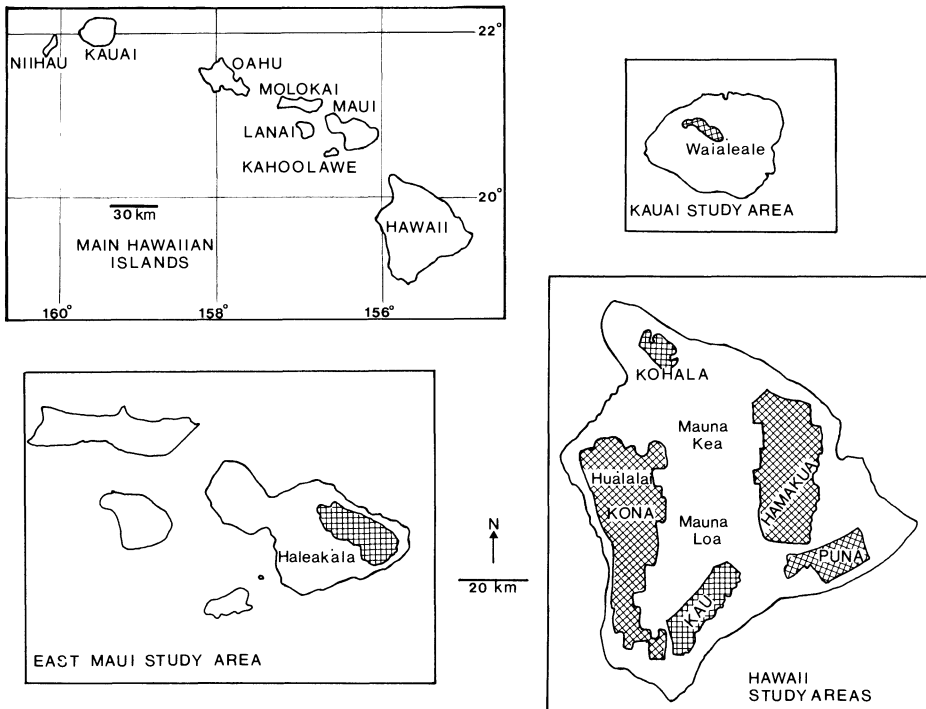
FIG. 2.   Location of study areas in the Hawaiian Islands.

otic shrubs and exotic grasses. It is fairly sedentary, and feeds on fruit, seeds, and less often on foliage insects.

STUDY AREAS

We conducted extensive surveys of the bird populations and habitat structure of native forests in five study areas on the island of Hawaii and one study area each on the islands of Maui and Kauai (Fig. 2). All study areas but one on Hawaii were located in wet, windward forests. All areas were sampled during the prolonged breeding season (May–August) typical of Hawaiian passerines (Berger 1981).

Wet forest study areas on the island of Hawaii

Hamakua study area.—This was the largest study area in wet forest, and occupied the eastern flank of Mauna Kea and the northeastern slopes of Mauna Loa. A total of 2422 stations on 21 transects were sampled from June to August 1977. The 1122-km² area extended from 430 to 2190 m elevation, and median annual rainfall ranged from 100 to 750 cm. The upper boundary lay near the inversion layer in dry disturbed pastures and grasslands. Dry mamane woodland dominated some areas at high elevation. Below these areas well-developed native forests were dominant, with koa forests on drier sites intergrading to ohia forests on wetter sites. Exotic plants were common at lower elevations. Matted ferns frequently dominated large areas

at low to mid-elevations where mass dieback of ohia had occurred.

Puna study area.—The Puna study area lay south and east of the Hamakua area on Pleistocene and Recent lava flows from Kilauea Volcano. A total of 651 stations on 10 transects were sampled from May to August 1979. The 270-km² area extended from 270 to 1170 m elevation, and median annual rainfall ranged from 90 to 400 cm. Ohia dominated both dry woodland and rain forest areas. Exotic trees and grasses were widespread on disturbed sites.

Kau study area.—The Kau study area lay on the southeast slopes of Mauna Loa, and consisted of fairly undisturbed wet forests isolated from other native forests by alpine desert, sugar cane fields, rangelands, and recent lava flows. A total of 867 stations on 11 transects were sampled from June to July 1976. The 329-km² area extended from 670 to 2130 m elevation, and median annual rainfall ranged from 90 to 400 cm. The top boundary of the study area lay near the inversion layer in dry, scrubby alpine grassland. Below this occurred subalpine scrubland, and then well-developed wet native forest. Koa was a dominant tree in the northeast half of the study area, and ohia was common throughout and sole dominant in the southwest half of the area.

Kohala study area.—The Kohala study area lay on the northern peninsula of Hawaii, and was well isolated from other native forests by extensive ranchlands and

arid disturbed scrub. This study area lay on the slopes of an old volcanic system deeply dissected by large valleys running northeast. A total of 210 stations on six transects were sampled from July to August 1979. The 124-km² area extended from 490 to 1670 m elevation, and median annual rainfall ranged from 120 to 480 cm. Most sites were dominated by ohia.

Other wet forest study areas

East Maui study area. — The East Maui study area lay on the eastern slopes of Haleakala, a massive shield volcano. A total of 785 stations on 19 transects were sampled in May to July 1980. The 290-km² area extended from 450 to 2500 m elevation, and median annual rainfall ranged from 120 to 900 cm. The upper boundary lay along the rim of Haleakala crater near the inversion layer in alpine grasslands situated above subalpine scrub and wet native forests. Most forest sites were dominated by ohia, although koa dominated small areas northwest of Koolau Gap and in Kipahulu Valley, mamane occurred along the crater rim, and exotic trees occurred at low elevations and along disturbed edges.

Kauai study area. — This study area was situated in the Alakai Swamp region, a high montane plateau dissected by numerous valleys and bordered by sheer canyons. A total of 140 stations on six transects were sampled in May 1981 in very wet, dense ohia forest. The 25-km² area extended from 1150 to 1510 m elevation, and median annual rainfall ranged from 250 to 750 cm.

Dry forest study area

Kona study area. — The Kona study area occupied the western slopes of the island of Hawaii on the Hualalai and Mauna Loa volcanoes. A total of 2786 stations on 33 transects were sampled from May to July 1978. The 1265-km² area extended from 210 to 2370 m elevation, and median annual rainfall ranged from 40 to 250 cm. Native forests in this area are fragmented from grazing, lumbering, and numerous historic lava flows. Forests reached their best development on the north and west slope of Hualalai and on the west slopes of Mauna Loa in the South Kona District. Elsewhere the habitat was generally arid. In mesic forests ohia, or koa and ohia, were dominant; in arid woodlands mamane, naio, and lama (*Diospyros ferrea*) were dominant. Exotic trees were common at low elevations, and eucalyptus and conifer plantations were also frequent. Exotic grasses were abundant in the dry area north of Hualalai and on several large ranches in the northern half of South Kona District.

METHODS

Bird population densities

In each study area sampling was conducted along transects placed 3.2 km apart at right angles to the elevational contour. Map location of the initial transect in a study area was determined by random placement. Due to more rapid geographic turnover of communities, transects on Maui were placed 1.6 km apart, and transects on Kauai were placed randomly with a minimum of 0.5 km between adjacent transects to ensure independent sampling.

Sampling stations were placed along transects at 134-m intervals in all study areas except Kau, where a 100-m interval was used. These distances were approximately twice the effective detection distance of the more conspicuous and vocal forest birds, and we felt that stations had a high degree of statistical independence. Sampling was conducted by separate teams of field workers specifically trained in bird or plant sampling to ensure uniformity among observers.

Each station was surveyed twice for birds during periods of good weather (wind speed <8 m/s and no appreciable noise from rain or water dripping from vegetation), for 4 h following sunrise. The variable circular-plot method (Reynolds et al. 1980) was used to estimate the population density of birds at each station. The estimated horizontal distance from the observer to every bird heard or seen during the two count periods was recorded, except for birds judged not to be using the area (e.g., birds flying high overhead). Since we were interested in an estimate of the density at a point, and not the density in a large area, two count periods were appropriate, not the larger values given in Reynolds et al. (1980:Table 1). An 8-min count period was used because it met the assumptions of an instantaneous count, and was 80–90% as effective as a 32-min count in detecting the forest birds in a given area (Hawaiian Forest Bird Survey data). Hawaiian forest passerines gave at least one and usually several calls in an 8-min period (Ralph 1981; Hawaiian Forest Bird Survey data).

Population densities derived from the station counts took into account the conspicuousness of individual bird species, canopy and understory vegetation density, and variation between observers. A full description of the derivation developed for us by F. L. Ramsey is given in Scott et al. (*in press*). Each station was assigned to 1 of 13 detectability classes based on canopy and understory conditions. 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 cells by species, observer, detectability class, and study area.

Detection distances were converted to the area searched. In each cell, detection areas were arranged in order of increasing magnitude and then used to construct a cumulative distance curve. We constructed the convex envelope of the cumulative distance curve by drawing a straight line from the origin to the point that gave the greatest slope of all points on the curve, and extending the line to the next point that gave the great-

est slope for all points beyond the first, etc. The slope of the envelope curve thus declined as the area searched increased. We used a likelihood ratio rule to decide when the decline in slope was significant. We then drew a line from the origin, through the first point where the slope significantly declined, to intersect the asymptote of the envelope. The detection area at that intersection was taken as the raw estimate of effective area surveyed (see also Ramsey and Scott 1979).

Burnham et al. (1980) 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 our data. Even with this cutoff, however, some cells had too few detections to produce raw estimates.

Missing cell values were estimated and available cell estimates were smoothed by fitting a linear ANOVA model that represented the influence of species, observer, and detectability code on the logarithm of effective area. To examine possible interactions, we fit models for the Kau, Hamakua, and Kona study areas that allowed for observer-by-detectability interactions and for different effects by seven abundant species (Red-billed Leiothrix, Hawaiian Thrush, Elepaio, Japanese White-eye, Common Amakihi, Iiwi, Apapane). The effects of observers and detectability codes were remarkably consistent among species and were independent of one another.

Density estimates derived by our procedures were subject to occasional sources of error: field misidentifications, inaccurate distance estimates, and inefficiency in estimating effective area. We considered the assumptions behind the density estimates to be satisfactorily met by the focal species in this study.

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

Habitat structure

Vegetation structure was sampled at each station within 2 wk of the bird counts in order to minimize temporal variation in phenology. Vegetation structure was quantified within a 50 m radius of the station using a habitat description format that permitted fairly rapid, detailed, and consistent assessment of the major habitat features (see Scott et al., *in press* for additional details). Observers were trained prior to sampling to calibrate estimates to crown covers of 5, 25, 60, and 80%; canopy heights of 2, 5, 10, and 25 m; and understory covers of 1, 5, 25, 50, 75, and 90%. Observers interpolated between these values in the field.

The habitat variables that entered the analysis as primary data for each station, with comments on their measurement or justification for their inclusion, were as follows.

Elevation.—Elevation above mean sea level was determined from the 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 topographic map.

Moisture.—On the basis of the field description of floristic components, each station was assigned to one of three moisture classes (dry, mesic, or wet) that represented the major differentiation of tree, shrub, and ground cover genera along the moisture gradient (Scott et al., *in press*). An extensive series of indicator species was used to determine the appropriate moisture class. Although we had initially sought to use precipitation (as given by standard rainfall maps) as the indicator of moisture, it became apparent that the maps were inaccurate in some areas and that substrate age, water-holding capacity of the soil, fog drip, local drainage, relative humidity, etc., interfered. A score of 2 was given to stations classified as dry, 4 for mesic, and 6 for wet. A small number (<1%) of stations were classified as intermediate to these three 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. A preliminary analysis using two dummy variables (dry/not dry and wet/not wet) showed that this assumption was appropriate for the focal species we analyzed.

Crown cover.—The percent crown cover.

Canopy height.—The height in metres of the highest canopy layer.

Canopy volume.—A measure of forest development was calculated as the product of canopy cover multiplied by canopy height. This variable also indexed foliage volume. Karr (1968), Sturman (1968), and Karr and Roth (1971) found foliage or canopy volume useful in analyzing avian habitat response.

Dominant tree species.—Five dominant tree types were entered into the analysis as the amount of canopy volume occupied by koa, ohia, naio, mamane, and exotic trees.

Understory components.—Understory variables were entered as percent cover. Eleven understory types were entered as separate variables in the analysis: native shrubs, exotic shrubs, ground ferns, matted ferns, tree-ferns, native vines, exotic vines, native herbs, exotic herbs, native grasses, and exotic grasses. In addition, two variables were constructed to summarize the general structure of the understory; shrub cover, the total cover of plants from 50 to 200 cm height, and ground cover, the total cover of plants below 50 cm height.

Phenology scores.—Phenology scores consisted of a 0–4 rating for ohia flowers, olapa (*Cheirodendron trigynum*) fruit, and mamane flowers of the 10 trees of each species that were nearest to the station. The scoring system was as follows: 0 = no flowers or fruit present; 1 = <1% of crown covered; 2 = 1–5% covered;

3 = 5–25% covered; 4 = >25% covered. The mean phenology score for the 10 trees nearest to the station was multiplied by the canopy volume of that species to serve as an index to the total number of ohia flowers, olapa fruit, and mamane flowers in the area.

Statistical analyses

Bird population densities and habitat variables entered the analysis as values for each sampled station and were taken as accurate values. In reality, an unknown error term accompanied each observation; Scott et al. (1981) suggested that the absolute value of the error term averaged 10% of the actual value. The effect of estimating, rather than measuring, variables tended to increase observed variability and decrease statistical efficiency, but did not introduce systematic bias and allowed us to survey a large number of stations.

Univariate distributions of the bird and habitat variables in each study area were examined for outliers and departures from the normal distribution. Multiple regression was performed on random subsets of 10–25% of the sample points. The residuals from the analysis were examined for nonlinear trends and heteroscedasticity. Because a tendency for the variance to increase with the mean appeared for many variables in the screening process, all bird densities and all habitat variables except elevation and moisture were transformed by $x' = \log(x + 1)$ in order to stabilize their variances. The logarithmic transformation was appropriate for population densities because population fluctuations are often analyzed on a logarithmic or percentage basis (Whittaker 1975).

Another important modification to the analytical design was necessary to account for a curvilinear response that many bird species exhibited to two important variables, elevation and canopy volume. Quadratic (x^2) terms for these variables were therefore included in the analysis to represent curvilinear response.

The techniques of multiple regression and partial correlation were applied to the bird and habitat data for each study area to evaluate the strength and sign of association between species after habitat effects have been removed. Multivariate partial correlation may be visualized as a multivariate regression using habitat variables as the independents, followed by an examination of the resulting partial correlations between bird variables (Morrison 1976). The partial correlations were more suitable indicators of species associations than regression coefficients (i.e., as if we had also entered bird variables into the regression as independent variables) because of surrogate effects that make interpretation ambiguous (Mosteller and Tukey 1977).

The model used was

$$B = a + \sum_i c_i h_i + c_b b_j + E,$$

where B is the density of focal species, a is a constant, c_i is the coefficient for habitat variable h_i, c_b is the the coefficient for the density b_j of species j, and E is random error. This model assumes a linear relationship among the independent and dependent variables. Binary, interval, and ratio habitat variables may be suitably included in the model because this model produces maximum likelihood estimates for the partial correlation coefficients (Draper and Smith 1981). We refer frequently to the statistical significance ($P < .05$, two-tailed test) of correlation coefficients, but these values are only approximate because the data do not conform exactly to the normal distribution. In order to avoid this problem in critical tests comparing groups of correlation coefficients, we resort to nonparametric tests based on the number of positive and negative correlations in a group. Since the model yields unbiased estimators of the correlations, these values are used as representative samples of the degree of positive or negative association among species in that group. In some comparisons, correlations from different study areas or different years are pooled. We did this in order to examine hypotheses on a broader scale (e.g., the general relationship of one species to another), and thereby implicitly assumed that correlations from different years or areas were independent samples from the same abstract population. In such cases we examined the consistency of such patterns across groups to avoid spurious results. Given the sporadic nature theorized for competition (Wiens 1977), the relatively aseasonal nature of the Hawaiian environment, sampling conducted only during the breeding season, and the similarity of bird-habitat responses observed between areas and years (Scott et al., *in press*) we feel that this assumption was justified.

Comparisons based on tabulations of species-pairs within a study area have inflated sample sizes, because the comparisons involve fewer species than pairs. This should not substantially affect the results, however, for the partial correlations of species-pairs within a study area were independent of one another, and sample sizes were at least an order of magnitude greater than the number of species-pairs.

In the presentation below, we refer to the simple correlations between species as "prehabitat correlations," and to the partial correlations after removing the effect of habitat variables as "posthabitat correlations."

RESULTS

Patterns within individual forests

Hamakua study area.—In this area eight passerines are common (Table 2), the greatest number in the study areas on the island of Hawaii, making 28 comparisons between species. From the general diets of these species (Table 1), we would expect interspecific competition to be most likely among those species that feed heavily on fruit (Melodious Laughing-thrush, Red-billed Leiothrix, and Hawaiian Thrush) and among those

TABLE 2.   Population densities (given as birds/km², $\bar{x} \pm$ SE) of focal birds in the study areas. "+" marks species that occurred at low densities in an area but were not included in the analysis.

Species*	Hamakua	Puna	Kau	Kohala	Kona	East Maui	Kauai
MLTH	6 ± 1	13 ± 1	. . .	15 ± 1	+	7 ± 1	15 ± 1
RBLE	58 ± 2	+	54 ± 3	88 ± 7	10 ± 1	74 ± 3	. . .
HATH	94 ± 2	74 ± 3	188 ± 5	. . .	+	. . .	+
ELEP	116 ± 4	40 ± 3	45 ± 3	148 ± 13	56 ± 2	. . .	247 ± 10
JWEY	601 ± 10	651 ± 13	421 ± 20	480 ± 37	268 ± 5	396 ± 14	544 ± 29
AMAK	174 ± 6	128 ± 15	439 ± 19	317 ± 21	327 ± 6	158 ± 7	87 ± 8
ANIA	. . .	. . .	. . .	. . .	. . .	. . .	254 ± 11
KACR	. . .	. . .	. . .	. . .	. . .	. . .	74 ± 9
MACR	. . .	. . .	. . .	. . .	. . .	175 ± 16	. . .
AKEP	+	. . .	+	. . .	+	+	67 ± 6
APAP	385 ± 11	570 ± 22	911 ± 27	209 ± 21	195 ± 5	389 ± 16	1201 ± 29
CRHO	. . .	. . .	. . .	. . .	. . .	20 ± 2	. . .
IIWI	234 ± 8	+	209 ± 10	+	47 ± 2	89 ± 5	231 ± 10
NOCA	+	23 ± 1	+	+	25 ± 1	+	+
Sample size	2422	651	867	210	2786	785	140

* Common and scientific names given in Table 1. Codes in italics indicate exotic species.

feeding extensively on nectar (Apapane, Iiwi, Japanese White-eye, and Amakihi). The prehabitat correlations (Table 3) show that 10 of the 28 species pairs have a significant negative association. If one did not account for habitat preferences, these correlations would be evidence for interspecific competition among pairs where dietary overlap is substantial, e.g., between the Melodious Laughing-thrush and the Red-billed Leiothrix, and between the Japanese White-eye and each of the following: Hawaiian Thrush, Elepaio, Amakihi, and Iiwi. A rather different view is found among the posthabitat correlations, however, for here only 2 of the original 10 negative correlations are still significantly negative: the Japanese White-eye/Elepaio and the Japanese White-eye/Iiwi pairs. Another striking feature is the large number of positive pre- and posthabitat correlations. For the prehabitat correlations, 17 species-pairs are positive; this rises to 24 pairs in the posthabi-

tat correlations. Clearly, positive association is the general pattern in Hamakua.

Puna study area. — In this area we examined interactions among seven species (Table 2), making 21 species-pairs. Compared to Hamakua, the frugivore group loses the Red-billed Leiothrix and gains the Northern Cardinal, while the nectarivores lose the Iiwi (probably due to avian disease [Scott et al., *in press*]). Prehabitat correlations are about evenly divided, 10 positive and 11 negative (Table 4). The Melodious Laughing-thrush, Elepaio, Amakihi, and Northern Cardinal are each involved in 4 negative correlations. In classical competition theory, this might be interpreted as evidence for diffuse competition. The posthabitat correlations, however, show a different pattern of 15 positive and only 6 negative correlations. The Elepaio is involved in 3 of these pairs, possibly suggesting diffuse competition.

TABLE 3.   Matrix of simple (prehabitat†) and partial (posthabitat†) correlations between the local geographic distributions of species-pairs in the Hamakua study area. Codes in italics indicate exotic species.

	MLTH						
RBLE	−0.14**	*RBLE*					
HATH	−0.07*	0.40**	HATH			Prehabitat correlation matrix	
ELEP	−0.10**	0.24**	0.48**	ELEP			
JWEY	0.18**	0.06*	−0.17**	−0.15**	*JWEY*		
AMAK	−0.20**	0.35**	0.39**	0.37**	−0.09**	AMAK	
APAP	−0.15**	0.43**	0.61**	0.42**	−0.04	0.53**	APAP
IIWI	−0.30**	0.48**	0.56**	0.45**	−0.20**	0.60**	0.60**
	MLTH						
RBLE	0.08**	*RBLE*					
HATH	0.16**	0.04*	HATH			Posthabitat correlation matrix	
ELEP	0.03	−0.01	0.31**	ELEP			
JEWY	0.10**	0.18**	0.03	−0.05*	*JWEY*		
AMAK	0.06*	0.04	0.17**	0.18**	0.05*	AMAK	
APAP	0.09**	0.06*	0.29**	0.21**	0.10**	0.22**	APAP
IIWI	−0.01	0.03	0.25**	0.23**	−0.06*	0.20**	0.19**

* $P < .05$; ** $P < .001$.

† "Prehabitat" and "posthabitat" refer, respectively, to correlations before and after removal from the analysis of correlations between abundance of a given species and a suite of habitat variables.

TABLE 4. Matrix of simple (prehabitat†) and partial (posthabitat†) correlations between the local geographic distributions of species-pairs in the Puna study area. Codes in italics indicate exotic species.

	MLTH	HATH	ELEP	JWEY	AMAK	APAP	NOCA
HATH	−0.10*	HATH					
ELEP	−0.14**	0.30**	ELEP		Prehabitat correlation matrix		
JWEY	0.15**	0.01	−0.01	JWEY			
AMAK	−0.22**	−0.44**	−0.14**	0.01	AMAK		
APAP	−0.52**	0.38**	0.17**	0.00	0.18**	APAP	
NOCA	0.44**	−0.09*	−0.04	0.17**	−0.10*	−0.38**	
	MLTH	HATH	ELEP	JWEY	AMAK	APAP	NOCA
HATH	0.05	HATH					
ELEP	−0.13**	0.15**	ELEP		Posthabitat correlation matrix		
JWEY	0.10**	0.00	−0.04	JWEY			
AMAK	−0.05	0.04	0.09*	−0.00	AMAK		
APAP	−0.17**	0.26**	0.23**	0.11*	0.15**	APAP	
NOCA	0.16**	0.07	−0.18**	0.06	0.01	0.05	

*,**,† See Table 3 for definitions and key to level-of-significance symbols.

Kau study area.—The focal species for this area (Table 2) are identical to those of Hamakua, except for the Melodious Laughing-thrush, which has not yet colonized this isolated forest. Positive interactions dominate both the prehabitat (14+, 7−) and posthabitat (15+, 6−) correlation matrices (Table 5). In the prehabitat matrix, all species have only 1 or 2 significant negative correlations except the Japanese White-eye, which has 4. In the posthabitat matrix, the negative Japanese White-eye/Iiwi correlation recalls a similar association in Hamakua.

Kohala study area.—The focal species for this area (Table 2) are a subset of those for Hamakua, excluding the Hawaiian Thrush which is now extirpated from the area, and the Iiwi which is rare. The prehabitat correlations are about evenly divided, 7 positive and 8 negative (Table 6). Not a single negative posthabitat correlation is significant, and only 3 positive ones are. The comparatively small sample size ($N = 210$) partly accounts for the few significant posthabitat correlations, but the dominance of positive association is further emphasized by ranking the correlations in absolute magnitude; of 15 species pairs, the largest negative correlation ranks 11th.

East Maui study area.—The Maui Creeper and Crested Honeycreeper are unique to this area (Table 2), but six other focal species also occur in Hamakua. Since the Crested Honeycreeper is probably involved in interference competition with the Iiwi and Apapane, we might expect the correlations among these pairs to be negative. The prehabitat correlations among the trio are all positive, although the posthabitat correlations indicate that the Crested Honeycreeper is distributed independently of the other two (Table 7). All four significant negative prehabitat correlations involve the Melodious Laughing-thrush, and all become positive or nonsignificant in the posthabitat analysis. Of 28 posthabitat correlations, 18 are significantly positive, and none are significantly negative. The partial correlation of 0.51 between the Apapane and Japanese White-eye is exceptionally high, and 3 other species-pairs have partials exceeding 0.30. Since these high correlations involve disease-resistant species that are fairly common at low elevations, this pattern may reflect higher densities in mosquito-infested areas due to the absence of disease-susceptible species and to the resulting higher resource levels.

Kauai study area.—The focal species in this area include three not studied elsewhere—the Anianiau, Kauai Creeper, and Akepa (Table 2). The large number

TABLE 5. Matrix of simple (prehabitat†) and partial (posthabitat†) correlations between the local geographic distributions of species-pairs in the Kau study area. Codes in italics indicate exotic species.

	RBLE	HATH	ELEP	JWEY	AMAK	APAP	IIWI
HATH	0.27**	HATH					
ELEP	0.08*	0.23**	ELEP		Prehabitat correlation matrix		
JWEY	0.15**	0.05	−0.13**	JWEY			
AMAK	−0.08*	−0.05	0.26**	−0.32**	AMAK		
APAP	−0.14**	0.20**	0.21**	−0.21**	0.46**	APAP	
IIWI	0.01	0.29**	0.33**	−0.37**	0.37**	0.43**	
	RBLE	HATH	ELEP	JWEY	AMAK	APAP	IIWI
HATH	0.07*	HATH					
ELEP	−0.04	0.10*	ELEP		Posthabitat correlation matrix		
JWEY	0.09*	0.04	−0.06	JWEY			
AMAK	0.03	0.05	0.12**	−0.05	AMAK		
APAP	−0.10*	0.22**	0.04	0.04	0.23**	APAP	
IIWI	−0.00	0.17**	0.13**	−0.08*	0.09*	0.11*	

*,**,† See Table 3 for definitions and key to level-of-significance symbols.

TABLE 6. Matrix of simple (prehabitat†) and partial (posthabitat†) correlations between the local geographic distributions of species-pairs in the Kohala study area. Codes in italics indicate exotic species.

	MLTH				
RBLE	−0.01	*RBLE*			
ELEP	−0.16**	0.47**	ELEP	Prehabitat correlation matrix	
JWEY	0.26**	−0.10	−0.48**	*JWEY*	
AMAK	−0.19**	0.36**	0.47**	−0.21*	AMAK
APAP	−0.05	0.17*	0.21*	−0.07	0.43**
	MLTH				
RBLE	0.09	*RBLE*			
ELEP	0.06	0.12	ELEP	Posthabitat correlation matrix	
JWEY	0.14	0.31**	−0.02	*JWEY*	
AMAK	−0.03	0.11	0.17*	0.10	AMAK
APAP	0.03	0.01	0.05	−0.05	0.25**

*,**,† See Table 3 for definitions and key to level-of-significance symbols.

of primary insectivores in this area presents a situation for investigating competition as a force in determining local variation in population densities. The small sample size compared to other areas ($N = 140$) appears to have resulted in relatively few significant relations (Table 8). Positive interactions characterize both pre- and posthabitat correlation matrices; not a single posthabitat correlation is significantly negative.

Kona study area.—This dry forest study area has seven focal species. The pool is similar to Hamakua, but includes the Northern Cardinal and excludes the Melodious Laughing-thrush and the Hawaiian Thrush. Positive interactions dominate both the prehabitat (17+, 4−) and the posthabitat (16+, 5−) matrices (Table 9). The Japanese White-eye has significant negative posthabitat relations with both the Apapane and Iiwi, and the Red-billed Leiothrix/Amakihi pair accounts for the remaining negative correlation.

The overall picture emerging from the analysis of individual study areas is that positive posthabitat interactions are far more frequent than negative ones. Of 170 posthabitat correlations, 10 are significantly negative, 78 positive. Nevertheless, 10 significantly negative posthabitat correlations are significantly more than

chance expectation. In a sample of 170 correlations, we would expect 4.25, or half of 5%, to be significantly negative in a two-tailed test; for the goodness-of-fit test, $\chi^2 = 8.0$ ($P < .005$, df = 1). The probability from the binomial distribution of at least 10 significant negative correlations out of 170 is 0.011. Of the 37 significantly negative prehabitat correlations, 24 become nonsignificant in the posthabitat analysis, 7 become significantly positive, and only 6 remain significantly negative. Of 41 nonsignificant prehabitat correlations, 32 remain so (21 of these relations are due to Kauai, where small sample size is probably responsible). Of 92 significantly positive prehabitat correlations, over two-thirds remain significantly positive, and none becomes significantly negative.

Analysis of interspecific association among Hawaiian forest birds shows fairly consistent trends across seven forested study areas. By partialing out the effect of habitat, the number of significant negative correlations between the 170 species-pairs (counting each forest occurrence as independent) is significantly reduced from 37 prehabitat to 10 posthabitat correlations ($\chi^2 = 20.8$, $P < 10^{-5}$, df = 1). This suggests that ≈70% of the observed instances of negative species association

TABLE 7. Matrix of simple (prehabitat†) and partial (posthabitat†) correlations between the local geographic distributions of species-pairs in the East Maui study area. Codes in italics indicate exotic species.

	MLTH						
RBLE	−0.08*	*RBLE*					
JWEY	0.35**	0.41**	*JWEY*		Prehabitat correlation matrix		
AMAK	−0.06	0.45**	0.30**	AMAK			
MACR	−0.25**	0.43**	0.09*	0.39**	MACR		
APAP	0.08*	0.53**	0.52**	0.55**	0.37**	APAP	
CRHO	−0.19**	0.29**	0.05	0.28**	0.51**	0.26**	CRHO
IIWI	−0.10*	0.50**	0.20**	0.47**	0.48**	0.48**	0.34**
	MLTH						
RBLE	0.12**	*RBLE*					
JWEY	0.39**	0.29**	*JWEY*		Posthabitat correlation matrix		
AMAK	0.11*	0.16**	0.23**	AMAK			
MACR	−0.01	0.08*	−0.00	0.04	MACR		
APAP	0.31**	0.24**	0.51**	0.33**	0.02	APAP	
CRHO	0.02	0.05	0.01	0.02	0.09*	0.01	CRHO
IIWI	0.09*	0.20**	0.10*	0.22**	0.14**	0.22**	0.05

*,**,† See Table 3 for definitions and key to level-of-significance symbols.

TABLE 8. Matrix of simple (prehabitat†) and partial (posthabitat†) correlations between the local geographic distributions of species-pairs in the Kauai study area. Codes in italics indicate exotic species.

	MLTH	ELEP	JWEY	AMAK	ANIA	KACR	AKEP	APAP	
ELEP	−0.20*	ELEP							
JWEY	0.36**	0.07	JWEY					Prehabitat correlation matrix	
AMAK	0.11	−0.02	0.21*	AMAK					
ANIA	−0.16	0.13	−0.10	0.08	ANIA				
KACR	−0.11	0.05	−0.22*	0.11	0.25*	KACR			
AKEP	−0.03	0.30**	0.11	0.17*	0.21*	0.36*	AKEP		
APAP	0.18*	0.21*	0.28**	0.02	0.14	−0.05	0.03	APAP	
IIWI	−0.13	0.21*	−0.06	0.08	0.05	0.08	0.11	0.25*	
	MLTH	ELEP	JWEY	AMAK	ANIA	KACR	AKEP	APAP	
ELEP	−0.04	ELEP							
JWEY	0.22*	0.17	JWEY					Posthabitat correlation matrix	
AMAK	0.11	−0.03	0.16	AMAK					
ANIA	−0.16	0.15	−0.02	0.09	ANIA				
KACR	−0.03	−0.03	−0.11	0.11	0.16	KACR			
AKEP	−0.01	0.27*	0.18	0.17	0.08	0.31**	AKEP		
APAP	0.19*	0.17	0.28*	−0.07	0.11	−0.08	−0.01	APAP	
IIWI	0.00	0.09	0.04	0.08	0.06	0.07	0.08	0.16	

*,**,† See Table 3 for definitions and key to level-of-significance symbols.

can be satisfactorily explained by different habitat preferences.

Patterns of individual species-pairs across forests

Although the analysis of individual study areas shows rather overwhelming neutral and positive association, the relations of the individual species that co-occur in several forests are instructive to examine. We therefore compiled the posthabitat correlations for the 32 species-pairs that occurred in two or more study areas. As expected, the relations were dominated by positive interactions. Of 32 species-pairs, 17 had no negative correlations, 8 had 1 negative correlation, 4 had 2 negative correlations, 2 had 3 negative correlations, and 1 had 4 negative correlations. Only 2 pairs had more negative correlations than positive ones, and only 1 pair had more than a single negative correlation that was statistically significant.

Of all species-pairs, the Elepaio/Japanese White-eye had the greatest number of negative correlations, but only 1 of these was significant. All 4 negative relations occurred in the wet forests of Hawaii, where a distinct race of the Elepaio occurs (Pratt 1980). The Elepaio/Japanese White-eye relation in Kona and in Kauai was positive. Japanese White-eyes are driven off Elepaio territories during the breeding season (Conant 1977), and this, combined with the sedentary nature of the Elepaio (Pratt 1980) and the substantial overlap in diet between the two species, may result in the negative correlations; moreover, this territorial defense is apparently most pronounced in the windward Hawaii subspecies (Conant 1977). When the four windward Hawaii study areas (Hamakua, Puna, Kau, and Kohala) are combined to test the significance of overall negative association between the two species, this relation is near significance [$\chi^2 = -2 \sum_{i=1}^{4} (\ln P_i) = 14.5$, $P = .06$, df = 8]. Interspecific competition is a reasonable mechanism to account for this pattern because the Elepaio feeds entirely on insects, and the abundant

TABLE 9. Matrix of simple (prehabitat†) and partial (posthabitat†) correlations between the local geographic distributions of species-pairs in the Kona study area. Codes in italics indicate exotic species.

	RBLE	ELEP	JWEY	AMAK	APAP	IIWI	
ELEP	0.24**	ELEP					
JWEY	0.15**	0.06*	JWEY			Prehabitat correlation matrix	
AMAK	−0.01	0.15**	−0.24**	AMAK			
APAP	0.22**	0.26**	0.01	0.22**	APAP		
IIWI	0.33**	0.40**	0.01	0.19**	0.51**	IIWI	
NOCA	0.15**	0.27**	0.26**	−0.06*	−0.02	0.09**	
	RBLE	ELEP	JWEY	AMAK	APAP	IIWI	
ELEP	0.02	ELEP					
JWEY	0.10**	0.03	JWEY			Posthabitat correlation matrix	
AMAK	−0.06*	0.13**	−0.04	AMAK			
APAP	0.04*	0.06*	−0.06*	0.21**	APAP		
IIWI	0.09**	0.21**	−0.10**	0.19**	0.27**	IIWI	
NOCA	0.05*	0.17**	0.15**	0.01	−0.03	0.03	

*,**,† See Table 3 for definitions and key to level-of-significance symbols.

Japanese White-eye very frequently feeds on insects. Both species tend to feed on foliage insects over most of the foliage column, but particularly at lower heights. Since Japanese White-eye densities average 3–16 times greater than Elepaio densities in these four areas (Table 2), Elepaio densities are probably more strongly depressed by interspecific competition from the Japanese White-eye than vice versa.

The Japanese White-eye/Iiwi pair has negative posthabitat correlations in three out of five study areas, and as in the Elepaio/Japanese White-eye pair, these areas are confined to a particular geographic region, in this case the higher elevations of Hawaii. The statistical test for an overall effect in these three areas (Hamakua, Kau, Kona) is highly significant ($\chi^2 = 53.2$, $P < 10^{-7}$, df = 6). Both the Japanese White-eye and the Iiwi frequently feed on nectar from flowering understory trees and shrubs. According to Pimm and Pimm (1982:1475), the Iiwi "remains specialized on high quality resources and probably cannot profitably exploit poor ones." The negative interaction between the Japanese White-eye and Iiwi may thus be reasonably attributed to interspecific competition for limited nectar resources. When ohia and mamane flowers are locally unavailable, the Iiwi relies heavily on alternate nectar sources (e.g., *Broussaisia, Eugenia, Ilex, Passiflora, Vaccinium*), unlike the Apapane or Amakihi which switch to insects or fruit. Hence, the Iiwi may be particularly vulnerable to the omnivorous foraging behavior of the Japanese White-eye at certain seasons. As with the Elepaio, since Japanese White-eye densities average 2–5 times higher than Iiwi densities in these areas (Table 2), competition is probably more keenly felt by the native species. The Hawaii populations of the Iiwi, though not subspecifically distinct from those on Maui and Kauai, do have a behavioral difference that may explain why posthabitat correlations of this species pair differ among the three islands. On Hawaii, the Iiwi undertake extensive daily migrations between roosting and feeding areas (MacMillen and Carpenter 1980), but these migrations are poorly developed on Maui and Kauai (C. B. Kepler, J. L. Sincock, *personal communications*). Iiwi on Hawaii hence have a greater opportunity to avoid areas with depleted nectar resources such as might occur through the activity of high Japanese White-eye populations. On Maui and Kauai, daily movement is greatly reduced by comparison with Hawaii, and Iiwi would have less opportunity to avoid low-nectar patches via daily redistribution across the landscape; this would tend to yield fewer negative correlations than on Hawaii due to decreased potential for avoidance on a geographical scale.

Among the remaining species-pairs, most negative posthabitat correlations are isolated instances in one forest balanced by positive relations in other forests. Although consonant with the concept that competition acts in a sporadic fashion in response to local resource shortages, meaningful patterns are virtually impossible

TABLE 10. Distribution of negative and positive posthabitat correlations across study areas by native or exotic status of the members of the species-pairs.

Study area	Exotic/ Exotic		Native/ Native		Native/ Exotic		P^*
	−	+	−	+	−	+	
Hamakua	0	3	0	10	4	11	0.075
Puna	0	3	0	6	6	6	0.034
Kau	0	1	0	10	6	4	0.003
Kohala	0	3	0	3	3	6	0.250
Kona	0	3	0	6	5	7	0.063
East Maui	0	3	0	10	2	13	0.230
Kauia	0	1	5	16	6	8	0.234
Overall	0	17	5	61	32	55	≪0.001

* Two-tailed test that native/exotic species pairs have a greater proportion of negative correlations than native/native pairs.

to resolve at this scale. One exception of note, however, is the Japanese White-eye/Amakihi pair with weak negative correlations in three forests. Here competition is obliquely implied, as both species feed at lower heights in the forest on insects, flowers, and fruit, but this evidence is not strongly convincing. Interestingly, the two larger negative correlations are from the only two study areas where average Amakihi densities exceed Japanese White-eye densities. All three pairs of species, then, that have some consistency in negative association across forests are primary potential competitors (Table 11), and all involve the Japanese White-eye.

Patterns between native and exotic species

King (1978) and Berger (1981) suggested that introduced birds might compete for food or other resources with native birds. To examine this hypothesis, we divided the species-pairs into three groups according to the native or exotic status of the species in each pair. We then examined for different overall patterns of positive or negative association in the native/native, native/exotic, and exotic/exotic species-pairs.

Interactions of native/native and exotic/exotic species-pairs have virtually no negative associations (Table 10). The five negative native/native posthabitat correlations all come from Kauai, and are negligible, with $P = .38$ for the most significant of the 5. Equally apparent is the substantial proportion (37%) of negative correlations among native/exotic species-pairs. To evaluate whether native/exotic species-pairs had a significantly higher proportion of negative correlations than native/native or exotic/exotic pairs, we applied the normal approximation of χ^2 (Steel and Torrie 1980: 502) to the tabulated correlations in Table 10. For the overall effect summed across seven forests, native/exotic pairs had significantly higher proportions of negative correlations than either native/native ($Z = 4.2$, $P < .00003$) or exotic/exotic pairs ($Z = 3.0$, $P < .003$). Native/native and exotic/exotic correlations did not

TABLE 11. Classification of native/exotic species-pairs as primary (1) or secondary (2) potential competitors, based on general dietary similarity. See Table 1 for species codes.

	MLTH	RBLE	JWEY	NOCA
HATH	1	1	2	1
ELEP	1	1	1	2
AMAK	1	1	1	2
ANIA	1	. . .*	1	. . .
KACR	2	. . .	1	. . .
MACR	1	1	1	. . .
AKEP	2	. . .	2	. . .
APAP	2	2	2	2
CRHO	2	2	2	. . .
IIWI	2	2	1	2

* Species that do not co-occur in the analysis.

differ significantly in their proportion of negative correlations ($Z = 1.2$, $P > .24$).

The proportion of negative correlations in native/native and native/exotic pairs was also compared within individual forests (Table 10); exotic/exotic pairs were too few for this analysis. In each forest, native/exotic pairs had a higher proportion of negative correlations than native/native pairs; the associated probability values are $P < .05$ for Kau and Puna, $.06 < P < .08$ for Hamakua and Kona, and $.20 < P < .25$ for East Maui, Kauai, and Kohala. The χ^2 summation for overall effect (substructured by individual forests) again showed a highly significant greater proportion of negative correlations among native/exotic pairs compared to native/native pairs ($\chi^2 = 37.5$, $P < .001$, df = 14). Because native/exotic pairs consistently showed across study areas and years a higher proportion of negative partial correlations than native/native or exotic/exotic pairs, we interpreted the competitive effect to be similar in operation across years and to have a scale of operation <25 km^2 (the smallest study area). This offered some support for our decision to pool data from different years and different size study areas in making certain comparisons, and further indicated the potential for competitive displacements to accumulate in time.

Since nearly all variation in the proportion of negative posthabitat correlations occurred among native/exotic species pairs, we used this group to test whether interactions between primary potential competitors (Table 11) accounted for more of the negative associations than interactions between secondary potential competitors. Although not overwhelmingly strong (overall effect, $Z = 2.1$, $P < .04$), this pattern was consistent across forests (Table 12). We interpreted this as evidence that competitive interactions between species for food was one primary cause of negative posthabitat correlations.

The negative correlations of primary and secondary potential competitors did not differ statistically in magnitude ($P > .50$), and the combined average negative

correlation was low ($r = 0.06$). This indicated that the small-scale geographic displacement (or depression of population density) between native and exotic species was rather minor (the area involved would be on the order of 1% of the species' range for total displacement, and larger if low densities coexisted). This was a measure of the displacement occurring at a given instant, however, and when patterns of negative association are maintained over time, the net effect would be competitive displacement of the less successful species from a region or habitat as displacements accumulated over time. Without periodic resampling, temporal displacement cannot be quantified.

We have relied on the sign of the partial correlations, rather than their magnitude, to estimate the presence of competitive displacement. The small magnitudes observed may merely indicate that our sampling period was small relative to the period over which competitive displacements accumulate. If, for example, we assume that the correlations represent the effect of competition over a 4-mo period, then an average negative correlation of 0.06 extrapolates to complete displacement over 93 yr (0.333 yr/$[0.06]^2$). Our methods thus indicated the presence, but not the magnitude or time scale, of competitive displacement.

DISCUSSION

The dominance of positive species associations

Over 50% of all species-pairs examined had significantly positive posthabitat associations. At a general level, at least three biological factors seem responsible for this result. First, species tend to be attracted to areas where resources are superabundant. In common with other tropical areas, the breeding seasons of Hawaiian birds are prolonged, with nesting recorded in some species over 9–10 mo of the year and concentrated breeding efforts over 3–5 mo (Baker 1938, Berger 1981). Hence there will be a less heavy demand on food re-

TABLE 12. Distribution across study areas of negative and positive posthabitat correlations of primary and secondary potential competitors in native/exotic species-pairs.

Study area	Primary potential competitors		Secondary potential competitors	
	−	+	−	+
Hamakua	3	6	1	5
Puna	4	2	2	4
Kau	4	2	2	2
Kohala	2	4	1	2
Kona	3	2	2	5
East Maui	2	5	0	8
Kauai	4	4	2	4
Overall*	22	25	10	30

* Primary potential competitors have overall a significantly greater proportion of negative correlations ($P < .05$).

sources at any instant than with a synchronized pulse of breeding, as in the migratory passerines of cool north temperate forests. In addition, Hawaiian birds may time their breeding cycles to coincide with seasonal resource superabundance, as Fogden (1972) suggested for forest birds in Sarawak.

Another factor is that resources of Hawaiian forests, particularly nectar and fruit, have patchy distributions in space and time, despite the superficial appearance of "eternal spring" in tropical montane rain forests. The Hawaiian Thrush, Apapane, Crested Honeycreeper, and Iiwi seem to have adapted to this phenomenon by travelling extensively to areas with superabundant flowers or fruit (Perkins 1903). In montane areas when ohia is not in bloom, a small grove (<1 ha) in heavy bloom will attract large numbers of Iiwi and Apapane. This shared attraction to resource "oases" leads to positive association which the regression analysis cannot fully remove, because the high densities depend not on the absolute flowering intensity of the resource oasis, but on the flowering intensity relative to the surrounding resource "desert." The positive association between Apapane and Iiwi is still curious, however, because several studies (Perkins 1903, Baldwin 1953, Pimm and Pimm 1982) found that the Iiwi aggressively displaces the Apapane from the crowns of the heaviest flowering trees. On Maui, the Crested Honeycreeper chases both Iiwi and Apapane from its feeding trees (Perkins 1903; J. H. Carothers, *personal communication*). Yet in East Maui and other study areas, posthabitat correlations between these species were all positive. The key to this enigma may lie in the postdisplacement behavior of the Apapane and Iiwi in a resource oasis/desert situation. After being driven from the defended ohia crown, many Apapane and Iiwi fly to a nearby tree or to the subcanopy of the same tree, and return shortly after the dominant bird relaxes its vigilance (Perkins 1903, Pimm and Pimm 1982; J. H. Carothers and S. Mountainspring, *personal observation*). Hence this mechanism blunts the effect of interference competition and permits large numbers of these species to co-occur in a limited area despite intense aggression, due to efficient feeding on the profuse nectar compared to the low rewards of foraging in nonflowering areas. Carpenter and MacMillen (1976) predicted that the feeding territoriality of the Iiwi would break down when flowers were extremely abundant, as when the whole landscape is in bloom.

A third factor is mixed-species flocks, particularly of insectivorous birds. During the post-breeding season, flocks of Amakihi, Maui Creeper, juvenile Apapane, and occasionally Japanese White-eye, are frequent; mixed flocks are most common on Maui (S. Mountainspring, *personal observation*). The former existence in the Hawaiian Islands of hawks and owls adapted to catching small birds (Olson and James 1982b) may be partly responsible for this flocking be-

havior, which will tend to increase the number of positively associated species-pairs.

A possible fourth factor is that the positive posthabitat correlations represent a common response to some unquantified habitat variable (e.g., insect levels).

Interspecific competition tends to be most acute when population densities are high enough relative to the resource base so that resources are in short supply. Since populations and resources fluctuate extensively, and many birds have a range of alternate resources ("survival food"), under normal conditions competition would probably have an effect at infrequent intervals, in some but not all forests, and for few species-pairs at any one time. Wiens (1977) and Schoener (1982) have argued this position by postulating ecological "bottlenecks" with attendant competition during infrequent lean periods (perhaps related to abnormal weather), and that outside these periods resources are adequate. In the climatically variable semideserts and grasslands of North America, Rotenberry and Wiens (1980) found no evidence of biological coupling between species, and concluded that the individual bird species responded independently to environmental gradients. From this point of view, we are not surprised that only 10 out of 170 species-pair posthabitat correlations were significantly negative, and that the distribution of negative correlations for a given species-pair was often sporadic across study areas. In the two species-pairs where competition could reasonably be argued to occur in several study areas (Elepaio/Japanese White-eye, Japanese White-eye/Iiwi), the focal species overlapped extensively in resource use.

Competitive interactions between native and exotic species

When we group species-pairs by the native or exotic origin of their component species, the resulting compilation offers an intriguing insight into more general and subtle processes; in effect, our analysis increases in its sensitivity to detect competition, at the expense of no longer focusing on individual species-pairs. Here the results (Table 10) dramatically show virtually no competitive interaction among native or among exotic species; instead, there is a broad and diffuse "front" of competition occurring between the native and exotic avifaunas. The role of competition is further indicated by the greater proportion of negative posthabitat correlations among primary potential competitors than among secondary potential competitors. We would characterize the relationships between native and exotic species as a combination of direct and diffuse (MacArthur 1972, Pianka 1974) competition, affecting about one-half (47% in Table 12) of the primary potential competitors among native/exotic species in a forest.

Consider first the exotic/exotic species pairs. Although the Hawaiian Islands have had more intro-

duced bird species established (45 definite, 25 probable) than any other area on earth (Long 1981), comparatively few of these species have yet penetrated the native montane forests. "Population waves" of the Japanese White-eye, Red-billed Leiothrix, and Melodious Laughing-thrush have only recently arrived in some areas and not yet arrived in others (Scott et al., *in press*). The four exotic species in our analysis tend to differ in general foraging behavior and resource use, and are not obvious competitors, except perhaps for the two babblers that differ in finer details of resource use, the larger Melodious Laughing-thrush (55 g) feeding more on insects, the smaller Red-billed Leiothrix (22 g) more on fruit. Thus the prevalence of positive posthabitat correlations and absence of negative ones among exotic/exotic pairs comes as no surprise. Moulton and Pimm (1983) suggest that competitive interactions do occur among exotic birds below 600 m elevation; exotic birds found in native forests at higher elevations may have already passed the exotic/exotic competitive challenge.

The native bird species have evolved in close ecological proximity with one another over millions of years (Bock 1970, Sibley and Ahlquist 1982). Resource partitioning mechanisms between species have achieved subtle and intricate structure (Perkins 1903, Pimm and Pimm 1982). Presumably these mechanisms permit species feeding on similar resources to co-occur with a minimum of competition, although it is highly likely that competition in the past motivated this interspecific differentiation during resource shortages (Bock 1970) and especially during climatically induced fluctuations in Pleistocene vegetation boundaries (Selling 1948). Thus in our "instantaneous" view, we find almost no evidence of ongoing competition among native species. But when highly successful lowland populations of exotic species continually send waves of propagules into the native forests to establish new populations, then the co-evolved native species may be stressed by competitive strategies and resource shortages they have not previously encountered. Since most exotic species have entered montane native forests in the last 10–50 yr (Berger 1981), the exotic and native avifaunas have probably not yet reached equilibrium. The significantly greater proportion of negative posthabitat correlations among native/exotic species-pairs than among native/native or exotic/exotic ones is consistent over the seven study areas, and tends to support this explanation.

Exotic species have a potent advantage over many native species in being resistant to avian diseases (van Riper et al. 1982). Moreover, exotic birds can act as carriers, reservoirs, and even vectors (for pox) of these diseases; this may partly account for the negative correlations among native/exotic secondary potential competitors (Table 12). The potential role for exotic birds as strong competitors in Hawaiian ecosystems is also suggested from the extinctions of exotic species

that may have been caused by competition with other exotic birds (Moulton and Pimm 1983).

The few native/native competitive interactions (partial correlations) that we found differ from the conclusions that Pimm and Pimm (1982) reached in their study of Amakihi, Iiwi, and Apapane where competition was strongly inferred. Perhaps because our results differ the Pimms studied a resource space, not a real space. They studied resource differentiation among the three species on two 0.5-ha plots, and made no attempt to quantify the effect of competition on population densities. Despite the occurrence of interspecific aggression among native species, this behavioral mechanism does not appear to yield negative associations on the geographic scale of our study.

Although co-adjustment of native and exotic populations and habitat responses may achieve equilibrium in ecological time and lead to a reduction in the number of negative posthabitat correlations, it is also possible that this equilibrium may not occur. First, new species are constantly being introduced, and ranges of some existing established lowland species will eventually expand to include montane native forests. Second, some exotic populations in the montane native habitats lie at the periphery of their range, are marginally successful, but are continually reinforced by dispersal from highly successful lowland populations. Further, most native birds are precluded from breeding at low elevations by avian diseases (Warner 1968, van Riper et al. 1982). Thus, it is possible that a dynamic tension between native birds and "satellite" colonies of exotic birds could be maintained through fluctuations in climate and the resource base that would affect the success of the satellite population, yielding negative posthabitat correlations and depressing native bird densities indefinitely on an irregular basis.

The exotic/native interactions of Hawaiian forest birds resemble the taxon cycle postulated by Ricklefs and Cox (1972) for West Indian birds. Ricklefs and Cox suggested that some species that recently (in evolutionary time) colonized from mainland areas had superior competitive ability compared to endemic species. These recent arrivals would thus eventually have a wide distribution in lowland habitat over many islands, displacing the affected endemic species to isolated montane habitats. In the Hawaiian Islands the exotics are also aided in their advance by habitat destruction and by the mosquito as a vector for avian diseases (Laird and van Riper 1981). Our analysis suggests Hawaiian birds are an example of the taxon cycle in operation, because of the broad, diffuse, and stochastic manner in which exotic birds compete with native ones. Lack (1976) proposed that potential colonizers of oceanic islands were often unsuccessful because they were excluded through competition with existing residents. The remarkable success of introduced birds in the Hawaiian Islands may thus in part derive from the extinction and decimation of the orig-

inal lowland avifauna due to Polynesian and Western disturbance (Olson and James 1982a, b).

The Japanese White-eye is the most abundant, widespread, and omnivorous forest passerine, and its negative posthabitat correlations with the Elepaio, Amakihi, Kauai Creeper, and Iiwi indicate that the Japanese White-eye is the "point-man" for the native/exotic encounter. If we restrict our scope to primary competitors, native/exotic pairs involving the Japanese White-eye have a significantly greater proportion (62%) of negative correlations (8+, 13−) than all other native/exotic pairs (17+, 8−; $Z = 2.03$, $P = .04$). To see whether it is reasonable to conclude that the Japanese White-eye is partly responsible for the decline of the endangered Hawaii Creeper (Oreomystis mana), as Dunmire (1961) suggested, we calculated the posthabitat correlation between the two species for the Hamakua study area, where >70% of the Hawaii Creeper population occurs (Scott et al., in press). Despite the rarity of the Hawaii Creeper (mean density = 23 ± 2 SE birds/km²), the posthabitat correlation was significantly negative ($r = -0.064$, $P < .003$), thus supporting the hypothesis. The Japanese White-eye is the most abundant bird in five study areas, and the second and third most abundant bird in the other two areas (Table 2). Such high densities coupled with facultative omnivory argue that the effect of this species on native birds is much greater than the effect of native species on it, further indicating the potent role that the Japanese White-eye plays in depressing native bird populations. Competition with exotic species must be included among the many factors causing the decline and extinction of native Hawaiian birds in this century.

Another relevant phenomenon is that sometimes exotic species undergo an explosive expansion of range and numbers early after introduction, only to decline in later years, perhaps as biological controls come into play. This is well documented for the Red-billed Leiothrix on Oahu by annual Christmas bird counts (e.g., Anonymous 1974). This species exhibited a drastic decline from ≈100 birds per annual count before 1968 to 0–1 birds after 1969. Perkins (1903) also described a population explosion of the Common Myna (Acridotheres tristis) into heavily forested areas, possibly adversely affecting the survival of some now-extinct species. Since then the Myna has declined and is not found in dense forests. If competition occurs between native and exotic species, it seems reasonable to expect it to be most severe during these population explosions. Competition during these explosions may reduce native populations to the point where they cannot recover their former abundance because of loss in genetic variability from inbreeding and small populations. As most exotic birds prefer disturbed areas and forest edges (Scott et al., in press), native birds may be buffered from violent fluctuations in exotic populations by refugia of undisturbed native forests. This has practical application in the management of endangered in-

sectivorous species such as the Hawaii Creeper, the Nukupuu (Hemignathus lucidus), and the Poo-uli (Melamprosops phaeosoma), by implementing a policy of preserving unbroken blocks of forest and reducing forest edges where feasible. Diamond and Veitch (1981) also noted the propensity of exotic birds to associate with disturbed vegetation in New Zealand.

The scale of competition

The effects of interspecific competition are manifested at many levels of resolution. On a spatial scale, interspecific competition creates patterns at the niche, community, landscape, and regional levels; on a temporal scale, competitive effects may be observed that are from seconds to millenia in duration. These levels of resolution are hierarchical, or nested within one another. A niche represents species behavior within a community; the community is the assemblage of niches and resources at a site; the landscape is a collection of communities; the region is comprised of landscapes. In Table 13 we present a general classification for a number of phenomena that may be affected or induced by competition and that are observed at different scales. This classification is meant to be illustrative, not exhaustive. Entries observable at one scale of resolution may be due to competitive operation at another scale (e.g., differential foraging behavior is observed on the scale of minutes to days, but may reflect long-term evolutionary adaptation prompted by competition), and all processes tend to integrate in both space and time toward the upper right corner. Our present study fits into this classification at about the landscape/months level of resolution, although it relies on auxiliary information (e.g., interspecific aggression, foraging behavior, regional dynamics of exotic birds) to broaden the perspective and suggest long-term trends. Because our study focused on only a small portion of the total spectrum of phenomena that interspecific competition can yield, it should not be surprising that positive correlations dominated the results and that negative correlations were small; the total effect of competition between native and exotic species covers a far wider scale than we studied.

Inferring interspecific competition from landscape patterns

Competition appears to be irregular in its operation due to variation in resource and population levels, and thus may be difficult to document with small data sets. Consider, for example, the results for the two smallest data sets, Kauai ($N = 140$) and Kohala ($N = 210$). Even with sample sizes that would be considered large in many studies, we found only 6 out of 36 posthabitat correlations to be significant in Kauai and only 3 out of 15 in Kohala, compared with 77 out of 119 for the other five study areas. Performing the analyses on just these two areas would be inconclusive, but Tables 10 and 12 show that the patterns within these areas fell

TABLE 13. Some phenomena of passerine birds that are affected or induced by interspecific competition at varying spatial and temporal scales of extent.

Spatial scale	Temporal scale				
	Seconds	Days	Months	Generations	Millennia
Region			seasonal migration	range dynamics	"equilibrial" island biogeography
Landscape			landscape distribution	competitive displacement from habitat	genetic adaptation to habitat
Community		flocking behavior	resource depletion	competitive exclusion from community	genetic adaptation to exploiting resources
Niche	interspecific aggression (contest competiton)	differential foraging behavior (scramble competition)	seasonal foraging strategies	response to recurrent resource bottlenecks	morphological character displacement

within the grand overall trend. This suggests that extensive studies in a series of "replicates" may be necessary to document subtle phenomena like competition that by their very nature occur sporadically and infrequently. The lack of a sufficiently large data set may underlie the failure of Rotenberry and Wiens (1980) to demonstrate competitive interaction or biotic coupling in an exceptionally variable environment, based on 26 10-ha plots.

Although our results tend to corroborate Terborgh and Weske's (1975) conclusion that diffuse competition limits some species, three important differences between our study and theirs should be noted. First, we used population densities as the index of a species' ecological success, whereas Terborgh and Weske used the distributional limits along an elevational gradient. These two indices may be correlated, but the distributional limits are susceptible to juvenile dispersal and random movement, and ignore the difference between low and high levels of abundance.

The second important difference is that Terborgh and Weske distinguished only four major physiognomic zones (elevational replacements) to aocunt for habitat response. Although elevation and gross physiognomy are major gradients of habitat structure, our detailed analysis of habitat response (Scott et al., in press) showed that Hawaiian forest birds had substantial response to particular elements, such as dominant tree species, various understory components, flower and fruit phenology, etc., in an individualistic manner for each species. The importance of "fine habitat structure," the detailed physiognomy, floristic composition, and phenological status of a site, is probably closely related to resource struture and microclimate, and has been suggested as a determinant of species response equal in importance to gross physiognomy or elevation (Balda 1969, Snow and Snow 1971, Lovejoy 1974, Tomoff 1974, Sabo 1980, Wiens and Rotenberry 1981, Karr and Freemark 1983). By removing the effect of habitat variables, 70% of the negative prehabitat cor-

relations in our study became positive or nonsignificant; pending a more detailed analysis of habitat preferences, we view with caution the interpretation of Terborgh and Weske that direct and diffuse competition account for over two-thirds of the distributional limits of Andean birds, because obviously their four physiognomic types each encompass a broad range of habitat variation.

The third critical difference is that the Andean avifauna is continental, and consists of an assemblage of both unrelated and closely related species far richer than the Hawaiian avifauna. The Andean avifauna should therefore have greater opportunities for competitive interaction, encouraged perhaps by dramatic Pleistocene shifts in vegetation zones, to account partly for the high frequency of competition reported (Haffer 1974). The large number of rare species in the Andes may make competition more difficult to demonstrate, however. Competition among native/native species-pairs in the Hawaiian Islands was probably also reduced by dramatic extinctions in the lowland native avifauna due to Polynesian activities that extirpated 70% of the endemic species (Olson and James 1982a, b).

A series of comparisons similar to the preceding could be made between our study and one by Diamond (1973) on New Guinea, where elevation was taken as the sole habitat gradient. Although the degree of competition is overestimated by not considering finer levels of habitat structure, competition would be expected to be more frequent in New Guinea than in the Hawaiian Islands because of the much larger species pool. This expectation was also suggested by Crowell (1962) in his comparison of Bermuda and North American bird communities.

In conclusion, then, our impression is that competition occurs sporadically, with only 37 of 170 posthabitat correlations being negative in this study. Detailed examination of patterns between species groups shows, however, that nearly half of the species-pairs of native/

exotic primary potential competitors in any given forest modify their distribution across the landscape in apparent response to interspecific competition. Although the relatively low magnitude of the negative partial correlations (most were not significant) suggests that this effect is mild and involves only slightly lower populations in areas of range and habitat overlap, this pattern represents an "instantaneous" view of the displacement at a particular time. As these displacements integrate through time, therefore, the successful species may eventually displace the losers from an area. Since the negative relations were found to be concentrated among native/exotic species-pairs, a phenomenon of recent appearance, areas at faunal equilibrium may less frequently have competition observable through the sort of analysis we used. Periodic resurveys would give insight into how the effects of negative relations accumulate through time.

ACKNOWLEDGMENTS

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