POPULATION DYNAMICS OF LAND BIRD POPULATIONS ON OAHU, HAWAII: FIFTY YEARS OF INTRODUCTIONS AND COMPETITION

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ABSTRACT. Data from the annual Christmas Bird Count between 1939 and 1989, around Honolulu, on the island of Oahu during late December, were analyzed to discover the annual rates of change and possible competitive interactions of introduced and native land bird species. Both total number of species and total number of individuals increased over the period. The proportion of species that were rare dropped, rose, and dropped again during the 50-year period, probably as a result of new introductions. Two species held steady, while 12 increased (about 9 linearly and 3 logarithmically). The higher rates of increase were 10-25% per year. Six species declined, but no well-established species became extinct. Negative correlations between populaton sizes indicated possible competition between the Japanese White-eye *Zosterops japonicus* and the native Apapane *Himatione sanguinea* and Elepaio *Chasiempis sandwichensis*, and between the Red-billed Leiothrix *Leiothrix lutea* and White-rumped Shama *Copsychus malabaricus*.
Keywords: Introduced birds, Hawaii, bird populations, extinction, population dynamics.

INTRODUCTION

The Oahu Christmas Bird Count, part of a nation-wide effort of standard censusing conducted in early winter, provided a unique opportunity for a study of populations of introduced birds; the Hawaiian avifauna has been liberally enriched by human introductions of birds (Berger 1981, Long 1981). During late December from 1939 to 1989, missing only 1941-1943, observers counted birds in 15-mile (24-km) radius circles in the city, suburbs, and forested mountains around Honolulu.

In her excellent compendium of Christmas Count data from North America, Root (1988) describes the usefulness of the data, when proper correction for observer effort is applied. Butcher et al. (1990) also examined the data and found it very useful for trends over large geographical areas. The Oahu Christmas Count data have been analyzed previously by Ralph (1980) and Williams (1987), but not in the detail presented here. To my knowledge no analysis has been conducted, however, of any other count over so many years.

The 50 years of data analyzed here contribute to a topic for which, as Hutchinson (1978:29) states "A very few cases are known where species have been introduced into, or have invaded, isolated areas and have been studied effectively." Among these few cases were Ring-necked Pheasants *Phasianus colchicus* in British Columbia (Einarsen 1942, 1945), and Collared Turtle-Dove *Streptopelia decaocto* in Britain and Ireland (Hudson 1965, 1972).

METHODS

These data were taken from the annual count in a 15 mile (24 km) circle. Birds are recorded primarily during daylight hours on a predetermined day. Observers are divided into "parties" which spend time in various habitats recording all individuals of all species seen or heard. The number of birds seen by all observers in all areas combined was divided by the total number of hours spent counting by the separate parties (party-hours), as recommended by Bock & Root (1981), and followed by all investigators since.

Between 1964 and 1971 observers made a conscious effort to count Common Myna *Acridotheres tristis* and Zebra Dove *Geopelia striata* in evening roosts. Through the courtesy of R.L. Pyle in obtaining original field forms, and from accounts published in *Elepaio*, the journal of the Hawaii Audubon Society, I have been able to determine which observers counted at roosts and to estimate the number seen at each roost. I have subtracted these birds from the total for those years to make years comparable.

During 1949-1953 the data included counts from the Poamoho Trail, a remote area of largely native forest in the Waianae Mountains, actually outside of today's count circle of 24 km. This area was excluded after 1953 as other native forests were covered. Since this was the only area of native forest covered during this earlier period, I felt it best to include these data, as did Williams (1987).

The land bird species used in this analysis were those which I felt have actually established breeding populations. I included in most analyses only those species with more than 250 individuals counted, all years combined. Several rare but persistent species, such as the Lavender Waxbill *Estrilda caerulescens*, which was more common in the 1960s and 1970s, were not included in many analyses. The waxbill has persisted in low numbers, or has been continuously reintroduced, since then. The Rock Dove *Columba livia* was excluded from analyses because in early years it was not counted by observers. The first two years of the Yellow-fronted Canary *Serinus mozambicus* were also not included in analyses, as they were probably a flock of introduced birds. I have omitted cordon-bleus *Uraeginthus* spp. and waxbills *Estrilda* spp. except the Lavender Waxbill since many observers have found them difficult to identify as to species.

Analytical methods

RATE OF POPULATION CHANGE. The measure of population change (Table 1) was the least squares regression using year as the independent variable and number of birds per party-hour as the dependent variable. Because zero has no logarithm, 1.0 was added to the birds per party-hour in all years for those species with no detections of birds in some years. A regression model was calculated using both untransformed and logarithmically transformed data. Year equalled 1 on the first year the species was detected on a census, excluding the canary, as mentioned above. The various R^2 values shown in Table 1 estimate the amount of variation in the bird population size explained by years. A relatively high R^2 value would indicate a population with relatively low between-year variation. Such a population might be less responsive to environmental variation, showing, for instance, a consistent growth during the study. A relatively low value could indicate a species fluctuating from year-to-year. In expanding or contracting populations, the slope of the line (ß) can be considered to be the rate of population increase of the species if the change is linear. The values allow the

TABLE 1 - Population changes of birds on Oahu, Hawaii, between 1939 and 1989 as calculated by: a regression analysis (the R^2 value, y-intercept, and slope (ß) of normal and the natural logarithm of the number of birds per party-hour); the years included in the model; and the type of food taken.

	Regression of population change							
	Non-transformed			Natural logarithm			Years	Foraging mode[a]
Species	R^2	y-int,	ß	R^2	y-int.	ß		
Unchanging population								
Japanese Bush-Warbler	0.009	0.252	0.005	0.058	-2.007	0.042	71-89	I
Northern Cardinal	0.005	2.322	-0.004	0.018	0.555	0.005	40-89	G
House Finch	0.482	0.382	0.069	0.454	-0.754	0.046	39-89	G
Expanding population								
Zebra Dove	0.623	-1.398	0.807	0.673	1.646	0.042	39-89	G
Spotted Dove	0.659	0.073	0.285	0.643	0.539	0.046	39-89	G
Red-vented Bulbul	0.919	-3.461	0.939	0.847	-1.931	0.262	68-89	I,F
Red-whiskered Bulbul	0.645	-0.965	0.179	0.791	-3.849	0.242	67-89	I,F
White-rumped Shama	0.629	-0.237	0.064	0.683	-2.107	0.084	54-89	I,F
Common Myna	0.424	7.121	0.531	0.473	2.000	0.032	39-89	I,F
Japanese White-eye	0.414	2.448	0.148	0.453	0.998	0.027	39-89	I,F,N
Red-crested Cardinal	0.633	-0.272	0.093	0.698	-1.342	0.064	40-89	G
Yellow-fronted Canary	0.659	-0.031	0.012	0.767	-3.870	0.109	67-89	G
House Sparrow	0.184	4.671	0.264	0.374	1.136	0.038	39-89	G
Java Sparrow	0.654	-1.880	0.432	0.831	-2.169	0.223	69-89	G
Contracting								
Elepaio	0.331	2.586	-0.059	0.447	1.167	-0.023	39-89	I
Northern Mockingbird	0.068	0,178	-0.002	0.042	-1.987	-0.014	57-89	I,F
Red-billed Leiothrix	0.302	4.493	-0.100	0.421	1.690	-0.036	40-89	F
Amakihi	0.191	2.211	-0.032	0.155	0.557	-0.018	39-89	I,N
Apapane	0.220	9.590	-0.213	0.362	1.889	-0.056	39-89	N,I
Nutmeg Mannikin	0.153	11.053	-0.143	0.097	2.143	-0.015	39-89	G

[a] Foraging mode is: G = granivore; I = insectivore; F = frugivore; and N = nectarivore (based on Berger 1981; Ralph, in press).

separation between populations expanding: at higher rates of increase with a high value of ß; and those expanding at lower rates, due either to the influence of limiting factors or lower intrinsic rates of increase.

TESTS FOR COMPETITION. To test for possible competition between species, I used the simple premise that if one species is affecting another, their populations could show corresponding negative statistical relations. I divided birds into granivores, nectarivores, frugivores, and insectivores (Table 1), under the assumption that negative correlations on a population basis would not likely occur between species with widely different foraging niches.

I used the General Linear Model Procedure of SAS (SAS Institute 1985), specifically the partial sums of squares (Type III sums of squares), whereby I performed a least squares regression of the number of birds per party-hour per year of a given species with all other species of similar foraging niche. The first analysis included using all species in a foraging group as multiple regression predictors for one of the component species. While many had significant positive associations, a few negative interactions were significant in this analysis. Such an analysis, however, includes many numerical interactions. I then regressed separately each species pair. I included only those species having negative slopes from the first analysis. That is, I included only those species in which the addition of individuals of one species was significantly correlated with the loss of individuals of another, as calculated by the Student's *t* value (and associated P value), for testing the null hypothesis that the slope equalled zero. A very small P value leads to the conclusion that the independent variable contributed significantly to the model. If all significance disappeared when the species were analyzed separately, without the influence of other species, then I considered the previous negative relationship to be spurious.

RESULTS

Population characteristics

TOTAL NUMBER OF SPECIES. The total number of species recorded by year (Figure 1) was 15-20 species in the early years. In the late 1960s a surge of newly introduced species started to appear in the counts, and the number has reached 25-30 species recently. Only three or four in any one year were native Hawaiian species; all others have been introduced by humans.

TOTAL NUMBER OF INDIVIDUALS RECORDED BY YEARS. The number of individuals of all species recorded per party-hour has gradually increased over the past 50 years (Figure 2). The number during the 1940s through the late 1960s was variable, but usually 30-100 birds per party-hour. Since then, the average has increased, with only one year below 80 birds per party-hour, reaching an average in the 1980s of about 150 birds (a regression of: $R^2 = 0.775$; $P < 0.0001$). This pattern of increasing numbers of birds was maintained even when I removed the rarest species from the analysis, removing the possibility that the increase was solely due to an influx of rare species. To do this, I deleted from the analysis all species with a total of less than 250 individuals recorded over the 50 year period. The average number of individuals still increased, indicating that not only the rare species were increasing, as they established themselves, but also the commoner species were becoming more abundant. This pattern of increase could result from an increase in observer ability, an increase in overall bird density, or both.

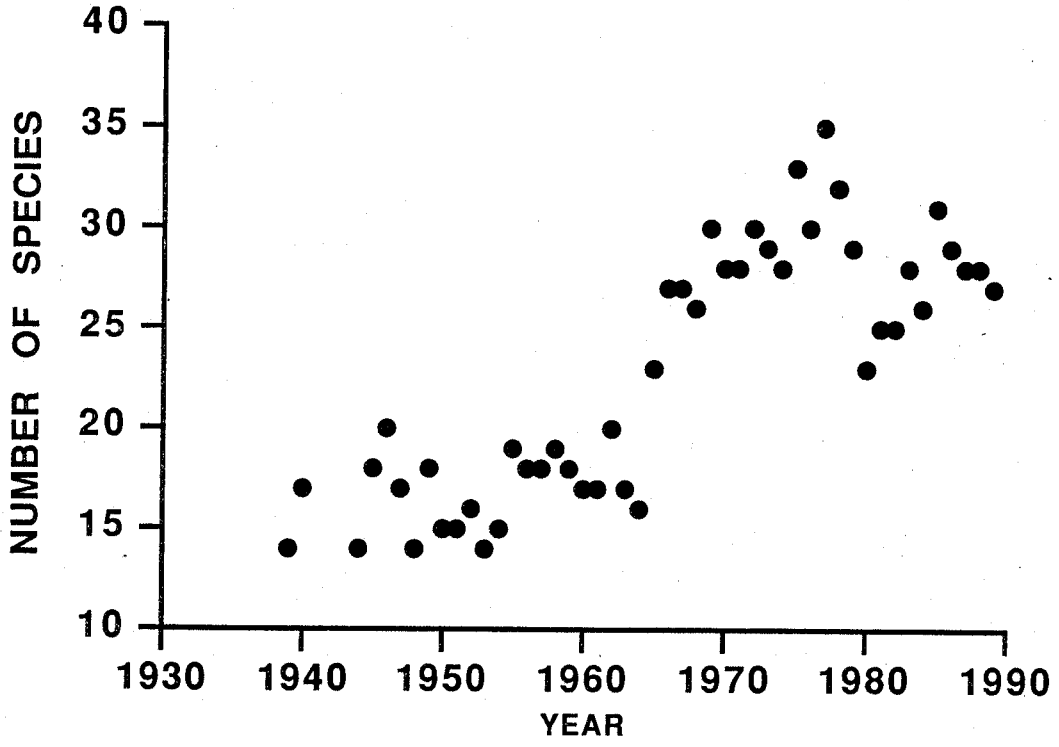

FIGURE 1 - Number of species recorded in each year on the Oahu Christmas Count.

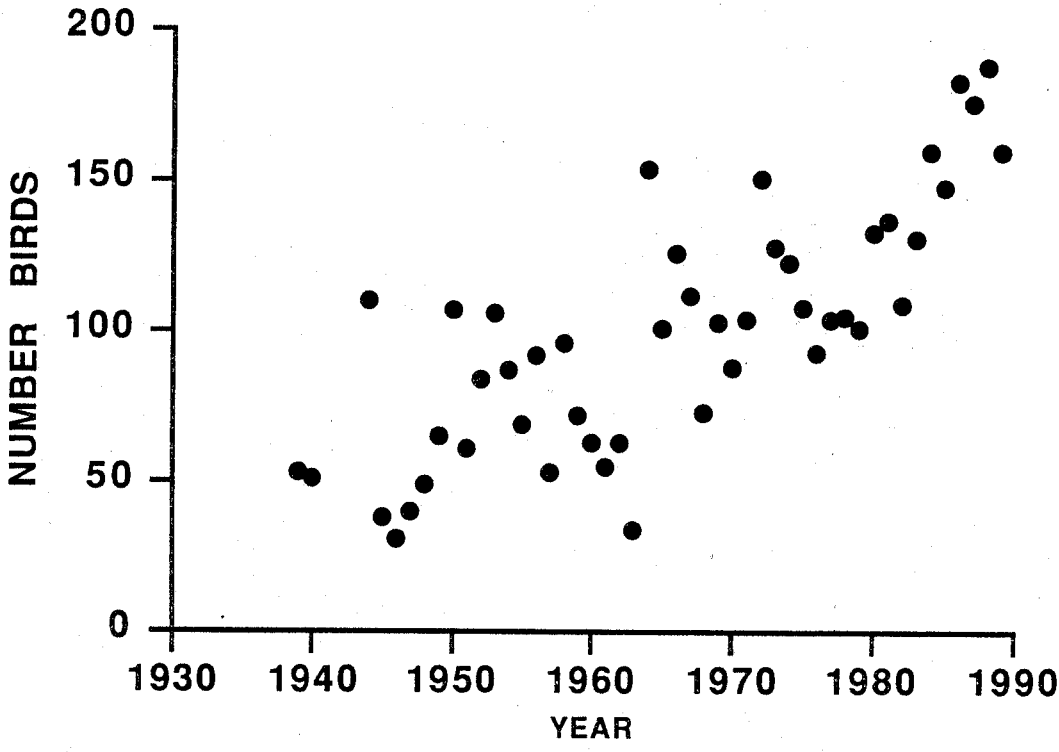

FIGURE 2 - Total number of individuals per party-hour of all species combined seen each year.

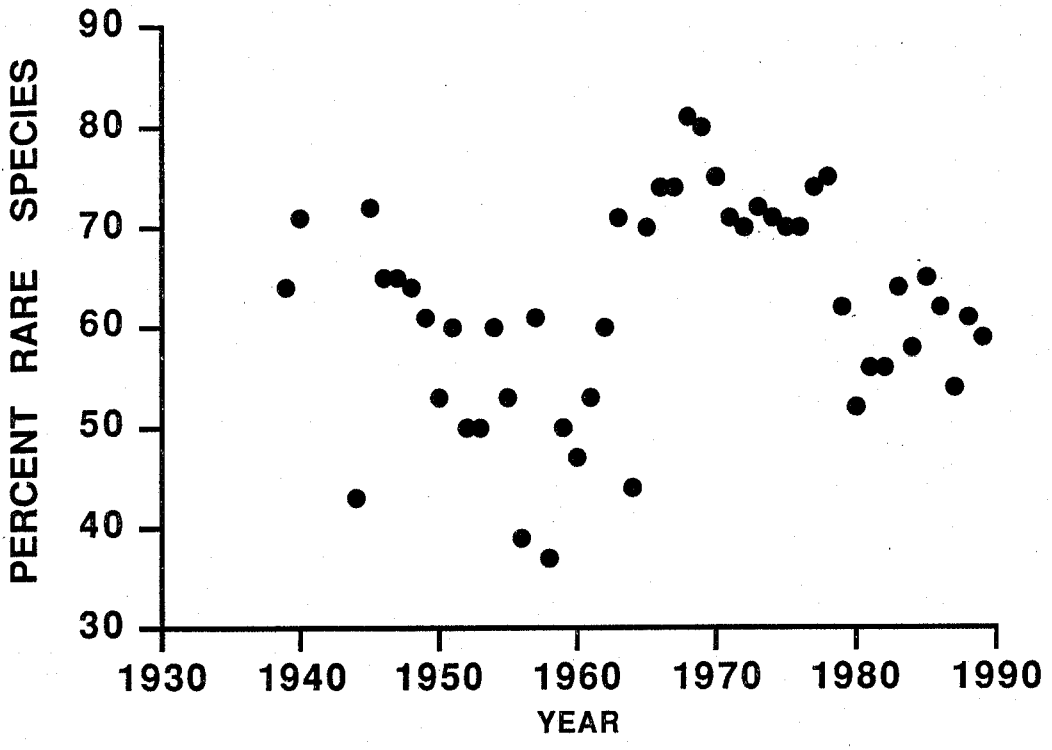

FIGURE 3 - Percent of rarer species (those with less than 2.5 individuals per party-hour) in each year.

NUMBER OF INDIVIDUALS/SPECIES. The least common species, defined here as those numbering less than 2.5 birds per party-hour in any one year (Figure 3), made up 64% of all species recorded from 1939 through the 1940s. During the 1950s this average dropped to 51%, as more species became more common. During the 1960s observers recorded a sharp increase in the number of newly introduced species, perforce in small numbers. The result was a marked increase in the percentage of rare birds, to 68% overall, and to about 80% in the last two years of the decade. Through the 1980s the proportion of rare birds again declined, as perhaps the community matured, to an average of 71% in the '70s and 59% in the '80s. Looking at it from another perspective, the average number of individuals per species per party-hour was significantly higher in the 1980s (mean = 5.6) and the 1950s (4.8), than in other decades (60s: 3.9; 70s: 3.6; and 40s: 3.1) by a Waller-Duncan multiple range test (T = 2.08, df = 1086).

Population changes

UNCHANGING POPULATIONS. Two species, the Japanese Bush-Warbler *Cettia diphone* and Northern Cardinal *Cardinalis cardinalis*, had constant populations (Table 1; Figure 4). The only change in the cardinal was a diminishing of the variance later in the period. The bush-warbler was unusual, in that it first appeared in counts in 1971 and remained fairly constant. Most species, once established, had a marked and constant increase in population. This cryptic species, usually detected only by voice, may have been overlooked in earlier counts.

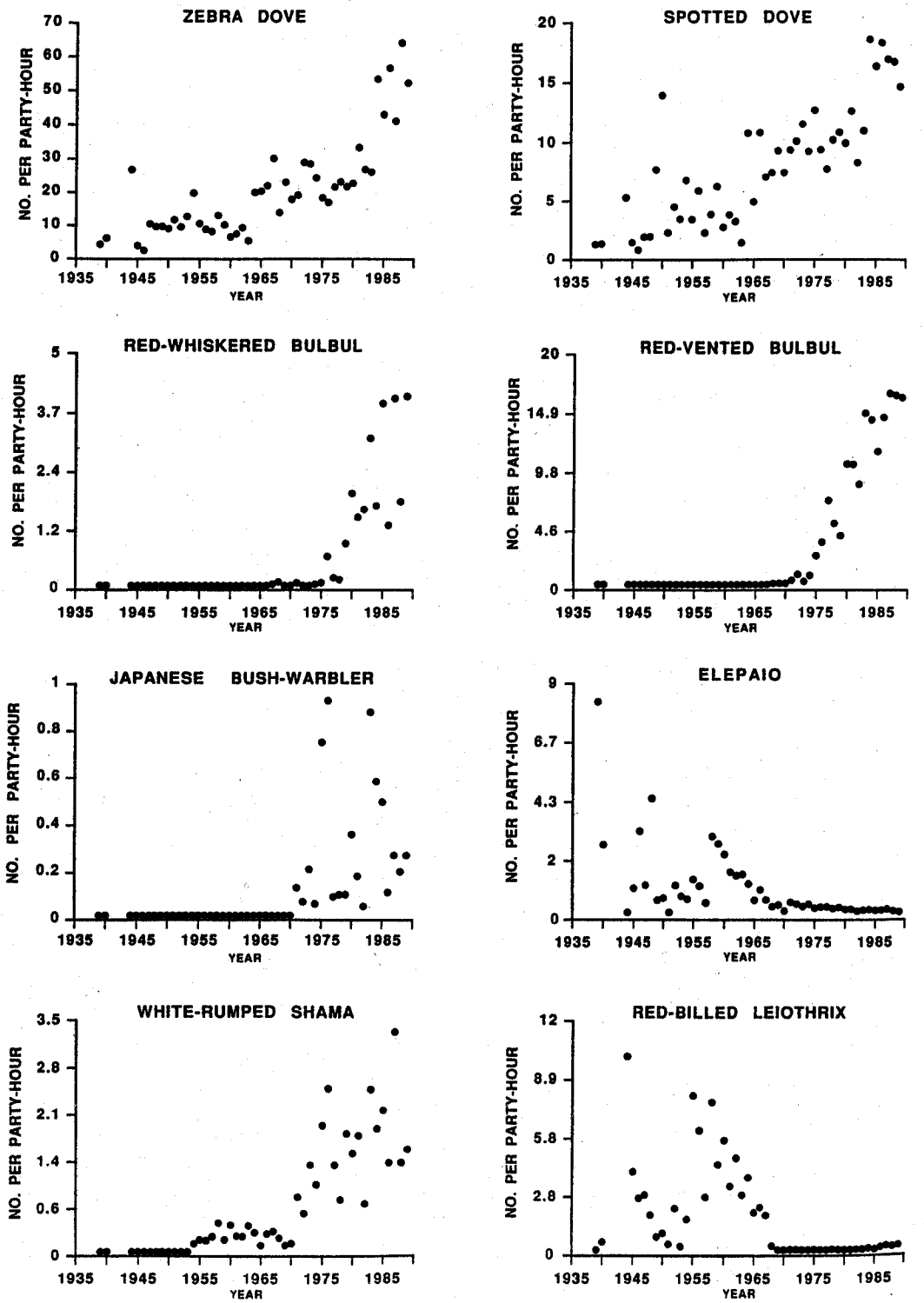

FIGURE 4 - Number of birds per party-hour detected of various species in the Honolulu Christmas Count between 1939 and 1989.

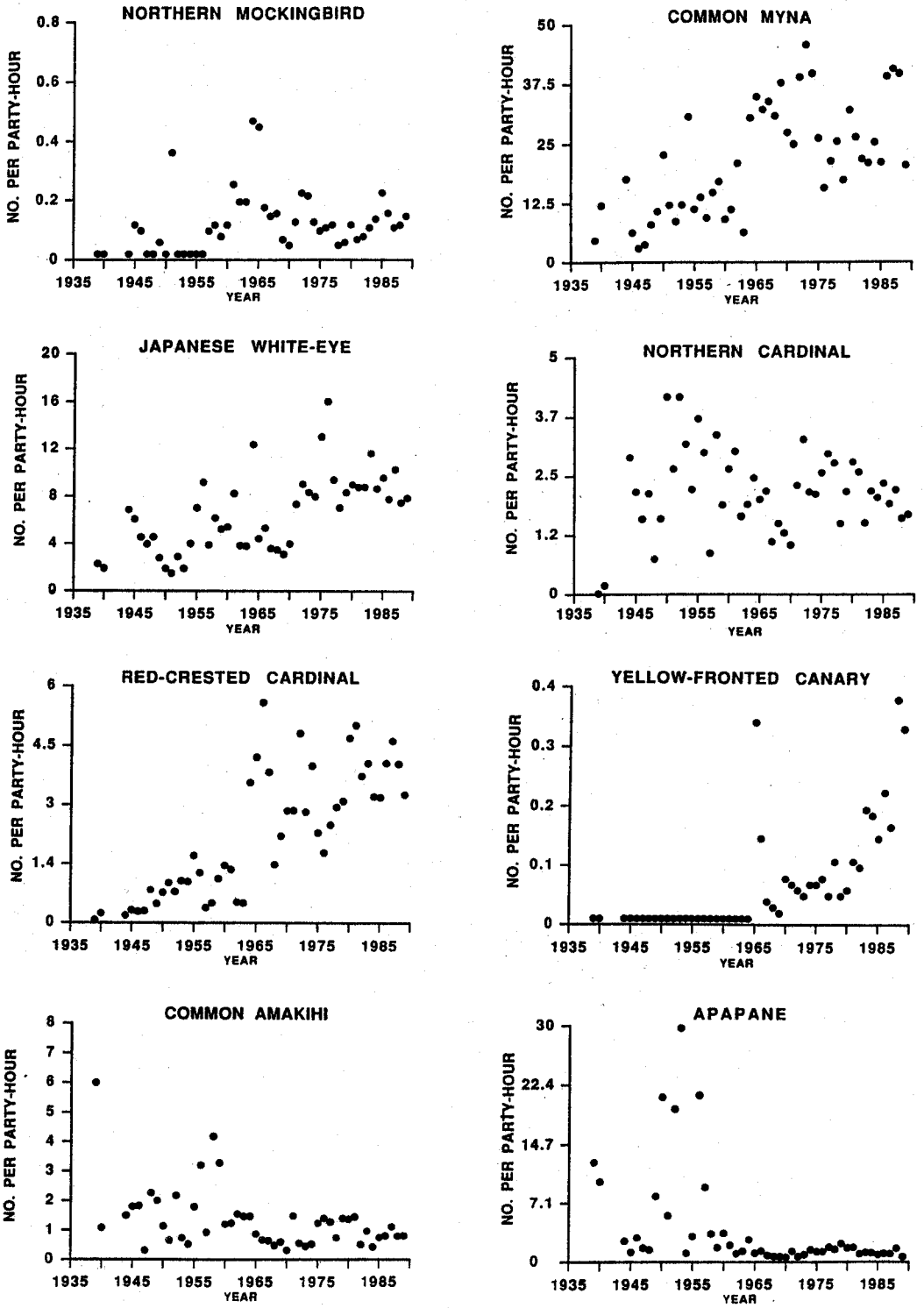

FIGURE 4 - Number of birds per party-hour detected of various species in the Honolulu Christmas Count between 1939 and 1989 (continued).

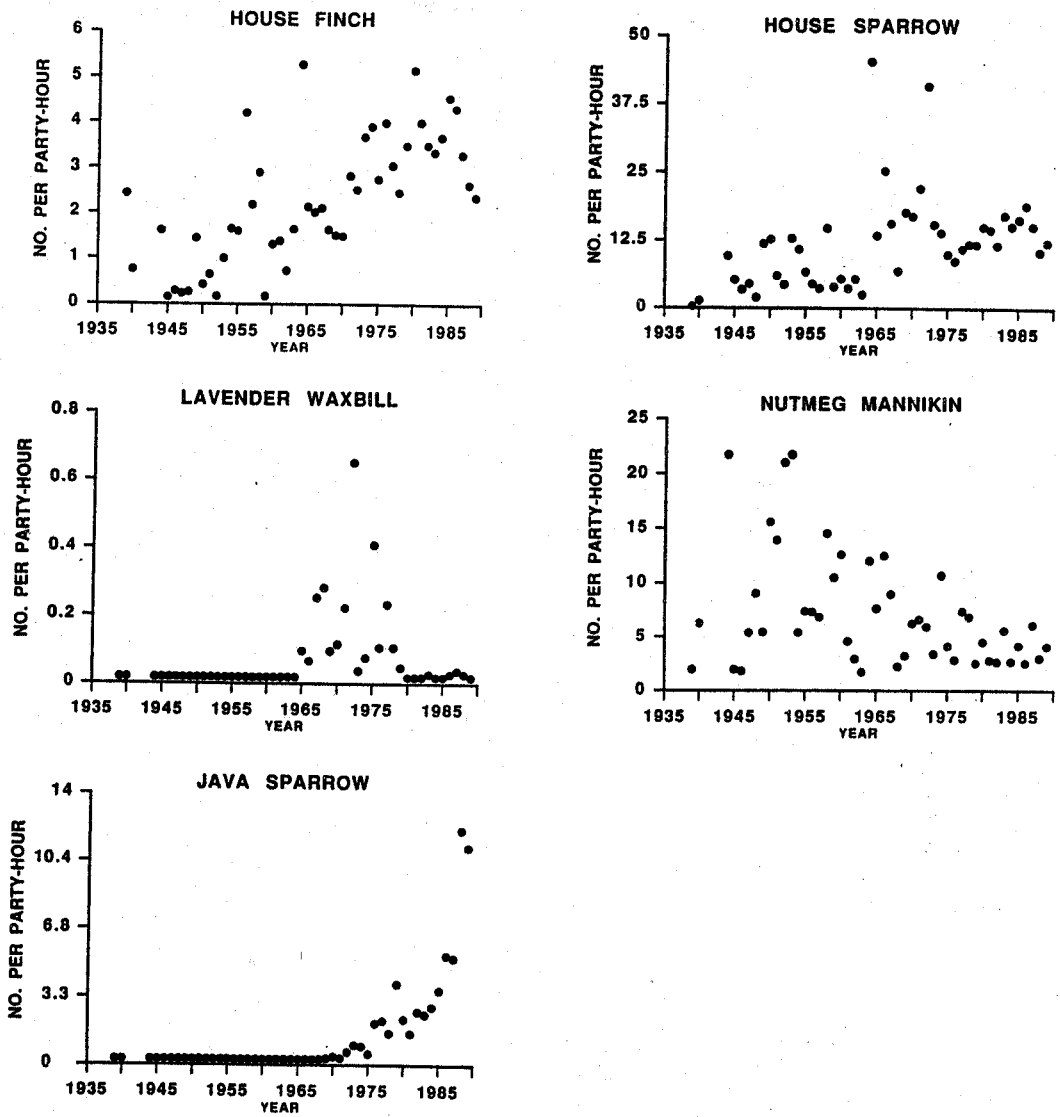

FIGURE 4 - Number of birds per party-hour detected of various species in the Honolulu Christmas Count between 1939 and 1989 (continued).

EXPANDING POPULATIONS. Several species showed rapid population increases, usually shortly after introduction. In many species with expanding populations, a large amount of their variation (R^2) could be explained by the passage of time. Of these expanding species, only the House Sparrow *Passer domesticus*, Japanese White-eye *Zosterops japonicus*, and Common Myna (Table 1), all long-time, abundant inhabitants of Oahu, had a R^2 lower than 60%.

The species with the highest values of R^2, and the most rapid growth (ß), the ones possibly under the least environmental resistance, from density dependent factors, were all introduced in the 1960s (the Red-whiskered *Pycnonotus jocosus*, and Red-vented *P. cafer*, bulbuls; Yellow-fronted Canary; and Java Sparrow *Padda oryzivora*).

TABLE 2 - Results of a multiple regression analysis between species having negative interactions, showing: (1) the slope of the negative interaction (Estimated Value), and the significance of it, and (2) the results of an overall model, with the amount of variation explained (R^2), and the significance of the model.

Dependent vs. Independent Species	Estim. value	T	P	Overall Model		
				F-value	P	R^2
Japanese White-eye				6.43	0.0035	0.222
v Apapane	-0.168	-2.49	0.016			
v Elepaio	-0.606	-2.03	0.048			
Apapane				8.19	0.0063	0.151
v Japanese White-eye	-0.770	-2.86	0.006			
Elepaio				5.98	0.0183	0.115
v Japanese White-eye	-0.152	-2.45	0.018			
Red billed Leiothrix				10.98	0.0018	0.193
v White-rumped Shama	-1.299	-3.31	0.002			

Except for the Red-vented Bulbul, these species also had the higher R^2 values with the logarithmic transformation of their numbers, possibly indicating populations still in their expansion phases, and not having encountered significant environmental resistance. Red-vented Bulbul may have reached a point of environmental resistance, with the population increase in recent years being slowed, and is best described by a logistic equation. In future years, other species could begin to show this phenomenon, apparently undocumented in the vertebrate literature.

Eight species showed steadily, but not rapidly, increasing populations with a growth rate (ß) of 2-8% in the logarithmic models, thus possibly interacting agaiinst a variety of limiting factors. These species were all equally well described (R^2) by a simple linear model with either transformed or untransformed population data; in the range of 35-70% of the variation was explained. They included the Zebra and Spotted *Streptopelia chinensis* doves, White-rumped Shama *Copsychus malabaricus*, Common Myna, Japanese White-eye, Red-crested Cardinal *Paroaria coronata*, House Finch *Carpodacus mexicanus* and House Sparrow.

CONTRACTING POPULATIONS. Of the six species which declined during the period but did not become extinct, three were native: the Elepaio *Chasiempis sandwichensis*, Apapane *Himatione sanguinea*, and Common Amakihi *Hemignathus virens*. Of the natives, the Apapane had the most precipitous decline (ß), about 5% per year by the logarithmic transformation. In the Elepaio, Red-billed Leiothrix *Leiothrix lutea*, and Apapane, the amount of variation explained (R^2) was 35-45%, at the lower end of those increasing species mentioned above that were possibly interacting against density dependent limiting factors. All three have declined to very low levels in recent years. The other three species Japanese Bush-Warbler, Common Amakihi, and Nutmeg Mannikin *Lonchura punctulata* had very little of their variation explained by the year variable, and their populations are probably responding to other, non-annual factors. The Northern Mockingbird's *Mimus polyglottos* population has declined only slightly.

EXTINCTIONS. To date, only two species have apparently become extirpated from the count area after establishing small populations: the Saffron Finch *Sicalis flaveola* and Pin-tailed Whydah *Vidua macroura* were last recorded about 1980. The Lavender Waxbill has declined to very low numbers after a few years of modest populations. It is unlikely that any of these species ever reached sufficient numbers to influence other species.

Interspecific interactions

The vast majority of interactions were positive and significant, as most introduced species increased their populations more or less in concert. Of the nine species in the granivore group, none interacted negatively with another. Interspecific competition seems unlikely. Three species in the insectivore group, however, had significant negative interactions (Table 2). These interactions included the very abundant and pervasive Japanese White-eye, and two native species, the Elepaio and Apapane. These models explained a relatively small (12-22%), but statistically significant, amount of the variation among those species. Both the Apapane and white-eye also feed on nectar.

In the group I considered to be frugivores, most members also taking considerable amounts of insects, the interaction between the two introduced species, the Red-billed Leiothrix and the White-rumped Shama, was significantly negative. The shama was present in moderate numbers from 1954 to 1970, then expanded rapidly. It was during the 1950s and early 1960s that the leiothrix population declined.

DISCUSSION

I used the data from the Oahu counts as a tool for the documentation of the arrival, spread, and changes in population which may indicate interspecific interactions at the population level of introduced birds, despite being taken by many observers, or perhaps in part because of it. The data apparently give the first approximation of population sizes from an entire community of species introduced into an isolated area that Hutchinson (1978) sought. As such, they give some insight into the natural potential for growth of some species. Of course, the real potential will depend upon many parameters not studied here such as clutch size, longevity, and fertility, but the range of values presented by this study was instructive.

The rates of increase of introduced birds differed. Some were high, possibly indicating species introduced into environments with relatively few constraints to population increase. Others increased at a slower rate, possibly as a result of interactions with various components of the environment, perhaps including competitors. The consistency of the increase, as measured by the R^2 value, indicated that newly introduced birds had a more consistent rate of increase than well-established species.

At the same time, the count documented the decline of some native birds and species from earlier introductions. There is circumstantial evidence that competition was involved with some of these changes, as the populations of some species with similar foraging niches were negatively correlated. In addition, the rate of decline of some species was similar to the rate of increase of some expanding species, perhaps suggesting a connection between the species or to common environmental factors.

The increasing number of individuals detected per party-hour during the study could indicate a gradual maturation or succession of the avian community. This maturation could be influenced by the introduction of more species, perhaps buffering the community against change. In addition, maturation might involve those species previously introduced having time to work out competition and niche exploitation patterns to fully utilize the relatively newly-colonized environment. While it is possible that observer efficiency increased as well, there is only the case of the Japanese Bush-warbler to support this.

Community maturation is also possibly the cause of the change in the distribution of the number of individuals per party-hour of the rarer species. It appeared that the community went through two cycles of this aspect of maturation during the study.

Robert Pyle (pers. comm.) has raised the possibility that increasing effort over the years in non-forested areas may have artificially deflated abundances of native birds and inflated abundances of birds of residential and park areas. However, Williams (1987) found no significant decline in percent of party hours in mountain forests

between 1967 and 1985. Further analysis may show that is involved to some extent, although I suspect it would be minor.

The interspecific interactions on a population scale were mostly positive associations; species pairs and groups responding in common to generally favorable or unfavorable environmental conditions. However, the Japanese White-eye, which has long been postulated as having a negative impact upon native birds, showed a slight, but significant, statistical effect upon two native species, the Elepaio and the Apapane. The white-eye was introduced in 1929 to Oahu (Caum 1933), and today is found abundantly everywhere from the dry, arid coasts to the wettest interior forests. Scott et al. (1986) also found slight, but significant negative interactions in habitat preference between the white-eye and two species, the Elepaio and the Liwi *Vestiaria coccinea* (the Liwi is very uncommon on Oahu). In another analysis (Mountainspring & Scott 1985), they found more negative interactions between native/introduced species pairs (37% of interactions), than between either native/native (8%), or introduced/introduced (0%) pairs. From these two separate lines of evidence, then, the case for the white-eye's involvement in competitive interactions seems likely.

The other negative interaction I found was between two introduced species. One, the Red-billed Leiothrix, had inexplicably declined during the study. The other, the White-rumped Shama, was introduced in 1940 (Harpham 1953), became common enough to be recorded on the count in 1954, and had a significant negative interaction with the leiothrix in my study. Lending credence to the possibility of these two species being in competition is the situation on Kauai Island. There, the shama has also been introduced, and the leiothrix, formerly abundant, is now virtually absent (Scott et al. 1986). On Hawaii Island, by contrast, the leiothrix is still abundant, and the shama has not been introduced (S. Conant, pers. comm.).

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