To the Graduate Council:

I am submitting herewith a dissertation written by Michael Platt Moulton entitled "Interspecific Competition And Community Structure In The Introduced Hawaiian Avifauna." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Zoology.

Stuart L. Pimm, Major Professor

We have read this dissertation and recommend its acceptance:

John C. Ehrlenmacht

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Gary F. McCracken

Accepted for the Council:

The Graduate School

INTERSPECIFIC COMPETITION AND COMMUNITY STRUCTURE IN THE INTRODUCED HAWAIIAN AVIFAUNA

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Michael Platt Moulton

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ABSTRACT

The role of interspecific competition in structuring the introduced Hawaiian avifauna is evaluated using four separate analyses.

In the first analysis I calculated the extinction rate (extinctions per year) for columbiform and passeriform species for the period 1861 to 1960. I show that this rate is significantly nonlinear. This result is consistent with the hypothesis that interspecific competition has affected extinctions.

In the second analysis I show that the morphologies of surviving species on each of the six main Hawaiian Islands are not more different from each other than expected by chance alone. This suggests that competition either does not operate on morphology or that its effects are not extensive enough to produce non-random patterns in the morphologies of surviving species.

In the third analysis I show that congeneric pairs of of species are less likely to coexist if the species do not differ greatly in bill length. This result is consistent with the hypothesis of limiting similarity, and supports the argument that competition has played a role in affecting extinctions.

In the final section I test the hypothesis that species abundances are independent of their morphological similarity to other species in the community. This test revealed a weak, but significant, positive relationship between logarithm of abundance and mean Euclidean distance from each species to every other species.

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I. INTRODUCTION

This dissertation is presented in four sections (excluding this introduction). Each section represents an independent analysis of the role of interspecific competition in structuring an essentially experimental community. I have made no attempt here at an overall synthesis. Such a synthesis will appear elsewhere (Moulton and Pimm 1985) as a part of a symposium on community ecology.

Section II of this dissertation has been published (Moulton and Pimm 1983). Section III has been incorporated in the synthesis (Moulton and Pimm 1985), and thus is in press. Section IV will be published by the journal Oikos (Moulton 1985), and Section V is under review by that journal presently (Moulton and Ellner ms).

Although each section is meant to stand alone, they are linked in that each deals with the introduced Hawaiian avifauna. This system is described in detail in Section II. This system basically consists of exotic speices of birds living in exotic habitats. The birds could be from any of six continents as could the plant species that make-up the habitats.

Section II involves an analysis of the extinction rate for these introduced species. I show that this rate is

nonlinear and argue that this is evidence that competition has affected each species' extinction probability.

In Section III I analyze the morphologies of surviving species, and show that these are not more different than expected by chance. This argues against the idea that competition is a major structuring force in this system.

Section IV deals with the coexistence of congeneric species introduced to the Hawaiian Islands. In this analysis I show that congeners that do not differ greatly in bill length do not tend to coexist.

Finally, in Section V I show that morphologically similar species tend to be less abundant than morphologically different species. This effect is weak, but significant and suggests that competition might affect many species but not with sufficient intensity to produce non-random morphologies at the community-wide level.

II. THE INTRODUCED HAWAIIAN AVIFAUNA: BIOGEOGRAPHIC EVIDENCE FOR COMPETITION

1. INTRODUCTION

David Lack (1976) succinctly expressed the basic observations about island avifaunas thus: "Oceanic islands . . . have far fewer resident species of land birds than the mainland, and they have fewer the smaller and more remote that they are" (p.1). Crowell (1961) and MacArthur and Wilson (1967) have interpreted these patterns as the result of a dynamic equilibrium: The number of species observed is obtained when immigration and extinction rates are equal. Larger islands have larger populations of any species than smaller islands, and small populations have a higher chance of extinction. Remote islands will have smaller immigration rates than islands near the mainland. A dynamic equilibrium, however, is not the only model for the variation in island species numbers. A second theory is that of Lack (1976) who argued that remote islands might be ecologically impoverished because of reduced plant immigrations. Schoener and Schoener (1983) suggested that increased exposure to wind and water might contribute to lower species diversity on distant islands. Of course,

larger areas of land always support more species than smaller areas--the familiar species-area curve.

These two theories are not mutually incompatible. Indeed, they differ only quantitatively, in regard to amount of turnover. MacArthur and Wilson view the distinct feature of island faunas to be their constant species turnover. Lack projects a more static view without denying that a small amount of turnover must be inevitable. There is no turnover rate below which one would accept one hypothesis and above which one would accept its alternative. It is also clear that examining species numbers on a range of islands over short periods of time is not going to be decisive: A variety of hypotheses can be generated which yield the same predictions as those of MacArthur and Wilson and Lack. Consequently, it is experimental studies that have been most informative (Simberloff 1976; Simberloff and Wilson 1969, 1970; Rey 1981; Wilson and Simberloff 1969; Crowell 1973; Crowell and Pimm 1976). One might debate the generality of these studies because the islands examined are very small and very close to source areas relative to the bulk of islands about which ecologists are interested. So here I consider the results of a remarkable experiment in biogeography on a large scale: the introduction of birds onto the Hawaiian Islands. I show that despite continued introductions, species numbers on some islands have tended

to remain constant through increased extinction rates. Moreover, the faunas are in a constant flux, with extinction a common event even in populations that had persisted for decades. These results are in close accord with MacArthur and Wilson's view of island faunas. I also demonstrate the effect of interspecific competition on extinction rate and, by extension, on the equilibrium numbers of species.

More species of birds have been introduced to the Hawaiian Islands than anywhere else (Long 1981). By the time most of these species were brought to the islands, native habitats below about 600 m had been severely altered. This alteration resulted from grazing by introduced mammals (Tomich 1969), deforestation for timber, principally sandalwood (Santalum sp.; Kuykendall and Day 1948; Rock 1913), and clearing of land for cultivation.

In conjunction with this disturbance there was a loss of native species of birds (Greenway 1967; Henshaw 1902). The native land birds were (and still are) closely associated with native habitats, and in the 1800s these were being replaced by cultivated land, pastureland, and exotic forests (Kuykendall and Day 1948; Schmitt 1977). Introduced species are found commonly in these disturbed habitats, but native species do not utilize these habitats to any great extent. In fact, today it is unusual to find native land birds below 900 m elevation (Berger 1981). For example,

on three Honolulu Christmas bird counts (1950, 1954, 1956) only four native passerine species were seen. Of the 8,379 individual passeriforms and columbiforms only 706 (<9%) were natives.

In addition to the effects of habitat loss, native land birds have also suffered from predation by three species of introduced rats, cats, and the small Indian mongoose (Herpestes auropunctatus; Tomich 1969). This evidence strongly suggests that native land birds have played, at most, a minor role in determining which species of introduced birds have succeeded or failed in the elevational zone below 600 m in the Hawaiian Islands. Thus a number of different species have been introduced into a set of confined areas with artificial habitats which supported few, if any, native species that would have any competitive advantage.

Many of the avian introductions to Hawaii were made intentionally with substantial numbers of individuals. In fact there was an organization, the Hui Manu, which existed solely for the purpose of introducing exotic birds into Hawaii. These conditions provide an interesting, if somewhat unfortunate, experiment to test the role of interspecific competition in shaping biogeographic patterns.

I would like to answer two questions: (1) Is the number of introduced bird species in Hawaii at a dynamic

equilibrium and (2) has interspecific competition modified the equilibrium numbers?

Equilibrium is defined as the condition where the number of species remains constant through time. This equilibrium will be considered dynamic if there continues to be a turnover in species composition, or static if there is no turnover. Thus, a dynamic equilibrium obtains if there is continuous extinction and immigration and these rates are equal. In a static equilibrium immigration and extinction rates are both equal to zero.

In natural systems immigrations to an island are drawn from a finite species pool. The immigration rate is the number of immigrating species that are new to the island per unit time. The rate of immigration will decrease with increasing numbers of species because, ultimately, none of the species immigrating to the island would be new to the island. In Hawaii the source of immigrants is essentially infinite: Birds from six continents, including species not usually considered cage birds, have been introduced. The species pool might exceed 1,000. Moreover, the immigration rate has varied with the perceived need by people in Hawaii to add to their fauna.

Because of the remoteness of these islands, natural immigration is essentially nonexistent. In fact, Berger (1981) lists only seven species of passerines as stragglers

to the Hawaiian Islands, and these were recorded, without exception, in the distant leeward islands and not the main islands considered here. Freed from the potential confusion caused by natural immigrations, one can see what effects experimental immigrations (i.e., introductions) have had on the numbers of species and their extinction rates. For the time period I examined (1861-1960), the immigration rate did not decrease (see table 1, Moulton and Pimm 1983). Indeed, 77 of 125 introductions occured in the last four decades. Because of constant or increasing immigration rate, the extinction rate might never be equal to the immigration rate and the islands might continue to accumulate species. With constant or increasing immigration, an indication that an equilibrium exists is a constant number of species.

How should interspecific competition affect extinctions? If there is no competition then one would expect a linear relationship between extinctions and the number of species present (Fig. 1). Equivalently, the chance of each species becoming extinct is a constant. Consequently, the more species that are introduced, the more there are to become extinct. In contrast, if there is competition then one would expect a curvilinear relationship between extinctions and number of species present (Fig. 1). The probability of any species becoming extinct would

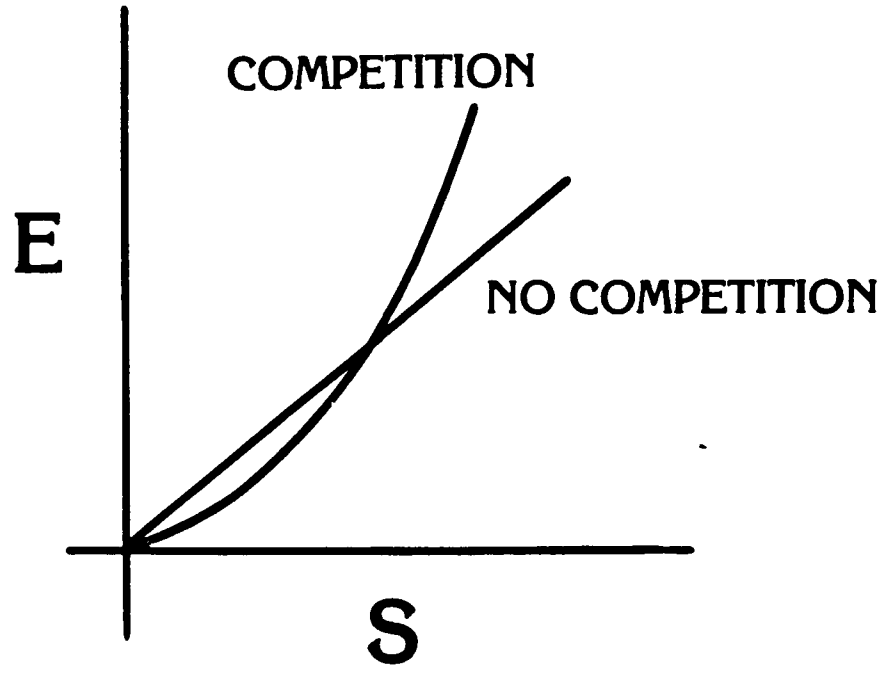


Figure 1. Extinction rate (E) as a function of the number of species (S) on an island.

increase with increasing numbers of interspecific competitors. By definition, competiton means reduced population sizes and this means an increased chance of extinction in the stochastic real world (MacArthur and Wilson 1967).

2. METHODS AND MATERIALS

I compiled lists of introduced species for each of the six largest islands of the Hawaiian archipelago: Oahu, Kauai, Maui, Hawaii, Molokai, Lanai. These lists, including dates of introductions and extinctions were taken from Henshaw (1902), Caum (1933), Munro (1944), Berger (1981), Bryan (1958), and the journal Elepaio (vol. 1, 1939 to present).

It was sometimes difficult to decide whether or not certain species should be included in this analysis. By force of circumstance my decisions were sometimes arbitrary.

My first concern was whether or not an adequate propagule (Simberloff 1969) was introduced to an island. If a species was intentionally introduced, I assumed that the propagule size was adequate.

Species that spread to different islands from their point of introduction were included only if they became established on the new islands. (These species are listed

in the Appendix of Moulton and Pimm 1983 under categories B and C). I included all species listed in the above references with the following exceptions. Species listed in Caum (1933) were not included in the analysis if: (1) only a single pair of birds was introduced (e.g., Copysychus saularis on Kauai); (2) the island of introduction was unknown (e.g., Starnoenas cyanocephala); (3) the species was not identified (e.g., "oriental thrush"). I excluded species from the analyses if I suspected that the propagule size (Simberloff 1969) at the time of introduction was inadequate. For example, in some cases a species was introduced onto one island and seen later on another. Paroaria coronata was intentionally introduced to Oahu in 1928. It was seen on Maui in 1951 (Bonsey 1951), again in 1961 (Bole 1961), and again in 1962 (Carpenter 1962). But, Berger (1981) claimed not to have seen it in several trips to Maui, and there is no evidence that this species established a viable population there. One could make an argument for including this species in my analysis of Maui, but I have elected to ignore such species. There is no evidence that an adequate propagule of this species arrived on Maui. The inclusion of such species could lead to an overestimate of extinctions.

I grouped introductions and extinctions into 10-yr periods. Often a species was introduced in more than one

year, and often I had to estimate the date of extinction. Although I could not be confident that extinctions or introductions occurred in a particular year, I usually could be certain to the nearest decade when they took place.

The date of introduction was determined in one of three ways. First, whenever possible, the exact date was taken from a reference. Second, before 1939 (first publication of Elepaio) when the exact date was not available, I averaged the earliest possible date with the first definite citation. For example, Streptopelia chinensis was listed by Henshaw (1902, p. 133) as "more or less abundant on all the islands." Caum (1933) reported that this species was common on Oahu as early as 1879. The date of introduction on the remaining islands was estimated by averaging 1879 and 1902, or 1890. Third, for first records after 1939, I used the first record in the Elepaio.

Before 1939, dates of extinctions were determined by averaging the date of introduction with the date of the first monograph after which there were no further records of the species. For example, Ocyphaps lophotes was intentionally introduced to Lanai in 1922 (Caum 1933). In 1933, Caum (1933) reported that it had not survived. The date of extinction was estimated as the midpoint between 1922 and 1933. If an author (Caum 1933 or Munro 1944) was not aware of the status of species, I used the date of the

monograph if there were no further references. For example, the Mongolian lark (Melanocorypha mongolica) was introduced to Kauai in 1914 where it became established near Lihue (Caum 1933). Munro (1944) listed this species as well established on Kauai, but there are no records of this species after 1944 and thus I have used this date as the date of extinction. On Oahu, for four species, I used 1939 (the first date of publication of the journal Elepaio) as the date of extinction. The status of these species (Grallina cyanoleuca, Sturnella neglecta, Luscinia komadori, and Passerina cyanea) was unknown to Caum (1933) or Munro (1944). Most of the reports in the journal Elepaio in the early years of its publication were for Oahu. There were no records for these species in Elepaio and it seems unlikely that these species would be overlooked. This was not the case for the other islands, from which there were far fewer reports. After 1939, the date of the last sighting listed in Elepaio was considered to be the date of extinction.

Only columbiform and passeriform species were included in my analysis. A number of psittaciform species were listed by Caum as introductions, but these were virtually all cage escapes. There is not reason to believe that adequate propagules existed for these species. Almost certainly, none of these species bred regularly and

successfully. By including these I believed that I would have overestimated extinctions.

To determine whether island size had an effect on extinctions I used the area of the islands below 600 m in elevation. As already mentioned, this zone is essentially devoid of native species of land birds and the habitats have been created largely by man. By confining my analysis to this zone I can eliminate any potential confusion that could be caused by interactions with native species. Moreover, the majority of the introduced species are confined to these lower elevations, and all of them occur there.

I assembled the data from the time period 1861-1960. I did not use data after 1960. The reason for this was that at least 22 new species were reported on Oahu in the 1960s. This more than doubled the number of species found there in 1960. Some of these species (e.g., Lonchura oryzivora, Pycnonotus cafer, Pycnonotus jocosus) have become well established. Some were reported fewer than five times and were probably just cage escapes (e.g., Paroaria gularis, Vidua chalybeata, Emblema guttata, Gubernatrix cristata). There were three introductions that might have been of males only (Gracula religiosa, Euplectes orix, Euplectes afer; Pyle 1981). Most of the remaining species were commonly kept cage birds (Bates and Busenbark 1970) and the possibility exists that there

were multiple introductions and extinctions. Moreover, many of the sightings of these species were from a single locality, Kapiolani Park in Honolulu near the Honolulu Zoo. The status of these species is thus unclear. Therefore, I have adopted the conservative approach and excluded these from my analyses. A similar situation occured on Hawaii where Orenstein (1968) reported seven new semiwild species, the status of which is also unclear.

I calculated extinction rate as the number of extinctions per year. I regressed extinction rate against the number of species, the square of the number of species, and the area of each island, below 600 m. I calculated apparent turnover (T) using the formula:

$$T = (I + E)/s_1 + s_2)t,$$

where I = introductions, E = extinctions, s_1 = the number of species present in the first interval, s_2 = the number of species present in the second interval, and t = the interval length (Diamond and May 1977). I calculated turnover rates for each decade for each island, and from these I calculated the mean for T for each island (see table 2 in Moulton and Pimm 1983). I regressed these means against area below 600 m to see if there was an area effect on turnover.

3. RESULTS

During the time period under consideration, forty-seven species were introduced a total of 125 times to the six main islands. There were 45 extinctions. (The dates of introduction and extinction are listed in the Appendix of Moulton and Pimm 1983). Thirty-five species were introduced to Oahu, 24 to Kauai, 21 to Maui, 19 to Hawaii, 13 to Molokai, and 13 to Lanai. There were 15 extinctions on Oahu, 10 on Kauai, 8 on Maui, 7 on Hawaii, 1 on Molokai, and 4 on Lanai.

There were no extinctions until the 1920s. Seven species were introduced to all the islands before 1920. In this group, there has been only one subsequent extinction, and that on only one island: Alauda arvensis on Kauai.

On four of the islands, the number of species appears to have leveled off by the 1960s. This does not appear to be the case on Molokai or Lanai (Fig. 2).

I found a significant positive relationship between extinction rate and the number of species present ($F = 44.3$, $p < .0001$). This relationship, however, was significantly improved by the addition of the square of species number ($F = 7.43$, $p < .01$, i.e., the relationship is significantly nonlinear). In contrast, the model with only S^2 is not improved by the addition of a term in only S ($F = 0.06$, $p >$

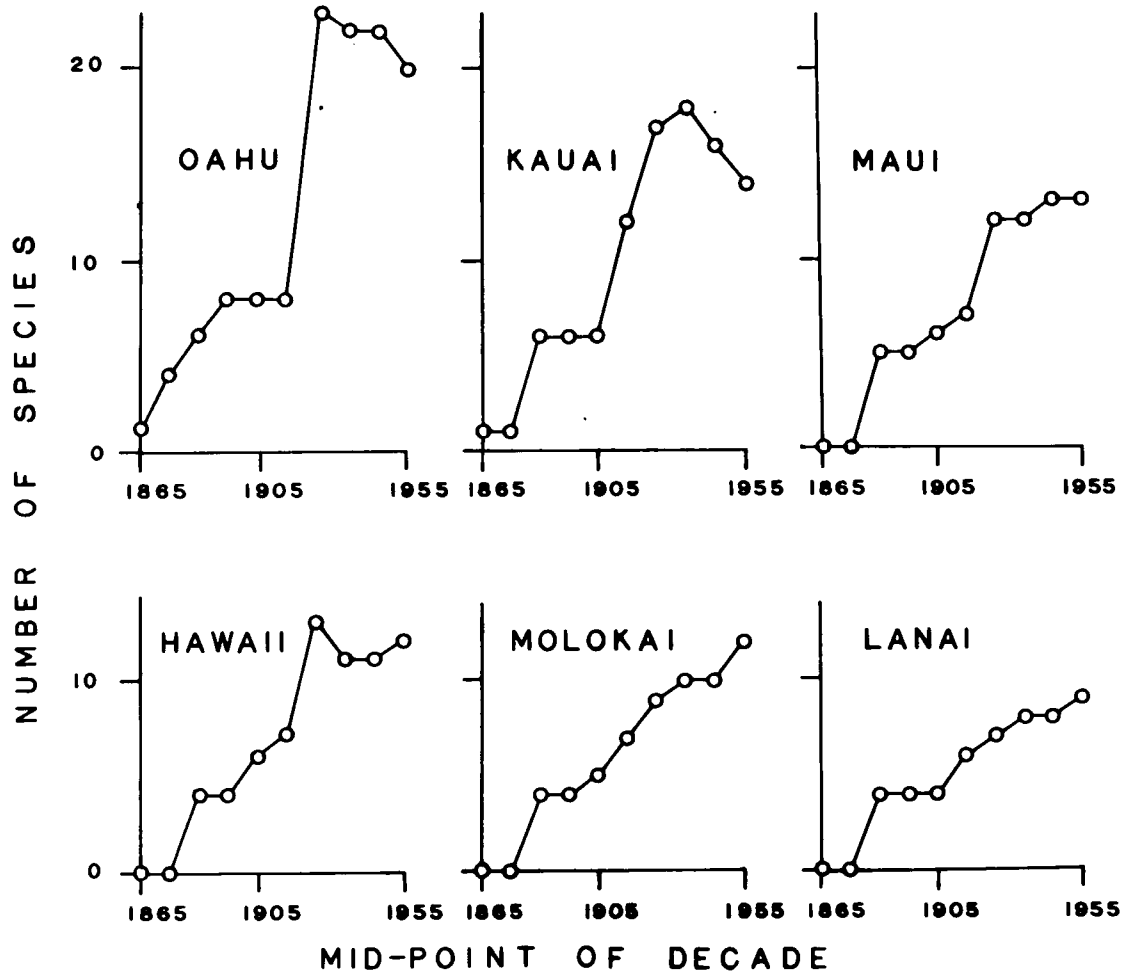


Figure 2. Number of species versus date for the six Hawaiian Islands.

.8). Thus, the best model is one with only S^2, i.e., the extinction rate increases faster than the number of species. Extinction rate was not significantly related to island size ($F = 0.03$, $p > .8$; see table 3 in Moulton and Pimm 1983) when the variable of species number was included in the model. Average turnover values (see table 2 in Moulton and Pimm 1983).) did not vary significantly with island area ($F = 1.64$, $p > .27$).

4. HAVE THE ISLAND AVIFAUNAS ACHIEVED DYNAMIC EQUILIBRIUM ?

(a) Does an Equilibrium Exist ?

If we assume that there were no species in the elevational zone that I studied on any island in 1861, then species were added to all six islands without an extinction in the first six decades. Subsequently, species numbers on four of the six islands appear to have leveled off. The exceptions are Molokai and Lanai, on which 13 species have been introduced with one and four extinctions, respectively. On the four remaining islands (Hawaii, Oahu, Maui, Kauai) species number has leveled off, but whether or not these are at equilibrium is unclear. Is the apparent constancy in species numbers because of extinction catching up with immigration (implying an equilibrium) or, more simply, is it that no more species have been introduced? Clearly, the

latter possibility says nothing about the existence of an equilibrium. To answer this question I consider each of the four islands in turn.

Hawaii (Fig. 2) has had 19 introductions and seven extinctions. All the extinctions came in one decade (1930s) and there has been only one introduction since the end of that decade. On Maui, there have been eight extinctions, six of which were columbiform species. Six species became extinct in the same decade in which they were introduced. Yet one species (Leucosarcia melanoleuca) persisted for at least 39 yr. None of the other columbiform species persisted for more than 5 yr. Finally, there has been only one introduction in the last two decades, and this species (Cardinalis cardinalis) is still present. Thus, on both Hawaii and Maui, the constant number of species might have resulted from a diminished immigration rate rather than a dynamic equilibrium.

On Kauai and Oahu, the number of species has leveled off because of continued extinctions in the later decades. Between 1941 and 1960, only one species was introduced to Kauai, and only two were introduced to Oahu, but there were five extinctions on both Kauai and Oahu in this same period. These two islands differ from the other four in that species number appears to have approached constancy through increased extinctions.

In summary, it appears that two islands (Molokai, Lanai) are definitely not at equilibrium; two islands (Kauai and Oahu) probably are at equilibrium; and on the remaining two islands the situation is unclear.

(b) Is the Equilibrium Dynamic ?

An alternative to a dynamic equilibrium (in which species composition changes, but species number does not) is a static equilibrium. One possible view of a static equilibrium is that one expects no extinctions until equilibrium is reached. After equilibrium is reached, one would expect it to be impossible for any new species to colonize the islands. In this system, turnover was common throughout the time period. However. it is difficult to compare my turnover values to those of other studies.

Terborgh and Faaborg (1973) calculated extinction rate Er (as an index of turnover) for the island of Mona using a different formula ($Er = 2e/[I + F]t$) where I and F stand for initial and final numbers of species, t stands for time, and e for the number of extinctions. They report an annual extinction rate of .23% for the period between 1901 and 1972. Using their formula and a time interval of 100 yr, the extinction rates in the Hawaiian Islands for introduced species are: 1.5% for Oahu, 1.4% for Kauai, 1.2% for Maui, 1.2% for Hawaii, .2% for Molokai, and .9% for Lanai. Only

one Hawaiian Island (Molokai) has an extinction rate lower than Mona, yet Mona is less than one-fifth the size of the smallest island in my study (61 km^2 for Mona, 333 km^2 for Lanai). I calculated turnover values, T, as described above for each decade; they ranged from 0%-10%. The mean value for T for Oahu was 2.3%, for Kauai 1.9%, for Maui 2.4%, for Hawaii 2.4%, for Molokai 1.9%, and for Lanai 2.2%).

For the Channel Islands of California, similarly calculated turnover values varied depending on interval width (Jones and Diamond 1976). These authors report average turnover values of 0.5% to 3.6% from all pairs of successive censuses for these islands. They examined eight islands and found higher turnover values on the four smaller islands. Between from .9%-5.6% for larger and smaller islands, respectively (Jones and Diamond 1976). In another study Diamond and Lecroy (1979) reported a turnover of 0.34% for Karkar Island. This value was calculated using a long interval (55 yr) between censuses. Elsewhere (Diamond and May 1977) the importance of interval length in estimating turnover rates has been emphasized: Long intervals lead to underestimates of turnover rates. In my data a thorough census was not conducted at each decade. Thus a species might be introduced and become extinct more

than once but I would record only one extinction. Consequently, my estimates of turnover could be low.

In answering the question of whether any equilibrium is static or dynamic, it becomes clear that there is no obvious turnover rate below which we can reject the notion that the fauna is maintained by dynamic processes. In viewing these results, however, it is hard not to conclude that faunas are in a remarkable state of flux. MacArthur and Wilson's (1967) view of a continuous turnover of species seems particularly compelling when at least 45/125 species introductions failed. These extinctions cannot be viewed as trivial consequences of introducing species to totally inappropriate habitats. There are many examples of species that were present for a reasonably long period of time (>10 yr) and subsequently became extinct (19 of 45, 42%; see Appendix in Moulton and Pimm 1983).

5. ISLAND SIZE AND EXTINCTION RATES

Other things being equal, small islands should have smaller populations of any species and thus small islands should have higher extinction rates than larger islands. However, I did not find a statistically significant higher extinction rate on smaller islands. One possible reason I did not get an area effect is that both the largest island

(Hawaii) and the smallest island (Lanai) might not be at equilibrium. Relatively few species have been introduced to these islands (19 to Hawaii, 13 to Lanai) and the remaining islands have fairly similar areas below 600m (see table 1 in Moulton and Pimm 1983).

6. DOES INTERSPECIFIC COMPETITION AFFECT THE EQUILIBRIUM NUMBER OF SPECIES ?

There are many reasons why a species should become extinct. Some species undoubtedly failed to find their appropriate habitats. For others, there may have been an insufficient propagule size. I have attempted to exclude the majority of such introductions from my analyses. For those included, many species probably found the right habitat but in such limited quantities that high population sizes were not possible. This possibility suggests a linear relationship between extinction rate and number of species; that is, the more species introduced, the more extinctions we should observe. The extinction rate, however, increased as the square of the number of species (Fig. 3). By chance alone, one would expect the extinction rate per species to be constant. Yet, the extinction rate per species increases with the number of species. This is strong evidence for interspecific competition because this relationship

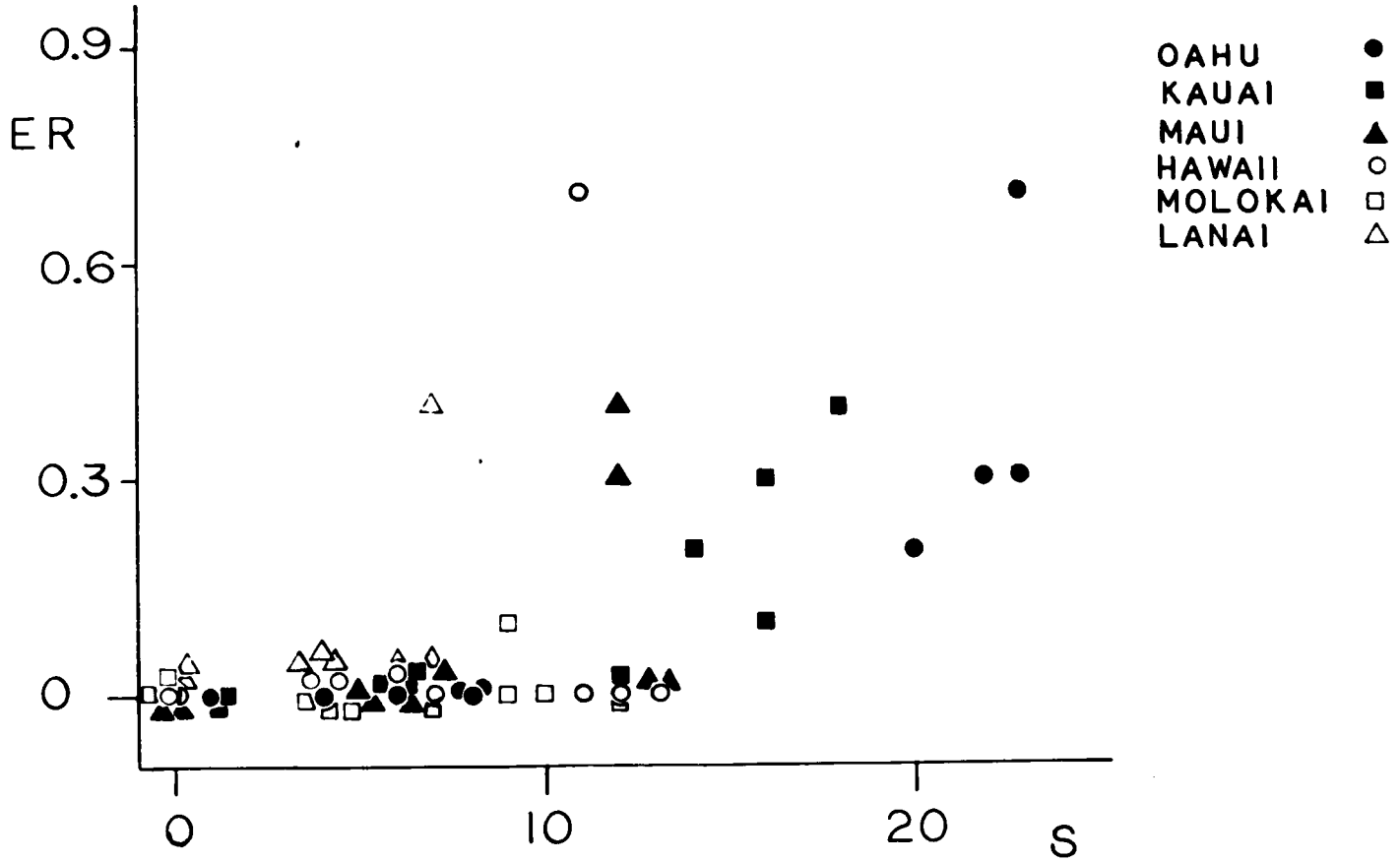


Figure 3. Extinction rate (Er) expressed as the number of extinctions per year, averaged over 10-yr periods versus the number of species on each island (S).

indicates that species modify each others' chances for extinction. This supports the prediction of Schoener's (1976) model, which incorporates the effects of species interactions in determining equilibrial species number on islands. The critical difference between his result and mine is that his was obtained indirectly. He had to assume a specific relationship between average population size (N) and the proportion of established species becoming extinct per unit time (μ_A). Since I know which species became extinct and when these extinctions occurred I am able to calculate extinction rate directly;

$$Er = .00089 \times S^2$$

where Er is the yearly extinction rate and S is the number of species on the island.

Anecdotal Evidence for Competition

Abbott and Grant (1976) noted that the simplest result of competition would be the replacement of one species by another, ecologically similar species. There are examples that suggest this is occurring in Hawaii.

On Kauai, Alauda arvensis was introduced in 1870 and well established by 1933 (Caum 1933). Sometime between 1933 and 1944 this species disappeared from Kauai, yet it is still found, often commonly, on all the other islands. What is different about Kauai, is that an ecologically similar

species, Melanocorypha mongolica, was introduced in 1914 (Caum 1933). Both of these species are members of the same family (Alaudidae); they are similar in size (Alauda 30-43.5 g, Melanocorypha 24-60 g); prefer similar habitats; and have similar diets (Long 1981). Melanocorypha also subsequently failed, with no further records after 1944. More probably, the loss of A. arvensis might have resulted from competitive pressure from the introduction of yet a third ecologically similar species, Sturnella neglecta. This species is larger than Melanocorypha and Alauda (99-112 g), but prefers open habitats and eats similar foods to those species (Long 1981). Sturnella neglecta was also introduced to Oahu in 1931. Interestingly, it became extinct on that island, yet Alauda arvensis survives there today.

Another example is that of Parus varius. This is a small (12-14 cm; 15.9-18.2 g) arboreal, insectivorous species (Long 1981). This species was introduced to Kauai in 1890 and was established there by 1933 (Caum 1933). In 1928, this species was also introduced to Oahu, Maui, and Hawaii where it persisted for about 10 yr (1928-1938). It disappeared on Kauai after 1958 and on Oahu after 1963 (outside the time period I considered). On each island where P. varius existed, an ecologically similar species Zosterops japonicus was also introduced. This is also a

small (10-12 cm, 10.0-12.5 g) arboreal, omnivorous species (Guest 1973). Zosterops japonicus is now one of the commonest species in forested habitats on all the islands (Berger 1981).

There are other examples, but like these they are anecdotal. Anecdotal evidence may be a consequence of staring too hard at the data and seeing apparent patterns that confirm the theory. Although I do find the above examples suggestive, I have no evidence that competition was responsible these particular extinctions. Rather, the strength of my argument lies in the statistical demonstration of the curved relationship between extinction rate and the number of species.

Other Possible Explanations for a Nonlinear Extinction Rate:

There are two possibilities other than interspecific competition which might explain this nonlinear extinction rate.

1. The first possibility involves habitat alteration. Species tended to accumulate through time; suggesting that there were more species in later decades than in the early ones on all islands (Fig. 2). Habitat alteration might accelerate through time with more extensive alterations and thus more extinctions when there were, coincidentally,

more species. Certainly, all the extinctions occurred in the last four decades. As discussed previously, the introduced species inhabit man-made habitats, such as cultivated land (which is mainly in sugar cane), pastureland, and exotic forest. Do the changes in these habitats correlate with the extinctions? It is evident from the data in table 4 of Moulton and Pimm (1983) that these habitats changed far more in the first five decades than in the last five. This is particularly true for exotic forest (forest reserve), and sugar cane fields. Simply, there were no extinctions when these habitats were changing the most, all extinctions occurred when the habitats were changing the least. This first possibility does not seem a plausible explanation for the nonlinear extinction rates.

2. The second possibility deals with factors intrinsic to each species. Some species have been successful nearly everywhere in the world that they have been introduced. Other species, perhaps highly specialized for restricted habitats, probably would fail no matter where they were introduced. The possibility exists that species characteristic of the former type were introduced early in the time period when there were few species, whereas species characteristic of the latter were introduced later when there were many species. If this were so, a nonlinear

extinction rate might result. There are three arguments against this possibility.

First, although many of these species had been introduced only to the Hawaiian Islands, there were 17 species which had been introduced elsewhere (see table 5 in Moulton and Pimm 1983). For these species I calculated the proportion of successful introductions using data in Long (1981). I included only those species which had been introduced in at least two places other than Hawaii. I then compared the success of species introduced to Hawaii between 1860 and 1920 to those of species introduced between 1920 and 1960. That is, I compared species introduced in the period with no extinctions to those introduced in the period with extinctions. There was no significant difference between the species introduced in these two time periods ($F = 1.37$, $p < 0.26$) in terms of how successful they had been in colonizing other areas.

Second, some species which have failed in Hawaii have been very successful elsewhere. For example, the collared dove (Streptopelia decaocto) was intentionally introduced to both Kauai and Oahu. It bred in small numbers on both islands but subsequently became extinct (Caum 1933). Yet, in the last century this species has spectacularly colonized all of mainland Europe, Scandinavia, the British Isles, and has been successfully introduced to Japan,

northern China, Korea, New Zealand, and the United States (Long 1981). Two other examples are Rhipidura leucophrys and Grallina cyanoleuca. Both were intentionally introduced to Oahu and both failed. Yet these species are found continent-wide in Australia, in a wide variety of habitats including cultivated areas and urban areas (Long 1981).

Third, and perhaps most persuasive, is that several species which are very common in Hawaii today were introduced after 1920. Zosterops japonicus is an obvious example. Furthermore, four species (Pycnonotus jocusus, Pycnonotus cafer, Lonchura oryzivora, and Lonchura malabarica) were introduced after 1960, and the first three species are common on Oahu, the fourth species on Hawaii, Maui, and Lanai.

These three arguments lend little support to the idea that species introduced early were intrinsically more likely to survive than those introduced later. I conclude that the nonlinear extinction rate is consistent with the idea interspecific competition has affected extinctions in the Hawaiian Islands and that two alternative explanations seem improbable.

III. MORPHOLOGICAL ANALYSIS OF COMMUNITY STRUCTURE

1. INTRODUCTION

When we say that competition affects community structure, we mean that competition should be reflected in the distributions of the species' use of their environment. With competition, these distributions should be non-random, because species too similar will be unlikely to coexist. A correlation between ecological and morphological similarity has been long recognized. Thus, if the species present in a community mutually affect each other's ecological strategies, then they should mutually affect what morphologies are possible, too. In this chapter I ask: are species in a given community more different morphologically than expected by chance alone?

Competition might affect morhological patterns through either of two mechanisms. First, the probability of a species' persistence might be decreased by the presence of morphologically similar species. Second, the species might undergo evolutionary shifts in some morphological characteristic in order to minimize competition. I am concerned with only the first mechanism because, in Hawaii, there have been many extinctions of introduced birds in too short a period to expect much evolutionary change. The

first mechanism is probably more important in cases where local extinctions are frequent.

Several studies have attempted to answer the question I pose above, (e.g. Karr and James 1975, Ricklefs and Travis 1980, Abbott et al. 1977, Grant 1969), but the results are contentious (Strong et al. 1979, Henrickson 1981, Grant and Abbott 1980). The contention stems almost entirely from the difficulty of defining an acceptable null hypothesis (i.e. "what is expected by chance alone"). By definition, a null hypothesis is simple enough that, given observed results, some statement can be made about its likelihood. The null model for community assembly is that species are selected independently from some larger set of species and that interspecific competition is either absent, or too weak, to subsequently modify the community. This larger set of species is called the species pool, and the "community" might be the assemblage of species in a fixed area, or habitat, or on an island.

The species pool contains more species (sometimes many more) than the community under scrutiny, and so there are many possible species combinations; each consisting of the same number of species as in the community under study. Each combination generates a value for a statistic that measures the morphological dispersion of the randomly drawn species; the values for all such combinations produce a

distribution of this statistic from which the probability of the observed value can be found. It is clear that what is expected by chance alone is due in no small part to the nature of the species pool. With this in mind, there are two basic problems in defining the species pool, which in turn complicate the construction of an acceptable null hypothesis.

The first problem involves the composition of the species pool. How does one decide which species should be included? One might, for example, ask if the morphologies of bird species in a deciduous Tennessee woodland were non-randomly distributed. (The assemblage of bird species in this particular Tennessee woodland is the community of interest.) But which species should comprise the species pool? The species pool might include all the species found in the same county as the woodland. One could argue that any species of bird found in the county is capable of reaching the woodland in question, and thus is a potential member of this community. But using this argument one could just as easily choose all the species in the state of Tennessee. Birds, after all, generally have above-average powers of dispersal. Alternatively one could argue that only "woodland birds" should make-up the species pool. It is possible that the species under study are adapted to live only in this particular habitat. With this in mind one

might choose all the species found in deciduous woodlands in the same county, or in all of Tennessee, or in all of North America, as the species pool.

A second problem, beyond that of the composition of the species pool lies in the mechanics of the testing procedure. Recall that a null distribution is established by drawing random combinations of species form the species pool. But although each species might be chosen in the testing procedure to participate in the community independently of all others, this does not mean in reality that all species should have an equal chance of being chosen. Other things being equal, better dispersers or more abundant species might enter a community more often than sedentary or rare species.

Virtually every study that I found in the literature suffers from either, if not both, of these two problems. And the gravity of these problems cannot be over-stated. Such analyses will always be contentious because whatever the outcome of the statistical test, the alternative outcome can often be obtained by simply altering the composition of the species pool and/or the probabilities of each species being chosen.

The introduced Hawaiian avifauna provides a unique data base for testing the hypothesis of non-random assembly of communities. The species pool for each island is known.

Thus the true composition of the species pools cannot be debated. Moreover, the species were physically brought to these islands. Thus the problems involved with probability of dispersal do not exist. With these two problems solved, for the most part, I can test the role of morphological similarity in effecting extinctions with a minimum of additional assumptions.

2. MATERIALS AND METHODS

This section is divided into three parts. In the first part, I discuss the morphological measurements. In the second part I explain how I defined new morphological variables from the original ones and why I think this is essential, and also how I calculated distances between species. The third part includes a description of how I used Minimal Spanning Trees (MSTs) and Monte Carlo computer simulations to test my hypothesis.

Measurements

I measured six morphological features of museum specimens from each of 15 columbiform and 32 passeriform species. The specimens I measured are housed at the United States Museum of Natural History, Washington, D.C. and The Museum at Texas Tech University. The measurements were:

tail, wing, tarsus, and length, width, and depth of bill. Tails were measured from the base of the tail to the tip of the longest rectrix; wings from the wrist to the tip of the longest primary. Bill length was measured from the base of the skull to the tip of the upper mandible. Bill width and depth were measured at the posterior margin of the nares. I obtained the means of these variables usually from 10 (and not less than three) individuals per species, usually from five males and five females. Why should these and only these six variables be chosen? Selecting the variables necessary and sufficient to give a morphological distance that best correlates with ecological similarity, may be impossible. Ultimately, any choice of variables is arbitrary. The measurements I chose are those usually taken on birds and this reflects my judgement (as well as other's) that these variables have an ecological basis. I discuss this later. In all subsequent analyses I treated columbiform and passeriform species separately. Ricklefs and Travis (1980) made the same judgement. These authors argued that non-passerines occupied different regions of morphological space from those of the passerines. Other authors have not separated these groups (Case et al. 1983). My decision to conduct this analysis at the ordinal level was arbitrary, and I elaborate on this point in the discussion.

Principal Components and Morphological Distances

It is possible to calculate distance between each pair of species using the original six variables. But such distances might not truly reflect ecological similarity. There are two reasons for this as follows. First, the scales of each of the six original variables are not comparable ecologically. For example, a difference of 5 mm in bill depth represents a much greater difference in ecology than a similar difference in tail length. For example, the largely insectivorous species in the analyses have tails varying over several centimeters, whereas most species with bills 10 mm deep or more are mainly granivorous, and those with bill depths less than 5 mm and mainly insectivorous. Thus, I standardized each of the six variables to have the same means (0) and standard deviations (1). (Logarithmic transformation of data, used by some authors, has a similar effect of equalizing variance because, in morphological data, standard deviations often increase linearly with the mean.)

Second, the variables are likely correlated and thus redundant. It is unlikely that the differences between a pair of species exist in each of the six original morphological variables. A simple change in size, for example, might cause changes in each of the six variables.

The true dimensionality of the data is likely to be less than six. To reduce the dimensionality I performed a principal components analysis on the standardized data, and obtained scores on each of two morphological dimensions. These scores are linear combinations of the original variables. For a discussion of how this is done see Schultz and Moulton (1984). It is on these new morphological dimensions that I estimate the morphological difference between species, and thus on which my results and conclusions depend.

The first two principal components accounted for at least 85% of the variance. The third principal component accounted for much less than an average amount of the total variance (the corresponding eigenvalue was $<<1$) so I did not consider it to calculate morphological distances (see Wiens and Rotenberry 1980). This implies that the dimensionality of the data is, indeed, much less than the six dimensions implied by the original six variables. These two new variables are orthogonal and can be represented by two dimensional plots (Fig. 4,5).

Although these analyses are statistically complex, the distances between species in these two dimensions, rank closely with my subjective judgements of their ecological relationships. Moreover, the dimensions are ecologically interpretable. Thus, in the passeriform analysis, the first

Figure 4. Positions of columbiform species in two-dimensional morphological space. The horizontal axis is Factor1 whereas the vertical axis is Factor2. Open circles represent extinct species and solid squares represent surviving species. Key to numbers: 1 Caloenas nicobarica, 2 Chalcophaps indica, 3 Gallicolumba luzonica, 4 Geopelia striata, 5 Geopelia cuneata, 6 Geopelia humeralis, 7 Geotrygon montanus, 8 Leucosarcia melanoleuca, 9 Leptotila verreauxi, 10 Ocyphaps lophotes, 11 Petrophassa smithii, 12 Petrophassa plumifera, 13 Phaps chalcoptera, 14 Streptopelia chinensis, 15 Streptopelia decaocto.

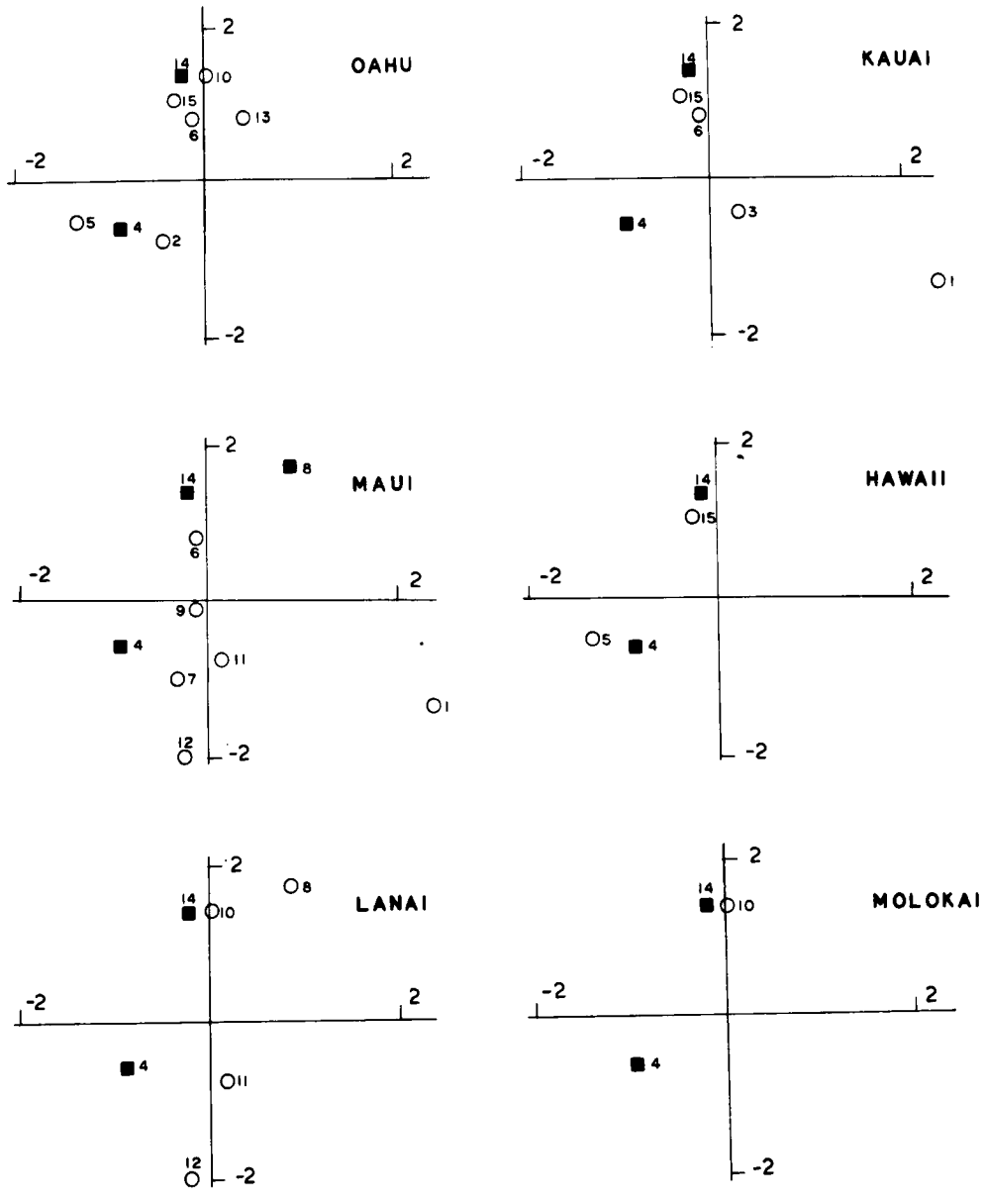
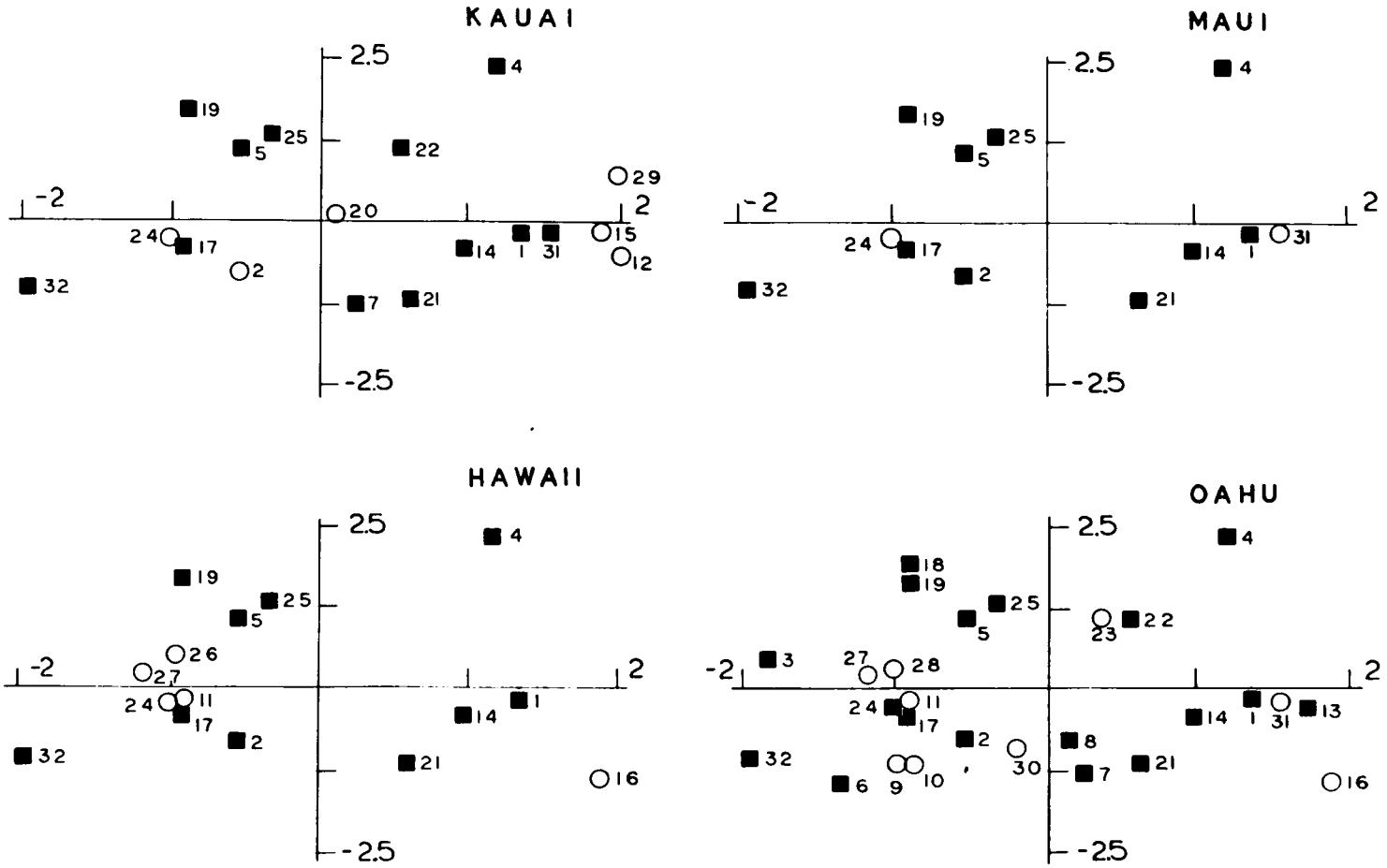


Figure 4.

Figure 5. Positions of passeriform species in two-dimensional morphological space. Symbols have same meaning as in Fig. 4. Key to numbers: 1 Acridotheres tristis, 2 Alauda arvensis, 3 Amandava amandava, 4 Cardinalis cardinalis, 5 Cardpodacus mexicanus, 6 Cettia diphone, 7 Copsychus malabaricus, 8 Copsychus saularis, 9 Luscinia akahige, 10 Luscinia komadori, 11 Muscicapa cyanomelana, 12 Garrulax albogularis, 13 Garrulax caerulatus, 14 Garrulax canorus, 15 Garrulax chinensis, 16 Grallina cyanoleuca, 17 Leiothrix lutea, 18 Lonchura malacca, 19 Lonchura punctulata, 20 Melanocorypha mongolica, 21 Mimus polyglottos, 22 Paroaria coronata, 23 Paroaria dominicana, 24 Parus varius, 25 Passer domesticus, 26 Passerina ciris, 27 Passerina cyanea, 28 Passerina leclancherii, 29 Pezites militaris, 30 Rhipidura leucophrys, 31 Sturnella neglecta, 32 Zosterops japonicus.


KAUAI
2.5
-2
2
-2.5
4
19
25
5
22
29
20
15
24
17
14
1
31
12
2
32
7
21
MAUI
2.5
-2
2
-2.5
4
19
25
5
24
17
14
1
31
2
32
21
HAWAII
2.5
-2
2
-2.5
4
19
25
5
26
27
24
11
17
14
1
2
32
21
16
OAHU
2.5
-2
2
-2.5
4
18
19
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22
3
27
28
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11
17
14
1
31
13
2
8
32
30
7
21
6
9
10
16

Figure 5.

principal component (Factor1) was positively correlated with all the original variables and thus represents a measure of overall size. In general, larger bodied species (for example the genera Garrulax, Sturnella, and Grallina) had high scores, whereas smaller bodies species such as Amandava amandava and Zosterops japonicus had small (i.e., most negative) scores. The vertical axis (Factor2) had high correlations with the orginal variables of bill depth and width (.81 and .80 respectively) and negative correlations with bill length, tarsus, tail, and wing (-.09, -.40, -.30. -.28 respectively). Not surprisingly, species with high scores on this second dimension tended to be largely granivorous, whereas species with small scores were generally insectivores characterized by slender bills. Species such as the bush warbler (Cettia diphone) and the mudlark (Grallina cyanoleuca) as well as species of the turdid genera Copsychus and Luscinia fell in with this group.

In the columbiform analysis the first dimension was, again, a measurement of overall size. The largest species was the pigeon Caloenas nicobarica whereas the smallest was the dove Geopelia cuneata. The second dimension was different from the passeriform analysis. The highest correlation between this second dimension and the original variables was tail length (.99). The distributions along

this second axis thus represent a separation of species with long tails from those with short tails. Species with negative scores on this second axis such as (Caloenas nicobarica, Geotrygon montana, and Petrophassa plumifera) are generally ground feeders, whereas those species with positive scores are more arboreal.

Minimal Spanning Trees and Monte Carlo Simulations

The minimal spanning tree (MST) is the shortest set of (n-1) lines that will connect all (n) points in a given space. In my analyses I used the principal component scores to plot species in two dimensional spaces. MSTs were calculated using these points. If extinctions of introduced birds have been non-random with respect to morphology because of competition, then, on average, the distances in the MSTs between the surviving species should be greater than the distances between all the species prior to extinctions. Unusually long MSTs imply that species involved are unusually different morphologically.

It would be unreasonable, however, to test the length of MSTs for surviving species against those for all species prior to extinction, because the average distance between points is sample-size dependent. Clearly, the more points there are in a space, the closer points will be to each other. Then, how does one decide if an increase in distance

between points is not a sampling artifact? The answer is to look at randomly constructed MSTs, representing random associations of species, with the same number of species as the actual MSTs for surviving species for each island. If the observed MST is longer than or equal to all but a small proportion of the random MST length, then one would conclude that the observed extinctions are unlikely to have been random morphologically. Convention, of course, set this "small proportion" at 5%. This provides a test that is free from any potentially confounding effects of sampling artifacts.

There is another problem too. In some of the analyses there were only a few possible MSTs. For example, in the columbiform analysis for Molokai (Fig. 4) three species were introduced and two survived. There are only three ways of drawing two species from three. In situations where there were only a few possible MSTs that could be calculated, I calculated every one and then compared these to the actual MST. In some of the other analyses, however, there was an enormous potential number of MSTs. For example, in the passeriform analysis for Oahu, 27 species were introduced and 18 survived. The combinations formula for calculating the number of possible ways of drawing r objects from a set of n objects where $n \geq r$ is:

$$C = \frac{n!}{(n-r)!r!}$$

Thus, there are 4,686,825 ways of randomly combining 18 species drawn from 27 species. In instances where there were so many possible MSTs the cost of computer time precluded the calculation of each possibility. Instead I randomly selected 200 combinations of introduced species and calculated their MSTs.

Next, I calculated the proportions of random MSTs that exceeded or equaled the observed MSTs in length. When the number of possible combinations is small (e.g. 3 for columbiforms on Molokai) it may be impossible for these individual proportions to be less than the 5% necessary to reject the null hypothesis. (For example, the smallest possible proportion for columbiforms on Molokai is 0.33). However, even though the individual probabilities for each island may be too large, combined they may deny the likelihood of the null hypothesis. By analogy, a coin that comes-up 'heads' when tossed once does not arouse suspicion. But if we repeat this experiment five more times and get 'heads' each time, we would want to examine that coin more closely! I used the Fisher combined probability test to test the hypothesis that extinctions over all islands combined were random morphologically. In this test, the natural logarithm of the proportion is multiplied by minus

two. These values are distributed chi-square with two degrees of freedom. The values and degrees of freedom are added for an overall test of the null hypothesis. (An example is given by Pimm (1980)). This test may be biased towards rejection of the null hypothesis for these data, because many of the extinctions included the same species but on different islands. Debatably these extinctions are not statistically independent of one another as the test requires.

3. RESULTS

In the time period under consideration, there were 45 extinctions of 29 introduced species birds in the Hawaiian Islands: 23 of these were columbiform species and 22 were passeriform species. Lists of dates of introductions and extinctions for each island are given by Moulton and Pimm (1983). Extinction rates were different between these two taxa. Columbiform species accounted for only 29% of the total introductions (36 of 125), yet these represented more than half the extinctions (23 of 45, chi-square = 16.92, $p < 0.01$).

Two columbiform species survived on all the islands (Streptopilia chinensis and Geopelia striata). Four islands (Maui, Molokai, Oahu, and Hawaii) share a core of

nine surviving passeriform species. Kauai is missing only one of these nine species (the skylark, Alauda arvensis). This species was released on Kauai in 1870 (Caum 1933) but probably became extinct around 1938 (Munro 1944). Three of these nine core species (Garrulax canorus, Leiothrix lutea, and Mimus polyglottos) were apparently missing from Lanai. It is unknown whether or not these species existed on Lanai during this time period, however Mimus polyglottos is common there now.

Proportions of random MSTs that exceeded observed MSTs in length for columbiforms and passeriforms are shown in Table 1. For columbiforms these proportions ranged from 0.25 on Oahu to 0.67 on Molokai. For passeriforms, proportions of random MSTs that equalled or exceeded actual MSTs ranged from 0.16 on Oahu to 0.52 on Kauai. Individually none of these proportions is small enough to warrant rejection of the null hypothesis. Moreover, even if the probable interdependence of these proportions is ignored, the combined probabilities are not even close to being significant at the 0.05 level (see Table 1). Thus based on this analysis, there is no evidence to reject the null hypothesis that the extinctions are random with respect to morphology.

Table 1. Results of Monte Carlo Simulations.

ISLAND	I[a]	S[b]	MST[c]	R>O[d]	P_i	X^2
COLUMBIFORMS						
Hawaii	4	2	1.90	2/6	0.33	2.21
Kauai	6	2	1.90	5/15	0.33	2.21
Lanai	6	2	1.90	7/15	0.47	1.51
Maui	9	3	3.21	102/200	0.51	1.35
Molokai	3	2	1.90	2/3	0.67	0.80
Oahu	8	2	1.90	7/28	0.25	2.77
						10.85 ns
						(0.9 < p < 0.5)
PASSERIFORMS						
Hawaii	15	10	7.88	55/200	0.27	2.62
Kauai	18	12	8.41	104/200	0.52	1.31
Maui	12	10	7.88	26/66	0.39	1.88
Oahu	27	18	10.39	32/200	0.16	3.67
						9.48 ns
						(0.5 < p < 0.1)

[a] Number of species introduced to the island.
[b] Number of species that survived.
[c] Minimal spanning tree length.
[d] Number of random trees that exceed the length of the observed MST.

4. DISCUSSION

Colwell and Winkler (1984) and Grant and Abbott (1980) have identified several pitfalls in detecting community structure using such morphological analyses. Two of these pitfalls do not apply to the introduced Hawaiian avifauna: I discuss these first, whereas other, more general problems I discuss later.

The first problem involves the pattern of extinctions in the species pool itself. It is possible that the species in the species pool have already suffered a number of competitively-mediated extinctions. This especially applies to communities on continental islands for which the species pool is assumed to be the set of species on the adjacent mainland. Most studies have no way of evaluating the magnitude of this problem. If this were the case, there might be few or no further extinctions in forming the island community. The species would already be different enough to guarantee coexistence (at least on the mainland). Tests for community structure via non-random morphologies would invariably fail to detect a pattern, because the pattern is already a property of the mainland community.

Extinction has been a common phenomenon in the introduced Hawaiian avifauna: 45 of 125 separate introductions failed (Moulton and Pimm 1983). Moreover, the

introductions came from five continents and not from some limited area where morphological divergence might have already occurred. It is certain that these extinctions have taken place, and it seems unlikely that these species--from so many different regions of the world--would already be so different morphologically as to make competitively-mediated extinctions a priori improbable.

The second problem deals with dispersal. For islands, dispersal ability might restrict the true species pool. The true species pool might be a nonrandom subset of the total set of potential colonists. This would be the result of correlations between morphology and dispersal ability. For example, species that disperse might invariably have long wings. So the island species might appear to be highly convergent (in all having long wings) relative to species in the assumed species pool that contains both long and short-winged species. Yet within long-winged species, those species on the island might be highly divergent. Related to this is the problem mentioned in the introduction concerning what area should be viewed as the source area for colonists?

For this study I know almost exactly what constitutes the species pool. It is reasonably certain that these islands were nearly devoid of land bird species at the start of the time period under study, in the elevational zone below about 600 m. And fairly complete records of

introductions and extinctions for each island are available (Moulton and Pimm 1983). It is possibile that a small number of species might have been released on one or more of the main islands that I do not know about. But I do not think this is a serious problem; there have been too many observers on these islands for extensive introductions to go unnoticed.

These possibilities (competitively-mediated extinctions in the species pool, and differences in dispersal powers) have reduced the likelihood in previous studies of finding a non-random pattern if one actually existed (this is the "power" of a statistical test). My analysis differs critically from other studies in its decidedly experimental nature. I do not need to infer which species have become extinct--I know the losses directly. Consequently, the finding that surviving species are apparently random with respect to morphology are not easily dismissed by questioning the composition of the species pool.

Nevertheless, four problems arise in interpreting these results that also arise in other studies. (1) do the mensural characteristics I used have an ecological basis? (2) is the multivariate analysis appropriate? (3) can one rely on museum specimens (rather than strictly Hawaiian material) for these analyses? (4) are the species in the species pool too distantly related for comparison?

1. I have no reason to believe that the characteristics used here lack an ecological basis. Several authors have argued the significance of bill dimensions in ecological separation (e.g. Abbott et al. 1977, Grant 1966, 1968). Other authors have shown the significance of other characteristics. Grant (1965) for example, discussed the significance of tarsus length in foraging. Wing and tail measurements probably reflect the overall size of the body, and this has been shown to be a predictor of prey size (e.g. Ashmole 1968, Hespenheide 1973, Schoener 1984). The characteristics I measured are standard for this type of analysis.

2. In using a multivariate approach I have followed Findley (1973), Karr and James (1975), and Ricklefs and Travis (1980). Findley (1973) argued that the ecological significance of only one set of characteristics might be obscured by constraints placed on the organism by some other set of characteristics. Consider two examples: (i) Ashmole (1968) pointed out that although the bills of two sympatric terns were similar in length, one of these species had a larger body and took larger prey. Thus body size, and not bill length, appears to be important in this case. (ii) I found in this study that certain species have similar overall body sizes, but very different bill shapes, suggesting different ecological strategies. Thus the finch

(Paroaria coronata: 22) and the thrush (Copsychus malabaricus: 7) are similar in body size (Factor1) but different in bill shape (Factor2), (see Fig. 5, Oahu). Thus it would seem that a single dimension is inadequate for describing the ecological differences the morphological characteristics are reckoned to reflect.

3. Wiens and Rotenberry (1980) have suggested that data sets based on museum specimens might be excessively heterogeneous. And that this variability might obscure basic patterns. Age, sexual, and geographical variation might be difficult to assess. The more similar species are in an analysis, the more serious a consdieration this should be. In Hawaii, introductions were often of unknown origin. It is therefore not only possible, but also probable that many of these introductions were heterogeneous samples. However my analysis deals with what are often relatively large interspecific differences, and thus should not be so sensitive to heterogeneity in my samples. I have no reason to believe that I have incorporated any systematic bias in this analysis by using museum specimens rather than specimens obtained from the islands.

4. Finally, there is the problem of including species in the species pool that are grossly different morphologically, and hence ecologically. Species with widely different morphologies are unlikely to compete

(although there are some spectacular exceptions--Brown et al. 1979). Nevertheless, the inclusion of morphologically bizarre species may obscure any non-random patterns in the data (Colwell and Winkler 1984). One might argue that species related only at the ordinal level do not usually compete. Grant and Abbott (1980) have championed the opinion of Darwin (1859), by claiming that the inclusion of species from different genera, let alone different orders, could obscure non-random patterns. But the birds included in my analysis come from five continents and suffer from the lack of a consistent systematic review. Thus it is not clear which species do in fact belong to a given genus. Consider the following pair of species: Acridotheres tristis (1) and Sturnella neglecta (31) (Fig. 5). The first species is a myna (a starling), whereas the second is a meadowlark (an icterid). Starlings are an old world family and icterids are from the new world. Yet no one who has seen these birds would deny their remarkable morphological and ecological similarity. In fact, at one time or another both species have been placed in the same genus Sturnus! (The former by Deignan and the latter by Linneaus).

It is clear that in these data one cannot ignore species from different genera when considering possible competitors. Unfortunately, it is not easy to decide a

priori which sets of species should be considered as potential competitors. The likelihood for potential competition can be argued in two ways. One could choose to look only at congeners, since these are likely to be similar in many ways. Alternatively, one could choose sets of species that are possibly very different phylogenetically but similar ecologically. But this is a tricky path to follow, and requires extensive knowledge of the species' natural history. For the species considered here such ecological information is not available. Afterall many of the species are extinct in Hawaii and thus such data can never be obtained. However, given the difficulties in the taxonomy of the species involved I believe that choosing the ordinal level is justified. But the most persuasive support for my choice is that I have shown previously that there is evidence for competitively-mediated extinctions for exactly the same data used in this morphological analysis (Moulton and Pimm 1983). One cannot deny the importance of Grant and Abbott's point. But while the patterns of extinctions set out in Moulton and Pimm (1983) strongly infer competition among these species, it does not manifest itself in the form of non-random morphologies.

My results show that at the community level morphology alone is an inadequate predictor of extinctions in the introduced Hawaiian avifauna. It is possible that

morphology plays a more subtle role in structuring communities and that this effect vanishes at the community level. Moreover, morphology might play a more important role in some habitats than in others, or it may operate in a multiplicative fashion with some unknown factors.

My analysis closely follows those of other authors with the exception of the detailed knowledge I have of the species pools for the Hawaiian islands. The uncertainty of the composition of the speices pool is the most serious draw-back to other studies. One could always retreat to the limits of the data as a means of not accepting the null hypothesis of no over-dispersion in morphology (= no competitive effect). But I have taken all reasonable precautions to reject the null hypothesis. Thus it seems reasonable to accept the null hypothesis that morphologies of surviving species of introduced birds are not more different than expected by chance alone. Competition might well operate on morphology, but if it does, it is neither intensive or extensive enough to produce community patterns such as non-random morphological dispersions via extinction.

IV. MORPHOLOGICAL SIMILARITY AND THE COEXISTENCE OF CONGENERS

1. INTRODUCTION

Islands support far fewer species than mainlands as Lack (1976) and MacArthur and Wilson (1967) have pointed-out. It is clear that this is often the result of dispersal problems. But in the case where differences in the powers of dispersal are likely to be small (e.g. congeneric species on near islands) other explanations must be sought. The variety of foods on islands is thought to be low and island populations are thought to be small, when compared to mainlands (Grant 1968, Schoener and Schoener 1983, Lack 1976, MacArthur and Wilson 1967). Thus competition between two ecologically similar species might be more severe than on the mainland, resulting in the extinction of one or both species (Grant 1966) and less diverse assemblages. Because species within the same genus are considered more similar on average than species of different genera this scenario is apt to be especially applicable to congeners (Darwin 1859, Grant 1968, Schoener 1965).

Of course, extinction of congeners, although possible, is not inevitable: coexistence between two species under

competition may occur provided that the species have diverged in some way that reflects their ecological strategies. One way this might be accomplished is through morphological differentiation. The fact that species in a given genus often differ in size, led Hutchinson (1959) to conclude that because of competition similar species must differ morphologically in order to coexist at a particular trophic level. In fact, he suggested that a ratio of roughly 1.3:1 in bill length might be necessary to allow birds to coexist. With this in mind Schoener (1965) found that sympatric congeneric species of birds in the West Indies showed large ratios in bill length.

Coexistence might be accomplished by other means as well. For example, species might occur allopatrically on an island, or they might use different habitats, or use the same habitats in different ways (Grant 1968). But the possibilities of habitat differentiation and/or resource variability undoubtedly vanish with decreasing island size (Grant 1966, 1968, Schoener 1965).

Nevertheless, chiefly due to Hutchinson's (1959) classic paper, a large difference in bill length between sympatric congeneric species of birds has been considered by many to be evidence that competition has played a role in determining species coexistence (Grant 1966, 1968, 1969, Schoener 1965, and examples in Simberloff and Boecklen

1981). But recently, the validity of Hutchinson's criteria for coexistence has been challenged (Simberloff and Boecklen 1981). These authors claim that despite a number of published examples of constant size ratios, there is reason to believe that cases of inconstant ratios might be ignored, emphasizing the seductive powers of theory. Moreover, they have shown that many published examples of constant size ratios do not differ from what is expected by chance alone. If constant size ratios can be obtained by chance alone, then inferences of competition based on such ratios are in jeopardy of being shown invalid. And the role of morphological differences in determining coexistence of congeners becomes suspect.

In this paper, I test the importance of morphological differences in determining coexistence of congeneric species of birds introduced to the six largest islands in the Hawaiian archipelago. Hereafter I shall refer to this hypothesis as the CLAM hypothesis (competition limits adjacent's morphology).

The introduced Hawaiian avifauna is ideally suited for testing the CLAM hypothesis for reasons specified in Moulton and Pimm (1983): (1) there have been numerous introductions and extinctions; (2) problems with differential dispersal powers are nonexistant since the species were physically transported to Hawaii; (3) the identities of all species

introduced to Hawaii are known. Because of these factors, arguments about whether species (and their bill lengths) are missing for islands due to chance, lack of dispersal, or competition obfuscate existing studies. Usually such studies can only infer extinctions. But in the introduced Hawaiian avifauna, extinctions are common and can be observed directly.

2. METHODS AND MATERIALS

I prepared a list of congeneric pairs of species using Berger (1981) with some modifications listed in Moulton and Pimm (1983). Other modifications are listed below. Each congeneric pair was categorized depending upon how many extinctions the pair had suffered. In group A, both species became extinct; in group B, one species became extinct; and in group C, neither species became extinct.

My tests use bill length as a measure of morphology following similar analyses (Grant 1966, 1968, 1969. Schoener 1965). Bill measurements were obtained at the U.S. Musem of natural history and The Museum at Texas Tech University. I tried to measure 10 individuals of each species, but often this was not possible. Percent difference in bill length was determined using Grant's (1969) procedure: for each pair I divided the length of the larger bill by that of the

smaller bill, subtracted 1, and multiplied by 100. Species or species pairs were not included in this analysis if:

1. Difficulty in field identification rendered sight observations suspect (Uraeginthus species; perhaps as many as three species have been introduced to Oahu, (Berger 1981); Estrilda troglodytes, possibly confused with E. astrild (Ord 1982);

2. The congeners were introduced to different islands (Paroaria coronata to Oahu and Kauai, and P. capitata to Hawaii;

3. One of the populations was not truly wild (Zenaida asiatica on Hawaii (Lewin 1971);

4. The species did not occur on the island at the same time. These were Passerina cyanea (extinct 1936) and P. leclancherii (introduced in 1941) on Oahu, and Garrulax albogularis (extinct 1959) and G. pectoralis on Kauai, and G. chinensis and G. pectoralis on Kauai.

5. The species occur allopatrically on an island (Lonchura punctulata and L. oryzivora on Oahu).

6. If both species became extinct, possibly due to the presence of a third, and successful congener, (Geopelia humeralis and G. cuneata both became extinct on Oahu, whereas G. striata survived, and Garrulax chinensis

and G. albogularis both became extinct on Kauai, whereas G. canorus survived.

Methods for determining dates of extinction before 1960 were the same as those used in Section II. After 1960 I considered a species to be extinct when a two year period passed with no observations reported in the journal Elepaio. All introduced species that have become extinct since 1960 occurred on Oahu in areas freuently visited by observers. These observations are reported regularly in the journal Elepaio. Thus a two year period with no reported observations seems a reasonable criterion for claiming that a species is extinct. If an individual of a species were suddenly observed after a two year absence, it would seem as likely to be a reintroduction.

3. RESULTS

Eighteen pairs of congeners met my criteria for inclusion. Of these there were three cases where both species became extinct (group A), nine cases where one species became extinct (group B), and six cases where neither species became extinct (group C). These results are listed in table 1 of Moulton (1985). Means and standard deviations of percent difference in bill length for the three groups are listed in table 2 of Moulton (1985).

Only three pairs of species were included in group A. These pairs were characterized by small differences (< 7%) in bill length. In group B, bill length differences varied from 1% (Garrulax albogularis and G. canorus) to 29% (Geopelia striata and G. humeralis). In this group mean difference in bill length should be small if competition has affected extinctions. Six of the nine pairs differed by 10% or less, and only one pair differs by more than 15% (G. humeralis and G. striata - 29 %).

In group C, percent differences in bill length ranged from 2% (Lonchura malacca and L. punctulata) to 38% (Lonchura oryzivora and L. punctulata). In this group mean difference in bill length should be large. And indeed there are only two cases that differ by less than 19% (Lonchura - 2% and Estrilda - 10%). By the CLAM hypothesis two congeners should not be able to coexist unless they have divereged ecologically, or have allopatric distributions. In the Lonchura case the two species are not allopatric (Berger 1981) and the species appear to be ecologically quite similar. It is probable that these species are competing presently. In the Estrilda case the situation is similar. Both species in this genus are rare and extinction of one or both seems imminent. I tested the equality of bill length differences using analysis of variance (ANOVA). The null hypothesis was that no

differences existed in mean percent bill length difference. The overall model was significant at $p < .05$ ($F = 3.932$; 2, 15 df).

The essence of the CLAM hypothesis is that through one to one competition one species forces the extinction of a congener. In the case where both species became extinct it seems possible that one (or both) species involved was doomed to extinction because of factors other than competition. Because of this possibility, I redid my analysis using only groups B and C. In this second analysis, groups B and C were significantly different at $p < .05$ ($F = 5.14$; 1,13 df).

4. DISCUSSION

Size ratios between sympartic congeners have been used as evidence of interspecific competition (e.g. Huthcinson 1959, Grant 1966, 1968, 1969, Schoener 1965). Simberloff and Boecklen (1981) have argued that many published examples of constant ratios between congeners do not differ from random expectation, and therefore alone are inadequate evidence for competition.

In contrast to such studies, the introduced Hawaiian avifauna provides a direct test of the CLAM hypothesis. The

species pool is known in detail, and any bias due to differences in dispersal powers does not exist.

Despite a significant result, there are two potential problems in interpretation. First, can a synthetic system be used for testing the CLAM hypothesis? And second, is there any evidence that suggests that the speices involved actually do compete?

1. Lack (1965) has cautioned against drawing certain ecological inferences from studies of non-natural circumstances, and there can be little doubt that the introduced avifauna of Hawaii is a system that exists largely due to severe disturbances of native habitats (Kirch 1982). But the introduction of exotic species into habitats different from those in which the species evolved, simulates the natural colonization process of oceanic islands. The problems faced by the first arrivals to an island (e.g. presence or absence of food, nesting sites, or competitors) are the same no matter how the birds get to the island. Thus the introduced Hawaiian avifauna seems to be exactly the type of system required to test the CLAM hypothesis.

2.) This result is entirely in accord with the results in Section II. And as stated previously those results supported the prediction of Schoener's (1976) competition model for determining equilibrial numbers of species on islands. The nonlinear extinction rate suggests that

species are influencing each other's extinction probabilities (= competition).

V. THE RELATIONSHIP BETWEEN MORPHOLOGICAL SIMILARITY AND SPECIES ABUNDANCE

1. INTRODUCTION

In 1859 Charles Darwin wrote that , "Rarity . . . is the precursor to extinction" (Darwin 1859). Since then ecologists have pondered the factors that lead to reduced species' abundances. One such factor is interspecific competition. In principle, the more similar species are, the more likely they are to compete. Thus in a community, under competition, relatively similar species should be rare when compared to relatively dissimilar species.

Recently several authors have attempted to compare real communities with model communities using morphological analyses to measure similarity among species (e.g. Findley 1973, 1976, Karr and James 1975, Ricklefs and Travis 1980, Ricklefs et al. 1981, Case et al. 1983). Typically, the null hypothesis in these studies is that the existing species in a community are not more different morphologically than expected by chance. By force of circumstance, when the null hypothesis is rejected it must be assumed that certain combinations of species (i.e. those involving morphologically similar species) cannot exist, because such combinations vanish under competitive

exclusion. Competitive exclusion in turn implies that local extinctions have taken place (Lack 1947).

If competitive exclusion has led to over-dispersed morphologies in a community, it must be assumed that local extinctions have occurred. Yet local extinctions in natural systems are often difficult to observe. Under certain circumstances, however, one might observe an intermediate step in the extinction process. This step involves the reduction of species' abundances. In this chapter I use the introduced Hawaiian avifauna to test hypotheses concerning the relationship between morphological similarity and species abundance. Are the more common species those species which, on average, are more different morphologically?

The introduced Hawaiian avifauna provides an essentially experimental system for testing this relationship (Moulton and Pimm 1983, Moulton 1985). A large number of species have been introduced into a variety of synthetic (man-made) habitats. In addition, there is a large quantity of published abundance data for the island of Oahu, in the form of Audubon Christmas Bird Counts (CBCs) (Bock and Root 1981).

2. METHODS AND MATERIALS

The Count Circle

The Honolulu CBC is a yearly census conducted in a circle with a diameter of 15 miles. This area includes a variety of habitats. However the terrestrial habitats can be generally categorized as wet forest or parks/residential. Native species of land birds are typically found only in wet forest, whereas exotic birds are found throughout the circle. Few alien species of birds are restricted in their habitat utilization; most of these species are found in the parks/residential habitats.

Abundances

I obtained raw abundances for 25 species of introduced passerines from CBCs for Honolulu, Hawaii, published in the journal Elepaio, for the period 1965 to 1982. My choice of this time interval (1965-1982) was arbitrary. In choosing this period I have attempted to simultaneously maximize the length of the interval and the number of species involved.

I standardized raw abundances by calculating the number of individuals (X) seen per 100 party hours (ph) (Bock and Root 1981). I then calculated the common logarithms of these standardized values (Bock and Ricklefs

1983). All my statistical results are based on thearithmetic means (for each species) of these log transformed abundances.

This time interval included 18 CBCs. Unfortunately not all the species were observed on all the counts. Thus some decisions had to be made concerning the calculation of the mean abundances. If a species was not observed on a particular count, should its abundance for that count be zero or should that count be ignored in calculating mean abundance? To solve this problem we assigned each species to one of five groups (see Appendix).

In group A all species were seen on all 18 counts. Calculation of mean abundance was straight-forward. The five species in group B were not observed on all counts, but I believe them to have been present throughout the time period. I believed that such species were 'missing' in some years because they either have low detectabilities(C. diphone), were genuinely rare in some years (E. melpoda, E. caerulescens, and L. lutea), or possibly both (G.canorus). Thus for counts where these species were not observed I assigned a value of zero for their abundances. Group C included seven species that were seen continuously throughout a portion of the interval, but not the whole interval. The absence of these species was considered to be due to their extinction (S.leucopygius,

V. macroura, L. senegala, E. troglodytes), or introduction after 1965 (L. oryzivora, P. cafer). The three species in group D are all present on Oahu today, but were not seen continuously throughout the time interval. Pycnonotus jocosus was first seen on the 1967 CBC, but was not seen on the 1969,1970,1972, or 1973 CBCs. Likewise S. flaveola was first seen on the 1967 CBC, but was not seen on the 1973 CBC. Lonchura malacca was seen first in 1977, but not in 1978, and has been observed on all counts since 1978. It is possible that absences of these species reflect extinction and reintroduction, but I believe this to be unlikely. Instead I have assigned a value of zero to these species for the CBCs on which these species were not observed. In the case of L. malacca, this species has been on Oahu since before 1940 (Berger 1981). I have treated it with this group because its range lies outside of the count area and has only recently been seen on the Honolulu CBC. Finally there is the case of Uraeginthus bengalus: the Red-cheeked Cordon-bleu. This species was reported on CBCs from 1965 until 1970, and in 1976 and 1977. Between 1971 and 1975 "Cordon-bleu" was reported, but these observation might have been due to any of three species in this genus (Berger 1981). To avoid over- or under-estimating the abundance of this species I ignored

those years in which "Red-cheeked Cordon bleu" was not explicity reported.

On certain CBCs some individuals of native species of passerines were observed. I have omitted these because the total number of individuals seen of these species is small. Recall that these species are restricted for the most part to the wet forest. I do not believe their omission seriously affects these results. I also ignored species seen on fewer than five CBCs.

Morphological Analysis

This morphological analysis was based on the arithmetic means of five characteristics taken from specimens housed at the U.S. National Museum. The measurements were length of wing (unflattened), bill, and tarsus, and width and depth of bill. Bill length was measured from the base of the skull to the tip of the upper mandible, and bill depth and width were measured at the posterior margin of the nares. Wing length was measured from the wrist to the tip of the longest primary. Damaged specimens, or specimens with extremely worn plumage were not used. I attempted to measure ten individuals (five females and five males) of each species, but often this was not possible. There was only one instance where fewer than seven individuals were measured (*E. caerulescens*, n=3).

I used a principal components analysis to define a morphological space. Following Ricklefs and Travis (1980) I factored the covariance matrix of log (10) transformed measurements. My analysis was based on mean values for each species. The first two principal components accounted for 94% of the total variance. I ignored principal components 3-5, because of their small relative contributions to the total variance (Ricklefs et al. 1981). Normalized factor scores for each species were calculated (using the SAS princomp procedure). I then calculated the Euclidean distances from each species to every other species. Further references to morphological distance in this chapter will mean these Euclidean distances in the two-dimensional principal component space.

Statistical Tests

I used linear regression to test the null hypothesis that the logarithms of mean abundances were not positively related to mean distance (in morphological space) from each species to every other species. I also tested this relationship using minimum distances between species.

3. RESULTS

Raw species abundances (X/ph) ranged from 42.7 (A.tristis) to 0.03 (G.canorus). The more abundant species lie roughly at the perimeter of the principal components space. Rare species are found throughout this space, but are concentrated in the upper left region.

The first principal component (Factor1) had positive loadings with all the original measurements, and thus represents a metric of body size. The second principal component (Factor2) had high positive loadings with log bill width and depth, and negative loadings with log wing, bill, and tarsus lengths. This factor can thus be interpreted as a metric of the ratio of bill shape to body size. The positions of the species may be represented simply by a two-dimensional plot (Fig. 6).

I found a significant positive relationship between log abundance and mean Euclidean distance (MDT) from each species to every other species ($F= 4.25$, $p< .03$, 1,23 df) A significant relationship was also found between log abundance and minimum morphological distance. A plot of log abundance versus mean distances between species is shown in Fig. 7. Not every species with a large MDT was common, nor was every species with a small MDT rare, but this was generally the case.

Figure 6. Positions of species in two-dimensional morphological space. Key to numbers: 1 A. tristis, 2 C. cardinalis, 3 C. mexicanus, 4 C. diphone, 5 C. malabaricus, 6 E. caerulescens, 7 E. melpoda, 8 E. troglodytes, 9 G. canorus, 10 L. senegala, 11 L. lutea, 12 L. malacca, 13 L. punctulata, 14 L. oryzivora, 15 M. polyglottos, 16 P. coronata, 17 P. domesticus, 18 P. cafer, 19 P. jocosus, 20 S. leucopygius, 21 S. mozambicus, 22 S. flaveola, 23 U. bengalus, 24 V. macroura, 25 Z. japonicus. See Appendix for complete names.

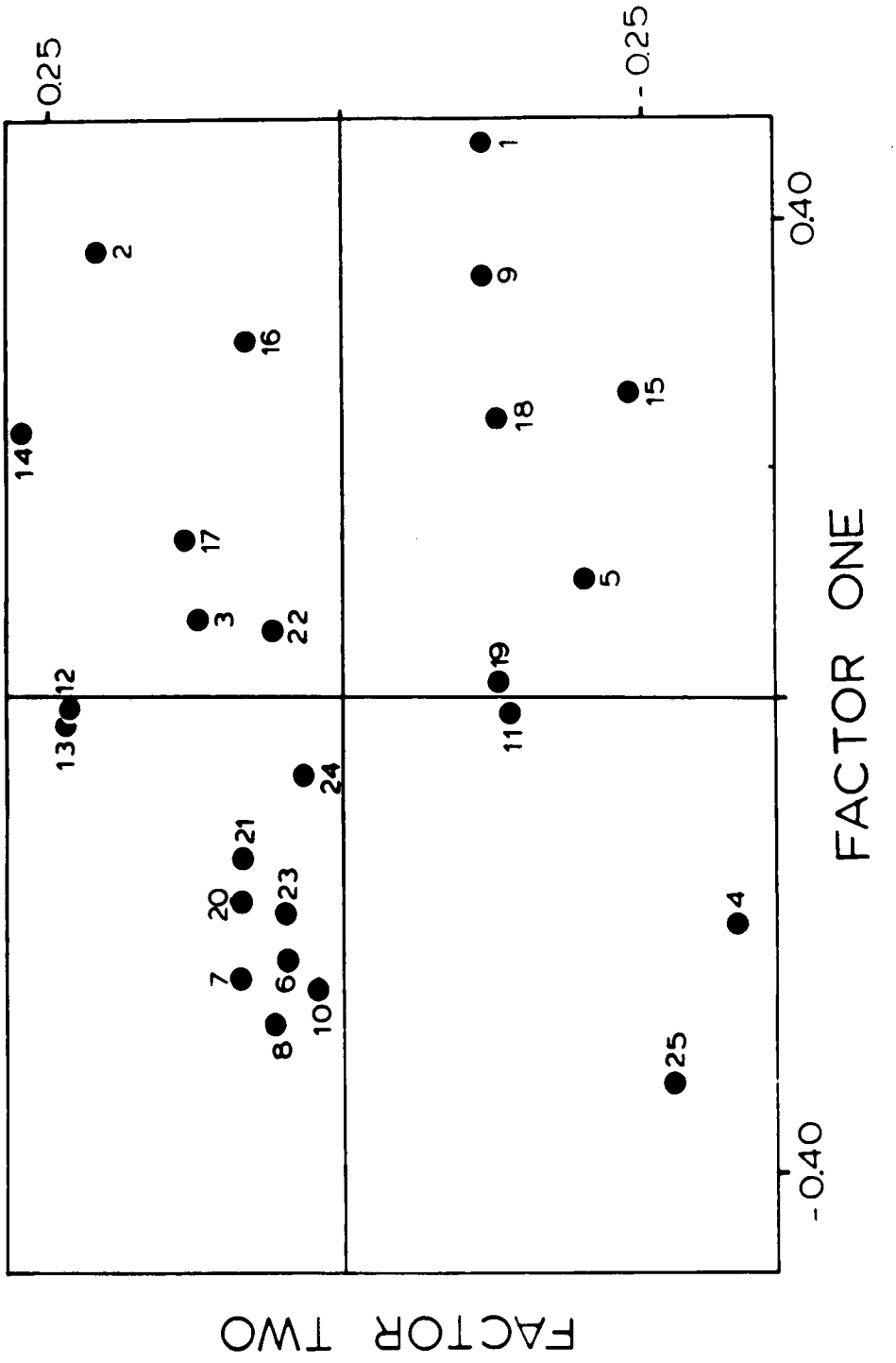
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Figure 6.

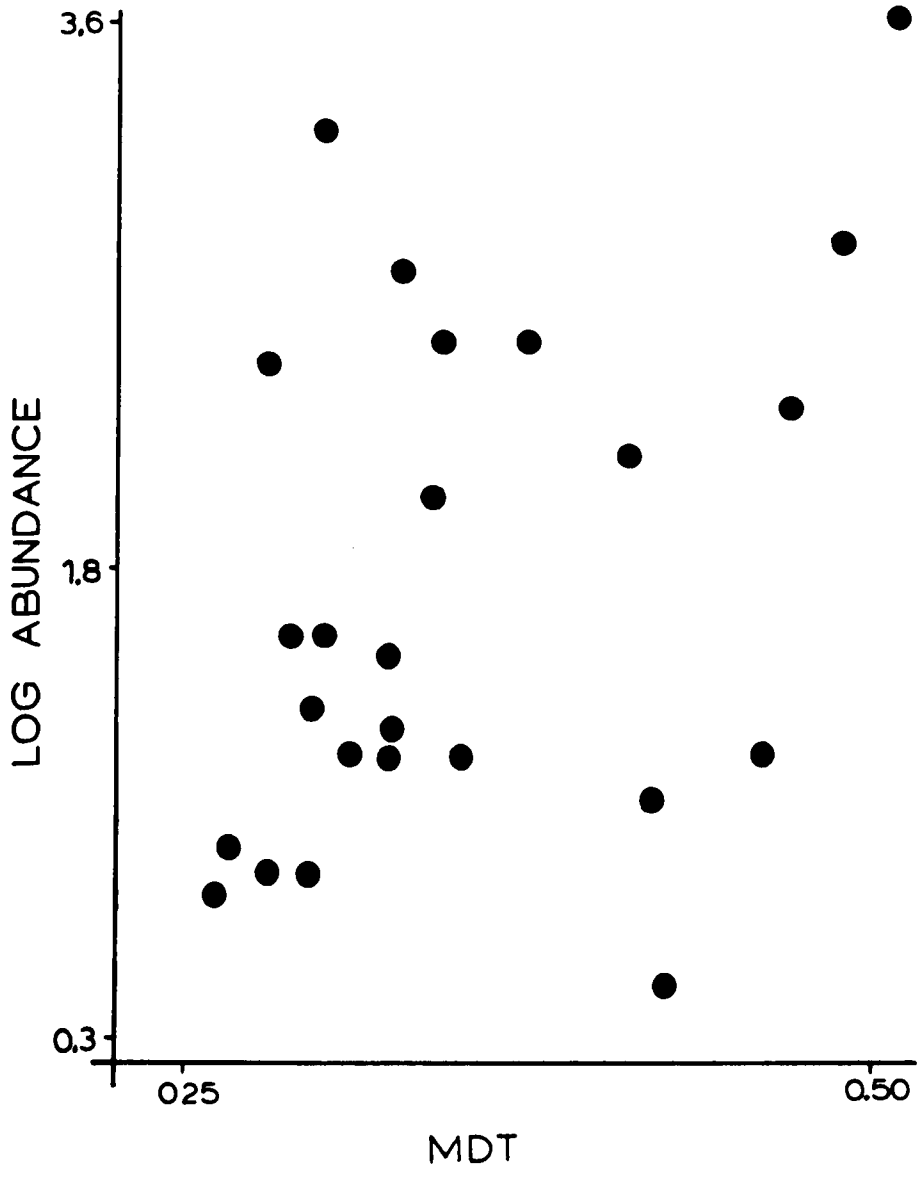

Figure 7. Log abundance versus mean morphological distance.

4. DISCUSSION

In this analysis I found that morphologically similar species are generally rare, whereas morphologically dissimilar species tend to be more abundant. Based on Darwin's idea (see Introduction), morphologically similar species should be more susceptible to extinction. For congeners in the introduced Hawaiian avifauna this has been tested directly (Moulton 1985). I have shown here that this morphological effect is apparently not restricted to congeners.

My results are consistent with the idea that interspecific competition is an on-going process in this system and that it operates on species' morphologies. My results rest on the following assumptions: 1. the morphological relationships among these species reflect ecological relationships; 2. the abundance estimates are valid; 3. that each species can interact with all other species. I discuss these individually below.

The relationship between ecological and morphological similarity has been well documented and there is no reason to rehash the arguments here. As Ricklefs et al. (1981) have pointed-out the exact nature of this relationship is unknown. But clearly, a great deal is known (e.g.

Hespenheide 1971, Grant 1966, Schoener 1965, Lack 1947, Schluter and Grant 1984, Ricklefs and Cox 1977). A second consideration involves using a multivariate versus univariate approach. I believe that when comparing phylogenetically different species a multivariate approach is superior to a univariate approach. Congeneric species are more likely to be similar in many biological characteristics and major ecological differences might be accurately represented by a single morphological dimension, such as bill size (Lack 1947). But this is probably not the case for heterogeneric species. Thus I have elected to use a multivariate analysis. This is in keeping with arguments advanced by Findley (1973) and Ricklefs and Travis (1980).

I have accepted the CBC data at face value, and I believe that these values are reasonably accurate in reflecting species abundances. Nevertheless there are problems in using such data. The principal problem lies in detectablility. 'Rare' species might truly be 'common' species that are difficult to observe. If this manifested itself in a specific region of the morphological space, the results might simply be statistical artifacts. Most of the species considered here occur in residential habitats and should not have especially low detectabilities. Low numbers of these species are likely due to rarity rather than sampling error. Only two species that occur consistently in

habitats where detection could be a problem are C. diphone and G. canorus. Thus I do not consider this to be a major problem in this data set.

A second problem involves the standardization of the raw abundances. Recall that I divided the number of individuals of a species observed by the number of party hours of observation. The problem arises when the true number of individuals of a species remains constant while the number of party hours of observation varies. Thus a total population of 50 individuals of a hypothetical species has an estimated abundance of 5 with 10 party hours of observation, and .5 with 100 party hours. The number of party hours for the counts here ranged from 44 (in 1966) to 130 (in 1979 and 1980). I do not know how extensive this problem is in these data, but I have tried to ameliorate its effect by using the mean of several CBCs. In using this standardization I follow Bock and Root (1981), and Bock and Ricklefs (1983).

My first statistical test (using MDT) assumes that each species could interact with every other species. In principle this might be a valid assumption, but in reality I doubt that competition is this extensive in the introduced Hawaiian avifauna. But I hasten to point-out that under the peculiar circumstances at hand (i.e. introduced species in exotic habitats), it would not be a simple matter to guess

which species never interact. Nevertheless, despite the fact that most of the species involved inhabit the same habitats there undoubtedly are cases where certain species do not co-occur. Rather than sift through the data exploring for such instances I elected to perform a second test using minimum Euclidean distance, the nearest neighbor distance (NND). I performed this second test for two further reasons. First, it is possible that the bulk of the MDT effect is due, in fact, to NND. Second, it is simpler when viewing pairs of species to make decisions concerning the potential for interaction (i.e. do the species occupy the same habitat?). Species and their nearest neighbors are listed in Table 2. A regression analysis revealed that log abundance was significantly related to NND ($F=2.97$; $p<.05$; 1,23 df) in a one-tailed test.

In nearly every case the species and their nearest neighbors occupy the same habitats (Berger 1981, and pers. field observations, MPM). A glaring exception to this is the pair of Common Myna (A. tristis) and the Melodious Laughingthrush (G. canorus). The myna occupies parks, pastures, and residential habitats whereas the laughingthrush is a denizen of dense forests. It is extremely unlikely that the rarity of the laughingthrush is due to the commoness of the myna. Removal of this pair does not alter the relationship, and in fact it improves the

relationship between log abundance and NND ($F=6.36$, $p<.01$). Moreover it emphasizes the general nature of this result; morphologically different species are not inevitably common, nor are morphologically similar species invariably rare.

The results of this study are consistent with hypotheses involving on-going interspecific competition. But they are also consistent with an alternative explanation, dealing with the distribution of resources. If each of the species considered here utilizes a different and unique set of resources then abundances would not be directly dependent on morphological similarity. I have no information concerning resource levels on Oahu. However, I believe it would be unlikely that individual resource distributions would be so well correlated with morphological distances. Moreover, based on field observations I believe that species overlap widely in their resource utilizations. A great deal of autecological study remains to be done to substantiate this claim.

Table 2. Species and nearest neighbors in morphological space.

SPECIES	NND[a]	MDT[b]	ABUN[c]
(1) Acridotheres tristis (9)[d]	.109	.509	3.63
(2) Cardinalis cardinalis (16)	.153	.468	2.33
(3) Carpodacus mexicanus (17)	.065	.280	2.46
(4) Cettia diphone (25)	.138	.462	1.23
(5) Copsychus malabaricus (19)	.121	.342	2.00
(6) Estrilda caerulescens (10)	.030	.312	1.18
(7) E. melpoda (6)	.035	.326	1.30
(8) E. troglodytes (7)	.044	.352	1.23
(9) Garrulax canorus (1)	.109	.423	0.48
(10) Lagonistica senegala (6)	.030	.325	1.20
(11) Leiothrix lutea (19)	.024	.297	1.54
(12) Lonchura malacca (13)	.015	.327	1.51
(13) Lonchura punctulata (12)	.015	.330	2.75
(14) Lonchura oryzivora (2)	.154	.410	2.14
(15) Mimus polyglottos (18)	.124	.419	1.08
(16) Paroaria coronata (2)	.153	.374	2.52
(17) Passer domesticus (3)	.065	.300	3.20
(18) Pycnonotus cafer (14)	.124	.347	2.53
(19) P. jocosus (11)	.024	.290	1.61
(20) Serinus leucopygius (21)	.037	.295	1.36
(21) S. mozambicus (20)	.037	.280	0.85
(22) Sicalis flaveola (3)	.065	.265	0.90
(23) Uraeginthus bengalus (6)	.033	.294	0.85
(24) Vidua macroura (21)	.077	.261	0.78
(25) Zosterops japonicus (4)	.138	.491	2.88

[a] Nearest neighbor distance in morphological space.
[b] Mean Euclidean distance to all other species.
[c] Common logarithm of the mean number of observations per 100 hours of observation.
[d] Number of nearest neighbor in Fig. 6.

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APPENDIX

APPENDIX

A. Species seen on all CBCs

Acridotheres tristis
Cardinalis cardinalis
Carpodacus mexicanus
Copsychus malabaricus
Lonchura punctulata
Mimus polyglottos
Paroaria coronata
Passer domesticus
Serinus mozambicus
Zosterops japonicus

B. Species not seen on every CBC, but believed present

Cettia diphone **
Estrilda caerulescens **
E. melpoda **
Garrulax canorus
Leiothrix lutea

C. Species seen continuously for part of the CBCs

Estrilda troglodytes *
Lagonistica senegala *
Lonchura oryzivora
Pycnonotus cafer *
Serinus leucopygius *
Vidua macroura

D. Species not seen throughout the time interval, and not seen continuously

Lonchura malacca
Pycnonotus jocosus
Sicalis flaveola

E. Miscellaneous oddity - see text

Uraeginthus bengalus *

* = presumed extinct
** = seen recently but very rare

1 all names follow Berger (1981)
2 see Goodwin (1982)

VITA

Michael Platt Moulton was born in Denver, Colorado on April 27, 1950. He was graduated from George Washington High School in June 1968. He subsequently received a Bachelor of Arts degree in Biology from The University of Colorado in August 1972. He received a Master of Science degree from Fort Hays State University in August of 1980. He began his doctoral work at Texas Tech University under the direction of S.L. Pimm in August 1980, and transferred with Dr. Pimm to The University of Tennessee, Knoxville in September 1982. He received the Ph.D. degree from The University of Tennessee in August 1984.