COMMUNITY ORGANIZATION IN HUMMINGBIRDS: RELATIONSHIPS BETWEEN MORPHOLOGY AND ECOLOGY

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ABSTRACT.—Hummingbird species inhabiting restricted geographic regions exhibit morphological patterns that differ significantly from those predicted by null models in which species are selected at random from appropriate species pools. Temperate North American hummingbirds are convergent: more similar in bill length, body weight, and wing length than predicted by several null models. These temperate species also are more similar to each other than they are to more closely related (congeneric) species from subtropical and tropical habitats. Hummingbirds of the Greater and Lesser Antilles show a nonrandom distribution of species among islands: all islands inhabited by hummingbirds have at least two species, and these fall into two distinctly different size categories. Allometric scaling of bill length with respect to body mass is distinctive in Antillean hummingbirds; bill length increases more rapidly with increasing body weight in West Indian hummingbirds than in random samples of hummingbirds of the world or in other birds. These morphological patterns appear to reflect two ecological processes: interspecific competition among hummingbirds and mutualistic coevolution with flowers. Hummingbird species of similar morphology use similar floral resources but rarely coexist in the same local areas. Species of divergent morphology exploit different food resources and frequently coexist locally. Length of the bill, which influences access to different kinds of flowers, is particularly important in the organization of these simple hummingbird associations. *Received 28 June 1983, accepted 5 July 1984.*

EVOLUTIONARY ecology has a long tradition of inferring dynamic processes of ecological interaction from static patterns in the morphologies and geographic distributions of closely related species (e.g. Lack 1947, Brown and Wilson 1956, Hutchinson 1959, MacArthur 1972). Such patterns have played a particularly important role in the development of current ideas about the role of competition and other interspecific interactions in the organization of natural communities (e.g. MacArthur 1972, Cody and Diamond 1975). Recently, however, these ideas have been criticized for two reasons. First, many of the purported patterns have not been rigorously tested against appropriate null models that assume they could result from random processes rather than deterministic biological mechanisms (e.g. Strong et al. 1979, Connor and Simberloff 1979, Simberloff and Boecklen 1981). Second, the relationship between morphology and ecology often is simply assumed or inferred from indirect evidence instead of being documented rigorously by observation and experiment (e.g. Lack 1947, Hutchinson 1959, Findley 1973, Cody 1974, Brown 1975, Karr and James 1975). These problems can be overcome in some cases by reanalyzing information already available for certain groups of organisms. Although these analyses are no substitute for careful experimental and observational field studies, they may clarify issues and focus future empirical work.

Hummingbirds, the nonpasserine avian family Trochilidae, provide an excellent system for addressing these issues. This presumably monophyletic group, containing more than 100 genera and 300 species, is widely distributed in the New World, attaining its greatest diversity in tropical latitudes. Hummingbirds are specialized for feeding on floral nectar and share a suite of characteristics including long, slender bills, tiny feet, and wings adapted for hovering flight. Because they are easily observed and their food resources can be monitored accurately, hummingbirds have been the subjects of many behavioral and ecological studies.

Several investigators have suggested that species in particular geographic areas exhibit morphological patterns that reflect evolutionary adaptations both for competitive interactions with other hummingbirds and for mutualistic interactions with bird-pollinated flowers

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(e.g. Grant and Grant 1968, Kodric-Brown and Brown 1978, and Brown and Kodric-Brown 1979 for temperate North America; Lack 1973, 1976, and Kodric-Brown et al. 1984 for Caribbean islands; Snow and Snow 1972, Colwell 1973, Feinsinger 1976, and Stiles 1975 for tropical America; and Feinsinger and Chaplin 1975, Feinsinger and Colwell 1978, and Feinsinger et al. 1979 for hummingbirds in general). Although these interactions have been studied carefully in certain instances, there has been little attempt to test the purported patterns of morphological organization against alternative models that assume no interspecific interactions. We performed such tests for the species inhabiting temperate North America and the Antillean islands, and the results are discussed here in terms of what is known about the processes of ecological interaction. Our analysis is based on three quantitative morphological traits that are known to be important in hummingbird ecology: culmen (bill) length, which influences the kinds of flowers from which the birds can forage; body weight, which indicates total energy requirements; and wing length, which together with body weight affects the aerodynamics of flight (Greenewalt 1975).

TEMPERATE NORTH AMERICAN ASSOCIATIONS

Eight species, belonging to four genera, have breeding ranges that extend well into temperate North America. Several other species, not considered further here, are primarily subtropical in distribution and reach their northern limits just across the Mexican-United States border. The collective breeding range of these temperate species extends from the deserts of the southwestern United States and northern Mexico to southern Alaska and from Florida to southeastern Canada. All of these species are migratory, wintering in Mexico and Central America.

Several investigators have noted that the north temperate hummingbirds are extremely similar in size and shape. Grant and Grant (1968; see also Brown and Kodric-Brown 1979) suggested that this similarity represents convergence among species to utilize a common set of widely distributed flower species, which also have converged in size, shape, and nectar rewards. Hummingbirds compete for these floral resources primarily by aggression and territoriality. This interference usually results in exclusive use of local areas by individuals and species, and its outcome depends largely on habitat (including flower density) and wing disc loading (the ratio of body weight to the area swept out by the wings in flight; Feinsinger and Chaplin 1975, Kodric-Brown and Brown 1978, Feinsinger et al. 1979).

The claim that temperate hummingbirds are convergent in morphology has not been tested rigorously against a null hypothesis. If the claim is correct, then temperate hummingbirds should be more similar to each other than a comparable number of species drawn at random from an appropriate species pool. We tested this hypothesis by comparing measurements of body weight, bill (exposed culmen) length, and wing length for the temperate species with sets of eight species randomly drawn from a large pool of species of hummingbirds of the world for which measurements were available (see Appendix). We conducted three tests of the null hypothesis that the temperate hummingbirds are no more similar in size than randomly assembled associations of species.

First, we used computer simulation techniques to draw 8 species at random 1,000 different times from the pool of 123 species for which all measurements were available. For each set of eight species we computed the variance for each of the three measurements, and we recorded the number of cases in which the variance for a null community exceeded that of the observed temperate assemblage. For all three characters, variance in the random communities was greater than in the real community for all 1,000 draws (Table 1). Clearly, temperate hummingbirds are much more similar in size and shape than a random subset of the hummingbirds of the world (Fig. 1).

A random draw from the global species pool may not be an appropriate method for evaluating certain null hypotheses, however. For one thing, the temperate species probably are more closely related to each other than to certain exclusively tropical groups. Thus, the similarity could be attributed to failure to diverge from a recent common ancestor rather than to convergence in response to similar ecological conditions. Biogeographic and taxonomic relationships suggest that temperate North American hummingbirds derived from tropical montane and subtropical ancestors that colonized from Mexico. The morphology of temperate hummingbirds also might be constrained by the de-

TABLE 1. Results of simulations testing the null hypothesis that the eight species of temperate North American hummingbirds are more similar than expected from a random draw of eight species sampled from the world species pool. Simulations compared the actual variances of morphological characters of temperate species against variances of the entire world species pool, the species pool that inhabits continental North America north of the Isthmus of Tehuantepec (biogeographic constraints), and species pool with wing lengths and body weights within the range observed for temperate species (morphological constraints).

		Number of random draws with variances greater than observed variance		
	Variance in 8 North American species	World species pool	Biogeographic constraints	Morphological constraints
Culmen length (mm)	1.75	1,000	996	1,000
Wing length (mm)	15.21	1,000	999	248
Weight (g)	0.203	1,000	999	523

mands of the fluctuating temperate climate or by the necessity to migrate from the temperate zones to winter in tropical and subtropical regions and survive in these habitats (see Feinsinger 1980). Such constraints would indicate that ecological factors influence the morphology and community organization of hummingbirds, but would suggest that other conditions probably are more important than biotic interactions with flowers or with other hummingbird species within the temperate zone of North America.

We then tested two null hypotheses that impose additional constraints on the species pool. Unfortunately there is no modern, generally accepted classification of the family Trochilidae that attempts to reconstruct phylogenetic relationships among the genera, so we did not feel confident restricting our species pool to some taxonomic subgroup within the family. Instead we drew random communities from a species pool limited by either biogeographic or morphological consraints. In a second test we limited the species pool to those 29 species (for which we have measurements out of a possible 38 species) that inhabit continental North America north of the Isthmus of Tehuantepec in southern Mexico (Peterson and Chalif 1973). Because many biogeographers recognize the region between the Isthmus of Tehuantepec and the United States-Mexican border as the area of subtropical transition between tropical South and Central America and temperate North America (Brown and Gibson 1983), this procedure defined a species pool consisting of 8 temperate North American species and 21 subtropical Mexican species. In a third test we limited the species pool to only those 28 species that had body weights and wing lengths within the range (2.66–4.25 g and 39.8–49.7 mm) for temperate species. Note that both the biogeographically and the morphologically constrained species pools are also taxonomically constrained, because they contain only 18 and 17 genera, respectively, of the 70 genera in the world species pool for which all measurements are available for at least one species.

When 1,000 draws of 8 species each are taken from either the biogeographically or morphologically constrained pools, the variation in the relevant traits is much greater than for the temperate hummingbirds (Table 1). This is true for all three characters in the test with biogeographic constraints, but of course only for culmen lengths in the test with morphological constraints (since all species in the pool were within the range of variation of the temperate species in both body weight and wing length).

The hypothesis that temperate hummingbirds are similar, not as a result of evolutionary convergence but simply because they have not diverged substantially from a common ancestor, also can be evaluated by comparing variation within and between genera. Two of the four genera of temperate hummingbirds have other species with exclusively tropical distributions. If temperate hummingbirds have not diverged significantly from a common ancestor, these tropical congeners should also be similar in size and shape to their temperate relatives. Clearly this is not the case (Table 2). Tropical species of the genera *Selasphorus* and *Calypte* are uniformly smaller than their temperate congeners. The temperate representatives of these genera are similar to each other and to the other two monotypic genera of tem-

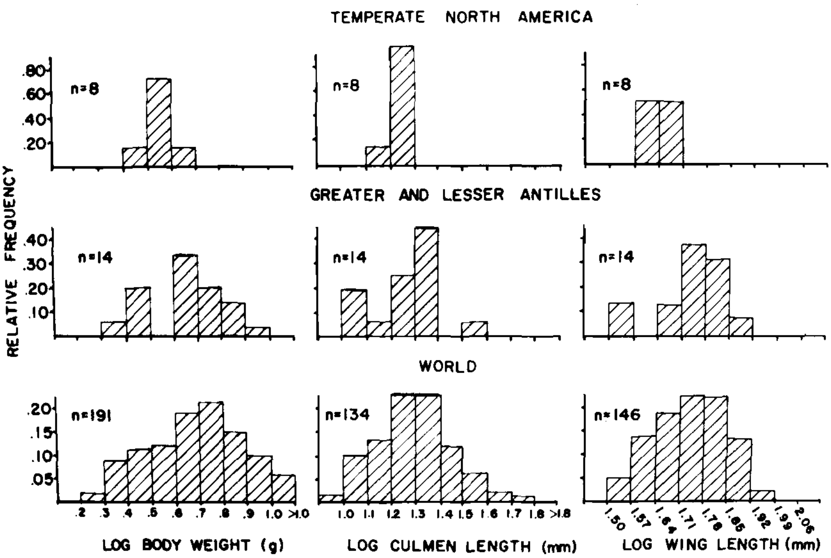

Fig. 1. Frequency distributions of body weights (g), culmen lengths (mm), and wing lengths (mm) for species of hummingbirds from temperate North America, the Greater and Lesser Antilles, and the world. Note the small variation among temperate species and the bimodal pattern for Antillean species compared to the world species pool.

perate hummingbirds, especially in bill length. The greater similarity among temperate species than among congeneric species provides strong evidence that the temperate hummingbirds have acquired their strikingly similar morphologies by evolutionary convergence.

These analyses demonstrate that temperate North American hummingbirds are much more similar in morphology, especially in bill length, than expected on the basis of several different null hypotheses. Because bill length is of primary importance in determining the kinds of flowers from which hummingbirds can forage (e.g. Snow and Snow 1972, Colwell 1973, Stiles 1975, Feinsinger and Colwell 1978, Kodric-Brown et al. 1984), these results also provide strong support for the idea (Grant and Grant 1968, Brown and Kodric-Brown 1979) that the birds have converged to use the same kinds of flowers. It seems highly unlikely that physiological adaptations to climate or migration would result in more precise convergence in bill length than in either body size or wing length.

ANTILLEAN COMMUNITIES

The tropical islands of the Greater and Lesser Antilles are inhabited by 14 species and 9 genera of hummingbirds (Bond 1971). All but 2 of these species are endemic to the Greater and Lesser Antilles. Other species not considered in the present analysis occur on islands around the periphery of the Caribbean Sea (the Bahamas, Old Providence, St. Andrew, Trinidad, and Tobago), but these islands differ conspicuously in habitat and geological history from the Antilles. As noted by Lack (1973, 1976), the Antillean hummingbirds appear to be distributed among the 36 islands in nonrandom patterns. Although Mona, a relatively large island between Puerto Rico and Hispaniola, has no hummingbirds, the remaining 35 have 2–5 species (Table 3). Lack noted that species occurring together on the same island tended either to differ substantially in body size and overlap widely in local distribution or to be relatively similar in size but occur in different habitats, usually at different elevations. Intensive work on Puerto Rico and more casual observations on other islands suggest that Antillean hummingbirds have morphologies that reflect both interspecific competition with other hummingbirds and coevolution with mutualistic flowers (Kodric-Brown et al. 1984). The situation is similar to that in temperate North America, except that in the Antilles there are two size categories of hummingbirds that are

TABLE 2. Mean ($\bar{x}$), range, and coefficient of variation (CV), with standard deviation (S_{cv})[a] in parentheses, for temperate hummingbirds and temperate, tropical, and combined species of *Selasphorus* and *Calypte*.

	Temperate hummingbirds (8 species, 4 genera)	Temperate *Selasphorus* and *Calypte* (5 species)	Tropical *Selasphorus* and *Calypte* (6 species)	All *Selasphorus* and *Calypte* (11 species)
Culmen length (mm)				
$\bar{x}$	17.66	17.61	11.77	14.72
Range	15.54–19.73	16.57–19.06	10.59–12.90	10.59–19.06
CV	0.0747 (±0.0188)	0.0521 (±0.0165)	0.0790 (±0.0228)	0.2201 (±0.0469)
Wing length (mm)				
$\bar{x}$	43.92	45.15	37.86	41.17
Range	39.77–49.68	39.77–49.68	31.61–41.57	31.61–49.68
CV	0.0887 (±0.0222)	0.0975 (±0.0308)	0.1033 (±0.0298)	0.1329 (±0.0283)
Weight (g)				
$\bar{x}$	3.29	3.46	2.17	2.98
Range	2.66–4.25	3.08–4.25	1.90–2.47	1.90–4.25
CV	0.1370 (±0.0343)	0.1349 (±0.0427)	0.1315 (±0.0379)	0.2578 (±0.0549)

[a] S_{cv} calculated from Sokal and Rohlf (1969).

highly specific pollinators of two distinct sets of hummingbird-pollinated plant species: small, short-billed hummingbirds can forage only from short-tubed flowers that have low rates of nectar secretion, whereas large, long-billed birds feed almost exclusively from long-tubed flowers that secrete more copious nectar.

The relationship between Antillean hummingbird morphology and ecology can be examined more rigorously by comparing the observed morphologies and distributions of species with those expected on the basis of null models that assume that insular communities are assembled at random, uninfluenced by interspecific interactions.

Comparison with the global species pool.—We first tested whether the morphologies of Antillean hummingbirds differ significantly from a random sample drawn from the entire pool of hummingbirds of the world. For each of the three measurements (body weight, culmen length, and wing length) we drew at random from the pool 14 species for which the relevant data were available. This was repeated 500 times. We quantified the maximum difference between the actual Antillean distribution and that for the entire world species pool, and then determined the number of random assemblages that were more different than this when also compared to the world species pool. We measured the difference using the D-statistic from the Kolmogorov-Smirnov two-sample test, which is the maximum cumulative deviation over corresponding intervals between two distributions (Siegel 1956). Depending on the trait, approximately 20–50% of the null assemblages were more different than the actual Antillean species when both were compared to the entire species pool (Table 4). This is hardly convincing evidence for the nonrandom assembly of Antillean communities, but note that fewer simulated distributions exceeded the observed difference for culmen length (102 out of 500; $P = 0.2$) than for the other two measurements.

Comparison with a randomized Antillean species pool.—We next tested whether the distribution of species morphologies differed from that expected if the 14 species were redistributed randomly among islands in the frequencies that they actually occur. There are 35 islands inhabited by hummingbirds, but the same combinations of species occur together on several different islands (Table 3). Thus, it is inappropriate for most tests to consider each island as an independent sample. To be rigorous and conservative we used only the nine different combinations to obtain the observed distributions for each measurement. We generated an expected distribution by drawing nine different combinations of species at random from the pool of 14 Antillean species (Table 3). This draw was constrained to have the same number of species in each combination as the real combinations (3 two-species, 4 three-species, 1 four-species, and 1 five-species combination). This procedure was repeated 750 times to generate an expected frequency distribution for each morphological trait. Because the birds in both the real and artificial assemblages differ in absolute size, and we wanted to evaluate the hypothesis

TABLE 3. The distribution of hummingbird species on 39 islands of the Greater and Lesser Antilles. From Bond (1971) and Lack (1973).

	Glaucis hirsuta	*Anthracothorax viridigula*	*Anthracothorax dominicus*	*Anthracothorax mango*	*Eulampis jugularis*	*Eulampis holosericeus*	*Orthorhyncus cristatus*	*Cyanophaia bicolor*	*Chlorostilbon ricordii*	*Chlorostilbon swainsonii*	*Chlorostilbon maugaeus*	*Trochilus polytmus*	*Mellisuga minima*	*Mellisuga helenae*
Grenada	X					X	X							
Carriacou						X	X							
Grenadines						X	X							
St. Vincent					X	X	X							
Barbados						X	X							
St. Lucia					X	X	X							
La Martinique					X	X	X	X						
Dominica					X	X	X	X						
Marie Galante						X	X							
La Guadeloupe					X	X	X							
Désirade						X	X							
Montserrat					X	X	X							
Antigua						X	X							
Barbuda						X	X							
Nevis					X	X	X							
Saba					X	X	X							
St. Eustatius					X	X	X							
St. Christopher					X	X	X							
Anguilla						X	X							
St. Martin						X	X							
St. Bartholomew						X	X							
Bequia						X	X							
Anegada						X	X							
St. Croix						X	X							
St. Thomas						X	X							
Puerto Rico		X	X			X	X				X			
Mona														
Hispaniola			X							X			X	
Île de la Gonâve			X										X	
Tortuga Island, Haiti			X										X	
Jamaica				X								X	X	
Cuba									X					X
Isle of Pines									X					X
Culebra						X	X							
Vieques						X	X							
St. John						X	X							

that coexisting species tend to differ in size more than expected on the basis of chance (Lack 1973, 1976), we expressed the differences in size between every pair of species in all combinations (both real and randomly assembled) as the difference in the logarithms for each measurement.

The observed and null distributions were compared and the significance evaluated with a Kolmogorov-Smirnov test (Fig. 2). Differences between observed and null are significant for culmen length ($P < 0.05$), marginally significant for body weight ($0.05 < P < 0.10$), and insignificant for wing length ($P > 0.10$). Note that it is particularly with respect to bill length that real communities represent nonrandom combinations of morphologies. Also, the observed distributions for both culmen

TABLE 4. Simulation results that tested whether 3 morphological characters of Antillean hummingbird species differ significantly from a sample of 14 species drawn at random from the world species pool.

Character	*D*-statistic	Number less	Number greater or equal
Wings	0.15	246	254
Weights	0.18	364	136
Culmens	0.20	398	102

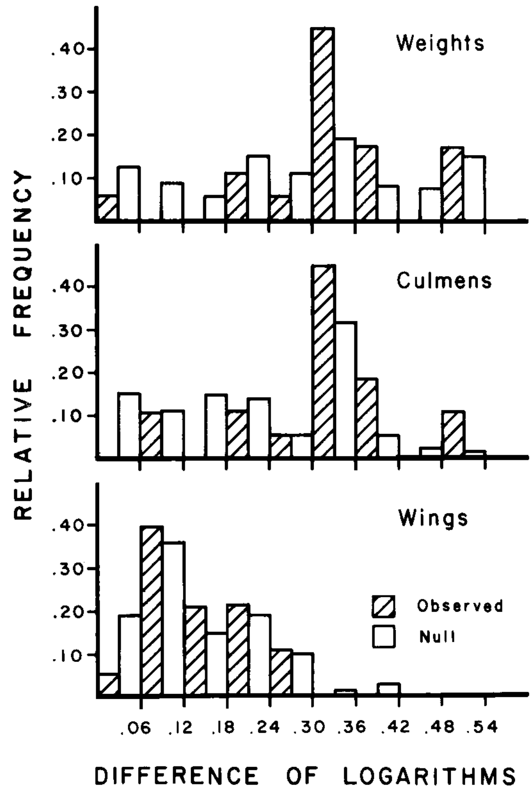

Fig. 2. Comparisons between observed distributions of measurements for Greater and Lesser Antillean hummingbird species and those measurements predicted from a null model that assumes that combinations of species are assembled at random from the pool of 14 Antillean species. Measurements are expressed as differences in the logarithms for each pair of species.

length and body weight differ conspicuously from the null assemblages in having a pronounced peak at a difference in logarithms of approximately 0.30, which corresponds to a body size ratio of about two. This is a conservative analysis in the sense that it incorporates all species within islands. When they occur on the same island, species of similar size often are segregated into different elevations and habitats (Lack 1973, 1975; confirmed on Puerto Rico by Kodric-Brown et al. 1984).

Distribution of species among islands.—We tested directly against a null model Lack's (1973, 1976) suggestion that the Antillean assemblages are nonrandom with respect to the number of species per island. Because there is one island (Mona) with no hummingbirds and many with two species (Table 3), Lack suggested that, in particular, the absence of islands with only one species was unlikely to be due to chance.

We tested the observed distribution of numbers of species among islands against a Poisson distribution. This null model predicts the independent distribution of rare events. It is appropriate here because the number of species per island is small and apparently not influenced significantly by island area or interisland distance (Lack 1973, Terborgh 1973). Results of this analysis indicate that the actual distribution differs ($P < 0.01$) from the predicted null distribution in having too few islands with only one species, too many islands with two species, and too few islands with three or more species (Fig. 3). This pattern is highly nonrandom ($\chi^2 = 27.26$, $P \ll 0.01$; Fig. 3 shows the data plotted by number of species per island, but some adjacent categories can be lumped to give sufficiently high expected values to meet the assumption of the Chi-square analysis). This pattern suggests that any island that can support one hummingbird species can be invaded successfully by at least one additional species. The precise reasons for this are obscure, but we suspect they have to do with the success in colonization by hummingbird-pollinated plant species as well as hummingbirds, and by the coevolution of the hummingbird-plant interactions within islands (see Kodric-Brown et al. 1984).

Allometry of bills and body size.—A conspicuous feature of Fig. 2 is the pronounced peak in observed measurements of both body weights and culmen lengths of coexisting combinations of species that occurs at a ratio of about 2.0, whereas the peak in wing length corresponds to a ratio of about 1.2. This indicates unusual allometric scaling of body parts in Antillean

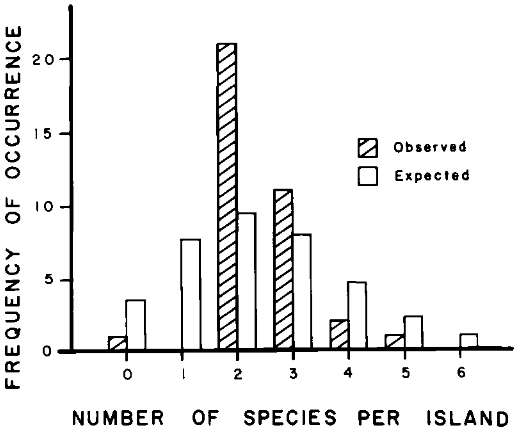

Fig. 3. Comparison between the observed number of hummingbird species among 36 islands of the Greater and Lesser Antilles and that predicted by a Poisson distribution.

hummingbirds. Because mass and volume scale as the cube of linear measurements, body weight ratios of about 2.0 usually are associated with ratios of linear measurements of 1.2–1.3. This typical allometry is observed for the relationship between body weight (a volumetric measurement) and wing length (a linear measurement), but bill lengths of different-sized Antillean hummingbirds are more different than would be expected on the basis of body weight ratios.

These relationships can be examined more rigorously by deriving the allometric equations from regressions fitted to the data. These equations take the form $l = CW^m$, where l is a linear dimension (bill length or wing length in mm), C is a fitted constant, W is a volumetric measurement (body weight in g), and m is the exponent relating the two variables (or the slope of the regression line fitted to log-transformed data). In Fig. 4 we have plotted fitted regression equations for log-transformed measurements of Antillean hummingbirds, hummingbirds of the world, North American corvids (crows and jays), and North American owls. We included the last two groups because we believe they are representative of the general allometric scaling of bill length and wing length in birds. Each of these two families exhibits a wide range of body sizes but does not use its bill for foraging in the same specialized way that hummingbirds do. The exponent (slope) for Antillean hummingbird bills (0.79) is nearly twice as high as the exponents for either bills or wings (0.32–0.53) of any of the other birds (Fig. 4). Statistically, the exponent for Antillean hummingbird bills can be readily distinguished from the exponents of all the other allometric relationships ($P < 0.01$), which are all much more similar to each other (Table 5). The bills of Antillean hummingbirds are much more different in length than would be expected on the basis of body weight. Also of interest, although it will come as no surprise to students of hummingbirds, is the great variation around the allometric relationships for bills ($r^2 = 0.39$) of hummingbirds in the global pool, compared to comparable relationships for either Antillean hummingbirds, owls, or corvids (all $r^2 > 0.79$). This indicates that differences in bill length (and shape) play such an important role in the ecology of hummingbirds that selection has produced morphologies of many species that deviate greatly from predicted allometric relationships (see also Feinsinger and Colwell 1978).

The unusual allometric scaling of bill length suggests a final and admittedly ad hoc test of the null hypothesis that Antillean hummingbirds represent a random sample of the hummingbirds of the world. We used Monte Carlo methods to draw 14 species at random from the 123 species for which both culmen length and body weight data were available. Then we calculated the correlation coefficient for the 14 pairs of log-transformed data. This procedure was repeated 1,000 times. In 996 of 1,000 sets of species assembled randomly from the world species pool the correlation coefficient was lower than the value (0.79) calculated for the real Antillean fauna, resulting in unequivocal rejection of the null hypothesis ($P = 0.004$).

All Antillean hummingbirds appear to conform to a special relationship between bill length and body size that is very different from comparable relationships both for hummingbirds in general and for other kinds of birds. Why should species that differ in body size be even more different in bill length than expected on the basis of the allometric relationship in other hummingbirds, unless species of different sizes tend to occur together and have been selected to diverge in bill length? Both Lack's qualitative observations and our quantitative analyses (Figs. 1–3) show that pairs of species of different size usually occur together on the same islands. Although these distribu-

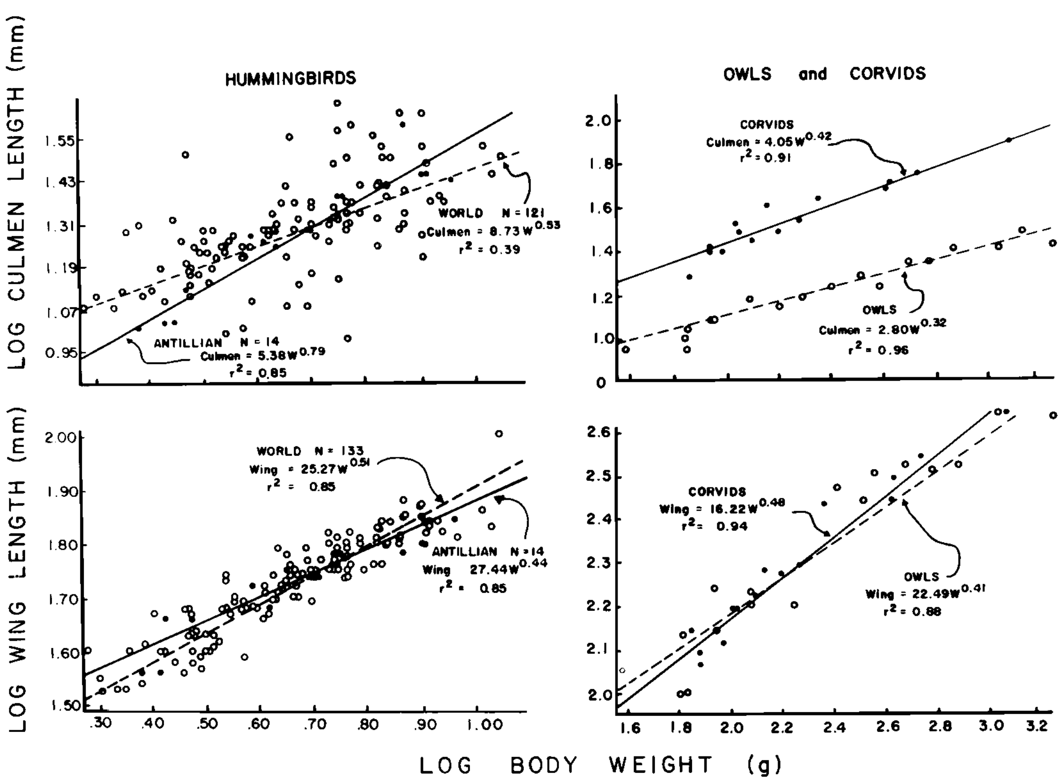

Fig. 4. Allometric relationships of culmen and wing length against body weight for Antillean hummingbirds, hummingbirds of the world, and North American owls and corvids. Note that the slope for Antillean hummingbird culmens (solid circles) is nearly twice that of either bills or wings of any of the other birds.

tions may reflect historical and contemporary biogeographic constraints as well as contemporary biotic interactions, these species appear to have adapted to coexistence by diverging in body size and especially in bill length. This is supported by taxonomic body size patterns. For example, *Chlorostilbon ricordii* on Cuba and *C. swainsonii* on Hispaniola, where they coexist with smaller hummingbirds, are much larger than *C. maugaeus* on Puerto Rico and other congeneric species on the tropical American mainland (see Appendix).

This interpretation also is consistent with the detailed ecological observations of Kodric-Brown et al. (1984) on Puerto Rican hummingbirds. They confirmed Lack's observation that species of similar size are segregated by habitat and elevation, whereas species of dissimilar size are broadly and locally sympatric. These pairs of coexisting species feed from almost completely nonoverlapping sets of flower species, and flower utilization is related to bill length. Only large hummingbirds with long bills can legitimately extract nectar from long-tubed flowers, which produce sufficient quantitites of nectar to make foraging rewarding for large birds. On the other hand, both large and small birds can feed from short-tubed flowers, but these produce such small quantitites of nectar that foraging is economical only for the smaller species. Thus differences among coexisting species in bill length and body size are functionally interrelated and appear to reflect selection both to diverge in resource utilization so as to reduce interspecific competition and to coevolve with specific flower species so as to provide effective pollination.

DISCUSSION

Our analyses demonstrate that specific morphological traits characterize the hummingbirds from particular geographic areas. Species from temperate North America differ from

TABLE 5. Results of *t*-tests that test the null hypothesis that slopes between culmen length or wing length and body weight are statistically ($P < 0.05$) equal. All comparisons were done on log-transformed data (see Fig. 3).[a]

	Culmens				Wings		
	Antillean hummingbirds	North American owls	North American corvids	Hummingbirds of the world	Antillean hummingbirds	North American owls	North American corvids
Culmens							
Antillean hummingbirds	—						
North American owls	5.87**	—					
North American corvids	4.63**	1.25	—				
Hummingbirds of the world	3.01**	2.37*	1.27	—			
Wings							
Antillean hummingbirds	4.37**	1.52	0.25	1.00	—		
North American owls	4.75**	1.13	0.13	1.25	0.37	—	
North American corvids	3.87**	2.01	0.87	0.36	0.50	1.16	—
Hummingbirds of the world	4.63**	1.26	0.13	1.25	0.25	0.13	1.05

[a] * $P < 0.01$, ** $P < 0.001$.

those inhabiting the tropical islands of the Greater and Lesser Antilles, and each of these groups represents a selected subsample of the hummingbirds of the world. These morphological patterns indicate that ecological processes severely limit the kinds of hummingbirds that comprise communities in different geographic areas. Ecological constraints, of which the most important is probably the number and kinds of floral resources, limit the range and combinations of morphological traits of the species that inhabit a region. Competitive interactions between hummingbirds, on the other hand, require species that coexist in local areas to differ in morphology sufficiently to exploit substantially nonoverlapping food resources. The eight hummingbird species in temperate North America utilize a large set of convergently similar floral resources (Grant and Grant 1968, Brown and Kodric-Brown 1979). Consequently they exhibit little variation in bill length and body size, and only one species normally is found within a local habitat (Kodric-Brown and Brown 1978, Brown and Kodric-Brown 1979). The Antillean islands are inhabited by two body size and bill length categories of hummingbirds that have coevolved with two distinct sets of flower species (Kodric-Brown et al. 1984). Hummingbirds of similar size tend not to occur on the same island, and when they do are normally found in different habitats, whereas hummingbirds of different size coexist locally to form the basic two-species community that is found on all islands with hummingbirds (Lack 1973, 1976; Kodric-Brown et al. 1984).

These results suggest that it should be possible to predict quite precisely the morphological characteristics of the hummingbird species occupying different habitats and geographic regions. Depending on the flowers and perhaps on other environmental conditions, only species with certain combinations of morphologies should be able to coexist to form stable communities. We have begun to characterize these traits for temperate North American and Antillean communities. We expect other hummingbird associations exhibiting different combinations of morphologies to inhabit other areas, especially tropical continental habitats where several species coexist locally. Available information suggests that tropical mainland communities often contain morphologically diverse hummingbird assemblages, with species exhibiting different combinations of body size, wing length, bill length, and bill shape (Snow and Snow 1972, Stiles 1975, Feinsinger 1976, Feinsinger and Colwell 1978).

Feinsinger and Colwell (1978) also have been impressed by the close correspondence between morphology and community ecology of hummingbirds. Based largely on their own experiences in continental tropical America, they have attempted to deduce the rules that govern the assembly of species into communities of increasing diversity. Interestingly, they describe the basic two-species tropical community as consisting of a territorialist and a low-reward trapliner or generalist, but these categories do not accurately characterize the two-species communities of the Antillean islands, where the main differences between locally coexisting species are in body size, bill length, and flower specialization. In fact, both large and small species tend to be trapliners, at least in the Greater Antilles (Kodric-Brown et al. 1984). Nevertheless, the ecological constraints and opportunities that affect the occurrence of hummingbirds in a particular region obviously are reflected in the morphologies of coexisting species, suggesting that it eventually may be possible to formulate community assembly rules that are both precise and general.

One general result of almost all of our analyses is that of the three morphological characteristics studied, bill length consistently shows the clearest, most nonrandom patterns. This may not seem surprising in view of the obvious importance of bill size and shape in the foraging of hummingbirds. Nevertheless, it emphasizes the roles of food resources, interspecific competition for food, and mutualistic plant-pollinator interactions in determining the morphological attributes and ecological roles of those species that coexist to form natural communities. Not only do these kinds of ecological interactions limit the morphological attributes of the species that occur within certain geographic areas, but they also influence the evolution of these traits. In the case of hummingbirds, mutualistic interactions between birds and flowers may be at least as important as competition among hummingbird species in the adaptive radiation of the entire family Trochilidae and the evolution of those subsets of species that inhabit the particular geographic regions. In fact, it is probably unrealistic to try to assess the relative importance of these two kinds of interactions because they are intimately interrelated; convergence or divergence in bill length and other aspects of morphology affect the relative abilities of different species to use particular kinds of flowers, and this in turn influences both the extent of interspecific competition and the efficiency of pollination.

The relationship between morphology and community ecology that we have documented for hummingbirds has several general implications. Recently there has been much debate about whether ecological communities exhibit nonrandom patterns of organization that reflect ecological processes such as interspecific competition. Several authors (e.g. Connor and Simberloff 1979, Strong et al. 1979, Simberloff and Boecklen 1981) have pointed out correctly that apparent patterns in the morphologies and distributions of species seldom have been tested to determine whether they differ significantly from appropriate null models that assume that species associate at random. However, here and elsewhere (Bowers and Brown 1982, Brown and Bowers 1984) we have shown that communities of both rodents and hummingbirds exhibit nonrandom organization that apparently reflects the role of interspecific competitive and (in the case of hummingbirds) mutualistic interactions. In both cases there already existed a large background of field studies on the ecology of these species that included analyses of the relationship between morphological traits and processes of resource exploitation and aggressive interference. This facilitated the formulation and testing of null hypotheses that are not only statistically rigorous but also biologically appropriate. It is hardly surprising that a good knowledge of the biology of the organisms concerned is a valuable aid in constructing and testing realistic null hypotheses and in elucidating the ecological processes that influence community organization.

In investigating the relationship between morphology and community ecology, it is often useful to restrict the analysis to closely related species. This is not to imply that only closely related species interact strongly to influence community organization. On the contrary, distantly related taxa often are involved in all classes of interspecific interactions, including competition. However, their morphologies may be so different that they provide little clue to their specific ecological roles. For example, on most Antillean islands a passerine bird, the bananaquit (*Coereba flaveola*), removes nectar from long-tubed flowers and presumably competes significantly with large hummingbirds (Kodric-Brown et al. 1984). In part because of its distant phylogenetic relationship, its morphology is adapted for a different manner of foraging: it cuts through the floral tube while perched, rather than probing through the flower opening while hovering as hummingbirds do. Consequently, its morphological characteristics provide little indication that it interacts much more closely with hummingbirds than any other Antillean passerine.

Closely related species often are so constrained by their common phylogenetic histories that they differ substantially in only a few characteristics. Often, especially in sympatric species, these differences reflect divergent mechanisms of resource utilization in response to interspecific competition. Therefore, they tell more about the role of ecological interactions in causing character displacement and adaptive radiation within phyletic lineages than they do about the organization of diverse communities containing many distantly related taxa. Analysis of morphological patterns among closely related species is useful because it may suggest mechanisms of ecological interaction that affect community structure, but other approaches will be necessary to explore the consequences of these interactions among distantly related taxa.

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APPENDIX. Wing length (mm), body weight (g), and culmen length (mm) of hummingbirds in the world species pool. Taxonomy follows the A.O.U. (1983; North American species) and Peters (1945). Measurements were taken from Ridgeway (1904, 1914), Wetmore (1968), Stiles (1973), Carpenter (1976), Feinsinger (1976), Waser (1978), Brown and Kodric-Brown (1979), and Feinsinger et al. (1979). J. H. Brown, R. K. Colwell, and R. Zusi contributed unpublished data. Temperate (T) and Antillean (A) hummingbird species are designated, as are those used in the biogeographically (B) and morphologically (M) constrained tests of null hypotheses for the temperate fauna.

Species	Character	$\bar{x}$	SD	n
Doryfera johannae	Wing	53.60	1.00	9
	Weight	4.10	0.10	9
	Culmen	—	—	—
D. ludoviciae	Wing	58.16	0.70	35
	Weight	5.72	0.20	20
	Culmen	36.13	—	16
Androdon aequatorialis	Wing	65.37	—	15
	Weight	8.00	—	1
	Culmen	39.77	—	15
Glaucis hirsuta (A)	Wing	59.22	2.10	76
	Weight	6.82	0.52	96
	Culmen	32.25	—	73
Threnetes leucurus	Wing	59.13	0.80	20
	Weight	5.59	0.10	42
	Culmen	29.50	—	—
T. ruckeri	Wing	56.85	—	45
	Weight	5.92	0.70	11
	Culmen	30.92	—	45
Phaethornis yaruqui	Wing	—	—	—
	Weight	6.00	—	1
	Culmen	—	—	—
P. guy	Wing	59.85	0.40	40
	Weight	5.66	0.24	64
	Culmen	42.50	—	20
P. syrmatophorus	Wing	—	—	—
	Weight	5.70	—	2
	Culmen	—	—	—
P. superciliosus (B)	Wing	59.74	1.34	268
	Weight	6.04	0.27	277
	Culmen	37.65	1.17	255

APPENDIX. Continued.

Species	Character	$\bar{x}$	SD	n
P. hispidus	Wing	56.90	0.60	22
	Weight	4.86	0.12	26
	Culmen	—	—	—
P. anthophilus	Wing	57.23	—	23
	Weight	4.60	—	1
	Culmen	35.30	—	23
P. ruber	Wing	—	—	—
	Weight	2.15	—	4
	Culmen	—	—	—
P. griseogularis	Wing	—	—	—
	Weight	2.00	—	1
	Culmen	—	—	—
P. longuemareus (M)	Wing	49.61	0.30	85
	Weight	2.97	0.38	58
	Culmen	31.19	—	79
Eutoxeres aquila	Wing	71.45	—	29
	Weight	10.83	—	3
	Culmen	27.09	—	29
E. condamini	Wing	68.10	0.80	22
	Weight	9.36	0.27	24
	Culmen	—	—	—
Phaeochroa cuvierii	Wing	69.34	—	51
	Weight	8.87	0.41	37
	Culmen	23.17	—	51
Campylopterus curvipennis	Wing	—	—	—
	Weight	6.40	—	7
	Culmen	—	—	—
C. largipennis	Wing	73.20	0.80	12
	Weight	8.32	0.21	29
	Culmen	—	—	—
C. rufus	Wing	72.56	—	9
	Weight	—	—	—
	Culmen	26.20	—	9
C. hemileucurus (B)	Wing	76.87	—	122
	Weight	10.46	0.50	56
	Culmen	32.48	—	123
C. ensipennis	Wing	—	—	—
	Weight	9.67	—	3
	Culmen	—	—	—
C. falcatus	Wing	—	—	—
	Weight	7.50	—	3
	Culmen	—	—	—
Eupetomena macroura	Wing	—	—	—
	Weight	8.74	—	29
	Culmen	—	—	—
Florisuga mellivora	Wing	67.41	—	88
	Weight	7.41	0.63	28
	Culmen	19.60	—	88
Melanotrochilus fuscus	Wing	—	—	—
	Weight	8.05	—	150
	Culmen	—	—	—
Colibri delphinae	Wing	70.55	—	50
	Weight	6.66	0.67	9
	Culmen	17.71	—	50
C. thalassinus (B)	Wing	63.79	—	65
	Weight	5.91	0.34	84
	Culmen	23.20	—	64

APPENDIX. Continued.

Species	Character	$\bar{x}$	SD	n
C. coruscans	Wing	75.20	—	2
	Weight	7.55	0.49	17
	Culmen	21.50	—	1
C. serrirostris	Wing	—	—	—
	Weight	6.75	—	45
	Culmen	—	—	—
Anthracothorax viridigula (A)	Wing	62.31	2.61	31
	Weight	7.46	0.49	25
	Culmen	24.53	1.70	31
A. prevostii (B)	Wing	65.45	—	109
	Weight	6.71	0.22	11
	Culmen	26.14	—	109
A. nigricollis	Wing	66.18	—	89
	Weight	7.00	0.55	51
	Culmen	24.18	—	88
A. veraguensis	Wing	66.75	—	8
	Weight	—	—	—
	Culmen	24.57	—	7
A. dominicus (A)	Wing	62.81	1.86	42
	Weight	5.66	0.41	32
	Culmen	24.13	0.75	42
A. mango (A)	Wing	68.31	—	21
	Weight	7.81	0.67	4
	Culmen	26.03	—	21
Eulampis jugularis (A)	Wing	73.21	—	45
	Weight	8.67	0.56	11
	Culmen	23.59	—	45
E. holosericeus (A)	Wing	60.00	2.04	92
	Weight	5.60	0.40	21
	Culmen	22.74	2.20	91
Chrysolampis mosquitus	Wing	54.57	—	48
	Weight	3.88	0.39	20
	Culmen	12.39	—	48
Orthorhyncus cristatus (A, M)	Wing	47.34	1.09	54
	Weight	2.71	0.18	23
	Culmen	10.72	1.18	54
Klais guimeti	Wing	47.77	—	64
	Weight	2.54	0.20	7
	Culmen	13.24	—	64
Abeillia abeillei	Wing	—	—	—
	Weight	2.67	—	3
	Culmen	—	—	—
Stephanoxis lalandi	Wing	—	—	—
	Weight	4.03	—	3
	Culmen	—	—	—
Lophornis ornata	Wing	—	—	—
	Weight	2.20	—	8
	Culmen	—	—	—
L. magnifica	Wing	—	—	—
	Weight	2.13	—	3
	Culmen	—	—	—
L. delattrei	Wing	37.54	—	25
	Weight	—	—	—
	Culmen	10.89	—	25
L. helenae	Wing	—	—	—
	Weight	2.60	—	4
	Culmen	—	—	—

APPENDIX. Continued.

Species	Character	$\bar{x}$	SD	n
L. adorabilis	Wing	—	—	—
	Weight	2.70	—	4
	Culmen	—	—	—
Popelairia langsdorffi	Wing	—	—	—
	Weight	3.00	—	3
	Culmen	—	—	—
Discosura conversii (M)	Wing	40.60	—	20
	Weight	3.00	0.40	5
	Culmen	13.85	—	20
D. longicauda	Wing	—	—	—
	Weight	3.00	—	1
	Culmen	—	—	—
Chlorestes notatus	Wing	—	—	—
	Weight	3.61	—	14
	Culmen	—	—	—
Chlorostilbon aureoventris (M)	Wing	43.33	—	6
	Weight	2.97	0.50	3
	Culmen	13.40	—	6
C. gibsoni	Wing	—	—	—
	Weight	2.72	—	5
	Culmen	—	—	—
C. ricordii (A)	Wing	51.50	—	22
	Weight	4.23	—	1
	Culmen	17.20	—	22
C. swainsonii (A)	Wing	54.51	—	14
	Weight	4.85	—	1
	Culmen	17.30	—	14
C. maugaeus (A, M)	Wing	47.53	—	45
	Weight	2.93	—	45
	Culmen	13.62	—	45
Cyanophaia bicolor (A)	Wing	58.58	—	26
	Weight	4.55	—	8
	Culmen	16.41	—	22
Thalurania furcata (A)	Wing	52.61	0.50	52
	Weight	4.35	0.24	72
	Culmen	20.19	—	36
T. watertonii	Wing	—	—	—
	Weight	4.50	—	2
	Culmen	—	—	—
T. glaucopis	Wing	—	—	—
	Weight	5.32	—	60
	Culmen	—	—	—
T. lerchi	Wing	—	—	—
	Weight	2.00	—	3
	Culmen	—	—	—
Panterpe insignis	Wing	64.47	—	68
	Weight	5.69	0.39	47
	Culmen	20.86	—	68
Damophila julie (M)	Wing	43.46	—	51
	Weight	3.31	0.15	51
	Culmen	15.17	—	51
Lepidopyga coeruleogularis (M)	Wing	48.76	—	21
	Weight	4.20	0.30	3
	Culmen	19.40	—	20
L. goudoti	Wing	50.00	—	1
	Weight	3.95	0.30	4
	Culmen	19.10	—	1

APPENDIX. Continued.

Species	Character	$\bar{x}$	SD	n
Hylocharis xantusii (B, M)	Wing	49.30	—	1
	Weight	3.53	0.18	11
	Culmen	17.00	—	1
H. leucotis (B)	Wing	57.00	—	1
	Weight	3.50	0.27	210
	Culmen	17.60	—	1
H. eliciae (M)	Wing	48.72	—	59
	Weight	3.60	—	13
	Culmen	18.24	—	59
H. sapphirina	Wing	—	—	—
	Weight	4.00	—	2
	Culmen	—	—	—
H. cyanus	Wing	—	—	—
	Weight	3.47	—	8
	Culmen	—	—	—
Goldmania violiceps	Wing	50.28	—	26
	Weight	3.63	0.20	6
	Culmen	18.73	—	26
Goethalsia bella	Wing	52.94	—	5
	Weight	—	—	—
	Culmen	17.86	—	5
Trochilus polytmus (A)	Wing	53.90	—	1
	Weight	4.10	—	1
	Culmen	19.80	—	1
Leucochloris albicollis	Wing	—	—	—
	Weight	6.45	—	26
	Culmen	—	—	—
Polytmus guainumbi	Wing	—	—	—
	Weight	4.70	—	3
	Culmen	—	—	—
Leucippus chionogaster	Wing	—	—	—
	Weight	3.80	—	7
	Culmen	—	—	—
Talaphorus tuczanowskii	Wing	69.90	—	1
	Weight	6.00	—	1
	Culmen	22.80	—	1
Amazilia candida (B, M)	Wing	49.00	—	1
	Weight	3.74	0.43	14
	Culmen	17.60	—	1
A. chionopectus	Wing	54.40	2.20	3
	Weight	4.72	—	62
	Culmen	—	—	—
A. versicolor	Wing	—	—	—
	Weight	4.00	—	1
	Culmen	—	—	—
A. fimbriata	Wing	51.60	—	1
	Weight	4.78	0.48	9
	Culmen	21.10	—	1
A. lactea	Wing	54.20	1.10	10
	Weight	4.55	0.10	11
	Culmen	—	—	—
A. amabilis	Wing	52.45	—	26
	Weight	4.32	0.55	18
	Culmen	19.20	—	26
A. cyaneotiocta	Wing	61.10	—	1
	Weight	5.84	0.63	13
	Culmen	19.90	—	1

APPENDIX. Continued.

Species	Character	$\bar{x}$	SD	*n*
A. franciae	Wing	50.60	—	1
	Weight	5.04	—	5
	Culmen	23.00	—	1
A. leucogaster	Wing	—	—	—
	Weight	4.90	—	6
	Culmen	—	—	—
A. cyanocephala (B)	Wing	61.10	—	1
	Weight	5.84	0.63	13
	Culmen	19.90	—	1
A. beryllina (B)	Wing	56.50	—	1
	Weight	4.94	0.40	7
	Culmen	19.40	—	1
A. saucerrottei	Wing	53.90	—	120
	Weight	4.49	0.37	139
	Culmen	23.16	—	120
A. tobaci (M)	Wing	47.00	—	1
	Weight	4.10	0.39	35
	Culmen	18.30	—	1
A. viridigaster	Wing	—	—	—
	Weight	6.70	—	5
	Culmen	—	—	—
A. edward	Wing	52.40	—	39
	Weight	4.70	0.20	58
	Culmen	19.43	—	39
A. rutila (B)	Wing	58.60	—	1
	Weight	4.71	0.54	11
	Culmen	23.40	—	1
A. yucatanensis	Wing	—	—	—
	Weight	3.57	—	7
	Culmen	—	—	—
A. tzacatl (B)	Wing	57.28	—	26
	Weight	5.03	0.28	105
	Culmen	22.56	—	36
A. amazilia	Wing	52.45	—	26
	Weight	4.32	0.55	18
	Culmen	19.20	—	26
A. violiceps (B)	Wing	58.40	—	1
	Weight	5.87	0.40	7
	Culmen	21.60	—	1
Eupherusa poliocerca	Wing	62.25	—	2
	Weight	—	—	—
	Culmen	18.00	—	1
E. eximia (B)	Wing	57.32	—	120
	Weight	4.27	0.30	126
	Culmen	21.37	—	114
E. nigriventris (M)	Wing	48.05	—	21
	Weight	3.00	—	1
	Culmen	15.43	—	21
Elvira chionura (M)	Wing	49.05	—	45
	Weight	2.99	0.21	16
	Culmen	15.75	—	45
E. cupreiceps (M)	Wing	46.58	—	26
	Weight	3.00	—	13
	Culmen	15.12	—	26
Microchera albocoronata (M)	Wing	40.77	—	17
	Weight	2.71	0.20	8
	Culmen	12.24	—	16

APPENDIX. Continued.

Species	Character	$\bar{x}$	SD	*n*
Chalybura buffonii	Wing	66.65	—	45
	Weight	6.20	0.40	6
	Culmen	25.39	—	45
C. melanorrhoa	Wing	66.70	—	20
	Weight	—	—	—
	Culmen	23.30	—	20
C. urochrysia	Wing	66.70	—	18
	Weight	7.00	—	1
	Culmen	25.54	—	18
Aphantochroa cirrochloris	Wing	—	—	—
	Weight	7.29	—	30
	Culmen	—	—	—
Lampornis clemenciae	Wing	—	—	—
	Weight	7.96	—	268
	Culmen	—	—	—
L. amethystinus (B)	Wing	67.23	—	13
	Weight	6.73	0.87	26
	Culmen	20.92	—	13
L. viridipallens	Wing	—	—	—
	Weight	5.42	—	11
	Culmen	—	—	—
L. hemileucus	Wing	61.69	—	18
	Weight	5.60	—	1
	Culmen	20.68	—	18
L. castaneoventris	Wing	62.15	—	20
	Weight	5.64	0.27	40
	Culmen	21.80	—	20
Adelomyia melanogenys	Wing	50.73	0.50	26
	Weight	3.77	0.31	35
	Culmen	16.10	—	1
Clytolaema rubricauda	Wing	—	—	—
	Weight	7.32	—	5
	Culmen	—	—	—
Polyplancta aurescens	Wing	58.80	0.80	8
	Weight	6.30	0.10	8
	Culmen	—	—	—
Heliodoxa rubinoides	Wing	—	—	—
	Weight	7.74	—	8
	Culmen	—	—	—
H. leadbeateri	Wing	66.40	0.70	24
	Weight	7.38	0.18	32
	Culmen	—	—	—
H. jacula	Wing	70.91	—	47
	Weight	8.30	0.40	10
	Culmen	23.22	—	47
Eugenes fulgens (B)	Wing	72.61	—	67
	Weight	6.80	0.46	38
	Culmen	30.68	—	67
Sternoclyta cyanopectus	Wing	—	—	—
	Weight	9.06	—	17
	Culmen	—	—	—
Topaza pella	Wing	—	—	—
	Weight	12.12	—	6
	Culmen	—	—	—
Oreotrochilus melanogaster	Wing	65.00	—	1
	Weight	4.40	—	2
	Culmen	17.70	—	1

APPENDIX. Continued.

Species	Character	$\bar{x}$	SD	n
O. estella	Wing	66.40	—	1
	Weight	8.11	0.39	37
	Culmen	18.50	—	1
Patagona gigas	Wing	132.30	—	1
	Weight	20.24	1.29	10
	Culmen	36.30	—	1
Aglaeactis cupripennis	Wing	80.10	—	1
	Weight	7.55	0.59	23
	Culmen	20.00	—	1
Lafresnaya lafresnayi	Wing	63.60	—	1
	Weight	4.50	—	2
	Culmen	25.60	—	1
Pterophanes cyanopterus	Wing	105.70	8.00	3
	Weight	11.17	0.50	6
	Culmen	30.50	—	1
Coeligena coeligena	Wing	70.76	0.60	27
	Weight	6.75	0.10	34
	Culmen	26.00	—	1
C. wilsoni	Wing	—	—	—
	Weight	7.00	—	1
	Culmen	—	—	—
C. torquata	Wing	73.27	0.80	19
	Weight	7.13	0.20	19
	Culmen	31.20	—	1
C. helianthea	Wing	70.10	—	1
	Weight	8.17	—	3
	Culmen	29.40	—	1
C. lutetiae	Wing	78.80	—	1
	Weight	8.13	—	3
	Culmen	33.00	—	1
C. violifer	Wing	74.78	1.60	6
	Weight	7.44	0.30	7
	Culmen	37.50	—	1
C. iris	Wing	77.90	—	1
	Weight	8.00	—	2
	Culmen	28.00	—	1
Ensifera ensifera	Wing	77.20	—	1
	Weight	11.83	0.50	3
	Culmen	—	—	—
Sephanoides sephanoides	Wing	—	—	—
	Weight	5.00	—	1
	Culmen	—	—	—
Boissonneaua flavescens	Wing	74.00	—	1
	Weight	8.05	0.90	8
	Culmen	16.30	—	1
B. matthewsii	Wing	—	—	—
	Weight	6.65	—	4
	Culmen	—	—	—
B. jardini	Wing	—	—	—
	Weight	8.20	—	2
	Culmen	—	—	—
Heliangelus amethysticollis	Wing	61.20	0.50	26
	Weight	5.27	0.10	28
	Culmen	—	—	—
H. exortis	Wing	—	—	—
	Weight	4.00	—	1
	Culmen	—	—	—

APPENDIX. Continued.

Species	Character	$\bar{x}$	SD	n
H. viola	Wing	—	—	—
	Weight	5.33	—	3
	Culmen	—	—	—
H. squamigularis	Wing	—	—	—
	Weight	5.00	—	1
	Culmen	—	—	—
Eriocnemis vestitus	Wing	58.90	—	1
	Weight	5.17	—	3
	Culmen	19.10	—	1
E. luciani	Wing	67.35	0.15	4
	Weight	6.26	0.16	8
	Culmen	21.40	—	1
E. mosquera	Wing	—	—	—
	Weight	5.80	—	1
	Culmen	—	—	—
Haplophaedia aureliae	Wing	58.75	0.50	41
	Weight	5.46	0.17	37
	Culmen	20.32	—	15
Ocreatus underwoodii (M)	Wing	44.14	0.50	8
	Weight	3.03	0.14	19
	Culmen	13.00	—	1
Lesbia victoriae	Wing	59.10	—	1
	Weight	5.10	—	1
	Culmen	15.00	—	1
L. nuna (M)	Wing	49.70	—	1
	Weight	3.75	—	6
	Culmen	10.40	—	1
Sappho sparganura	Wing	57.50	—	1
	Weight	5.88	—	4
	Culmen	19.20	—	1
Polyonymus caroli	Wing	56.80	—	1
	Weight	5.03	—	4
	Culmen	20.00	—	1
Metallura phoebe	Wing	—	—	—
	Weight	5.35	—	2
	Culmen	—	—	—
M. theresiae	Wing	64.10	—	1
	Weight	5.00	—	2
	Culmen	11.80	—	1
M. eupogon	Wing	59.60	0.80	10
	Weight	4.60	0.10	10
	Culmen	—	—	—
M. williami	Wing	55.60	—	1
	Weight	4.56	0.20	5
	Culmen	11.80	—	1
M. tyrianthina	Wing	55.24	0.11	10
	Weight	3.52	0.33	21
	Culmen	10.10	—	1
Chalcostigma stanleyi	Wing	66.70	—	1
	Weight	5.84	—	11
	Culmen	9.80	—	1
Oxypogon guerinii	Wing	61.40	—	1
	Weight	5.00	—	3
	Culmen	7.50	—	1
Aglaiocercus kingi	Wing	56.85	0.60	4
	Weight	4.76	0.58	17
	Culmen	13.70	—	1

APPENDIX. Continued.

Species	Character	$\bar{x}$	SD	*n*
A. emmae	Wing	66.90	—	1
	Weight	5.70	—	1
	Culmen	14.40	—	1
Oreonympha nobilis	Wing	—	—	—
	Weight	9.00	—	1
	Culmen	—	—	—
Augastes scutatus	Wing	—	—	—
	Weight	3.00	—	1
	Culmen	—	—	—
A. lumachellus	Wing	—	—	—
	Weight	4.00	—	2
	Culmen	—	—	—
Schistes geoffroyi	Wing	51.40	1.00	8
	Weight	3.62	0.22	13
	Culmen	—	—	—
Heliothryx barroti	Wing	66.15	—	76
	Weight	5.47	0.20	9
	Culmen	17.98	—	76
H. aurita	Wing	68.60	0.30	4
	Weight	5.43	0.30	7
	Culmen	—	—	—
Heliactin cornuta	Wing	—	—	—
	Weight	7.80	—	4
	Culmen	—	—	—
Loddigesia mirabilis	Wing	38.50	—	1
	Weight	3.00	—	1
	Culmen	14.70	—	1
Heliomaster constantii (B)	Wing	68.00	—	1
	Weight	7.30	—	2
	Culmen	41.00	—	1
H. longirostris (B)	Wing	59.24	—	16
	Weight	6.55	0.68	8
	Culmen	35.18	—	16
H. squamosus	Wing	—	—	—
	Weight	5.00	—	1
	Culmen	—	—	—
H. furcifer	Wing	—	—	—
	Weight	5.00	—	1
	Culmen	—	—	—
Rhodopis vesper (M)	Wing	49.30	—	1
	Weight	3.88	—	4
	Culmen	17.40	—	1
Thaumastura cora	Wing	36.10	—	1
	Weight	2.00	—	1
	Culmen	12.80	—	1
Calliphlox evelynae	Wing	36.10	—	—
	Weight	2.40	—	2
	Culmen	—	—	—
C. bryantae (M)	Wing	41.50	—	8
	Weight	3.29	—	21
	Culmen	19.30	—	8
Philodice mitchellii	Wing	37.80	—	1
	Weight	3.13	0.10	3
	Culmen	15.00	—	1
Doricha enicura	Wing	35.26	—	29
	Weight	2.40	—	1
	Culmen	20.41	—	29

APPENDIX. Continued.

Species	Character	$\bar{x}$	SD	*n*
Tilmatura dupontii (B)	Wing	34.33	—	19
	Weight	2.23	0.15	12
	Culmen	13.11	—	19
Calothorax lucifer (B)	Wing	39.28	—	19
	Weight	2.80	—	3
	Culmen	21.05	—	19
C. pulcher (B)	Wing	37.08	—	12
	Weight	2.93	0.30	3
	Culmen	18.07	—	12
Archilochus colubris (T, B, M)	Wing	41.05	—	26
	Weight	3.19	0.30	35
	Culmen	17.96	—	27
A. alexandri (T, B, M)	Wing	44.21	1.19	119
	Weight	3.20	0.19	76
	Culmen	19.73	0.55	137
Calliphlox amethystina	Wing	—	—	—
	Weight	2.43	—	24
	Culmen	—	—	—
Mellisuga minima (A)	Wing	37.10	—	17
	Weight	2.43	0.10	6
	Culmen	10.45	—	17
M. helenae (A)	Wing	31.61	—	13
	Weight	—	—	—
	Culmen	10.76	—	13
Calypte anna (T, B, M)	Wing	49.56	0.97	71
	Weight	4.25	0.33	79
	Culmen	19.06	0.95	71
C. costae (T, B, M)	Wing	44.45	0.82	76
	Weight	3.08	0.29	58
	Culmen	17.71	0.56	107
Stellula calliope (T, B, M)	Wing	40.31	0.80	71
	Weight	2.66	0.32	51
	Culmen	15.54	0.70	71
Atthis heloisa (B)	Wing	35.12	—	25
	Weight	—	—	—
	Culmen	11.77	—	25
Myrtis fanny	Wing	40.80	—	1
	Weight	2.30	—	1
	Culmen	19.20	—	1
Acestrura mulsanti	Wing	39.55	—	2
	Weight	3.75	—	6
	Culmen	16.20	—	1
A. heliodor	Wing	32.40	—	20
	Weight	—	—	—
	Culmen	15.00	—	20
Selasphorus platycercus (T, B, M)	Wing	49.68	—	58
	Weight	3.43	0.31	86
	Culmen	17.51	0.45	145
S. rufus (T, B, M)	Wing	42.30	0.84	326
	Weight	3.36	0.31	68
	Culmen	16.57	0.67	326
S. sasin (T, B, M)	Wing	39.77	0.83	111
	Weight	3.16	0.21	38
	Culmen	17.20	0.60	111
S. flammula (M)	Wing	41.57	—	40
	Weight	2.47	—	3
	Culmen	12.90	—	40

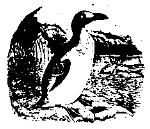
APPENDIX. Continued.

Species	Character	$\bar{x}$	SD	*n*
S. torridus	Wing	40.50	—	8
	Weight	1.90	—	1
	Culmen	11.89	—	8
S. simoni	Wing	38.68	—	11
	Weight	—	—	—
	Culmen	10.59	—	11

APPENDIX. Continued.

Species	Character	$\bar{x}$	SD	*n*
S. ardens	Wing	40.17	—	19
	Weight	—	—	—
	Culmen	12.54	—	19
S. scintilla	Wing	34.60	—	43
	Weight	2.15	0.16	39
	Culmen	11.93	—	43

100 Years Ago in The Auk



[From "Sexual selection and the nesting of birds," by J. A. Allen (1885 Auk 2: 129-139):

"Mr. Wallace, and after him Mr. Dixon and others, in discusing [sic] the question How do young birds learn to build their first nest? claim that 'instinct' has nothing to do with the matter,—that they learn by observation and are guided by memory! Says Mr. Wallace: 'It has, however, been objected that observation, imitation, or memory, can have nothing to do with a bird's architectural powers, because the young birds which in England are born in May or June, will proceed in the following April or May to build a nests [sic] as perfect and as beautiful as that in which it was hatched, although it could never have seen one built. But surely the young birds *before* they left the nest had ample opportunities of observing its *form*, its *size*, its *position*, the *materials* of which it was constructed, and the manner in which those materials were arranged. Memory would retain these observations till the following spring, when the materials would come in their way during daily search for food, and it seems highly probable that the older birds would begin building first, and that those born the preceding summer would follow their example, learning from them how the foundations of the nest were laid and the materials put together. Again we have no right to assume that young birds generally pair together,' etc. Mr. Dixon restates the case in much the same way. Alluding to 'blind instinct' as a factor in the case, he says: 'To credit the bird with such instinct, which because it seems so self-evident is taken to be matter of fact, is to admit that it possesses intellectual powers infinitely superior to those of man; whilst the evidence that can be gathered on the subject all goes to show that its intellectual powers are of precisely the same kind as man's, but some of them, of course, are infinitely inferior in degree, whilst others are unquestionably superior.' He assumes that *imitation*, *memory*, and hereditary habit, 'play the minor parts.' 'To credit birds,' he says, 'with such marvellous power as blind and infallible instinct in building their nests would be to place them far beyond man himself in intelligence, and allot to them a faculty which is superhuman . . . . A bird's intellectual powers advance towards maturity much more quickly than in the human species. A young bird three or four days old is capable of considerable powers of memory and observation, and during the time that elapses in which it is in the nest it has ample opportunity of gaining an insight into the architecture peculiar to its species. It sees the position of the nest, it notes the materials, and when it requires one for itself, is it so very extraordinary that, profiting by such experience, it builds one on the same plan? Again, birds often return to the place of their birth the following season, and possibly see the old home many times ere they want one for themselves. This, aided by the strong hereditary impulse to build a nest similar to the one in which they were born, inherited from their parents, aids them in their task.' This reasoning, I am free to confess, strikes me, to say the least, as extraordinary! A degree of mental power, at least of memory and of imitation, is ascribed to young birds which is not only 'superhuman,' but of which there is neither proof, nor even possibility of proof. Mr. Dixon has the 'three or four days old' nestling taking note of and memorizing its surroundings before, in the case of the higher Oscines, *it has the power to even open its eyes*! Yet with all this ascribed precosity and keenness of observation, and this wonderful power of memory and imitation in young birds, Mr. Dixon finds it neccessary [sic] to call in the aid of 'a strong hereditary impulse to build a nest similar to the one in which they were born,' which is more

(*continued on p. 322*)