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The ecological morphology of birds: a review

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The study of the ecological morphology of birds requires an integration of information about phylogenetic relationships among taxa and their adaptations to environments. Parallel or convergent morphological evolution can be demonstrated either by comparisons of the size and shape of birds in different lineages that occupy the same microhabitat or by comparisons of taxa that occupy similar but distant environments. The common notion that interspecific constraints affect adaptive radiation in a lineage is probably incorrect because it rests on unsupported evidence of character displacement.

At the generic level, wherein differences in morphology between species can be judged against the standard of recent common ancestry, very small differences in the shape of the feeding, wing, and/or leg complexes may be correlated with species-specific differences in foraging behavior. Morphological relationships among species in communities are more difficult to interpret. Many purported regularities in the size ratios of coexisting species cannot be distinguished from randomly distributed arrays of species sizes. Such size ratios are too crude a measure of ecological differences to be very meaningful, and the demonstration of nonrandomly distributed sizes of coexisting species is not sufficient evidence that such patterns are caused by interspecific interactions. The analogy between morphological relationships among species in a community and peaks of fitness in different populations of a single species is unfortunate because it implies that communities evolve in concert. Quantitative studies of morphological relationships among coexisting species should be extended to include consideration of the levels of abundance and rarity of the species over time.

At the intraspecific level there are many well documented cases of parallel geographic size variation. Unfortunately, we do not know the extent to which these cases are regulated by natural selection. Recently developed methods of size and shape analysis, and the possibility of field experiments designed to estimate the genetic and nongenetic components of the observed morphological variation, will probably permit new insights into the mechanisms underlying the morphological differentiation of birds in the next few years.

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1. Introduction

The study of ecological morphology is an attempt to understand the functional relationship between morphological variation in animals and their ecology. It requires an integration of information about phylogenetic relationships among taxa (Payne & Risley 1976) and adaptations to environments. Two good examples of research in this field are the study of Mares (1976) comparing the morphological relationships in two desert and one forest assemblage of rodents, and that by Leisler and Thaler (this issue) comparing the external morphology, skeletal elements, and foraging ecology of two species of *Regulus*. Additional examples would include comparisons of families that appear to be filling the same role on different continents and experiments about the genetic and nongenetic contributions to clinal variation within species.

The broader aspects of ecological morphology use the comparative approach to search for morphological trends in different lineages and environments. The results are usually presented in graphic form (e.g. Karr & James 1975) or, most recently, as statements that can be tested in relation to null hypotheses (Simberloff & Boecklen 1981). This approach precludes statistical replication or randomization of experimental units, so inferences about the causes of observed patterns in "natural experiments" are necessarily weak (Simberloff, this volume, Wiley & Cruz 1980, Orians & Solbrig 1977). Nevertheless, proper statistical use of the comparative approach is useful for formulating empirical generalizations and making predictions.

The best possibilities for analyzing the mechanism(s) that underlie the relationship between morphology and ecology are at the level of field experiments at the intraspecific level.

There are surprisingly few cases of natural selection in which the selective agent and the object of selection are known with certainty (Wright 1978, Boag & Grant 1981, Fleischer & Johnston 1982). My objective is to review the literature on the ecological morphology of birds. I will occasionally use examples about mammals, but will not attempt to discuss related papers on other groups (e.g. Pianka 1975, Brown 1965, Patterson 1981). I hope the reader will realize that comments about methods of analysis and criteria for tests of patterns of variation apply to research on other taxa.

Similarities in the skeletal and external morphology of birds that behave in similar ways can be demonstrated either by comparisons of the size and shape of birds occupying the same microhabitat or by comparisons of taxa in similar but distant environments. The tarsometatarsus (distal leg element) is relatively shorter in most birds that forage on the trunks of trees (Piciformes, Dendrocolaptidae, and Certhiidae; Richardson 1942) or hang from slender branches (Palmgren 1932) than in birds that forage on the ground (Rüggeberg 1960, Dilger 1956) or use rigid perches (Grant 1966, 1971). And the wings are more rounded in birds that maneuver through closed habitats (Phasianidae, Strigiformes) than in birds that forage above the vegetation (Hirundinidae) (Savile 1957). A particularly striking example of convergent evolution in unrelated taxa is the similarity in morphology, plumage, habitat, and behavior between the American icterid meadowlarks (*Sturnella*) and the African motacillid longclaws (*Macronyx,* Friedmann 1946). Some of the other well known examples are the similarities between the New World wood warbers (Parulidae), certain tyrant flycatchers (Tyrannidae), and American vultures (Cathartidae) and their apparent counterparts among the Old World warblers (Sylviidae), flycatchers (Muscicapidae) and vultures (of the Accipitridae). Reviews by Mayr (1946), Lack (1968), Lein (1972), and Cody (1974) cite many more examples.

The classical works in biogeography contain insightful observations about patterns of morphological variation among lineages. First, Alfred Russel Wallace (1869) noted not only apparent convergences of taxa in similar but distant environments but also parallel geographic variation in pairs of species, a phenomenon he attributed to mimicry. Second, Rensch (1936) and Huxley (1942) wrote extensively about parallel geographic trends of intraspecific variation in many species of birds. These studies of parallelism and convergence (Mayr 1963) should be reviewed thoroughly and integrated with modern studies of allometric constraints on variation (see Wake 1978, Gould 1971, Mosimann & James 1979, Hills 1982).

2. The role of the associated fauna

Assuming wing length to be a general indicator of size and bill length an indicator of the kind and sizes of food eaten, Keast (1972) plotted the species of African and Australian insectivorous species in the graphic morphological space that was encompassed by the tyrant flycatchers of South America. He argued that in South America the tyrannids were able to radiate widely because of isolation from competitors, but in Africa a series of invasions of birds already adapted for catching insects in certain ways precluded a wide radiation by any one family. Keast's argument is weakened by the fact that approximately the same number of insectivorous taxa occur in the isolated continent of Australia as in Africa. Moreover, the richness of the South American woodpecker fauna does not seem to have prevented the wood-

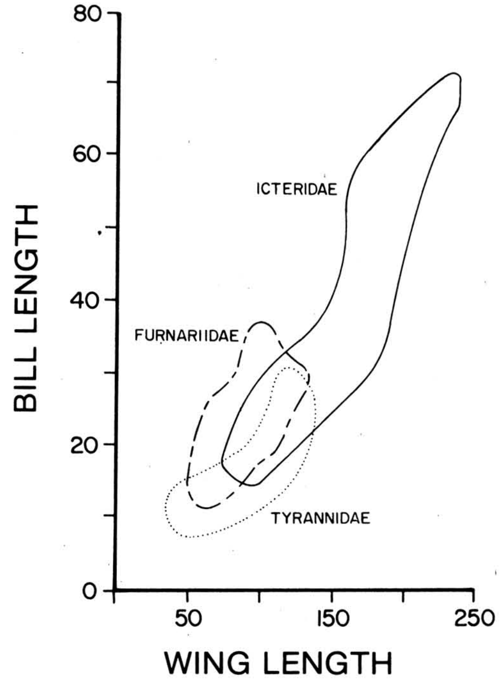

Fig. 1. A comparison of the extent of morphological radiation in three families of birds in South America: a) Tyrannidae, > 370 species (redrawn from Keast 1972); b) Furnariidae, >215 species (from data in Vaurie 1980); and c) Icteridae, 95 species. The icterid data include some North and Central American species but do not include several large icterids in the genus *Psaricolius* whose bill and wing measurements (mm) exceed the maximum shown here (see footnote to Table 1).

creepers from radiating there, and the absence of woodpeckers has not led to the diversification of creeper-like birds in Australia (Lein 1972). The classical solitary radiations of the honeycreepers (Drepanididae) on the Hawaiian Islands (Amadon 1950) and the Galápagos finches (Geospizinae; Lack 1947, Bowman 1961) are no more extreme than those of the South American blackbirds (Icteridae; Beecher 1951) or ovenbirds (Furnariidae; Vaurie 1980). These last two families, plus Keast's example of the tyrant flycatchers, have evolved in the midst of the largest continental avifauna on earth (Fig. 1). Evidence that the cooccurrence of other species affects allopatric speciation seems to be based on selected examples and many counterexamples are available.

If preemption of resources by one or more taxa were restricting the process of speciation in another taxon (Keast 1977), the phenomenon would entail successive cases of interspecific constraints on morphological differentation (Brown & Wilson 1956). Lack (1947) and many subsequent authors have assumed that such a process accounts for ecomorphological patterns. Some authors also contend that interspecific constraints cause convergences (see Patterson 1981 on chipmunks, *Eutamias*; Cody & Mooney 1978). But Grant (1972) made a detailed review of all published information about morphological character displacement and found that there are no unequivocal cases demonstrating that such a process exists (see also Grant 1975). The evidence that interspecific relationships among birds affect differentiation is very weak.

3. Differences at the generic level

The generic level is especially appropriate for the analysis of ecological morphology because differences among closely related species can be judged against the standard of their recent common ancestry (Inger 1958). The best examples for birds are the studies of tits (Paridae) by Partridge (1976) and of warblers (Sylviidae) by Leisler (1977, 1980a, b, c, 1981). Leisler combines field work with behavioral studies in aviaries, and studies of external and skeletal morphology. By studying many variables of the feeding, wing and leg complexes, he can show that the reed-dwelling genus *Acrocephalus* has differentiated in foot morphology more than the genus *Locustella* and that the major difference between *Sylvia* and *Hippolais* is in the shape of the wing (Fig. 2). Subtle morphological differences within genera are correlated with species-specific foraging behavior. That these differences are important correlates of habitat selection is clear from the study by Bairlein (1980) showing that each species occurs in an extremely narrow range of habitats even during migration (see also Baker 1979).

Morphological correlates of foraging behavior are also apparent in the wood warblers (Parulidae). Small differences in the length of leg bones divided by the cube root of body weight fit predictions based on behavioral observations (Osterhaus 1962). Similarly, Cruz (1978) compared the external morphology of the Jamaican Blackbird (*Neospar nigerrimus*) with that of other icterids. Its relatively long bill, short legs, curved claws and long hallux permit it to forage efficiently in bromeliads along the trunks of trees, and in these respects it differs from its closest relatives in *Agelaius* (see also Wiley & Cruz 1980). Of course these detailed studies are also relevant to analyses of assemblages of species. Norberg (1979) was able to predict the microlocation of each species within a feeding assemblage wintering in European coniferous forests on the basis of subtle differences

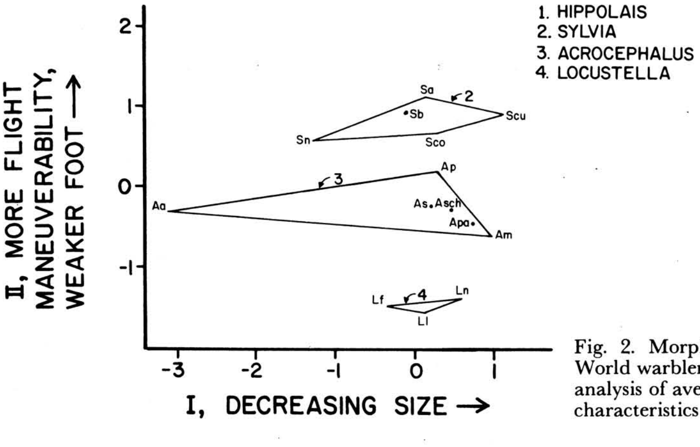

Fig. 2. Morphological variation in several genera of Old World warblers (Sylviidae), based on a principal components analysis of averages for 42 characters of external and skeletal characteristics (redrawn from Leisler 1980a, Fig. 9).

in wing, tail, and leg morphology. But species that are known to compete for food need not always differ in morphology. A very detailed study of the functional morphology of the feeding mechanism in several species of wheatears (*Oenanthe*) (Potapova & Panov 1977) revealed no differences.

4. Relationships within and among assemblages of species

To analyze morphological relationships within communities is a far more difficult problem than to analyze differences within lineages. First, there are only vague criteria for defining the boundaries of communities. When these are standardized, estimates of the resources of a habitat, such as those based on the structure of the vegetation, can be used to predict the general species richness and relative abundance of birds present (James & Rathbun 1981). But the history of the fauna and the dispersal capabilities of the species (Pregill & Olson 1981, Travis & Ricklefs, in press) underlie the establishment of such patterns.

Wiens & Rotenberry (1980) examined their data for breeding bird communities in grassland and shrubsteppe habitats of the central United States and were unable to find support for several published generalizations about ecomorphological relationships at this level. For example, they found that bill size was not positively correlated with prey size (Schoener 1965, Hespenheide 1966, 1973) and that smaller species were not more specialized in their diet than larger ones (Kear 1962). Their tests for clinal variation were based on only five localities, so in this case their negative result was not an adequate test of whether clines exist. In fact, clinal variation has been well documented elsewhere for two of their five species (*Sturnella magna* James 1970; *Eremophila alpestris,* Niles 1973). Nevertheless, Wiens and Rotenberry point out that some processes operating at the community level are not as tightly coupled to morphological differences among the member species as was implied by the analysis of Ricklefs & Cox (1977) in their study of a community of birds on St. Kitts.

5. Limiting similarity

Whether behavioral interactions between species result in restrictions on the sizes that occur in a community or assemblage has been a controversial topic. Hutchinson (1959) thought such regularities occurred and suggested that the sizes of coexisting species, when ranked in a decreasing array, generally show minimal limits of similarity. Simberloff & Boecklen (1981) contend that the published evidence for such purported regularities in size ratios cannot usually be distinguished from randomly distributed arrays of species sizes. But Brown (in press), Schoener (1965, 1974, in press), and Oksanen et al. (1979) not only find such patterns, they attribute them to interspecific interactions. The strongest case is made by Bowers & Brown (1982) on the basis of experimental manipulations of desert assemblages of rodents.

Schoener (1965) does not expect patterns of limiting similarity among the sizes or bill lengths of assemblages of breeding songbirds because in songbird assemblages resources do not seem to be limiting. This is only one of several possible arguments. First, single measurements of external morphology are not adequate to estimate differences among species (Root 1967; Wiens, this issue), and second, morphological differences need not be adaptations to conditions of the breeding season (Lack 1954, 1966, Fretwell 1972). Finches can be used as an example for both of these cases. Almost all songbirds eat invertebrates in the breeding season, including the four lineages that have conical bills and are adapted to eating seeds in the nonbreeding seasons. Each of the four groups has a unique method of ingesting seeds. Fringillids prefer the seeds of dicots, which they slice with sharp mandibles; emberizids, ploceids, and estrildids prefer grass seeds, which they squeeze in different ways against a stiffened tongue (Ziswiler 1980). The size ratios of the bill length of birds with conical bills, in all four groups, are too crude a measure to provide meaningful estimates of these ecological differences (Kear 1962, Newton 1967, Root 1967), and the relevance of differences in bill length to patterns of coexistence during the breeding season is doubtful. Similar examples could be developed for other taxa.

Strong et al. (1979), Strong & Simberloff (1981), and Simberloff & Boecklen (1981) insist that, before assigning causes to observed morphological relationships, one should conduct tests of whether the relationships are different from those that would occur by chance. Gatz (1981) followed this advice and demonstrated a nonrandom pattern of morphological relationships among fish communities. Then he assumed that this demonstration of a pattern was sufficient evidence that its underlying cause was interspecific interactions. Obviously, the relative importance of other potential causes needs to be evaluated as well.

6. The Hutchinsonian model

In 1957 Hutchinson proposed that the ecological niches of associated species could be located in a hypothetical n-dimensional resource space in such a way that their fitness relationships would be represented (he was careful to emphasize that this model could not be used to test the validity of the Gause-Volterra competition principle on which it is based). In 1968 Hutchinson suggested further that morphological relationships among coexisting species, as determined by numerical taxonomic methods, could provide a similar space. Assuming that functions exist that permit the transformation of the morphological relationships to values of environmental variables, the morphological and niche spaces would be interchangeable, and the positions of species would correspond to adaptive peaks in the sense of Wright (1932). This analogy, between the morphological relationships among species in a community and peaks of relative fitness in different populations of a single species, is unfortunate because it implies that communities evolve in the same neo-Darwinian way that we think populations and lineages evolve. Because there is no evidence that species evolve in concert, the term "evolution of communities" means only the history of species associations. Nevertheless, the Hutchinsonian model has focussed attention on the quantitative analysis of morphological relationships among sets of species that coexist. Furthermore, ecological and behavioral interactions may affect assemblages (Cody 1974, 1978, Noon 1981, Pulliam 1975; Birch 1979 reviews the experimental evidence).

One of the first multivariate comparisons of morphological relationships among faunas was constructed by Findley (1973) for bats in order to discover whether more speciose faunas are more tightly packed into their overall morphological niche space than less speciose faunas are. Gatz (1980) pointed out that the method Findley (1976) used is preferable because he calculated Euclidean distances between taxa rather than summing branches of a Prim network. Using this method, Gatz (1979) concluded that more speciose fish communities are not more tightly packed, confirming a prediction of Schoener (1965). Karr & James (1975) showed that the results of such analyses depend partly on which characters are selected for study.

There has been a series of attempts to quantify the extremely complex situation in which sets of species in similar but distant environments appear to have ecologically equivalent taxa that are unrelated. But Orians & Solbrig (1977) concluded that there is as yet no theory that accounts for the "evolution of convergent ecosystems." Cody & Mooney (1978) and Cody (1974) discussed similarities among bird communities occupying scrub habitats in California, Chile, and the Mediterranean region, but gave no comparisons with communities that are presumed to be less convergent. Karr & James (1975) compared one temperate and two tropical bird communities in terms of morphological relationships but give no tests. Mares (1976) compared a desert assemblage of rodents in Argentina with another assemblage in the Sonoran Desert of the southwestern United States and a nearby assemblage in a coniferous forest. He showed that the degree of desert adaptation is apparently less in Argentina than in the Sonoran desert, as would be expected from the known history of the faunas. Niemi (ms) is taking a different comparative approach in his study of birds breeding in New World (Minnesota) and Old World (Finland) peatlands. He compares species in the peatlands with their congeners in other habitats, in order to discover morphological trends that may be associated with adaptations to peatland habitats. Ricklefs & Travis (1980) analyzed morphological relationships among 11 communities studied by Cody (1974) in chaparral habitats of California and matorral habitats in Chile. They presented a statistical test of community convergence based on whether the morphology of birds in presumed convergent communities is more similar than combinations of the same species that do not actually cooccur. In one case their model does not detect the difference between real birds and a random combination of parts of birds. This result emphasizes that we do not yet have null models that are sufficiently sensitive to detect whether the phenomenon of interest exists.

In most studies of limiting similarity, phenetic packing, and multivariate morphological relationships among coexisting species, there is no consideration of the relative abundance of the component species. Certainly if interspecific interactions affect bird distribution sufficiently to account for patterns of species distributions (Diamond 1975), and the relationships are based on morphological similarities (Cody 1974), we need studies to determine whether species of similar morphology have reciprocal levels of abundance and rarity. James & Boecklen (in press) examined one community of twenty species breeding in a 12 ha upland deciduous forest in Maryland. A few pairs of species showed reciprocal densities over time, but there was no morphological evidence that either the community as a whole or guilds within the community were organized by interspecific interactions. Consideration of the abundant versus the rare species did not indicate that morphological relationships constrained community structure.

7. Intraspecific variation

There are many well-documented cases of parallel geographic size variation in different species of birds (Rensch 1936, 1960, Huxley 1942, James 1970, and others). Species that vary geographically are generally larger in either cooler or drier areas, where the evaporation is greatest (Hamilton 1958, 1961, Power 1969), such as deserts, mountains, and high latitude locations (James 1970). Because these trends can be seen on a scale of even 1 degree latitude-longitude blocks across broad continental regions, and because species of very different ecology (songbirds, owls, woodpeckers) have the same patterns, adaptations to the physical environment are implicated (Mosimann & James 1979). Bergmann's Rule as formulated by Mayr (1963) (that races in cooler climates tend to be larger than races of the same species in warmer climates) is an inadequate expression of our current knowledge of clinal variation in birds, because consideration is limited to dry-bulb temperature. When additional avenues of heat exchange between the organism and the environment are considered, the size/climate relationships become more impressive, and many exceptions are accounted for. Nevertheless, judgments about the adaptive nature of observed patterns often involve circular reasoning (Rothstein 1982), and the possibility that the variation is a passive byproduct of other processes leaves nagging doubts.

There have been only a few attempts to quantify the total phenotypic variation for a single species (Johnston & Selander 1973) and a few hints at its significance (Johnston 1972, 1973, Gould & Johnston 1972, Baker & Moeed 1979). Selander (1966) reviewed the arguments for ecological interpretations versus sexual selection in the analysis of patterns of sexual dimorphism in size and shape. Baker (1979), Selander & Johnston (1967), and Johnston & Fleischer (1981) have made detailed analyses of sexual dimorphism in the House Sparrow (*Passer domesticus*).

In spite of the large literature describing patterns of ecological and morphological covariation and the many neo-Darwinian studies documenting shifts in gene frequency when environments change, we do not really know the extent to which natural selection regulates variation in adult phenotypes (Maze & Bradfield 1982, Wake 1978, Wright 1978). Changes in the average phenotypic value of a trait can be caused by selection for a covarying trait (perhaps physiological or developmental; Løvtrup 1974, Wake 1978) by genetic drift (Lande 1976) and by nongenetic processes (Harrison 1959). Even the assumption that clines of character variation are entirely the result of a balance between natural selection and gene flow (Endler 1979) is not sacrosanct. By exchanging eggs of Red-winged Blackbirds (*Agelaius phoeniceus*) between nests in northern and southern Florida, and following the subsequent development of nestlings, I have been able to show that a substantial amount of the differences in shape between the populations of nestlings is nongenetic (James, unpubl.). Also, Berven et al. (1979) reported similar results in a study of variation in the green frog (*Rana clamitans*). They showed that a size cline increasing with elevation in the Appalachian mountains was an environmentally-induced growth response to a temperature gradient and that natural selection for early metamorphosis was operating in the opposite direction from the cline. The nongenetic effects of food and the physical environment on the morphology of wild birds need more study, and we need experiments designed to compare different populations of the same species. Recent work on the heritability of morphological characters in natural populations is an important contribution to this effort. But which of the many sets of correlated characters might be the object of selection is rarely known. New work by Smith & Zach (1979), Smith & Dhondt (1980), Van Noordwijk et al. (1980), Findlay & Cooke (1982), Dhondt (1982) and Boag & Grant (1981) indicates that this area of research will develop rapidly in the next few years.

8. Size and shape analysis

Studies of morphological patterns can be expressed by simple bivariate plots of two of the characters (e.g. Fig. 1), but such plots show only a small part of the differences that are apparent when comparisons are made visually. Fenton (1972) was able to express more of the observed variation in his study of bat faunas by using ratios as variables and having an accompanying index to size differences. With multivariate methods, such as principal components analysis, many variables can be studied simultaneously, and the resulting plots can express covariation in sets of characters. Atchley et al. (1976; see also Ricklefs & Travis 1980) object to using ratios as variables in multivariate analysis because ratios are frequently not normally distributed (see Hills 1978 for a response). Ratios and proportions are very basic variables in morphological analysis, so their proper mathematical treatment is an

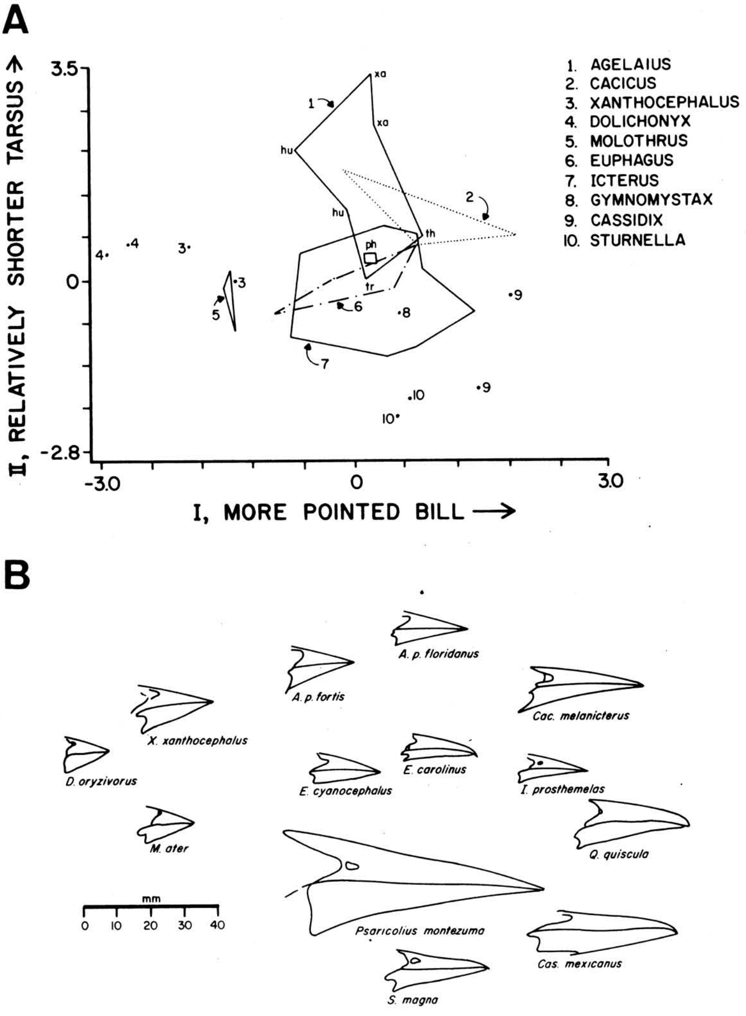

Fig. 3. Morphological variation in shape among 39 species in the American family Icteridae (oropendolas, caciques, blackbirds, meadowlarks, orioles, and cowbirds). — A: A principal components analysis of variation in shape gives overall morphological relationships. Intraspecific variation in the Red-winged Blackbird, *Agelaius phoeniceus* (ph) was added by weighting average measurements for extreme populations by the coefficients in Table 1. — B: Outlines of the bills of selected taxa arranged in a similar space show how the extremes of intraspecific variation in *Agelaius phoeniceus* (e.g. *A. p fortis,* northern Great Plains; *A. p. floridanus,* southern Florida) fit into the pattern of interspecific variation.

important concern.

Mosimann (1970, 1975a, b) proposed a method of defining size and shape in a way that is geometrically meaningful and that permits the study of their joint statistical distribution. A size variable can be any measurement, sum of measurements, or geometric mean that has intuitive appeal. Shape variables are ratios or proportions, and isometry is defined as the lack of statistical association of shape with a specified size variable. The choice of the size variable is very important, and no one measure is ideal for all cases (Mosimann & James 1979). If the original data follow a multivariate lognormal distribution, their logs jointly follow a multivariate normal distribution, and a wealth of statistical methods is available. For example, Mosimann & James (1979) used the multiple correlation coefficient to test for and measure the extent of the association of shape with a variety of size variables. The goal of size and shape analysis is not to produce uncorrelated size and shape variables, but to define size and shape precisely and then analyze how they are related. It would be interesting to combine size and shape analysis with studies of spatial autocorrelation (Cliff & Ord 1973, Sokal & Riska 1981).

For an analysis of geographical variation in Red-winged Blackbirds in Florida (Mosimann & James 1979), wing length was the best size variable because it had the highest between-locality/within-locality variance ratio. We could then analyze bill shape in relation to size variation. If Beecher (1951) was correct in his idea

Table 1. Principal components analysis of general shape relationships among species of the family Icteridae based on single specimens of each sex.[1] PCI accounts for 46 % of the variance, PCII for an additional 35 %.

Shape Variable[2]	Correlations PCI	Correlations PCII	Coefficients PCI	Coefficients PCII
log wing length — log tarsus	0.04	0.84	0.02	0.60
log central toe — log tarsus	0.15	0.82	0.08	0.59
log bill length — log bill depth	0.95	−0.07	0.52	−0.05
log bill depth — log bill width	0.95	−0.10	0.52	−0.07

[1]) Data include only those 39 species available in the collection of the Florida State Museum. For a few species no female specimens were available. The family contains a total of 95 species.

[2]) Differences between logs are equivalent to ratios. See Mosimann and James (1979) for methods.

that the Icteridae as a whole have undergone radiation from a seed-eating finch-like ancestor into fruit-, nectar-, and insect-eating forms, the increase in size might have followed a change in bill shape even in intraspecific differentiation. But the fact that many other species of diverse diet have the same clines of size variation (James 1970) suggests that the shape variation may be merely an allometric by-product of clinal size variation. We cannot choose among these ideas on the basis of empiricial observations, but to be able to analyze the covariation of size and shape is a considerable aid in ecomorphological work.

Fig. 3 gives an example of how shape can be studied by principal components analysis. Fig. 3a gives the variation in shape among 39 species of icterids based on a principal components analysis of shape variables for study skins of one male and one female for each species (Table 1). (The data for bill width and wing length are the same as in Fig. 1, where size differences dominate the graph.) I have included the extremes of intraspecific variation in the shape of the widespread Red-winged Blackbird (*Agelaius phoeniceus*). Fig. 3b gives outlines of the bill size and shape for a subset of these species arranged in a comparable way. Here the extremes of bill shape in populations of Red-winged Blackbirds, those in the central Great Plains and southern Florida, can be compared in the context of variation in the family as a whole.

9. Conclusions

At the broad comparative level, studies of assemblages or between faunas can detect interesting patterns of parallelism and convergence in the morphology of birds, but the discovery of such relationships is unlikely to suggest the mechanisms that underlie the establishment of these patterns. Ecologists tend to become either overly concerned with arbitrary size comparisons or mired in matrices in which size and shape relationships are confounded, and systematists seem overly concerned with constructing branching diagrams. To cladists the parallelisms and convergences that are the object of study in ecological morphology are just a hindrance to creating a natural classification (Ashlock 1974) or to understanding historical biogeography (Rosen 1978). The job of quantifying and analyzing the relationship between the legacy of phylogenetic attributes of taxa in relation to potential sources of change, and then relating the results to past and present environmental conditions, requires behavioral studies, analysis of the covariation of size and shape, quantification of resources, and determination of the genetic and nongenetic components of morphological variation. These are promising areas of research in evolution, but the analytical problems are so complex that it is not surprising that comparisons for members of communities of unrelated birds are frequently unsatisfying. Evolutionary relationships are best studied within and between lineages where phylogenetic relationships based on anatomical comparisons can be used as a standard against which differences can be judged.

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References

Amadon, D. 1950: The Hawaiian honeycreepers (Aves, Drepanididae). — Bull. Amer. Mus. Nat. Hist. 95.

Ashlock, P. D. 1974: The uses of cladistics. — Ann. Rev. Ecol. Syst. 5: 81-99.

Atchley, W. R., Gaskins, C. T. & Anderson, D. T. 1976: Statistical properties of ratios. I. Empirical results. — Syst. Zool. 25: 137-148.

Bairlein, F. 1980: Ecosystem analysis of resting areas of migratory birds: description and interpretation of trapping stations of the "Mettnau-Reit-Illmitz-Program." — Ökol. Vögel 3: 7-137.

Baker, M. 1979: Morphological correlates of habitat selection in a community of shorebirds (Charadriiformes). — Oikos 33: 121-126.

Baker, A. J. & Moeed, A. 1979: Evolution in the introduced New Zealand populations of the common myna Acridotheres tristis. — Can. J. Zool. 57: 570-584.

Beecher, W. J. 1951: Adaptations for food-getting in the

American blackbirds. — Auk 68: 411-440.

Berven, K. A., Gill, D. E. & Smith-Gill, S. J. 1979: Countergradient selection in the green frog, Rana clamitans. — Evolution 33: 609-623.

Birch, L. C. 1979: The effect of species of animals which share common resources on one another's distribution and abundance. — Fortschr. Zool. 25: 197-221.

Boag, P. T. & Grant, P. R. 1981: Intense natural selection on a population of Darwin's Finches (Geospizinae) in the Galápagos. — Science 214: 82-85.

Bowers, M. A. & Brown, J. H. 1982: Body size and coexistence in desert rodents: chance or community structure? — Ecology 63: 391-400.

Bowman, R. I. 1961: Morphological differentiation and adaptation in the Galápagos finches. — Univ. Calif. Berkeley Publ. Zool. 58: 1-302.

Brown, J. H.: Patterns and processes in three guilds of terrestrial vertebrates. — In: Strong, D. R., Simberloff, D. & Abele, L. G. (eds.), Ecological communities: conceptual issues and the evidence. — Princeton Univ. Press, Princeton. In press.

Brown, W. H. & Wilson, E. O. 1956: Character displacement. — Syst. Zool. 5: 48-64.

Brown, W. L., Jr. 1965: Numerical taxonomy, convergence, and evolutionary reduction. — Syst. Zool. 14: 101-109.

Cliff, A. D. & Ord, J. K. 1973: Spatial autocorrelation. — Pion Limited, London.

Cody, M. L. 1974: Competition and the structure of bird communities. — Princeton University Press, Princeton, N.J. 318 pp.

—»— 1978: Habitat selection and interspecific territoriality among the sylviid warblers of England and Sweden. — Ecol. Monogr. 48: 351-396.

Cody, M. L. & Mooney, H. A. 1978: Convergence versus nonconvergence in Mediterranean-climate ecosystems. — Ann. Rev. Ecol. Syst. 9: 265-321.

Cruz, A. 1978: Adaptive evolution in the Jamaican Blackbird Neospar nigerrimus. — Ornis Scand. 9: 130-137.

Dhondt, A. A. 1982: Heritability of blue tit tarsal length from normal and cross-fostered broods. — Evolution 36: 418-419.

Diamond, J. M. 1975: Assembly of species communities. — In: Cody, M. L. & Diamond, J. M. (eds.), Ecology and evolution of communities: 342-444. Harvard Univ. Press, Cambridge, Mass.

Dilger, W. C. 1956: Adaptive modifications and ecological isolating mechanisms in the thrush genera Catharus and Hylocichla. — Wilson Bull. 68: 171-199.

Endler, J. A. 1979: Gene flow and life history patterns. — Genetics 93: 263-284.

Fenton, M. B. 1972: The structure of aerial-feeding bat faunas as indicated by ears and wing elements. — Can. J. Zool. 50: 287-296.

Findlay, C. S. & Cooke, F. 1982: Breeding synchrony in the Lesser Snow Goose (Anser caerulescens caerulescens). I. Genetic and environmental components of hatch date variability and their effects on hatch synchrony. — Evolution 36: 342-351.

Findley, J. S. 1973: Phenetic packing as a measure of faunal diversity. — Amer. Natur. 107: 580-584.

—»— 1976: The structure of bat communities. — Amer. Natur. 110: 129-139.

Fleischer, R. C. & Johnston, R. F. 1982: Natural selection on body size and proportions in house sparrows. — Nature 298: 747.

Fretwell, S. 1972: Populations in a seasonal environment. — Monogr. Pop. Biol., Princeton Univ. Press.

Friedmann, H. 1946: Ecological counterparts in birds. — Sci. Monthly 63: 395-398.

Gatz, A. J., Jr. 1979: Community organization in fishes as indicated by morphological features. — Ecology 60: 711-718.

—»— 1980: Phenetic packing and community structure: a methodological comment. — Amer. Natur. 116: 147-149.

—»— 1981: Morphologically inferred niche differentiation in stream fishes. — Amer. Midl. Nat. 106: 10-21.

Gould, S. J. 1971: Geometric scaling in allometric growth: a contribution to the problem of scaling in the evolution of size. — Amer. Natur. 105: 113-136.

Gould, S. J. & Johnston, R. F. 1972: Geographical variation. — Ann. Rev. Ecol. Syst. 3: 457-498.

Grant, P. R. 1966: Ecological incompatibility of bird species on islands. — Amer. Natur. 100: 451-462.

—»— 1971: Variation in the tarsus length of birds in island and mainland regions. — Evolution 25: 599-614.

—»— 1972: Convergent and divergent character displacement. — Biol. J. Linn. Soc. 4: 39-68.

—»— 1975: The classical case of character displacement. — In: Dobzhansky, T., Hecht, M. & Steere, W. C. (eds.), Evol. Biol. 8: 237-337. Plenum Press.

Hamilton, T. H. 1958: Adaptive variation in the genus Vireo. — Wilson Bull. 70: 307-346.

—»— 1961: The adaptive significances of intraspecific trends of variation in wing length and body size among bird species. — Evolution 15: 180-195.

Harrison, G. A. 1959: Environmental determination of the phenotype. — In Cain, S. A. (ed.), Function and taxonomic importance. Syst. Assoc. Publ. No. 3: 81-86. Oxford Univ. Press.

Hespenheide, H. A. 1966: The selection of seed size by finches. — Wilson Bull. 78: 191-197.

—»— 1973: Ecological inferences from morphological data. — Ann. Rev. Ecol. Syst. 4: 213-229.

Hills, M. 1978: On ratios — a response to Atchley, Gaskins, and Anderson. — Syst. Zool. 27: 61-62.

—»— 1982: Allometry. — In: Encyclopedia of statistical sciences, Vol. 1. John Wiley and Sons, N.Y.

Hutchinson, G. E. 1957: Concluding remarks. — Cold Spring Harbor Symp. Quant. Biol. 22: 415-427.

—»— 1959: Homage to Santa Rosalia, or why are there so many kinds of animals? — Amer. Natur. 93: 145-159.

—»— 1968: When are species necessary? — In: Lewontin, R. C. (ed.), Population biology and evolution. Syracuse Univ. Press.

Huxley, J. 1942: Evolution: the modern synthesis. — Allen and Unwin, London.

Inger, R. F. 1958: Comments on the definition of genera. — Evolution 12: 370-384.

James, F. C. 1970: Geographic size variation in birds and its relationship to climate. — Ecology 51: 365-390.

James, F. C. & Boecklen, W. J.: Interspecific morphological relationships and the densities of birds. — In Strong, D. R., Simberloff, D. & Abele, L. G. (eds.), Ecological communities: conceptual issues and the evidence. Princeton Univ. Press, Princeton. In press.

James, F. C. & Rathbun, S. 1981: Rarefaction, relative abundance and diversity of avian communities. — Auk 98: 785-800.

Johnston, R. F. 1972: Ecologic differentiation in North American birds. — In Allen, R. T. & James, F. C. (eds.), A Symposium on Ecosystematics. Univ. Ark. Museum Occ. Pap. 4: 101-126, Fayetteville.

—»— 1973: Evolution of the House Sparrow IV. Replicate studies in phenetic covariation. — Syst. Zool. 22: 219-226.

Johnston, R. F. & Fleischer, R. C. 1981: Overwinter mortality and sexual size dimorphism in the House Sparrow. — Auk 98: 503-511.

Johnston, R. F. & Selander, R. K. 1973: Evolution in the House Sparrow. III. Variation in size and sexual dimorphism in Europe and North and South America. — Amer. Nat. 107: 373-390.

Karr, J. R. & James, F. C. 1975: Ecomorphological configurations and convergent evolution. — In: Cody, M. L. & Diamond, J. M. (eds.), Ecology and evolution of communities. Harvard University Press.

Kear, J. 1962: Food selection in finches with special reference to interspecific differences. — Proc. Zool. Soc. London 138: 163-204.

Keast, A. 1972: Ecological opportunities and dominant families, as illustrated by the neotropical Tyrannidae (Aves). — In: Dobzhansky, T., Hecht, M. K. & Steere, W. C. (eds.), Evolutionary Biology 5: 229-277.

—»— 1977: Zoogeography and phylogeny: the theoretical background and methodology to the analysis of mammal and bird fauna. — In: Hecht, M. K., Goody, P. C. & Hecht, B. M. (eds.), Major patterns in vertebrate evolution. Plenum Press, New York.

Lack, D. 1947: Darwin's Finches. — Cambridge Univ. Press, Cambridge.

—»— 1954: The natural regulation of animal numbers. — Oxford.

—»— 1966: Population studies of birds. — Clarendon Press.

—»— 1968: Ecological adaptations for breeding in birds. — Methuen, London.

Lande, R. 1976: Natural selection and random genetic drift in phenotypic evolution. — Evolution 30: 314-334.

Lein, M. R. 1972: A trophic comparison of avifaunas. — Syst. Zool. 21: 135-150.

Leisler, B. 1977: Die ökologische Bedeutung der Lokomotion mitteleuropäischer Schwirle (Locustella). — Egretta 1: 1-25.

—»— 1980a: Morphological aspects of ecological specialization in bird genera. — Ökol. Vögel 2: 199-200.

—»— 1980b: Ökomorphologische Freiland- und Laboratoriumsuntersuchungen. — Acta XVII Congr. Int. Ornithol., pp. 202-208.

—»— 1980c: Morphologie und Habitatnutzung europäischer Acrocephalus-Arten. — Acta XVII Congr. Int. Ornithol., pp. 1031-1037.

—»— 1981: Die ökologische Einnischung der mitteleuropäischen Rohrsänger (Acrocephalus, Sylviinae). I. Habitattrennung. — Vogelwarte 31: 45-74.

Løvtrup, S. 1974: Epigenetics, a treatise on theoretical biology. — Wiley.

Mares, M. A. 1976: Convergent evolution of desert rodents: multivariate analysis and zoogeographic implications. — Paleobiology 2: 39-63.

Mayr, E. 1946: History of the North American bird fauna. — Wilson Bull. 58: 3-41.

—»— 1963: Animal species and evolution. — Harvard Univ. Press.

Maze, J. & Bradfield, G. E. 1982: Neo-Darwinian evolution — panacea or popgun. — Syst. Zool. 31: 92-95.

Mosimann, J. E. 1970: Size allometry: Size and shape variables with characterizations of the lognormal and generalized gamma distributions. — J. Amer. Stat. Assoc. 65: 930-945.

—»— 1975a: Statistical problems of size and shape. I. Biological applications and basic theorems. — In Patil, G. P., Kotz, S., & Ord, K. (eds.), Statistical distributions in scientific work 2: 187-217. D. Reidel Publ. Co., Dordrecht-Holland.

—»— 1975b: Statistical problems of size and shape. II. Characterizations of the lognormal and gamma distributions. — In Patil, G. P., Kotz, S., & Ord, K. (eds.), Statistical distributions in scientific work 2: 219-239. D. Reidel Publ. Co., Dordrecht-Holland.

Mosimann, J. E. & James, F. C. 1979: New statistical methods for allometry with application to Florida red-winged blackbirds. — Evolution 33: 444-459.

Newton, I. 1967: The adaptive radiation and feeding ecology of some British finches. — Ibis 109: 33-98.

Niles, D. M. 1973: Adaptive variation in body size and skeletal proportions of horned larks of the southwestern United States. — Evolution 27: 405-426.

Noon, B. R. 1981: The distribution of an avian guild along a temperate elevational gradient: the importance and expression of competition. — Ecol. Monogr. 51: 105-124.

Norberg, U. M. 1979: Morphology of the wings, legs, and tail of three coniferous forest tits, the goldcrest, and the treecreeper in relation to locomotor pattern and feeding station selection. — Phil. Trans. Royal Soc. London 287: 131-165.

Oksanen, L., Fretwell, S. D. & Järvinen, O. 1979: Interspecific aggression and the limiting similarity of close competitors: The problem of size gaps in some community arrays. — Amer. Natur. 114: 117-129.

Orians, G. H. & Solbrig, O. T. (eds.) 1977: Convergent evolution in warm deserts: an examination of strategies and patterns in deserts of Argentina and the United States. — Dowden, Hutchinson, and Ross, Stroudsburg, Penn.

Osterhaus, M. B. 1962: Adaptive modifications in the leg structure of some North American warblers. — Am. Midl. Nat. 68: 475-486.

Palmgren, P. 1932: Zur Biologie von Regulus r. regulus (L.) und Parus atricapillus borealis Selys. Eine vergleichend-ökologische Untersuchung. — Acta Zool. Fennica 14: 1-113.

Partridge, L. 1976: Some aspects of the morphology of blue tits (Parus caeruleus) and coal tits (Parus ater) in relation to their behavior. — J. Zool. 179: 121-133.

Patterson, B. D. 1981: Morphological shifts of some isolated populations of Eutamias (Rodentia: Sciuridae) in different congeneric assemblages. — Evolution 35: 53-66.

Payne, R. B. & Risley, C. J. 1976: Systematics and evolutionary relationships among the herons (Ardeidae). — Misc. Publ. Mus. Zool. Univ. Michigan, No. 150.

Pianka, E. R. 1975: Niche relations of desert lizards. — In Cody, M. L. & Diamond, J. M. (eds.), Ecology and evolution of communities: 292-314. Harvard Univ. Press.

Potapova, E. & Panov, E. 1977: Jaw structure features of wheatears, genus Oenanthe, relative to the modes of reduction of food competition between affiliate species. — Zool. Zhurn. 56: 743-752.

Power, D. M. 1969: Evolutionary implications of wing and size variation in the red-winged blackbird in relation to geographic and climatic factors: a multiple regression analysis. — Syst. Zool. 18: 363-373.

Pregill, G. K. & Olson, S. L. 1981: Zoogeography of West Indies vertebrates in relation to Pleistocene climatic cycles. — Ann. Rev. Ecol. Syst. 12: 75-98.

Pulliam, H. R. 1975: Coexistence of sparrows: A test of community theory. — Science 189: 474-476.

Rensch, B. 1936: Studien über klimatische Parallelität der Merkmalsausprägung bei Vögeln und Säugern. — Arch. Naturgesch., N.F. 5: 317-363.

—»— 1960: Evolution above the species level. — Columbia Univ. Press, NY.

Richardson, F. 1942: Adaptive modifications for treetrunk foraging in birds. — Univ. Calif. Publ. Zool. 46: 317-368.

Ricklefs, R. E. & Cox, G. W. 1977: Morphological similarity and ecological overlap among passerine birds on St. Kitts, British West Indies. — Oikos 28: 60-66.

Ricklefs, R. E. & Travis, J. 1980: A morphological approach to the study of avian community organization. — Auk 97: 321-338.

Root, R. B. 1967: The niche exploitation pattern of the blue-gray gnatcatcher. — Ecol. Monogr. 37: 317-350.

Rosen, D. E. 1978: Vicariant patterns and historical explanation in biogeography. — Syst. Zool. 27: 159-188.

Rothstein, S. I. 1982: Successes and failures in avian egg and nestling recognition with comments on the utility of optimal reasoning. — Amer. Zool. 22: 547-560.

Rüggeberg, T. 1960: Zur funktionellen Anatomie der hinteren Extremität einiger mitteleuropäischer Singvogelarten.

— Zeitschr. Wiss. Zool. 164: 1-106.

Savile, D. B. O. 1957: Adaptive evolution in the avian wing. — Evolution 11: 212-224.

Schoener, T. W. 1965: The evolution of bill size differences among sympatric congeneric species of birds. — Evolution 19: 189-213.

—»— 1974: Resource partitioning in ecological communities. — Science 185: 27-39.

—»— Size differences among sympatric, bird-eating hawks: a worldwide survey. — In: Strong, D. R., Simberloff, D. & Abele, L. G. (eds.), Ecological communities: conceptual issues and the evidence. Princeton Univ. Press, Princeton. In press.

Selander, R. K. 1966: Sexual dimorphism and differential niche utilization in birds. — Condor 68: 113-151.

Selander, R. K. & Johnston, R. F. 1967: Evolution in the house sparrow I. Intrapopulation variation in North America. — Condor 69: 217-258.

Simberloff, D. & Boecklen, W. 1981: Santa Rosalia reconsidered: size ratios and competition. — Evolution 35: 1206-1228.

Smith, J. N. M. & Dhondt, A. A. 1980: Experimental confirmation of heritable morphological variation in a natural population of song sparrows. — Evolution 34: 1155-1158.

Smith, J. N. M. & Zach, R. 1979: Heritability of some morphological characters in a song sparrow population. — Evolution 33: 460-467.

Sokal, R. R. & Riska, B. 1981: Geographic variation in Pemphigus populitransversus (Insecta: Aphidae). — Biol. J. Linn. Soc. 15: 201-233.

Strong, D. R. & Simberloff, D. 1981: Straining at gnats and swallowing ratios: Character displacement. — Evolution 35: 810-812.

Strong, D. R., Jr., Szyska, L. A. & Simberloff, D. S. 1979: Tests of community-wide character displacement against null hypotheses. — Evolution 33: 897-913.

Travis, J. & Ricklefs, R. E. 1983: A morphological approach to the study of avian organization II. Effects of locale and habitat on patterns in tropical assemblages. — Oikos, in press.

Van Noordwijk, A. J., Van Balen, J. H. & Scharloo, W. 1980: Heritability of ecologically important traits in the great tit, Parus major. — Ardea 68: 193-203.

Vaurie, C. 1980: Taxonomy and geographical distribution of the Furnariidae (Aves, Passeriformes). — Bull. Amer. Mus. Nat. Hist. 116: 1-357.

Wake, D. B. 1978: Shape, form, development, ecology, genetics, and evolution. — Paleobiology 4: 96-99.

Wallace, A. R. 1869: The Malay Archipelago. — Harper, NY.

Wiens, J. A. & Rotenberry, J. T. 1980: Patterns of morphology and ecology in grassland and shrubsteppe bird populations. — Ecol. Monogr. 50: 287-308.

Wiley, R. H. & Cruz, A. 1980: The Jamaican Blackbird: a "natural experiment" for hypotheses in socioecology. — In Hecht, M. K., Steere, W. C. & Wallace, B. (eds.), Evolutionary Biology 13: 261-293. Plenum Press, NY.

Wright, S. 1932: The roles of mutation, inbreeding, crossbreeding, and selection in evolution. — Proc. VI Int. Congr. Gen. I: 356-366.

—»— 1978: Evolution and the genetics of populations. Vol. 4. Variability within and among natural populations. — University of Chicago Press, Chicago.

Ziswiler, V. 1980: Uses of adaptational analysis in evolutionary and phylogenetic study. — Acta XVII Congr. Int. Ornithol., pp. 209-213.

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