

A view of avian ecomorphological hypotheses

Betrachtungen ökomorphologischer Hypothesen

By Roger J. Lederer

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Summary

The ecological dynamics of bird species have often been measured or predicted by the analyses of one or more morphological features of the birds. There are a number of hypotheses based on the premise that morphology defines the niche. However, many of these hypotheses are weak because there often is little direct correlation between morphology and ecology. The same morphological structure can be used in many ways, depending on the birds' food requirements, habitat, and behavior. Ecomorphological studies must take into account many morphological and ecological measurements rather than a few and should, until more evidence is gathered, be restricted to small communities or taxonomic groups until it can be shown that the hypothesis is broadly applicable.

Zusammenfassung

Untersuchungen eines oder mehrerer morphologischer Merkmale werden häufig als indirekter Weg benutzt, um die ökologischen Ansprüche von Vogelarten abzuschätzen oder zu messen. Eine Reihe von Hypothesen beruhen auf der Annahme, daß der Körperbau die Nische einer Art bestimmt. Viele dieser Hypothesen sind jedoch wenig allgemein gültig, da häufig die direkte Beziehung zwischen Morphologie und Ökologie schwach ist. Dieselbe morphologische Struktur kann verschiedene biologische Rollen erfüllen, abhängig von den Nahrungsansprüchen, dem Habitat und dem Verhalten einer Art. Ökomorphologische Untersuchungen sollten daher eher viele als wenige morphologische und ökologische Messungen berücksichtigen.

Solange nicht gezeigt werden kann, daß eine Hypothese allgemein gültig ist, sollten sich ökomorphologische Untersuchungen auf kleine einheitliche Vogelgemeinschaften (Gilden) oder taxonomische Gruppen beschränken.

Introduction

The past 20 years have seen a trend towards predicting the ecological dynamics of a species, community, or guild by measuring one or more morphological features of birds. The purpose of these studies was to define species' niches since the birds' habitats, foraging behavior, food and other ecological characteristics intuitively seem to reflect the constraints of their morphological features. In other words, morphological features define the niche (KEAST 1970).

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Hypotheses

We find a number of hypotheses based on this premise. For example, it has been stated that ecologically similar species should differ in body size or bill size by some relatively constant proportion (1:1.3) in order to coexist (HUTCHINSON 1959, DIAMOND 1973, MAIORANA 1978). DIAMOND's work on fruit pigeons (Table 1) more or less substantiates this ratio but other studies weaken this constant proportion idea. MAIORANA (1978) and HORN & MAY (1977) have found that 1:1.3 ratios also exist among artifacts such as figurines, kitchen skillets, recorders and violins, implying that the ratio may be somewhat artificial. I have found that sets of 2, 3 or 4 Tyrannid flycatchers exhibit ratios of 1 to 1.4 during the breeding season, but during migration range to 2.0. WIENS & ROTENBERRY (1981) found ratios of grassland birds to vary from 1.03 to 3.19 for bills and 1.12 to 3.97 for body sizes.

Table 1. Body Weight of Fruit Pigeon Species (from DIAMOND, J. M. 1973).
Tabelle 1. Körpergewicht von Fruchttauben.

Species	Wt. in Grams	Ratio Between Adjacent Size Species
<i>Ptilinopus perlatus</i>	245	
<i>Ducula rufigaster</i>	414	1.69
<i>Ducula zoeae</i>	592	1.43
<i>Ducula pinon</i>	802	1.35

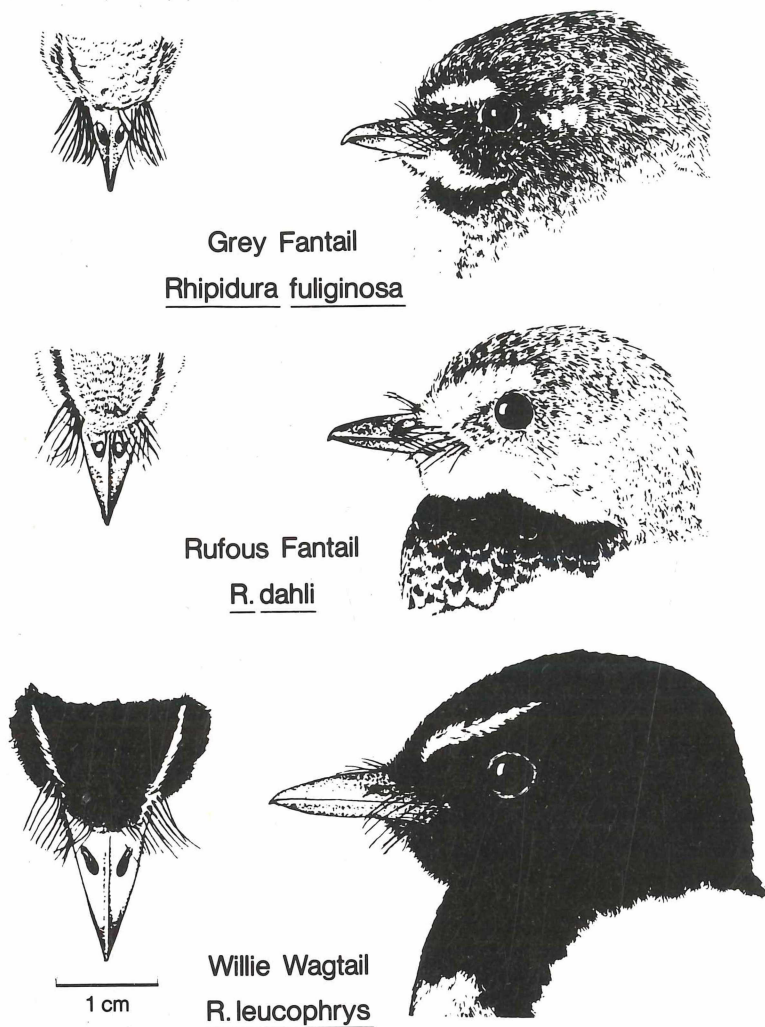
Another generally accepted hypothesis is that differences in bill size are closely related to differences in the size of the prey captured (ABBOTT 1977, BEAVER & BALDWIN 1975, GRANT 1967, 1968, HERRERA 1978, HESPENHEIDE 1973, SCHOENER 1965, 1968, SMITH & ZACH 1979). Although this hypothesis seems intuitively logical, a search of the literature revealed only indirect, vague, and often very qualified data. There are numerous exceptions to and modifications that must be made of this hypothesis. For example, the length of the bill may not be due to the size of the prey but to the mobility of the prey as larger jaws close faster (BEECHER 1962, BOCK 1964, LEDERER 1965). Body size may be a better indicator of prey size than bill size (HESPENHEIDE 1973).

The relationships between trophic structure (or body size) and food size also vary among taxa (STRONG, SZYSKA & SIMBERLOFF 1979). SMITH & VUILLEUMIER (1971) found that flycatchers (*Tyrannidae*) living in wetter and denser habitats have broader bills than those in drier and more open habitats (Table 2). The relationship between bill size and food becomes even

Table 2. Bill Shapes and Habitat of South American Ground Tyrants (from SMITH & VUILLEUMIER 1971).
Tabelle 2. Schnabelform, Ernährungsweise und Habitate südamerikanischer bodenlebender Tyranniden.

Species	Bill Shape	Diet	Habitat
<i>Ochthoeca cinnamomeiventris</i>	Short and broad	Insectivorous	Wet Forest
<i>Muscisaxicola alpina</i>	Thin and narrow	Insectivorous	Dry, non-forested
<i>Xolmis cinerea</i>	Long and broad	Partially insectivorous	Moderately dense
<i>Agriornis livida</i>	Long, narrow, hooked	Varied	Non-forest

less clear when methods of foraging are considered. CAMERON (1980) found interesting differences between three species of flycatchers (*Rhipidurinae*) (Fig. 1). *Rhipidura fuliginosa* has the shortest and narrowest bill and feeds most consistently by aerial hawking. *R. dahl* feeds in dense vegetation by gleaning and hover gleaning and has a wider bill than *R. fuliginosa*. *R. leucophrys* has the widest and longest bill of the three species and takes the largest prey by pecking on the ground among rocks.



From: Cameron, E. 1980. Flying catchers. Australian Natural History 0:298-303.

Fig. 1: Bill sizes and shapes of 3 species of Australian flycatchers. From: CAMERON, E. (1980): Flying catchers. Australian Natural History 9: 298-303.

Abb. 1: Schnabelgröße und -form von drei australischen Fächerschwanzarten.

HULSMAN (1981) showed that in some terns the width of the gape and length of the esophagus were more closely related to the size of the prey than bill length; there may even be a negative correlation between bill length and size of prey because shorter bills are usually stronger. And bills that are used to expose or reach prey (gaping as in Starlings and Meadowlarks, probing as in shorebirds, creepers, and nuthatches, and pecking as in woodpeckers) would seem to have bills related to foraging method and not size of prey. Even if we limit the studies to comparable groups of birds feeding on similar foods, we find conflicting results. MORRIS (1955) found that finch bill size is related to seed size eaten; WILLSON (1971) did not. Thus, the hypotheses of a fixed ratio of difference between species and the correlation of food size to bill length seem to be weak and limited in their applicability. There are several other hypotheses with similar weaknesses; see WIENS & ROTENBERRY (1979).

Townsend's Solitaires and American Robins: an example

For 5 winter seasons I studied the feeding behavior of Townsend's Solitaires (*Myadestes townsendi*) and American Robins (*Turdus migratorius*), two species of Turdidae (LEDERER 1977). In the breeding season these birds are omnivorous, eating both fruits and insects. The solitaire is more insectivorous and does considerably more flycatching than the robin. Both species have unspecialized bills, as one would expect of omnivores. Considering the generalized bill shape it did not seem fruitful to make any bill measurements. Instead, I studied their foraging behavior.

Both species are totally frugivorous in the winter. Robins feed like most frugivorous birds, hopping along branches for berries and picking the berries at their feet. Solitaires, however, feed like hover-gleaning insectivores, hovering under branches and picking berries from above. I doubt whether this behavior could have been predicted by morphological measurements of any sort. These two species do not seem to support any extant hypothesis.

What I propose is that we retreat from these overly broad hypotheses until more information is gathered. Although present hypotheses are too simplistic and apply only narrowly, they do hold in some cases. I suggest, then, that a series of hypotheses be developed based on the ecomorphology of guilds of birds, each guild by a somewhat different approach. Let me develop this idea with an example.

The ecomorphology of insectivorous and frugivorous birds

Fruit-eating by birds generally results in the dispersion of seeds, thus leading to adaptations by the plants for attracting birds. Insect-eating, on the other hand, promotes anti-predator adaptations by insects such as cryptic coloration, distastefulness, or escape mechanisms (MORTON 1973). Thus, insectivorous birds have evolved specializations to find, capture, and hold insect prey but fruit-eaters are much more generalized as their food is so much more accessible. It may be a useful exercise to compare the relative importance of various morphological features to frugivore and insectivore guilds.

Bill shape and size

Bill length differences are at least partly due to the nature and abundance of food items (GRANT 1968). The length of the insectivorous bird's bill is sometimes related to the necessity for capturing faster, and perhaps larger, prey. The force at the bill tip decreases with the length of the bill, so larger, but not necessarily stronger, insects may be captured. For example, large soft-bodied larvae may be handled, but not large hard-bodied adults. Foliage gleaners have thinner bills than hover-gleaners or salliers, which have thinner bills than aerial foragers. The width of the bill seems related to the agility required to capture prey — wider bills for faster or stronger prey.

For frugivorous birds, the length of the beak is often related to the ability to reach fruits or seeds, e.g. *Stemmadenia* fruits of Central America are woody and a slit-like opening exposes seeds to only woodpeckers, jays, motmots and others with long beaks. The width of the beak may be related to what size fruit the bird can swallow. The depth and/or cross-sectional area of the beak determines its force and thus what fruits or insects it will be able to pick or take pieces from.

Jaw kinesis

Kinesis among insectivorous birds may have three functions: (1) maintaining line of sight as the jaw is opened; (2) for gaping to expose insects in grass, buds, fruits, or substrate; (3) to close the jaws rapidly (Bock 1964). (1) and (3) are important to insectivores while (2) is important to both guilds. Frugivorous birds may make use of the kinetic mechanism to open fruits to expose seeds or to bite chunks out of large fruits.

Jaw musculature

The jaw musculature of most insectivores and frugivores is oriented towards adduction, but the relative strength of adduction (or abduction) depends on the size and arrangement of the muscles and the shape of the jaws. Flycatching insectivores may have a quite different muscle arrangement than those insectivores that probe in short grass for prey. Similarly, frugivores that pick and eat whole small fruits would be expected to have different musculature than those birds that bite chunks out of larger fruits.

Wing and tail shape and size

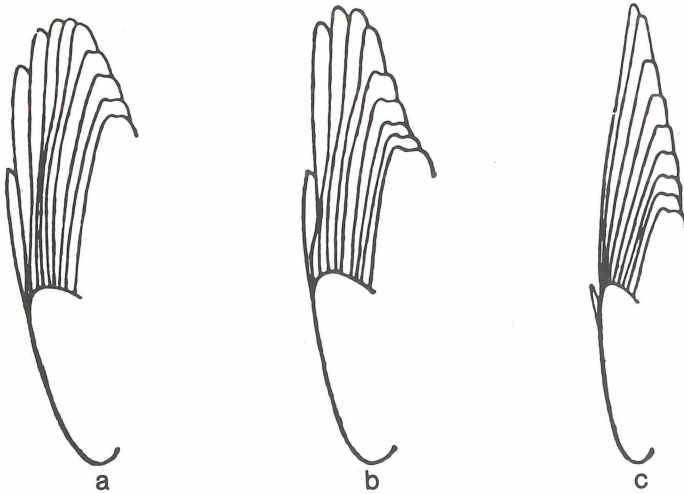
A long wing tip and chord of wing indicate good flying ability and are characteristic of insectivores that hawk, sally and hover-glean. Hawkers have longer wings than salliers and salliers are longer-winged than hover-gleaners. Frugivores that fly from one part of the canopy to another have longer wings than those that thread through vegetation.

Rounded, short wings are characteristic of insectivores that thread their way through vegetation and glean as short, rounded wings are helpful in maneuvering in small, dense areas and for hovering. Rounded, short wings are also characteristic of frugivores that thread through vegetation or feed on the ground. Long tails seem to be characteristic of poor fliers that thread through vegetation — used perhaps for balance, lift, and/or steering.

Figure 2 shows examples of wing configurations of 3 species of bee eaters. *Nyctiornis* is a forest bird with maneuvering flight. *Mellitophagus* inhabits forest edges and savannahs, and *Melospiza* is an aerial feeder. These configurations suggest that thinner, more pointed wings are related to open habitats and aerial habits. MORRISON (1982) suggests, however, that the wing length differences between two warbler species may be due to the distance they fly during migration and not to their ecology on their breeding grounds.

Leg structure

In general, the tarsus is long in terrestrial birds or those that do part of their feeding on the ground and is true for both insectivores and frugivores. But there seems to be a lot more difference in tarsus length among insectivorous birds than frugivorous ones. The tarsus is shorter in birds that need more support — the more aerial birds need less support and have longer tarsi. Salliers, e.g., have shorter tarsi than hover-gleaners. Those birds foraging on flimsy twigs and thin branches have shorter tarsi than those using heavier and rigid perches and shortest in those clinging to vertical trunks. Those that cling to marsh vegetation or to leaves or petioles have longer toes and claws. Walkers have short toes and claws (LEISLER 1980). The relative length of the legs and feet is thus molded by the characteristics of the perch site.



a. Nyctiornis sp.

b. Mellitophagus sp.

c. Meropsapiaster

From: Kokshaysky, N.V. 1973. Functional aspects of some details of bird wing configuration. Syst. Zool. 22: 442-450

Fig. 2: Wing sizes and shapes of 3 species of bee-eaters. From: KOKSHAYSKY, N. V. (1973): Functional aspects of some details of bird wing configuration. Syst. Zool. 22: 442-450.

Abb. 2: Flügelgröße und -form von drei Bienenfresserarten.

Conclusion

It seems clear to me that present ecomorphological hypothesis cannot be applied in the same way to frugivores as it is to insectivores. Even within the frugivore guild one hypothesis would have many exceptions. In many admirable attempts at developing predictive hypotheses, we have erred by oversimplifying. It is tempting indeed to measure bill lengths and food sizes or foot length and perch sizes and then draw intuitively logical conclusions. What has resulted, however, is a large number of hypotheses, each with a large number of exceptions. I am suggesting that we rethink the way in which we develop these hypotheses.

More recent studies have tried to combine various morphological attributes, rather than relying on one. RICKLEFS & COX's 1977 study showed that foraging method overlaps were strongly correlated with similarity in wing/tarsus ratio; overlap in feeding location was correlated with similarity in bill structure; but habitat was not related to morphological similarity. RICKLEFS & TRAVIS (1980) found that in small communities, morphological separation and ecological overlap were inversely related, but the relationship became less clear in larger communities.

Ecology and morphology are related, but not in some simple and general way. The use of morphology to predict ecological relationships has been based on the premise that morphological differences bear the same relationship to ecological differences in all groups of birds. But any relationship between morphological similarity and ecological overlap will likely apply only to a narrow set of conditions which must be strictly defined (STRONG et al. 1979). Any correlations of morphology and ecology must include not only size distributions, morphological differences and habitats, but functional anatomy, foraging methods, and food types and sizes. One approach suggested by HESPENHEIDE (1973) is to characterize micro-communities exploiting a single food source. PIKE, PULLIAM & CHARNOV (1977) have suggested that only when animals are foraging for a single source of energy such as nectar or for different sizes of one kind of food, will optimal foraging theories be predictive. I suggest that only when animals forage for a single source of food with a very limited number of foraging tactics will ecomorphological theories be predictive.

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