

Behavioral and Theoretical Considerations

A FUNCTIONAL APPROACH TO FORAGING: MORPHOLOGY, BEHAVIOR, AND THE CAPACITY TO EXPLOIT

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Abstract. To understand the foraging behavior of birds, one needs to examine the relationships between morphology and foraging behavior, and between foraging behavior and resource use. A basic working principle is that morphological specialization for certain types of foraging maneuvers reduces the ability to perform other maneuvers. A second working principle is that birds select food on a benefit to cost basis. A bird's abilities affect its efficiency in searching for and capturing food items in a given microhabitat. As such, the cost/benefit depends on the context in which food is found. I use three groups of birds as examples of the connection between morphology and foraging behavior and show how this connection can be used to interpret patterns of resource use. Aerial insectivores, such as swallows and swifts, show several dichotomies in morphology that influence their foraging behavior and diet. Foliage insectivores show that resource partitioning is based on subtle differences in wings, legs, and feet that can be correlated with their ability to use particular microhabitats. Studies of fruit-eaters in aviaries have shown that slight differences in ability influence several aspects of food choice. Such results can be used to interpret field observations of food capture behavior to assess resource use by different species. By studying how birds feed in varying contexts, one can infer how morphology restricts their foraging behavior and influences their pattern of resource use.

Key Words: Adaptations; aerial insectivore; ecomorphology; feeding behavior; foliage insectivore; foraging; fruit-eater; jack-of-all-trades; resource partitioning.

Ecomorphology (Leisler and Winkler 1985) is a term for a mechanistic approach to understanding the interface between morphology and ecology (see also Hespeneide 1973b, Karr and James 1975, Ricklefs and Travis 1980, James 1982, Winkler and Leisler 1985, Moermond 1986). Both morphology and habitat structure influence foraging and resource use (e.g., Moermond 1979a, b; Grubb 1979; Robinson and Holmes 1984). With birds, one key to understanding these connections is through functional studies of foraging behavior. The usefulness of foraging behavior for understanding the integration of morphology, behavior, and resource use depends on how well the mechanistic basis for the foraging maneuvers is operationally defined (e.g., Partridge 1976a, b; Norberg 1979, 1981; Robinson and Holmes 1982; Holmes and Recher 1986a, b; Moermond and Howe, in press). In this paper, I discuss the procedures and values of mechanistic approaches, focussing on two important connections between (1) morphology and foraging behavior and (2) foraging behavior and resource use; the latter includes the portion of habitat or microhabitat used. We can ask, then: How tight is the connection between a bird's morphology and its foraging behavior repertoire? How do we recognize limitations or restrictions, and what are the consequences of such constraints?

Studies of resource partitioning in ecologically closely related birds nearly always show differences in the frequency of use of foraging maneu-

vers (e.g., MacArthur 1958, Root 1967, Lack 1971). Such differences are usually related to differences in the abilities of each species to perform various maneuvers. The basic concept supporting such an assumption is the jack-of-all-trades, master of none principle (MacArthur 1965; Moermond 1979b, 1986). Theory and empirical assessment of adaptations dictate that morphological features designed to perform one type of movement well are unlikely to be well designed for other types of movements. The ecological consequences of this principle can be observed in several different aspects of studies of resource use by birds. For example, one may examine the foraging behavior of a group of species to look for dichotomies in foraging maneuvers. The foraging maneuvers employed by one subgroup may be mutually exclusive of those employed by a different subgroup. Even within a guild, one finds differences in the relative frequencies of foraging maneuvers used. Are such differences important to their relative abilities to exploit the same resources? I shall illustrate at least some possible answers with the series of examples to follow.

To understand the connection between foraging behavior and resource use, one needs to know what foods birds use and what factors influence their selection (Grubb 1979). Optimal foraging theory has shown that birds often select food based on energy, time, and effort (Pyke et al. 1977, Krebs 1978). Optimal foraging predictions can be demonstrated in controlled labo-

ratory situations; however, clear demonstrations in the field are rarely possible and often problematic (Krebs et al. 1983).

AERIAL INSECTIVORES

Aerial insectivores show a dichotomy in morphology and foraging behavior. Swallows (*Hirundinidae*) and swifts (*Apodidae*) (which I shall call "screeners" after Emlen 1977) hunt by flying continuously for long periods, often taking multiple prey items per flight. By contrast, sallyers (called "hawkers" by some authors) usually hunt from a perch from which the surrounding air or vegetation can be scanned. Prey are taken by a rapid flight to the item, followed by a return to a perch; usually only one prey item is taken per flight.

Screeners and sallyers have different wing and bill morphologies. The screeners' wings have a higher aspect ratio with a narrow-pointed tip; the sallyer has a broader wing with a rounded, more slotted tip. The screener has a shorter, flatter, wider bill with a large gape; the sallyer has a stronger, longer, narrower bill. Both types of differences are congruent with their different hunting styles: the sallyer's broader, more slotted wings allow rapid acceleration and deceleration; the long, narrow wing of the screener allows more efficient flight at the cruising speed of its extended flights (Burton 1976, Hails 1979).

The dichotomy in foraging behavior between screeners and sallyers is likely to be based on the differences in their wings and the associated differences in costs and effectiveness of different foraging maneuvers. I was unable to find any records of such specialized screeners as swallows and swifts ever sallying. Likewise, most species of sallyers such as tyrannid or muscivorous flycatchers rarely, if ever, hunt like screeners. Although both screeners and sallyers depend on aerial insects for food and both take their prey on the wing, their morphologies and foraging methods are virtually mutually exclusive.

The few exceptions to the screener-sallyer dichotomy provide support for the mechanistic explanation of the dichotomy. I have seen Gray Kingbirds (*Tyrannus dominicensis*) engage in series of long flights in which multiple prey were taken when flying insects were available in unusual aerial swarms (unpublished data). Similar observations have been made for Phainopepla (*P. nitens*) (Walsberg 1977), Swallow-wing (*Chelidoptera tenebrosa*) (Burton 1976), Eastern Kingbird (*Tyrannus tyrannus*), Fork-tailed Flycatcher (*Muscivora tyrannus*) (pers. obs.), and Cedar Waxwings (*Bombycilla cedrorum*) (pers. obs.). Several species of bee-eaters (*Meropidae*) often employ both screening and sallying (Fry 1984, pers. obs.). All of these exceptions occur in species that sally in open areas with long sallies as com-

pared with forest species, and all have relatively long, narrow, pointed wings for sallyers (e.g., see Fitzpatrick 1985), thereby using intermediate morphologies that incorporate some of the advantages of both screeners and sallyers. The advantages of the typical sallyer's short, broad wing for maneuverability and acceleration may be outweighed by the greater economy and maximum speed of the longer, narrower wing when employed in long sallies. The longer wing of these long-distance sallyers is convergent on that of the typical screener, but not identical. Instances of sallyers using screening or long, multiple-prey sallies should be carefully recorded as indicative of exploitation behavior beyond normal constraints. The descriptions of high aerial food densities that appear to induce screening behavior in the Lewis' Woodpecker (*Melanerpes lewis*) (Bock 1970) suggest the conditions under which the screening may be the more profitable choice.

Within the screeners, swifts have longer, narrower, stiffer wings than swallows that may allow faster, cheaper cruising flight (Hails 1979). Such advantages may allow the long-distance foraging flights observed for some swifts. The advantages of relatively wider, more flexible wings for swallows may be in greater maneuverability, which in turn may mean higher capture rates of certain types of aerial prey or the ability to maneuver closer to obstacles and the ground (Waugh 1978).

Within the swallows, subtle differences in wing and tail shape (Waugh 1978) are apparently related to differences in hunting flight patterns among genera such as the maneuverability of long, fork-tailed *Hirundo* species compared to the straight-line cruising of some square-tailed species (Waugh 1978). Even such subtle differences are associated with differences in resource use such as foraging site and prey type.

Morphological variation in the sallyers also appears to influence resource use (see Fitzpatrick 1980, 1985). The range of foraging behaviors described by Fitzpatrick for tyrannid sallyers appears to be associated with differences in bill, wing, and leg morphology; these differences likely account for observed differences in prey type and diet breadth (Sherry 1984).

FOLIAGE INSECTIVORES

The maneuvers used to take prey from foliage differ substantially among species. For example, many sallyers may snatch or hover-glean prey from foliage (Fitzpatrick 1980), whereas warblers (*Sylviinae*, *Parulinae*) primarily glean their prey from a perched position. Birds that habitually glean prey from small twigs and foliage often take only a small percentage of items on the wing, either from the air or from foliage. Species that habitually sally take the great majority of their

prey on the wing (Eckhardt 1979, Recher et al. 1985). This dichotomy appears to be quite distinct, even among a single group. For example, Schulenberg (1983) identified a suite of morphology and behavioral characteristics that distinguished the sally-gleaning *Thamnomanes* antshrikes from the more typical perch-gleaning genera. The suite was so evident that he convincingly argued that two atypical *Thamnomanes* were perch-gleaners and not allied to the other sally-gleaning *Thamnomanes*.

Foliage gleaners must move among leaves and twigs arrayed in a variety of patterns that often require special modifications of wing, legs, and feet (e.g., Gaston 1974, Pearson 1977a, Leisler 1980, Winkler and Leisler 1985). Norberg's (1979, 1981) analysis of bark and twig gleaners demonstrated a number of subtle, but important and relevant, differences in morphology that correspond to differences in their use of microhabitats. MacArthur (1958) described differences in movement and microhabitat use for a series of *Dendroica* species (Parulinae) exhibiting only minor differences in morphology. Morrison (1982) attributed differences in wing shape between Black-throated Gray (*D. nigrescens*) and Hermit (*D. occidentalis*) Warblers to differences in habitat use. In my lab, we demonstrated distinct differences in the reaching ability of Yellow-rumped (*D. coronata*) and Palm (*D. palmarum*) warblers that were correlated with minor differences in leg morphology and that corresponded to differences in each species' use of foraging maneuvers in the field (Moermond and Howe, in press). The minor differences in leg morphology were of the same magnitude as those reported by Pearson (1977a) for antwrens (*Myrmotherula* spp.: Formicariidae) occupying different microhabitats.

Winkler and Leisler (1985) demonstrated that for European sylvian warblers that foraged high in trees or shrub vegetation (e.g., *Sylvia* spp.), wing morphology varied considerably with associated habitat differences. For species that used low, dense vegetation (e.g., *Acrocephalus* spp.), differences in leg morphology appeared more critical. This work suggests that the foraging maneuvers that can be successfully applied to these two categories of vegetation are quite different, requiring a different suite of morphological adaptations. The rules that may govern such adaptations appear to include those that influence the performance of birds negotiating different microhabitats. Such differences are likely involved in determining the habitat type and range of birds (Winkler and Leisler 1985).

FRUIT-EATING BIRDS

The taking of fruits provides a clear example of morphological constraints. In the Neotropics,

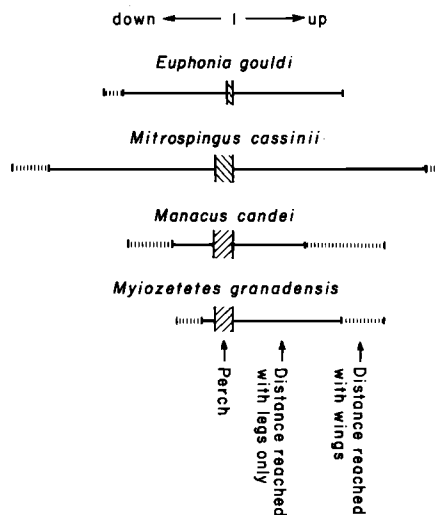


FIGURE 1. The ability of captive individuals of four species of birds to reach for fruits above and below a perch. The solid line shows the distance reached without using the wings. The broken line shows the additional distance reached with the use of the wings. The perch diameter was 3 mm for *Euphonia gouldi* and 12 mm for the others. Two individuals were tested for each species with the maximum reaches shown. Adapted from Moermond et al. (1986).

the dichotomy between birds taking fruits from a perch versus those taking fruits on the wing is sharp (Moermond and Denslow 1985, Moermond, in press). Species taking fruits from a perch apparently use only simple actions. Fruits at the level of a sturdy perch can be taken with only a slight downward lean, but fruits below the perch require a more extreme extension of the body. The ability to reach varies considerably. Among small Neotropical fruit-eating birds we tested, some tanager species (e.g., *Euphonia gouldi*, *Thraupis palmarum*) were able to extend their entire bodies below the perch; whereas a tyrannid flycatcher (*Myiozetetes granadensis*) and a manakin (*Manacus candei*) were unable to reach more than a small distance down from a perch (Fig. 1) (Moermond and Denslow 1985, Moermond et al. 1986). The added cost to a bird of obtaining a particular fruit placed below a perch may cause a switch in preference from that fruit to a fruit of lesser quality that is easier to obtain (Moermond and Denslow 1983). The decision as to which fruits to take or not appears to be a cost/benefit choice that is influenced by the morphological abilities of each bird species (Moermond et al. 1986, 1987).

When a fruit cannot be taken from a perch, then it must be taken on the wing. How restrictive the choice is for such fruits depends on the ability of the bird. In the spring of 1986 in central

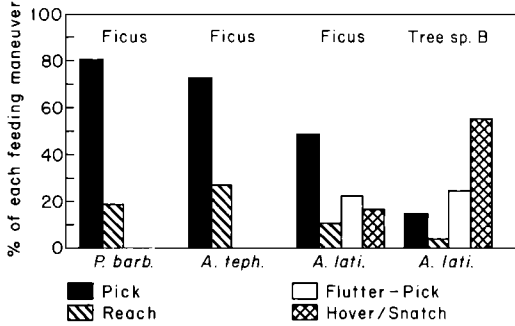


FIGURE 2. Feeding maneuvers used by three species of bulbuls (*Pycnonotus barbatus*, *Andropadus tephrolaemus*, and *A. latirostris*) feeding on cauliflorous fruits of *Ficus* and pendant fruits of *Prunus africanus* (Tree sp. B). Picks, reaches, and flutter-picks were performed while clinging to a perch. Hover-gleans and snatches of fruits were all done in flight. The total sample sizes for each case shown from left to right are 53, 75, 90, and 48, respectively.

Africa (in the Nyungwe forest of Rwanda), I observed three species of bulbuls (*Pycnonotus barbatus*, *Andropadus tephrolaemus*, *A. latirostris*) feeding actively on a *Ficus* with large, cauliflorous fruits (Moermond, in press). *P. barbatus* and *A. tephrolaemus* took all their fruits from a perch while *A. latirostris* relatively frequently used its wings to pick a fruit with a flutter (23%) or while flying by (16%, Fig. 2). The use of wings by *A. latirostris* corresponded to its frequent use of its wings while hunting insects among foliage. The other bulbul species rarely use aerial maneuvers while foraging for insects or fruit.

During the same period, fruits were simultaneously available on a nearby tree; however, these fruits were pendant below thin, flexible perches. *A. latirostris* fed extensively on these fruits also, but it frequently used aerial maneuvers (snatches and hover-gleans) to obtain the fruits (56%, Fig. 2, tree B). During the time I observed over 100 feedings of *A. latirostris* in tree B (*Prunus africanus*), I never observed any feeding by *A. teph-*

rolaemus and only six feedings by *P. barbatus*. Four of these six feeding maneuvers were aerial snatches. These data suggest that feeding on fruits that require more aerial maneuvers is restricted to the species with more ability to use its wings. Although all three bulbuls are very similar in size and morphology, what appear as minor or subtle differences in frequency of feeding maneuvers of fruit-eaters can be shown to influence food type and diet breadth (Moermond et al. 1986).

CONCLUSIONS

The combination of constraints of morphology on foraging behavior and the influence of foraging on food exploitation has many implications for our understanding of bird communities such as the divisions between species guilds (Ford 1985, Holmes and Recher 1986b, Terborgh and Robinson 1986) or the barriers to niche shifts (e.g., Diamond 1970). On a finer scale, the connections between morphology and foraging ability probably rarely determine diet and habitat use, but act as a directing influence often enabling appropriate responses to environmental context (e.g., Moermond et al. 1987). The conclusion of this approach is that foraging behavior offers important clues to assessing and interpreting the food exploitation patterns and capabilities of birds. These clues will be most insightful when the observations of foraging are keyed to how the bird is responding to resources in a given context.

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