

A CLASSIFICATION SCHEME FOR FORAGING BEHAVIOR OF BIRDS IN TERRESTRIAL HABITATS

J. V. REMSEN, JR. AND SCOTT K. ROBINSON

Abstract. Studies of avian foraging behavior in terrestrial habitats suffer from a lack of standardization in the kinds of data gathered and in the terminology used to classify different activities. These inconsistencies partially reflect the variety of questions asked about foraging. If a standard terminology were used, then data on foraging behavior could be included among the standard data (e.g., clutch size, body weight, and mating system) routinely recorded for the biology of a bird species.

We propose a system for gathering foraging data for landbirds in which the five basic, sequential components of foraging (search, attack, foraging site, food, and food handling) are quantified separately. Data on searching behavior involve measuring continuous variables and are particularly critical for studies of energetics. The "attack" component is most in need of standardized terminology. The system that we propose separates the attack perch from the attack maneuver, and further subdivides the maneuvers into near-perch, subsurface, and aerial maneuvers. Each of these general categories is further subdivided according to details of attack movements and ways in which substrates are manipulated. Data on attack methods are primarily useful for studies of ecomorphology, but may also be important in bioenergetic and community-level studies.

Quantifying the foraging site involves measuring the following variables: general habitat (location in a study area), vertical position, foliage density, and substrate. Although identification and quantification of foods taken in the field is difficult, it can provide valuable information on food size (and taxon for larger items). Dietary data from stomach samples are useful for studies of resource partitioning when they show dramatic differences, but overlapping diets do not necessarily indicate that two birds forage in the same way. Food-handling behavior is seldom measured in the field, but is valuable in studies of optimal foraging behavior and ecomorphology.

Intercorrelations between each of these aspects of foraging can be determined from standard multivariate analyses. How finely to subdivide categories depends upon the kinds of questions being asked.

Key Words: Foraging behavior classification; foraging maneuvers; search; attack; foraging site; diet; food-handling; glean; sally; probe; manipulate.

There are almost as many ways of classifying and quantifying foraging behavior as there are papers on the subject. In part, this variety reflects the fact that no two species or groups of species forage in exactly the same way, and that no two habitats present exactly the same foraging opportunities. It is difficult, for example, to quantify the foraging methods of bark-foragers in the same way that one quantifies the foraging of foliage-foragers (Jackson 1979). Another factor contributing to the lack of standardization is that different kinds of questions often require different kinds of data. Many studies that focus on resource partitioning record only the details of foraging site selection and omit data on search and attack movements (e.g., Hertz et al. 1976). In contrast, studies of ecomorphology emphasize prey-attack methods (e.g., Osterhaus 1962; Fitzpatrick 1980, 1985), whereas bioenergetic and optimal foraging studies emphasize searching movements as well as prey handling (e.g., Sherry and McDade 1982, Robinson 1986). Even studies addressing the same questions in ecologically similar birds do not always measure the same variables.

This lack of standardization, however, reflects fundamental inconsistencies in the importance attached to the individual variables used to

quantify foraging. For example, the "hawk" category of Sherry (1979) and Holmes et al. (1978, 1979b) includes attacks on prey animals that were flying when first seen, attacks on prey flushed from foliage by the foraging activities of the bird, and chases after prey that the bird attacked and missed. Later papers by Robinson and Holmes (1982, 1984) and Sherry (1983, 1984), however, showed that differences among these aerial maneuvers have important implications for diet. Remsen (1985) showed that the fine details of substrate use (e.g., dead leaves, moss) that are often ignored in many community studies were particularly important in resource partitioning in a tropical bird community. Rosenberg (this volume) further showed that even within a group as specialized as dead-leaf foragers, species differ in the kinds of suspended dead leaves that they search. The classification of foraging behavior, therefore, is more than a semantic problem: one can reach different conclusions simply by classifying foraging methods differently.

In this paper, we propose a system for measuring and classifying foraging behavior for non-raptorial landbirds. Our goal is to standardize data-gathering methods and terminology to permit among-site and among-species comparisons that are currently handicapped by the absence of

a common vocabulary. If some standard system and terminology were used by those studying foraging behavior, then we could ask questions concerning the frequencies of various behaviors among communities. Such comparisons may provide important insights into community organization: in a field such as foraging behavior, in which community-wide experimental manipulations are difficult or limited, a comparative approach among species and communities may be the only method available for testing many hypotheses.

The system presented here separates five sequential components of foraging behavior, each of which is quantified separately when data are gathered in the field: (1) search (movements leading up to sighting of food or food-concealing substrates); (2) attack (movements directed at food item or the substrate that conceals it once sighted); (3) foraging site (including general location and specific substrate); (4) food (including type and size); and (5) food handling (after food item obtained). We recognize that many of these components are not necessarily independent, but we prefer to quantify each separately and to allow subsequent analyses to show intercorrelations.

At the outset, we recognize that any classification system inflicts typology on what may be gradients of behavior, but we see no other practical solution for organizing foraging information. Our goal is to distinguish among what we subjectively perceive to be functionally different categories. By using standardized terminology, data on foraging behavior can be included among the standard biological data reported for bird species. At present, reference works on birds, which typically include detailed, quantitative data on variables such as clutch size, body weight, molt and migration schedule, and mating system, tend to omit, or describe in superficial, qualitative ways, all aspects of foraging behavior except perhaps diet. Foraging data should be included in such reference works, because foraging behavior is an integral part of a species' biology, and because it relates to time-activity budgets, morphology, habitat selection, and social system. The foraging behavior of many species may also be as "typical" of that species as any other aspect of its biology. A standard vocabulary will eventually allow a more sophisticated review of the prevalence of various foraging behaviors in birds; such a review will be able to replace the often anecdotal, "who-does-what" approach with quantitative comparisons between taxa and regions.

The heart of this paper is the section on the attack, which is the phase of foraging that is most in need of a standard terminology based on functionally different categories (cf. Moermond, this

volume). We discuss briefly data on bird diets, and also propose a standard terminology for food-handling techniques. The final section of our paper deals with some of the ways in which data can be analyzed to address questions of resource-partitioning, bioenergetics, and ecomorphology.

SEARCHING BEHAVIOR

Searching behavior includes those movements used to search for food or substrates that hide food; under our definition of searching behavior, "search" ends once food or food-hiding substrates are sighted and attacked. Searching methods have usually been quantified by recording the lengths and rates of movements between perches and the time intervals between movements (e.g., MacArthur 1958, Cody 1968, Williamson 1971, Fitzpatrick 1981, Robinson and Holmes 1982). Other variables are: (1) distance covered per unit time; (2) number of stops and time-spent-stopped per unit time; (3) number of attacks (and % successful) per unit time; (4) direction of movement between stops, in three dimensions if appropriate; (5) sequential distribution of locations of stops (to calculate return rates to previous stops). Between-foraging-site movements can be categorized as: (1) walk, (2) hop, (3) jump (leg-powered leaps that cover more space than the typical hop), (4) run, (5) climb (with notations on whether or not the tail is used as a brace), (6) glide, (7) flutter, and (8) fly. Robinson and Holmes (1984) further distinguished between hops in which American Redstarts (*Setophaga ruticilla*) fanned their tails and lowered their wings, and hops in which there were no extra movements. Some birds also use their wings for support when hopping on thin, weak perches, a movement that could be called a "flutter-hop" (Robinson, unpubl. data). Also of interest are postures during searching that are seldom qualitatively described (for exceptions, see any E. O. Willis reference) or quantified but that may have subtle morphological correlates. Postures are particularly difficult to categorize because most species move and change postures frequently, and because head, wing, and tail orientations are all simultaneously involved. Perhaps the advent of telephoto video-cameras will permit such analyses; in this paper we deal with postures only peripherally. More amenable to quantification are changes of orientation while searching from a perch, either with head or body movements. For example, many species have characteristic side-to-side movements, whereas others maintain a straight-ahead orientation. Many species have characteristic wing-flicking or tail-wagging movements that accompany foraging, the significance of which is not often understood; the frequency of such actions could also be quantified. There is also a parallel literature on the searching behavior of various lizards (Moermond 1979, Huey and Pianka 1981).

In general, searching movements of birds form a continuum from "active" to "passive" modes (Eckhardt 1979). Active foragers change perches at a high rate, including many hops (or steps in species that walk), and most flights are short. Passive foragers seldom change perches, but fly long distances when they do move. The subset of birds that Eckhardt (1979) chose from the community that he studied fit into active

(primarily wood-warblers) and passive (primarily tyrannids) foragers. A subsequent study of a different forest bird community (Robinson and Holmes 1982), however, found that many species did not fit cleanly into either category. Tanagers and vireos, for example, were intermediate in their rates of hopping and flying and in the lengths of their flights. Another species, the American Redstart appeared to add many movements of its wings and tail designed to flush prey to its already active foraging behavior. Furthermore, the searching movements of the Black-capped Chickadee (*Parus atricapillus*) depended upon the distribution of whatever substrate (e.g., dead leaves) an individual of this species was searching at the time. Searching movements, therefore, cannot necessarily be categorized typologically in the same way as attack maneuvers (see below). We agree with the approach of most authors who quantify and present data on searching movements separately (e.g., Robinson and Holmes 1982, Landres and MacMahon 1983, Holmes and Recher 1986b).

Many birds use food-searching methods that are similar to attack methods (see below). Robinson (1986), for example, quantified the rate at which Yellow-rumped Caciques (*Cacicus cela*) used the following search tactics: "probe-searches," in which an individual searched a dense cluster of leaves; "hover-searches," in which an individual searched the tips of foliage while hovering under them in stationary flight; and "hang-searches," in which an individual searched a nearby substrate while suspended below it. If any of these searching tactics led to a prey capture, then they were quantified separately as prey attack maneuvers. The only difference between a "probe-search" and a "probe-attack" (see below) was in whether or not prey was located. This illustrates a problem in distinguishing between searching and attack methods in species that search for concealed food: any classification system inevitably includes data on both searching and attacking behavior. Woodpeckers, for example, both search for and attack prey by removing an outer layer of bark. We have chosen to classify these methods as attacks (see below) on food-concealing substrates. Distinguishing between search and attack phases, however, represents an unresolved issue in some parts of our classification scheme, especially for those species that peer closely and unambiguously at particular substrates, such as curled leaves, leaf tops, and crevices. Although these species search a particular substrate in a manner that is analogous to any of the substrate-manipulation maneuvers outlined in the attack maneuver section (see below), our scheme does not include "peering" or "scanning" as an attack maneuver. In the field, we record substrates that are unambiguously searched with the notation "visual search," but we are uncertain as to how to include such data in analyses. Certainly, such visual searches are important in analyses of substrate use.

Several other kinds of search behavior are sufficiently distinct to warrant separate treatment. Many birds follow disturbances that expose prey; such disturbances include fires, other animals (particularly other bird species, ungulates, monkeys, and army ants), and humans and their machines. Many recent studies place disturbance-followers in a separate guild (e.g., Karr 1980, Terborgh 1980a, Terborgh and Robinson 1986).

Many birds steal food from other birds, and some species rely on this tactic (kleptoparasitism) for locating and capturing food (see Brockman and Barnard [1979] for review). Finally, some landbirds form mutualistic food-searching associations either with conspecifics (e.g., Kilham 1979, Mindell and Black 1984) or other bird species (Jackson 1985), especially within mixed-species flocks (e.g., Munn 1986). These sorts of associations should always be recorded.

ATTACK BEHAVIOR

We define the "attack" phase as that portion of foraging behavior from the moment when a food item, or food-concealing substrate, is sighted to the moment when a capture attempt is made. Thus, we include within "attack" phase those behaviors aimed at dislodging or revealing food before it is sighted, such as various kinds of substrate manipulation (e.g., flaking, hammering, gaping). We further subdivide the attack phase into (1) perch and (2) maneuver.

Few studies have quantified parameters concerning the characteristics of the perch from which an attack is launched. The numerous studies by E. O. Willis (see references) have shown that a species' presence in a particular habitat or microhabitat may be determined in part by availability of suitable perches. Certain species may also specialize on perch types not used by other species. For example, two small tanagers (*Hemispingus xanthophthalmus* and *H. verticalis*) that characteristically search the uppersides of leaves in dense clusters do so by perching on the clusters themselves (Parker and O'Neill 1980; Parker et al. 1980, 1985). Several species in the vireonid genus *Hylophilus* characteristically grasp the margins of leaves for perches to reach the undersides of these leaves (T. A. Parker and JVR, unpubl. data). Furthermore, studies such as those by Partridge (1976a; cf. Leisler and Winkler 1985) have revealed important morphological adaptations associated with particular perch types.

Perch type can be quantified using the same variables as those used in our scheme for "substrate" (see below). In practice, most measurements taken for the substrate will be the same as those for the perch except for the details of perch angle and diameter; therefore, the increase in volume of data to be recorded in the field is minimal. Those species that search while moving do not really have a "perch" *per se*; for instance, some species search and attack while in continuous flight ("screening," see below) or while hovering (e.g., Say's Phoebe [*Sayornis saya*], Grinnell and Miller 1944; bluebirds [*Sialia* spp.], Power 1980; and Restless Flycatcher [*Myiagra inquieta*], Ford et al. 1986).

Our classification of attack maneuvers categorizes them with respect to the complexity and required agility of each behavior. For example, we assume that aerial maneuvers and substrate manipulation require greater agility and more energy than those maneuvers in which a food item is removed from a substrate next to the bird's perch. Our classification also attempts to remove where possible the influence of substrate; thus, foraging motions that appear similar, but are directed at different substrates, are grouped together. Such similarities may be superficial, and foraging motions are certainly influenced by the types of substrates at which they are directed. Nevertheless, we prefer to group to-

TABLE 1. PROPOSED CLASSIFICATION SCHEME FOR ATTACK METHODS OF THE FORAGING BEHAVIOR OF NON-RAPTORIAL LANDBIRDS, WITH SYNONYMS OR PRESUMED SYNONYMS FROM OTHER STUDIES (SEE TEXT)

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- I. Near-perch maneuvers
- A. Surface maneuvers
1. Glean (= pluck, perch-glean, pick)
 2. Reach (= stretch)
 - a. Reach-up (= crane)
 - b. Reach-out
 - c. Reach-down (= lean, duck-under)
 3. Hang (= hang-glean)
 - a. Hang-up (= hang vertical, hang head-up, vertical clinging)
 - b. Hang-down (= hang head-down)
 - c. Hang-sideways (= hang-side, vertical clinging)
 - d. Hang-upsidedown (= hang horizontal)
 4. Lunge (= dart, rush)
- B. Subsurface maneuvers: no substrate manipulation
1. Probe
- C. Subsurface maneuvers: substrate manipulation
1. Gape
 2. Peck (= tap)
 3. Hammer (= drill)
 4. Chisel
 5. Flake (= bill-sweep, toss)
 6. Pry
 7. Pull
 8. Scratch
- II. Aerial maneuvers
- A. Leg-powered maneuvers
1. Leap (= jump-glean, jump). Include leap-distance and leap-angle.
- B. Wing-powered maneuvers
1. Sally (= hawk, snatch, flycatch, hover-glean, hover). Include sally-distance and sally-angle.
 - a. Sally-strike (= outward strike, upward strike, snatch)
 - b. Sally-glide
 - c. Sally-stall (= hover, hover-glean)
 - d. Sally-hover (= hover, hover-glean)
 - e. Sally-pounce (= land-and-glean, pounce, dive-glean)
 2. Flutter-chase
 3. Flush-pursue
 4. Screen (= hawk)
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In general, studies of attack behavior in landbirds have distinguished the conspicuous aerial maneuvers from other attack behaviors, but the nonaerial attack maneuvers have often been lumped in one category, usually "glean." Such merging of nonaerial maneuvers into one or a few categories might obscure important behavioral differences among species that have implications for adaptive morphology (e.g., Richards and Bock 1973, Partridge 1976a, Leisler and Winkler 1985), search tactics, niche overlap, and food selection.

Our classification (Table 1) does not include certain maneuvers that appear to be rare, such as digging in ground by using a strongly curved bill in a hoe-like motion (Engels 1940), using spines and twigs as tools for probing (reviewed by Boswall 1977), using the head as a brace to provide leverage for foot scraping (DeBenedictis 1966, Kushlan 1983) or as a buttress to move or dislodge substrate (Keast 1968), vibrating feet to startle prey in leaf-litter (Hobbs 1954, Wall 1982 as cited by Edington 1983), rustling leaf-litter to startle prey (Potter and Davis 1974), and crushing twigs with the bill to expose prey therein (Mountainspring 1987). The system in Table 1 can be expanded as needed to include any such rare behaviors.

Many studies of foraging behavior that make interspecific comparisons, or intraspecific comparisons among seasons or habitats, have presented their data in the form of a diversity index and have not included the original data with percentage of observations in each foraging category. Other studies have identified the number of species in a community associated with various foraging categories, but have neglected to identify which species belong in each category. We think that the original data themselves should be presented to facilitate comparisons with other studies; they should at least be published as appendices.

An outline of the categories with definitions of each attack behavior follows. Some categories are not mutually exclusive. For example, a bird that "sally-hovers" might also "probe" while hovering. Therefore, many attack maneuvers can have compound names, such as "sally-hover-probe" or "reach-out-gape."

Each maneuver category is accompanied by some examples from the literature. Our literature survey is intended to be illustrative rather than encyclopedic. We tend to cite examples from recent, quantitative studies, rather than older, more qualitative material. Although the descriptive sections of the latter are often superior, much of the older material is contained within more general life-history studies and is therefore more difficult to locate.

In choosing a standard vocabulary, we have attempted to use simple, descriptive terms, which, if possible, are already frequently used in studies of foraging behavior; we have not hesitated to "synonymize" many favorite terms, including many of our own.

I. Near-perch maneuvers (target food item can be reached from bird's perch)

A. Surface maneuvers

1. *Glean*: to pick food items from a nearby substrate, including the ground, that can be reached without full extension of legs or neck; no acrobatic movements are involved. Emmlen's (1977) and Mountainspring's (1987)

gether similar-appearing behaviors to alert morphologists to these potential similarities, rather than to allow the substrate category to separate automatically such behaviors. Because the system presented here also requires that the substrate also be recorded, no information is lost by excluding substrates from the behavior categories.

“pluck,” Fitzpatrick’s (1980) “perch-glean,” and Moermond and Denslow’s (1985) and Remsen’s (1985) “pick” are synonyms. Perhaps the majority of maneuvers performed by most foliage- and ground-searching birds are “gleans.” For example, 51% of the forest species studied in the Andes by Remsen (1985) and 53% of the forest species studied in Australia by Ford et al. (1986) used glean as their principal foraging maneuver. Because gleaning is presumably the least costly maneuver in terms of energy expenditure, it is not surprising that it is used so frequently (Remsen 1985; Moermond, this volume).

2. *Reach*: to extend completely the legs or neck upwards, outwards, or downwards to reach food (after Moermond and Denslow 1985, Remsen 1985). Because most studies seldom distinguish “glean” from “reach,” the frequency with which “reach” maneuvers are used is not generally known. Strong interspecific differences among congeners in ability to reach are associated with morphological differences (Snow and Snow 1971, Moermond and Denslow 1985). Some frugivores, especially toucans and some tanagers, obtain their food by reaching (Moermond and Denslow 1985). Morse (1967b), who distinguished “stretching”—which is probably equivalent to our “reaching”—from gleaning, found that it was used seldomly (0–5% of all maneuvers) in the six species of wood-warblers studied. Three further subdivisions may be made with respect to direction:
 - a. *Reach-up*: to reach above the bird. This is synonymous with the “crane” of Greenberg (1987b). This maneuver is used especially frequently to pick prey from undersides of leaves. The Pale-legged Warbler (*Basileuterus signatus*) uses this motion, along with the next, more frequently than any other maneuver (Remsen 1985).
 - b. *Reach-out*: to reach lateral to the bird. A maneuver used especially frequently to pick prey from nearby leaves and branches.
 - c. *Reach-down*: to reach below the plane of the feet. This is synonymous with the “lean” of Greenberg (1987b) and probably the “ducking-under” of Rabenold (1980). This maneuver is used by many tanagers, especially *Tangara*, when foraging on branches (Snow and Snow 1971; Skutch 1981; Parker and Parker 1982; Remsen 1984, 1985; Hilty and Brown 1986; Isler and Isler 1987); tanagers often reach-down alternately on opposite sides of a branch as they move along the branch, as does the wren *Odontorchilus branickii* (Parker et al. 1980). A bird-of-paradise (*Parotia carolae*) apparently uses a similar maneuver when searching

branches (Forshaw and Cooper 1979). At least one hummingbird (*Metallura tyrianthina*) uses reach-down maneuvers to reach more than a third of its flowers (Remsen 1985).

3. *Hang*: to use legs and toes to suspend the body below the feet to reach food that cannot be reached from any other perched position. “Hang-glean” of Recher et al. (1985) and Robinson (1986) is a synonym. Differences in frequency of use of “hang” among similar species may have subtle consequences for morphology (Partridge 1976a, Leisler and Thaler 1982). Parrots use “hang” frequently (Forshaw 1973 and references therein). Chickadees and titmice (Paridae), bushtits (Aegithalidae), and some thornbills (*Acanthiza*) frequently “hang” to reach undersides of branches and leaf tips (e.g., Gibb 1954; Root 1964, 1967; Grant 1966; Sturman 1968; Partridge 1976b; Rabenold 1978; Moreno 1981; Alatalo 1982; Bell 1985b; Recher et al. 1985, 1987; Laurent 1986). The Palm Tanager (*Thraupis palmarum*) in Trinidad “hangs” almost exclusively when searching for insects in foliage (Snow and Snow 1971). The Blue-backed Conebill (*Conirostrum sitticolor*; Thraupinae) also uses this maneuver as its primary means of attack (Remsen 1985). Other insectivores that use “hang” regularly include: Rufous-browed Wren (*Troglodytes rufociliatus*; Skutch 1960), some wood-warblers (Root 1967, Ficken and Ficken 1968, Elliott 1969, Andrie and Andrie 1976, Rabenold 1980), Speckled Tanager (*Tangara guttata*; Snow and Snow 1971); some white-eyes (*Zosterops*; Gill 1971, Earlé 1983); Ruby-crowned Kinglet (*Regulus satrapa*; Rabenold 1978); the furnariid *Siptornis striaticollis* (Eley et al. 1979); and Sharpbill (*Oxyruncus cristatus*; De L. Brooke et al. 1983, Stiles and Whitney 1983). Some vireos “hang” when grasping the margins of leaves to reach food that cannot be reached from branches (*Vireo griseus*, Nolan and Wooldridge 1962; *V. huttoni* and *V. gilvus*, Root 1967); several tropical vireos (*Hylophilus*) use this maneuver frequently if not predominately (Greenberg 1984a; T. A. Parker and JVR, unpubl. data). Many species that extract prey from hanging dead leaves “hang” (and “reach”) to investigate isolated dead leaves (Skutch 1969 for *Automolus ochrolaemus*; Greenberg 1987b; K. V. Rosenberg, unpubl. data; JVR, unpubl. data). Among frugivores that “hang” to reach fruit are *Euphonia violacea* (Snow and Snow 1971) and two species of woodpeckers (Moermond and Denslow 1985). Several hummingbirds “hang” to reach flowers (Parker and O’Neill 1980, Parker and Parker 1982, Parker et al. 1985, Remsen 1985). Four types of “hang” maneuvers (Fig. 1) should probably be distinguished (modified after Partridge 1976b,

Rabenold 1980, Alatalo 1982, Earlé 1983, and Greenberg 1987b):

- a. *Hang-up*: to hang, head-up.
- b. *Hang-down*: to hang, head-down. This differs from reach-down only in that the bird is clinging to a vertical surface or side of a horizontal surface, rather than perching on the upperside of a surface in reach-down. There is probably a continuum between the two maneuvers, and in fact, Moermond and Denslow's (1985) "reach" would include maneuvers here considered to be "hang-down."
- c. *Hang-sideways*: to hang on the side of a substrate with body axis parallel to the ground and with the bird's side oriented upwards.
- d. *Hang-upside-down*: to hang, belly-up, on underside of horizontal or diagonal surface.

These same four categories may also be applied to the foraging behavior of all specialized bark-foraging birds (e.g., woodpeckers, dendrocolaptids, certhiids) that characteristically hang while searching and attacking; in bark-foraging birds, these maneuvers are probably best considered postures rather than maneuvers.

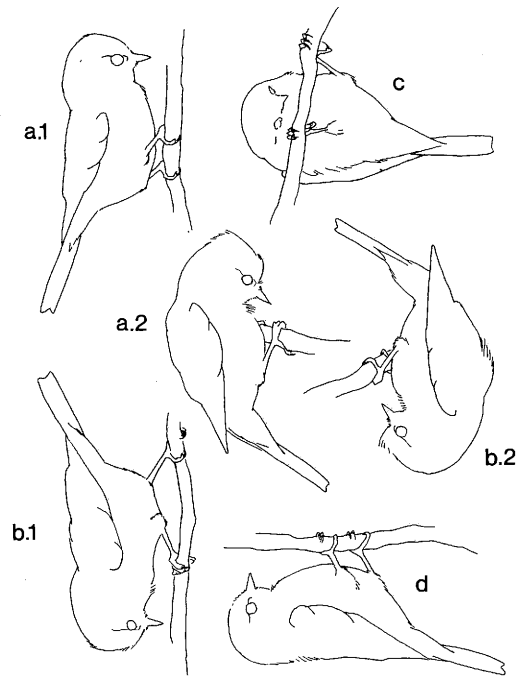


FIGURE 1. "Hang" maneuvers: (a.1) = "hang-up" on vertical perch; (a.2) = "hang-up" on horizontal perch; (b.1) = "hang-down" on vertical perch; (b.2) = "hang-down" on horizontal perch; (c) = "hang-sideways"; (d) = "hang-upside-down." Drawing by Donna L. Dittmann.

4. *Lunge*: those maneuvers in which the food item is beyond the range of "reach," but rapid leg movements rather than flight are used to approach and capture the prey. This is synonymous with the "lunge" of Greenberg (1984a), except that Greenberg's lunge would include movements that we call "reach-out." Root's (1967) "rush" is a combination of our "sally-pounce" (see below) followed by our "lunge." Some studies have used "dart" for foliage-gleaning birds and "rush" for ground-foraging birds as presumed equivalents. Several ground-foraging birds, particularly thrushes (Heppner 1965; Smith 1973; Tye 1981; Willis 1985a, 1986) and ground-cuckoos (*Neomorphus*: Willis 1982a), and also some bulbuls (*Bleda*; Willis 1983a), tyrannids (*Muscisaxicola*, Smith and Vuilleumier 1971; *Corythopsis torquata*, Willis 1983b), and antbirds (*Gymnopathys*, Willis 1968; *Grallaricula nana*, Parker et al. 1985) use the lunge maneuver regularly. Arboreal birds that also regularly lunge include: Red-crowned Ant-Tanager (*Habia rubica*; Willis 1960), Plain-brown Woodcreeper (*Dendrocincla fuliginosa*; Willis 1972), Chestnut-crowned Gnatcatcher (*Conopophaga castaneiceps*; Hilty 1975); Black-headed Grosbeak (*Pheucticus melanocephalus*; Airola and Barrett 1985), the tiny, canopy antwrens of the *Terenura callinota* superspecies (Remsen et al. 1982; Stiles 1983; T. A. Parker, unpubl. data), White-shouldered Tanager (*Tachyphonus luctuosus*; Greenberg 1984a; JVR, unpubl. data), and an undescribed species of *Cercomacra* (Formicariidae; Parker and Remsen 1987).

- B. Subsurface maneuvers (bird penetrates or manipulates the substrate rather than removing food from its surface; the attack is directed at food that cannot be seen from the surface without substrate manipulation).

1. *Probe*: to insert the bill into cracks or holes in firm substrate or directly into softer substrates such as moss or mud to capture hidden food. This tactic is often associated with specialized morphologies adapted for specific substrates. Most probes have long, slender, decurved bills for reaching deep into crevices, tubes, holes, and soft substrates such as mud or moss. Those that probe bark often have specialized hindlimb morphology and tail structure for climbing on and bracing against branches (Richardson 1942, Bock and Miller 1959, Feduccia 1973, Norberg 1979). Several unrelated groups have converged on similar morphology associated with bark probing: the creepers (Certhiidae), some woodcreepers (Dendrocolaptidae), and the Australian treecreepers (*Climacteris* spp.). The scythebills (*Campylorhamphus* spp.) and the Long-billed Woodcreeper (*Nasica longirostris*), with some of the longest bills relative to body size of any passerines, use their bills for probing deep into holes in tree trunks and

bamboo stems and into large bromeliad clusters (Pierpont 1986; T. A. Parker, unpubl. data; JVR, unpubl. data). Some woodpeckers do more probing (and gleaning) than the more "typical" woodpecker maneuvers, such as "peck" and "hammer" (e.g., Bock 1970; Short 1973, 1978; Cruz 1977; Alatalo 1978; Cruz and Johnston 1979, 1984; Stacey 1981; Askins 1983; Pettersson 1983; Kattan 1988). Bark-foraging birds that also probe epiphytic vegetation include the Brown Creeper (*Certhia familiaris*; Stiles 1978), many woodcreepers (Willis 1983c, d), and some woodpeckers (Kilham 1972, Short 1973, Cruz 1977, Askins 1983), and certain furnariids (Skutch 1969, Eley et al. 1979, Parker et al. 1985, Remsen 1985). Some species without obvious morphological adaptations for climbing also frequently probe bark or epiphytes on branches. Although examples include continental birds, such as the Sharpbill (Stiles and Whitney 1983), some wrens (Root 1964, Parker 1986a), and the Red Warbler (*Ergaticus ruber*; Elliott 1969), they are particularly frequent on islands or in regions such as New Guinea and Australia where specialized bark-searching taxa are rare or absent (Keast 1968, Zusi 1969, Cruz 1978). Examples include: a pachycephalid (*Colluricincla harmonica*), a scrub-wren (*Sericornis magnus*), and some meliphagid honeyeaters (Keast 1968, Recher et al. 1985); a mimid (*Cinlocerthia ruficauda*; Zusi 1969); some Hawaiian honeycreepers (Richards and Bock 1973); some icterids (*Nesopsar nigerrimus* and *Icterus leucopteryx*; Cruz 1978); and several birds-of-paradise (*Ptiloris* spp., *Astrapia mayeri*, *Pteridophora alberti*, *Diphyllodes magnificus*; Forshaw and Cooper 1979). Many species that search hanging dead leaves for hidden arthropods probe into these curled leaves (Remsen and Parker 1984 and references therein; K. V. Rosenberg, unpubl. data; T. A. Parker, unpubl. data). Similarly, some species of small tanagers (*Dacnis* spp. and *Cyanerpes* spp.; Snow and Snow 1971, Isler and Isler 1987) use their slender bills to probe inside curled living leaves. Some populations of Yellow-throated Warbler (*Dendroica dominica*) probe pine cones (Ficken et al. 1968, Emlen 1977) or dense clusters of pine needles or small leaves (Lack and Lack 1972). Some ground-foraging birds probe in soil, mud, or deep leaf-litter; examples include thrashers (*Toxostoma*, Mimidae; Fischer 1981), White's Thrush (*Zoothera dauma*; Edington 1983), Rook (*Corvus frugilegus*; Waite 1984b), White-winged Chough (*Corcorax melanorhamphos*; Ford et al. 1986), and the woodcocks (*Scolopax* spp.; Sheldon 1971). The furnariid *Cinclodes excelsior* probes moss and lichens on rocks and the ground (Fjeldsá et al. 1987). Hundreds of species of nectar-

feeding birds around the world probe flowers, especially in the Trochilidae, Nectarinidae, and Meliphagidae. Woodpeckers and hummingbirds also extend their tongues to probe crevices, holes, and flowers; such probing could be labelled "tongue-probing."

C. Subsurface maneuvers with *Substrate Manipulation* (maneuvers in which the substrate is manipulated beyond insertion of a probe).

1. *Gape*: to insert the bill into the substrate as in a probe, but the bill is opened to widen the opening. This maneuver is characteristic of many starlings and American blackbirds (Icteridae), which have bills and jaw musculature adapted for gaping (Beecher 1951, 1978; Orians 1985b). Various icterids use their bills to open holes in curled living and dead leaves (e.g., orioles [*Icterus* spp.]), dead branches and stems, moss, bromeliad clusters, seed clusters, leaf-litter, soil (*Sturnella* spp.), clumps of grass, flowers, and large fruits (Cruz 1978; Orians 1985b; Robinson 1985, 1986, 1988); they also use "gape" to turn over stones, twigs, dung, and other objects that might conceal prey on the ground (Orians 1985b). Several species of wood-warblers, including several *Vermivora* spp. (Ficken and Ficken 1968), the Swainson's Warbler (*Limnithlypis swainsonii*; Meanley 1970), and the Worm-eating Warbler (*Helmintheros vermivorus*; Greenberg 1987b), use the gape maneuver for probing buds, dead leaves, and flowers. The Sharpbill "gapes" to open tightly rolled young leaves and dead leaves (Stiles and Whitney 1983), as does the woodhoopoe *Phoeniculus bollei* to open crevices in loose bark (Löhrl 1972). Instances of gaping are occasionally reported in other taxa, such as Meliphagidae (Keast 1968) and Dendrocolaptidae (Willis 1983c).
2. *Peck*: to drive the bill against the substrate to remove some of the exterior of the substrate. This maneuver is characteristic of many woodpeckers (Picidae) that excavate holes in bark or wood to expose prey. "Peck" is synonymous with the "tap" maneuver of some studies of woodpeckers; we recommend restricting "tap" to those motions that are probably exploratory pecks for detecting wood-borer tunnels or movements, as described by Davis (1965) and Kilham (1972). Many parids and at least one icterid (*Nesopsar nigerrimus*; Cruz 1978) also peck to excavate holes in rotted wood. Ground-foraging birds use this maneuver in combination with "flake" (see below) to dig small holes to reach food in the ground (e.g., thrashers [*Toxostoma*], Engels 1940, Fischer 1981; and some thrushes, Tye 1981). Some frugivorous birds use "peck" to break the outer skin of large fruit (Snow and Snow 1971). The Bananaquit (*Coereba flaveola*; Gross 1958), some hummingbirds (Colwell 1973, Stiles 1985c), some white-eyes (*Zos-*

- terops*; e.g., Gill 1971), and icterids (Robinson, unpubl. data) may use this maneuver, usually described as “piercing,” to make a hole in the base of flower corollas for “stealing” nectar, but the actual maneuver used to make the hole is uncertain. The flower-piercers (*Diglossa*) hold the flower with their hooked upper mandible and pierce with their sharp, upturned lower mandible (Skutch 1954).
3. *Hammer*: to deliver a series of pecks without pausing between pecks. This maneuver is mainly restricted to certain woodpeckers that use it for excavation of deep holes to reach bark- or wood-dwelling insects or sap. The twig-foraging furnariid *Xenops minutus* also uses this maneuver frequently (Skutch 1969). Some chickadees and titmice (Paridae) may use this maneuver occasionally to open acorns, galls, seeds, and fruits (e.g., *Parus inornatus* and *P. rufescens*; Root 1964, 1967), but the pecks are not delivered as rapidly as in woodpeckers. The distinction between hammer and peck, which rests on whether there is a pause between pecks, may be vague. Counting the number of pecks per unit time, and thereby eliminating the “hammer” category, is an alternative treatment.
 4. *Chisel*: like “peck,” but rather than the bill being pounded almost perpendicularly into the substrate, it is aimed more obliquely at the substrate—usually bark or dead stems—and the bill is used as a chisel or lever to dislodge portions of the substrate. The direction of head movements is forward and upwards. Slightly to strongly upturned lower mandibles that give the bill a somewhat chisel shape are often associated with species specialized on chiseling. Species that seem to have converged on this foraging behavior and morphology are some *Xenops* spp. (Furnariidae; Skutch 1969), the dendrocolaptid *Glyphorhynchus spirurus* (Skutch 1969), the furnariid *Simoxenops ucayali* (JVR and T. A. Parker, unpubl. data), and the antbird *Neotantes niger* (Hilty and Brown 1986); and to a lesser degree, nuthatches (*Sitta* spp.) and sitellas (*Sitella* spp.; Holmes and Recher 1986a, b). We invented this category to match our expectations of how chisel-shaped bills are used rather than on any data on movements used by these species. Although some brief descriptions (e.g., *Glyphorhynchus*; Skutch 1969) fulfill our expectations, the reality of our “chisel” maneuver remains unclear.
 5. *Flake*: to brush aside loose substrate with sideways, sweeping motions of the bill. Not as much force is required as in chisel or pry because the substrate dislodged is already loose or unattached. This category combines two types of motions that are often difficult to distinguish in the field: the closed bill tip is used to brush aside the substrate, and the substrate is grasped briefly between the mandibles (which can be called “toss” when the distinction can be made). “Flake” is synonymous with “bill-sweeping” (Clark 1971) except that it applies to substrates other than leaf-litter. “Flake” is also apparently synonymous with R. J. Craig’s (1984) “leaf-pull.” Many bark-foraging woodpeckers “flake” to dislodge loose sections of bark (Tanner 1942; Kilham 1965, 1983; Conner 1981). The term “scaling” used in many studies of woodpeckers to describe removal of loose bark presumably refers to a combination of our “pecking,” “flaking,” and “prying.” Some dendrocolaptids (Willis 1983c, Pierpont 1986), furnariids (JVR, unpubl. data), and a meliphagid (*Melithreptus brevirostris*; Keast 1968) use this maneuver to search through debris clusters and loose bark. Ground-foraging birds that “flake” leaf-litter include some thrushes (*Turdus* [Skutch 1960, 1981; Clark 1971; Tye 1981]; *Hylocichla* [Clark 1971; Holmes and Robinson 1988]; *Alethe* [Willis 1986]), antbirds (*Formicarius*, Skutch 1969, Willis 1985b; *Rhopornis*, Willis 1981a), leaflossers (*Sclerurus*, Furnariidae; Skutch 1969, Hilty and Brown 1986), thrashers (*Toxostoma*; Clark 1971, Fischer 1981), bulbuls (*Bleda*; Willis 1983a), the waterthrushes (*Seiurus*; R. J. Craig 1984), and horneros (*Furnarius*; Robinson, unpubl. data). The Dune Lark (*Mirafra erythrochlamys*) uses “flake” to dislodge sand to excavate small craters to expose hidden seeds (Cox 1983). The furnariid *Cinclodes excelsior* “flakes” moss and lichens from rocks (Fjeldså et al. 1987).
 6. *Pry*: to insert the bill into a substrate and use it as a lever to lift up portions of the substrate. This differs from “flake” in that the sides of the bill, rather than the tip, accomplish the movement of the substrate while the tip remains relatively stationary. Substrates for which “pry” is needed are generally more firmly attached than those dislodged when a bird “flakes.” “Pry” differs from “chisel” in that the tip of the bill is stationary, instead of moved forward and upward as in chisel. Examples of species that use “pry” are: Band-backed Wren (*Campylorhynchus zonatus*; Skutch 1960), some species of dendrocolaptids (Skutch 1945; Willis 1983c, d), a meliphagid (*Melithreptus validirostris*; Keast 1968), many woodpeckers (e.g., Short 1973), and a bird-of-paradise (*Astrapia mayeri*; Forshaw and Cooper 1979), all of which pry up sections of loose bark; and Sharpbill, which pries moss from branches (Stiles and Whitney 1983).
 7. *Pull*: to grasp, pull, or tear, and thereby remove or dislodge sections of the substrate with the bill. Pulling differs from “flaking” in that the target substrate is grasped in the bill because extra force is needed to dislodge

more firmly attached portions of substrate. Birds that pull off loose bark or lichens to attack hidden insects include Band-backed Wren (Skutch 1960), Plain Titmouse (*Parus inornatus*; Root 1967), Crested Shrike-Tit (*Falcunculus frontatus*; Recher et al. 1985, Ford et al. 1986), a bird-of-paradise (*Macgregoria pulchra*; Forshaw and Cooper 1979), some orthonychids (Holmes and Recher 1986a), some dendrocolaptids (Willis 1983c, d) and Giant Cowbird (*Scaphidura oryzivora*; Robinson 1988). The Plain Titmouse also pulls apart leaf galls, flowers, lichens, and curled dead leaves (Root 1967). *Thripadectes rufobrunneus* (Skutch 1969) and several other furnariids (T. A. Parker, unpubl. data) pull leaves from bromeliads to expose prey. Most New World barbets (*Capito*, *Eubucco*) also pull open large dead leaves, twig galls, and sections of rotting wood to search for prey (Remsen and Parker 1984; T. A. Parker, unpubl. data; SKR, pers. obs.). The Plush-capped Finch (*Catamblyrhynchus*) pulls the leaf whorls at the nodes on bamboo stems, presumably to reveal insects (Hilty et al. 1979, Remsen 1985). The ground-foraging Song Thrush (*Turdus philomelos*) uses "pull" in its foraging repertoire (Henty 1976). Many parrots use "pull" for opening fruits, seeds, flowers, and rotting wood (Forshaw 1973 and references therein).

8. *Scratch*: to dislodge section of substrate with foot movements. This maneuver is used by many ground-foraging birds around the world; examples include: some orthonychids (Zusi 1978, Frith 1984), Australian lyrebird (Menuridae; Recher et al. 1985, Holmes and Recher 1986b), and some megapodes (e.g., *Alectura lathami*; Frith 1984). Although most species scratch using one foot at a time, many emberizid sparrows (Davis 1957, C. J. O. Harrison 1967, Hailman 1973, Greenlaw 1976 and references therein) and occasionally some thrushes (*Turdus*; Clark 1983) and icterids (Greenlaw 1976) move both feet simultaneously to expose food under leaf-litter or snow.

II. Aerial maneuvers (bird must leave substrate to reach food)

A. Leg-powered maneuvers

1. *Leap*: to launch into the air to reach a food item too far for a "reach" but too close for a "sally." This differs from "sally" in that the upward thrust seems to come mostly from leg movements rather than wing movements (Davies and Green 1976); it is equivalent to the "jump-glean" of Holmes and Robinson (1988) and presumably the "jump" of Hutto (1981b). Distinguishing "leap" from short sallies is often difficult. Davies and Green (1976) found that "leap" was the most frequent maneuver used by Reed Warblers (*Acrocephalus scirpaceus*), and Greenberg (1984a) found that it com-

prised 25% of the maneuvers of Chestnut-sided Warblers (*Dendroica pensylvanica*) in winter. Holmes and Robinson (1988) found that about one-fifth of all maneuvers used by Ovenbirds (*Seiurus aurocapillus*) and Dark-eyed Juncos (*Junco hyemalis*) were leaps. Greenberg and Gradwohl (1980) considered leaping (from ground to foliage) to be the primary foraging maneuver of Kentucky Warblers (*Oporornis formosus*) and Chestnut-backed Antbirds (*Myrmeciza exsul*). The Chestnut-crowned Gnatcatcher (*Conopophaga castaneiceps*) leaps to nearby perches to attack prey (Hilty 1975). Many species that follow army-ant swarms probably "leap-down" from low perches above the ants to capture flushed insects (e.g., *Gymnophis*, Willis 1968; *Rhegmatorhina*, Willis 1969; *Phlegopsis*, Willis 1981b; *Dendrocincla*, Willis 1972, 1979). Some seed-eating species apparently leap onto stems to pull seed heads to the ground (Emlen 1977). The direction and distance of the leap should be recorded, just as it is for "sally" (see next account), particularly because a "leap" downward (i.e., dropping) probably requires only a fraction of the energy than does an upward or outward leap against gravity.

B. Wing-powered maneuvers

1. *Sally*: to fly from a perch to attack a food item (and then return to a perch). Most authors have used separate terms to distinguish sallies directed at aerial prey from those aimed at nonflying prey. We do not, because the foraging site (i.e., air vs. anything else) will automatically be recorded more appropriately in our scheme under the "substrate" category (see below); and the maneuver itself appears to us to be very similar whether directed at air or hard substrate. Although we acknowledge that the movements directed at flying vs. nonflying food may be different, we prefer to remove the substrate-bias from terminology as much as possible. Another difference between our system and others is that the term "hawk" has been used frequently to describe what we here call "sally" (e.g., Holmes et al. 1979b). We use "sally" rather than "hawk" because: the dictionary definition of "sally" is closer to this behavior than is "hawk," and hawks rarely if ever fly from a lookout perch to attack flying prey. Similarly, the term "flycatch" has been used frequently for sallies after flying prey, but most "flycatchers," whether tyrannids or muscicapids, do not "flycatch" *per se*, but instead glean or sally to substrates (e.g., Fitzpatrick 1980). Greenberg (1984a) distinguished sallies in which a bird returned to the perch from those in which the bird continues in the same direction by calling the latter "darts." There is probably more among-author variability in terms used to describe aerial maneuvers (e.g., hawk, hover, hover-glean, snatch, sally, flycatch) than

in any other broad category of foraging behavior.

Many species have characteristic directions or distances associated with their sallies that provide an index of the average search radius (Fitzpatrick 1981, Robinson and Holmes 1982), and these are important to record (after Fitzpatrick 1980):

- a. *sally-distance* (distance of the sally from perch to food item).
- b. *sally-angle* (the qualitative divisions "up," "down," "horizontal," "diagonal-up," and "diagonal-down" probably represent maximum possible resolution under most field conditions). Certain species or species groups may have characteristic sally angles. Willis (1984), for example, noted that most manakins (Pipridae) typically sally only at a horizontal angle, and Holmes and Recher (1986a) found that two species of thornbills differed in the angles of their sallies.

Sally-distance and sally-angle should refer to the initial attack attempt only; subsequent pursuit of a missed target should be recorded separately. We distinguish five types of sallies based on the bird's foraging motion at the end of the sally:

- a. *Sally-strike*: to attack in a fluid movement without gliding, hovering, or landing (after the "outward striking" and "upward striking" of Fitzpatrick [1980] and the "snatch" of Moermond and Denslow [1985]). The "sally-strike," whether aimed at flying prey or stationary substrates, is the characteristic attack behavior of many Tyrannidae (Hespenheide 1971; Fitzpatrick 1980, 1985; Sherry 1984), Muscicapinae and other Old World "flycatchers" (e.g., Croxall 1977, Davies 1977b, Fraser 1983, Moreno 1984), Pipridae (Skutch 1969), Bucconidae (e.g., Skutch 1948; Willis 1982b, c), Galbulidae (Hilty and Brown 1986), Meropidae (Fry 1984), Momotidae (e.g., Skutch 1947; Willis 1981c), Alcedinidae (Fry 1980), and Conopophagidae (Willis 1985b). Numerous species in other families use the sally-strike maneuver to varying degrees, accompanied by morphological adaptations that parallel those seen in more typically sally-striking groups (Partridge 1976b, Norberg 1979, Schulenberg 1983). Most species that use this maneuver are sit-and-wait predators that watch for prey while sitting motionless on an elevated perch, although others search more actively (e.g., tree-climbing dendrocolaptids [Willis 1972, 1982d; Pierpont 1986] and some vireos [Robinson and Holmes 1982]). Ground-foraging birds that "sally-strike" to capture insects on foliage above them include the tyrannid *Corythopsis torquata* (Fitzpat-

rick 1980, Willis 1983b) and *Catharus* thrushes (Paszowski 1984, Holmes and Robinson 1988). Other ground-foraging birds "sally-strike" to catch flying insects. Examples include ground-tyrants (*Muscisaxicola* spp. [Smith and Vuilleumier 1971; Fitzpatrick 1980, 1985]), *Rhipidura leucophrys* (Ford et al. 1986), and wheatears (*Oenanthe* spp.; Leisler and Seibenrock 1983). Some species also use this maneuver to obtain fruit (Skutch 1969; Fitzpatrick 1980, 1985). Sally-striking species often have wide, scoop-like bills and wide gapes that presumably facilitate prey capture in flight (Fitzpatrick 1985).

- b. *Sally-glide*: like sally-strike except the final approach at the target is a glide (vs. continuous flapping in sally-strike). Moermond and Denslow (1985) pointed out that many sally-strikers do not use continuous, flapping flight in their approach, and they made a convincing case for distinguishing those species that used a brief glide from those that did not. It is likely that some or many of the examples of sally-strikers above are actually sally-gliders. Other than Moermond and Denslow's (1985) data on frugivores, the prevalence of sally-gliding (which they called "sally-scooping") vs. sally-striking will be revealed only by careful observations.
- c. *Sally-stall*: to stall in front of the target briefly with fluttering motions at the end of the sally. Moermond and Denslow (1985) noted that many species usually considered to sally-hover (see below) do not engage in true hovering (flying in place), but rather flutter awkwardly in a stalling motion after a steep attack angle at the final approach of the sally. Such species, mainly trogons and some cotingas, use different flight motions and have different morphological adaptations from those that hover. We suspect that many of the examples of "sally-hover" noted below may actually be "sally-stalling." As with sally-gliding, only careful observations (or high-speed photography?) will reveal its true prevalence among sallying birds.
- d. *Sally-hover*: like other sallies except that the bird hovers at the target substrate at the end of the sally. This is synonymous with Fitzpatrick's (1980) "hover-glean." Most studies do not distinguish between sally-strike and sally-hover (much less sally-glide and sally-stall), and many other studies appear to label all sallies to foliage as "hovering" (e.g., Holmes et al. 1979b), even though few of these maneuvers actually involve hovering flight. Unless these maneuvers are distinguished, the possibility that they require

- different morphological adaptations, as found for frugivores by Moermond and Denslow (1985), cannot be addressed. Some tyrannids use the sally-hover maneuver regularly (Fitzpatrick 1980, 1985), as do kinglets (*Regulus*; Rabenold 1978, Moreno 1981, Franzreb 1984), the Blue-gray Gnatcatcher (*Polioptila caerulea*; Root 1967), some sylviid warblers (*Phylloscopus*; Gaston 1974), some wood-warblers (*Ergaticus ruber*, Elliott 1969; *Dendroica*, Rabenold 1978, 1980; Greenberg 1984a); an acanthizid (*Sericornis magnirostris*; Frith 1984), the Restless Flycatcher (*Myiagra inquieta*; Ford et al. 1986), and some puffbirds (Sherry and McDade 1982; Willis 1982c, e). Bell (1984) found that at a forest site in New Guinea, 5 of 83 bird species studied in detail used this maneuver in 18–24% of his foraging observations: two monarch-flycatchers (*Monarcha* and *Arses*), a cracticid (*Peltops*), a meliphagid (*Melilestes*), and a drongo. Similarly, Remsen (1985) found that at a forest site in the Andes, 4 (all tyrannids) of 33 species studied in detail used this maneuver in 16–33% of their foraging observations. In contrast, hovering accounted for only 1% of all prey attacks observed in an Australian eucalypt forest where 41 species were studied in detail (Recher et al. 1985). Many species use this maneuver when taking fruit. Examples include many tyrannid flycatchers, manakins, and some tanagers (Fitzpatrick 1980, Willis 1984, Moermond and Denslow 1985). Some species, including kinglets (Leisler and Thaler 1982, Franzreb 1984), some wood-warblers (Morton 1980a), and the Yellow-rumped Cacique (Robinson 1986), occasionally hover under surfaces to search for food that cannot be seen from a perch. Hummingbirds, of course, use this maneuver extensively when feeding at flowers or searching foliage and branches; for nectar-feeding, however, the parameters “sally-distance” and “sally-angle” are usually irrelevant.
- e. *Sally-pounce*: to land briefly at the end of the sally to take food from substrate. Although the bird is perched when it takes the food item, we classify this maneuver as a “sally” because it involves a flight after food is spotted at a distance from the lookout perch. It is probably synonymous with Fitzpatrick’s (1980) “landing-and-gleaning,” Recher et al.’s (1985) “pounce,” and Holmes and Robinson’s (1988) “dive-glean.” Examples of birds that use this maneuver are: many open-country tyrannids and muscicapids (Fitzpatrick 1980, 1985; Fraser 1983), bluebirds (Power 1980), Australian robins (*Petroica*, *Eopsaltria*; Recher et al. 1985, Ford et al. 1986, Holmes and Recher 1986b), and Fan-tailed Cuckoo (*Cuculus pyrrhophanus*, Recher et al. 1985), some *Catharus* thrushes (Dilger 1956, Paszkowski 1984), some puffbirds (Willis 1982b, c), and the Field (*Spizella pusilla*) and Chipping (*S. passerina*) sparrows when foraging for insects (Allaire and Fisher 1975). Some vireos (Vireonidae) use this maneuver when attacking prey on branches (James 1976, Robinson and Holmes 1982). Some tropical vireos (*Hylophilus*) characteristically use this maneuver followed immediately by hanging on leaf margins when attacking undersides of leaves (T. A. Parker and JVR, unpubl. data). A special kind of sally-pounce is used by some seed-eating birds that sally to a grass stem, grasp the stem in their feet, and then allow their weight to pull the stem to the ground, where seeds can be removed more effectively (Allaire and Fisher 1975).
2. *Flutter-chase*: to flush or dislodge prey from a substrate and to then chase the prey. This maneuver is used regularly by foliage-gleaning birds that flutter after a falling or flying prey item that has escaped their normal attack behavior and is often preceded by a lunge. Root’s (1967) “tumble” is synonymous (because “tumble” refers to out-of-control, somersaulting movements, we have chosen a new term). Root (1967) found that Blue-gray Gnatcatchers (*Polioptila caerulea*) used this maneuver in 23% of all sallies directed at insects in the air; however, Root suspected that the frequent tail-flashing of this species may function to startle insects, therefore making these “flutter-chases” into “flush-pursuits” (see below) in our scheme. Morse (1968) found that four wood-warblers (*Dendroica*) used this maneuver in about 5% of their foraging motions. We see this maneuver most frequently in foliage-gleaning birds in mixed-species flocks in the canopy of tropical forests; apparently, the escape behavior of many of their arthropod prey involves falling from the substrate at the approach of a bird predator. In particular, the White-shouldered Tanager (*Tachyphonus luctuosus*) uses the flutter-chase maneuver frequently (Snow and Snow 1971; JVR, unpubl. data). We use this term mainly for species that are not typically salliers. We recommend recording the distance and angle of the chase, just as in the sally maneuvers.
3. *Flush-pursue*: similar to “flutter-chase” except that species that use this maneuver deliberately (vs. accidentally) flush prey from hiding places and then pursue the flying or falling prey. This maneuver tends to be prominent in the foraging repertoire of species that use it, most of which have conspicuous wing or tail spots or stripes that are flashed to startle hidden prey. Distin-

- guishing this maneuver from "flutter-pursuit" may be difficult, but because each involves fundamentally different tactics, we believe that to do so where possible is valuable. Among North American species, the American Redstart (*Setophaga ruticilla*; Robinson and Holmes 1982) and, on the ground, the Northern Mockingbird (*Mimus polyglottos*; Hailman 1960) most frequently use this maneuver. Other examples include: *Dendrocincla* woodcreepers (Willis 1972, 1979), fantails (*Rhipidura*; Recher et al. 1985, C. J. O. Harrison 1976, Holmes and Recher 1986a), *Monarcha* flycatchers (Pearson 1977b), *Myiobius* tyrannids (Fitzpatrick 1980), Ruddy-tailed Flycatcher (*Terentriacus erythrorus*, Sherry 1984), and the *Myioborus* redstarts (Parulinae; Remsen 1985).
4. *Screen*: to attack in continuous flight (after Emlen 1977, Fitzpatrick 1980). (Note that this is a searching behavior as well as an attack maneuver.) This is synonymous with "hawk" as used by Remsen (1985) and others for birds that feed in flight. Swallows, swifts, and nighthawks (*Chordeiles*, Caprimulgidae) use this maneuver almost exclusively. Other birds that may use this maneuver occasionally include European Starling (*Sturnus neglectus*; Cayonette 1947), Golden-naped Woodpecker (*Melanerpes chrysauchen*; Skutch 1969), Lewis' Woodpecker (*M. lewis*; Bock 1970), some tyrannids (Fitzpatrick 1980), and probably the puffbird *Chelidoptera tenebrosa* (Burton 1976).

FORAGING SITE

We suggest recording the following parameters with respect to the foraging site used by a foraging bird: (1) general habitat, (2) vertical position, (3) horizontal position, (4) foliage density, and (5) the precise substrate from which the food was taken. We discuss each category briefly.

- I. *Habitat*: Many study areas contain more than one habitat or microhabitat. Each foraging record should be assigned to one of the investigator's general habitat or microhabitat categories to permit examination of the influence of habitat on foraging behavior (e.g., Bilcke et al. 1986). Classification of habitats, a complex and critical topic, is beyond the scope of this paper.
- II. *Vertical position*: It has been recognized for decades that important differences in vertical position separate the foraging activities of many closely related birds. Furthermore, foraging behavior may change with changes in height above ground. Therefore, every foraging record should be assigned two values to allow its position to be plotted: (1) height-above-ground and (2) distance-to-canopy (above bird). We have also found a third parameter to be of interest: (3) height of the individual plant in which the bird was foraging. This allows us to distinguish species that frequently use small trees or saplings within the foliage column from those that use the lower foliage of canopy trees at the same height as the small trees. Provided that only one observer records the data, a visual estimate of height (vs. precise measurements) may be the only practical way to obtain such data. Not only does the time required to make precise measurements reduce the volume of data that can be collected, but it seems unlikely that the birds recognize vertical subdivisions sufficiently precisely to warrant such a time investment. Heterogeneity in canopy height, light penetration, and foliage distribution obliterate such precise boundaries. However, differences among observers in the accuracy of such visual estimates (Block et al. 1987) reveal the unreliability of such visual estimates and provide support for use of objective measures of height.
- III. *Horizontal position*: Many researchers have recorded the "horizontal" position (e.g., "inner," "middle," "outer") of the bird in the tree or bush. Many species of foliage- and branch-gleaning birds characteristically favor one of these foraging zones (e.g., MacArthur 1958 and numerous other studies). Whether birds select such zones *per se*, or are keying on differences in foliage density (next category) is unknown. It is possible that "horizontal position" and "foliage density" measures are largely redundant. However, Greenberg and Gradwohl (1980) and Holmes and Robinson (1981) showed the importance of branch and leaf arrangement around the bird in determining which surfaces can be attacked effectively. Greenberg (1984a) used a system for "horizontal" position designed specifically to place the foraging bird in categories with respect to foliage and branch geometry.
- IV. *Foliage density*: Foliage density at the point of foraging observation can be recorded using a qualitative scale. For example, the system that we have found to be useful (e.g., Remsen 1985; modified from Wiley 1971) is a scale from "0" to "5" of increasing foliage density within a one-meter radius around the bird: "0" = no vegetation within the imaginary 1-m sphere; "1" = very low vegetation density within the sphere (e.g., 95–99% of all light passes through sphere); "2" = low density, 75–95% of light passes; "3" = moderate density, 25–75% of all light passes; "4" = high density, only 5–25% of light passes; and "5" = extremely dense, 0–5% of light passes.
- V. *Substrate*. We have found the following substrate categories to be useful:
 - A. *Living Foliage*
 1. *Plant species* or "type" (species, genus, or family when possible; otherwise "broad-leaf tree," "vine," "palm," "grass," "bamboo," "fern," "cactus," and the like; note if epiphytic). Many studies (e.g., Hartley 1953; Gibb 1954; Willson 1970; Reller 1972; Holmes and Robinson 1981; Woinarski and Rounsevell 1983; Robinson and Holmes 1984; Franzreb 1984; Bell 1985b; Morrison et al. 1985, 1987b) have emphasized the importance of distinguishing plant species. In the tropics, many bird species specialize on distinctive plant types such

as bromeliads, bamboo (Parker 1982, Remsen 1985), and palms.

2. *Leaf size* (visual estimate of length and width of leaf searched). This is probably necessary mainly in areas where complexity of plant communities prevents quick taxonomic identification of plant species (and therefore subsequent, more accurate assessment of leaf size). Leaf buds should also be distinguished, although these can be "food" as well as substrate.
 3. *Top or Bottom*. See Greenberg and Gradwohl (1980) and Greenberg (1984a) for the importance of distinguishing leaf tops from leaf bottoms. Greenberg and Gradwohl (1980) also found that a foliage-gleaning tanager (*Dacnis cayana*) may inspect brown, insect-damaged areas on leaves; therefore, observers should be careful to record when such leaf sections are investigated.
- B. *Dead foliage*. See Gradwohl and Greenberg (1982b), Remsen and Parker (1984), and Rosenberg (this volume) for the importance of distinguishing live from dead leaves. Size of leaf should also be recorded, as well as condition (curled, tattered, or entire; see Rosenberg, this volume) and general type (e.g., palm, broadleaf, bamboo).
- C. *Bark or stem surfaces*. Observers should note that careful observations often reveal that many species generally thought to be foliage-searchers direct considerable proportions of their attacks at branches and stems, such as some species of vireos (Nolan and Woodridge 1962; Root 1967; James 1976, 1979; Robinson and Holmes 1982; Airola and Barrett 1985), tanagers (Snow and Snow 1971, Isler and Isler 1987), wood-warblers (Morse 1967a, b, 1968; Lack and Lack 1972; Emlen 1977; Greenberg 1984a), sylviids (Earlé 1983), Hawaiian honeycreepers (Richards and Bock 1973), shrikes (Earlé 1983), chats (Frith 1984), Old World sallying flycatchers and drongos (Bell 1984), honeyeaters, whistlers, and babblers (Keast 1968, Thomas 1980, Wooller and Calver 1981), and thornbills (*Acanthiza*; Bell 1985b, Recher et al. 1987). When recording use of this substrate category, the observer can record:
1. *Diameter* (visual estimate)
 2. "*Angle*" of branch (i.e., vertical, horizontal, or diagonal).
 3. *Upper or Lower side* (for horizontal or diagonal branches). Some species may characteristically forage on the undersides of limbs, such as the woodcreeper *Xiphorhynchus lachrymosus* (Willis 1983c).
 4. *Plant species*, when possible, or plant type (see A.1. above). See Jackson (1979) and Morrison and With (1987) for examples of the importance of tree species for woodpecker feeding-site selection.
 5. *Surface type and texture* (especially critical where identification of plant species is not possible). Examples include: (a) smooth-green; (b) smooth bark; (c) rough bark (with perhaps a qualitative scale to indicate degree of corrugation); (d) seam between two closely growing branches or between vine and supporting trunk (such seams appear to be particularly favored foraging sites for some dendrocolaptids; e.g., *Hylexetastes perrotii* [Willis 1982f]); (e) lichen- or moss-covered (mossy branches are favored sites for furnarids, dendrocolaptids, several birds-of-paradise, and tanagers [Skutch 1969, 1981; Forshaw and Cooper 1979; Parker and O'Neill 1980; Remsen 1984; Parker et al. 1985; Remsen 1985]); (f) hard, dead wood with bark removed; (g) soft, rotted dead wood (see Alatalo [1978], Cruz and Johnston [1979], Pettersson [1983], and Morrison et al. [1987b] for examples of the importance of distinguishing live from dead branches in bark-foraging birds; the furnariid *Xenops minutus* seems to be specialized on dead branches, especially those that have fallen but are caught up in the canopy [Skutch 1969; T. A. Parker and JVR, unpubl. data]); and (h) holes (favored foraging sites for some dendrocolaptids [Willis 1982d, f]).
- D. *Ground*
1. *Surface type* (e.g., mud, bare soil, leaf-litter, moss, gravel).
 2. *Distance to nearest cover*.
 3. *Slope* (e.g., flat, moderate slope, steep slope).
- E. *Rock*
1. *Size*.
 2. *Surface type* (e.g., smooth, rough, crevice).
 3. *Surface "angle"* (top, bottom, side; vertical or diagonal slope).
- F. *Air*
- G. *Flower* (when identification of plant unknown); as noted by Emlen (1977), it is often difficult to distinguish whether some species use flowers as sources of food (nectar feeding) or as substrates for searching for arthropods.
1. *Corolla length*.
 2. *Color*.
 3. *Flower density* (estimate no. flowers/unit area; e.g., per 0.5 m²).
- G. *Miscellaneous*. Almost every habitat will have some substrates that do not fit into the above scheme. For example, some species of birds search pine cones (Morse 1967a, Ficken and Ficken 1968, Emlen 1977, Moreno 1981), termite nests (Bell 1984), wasp nests (Willis 1982f), spider webs (Young 1971, Burt et al. 1977, Douglass 1977, Waide and Hailman 1977, Bell 1984, Brooks 1986, Tiebout 1986, Parrish 1988, Petit and Petit 1988), dung (Anderson and Merritt 1977), and even the skin of other vertebrates (Rice and Mockford 1954, Orians 1983, Isenhardt and DeSante 1985 and references therein, Robinson 1988). For fruit-eating birds, we do not record a substrate *per se*, but note certain characteristics of the fruit under "food taken" (see next section).

Although the number of parameters to be recorded in this classification of foraging maneuvers and sub-

Remsen, Rufous-tailed Xenops
 J.V. Xenops milleri
 1985

Tambopata Wildlife Reserve, Rio Tambopata, Depto. Madre de Dios, PERU

| | HT | DC | FD | Substrate | AHact | | |
|---|----|----|-------------|------------------|------------------|--|-----------|
| 4 July | 60 | 40 | 1 | x vine 2" | hang-up | | |
| | 55 | 45 | 1 | x vine 3" | hang-up / peck | | |
| | 55 | 45 | 1 | x 1" | hang-up | | |
| | 55 | 45 | 1 | x 2" at epiphyte | glean | | |
| This species is an extremely active, rapidly moving forager | | | | | | | |
| 12 July | 20 | 40 | 1 | x 3" | reach-down | | |
| | 60 | 20 | 1 | x 2" | | | |
| 18 July | 50 | 15 | 2 | DL 10x5 cluster | vs | | |
| | | | 2 | DL 3x2 | hang-up-sidedown | | |
| | | | 2 | DL 6x3 | | | |
| | | | 2 | DL 5x2 | hang-down | | |
| | | | 1 | x 1" | reach-down | | |
| | | | 1 | x 1" | | | |
| | | | 40 | 50 | 2 | DL 3x2 | hang-down |
| | | | 1 | 1 | 1 | small dried epiphyte 4x4 | |
| | | | 1 | 1 | 1 | x dried moss 5x5 | glean |
| | | | 1 | 1 | 1 | 1 with orthopteran 1/2-2" long. Claspd | |
| 40 | 60 | 1 | x 1" | hang-down | | | |
| | | 2 | x 1/2" dead | vs | | | |
| | | 2 | x 3" | vs | | | |
| | | 50 | 100 | 1 | x 1" | vs | |
| | | 1 | 1 | 1 | x 1" | vs | |
| | | 60 | 50 | 2 | x | hang-down | |
| | | 2 | 2 | x | reach-down | | |
| | | 2 | 2 | DL 3x2 | glean | | |
| | | 2 | 2 | DL 4x3 | | | |
| | | 2 | 2 | x moss | hang-up | | |
| 2 | 2 | x | glean | | | | |

FIGURE 2. Sample foraging data transcribed from microcassette to field notes. Codes: "HT" = height above ground, "DC" = distance-to-canopy above bird, "FD" = foliage density, "DL" = dead leaf, and "vs" = visual search. Vertical brackets near left margin group consecutive observations on same individual. The thin lines under the "Substrate" column record branch "angles," and tiny "x" marks record position of bird with respect to branch. (Height variables are in feet, and substrate variables are in inches.)

strate characteristics may seem complex and overwhelming, the advent of microcassette tape-recorders facilitates recording such volumes of data in the field. Also, transcription of the data can be simplified by using codes and symbols (Fig. 2).

FOOD TAKEN

Data on diets are useful for virtually every kind of foraging study. Differences in food taken may provide information on niches, morphology (principally of the bill), and energetics. Unfortunately, dietary data are usually difficult to obtain in the field, especially for insectivores.

For many species that eat small insects, it can even be difficult to determine whether or not a prey item was captured at the end of an attack. For these reasons, most field studies of insectivores include only limited data on prey. Variables measured include prey size (usually in relation to bill length, but see Bayer [1985] and Goss-Custard et al. [1987] for cautions) and prey type (for large prey items such as caterpillars and orthopterans). Some authors (e.g., Greenberg 1984a) recorded each time that a bird wiped its bill after a prey attack as an index of success. Reasonably accurate estimates of capture rates can be obtained for large prey, such as orthopterans that require extensive handling

before they are eaten (Robinson 1986). Many neotropical insectivores evidently obtain most of their energy from large katydids (Orthoptera: Tettigoniidae) and have bills adapted specifically to handle them (Greenberg 1981a). Most temperate-zone insectivores, on the other hand, have smaller bills, presumably adapted for the smaller arthropods or less agile larvae available during the breeding season. Because large food items have more biomass than small items, we think that food size should always be recorded where feasible.

For frugivores, the most important variable is the plant species. Secondary variables include the color (as a measure of ripeness), size (especially if the plant species is unknown), and shape of the fruit. For nectarivores, the plant species is again the primary variable of interest. If this is unknown, then color, shape, and corolla length should be recorded.

Data obtained from stomach samples are discussed elsewhere in this volume (Rosenberg and Cooper). Here we wish only to emphasize that stomach samples can be very useful when they reveal major ordinal levels of dietary differences among species being compared. Sherry (1984), for example, showed that species that are generally similar in size and foraging behavior can differ strikingly in their diets. Dietary analyses of Least Flycatchers (*Empidonax minimus*) and American Redstarts, which are strikingly similar in many aspects of their foraging behavior and foraging-site selection (Sherry 1979), revealed surprisingly little overlap (Robinson and Holmes 1982). In this case, knowledge of diet from stomach samples (redstarts catch many Heteropteran leafhoppers) provided information on the functional significance of the "flush-chase" attack maneuver described previously.

Data from stomach samples should, however, be treated with caution. Because prey items in stomach samples can usually only be identified to the level of order or family, the categories are crude. It is quite possible that two species that eat the same orders, families, or even genera of insects could overlap very little in other aspects of their foraging behavior, particularly substrate use. Information on diet in the absence of data on other components of foraging (e.g., Wiens and Rotenberry 1979) therefore could be misleading.

FOOD-HANDLING TECHNIQUES

Once food is "captured," it may be eaten, delivered to offspring or mate, stored (cached), or rejected. We here consider only the techniques associated with the first of these options. The way that food is handled is important because (1) food-handling time must be considered in the cost : benefit ratio of any food type (e.g., Sherry and McDade 1982), (2) it is a factor in studies of adaptive morphology (e.g., Sherry and McDade 1982, Moermond and Denslow 1985, Foster 1987), and (3) it has important implications for the study of plant-frugivore interactions (Howe and Smallwood 1982, Moermond and Denslow 1983, Levey 1987b). Food-handling techniques, however, have been largely ignored in studies of arthropod-foraging behavior (for exception, see Sherry and McDade 1982). Fortunately, the detailed descriptions by some observers (e.g., E. O. Willis and A. F. Skutch) have revealed the distinctive behaviors associated with handling of various food types. The lack of data on food-handling techniques,

particularly in insectivores, prevents an evaluation of their relative frequencies of use. In addition to quantifying the time taken to manipulate food before swallowing, we recommend the following terms to describe techniques that we feel are appropriate for field observations of landbirds:

1. *Engulf*: to capture and swallow in one continuous motion, without being held by the bill.
2. *Gulp* (after Moermond and Denslow 1985): to swallow upon capture without any noticeable manipulation other than being held briefly by the bill.
3. *Snap*: to pinch momentarily, usually between tips of mandibles and usually to kill prey before further handling.
4. *Mash* (after Moermond and Denslow 1985): to squeeze or move around between the mandibles before swallowing (apparently to kill prey or remove undesirable portions, such as wings, legs, shells, and husks); sometimes, juices or pulp are squeezed out of the food and solid portions discarded (Moermond and Denslow 1985, Foster 1987). This category almost certainly lumps distinct types of mandibulation that could be revealed by analysis of high-speed photography of food-handling.
5. *Shake*: to shake food item violently (to remove undesirable portions).
6. *Beat*: to beat food item against hard substrate (as in above, to kill or remove undesirable portions). Many small insectivorous birds typically beat insects against branches in a diagonally downward-facing position (e.g., Root 1967).
7. *Rub*: to rub food along substrate (usually to remove distasteful substances or undesirable portions such as hairs and stingers [Sherry and McDade 1982]).
8. *Jab*: to peck food item with bill tip (to kill it or open it), usually while clasped with feet.
9. *Tear*: to eviscerate or dissect food item into smaller pieces, usually while the food is clasped by one or both feet.
10. *Bite*: to bite and remove a section of food item (after Foster 1987). This technique applies as far as we know only to frugivores that take bites from fruit too large to swallow whole.
11. *Juggle*: to reposition food item, sometimes by tossing into air and catching it (to allow or facilitate swallowing; many species juggle prey to maneuver it into a head-first position before swallowing).
12. *Clasp*: to hold food item with feet.
13. *Anchor*: to immobilize food item by fixing it to substrate, such as by impaling with sharp objects or by wedging food item into crack.
14. *Drink*: intake of liquid food, such as fruit juices and nectar.

In practice, we have found that in the field, we have time to note only those food-handling behaviors that are not "gulping," which seems to be the predominant food-handling technique in most insectivorous and frugivorous birds, with the notation that all "blank" records refer to gulping. Our scheme leaves out certain techniques that are presumably very rare, such as scraping (to remove fruit pulp in snake-like jaw motion; Schaeffer 1953), dropping (to break open), soaking, and drowning.

ANALYSES OF FORAGING DATA

This classification system contains many finely subdivided categories. Although too many can create problems (e.g., small or empty data cells) for statistical analyses, we think that fine subdivisions are preferable during the data-gathering stage. Their retention allows maximum data resolution, which in turn, even if sample sizes are too small for statistical analysis, might generate insights that can be developed to answer specific questions in subsequent studies. Here we provide examples of how categories might be combined or subdivided.

I. *Ecomorphological studies.* Fine subdivisions of attack methods, foraging substrate, and searching behavior are most likely to be useful in studies of adaptive morphology. Fitzpatrick (1985), for example, showed that many aspects of bill and wing shape were strongly associated with the details of aerial attack methods (see Table 1) and substrate in tyrannids, whereas leg morphology was more closely related to searching movements and perch types. Fitzpatrick's (1985) classification system of foraging methods, therefore, combined searching movements, perch types, substrate type, and attack method in an attempt to include all of the variables that affect flycatcher ecomorphology. The bill morphologies of bark-foraging birds are also affected by the methods used to manipulate the substrate to attack concealed food. The finer subdivisions of near-perch maneuvers (see Table 1) also may be related to leg and foot morphology (Partridge 1976a, Leisler and Winkler 1985). The bill shapes of frugivores and some insectivores may also be associated with particular kinds of food (Greenberg 1981, Moermond and Denslow 1985, Foster 1987).

II. *Community-level studies.* Community-level studies probably require the least finely subdivided categories. Communities in wooded habitats are likely to include birds that use most of the attack methods described in Table 1. If each method were to be broken down by substrate, the resulting data matrix would be prohibitively large and would contain many zero values. For this reason, most studies that seek to identify guilds use only a few general attack categories (e.g., Holmes et al. 1979b) or use only data on foraging site (Anderson and Shugart 1974). Holmes et al. (1979b), for example, divided the attack methods of birds in a northern hardwoods forest into "gleans" (lumping all "near-perch" maneuvers in Table 1), "hovers" (all sallies to substrates other than air in Table 1), "probes" (including all subsurface maneuvers in Table 1), and "hawks" (all sallies directed at flying prey in Table 1). Each of these attack methods was then combined with a foraging site. The resulting

analysis showed that such variables as substrate and tree species were more important in assigning species to guilds than attack methods. By contrast, in a similar analysis of an Australian bird community, which added categories for flush-chase and manipulative prey-attacks, Holmes and Recher (1986a) found that attack methods were also important. The different guild structures in the two areas may have been influenced, therefore, by their differing classification systems. In general, we recommend that manipulative attack-methods be distinguished from methods in which food is simply plucked from surfaces or the air in studies of entire communities.

III. *Single-guild studies* (taxonomic guilds, *sensu* Terborgh and Robinson 1986). Studies that focus on ecologically similar species should benefit from fine subdivisions of substrates and attack methods. The members of a guild are only likely to use a subset of the attack methods shown in Table 1, which should simplify the matrices and allow finer subdivisions. Rosenberg (this volume), for example, included data on the size and shape of dead leaves searched, and Greenberg's (1987a, b) study of a dead-leaf forager included data on searching postures similar to the subdivisions of near-perch attacks shown in Table 1. Conner's (1980, 1981) studies of bark foragers showed the importance of different methods of manipulating substrates in distinguishing among species. Fitzpatrick (1980, 1981) showed the different ways that syntopic tyrannids differ in the subtle details of how they sally to catch prey.

IV. *Foraging modes* (*sensu* Huey and Pianka 1981) or adaptive syndromes (*sensu* Eckhardt 1979). Studies of foraging modes seek to identify suites of intercorrelated foraging variables. Many researchers have shown that the rates and lengths of searching movements are associated with the lengths and kinds of attack methods (e.g., Williamson 1971; Eckhardt 1979; Fitzpatrick 1981; Robinson and Holmes 1982; Holmes and Recher 1986b; Holmes and Robinson 1988; see also Moermond 1979a and Huey and Pianka 1981 for similar analyses of foraging in lizards). In general, birds that move short distances between perches also obtain food on nearby substrates. Similarly, species that fly long distances between perches also search and attack over long distances. Studies of adaptive syndromes therefore include detailed data on searching movements (including rates and lengths), attack tactics (including lengths of attacks), and the use of special foraging tactics such as tail-fanning. Table 2 gives examples of adaptive syndromes or foraging modes that have been identified in New World insectivorous birds (modified from Eckhardt [1979], Fitzpatrick [1981], and Robinson and

TABLE 2. ADAPTIVE SYNDROMES OR FORAGING MODES OF INSECTIVOROUS BIRDS

| Foraging mode | Search movements | Associated prey-attacking maneuvers |
|---------------------------------|---|--|
| Open perch or passive searching | Infrequent, long flights | Long sallies |
| Medium-distance searching | Frequent medium-length flights and bouts of hopping | Sallies and near-perch gleans |
| Near-surface searching | Frequent hops and short flights | Near-perch maneuvers, probes |
| Flush-Chasing | Conspicuous, frequent flights and hops, wing and tail flicking | Flush-chases |
| Manipulative | Short periods of movement between long periods at the substrate | Flake, peck, tear, hammer, scratch, chisel |

Holmes [1982]). Whether these relationships have global generality remains to be determined.

V. *Energetics and optimal foraging.* Studies of energetics or optimal foraging primarily use data on time intervals between movements and food-capture rates. Robinson (1986), for example, measured intervals between flights of at least one meter as an index of foraging speed and prey-capture rate, and prey size as an index of foraging success. Energetic studies therefore require long, timed sequences on individual birds in which the length and kinds of every movement are recorded. As already noted, food-handling time is a critical variable in studies of optimal diet selection (e.g., Sherry and McDade 1982).

CLOSING REMARKS

Although portions of our classification scheme have been used by us or other researchers for many years, other portions were novelties generated by rethinking the underlying logic of ear-

lier versions or by incorporating suggestions from other researchers. We regard this scheme as a first step towards standardization of the organization and vocabulary of studies of foraging behavior of birds. We anticipate that it will be modified as it is tested and refined by us and, we hope, other researchers.

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