Condor, 82:43–57

FORAGING BEHAVIOR OF NEOTROPICAL TYRANT FLYCATCHERS

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ABSTRACT.—An overview of the foraging characteristics of tyrant flycatchers (Tyrannidae) is presented in three parts. First, the physical techniques of different prey capture methods are described, and a standardized nomenclature for these techniques is suggested. Second, ten predominant "foraging modes" are defined according to the comparative frequencies with which each prey capture method is used by different species. Certain species use specialized foraging modes, in that their foraging behavior is confined to a single capture method. Other more generalized foraging modes are characterized by the use of several or many capture methods with similar frequency. Third, the distribution of these foraging modes within the family as a whole is summarized in a genus by genus outline, with genera grouped according to a recent systematic revision of the family. The resulting pattern shows that each of the three subfamilies contains certain behaviorally generalized genera as well as radiations into related, but more specialized, foraging modes.

Tyrant flycatchers (Tyrannidae) form one of the largest and most diverse bird families in the world. The 375 species (Traylor 1977) include one tenth of South America's entire land bird fauna (Meyer de Schauensee 1966), and their range of body forms and ecological roles is rivaled in the New World only by the Furnariidae (Feduccia 1973). This diversity, coupled with the ubiquity and numerical dominance of tyrannids throughout the Neotropics, makes the family ideally suited for a variety of studies regarding adaptive radiation in a continental avian group. Keast (1972) presented a brief overview of the tyrannid radiation, and several authors have analyzed evolution within selected flycatcher groups in greater depth (e.g., Lanyon 1967, 1978, Smith and Vuilleumier 1971, Fitzpatrick 1976). However, the scarcity of basic information on tyrannid biology, particularly among tropical species, has until now prohibited any comprehensive evaluation of the family's radiation.

With this paper I initiate a series of reports on ecological and evolutionary trends in the Tyrannidae by describing and classifying the foraging tactics that characterize the family (see also Fitzpatrick 1978). By necessity the bulk of this report is descriptive, my intent being to propose a standard by which tyrannid foraging behavior may be quantitatively described and analyzed from a variety of perspectives (see Discussion). The paper is presented in three sections, beginning with descriptions and suggested nomenclature for each of the prey capture techniques used by flycatchers. This is followed by an outline of the predominant ways that different tyrannids combine these individual techniques into discrete "foraging modes," each mode represented by a characteristic combination of prey capture techniques. Certain foraging modes are shown to reflect behavioral specialization, while other modes are more generalized. I conclude by reviewing the occurrence of these foraging modes within each of the major phyletic groups in the Tyrannidae, based on my own field studies, published information, and the recent systematic review of the family by Traylor (1977).

STUDY SITES AND METHODS

Data discussed in this report were accumulated over ten months of field work in an Amazonian forest site in southeastern Peru (Cocha Cashu Biological Station, Manu National Park, dept. Madre de Dios) where 61 tyrannid species have been recorded; two months in extreme northern Peru in a subtropical montane forest (Cordillera del Condor, dept. Cajamarca); four months in semi-arid scrub and deciduous forest sites in northwestern Venezuela (Falcón and Aragua); two months in cerrado, campo, and caatinga sites in southeastern and east-central Brasil (Santa Barbara do Rio Pardo, São Paulo; Parque Nacional de Brasilia; Exú, Pernambuco). Field work was conducted between June 1974 and September 1977. I was present in southeastern Peru and northern Venezuela during both wet and dry seasons, but worked in northern Peru and in Brasil only during their dry periods, from June to September.

I observed 167 flycatcher species in the wild. These represent all three subfamilies (Traylor 1977) and 71 of the 88 currently recognized tyrannid genera. I gathered quantitative data on foraging behavior for 90 tyrannid species at the above-mentioned sites. I watched flycatchers with the naked eye or through 9 × 35 power binoculars, and dictated observations into a portable tape recorder for later transcription. Foraging data were recorded only from individuals I judged to be actively foraging, primarily during morning and late afternoon peaks of activity. Sluggishness, resting, or

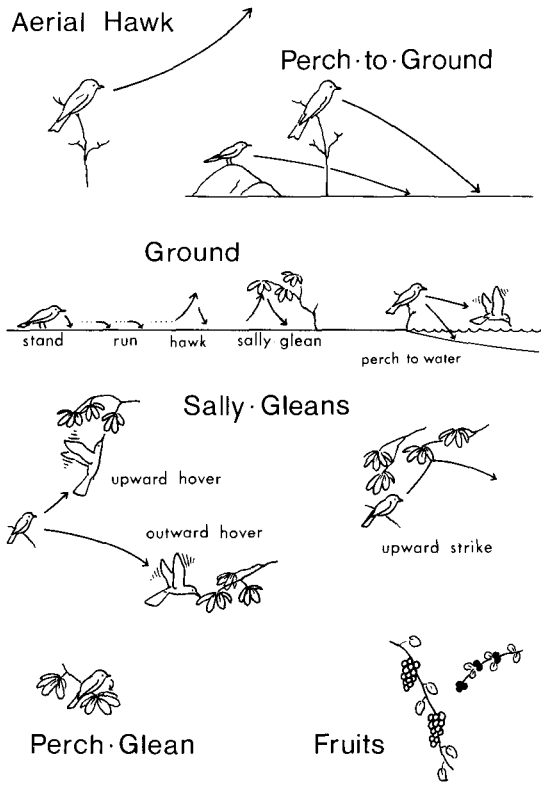


FIGURE 1. Important prey capture techniques used by tyrant flycatchers. Each capture is preceded by a stationary search period on the perch.

frequent preening were assumed to indicate less than active foraging. I followed easily observable species for periods ranging from 15 min to one hour. At Cocha Cashu I followed each of four species of large-bodied tyrannine flycatchers for full days during each of five months, as part of a longer-term study of their social systems. Less conspicuous species were followed until lost from sight.

Each time a foraging bird stopped on a new perch, I attempted to record the habitat, perch height, vegetation characteristics surrounding the perch, and the search time on the perch. Search times were measured with wrist- or stop-watch, or counted by using a portable, audible timer that clicked at one-second intervals. For search periods ending in a foraging maneuver, I recorded the sally type (see Results), its distance and angle from the horizontal, and the distance moved after the sally. If the perch was abandoned I noted the distance to the new perch. In practice, not all measures could be accurately noted while following rapidly moving birds, but I tried to include representative samples of all measures for each species. I did not attempt to distinguish between successful and unsuccessful sallies, as prey items could be seen and identified only rarely.

The descriptions and data presented herein, while intended as a review of the known foraging habits of flycatchers, are primarily taken from my own notes. A few published studies describe tyrannid foraging movements with enough detail to be usable in this analysis, and results from these accounts are incorporated where they supplement my own.

RESULTS

METHODS OF PREY CAPTURE

The descriptions in this section are limited to the physical acts involved in each type of prey capture by flycatchers. I present them in the context of a classification whereby each individual foraging maneuver can be assigned to one and only one category. This affords a means of quantitatively comparing the foraging repertoires of various species, as discussed in the next section.

Given the family's size and diversity, tyrannids seem more remarkable for the foraging techniques they do *not* employ than for the ones they do. Creeping along bark, scratching in leaf litter, searching among dead leaves, gaping and probing, all common techniques in other sub-oscine families, are absent from the Tyrannidae. The family shows comparatively few modifications on a stereotyped search-and-capture technique, characterized by stationary, often long search periods on a perch, followed by either an attempt at prey capture (usually through an approach flight or "sally") or a move to a new perch. For this reason I stress certain, seemingly minor distinctions between capture techniques. These subtle differences appear to account for many of the morphological and ecological features of this diverse family (Fitzpatrick 1978). The following descriptions are diagrammatically summarized in Fig. 1.

Aerial Hawking. Often referred to as "true flycatching" (e.g., Skutch 1960, Slud 1964), this encompasses all sallies in which aerial prey is pursued and captured in flight. Aerial prey is located while the bird searches from an exposed perch. Prey is snapped from the air after a rapid, direct flight off the perch. Especially after long sallies the bird may hover, glide, or float briefly at the point of capture. Escaping prey often are pursued with quick turns or a tumbling series of acrobatic maneuvers. Large prey items are carried to the perch for handling. No tyrannid is known to habitually make multiple prey captures while searching on the wing, although this does occur occasionally in certain genera (e.g., *Contopus, Tyrannus*). This distinguishes Aerial Hawking from true aerial foraging that characterizes swallows (Hirundinidae) and swifts (Apodidae), for which I agree with T. C. Moermond (unpubl. data) in preferring the term "screening" (Emlen 1977, p. 103).

Perch-to-Ground Sallying. Terrestrial prey is located during a stationary search period

on an elevated perch (exposed twigs, earth or rock mounds, utility poles or wires, rooftops). The bird flies, glides, or hops to the ground after spotting prey, which is picked up as the bird lands or, more frequently, while the bird stands on the ground. The bird occasionally lands a short distance from the prey item and hops toward it before capture. A short chase along the ground may ensue. Larger prey are handled after the bird returns to an elevated perch.

Ground Foraging. Prey is found while the bird stands, walks, hops, or runs on the ground. Prey may be picked from the vegetation during a short jump or flight (*Ground Sally-gleaning*) or snatched from the air (*Ground Hawking*), after which the bird returns to the ground. Prey also may be picked from the ground or vegetation (*Standing* or *Running Ground Gleaning*). The bird may search for prey some distance away and fly rapidly to capture it. This frequently terminates in a short, fluttering pursuit along the ground or into the air as prey attempts to escape (*Flutter-pursuit*).

Perch-to-Water Sallying. Aquatic prey is spotted while the bird searches from an exposed vantage-point over or very near the water. In *Surface Gleaning,* the approach flight is directed toward a position several centimeters over the surface prey, which is picked from the water with a smooth downward head motion, during a brief hover. Rarely, prey is taken from well below the water surface during a *Dive* straight down from the perch. Prey is captured in the bill, and usually only the head submerges before the bird instantly returns to an exposed perch to handle prey or resume searching. Several species have been recorded *Wading* in search of aquatic prey in shallow water (Hudson 1920:179, Skutch 1960:356, Smith 1971:261).

Sally-gleaning. This category encompasses several widespread capture techniques in which prey is picked off a substrate during a flight from the perch. Four types of Sally-gleans are recognized here, although even finer subdivisions could be made. (1) *Outward Hover-gleaning.* The bird searches from an exposed, usually well-lighted site, looking primarily outward or downward. The approach flight is rapid and direct, and prey is snatched from an exposed surface (upper side of a leaf, a twig, or weed top) during a short hover in which the bird may still be moving forward. Often, during the hover and capture, the bird crashes into the substrate, slowing down only slightly while snapping the prey. The follow-up flight is a continuation of the sally, carrying the bird well away from its former perch. (2) *Upward Hover-gleaning.* The bird searches from an enclosed position within the vegetation. The approach flight is either horizontal or upward. While the approach may be rapid, the hovering bird does not move forward at the point of capture. The hover may begin well before the capture, and may last several seconds as the bird positions itself almost vertically under the prey item. Capture occurs with a quick snap, and repeated attempts may occur during a single hover. The follow-up flight may be a momentary return to the former perch, but active searching usually begins only after a move to a new perch. (3) *Outward Striking.* The bird snaps stationary prey off an exposed surface during a direct, horizontal or downward approach flight. No hover is used during prey capture and the follow-up flight usually carries the bird away from the original perch. (4) *Upward Striking.* Searching occurs among enclosed, often dense vegetation. The approach is explosively rapid, and prey is snapped or scraped off the under-surface of leaves without hovering. Only one capture attempt is made as the bird moves rapidly through to a new perch.

Perch-gleaning. This category includes foraging maneuvers in which stationary prey is taken from the substrate while the bird remains perched. (1) *Simple Perch-gleaning.* Searching occurs between rapid movements through the vegetation, with perches chosen in a variety of exposed and enclosed situations. Prey is located only with visual searching, the bill rarely being used for probing. Prey is removed from the substrate with no approach flight. The bird may employ body movements during both search and capture. Usually this involves an upward or downward lean, but occasionally even results in a somersault around the perch to retrieve prey from below. Escaping prey are rarely pursued. (2) *Landing-and-gleaning.* After spotting prey too far away for a Simple Perch-glean, the bird perches within reach of the prey and picks it off the substrate immediately after landing.

Frugivory. I place all instances of frugivory by tyrannids into a single category, although the actual feeding techniques vary considerably. Some individuals or species hover at fruit clusters, some strike the fruit and continue to a new perch, some perch and pick at fruit without sallying, and a few

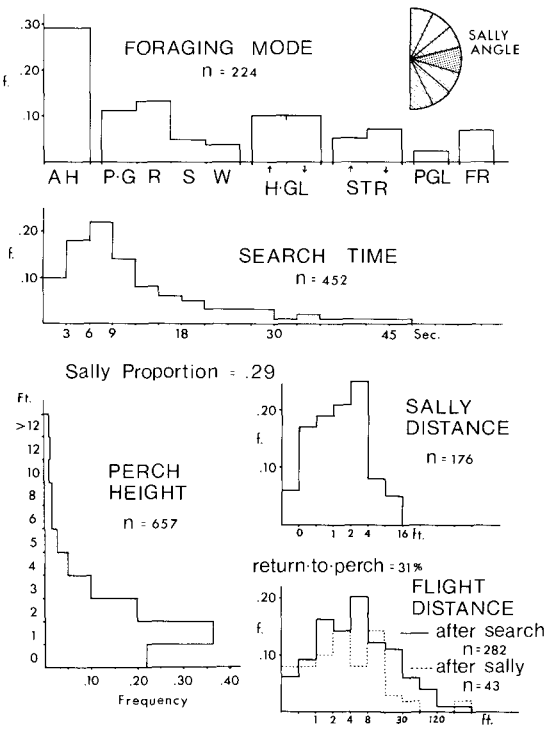


FIGURE 2. Foraging Mode Profile for *Ochthoeca* (=*Ochthornis*) *littoralis*, a Near-ground Generalist, in Amazonian Peru. The species' "foraging mode" is shown by the frequencies with which each prey capture technique is used (top of figure). Prey capture codes: AH = Aerial Hawk; P-G = Perch-to-ground; R = Running; S = Standing Ground Glean; W = Perch-to-Water; H-GL = Hover-glean (Upward and Outward, shown by arrows); STR = Strike (Upward and Outward); PGL = Perch-glean; FR = Fruit. See text for definitions of terms. Sample sizes (n) are shown for each measure. Sally Angle frequencies: hatched = .05–.15; stippled = .16–.30.

species eat only a portion of the fruit without removing it from the plant. Several features common to these techniques argue for their inclusion into one behavioral category. The "prey items" are immobile and conspicuous, and are available to any bird that passes close enough to find them. Individuals occasionally find fruit by being attracted to other birds at fruit concentrations. Whether a fruit is taken as food depends on the micro-habitat and dietary preferences of the bird species, and not on the species' searching behavior and sallying technique. Interspecific differences in techniques of frugivory have little functional significance in the Tyrannidae, and usually reflect each species' typical capture techniques during insect foraging.

TYRANNID FORAGING MODES

I refer to the frequencies with which a species uses each of the above prey capture techniques as that species' *foraging mode*. Foraging "specialists" use only one of the sallying methods for most prey captures, while "generalists" regularly employ several of them, without specializing in any one (see Appendix). Although intermediates exist between these two extremes, the Tyrannidae actually are charactertized by a relatively small set of distinct foraging modes. In this section I describe these predominant methods, drawing examples from the prey capture distributions of some species I have studied.

Besides the frequency distributions of prey capture techniques, additional measurements are useful in quantitatively describing the foraging habits of a given species. Taken together, these measures comprise what I call the *foraging mode profile* for a species. A sample of such a profile is demonstrated in Fig. 2. In Fig. 2 and below, I refer to several terms that require definitions at this point.

Search Time. Nearly all tyrannids forage by pausing on each perch to search for prey. The duration of each pause, which may precede either a foraging maneuver or a flight to a new perch, is easily measured and constitutes the search time on that perch. Each species has a characteristic, positively skewed frequency distribution of search times, which varies only slightly between foraging bouts or geographic sites (e.g., Fig. 2; Fitzpatrick, in press; Davies 1977). I have explored this important aspect of tyrannid foraging behavior in greater detail elsewhere (Fitzpatrick 1978, in press).

Sally Proportion. This measure is expressed as the fraction of the total number of observed search periods that resulted in an attempted prey capture, as opposed to a give-up flight to a new perch. Species that give up many more times than they attempt a capture (proportions below 0.4) may be pictured as "searchers" (MacArthur 1972), while those that search at nearly every perch until they sally (proportions above 0.7) represent "sit-and-wait" predators.

Sally Distance. The distances travelled between perch and prey form an approximately log-normal distribution for every species. The median may be taken as a measure of the average radius within which a species customarily searches for prey.

Sally Angle. The angle above or below the horizontal followed during a sally toward a prey item.

Give-up Flight. During active foraging, the distances moved from one unsuccessful perch to a new perch also are distributed

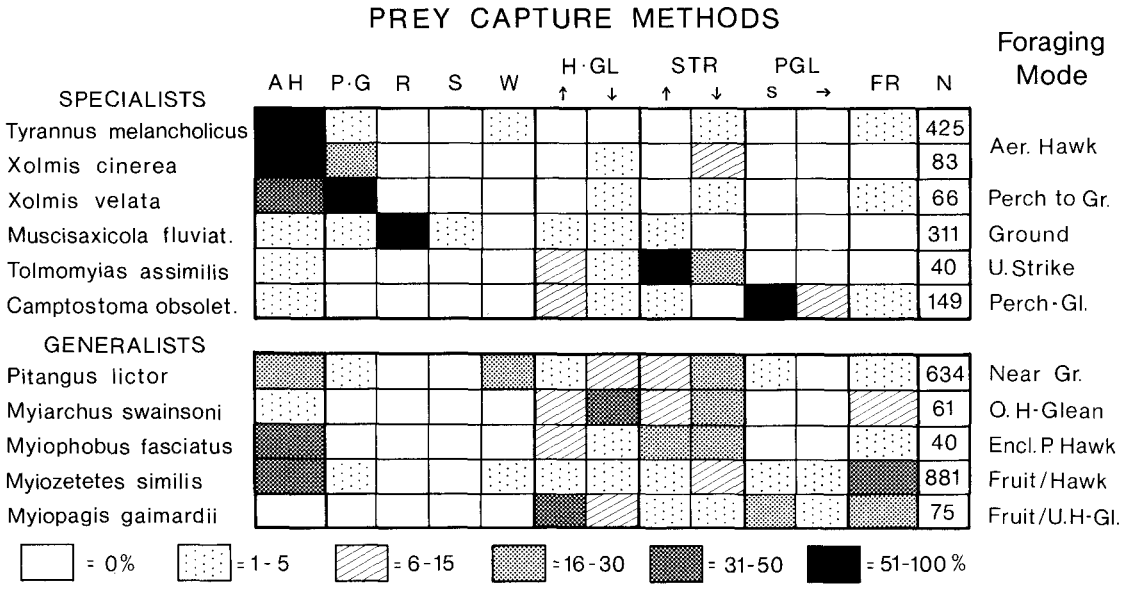


FIGURE 3. The ten predominant foraging modes found in the Tyrannidae, illustrated with data from the five kinds of specialists (over 50% use of one capture technique) and five kinds of generalists. Prey capture codes as in Figure 2, with Perch-gleans separated here into Simple Perch-gleans (S) and Land-and-gleans (arrow). Foraging mode codes in Figures 3 and 4: Aer. Hawk = Aerial Hawking; Perch-to-Gr. = Perch-to-Ground; Ground = Ground Foraging; U. Strike = Upward Striking; Perch-Gl. = Perch-gleaning; Near Gr. = Near-Ground Generalist; O. H.-Glean = Outward Hover-gleaning; Encl. P. Hawk = Enclosed Perch Hawking; Fruit/Hawk = Frugivory and Aerial Hawking; Fruit/U. H.-Gl. = Frugivory and Upward Hover-gleaning.

log-normally, with a characteristic median for each species (Flight Distance after Search in Fig. 2).

Follow-up Flight. This measures how far an individual moves before landing on a new perch following a prey capture (Flight Distance after Sally in Fig. 2).

Return-to-perch Frequency. The percentage of sallies that are followed by a return to the former perch.

Figure 3 depicts frequencies of different types of prey capture techniques used by some sample tyrannids, illustrating most of the foraging modes described below. The following comparisons are based on complete foraging mode profiles for 90 tyrannids, together with less complete notes and published accounts of additional species. The numerical data for 43 representative genera are presented in the Appendix.

Aerial Hawking. Specialists in this foraging mode may use the Aerial Hawk for up to 100% of their sallies (Appendix). Such species habitually use a small number of favored perches, to which they return after each sally (Fitzpatrick, in press). In most cases (e.g. *Tyrannus* spp., Fig. 3; also *Contopus, Colonia, Knipolegus, Hirundinea*) these species inhabit edge or canopy situations, where light is very bright and prey can be spotted against solid, light backgrounds of sky or water. A few Aerial Hawkers (*Mitrephanes, Pyrrhomyias,* certain *Ochthoeca* and *Contopus*) occupy true forest habitats, where they hunt from exposed perches near small forest openings, cliffs, stream margins, or in a broken canopy. Aerial Hawkers remain still for long periods, searching all angles for prey and rarely changing positions. Their search times and sally proportions are the highest in the family (Fitzpatrick, in press). Pursuit flights are fast, powerful, and on the average longer than those of other equivalent-sized tyrannids. Many Aerial Hawkers employ a long, floating glide immediately preceding the prey capture, apparently in preparation for the abrupt aerial maneuvers required to pursue and capture an escaping insect.

Perch-to-Ground Sallying. One large assemblage of open country tyrannids (*Agriornis, Xolmis, Neoxolmis, Myiotheretes,* certain *Ochthoeca*) consists primarily of Perch-to-Ground specialists, exemplified in Fig. 3 by *Xolmis velata.* Various authors, summarized by Smith and Vuilleumier (1971), indicate that some of these species forage almost exclusively in this fashion. These "ground gazers" (Hudson 1920) hunt in open pastures, rocky slopes, or low brush and scan the ground from exposed, slightly elevated perches. As reported by Smith and

Vuilleumier (1971), most Perch-to-Ground Salliers frequently take some aerial prey, a habit that varies with local conditions. At two Brasilian sites I found *Xolmis cinerea*, elsewhere described as a Perch-to-Ground specialist, taking more prey from the air than from the ground (Fig. 3). In addition, certain open country species that are primarily Aerial Hawkers (e.g., *Gubernetes yetapa*, *Knipolegus* spp., *Pyrocephalus rubinus*) make facultative use of Perch-to-Ground Sallies, and occasionally forage exclusively in this manner where locally heavy concentrations of ground prey are found (e.g., recently burned pastures, tidal flats, rich, wet meadows). Thus a continuum exists in the degrees to which various species use the two "sit-and-wait" foraging modes of Aerial Hawking and Perch-to-Ground Sallying (see Appendix). Some evolutionary consequences of this continuum are discussed in Fitzpatrick (1978).

Ground Foraging. The use of the ground as a foraging substrate has evolved independently in three major tyrannid groups (Fitzpatrick 1978). True ground specialists habitually walk or run, hopping only where it is required by a broken terrain. In most cases (e.g., *Muscisaxicola*, Fig. 3; also *Muscigralla*, *Machetornis*, *Fluvicola nengeta*) the bird picks prey from open ground or grass clumps while standing or after a short run. Flutter-pursuits are frequently employed by *Lessonia rufa* and *Fluvicola nengeta*. Smith (*in* Smith and Vuilleumier 1971) reported occasional aerial sallies up to 35 m long by certain species of *Muscisaxicola*, which otherwise are pipit-like ground specialists. One aberrant genus (*Corythopis*) forages by walking along the ground in the forest interior, picking prey from leaf litter and, more frequently, Upward Striking off the undersides of ground story vegetation. Search times for ground foragers are extremely brief, apparently reflecting their tiny searching radius at any one stopping point (Fitzpatrick, in press). Pausing to search often gives way to continuous walking, especially in *Machetornis* and *Corythopis*. The Cattle Tyrant (*Machetornis rixosus*) regularly follows livestock in pastures, picking or sallying after prey under their feet, and even riding their backs while searching for insects kicked up from the grass.

Foliage Gleaning. The vast majority of tyrannids forage by moving through vegetation, pausing briefly to search on each perch and gleaning stationary prey from nearby surfaces. Certain species specialize in only a single gleaning technique, while others use several with equal frequency. In Fig. 3 the foraging modes of three Amazonian, canopy-dwelling flycatchers illustrate the three most common modes of foliage gleaning:

(1) *Outward hover-gleaning.* Nearly all species of *Myiarchus*, and the related genera of medium-sized tyrannids (*Sirystes*, *Attila*, *Rhytipterna*, *Casiornis*), habitually use the Outward Hover-glean. Forty to 80% of their foraging maneuvers are of this type, the remainder consisting largely of other sally-gleaning variations. These species favor leafy micro-habitats with high light intensity, including scrub, forest openings and subcanopy, and river or lake margins. They choose exposed perches close to foliage, peering in all directions with a characteristic head-bobbing motion. Prey tend to be large, including caterpillars, moths, orthopterans, and arboreal lizards. Many of these generalists regularly eat fruit.

(2) *Upward striking.* One of the most stereotyped foraging modes in the Tyrannidae, Upward Striking is especially characteristic of the medium- to small-bodied species formerly comprising Hellmayr's (1927) subfamily Euscarthminae (see Traylor 1977). These include the genera *Platyrinchus*, *Tolmomyias* (Fig. 3), *Todirostrum*, *Hemitriccus* (including *Idioptilon*), and relatives (cf. genera in Appendix). Species using this foraging mode occupy nearly every foliated habitat in the Neotropics, and micro-habitat subdivisions between species are extremely sharply defined (Fitzpatrick, unpubl. data). Perches are chosen close to leaves and searching is directed upward. Sixty to 90% of the sallies are Upward Strikes, and the remainder mostly are Upward Hover-gleans. Search times are comparatively long, and sally proportions (around 0.3) place these species toward the "searcher" end of the foraging mode spectrum.

(3) *Perch-gleaning.* Several groups of tyrannids in the subfamily Elaeniinae (Traylor 1977) specialize in Perch-gleaning (e.g. *Camptostoma*, Fig. 3), a foraging mode more characteristic of vireos (Vireonidae) and warblers (Parulidae) than of flycatchers. Perch-gleaners move rapidly with short hops or flights, searching only the area they can reach without sallying. They choose scrub, canopy, or edge habitats where foliage is dense and light is bright. Most Perch-gleaners are highly frugivorous during appropriate seasons, and they frequently associate with mixed species flocks in the forest canopy.

Enclosed Perch Hawking. A number of medium- to small-bodied generalist species frequently use the Aerial Hawk while foraging inside dense vegetation. These species forage by perching in relatively small openings within the foliage, where light intensity and dappled backgrounds are less favorable for spotting aerial prey than are the open habitats of true Aerial Hawkers. For this reason, these species use sally-gleans (mostly Upward Strikes and Upward Hover-gleans) at least as often as Aerial Hawks (Appendix). Aerial Hawking becomes more frequent when they wander into larger openings or move along the edges of clearings. Enclosed Perch Hawkers include *Myiophobus* (e.g., *M. fasciatus*; Fig. 3), *Empidonax, Cnemotriccus, Terenotriccus, Myiotriccus.*

Certain species of *Myiobius* use a unique variant of this foraging mode by moving through forest understory with extremely rapid flights, short pauses, and active wing and tail flashing in the manner of redstarts (*Setophaga* and *Myioborus*). Skutch (1960) interpreted these rapid, erratic flights as Aerial Hawks. However, my experience shows the most common sally techniques to be Outward and Upward Strikes, followed by rapid pursuits of dislodged, escaping prey. This peculiar, poorly understood foraging mode, characterized by very brief search times, portrays *Myiobius* as a behaviorally aberrant member of the Tyrannidae (Fitzpatrick 1978, in press).

Near-ground Generalists. This heterogeneous group includes a number of species whose foraging repertoires are generalized but depend upon being close to the ground. Included are many of the species in *Ochthoeca* (including *O. littoralis*, Fig. 2), *Sayornis, Pyrocephalus, Arundinicola, Fluvicola, Pitangus lictor* (Fig. 3), *Pseudotriccus,* and the *Serpophaga cinerea* species group (Smith 1971). These species, many of which habitually forage near or over water, use most of the capture techniques described above. They typically employ moderate to high percentages of Aerial Hawks and Perch-to-Ground Sallies (Appendix). Perches are low, permitting the bird to scan the ground, water surface, and low vegetation. Sallies are usually outward or downward. Home ranges are often linear along streams, river banks, or lake edges. Search times, sally proportions, and return-to-perch frequencies vary according to body size and the amount of Aerial Hawking employed.

Partial Frugivory. No tyrannid is known to rely exclusively on fruit, but several groups of genera feed on it heavily during most or all of the year. Each group has its own repertoire of insect foraging to supplement frugivory, and three discrete foraging modes can be recognized. (1) The most frugivorous tyrant flycatcher appears to be *Legatus leucophaius* (e.g., Morton 1977). Many of its large-bodied tyrannine relatives (e.g., *Myiozetetes similis*, Fig. 3) are foraging generalists in the truest sense: all are largely frugivorous, they use the Aerial Hawk extensively, and they facultatively employ every other prey capture technique regularly. This group of frugivorous generalists includes *Empidonomus, Conopias,* and *Myiozetetes* as well as *Legatus.* (2) The genus *Elaenia* shows a similar repertoire, also taking fruit extensively during much of the year, but is more restricted to densely foliated edge or canopy micro-habitats. Aerial Hawking is less important than in the former group, and is replaced by Perch- and Sally-gleaning techniques. One assemblage of strictly canopy-dwelling, small-bodied *Elaenia* relatives (*Phyllomyias, Zimmerius, Tyrannulus, Phaeomyias*; Traylor 1977) uses Perch-gleans and Upward Hover-gleans exclusively during insect foraging, but feeds mostly on small berries, especially of mistletoes (Loranthaceae). (3) A third highly frugivorous group, primarily represented by the expanded genus *Mionectes* (includes *Pipromorpha*), uses the Upward Hover-glean when foraging for insects in the forest understory. These species feed heavily on melastome fruit where available, and are often associated with forest understory mixed flocks of antbirds (Formicariidae) and ovenbirds (Furnariidae; Munn and Terborgh 1979).

Pitangus sulphuratus. The Great Kiskadee, a supreme generalist, is so uniquely variable in its foraging behavior that it represents its own foraging mode in this classification. The species is widespread throughout tropical Central and South America, and shows tremendous versatility throughout its distribution. I have seen it scavenging dead fish, hunting for live fish, preying on tadpoles, frogs, and terrestrial lizards, Aerial Hawking, Perch-gleaning, Sally-gleaning with all variations, foraging over army ants (see also Slud 1964), and feeding on a vast array of fruits, from small melastomes up to large figs. Other investigators have found the species exclusively Aerial Hawking (R. Bailey, pers. comm.), wading in shallow ponds (Hudson 1920), preying on passerine nestlings (Skutch 1960, ffrench 1976), eating refuse from gar-

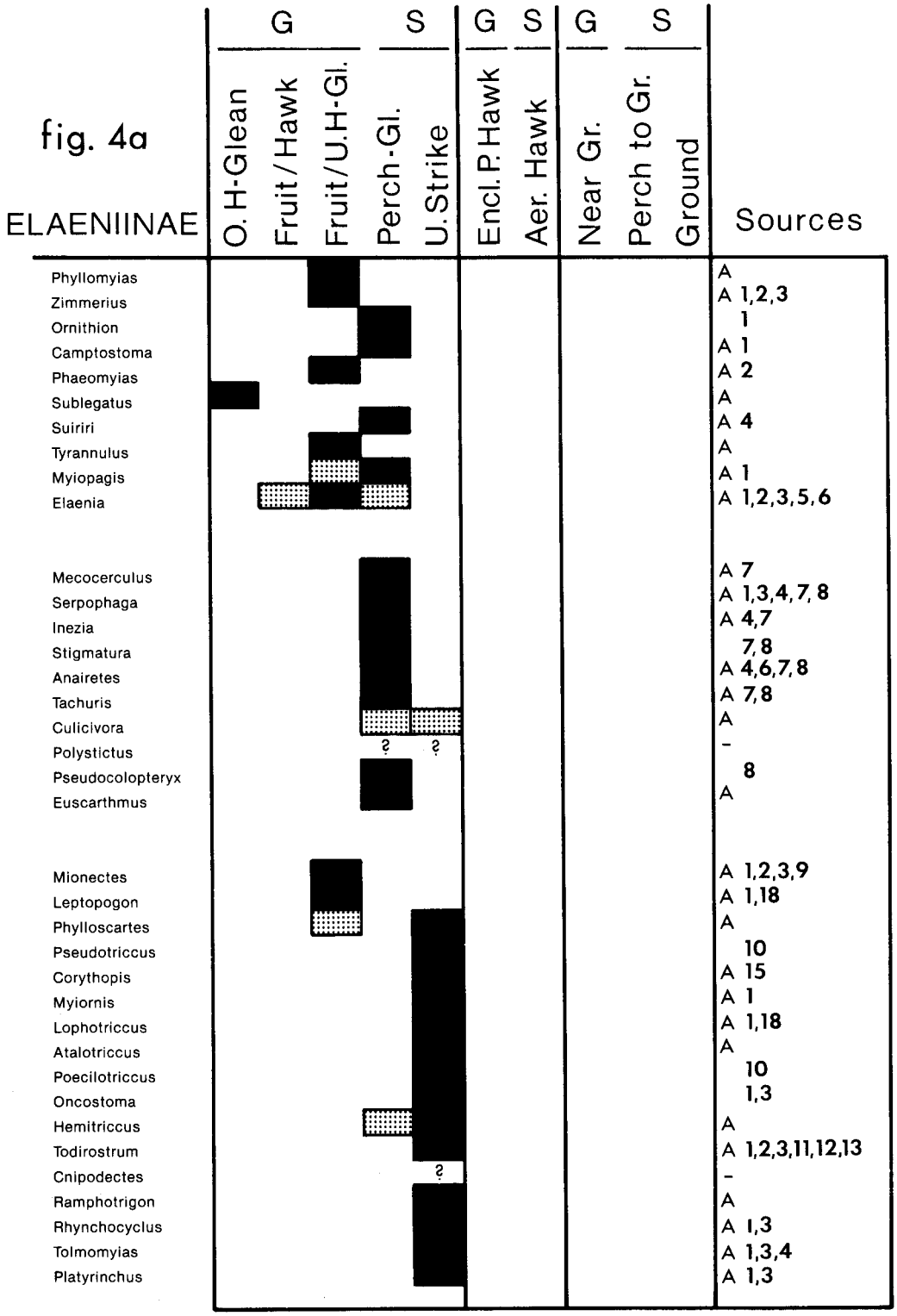
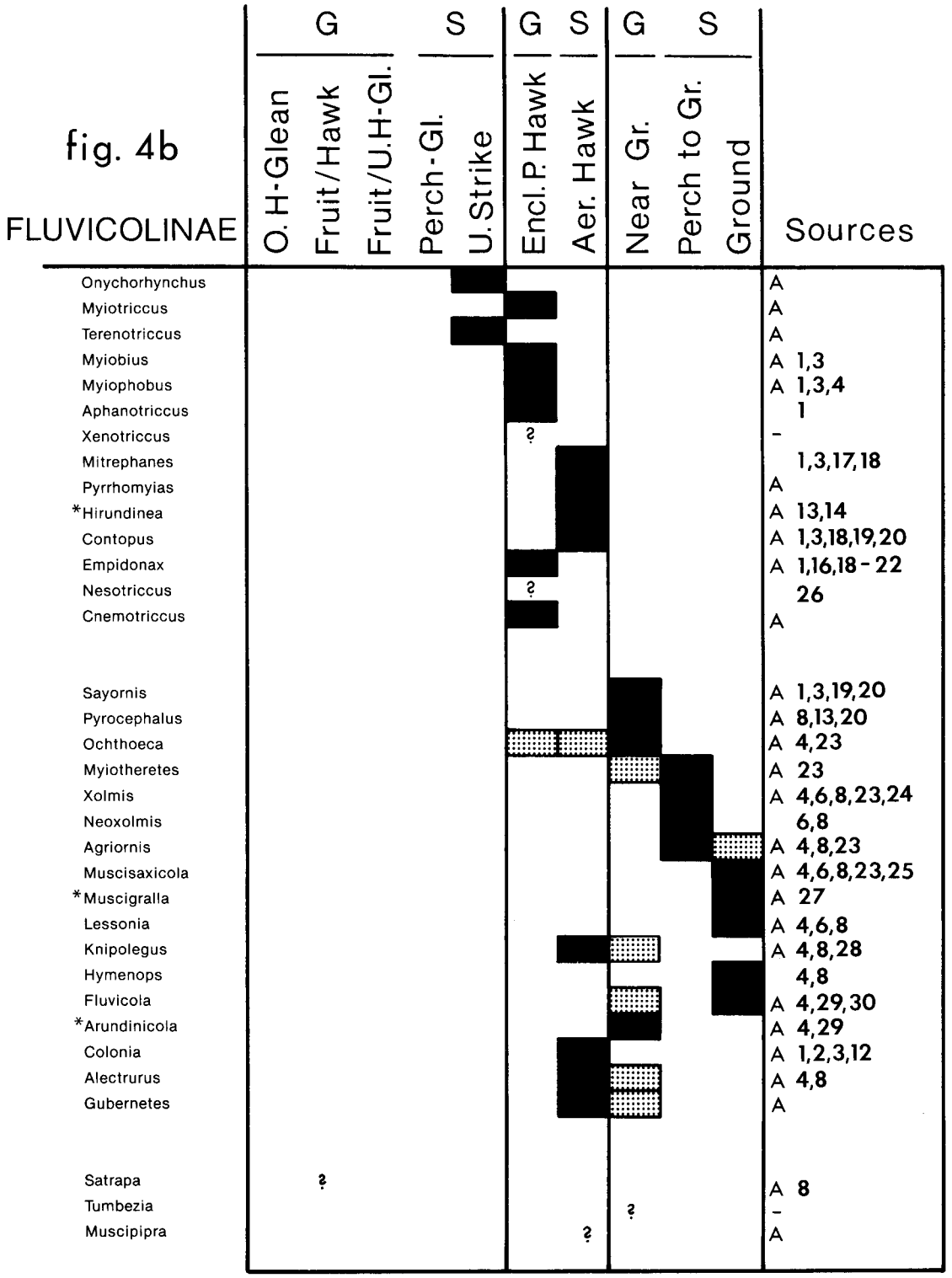
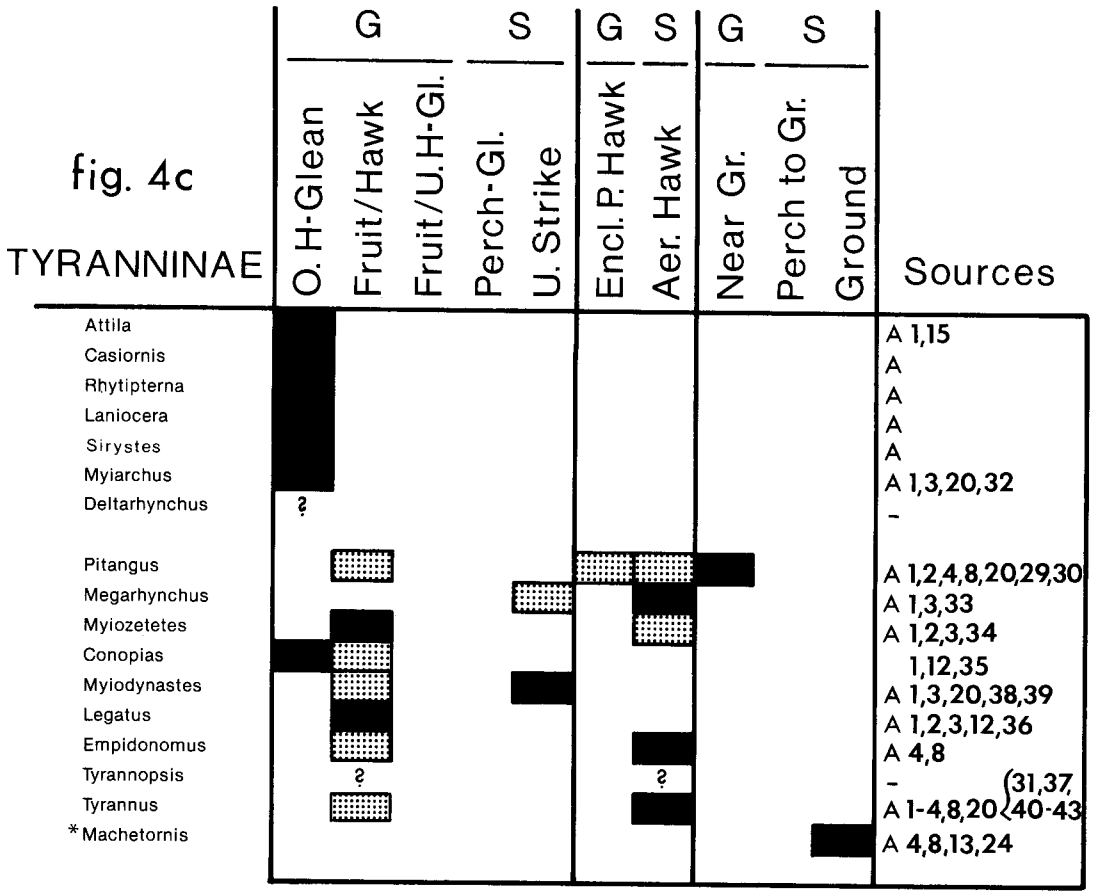


FIGURE 4. Characteristic foraging modes of the tyrannid genera (see text). Genera are listed in the subfamilies Elaeniinae (Fig. 4a), Fluvicolinae (Fig. 4b), and Tyranninae (Fig. 4c) according to the classification of Traylor (1977) except where noted with an asterisk (*). Foraging modes, coded as in Figure 3, are grouped into three behavioral categories in which related generalized (G) and specialized (S) modes are shown together. Black bars indicate the foraging mode most typical of each genus; stippled bars indicate less important modes for certain



genera. Question marks show probable foraging modes for genera where behavioral data are lacking. Sources: A = Author's field data; 1: Slud (1964); 2: Haverschmidt (1968); 3: Skutch (1960); 4: Wetmore (1926); 5: Crowell (1968); 6: Crawshay (1907); 7: Smith (1971); 8: Hudson (1920); 9: Willis et al. (1978); 10: personal communication, O'Neill, Terborgh, Willis; 11: Skutch (1930); 12: Skutch (1972); 13: Mitchell (1957); 14: Meyer de Schauensee, Phelps, and Tudor (1978); 15: Oniki and Willis (1972); 16: Willis (1966); 17: Webster (1968); 18: Skutch (1967);



19: Verbeek (1975); 20: Bent (1942); 21: Beaver and Baldwin (1975); 22: Johnson (1963); 23: Smith and Vuilleumier (1971); 24: Gibson (1918); 25: Humphrey et al. (1970); 26: Slud (1967); 27: Short and Morony (1969); 28: Willis (1976); 29: ffrench (1976); 30: Wetmore (1972); 31: Leck (1971); 32: Lanyon (1975); 33: Skutch (1951); 34: Cracraft (1967); 35: E. T. Thomas (1979); 36: Morton (1977); 37: Smith (1966); 38: Gross (1950); 39: Ligon (1971); 40: Morton (1971); 41: Fitch (1950); 42: Hespenheide (1964); 43: Skutch (1954).

bage dumps (ffrench 1976), and even pirating from other birds (J. P. Myers, pers. comm.). The species appears to develop short-term foraging specialities according to local and seasonal conditions of food availability. It occupies a spectrum of habitats from desert to rain forest, and is the most common native passerine along the central boulevards of São Paulo, South America's largest city. The Great Kiskadee exhibits an omnivorous foraging versatility more typical of the Corvidae than of a suboscine passerine.

FORAGING CHARACTERISTICS OF TYRANNID GENERA

As shown above, prey capture techniques are combined in different ways by tyrannids to form behaviorally and ecologically distinct foraging modes (see Appendix). It is of both ecological and evolutionary interest to examine how these habits occur within the Tyrannidae as a whole. Ecologically, a foraging mode classification of the tyrannid genera can be used in analyses of neotropical bird community compositions, as I will discuss in later papers. Evolutionarily, the range of foraging styles within groups of related species, and the morphologic adaptations and constraints associated with these behaviors, can indicate the paths through which the family has radiated (Fitzpatrick 1978). To these ends, I present below, and in Fig. 4, a summary of the foraging modes that are known to characterize each tyrannid genus.

Figure 4 lumps the different foraging modes, each of which is described above and exemplified in Fig. 3, into three categories. From left to right in the figure these correspond to foliage gleaners, aerial salliers, and ground-related foragers. Within each category, specialized foraging modes (S) are distinguished from generalized ones (G) as defined above and statistically veri-

fied in the Appendix. For each genus, a black bar is placed under the foraging mode that best describes the foraging habits of that genus. Question marks indicate genera for which adequate information on foraging techniques is lacking. References to the best available descriptions of foraging styles also are given for each genus in Fig. 4.

As with any broad categorization of a complex natural spectrum, Fig. 4 contains certain simplifications. Most important, this summary fails to show the behavioral variations present within some of the tyrannid genera. Intra-generic variability is especially prevalent among the generalists, where two species often differ quantitatively in their dependence upon a given set of capture techniques. In certain cases these variations appear to be ecologically important among the assemblages of congeneric tyrannids in South America. These behavioral details require a fine-grained treatment that is outside the scope of this review. In Fig. 4, this problem is dealt with in part by showing a major (black bar) and a minor (stippled bar) foraging mode for certain genera (e.g. *Elaenia, Serpophaga, Phylloscartes,* and *Fluvicola* as shown in the Appendix) in which site-to-site or species-to-species variation is pronounced. The Appendix presents supporting data for many of the genera mentioned below.

Elaeniinae. This group contains small- to medium-sized, predominantly foliage-gleaning species. Three elaeniine lineages are suggested in Traylor's (1977) classification (Fig. 4a). The *Elaenia* relatives (*Phyllomyias* through *Elaenia*) are primarily generalized frugivores. They forage heavily or exclusively on small berries during seasonal fruiting peaks, and use Perch-gleans, Upward Hover-gleans, and short Aerial Hawks during insect foraging. Four genera, two of them monotypic, have specialized into a Perch-gleaning foraging mode. Of the tit-tyrants and relatives (*Mecocerculus* through *Euscarthmus*), nearly all are Perch-gleaning specialists. These genera, along with *Camptostoma* and *Ornithion* of the previous lineage, represent the most "warbler-like" tyrant flycatchers. Only the aberrant *Culicivora,* and presumably its close relative *Polystictus,* shows more generalized foraging, using Striking and Hover-gleaning at least as often as Perch-gleaning (see Appendix). These two peculiar genera are also unique in being restricted to purely open grass habitats. The lineage *Mionectes* through *Platyrinchus* includes the most behaviorally stereotyped generic assemblage in the family. *Mionectes* (including *Pipromorpha*), *Leptopogon,* and a few *Phylloscartes* combine frugivory with Upward Hover-gleaning. The latter mode, together with Upward Striking, characterizes most *Phylloscartes.* The entire remainder of the lineage, from *Pseudotriccus* through *Platyrinchus,* consists of extremely stereotyped Upward Strikers. The aberrant genus *Corythopis,* a strictly terrestrial form which uses this capture technique from the ground (Appendix), was tentatively placed in this group by Traylor (1977) in part *because* of this behavior.

Fluvicolinae. Traylor (1977:159) recognized two fluvicoline lineages, as shown with minor changes in Fig. 4b. Although I follow Traylor's linear order exactly, I agree with Smith (1970) and Smith and Vuilleumier (1971) that *Sayornis* and *Pyrocephalus* represent primitive members of the ground-tyrant radiation (*Sayornis* through *Gubernetes* in Fig. 4b). Traylor included these two genera with the other fluvicoline lineage (*Onychorhynchus* through *Cnemotriccus* in Fig. 4b). The latter lineage contains an assortment of forest-inhabiting genera ranging from generalized Enclosed Perch Hawkers (*Myiobius, Myiophobus, Empidonax, Cnemotriccus* etc.) to Aerial Hawking specialists that occupy forest borders and openings (*Pyrhomyias, Mitrephanes, Contopus*). As discussed in Fitzpatrick (1978) and Smith (unpubl. data), the most specialized Aerial Hawking flycatcher, *Hirundinea,* appears to be closely related to *Pyrrhomyias* as reflected in Fig. 4b. The second fluvicoline lineage consists of Near-Ground Generalists (*Sayornis, Pyrocephalus, Ochthoeca,* certain *Knipolegus, Arundinicola*) and a large radiation into Perch-to-Ground specialists (*Myiotheretes* through *Agriornis*) and pure Ground Foraging specialists (*Muscisaxicola, Muscigralla, Lessonia, Hymenops, Fluvicola*). As discussed elsewhere (Fitzpatrick 1978, in press), sit-and-wait behavior of the open country Perch-to-Ground species leads also to the evolution of certain Aerial Hawking specialists (*Colonia, Alectrurus, Gubernetes*; see continuum between these modes in the Appendix). *Muscipipra* may also belong here, but it must at present remain in the small group of confusing genera, about which we know too little, placed by Traylor (1977) at the end of the Fluvicolinae.

Tyranninae. Traylor (1977:166) summarized the strong evidence that two lineages comprise this subfamily (Fig. 4c). The *Myiarchus* group (*Attila* through *Myiar-*

chus) is a homogeneous assemblage of Outward Hover-gleaning generalists. The behavior of the monotypic genus *Deltarhynchus* is unknown, and its inclusion in this group remains tentative (Traylor 1977:166). The remaining genera comprise a tremendously successful, heterogeneous lineage in which nearly every foraging mode is represented by at least one species. The group includes an Outward Hover-gleaning generalist (*Conopias*), Upward Strikers of sorts (*Myiodynastes*), a Near-Ground Generalist (*Pitangus lictor*), many frugivorous generalists (especially *Myiozetetes* and *Empidonomus*), at least one frugivorous specialist (*Legatus*; Morton 1977), Aerial Hawking specialists (*Tyrannus*), and, as argued in Fitzpatrick (1978), one Ground Foraging specialist (*Machetornis*). Finally, as described earlier, this group contains the single, omnivorous species that appears to use various foraging modes facultatively, and whose overall repertoire encompasses nearly the entire range of tyrannid foraging techniques (*Pitangus sulphuratus*).

DISCUSSION

Traylor's (1977) full scale revision of the Tyrannidae is based upon features that are, so far as we know, largely independent of foraging characteristics. Traylor relied heavily upon the anatomical comparisons of Warter (1965) and Ames (1971), supplementing these studies with comparisons of nest characteristics and plumage patterns. For this reason the behavioral catalog presented here is especially revealing, and it strikingly supports Traylor's conclusions. Foraging modes are not randomly distributed within his phylogenetic lineages. Rather, with the exception of the tyrannine group of ecological generalists (*Pitangus* through *Machetornis* in Fig. 4c), foraging styles are remarkably restricted within each of the taxonomic groups hypothesized independently by Traylor (1977).

Figure 4 presents each specialized foraging mode next to the more generalized ones to which it is behaviorally related. Aerial Hawkers, for example, specialize on a capture technique used extensively by Enclosed Perch Hawkers. Similarly, both Perch-to-Ground and Ground foraging are stereotyped specializations upon a few capture techniques used by Near-Ground generalists. When these generalist-specialist relationships are overlaid onto the systematic list of Traylor (1977) (Fig. 4) the distinctive behavioral characteristics of each phylogenetic line clearly emerge. As summarized above, each major lineage contains assemblages of behavioral generalists and radiations into related but more specialized modes. This pattern strongly suggests that certain lines of ecological radiation are preserved among present-day tyrannid forms. This suggestion is supported by the patterns of morphological adaptations within each group (Fitzpatrick 1978).

This brief catalog of tyrannid foraging behavior will be amended and refined as new information accumulates. However, it is already an adequate foundation for a variety of analyses of the tyrannid radiation. Topics that depend on this descriptive framework include (1) the analysis of morphological adaptations in relation to different foraging styles; (2) phylogenetic patterns of radiation in structure and behavior, and the use of foraging characteristics as a tool in solving certain taxonomic problems; (3) relationships between foraging mode and microhabitat characteristics, and the effects of these patterns on flycatcher community compositions; (4) the effects of foraging mode on home range and territorial habits; (5) quantitative differences in the optimal searching behavior associated with different foraging modes. These topics will be explored in subsequent papers.

ACKNOWLEDGMENTS

I am extremely grateful to the Peruvian Ministerio de Agricultura, Dirección General Forestal y de Fauna, for permitting my fieldwork in the pristine splendor of the Gran Parque Nacional del Manu. I also thank Manuel Plenge (Peru), the late Paul Schwartz (Venezuela), Paulo Vanzolini (Brazil), and Maria Tereza Jorge Padua (Brasilia, Brazil) for their kind logistical assistance in their countries.

This paper is drawn from a doctoral dissertation approved by the Biology Department of Princeton University. The study benefitted from encouragement and helpful criticism from all members of my dissertation committee, especially Henry S. Horn and John W. Terborgh. I thank them and the students and faculty in Princeton's Ecology and Population Biology group. For sharing information on the behavior of certain flycatchers, I thank Peter Alden, Eugene Eisenmann, Steve Hilty, Wesley Lanyon, John O'Neill, Ted Parker, Chris Parrish, Lester Short, W. John Smith, John Terborgh, Betsy Thomas, John Weske, and Edwin Willis. I am grateful to Melvin A. Traylor and especially Henry Hespenheide and Tom Sherry for criticizing an earlier draft, and to Debra Moskovits for her tremendous help both in the field and with all drafts of this paper.

Fieldwork was supported by a dissertation grant from the National Science Foundation, and research grants from the Frank M. Chapman Memorial Fund and Princeton University.

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APPENDIX. Abridged foraging mode profiles of some representative South American tyrant flycatchers.[a]

Foraging mode	Prey substrate: / Capture method[b]:	Air	Ground			Foliage					Fruit
		Aerial hawk	Perch-ground	Ground	Water	Up hover	Down hover	Up strike	Down strike	Perch glean	Fruit
Aerial Hawk/Perch-to-Ground											
Hirundinea ferruginea											
	R, SJ[d] (24)[e]	**100***[c]									
Tyrannus melancholicus											
	M (425)	**94***	<		1				2		3
Colonia colonus											
	B (53)	**92***				2					6
Contopus virens (winter)											
	M (164)	**88***				4	2	4	1		
Pyrocephalus rubinus											
	M, V (249)	**79***	10		1	2	2	1	5	<	
Gubernetes yetapa											
	S, B (96)	**51**	18				2	3	15		11
Knipolegus lophotes											
	B (37)	38	32				19		11		
Xolmis velata											
	S, B (66)	35	**61**				2		2		2
Ground Foraging											
Muscigralla brevicauda											
	P (103)			**100***							
Muscisaxicola fluviatilis											
	M (311)	5	1	**92***	<	2		1			
Machetornis rixosus											
	V, E (63)	5	8	**87***							
Lessonia rufa											
	C (24)	17		**83***							
Fluvicola nengeta											
	E (120)	11	3	**73***	4		3	3	3	1	
Upward Strike											
Platyrinchus coronatus											
	M (44)					5	5	**82***	8		
Atalotriccus pilaris											
	V (48)					6	2	**73***	17		2
Todirostrum maculatum											
	M (62)	6				2		**63***	19	2	8
Ramphotrigon fuscicauda											
	M (23)					13	4	**65**	17		
Tolmomyias assimilis											
	M (40)	3				15	3	**63**	18		
Hemitriccus zosterops											
	M (30)	3				10	3	**63**	20		
Onychorhynchus coronatus											
	M (17)					6		65	29		
Myiornis ecaudatus											
	M (34)	3				9	12	50	27		
Corythopis torquata											
	M (20)	5		30				65			

APPENDIX. Continued.

Foraging mode	Prey substrate: / Capture method[b]:	Air: Aerial hawk	Ground: Perch-ground	Ground: Ground	Ground: Water	Foliage: Up hover	Foliage: Down hover	Foliage: Up strike	Foliage: Down strike	Foliage: Perch glean	Fruit: Fruit
Perch-glean											
	Camptostoma obsoletum										
	V, M (149)	1				6	5	2		**83***	3
	Suiriri suiriri										
	B, S (58)	7				9	5			**79***	
	Inezia tenuirostris										
	V (88)	1				23	5	9	1	**61***	
	Serpophaga subcristata										
	S (37)	11				14		14	11	**51**	
Grassland Specialist[f]											
	Alectrurus tricolor										
	S, B (135)	45	1				10		42		
	Culicivora caudacuta										
	B, S (62)	13				8	8	23	23	26	
	Tachuris rubrigastra										
	P (20)	25				15				60	
Near-ground Generalist											
	Arundinicola leucocephala										
	E (73)	**41**	1		22	1	10	2	21	1	
	Ochthoeca littoralis										
	M (224)	**29**	11	17	3	15	7	8	5	2	7
	Pitangus lictor										
	M (634)	21	3		18	5	13	11	25	<	3
	Fluvicola pica										
	V, M, E (89)	14	8	31	19	7	3	9	3	4	
Hover-glean Generalist											
	Myiarchus swainsoni (winter)										
	M (61)	2				11	46	7	25		10
	Sirystes sibilator										
	M (14)	14				14	50		21		
	Attila bolivianus										
	M (17)	18				24	42	6	6	6	
	Sublegatus arenarum										
	V (101)	13	10	1		33	23	12	5	1	4
Enclosed Perch Hawk											
	Myiophobus fasciatus										
	V, B (39)	49				11		31	13		
	Myiobius barbatus										
	R, B (27)	37				11	4	44	4		
	Cnemotriccus fuscatus										
	V (26)	27	15			19	4	31	4		
Fruit/Aerial Hawk Generalist											
	Myiozetetes similis										
	M (881)	**47**	1		2	2	4	5	7	2	31
Fruit/Hover-glean Generalist											
	Phaeomyias murina										
	V, E (65)	2				20	12	8	3	20	35
	Elaenia cristata										
	M (54)	19				24	9	7		20	20
	Myiopagis gaimardii										
	V (75)					35	11	3	3	34	16

[a] Data for 43 genera (44 species) show the range of foraging modes I encountered. One example (*Fluvicola*) shows a genus containing more than one foraging mode. See text for discussion of the foraging mode categories by which these species are grouped.

[b] Frequency of each prey capture method is expressed as a percentage of the total number of captures observed for each species; < denotes non-zero percentage less than 0.5.

[c] Prey capture methods used significantly more frequently than any other (boldfaced numerals; chi square, $P < .05$), or more frequently than all others combined (boldfaced, *; $P < .01$), show tendencies toward foraging specialization.

[d] Key to study site symbols as listed beneath each species: M = Manu National Park, dept. Madre de Dios, Peru (forest and riparian habitats); B = Parque nacional de Brasilia, D.F., Brasil (cerrado, campo, gallery forest); C = near Cusco, dept. Cusco, Peru (arid grassland); E = Exú, Pernambuco, Brasil (caatinga, seasonal ponds); R = Rio de Janeiro, Brasil (subtropical forest); P = near Paracas Peninsula, dept. Ica, Peru (arid coastal zone); S = Santa Barbara do Rio Pardo, São Paulo, Brasil (cerrado, campo); SJ = San José de Lourdes, dept. Cajamarca, Peru (subtropical forest); V = Venezuela, state of Falcón (desert, thorn forest, mangrove flats).

[e] Sample size of prey captures shown in parentheses.

[f] Grassland specialists, rare and little-studied tyrannids, show three foraging modes: *Tachuris* represents a specialized Perch-gleaner; *Alectrurus* uniquely combines Aerial Hawking with Outward Striking; *Culicivora* shows generalized foliage-gleaning.