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Author(s): John W. Fitzpatrick

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FORM, FORAGING BEHAVIOR, AND ADAPTIVE RADIATION IN THE TYRANNIDAE

JOHN W. FITZPATRICK

Division of Birds, Field Museum of Natural History, Chicago, Illinois 60605 USA

ABSTRACT. Relationships between foraging behavior and external measurements of the bill, wings, tarsus, and tail are analyzed for 94 representative species of tyrant flycatchers (one quarter of the family). Results are presented in three parts: (1) Allometric relationships are summarized for external measurements, followed by general correlations between measurements (corrected for body size) and foraging mode. Upward-strikers have wide bills, short wings, long tarsi, and reduced tails; perch-gleaners and ground-foragers both have narrow bills, and with the latter also showing substantially longer legs; aerial-hawkers have triangular bills, extremely long wings (as do long-distance migrants), and short legs. Generalists, using many prey capture techniques, have intermediate structural features. (2) Using three sample analyses I show that relative sizes of certain characters vary continuously among species along a quantitative scale of foraging behavior. The morphology-behavior functions suggest adaptive interpretations for much of the observed structural variation. Evolutionary change in structure appears to accompany fine-scale changes along behavioral spectra. Extreme structural peculiarity characterizes the most behaviorally specialized forms, and even could limit evolutionary flexibility at the end-points. These relationships support the notion that evolution proceeds most easily from generalized form and behavior, through intermediate conditions, to the most extreme behavioral and morphological specializations. (3) I speculate on the directions along which increasingly specialized descendants evolved from generalized ancestors in the Tyrannidae, suggesting that these pathways are still visible in present-day forms. The great diversity within the Tyrannidae results, in part, from the unusually competitor-free environment within which the nonoscine lineages may have evolved. This environment allowed various flycatcher species to stop along certain routes toward specialization, remaining or even proliferating at stable intermediate points while certain others continued to specialize further. In this way, today's family Tyrannidae may illustrate pathways of morphological and behavioral specialization long since obliterated in most other modern bird families.

RESUMEN. Se analiza la relación entre el comportamiento de alimentación y medidas externas del pico, alas, tarso y cola para 94 especies representativas de atrapa moscas tirano (un cuarto de la familia). Los resultados se presentan en tres partes: (1) Se resumen las relaciones alométricas para medidas externas, seguido por una correlación entre medidas (corregidas para el tamaño del cuerpo) y el modelo empleado para alimentarse. Las especies que picotean hacia arriba ("upward-strikers") tienen picos anchos, alas cortas, tarsos largos y cola reducida; aquellas aves que picotean posadas en ramas ("perch-gleaners") así como las que se alimentan en el suelo ("ground-foragers") tienen picos angostos y estas últimas aves muestran patas singularmente largas; las que cazan en el aire ("aerial-hawkers") tienen picos triangulares, alas extremadamente largas (tal como las que migran grandes distancias) y patas cortas. Aquellas aves que usan técnicas diferentes para la captura de sus presas ("generalists") presentan componentes intermedios. (2) Utilizo análisis de tres ejemplos para mostrar que los tamaños relativos de ciertos caracteres varían continuamente entre especies a lo largo de una escala cuantitativa de comportamiento de forraje. Las funciones de comportamiento-morfología sugieren interpretaciones adaptativas para la mayoría de las variaciones estructurales observadas. Los cambios evolucionarios en la estructura, parecerían acompañar cambios muy pequeños en los espectros de comportamiento. La presencia de peculiaridades estructurales externa caracteriza a las formas con comportamientos más especializados e inclusive podrían limitar la flexibilidad evolucionaria en los puntos de los espectros. Estas relaciones soportan la idea de que evolución avanza más fácilmente desde formas y comportamientos generalizados a través de las condiciones intermedias hacia las especializaciones más extremas de comportamiento y morfología. (3) Especulo sobre las direcciones a lo largo de las cuales evolucionaron los descendientes mayormente especializados de ancestros generalizados en los Tyrannidae, sugiriendo que esas direcciones aún son visibles en formas de la actualidad. La gran diversidad en Ty-

rannidae resulta en parte por la inusual falta de competidores en el medio en el cual es posible que hayan evolucionado los linajes de no-oscines. Este medio permitió que varias especies de atrapa moscas se detuvieran a lo largo de determinadas rutas de especialización permaneciendo o inclusive proliferando en puntos intermedios estables, mientras que otras continuaron especializándose aún más. De esta manera, la familia actual de Tyrannidae puede ilustrar rutas de especialización de comportamiento y morfología que hace mucho han sido obliteradas en otras familias de aves actuales.

Morphological radiation and gradually increasing ecological diversity within certain successful lineages are principal hallmarks of evolution. We would learn a great deal about the process of adaptation if only we could study through time the pathways by which such radiations occur. Such a feat is impossible, of course, because proliferation of many descendant species from a common ancestor occurs too slowly to observe directly. However, an alternative exists; available for study are numerous examples of diverse phylogenetic lineages that we can study in "cross-section" in present-day time. Many lineages currently are at revealing points along their individual histories of proliferation or decay. Comparative analysis of structure and function within such groups gives us a picture, albeit an indirect one, that allows us to infer some of the pathways and processes of adaptive radiation. In this context, I began studying the relationships between body form and foraging habits in the enormously diverse family Tyrannidae, the tyrant flycatchers.

The 375 tyrant flycatcher species are largely neotropical, and they span a range of ecological roles and morphological forms as great as that of any bird family. They form the subject of several preliminary studies on radiation, both at the family-wide level (Keast 1972) and within several important lineages within the family (e.g., Johnson 1963, 1980; Smith 1966; Lanyon 1967, 1978; Smith and Vuilleumier 1971). An overview of the tyrannid radiation is provided in Traylor and Fitzpatrick (1982).

In prior papers I described and classified the patterns of foraging behavior found in the family (Fitzpatrick 1980), and analyzed some quantitative aspects of flycatcher foraging strategies (Fitzpatrick 1981a). In the present paper I present a preliminary analysis of the external shapes of flycatchers as they relate to foraging. Patterns that are suggested by this study indicate that much of the variation in tyrannid body form is closely related to variation in foraging techniques. Despite the caution advised by Gould and Lewontin (e.g., 1979) in such matters, I interpret close correlations between features of form and behavior within a variable group of close relatives as evidence for *adaptive* radiation within the group.

Demonstration that form and function vary together among related species remains a crucial first step in any careful analysis of adaptation. In this regard, I emphasize that the present study is only a beginning. I focus on the broad patterns of functional correspondence between form and behavior within the Tyrannidae. These overall relationships can be illustrated rather clearly with visually comprehensible diagrams and bivariate statistics. However, such methods only crudely assess the degree to which morphological features vary together with one another and with behavior to form true adaptive character-suites. More sophisticated statistical treatments of this question, using a multi-variate approach and an expanded set of morphologic and behavioral data, currently are in progress.

METHODS

This paper combines field measurements of flycatcher foraging behavior with physical measurements of museum specimens representing the same species. Field sites and procedures are described in detail elsewhere (Fitzpatrick 1980, 1981a) and will be summarized only briefly here. To date, I have observed more than 200 flycatcher species in the wild, principally in Peru, Venezuela, and Brazil. I have quantitative foraging data for about 120 of these species. Data recorded for a foraging tyrannid include overall habitat and micro-habitat descriptions and the following variables for each perch used during a continuous foraging bout, usually lasting as long as the bird can be kept in sight: perch height, distance to nearest leaf above the bird, search time at perch (minus any handling time for captured prey), distance moved to next perch (after a sally or a give-up), sally angle, sally distance, and sally type. These data are organized into a "foraging mode profile" for each species (Fitzpatrick 1980). This permits each species to be classified on a gross level as a specialist or a generalist. Specialists use predominantly one prey-capture technique; generalists use several or many techniques with

TABLE 1
FORAGING MODES AND THEIR DISTRIBUTION AMONG GENERA IN THREE SUBFAMILIES OF
TYRANT FLYCATCHERS¹

	Elaeniinae (37)	Fluvicolinae (34)	Tyranninae (17)
Foliage-gleaning			
Generalized modes:			
Outward hover-gleaners	1		7
Frugivorous aerial-hawkers	*2		2
Frugivorous upward hover-gleaners	7		
Specialized modes:			
Perch-gleaners	13		
Upward-strikers	15	2	1
Aerial-foraging			
Generalized mode:			
Enclosed-perch-hawkers		7	*
Specialized mode:			
Aerial-hawkers		8	3
Ground-foraging			
Generalized mode:			
Near-ground generalists		5	1
Specialized modes:			
Perch-to-ground specialists		4	
Terrestrial specialists		5	1
Unknown	1	3	2

¹ Subfamilies defined in Traylor (1977) and Traylor and Fitzpatrick (1982). Numbers in parentheses show total number of currently recognized genera within each subfamily.

² Asterisk (*) shows foraging modes of secondary importance to one or more genera within subfamily. From Fitzpatrick (1980).

equal frequency. The actual frequencies of use of perching positions, sally types, etc. provide data for numerous comparisons along continuously varying behavioral scales.

Linear measurements used in this paper (mm) are averages from two typical, but otherwise randomly chosen males for each species, collected from the geographic regions where I studied them. I measured 94 species (one-quarter of the family), including members of 72 of the 87 genera recognized by Traylor (1977, 1979) and representing essentially the entire range of body form variation within the family. I measured wing chord, length of innermost and outermost rectrices, tarsus length, length of hallux and claw, culmen length from base and from anterior edge of nostril opening, bill width at base and half-way to the tip, and bill depth at the nostril.

Body weights were obtained primarily from birds mist-netted in Peru and Venezuela. For species I never caught, I used weights listed in Weske (1972), French (1976), or recorded on specimen labels at the American Museum of Natural History, Field Museum of Natural History, and Louisiana State University Museum of Zoology.

Aspect ratios were calculated from wing tracings made from live or recently collected specimens in the field, with the anterior edge of the wing held as nearly straight (extended) as possible. To correct for variability, I made two separate tracings for each individual, and traced as many individuals as possible (N = 1 to 19). Wing areas were measured from these tracings with a compensating polar planimeter; aspect ratios were calculated as the square of the total length of the extended wing divided by wing area (i.e., wing length/mean aerodynamic width). These measures are proportional, but not identical, to the aspect ratios used in technical aerodynamic equations (e.g., Greenewalt 1975), because I measured only one wing instead of total wing area including the body.

To compare the sizes and shapes of external body parts across numerous species I relied principally upon bivariate statistics and bivariate graphs. Of special interest are the three body parts most directly associated with food-gathering: bill, wing, and tarsus. In all figures and

TABLE 2
SIZES AND ALLOMETRIC RELATIONSHIPS IN THE TYRANNIDAE¹

	Wing	Tail	Tarsus	Bill			Body weight
				Length	Width	Half-width	
Median	69.5	57.0	18.0	14.7	8.5	4.7	13.3
Minimum	30.5	14.0	11.7	8.9	4.0	2.5	4.7
Maximum	138.0	280.0	37.3	31.6	16.6	11.2	72.0
Allometric regressions:							
<i>Untransformed linear measurements vs log₁₀ body weight</i>							
Slope	77.23	86.27	7.96	13.38	7.48	3.58	—
Intercept	−17.33	−34.58	9.51	0.46	−0.06	0.67	—
r ²	0.86	0.38	0.27	0.67	0.70	0.39	—
<i>Untransformed linear measurements vs √body weight</i>							
Slope	37.89	42.77	3.95	6.77	3.68	1.77	—
Intercept	−22.35	−41.32	8.87	−0.94	−0.57	0.41	—
r ²	0.85	0.38	0.28	0.70	0.70	0.39	—
<i>Log₁₀ measurements vs log₁₀ body weight</i>							
Slope	0.45	0.52	0.17	0.33	0.37	0.32	—
Intercept	1.31	1.16	1.07	0.81	0.49	0.30	—
r ²	0.87	0.58*	0.28	0.67	0.69	0.43	—

¹ Based on measurements of 94 representative species. Measurements in millimeters, body weights in grams. Asterisk (*) marks the only case in which one regression shows a substantially better fit than the others in its column, thereby favoring one of the transformations over the other two.

graphs, each plotted point represents a species; its position on the graph reflects that species' morphological or behavioral position relative to the other species measured. Species are symbolized on some graphs according to their foraging modes, using the behavioral categories described in detail in Fitzpatrick (1980, 1981a). Those foraging modes and their frequencies within the three tyrannid subfamilies of Traylor (1977)—the Elaeniinae, Fluvicolinae, and Tyranninae—are listed in Table 1.

To test for correspondence between foraging mode and morphology I used two approaches. In the first ("Character Variation") I searched bivariate graphs for non-random clustering among species that share a foraging mode. The null hypothesis in these examples is that species with similar foraging characteristics plot randomly with respect to one another inside the two-dimensional space mapped by the family as a whole. Put conversely, I searched for statistical correlations between size-correct mensural traits and certain discrete categories of foraging behavior. In the second approach ("Morphology as a Function of Behavior") I plotted selected morphological measurements directly against continuously varying behavioral axes. Positions of species along these axes were determined from frequency distributions of their respective use of various prey capture maneuvers. The resulting correlations are examined largely by eye in this paper.

In one case (see Fig. 8), values for relative tarsus length represent residuals, based upon a tarsus-length versus body-weight regression calculated earlier (Fig. 5). The values were derived by subtracting 9.40 mm from the actual length and dividing by log body weight. The Y-intercept of the Figure 5 regression is 9.40. Thus, a tarsus of exactly average length for its body weight produces a value of 8.05 by this formula, which is the slope of the regression in Figure 5.

CHARACTER ANALYSES AND INTERPRETATIONS

ALLOMETRIC RELATIONSHIPS

In any analysis of body form variation, the effects of size upon shape must be considered. The sizes of individual characters tend to be strongly correlated with overall body mass, but the correlations are neither perfect nor similar to one another across characters. To make meaningful functional analyses of shape, we must factor out the overriding effects of size from our measurements. (Functional analyses of size per se also can be informative, but shall not be attempted here.)

The ranges of sizes and shapes contained within the Tyrannidae are summarized in Table 2. The results of a series of bivariate regression analyses indicate how each of five external characters varies against body weight across the family. Not surprisingly, all regressions show highly significant correlations between mensural characters and body weight (lowest correlation coefficient, r , is .52, d.f. = 92, $P < 0.01$ throughout), although the amount of variation "explained" by body weight alone (r^2) varies considerably among characters. Three types of allometric analyses are shown for the same set of measurements, using different transformations. Untransformed linear measurements were plotted against \log_{10} body weight and against cube root of body weight, and \log_{10} transformed measurements were plotted against \log_{10} body weight. Not shown are regression results using untransformed body weight data, as these yielded substantially poorer fits. In general, the linear regression model fits all three data transformations equally well. This can be seen by comparing the three r^2 values for the three separate regressions within each column.

If the values of r^2 in Table 2 were 1.0, or close to it, then this paper would end here. Differences in shape would strictly reflect differences in body size. The remainder of this report analyzes the various components of variation in shape not explained by size alone. To do this, size is factored out of the mensural data, usually by dividing them by \log_{10} body weight.

CHARACTER VARIATION

Bill shape.—Perhaps the most ecologically revealing morphological feature of a bird is its bill, the tool with which potential food is handled and ingested (e.g., Schoener 1965; Pulliam 1975). Variations, specializations and convergences in bill structure are widely known to reflect gross ecological roles (Storer 1971), and even small behavioral differences related to foraging tactics (e.g., Engels 1940) or food choice (reviewed by Hespeneide 1973; Abbott et al. 1975; Karr and James 1975).

Among flycatchers, most of which are predominantly or entirely insectivorous, bill structure varies only in subtleties of length and width measurements, rather than in over-all form (Traylor and Fitzpatrick 1982). Whereas Hespeneide (1971) showed prey sizes to be correlated at least grossly with bill size among tyrannids (in his species, larger birds have larger bills, but prey sizes are more closely correlated with body sizes), he also stressed the effects that subtle differences in foraging style can have on prey choice and community assembly among grossly similar species (Hespeneide 1975). It is, therefore, of ecological as well as evolutionary interest to determine how foraging style differences *themselves* relate to bill size and shape.

I plotted relative bill widths and lengths of 94 representative species of tyrant flycatchers in Figure 1. Body size effects were removed from this analysis by dividing both bill width and bill length by \log_{10} body weight.

Seven foraging mode distinctions are made among the 94 species I considered. Bill shapes of the species using these modes fall within distinct subsets of the total morphological space defined by the family as a whole (Fig. 1). Bills of upward-strikers are relatively long and wide, whereas those of perch-gleaners are nearly as long, but relatively narrow. The highly frugivorous tyrannids (including species in all three subfamilies) have short, stubby bills relative to body size. Ground-foragers and perch-to-ground specialists show almost complete overlap with perch-gleaners in possessing relatively long, narrow bills, slightly wider at the base. Aerial-hawkers show wide variation in bill length, but uniformly intermediate bill widths, reflecting bill shapes that are all minor variants upon a broad isosceles triangle, providing a relatively wide gape.

Some simple functional interpretations of the above general pattern are available. Upward-strikers forage with highly stereotyped, explosive sallies upward toward leaf undersurfaces, clearly relying on surprising unwary insects. Their spatulate bills would seem to provide the necessary room for error during split-second contact with the prey substrate, during which the insect is literally scooped from the leaf. In contrast, both directional and temporal precision are smaller problems for a perch-gleaner, because no sally is made at all. In these species, the thin, pointed bill permits accurate picking and probing as the bird searches vegetation within its reach, in much the same way that tweezers are used by humans.

As a sidelight to the above, well-developed rictal bristles characterize the upward-strikers, and are conspicuously absent from tyrannid perch-gleaners. The role of these bristles in prey capture remains unclear (Stettenheim 1974); they may serve in part as protective devices about the eyes and face of a sallying flycatcher (Conover and Miller 1980), as well as expanding the effective area swept by an open bill in motion. The observation that bristles are best

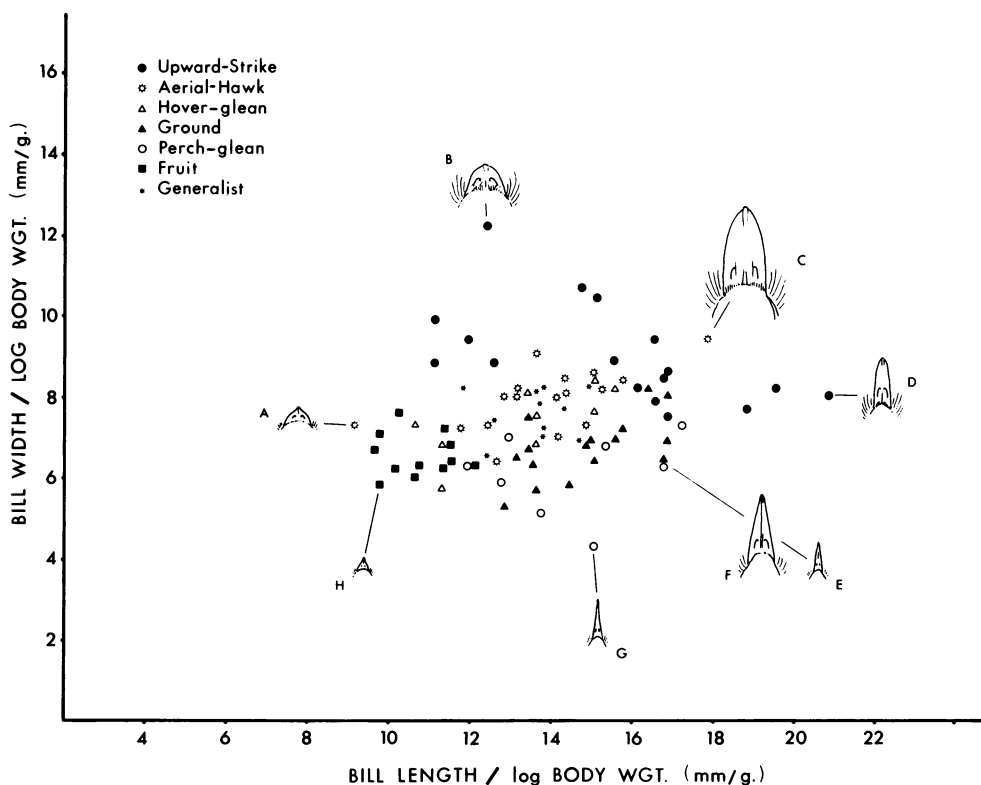


FIG. 1. Relative bill width at base plotted against relative bill length (from base) for 94 species of tyrant flycatchers, each assigned to one of seven foraging mode categories (upper left). Extreme bill shapes, drawn to scale: A = *Colonia colonus*, B = *Platyrinchus platyrhynchos*, C = *Megarynchus pitangua*, D = *Todiostrostrum cinereum*, E = *Anairetes paulus*, F = *Agriornis montana* (closed triangle), G = *Tachuris rubrigastra*, and H = *Tyrannulus elatus*.

developed among upward-strikers, and least among perch-gleaners, is consistent with both functions.

The bill-shape dichotomy just discussed suggests why most perch-gleaners, when they do sally after a prey item, usually do so with an upward-hover-glean (Fitzpatrick 1980). With a narrow, pointed bill, individuals presumably must become virtually stationary to use the bill tip accurately. During a sally, this can be accomplished only by hovering. Furthermore, because hovering presumably gives some kinds of insects a chance to escape, this restriction may have implications regarding the range of prey items usable by perch-gleaners versus upward-strikers. This point was stressed by Sherry (1982), who documented just such differences between the diets of these two ecological groups.

Method of prey capture used by ground-foraging flycatchers usually is similar to that of perch-gleaners. The simple picking motion is slower and more easily directed than in the sally-gleaners. The fact that many perch-to-ground salliers are large, and feed on relatively large prey items, probably explains the relatively wide gapes among bills of ground-foragers, whose bills otherwise closely match those of perch-gleaners (Fig. 2).

Aerial-hawkers in a number of avian groups show relatively wide gapes, presumably affording a means of sweeping a wider area with the open bill (Storer 1971). Possibly, this constraint leaves only bill length to vary functionally with prey size (Fig. 2). This interpretation predicts that bill length is a better indicator of prey size among aerial-hawkers than among other tyrannid foraging modes less constrained to a wide gape.

MacArthur (1971) pointed out that one "fundamental law of functional morphology"—that jacks-of-all-trades are masters of none—still remains to be "clearly enunciated." In this regard

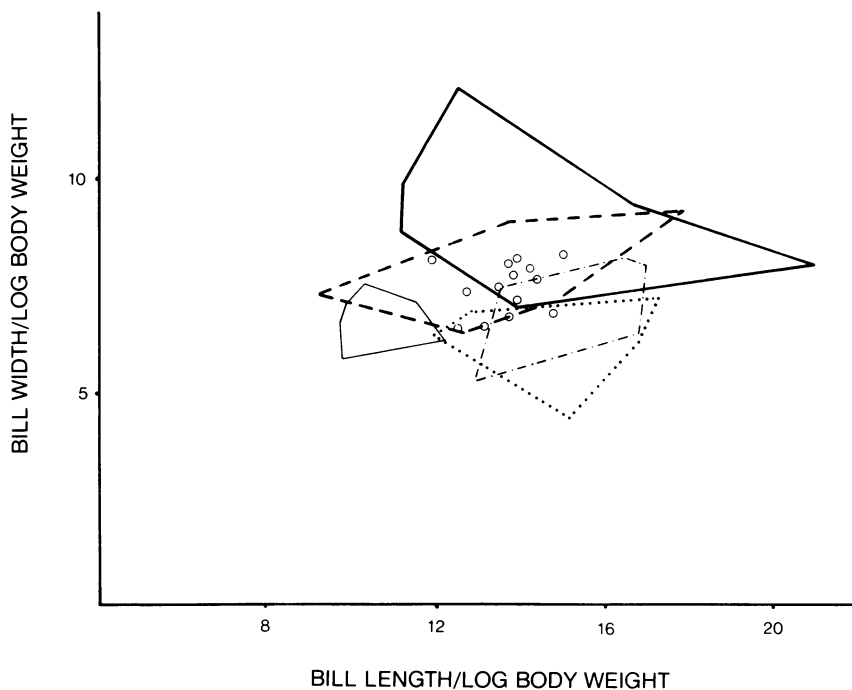


FIG. 2. Relative bill shapes of tyrant flycatchers, based on the data plotted in Figure 1. Lines enclose all values within the following foraging mode categories: upward-strike (thick solid line), aerial-hawk (thick dashed line), ground-related foraging (dot-and-dashed line), perch-glean (dotted line), frugivorous generalists (thin solid line). Foraging mode generalists are plotted as open circles.

it seems worth emphasizing that the tyrannid behavioral generalists (those species that use several sally techniques) do, in fact, fall in the very middle of their family's bill-shape spectrum (Fig. 2). Generalists appear to have settled on a "morphologically average" bill shape, in which the differing structural requirements of distinct behavioral traits combine to produce a master-of-none-of-them. This morphological intermediacy among behavioral generalists reappears throughout the analyses discussed in this paper.

Wing shape.—Severe aerodynamic constraints have resulted in remarkable uniformity in wing form within any taxonomic group of birds. Indeed, regressions of wing length, area, and aspect ratio against body weight show that a single power function defines wing structures within the entire class Aves, spanning four orders of magnitude in body weight (Greenewalt 1962, 1975). Because of aerodynamic constraints, variation in wing shape within the Tyrannidae is comparatively slight. This is immediately apparent from the fact that body size alone accounts for much more of the variation in the tyrannid wing length than it does for any other character I measured (Table 2). Nevertheless, the family still shows more variation in wing design than does any other passerine family (Hartman 1961). This variation principally relates to migratory habits and reliance upon aerial foraging techniques.

The Tyrannidae, like other passerines, show minor variations on the elliptical wing, a design that provides maximum lift and maneuverability at low air speed, and allows for rapid acceleration during a sally (Savile 1957). However, maximum power during open-air, high velocity flight is provided by longer, more pointed wings. One ecological subset of flycatchers, aerial-hawking species ($N = 19$) and species of other foraging modes known to migrate great distances each year ($N = 11$; Kipp 1958), approaches this latter design in having relatively long wings compared to the rest of the family (Fig. 3). Analyzed separately, the hawkers and the migrants show virtually identical regressions; pooled, their regression line shows the same slope but is significantly above that of the remainder of species (Fig. 3; $F = 7.08$; $P < 0.01$).

The regression for upward-strikers (Fig. 3, open triangles) shows a trend toward relatively

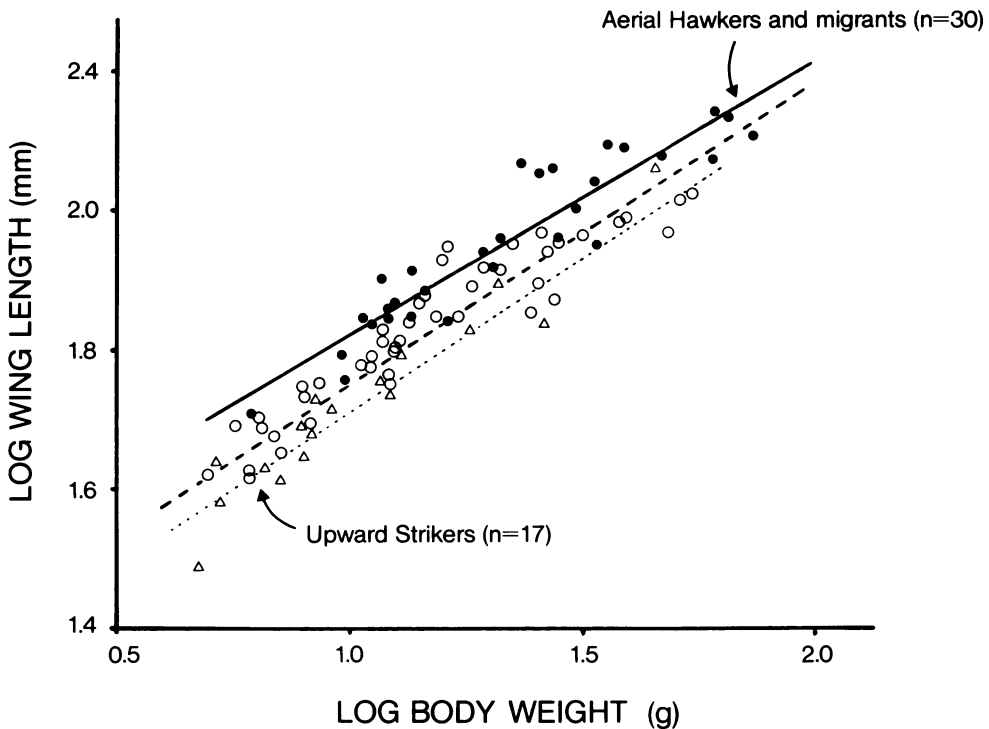


FIG. 3. Log-log plot of wing length versus body weight in 94 species of tyrant flycatchers, categorized as aerial-hawkiers or long distance migrants (closed circles), upward-strikers (open triangles), or others (open circles). Regression lines are shown for all three categories.

short wings compared to other tyrannids. Although not statistically significant, this trend is consistent with Savile's (1957) model for species that require rapid take-offs in dense foliage.

Wing designs differ more in aspect ratio than in simple wing length (Fig. 4). Even among the limited set of species for which I obtained both wing tracings and foraging data, some clear patterns emerge. The four aerial-hawking specialists have substantially more elongate wings than the other species (Fig. 4). Species that capture aerial prey between 20 and 80 percent of the time I consider to be facultative aerial-hawkers (Fig. 4, open stars). Just as generalists exhibit intermediate bill shapes (preceding section), the aspect ratios of facultative hawkers fall below those of aerial-hawking specialists but, on average, above those of species that rarely hawk.

The four aerial-hawking specialists plotted in Fig. 4 belong to two genera, *Contopus* (left-hand pair) and *Tyrannus* (right-hand pair). These pairs illustrate the cumulative effects of foraging strategy and migratory habits; each pair contains a resident species (*C. cinereus* and *T. melancholicus*) and a long-distance migrant (*C. virens* and *T. tyrannus*). In both genera the migrant, as predicted, has a substantially greater aspect ratio, despite being nearly identical in body weight.

Functional interpretations of these results are straightforward and parallel the discussion by Savile (1957). Longer wings generate power more efficiently during sustained, high speed flight, while shorter, rounded wings provide better lift at take-off and low velocities, and also permit greater mobility through dense vegetation. As expected for these mechanical reasons, aerial-hawkers and migrants show the relatively longest wings for their body size, while foliage-gleaning specialists show the shortest.

Tarsus length.—In contrast to wing form, which for aerodynamic reasons is restricted to minor variation in the family, tyrannid tarsi span a wide morphological range. Tarsus length and body weight are only weakly correlated across the family as a whole (Fig. 5, Table 2). A major portion of the variation is related to the use of the ground as a foraging substrate, a

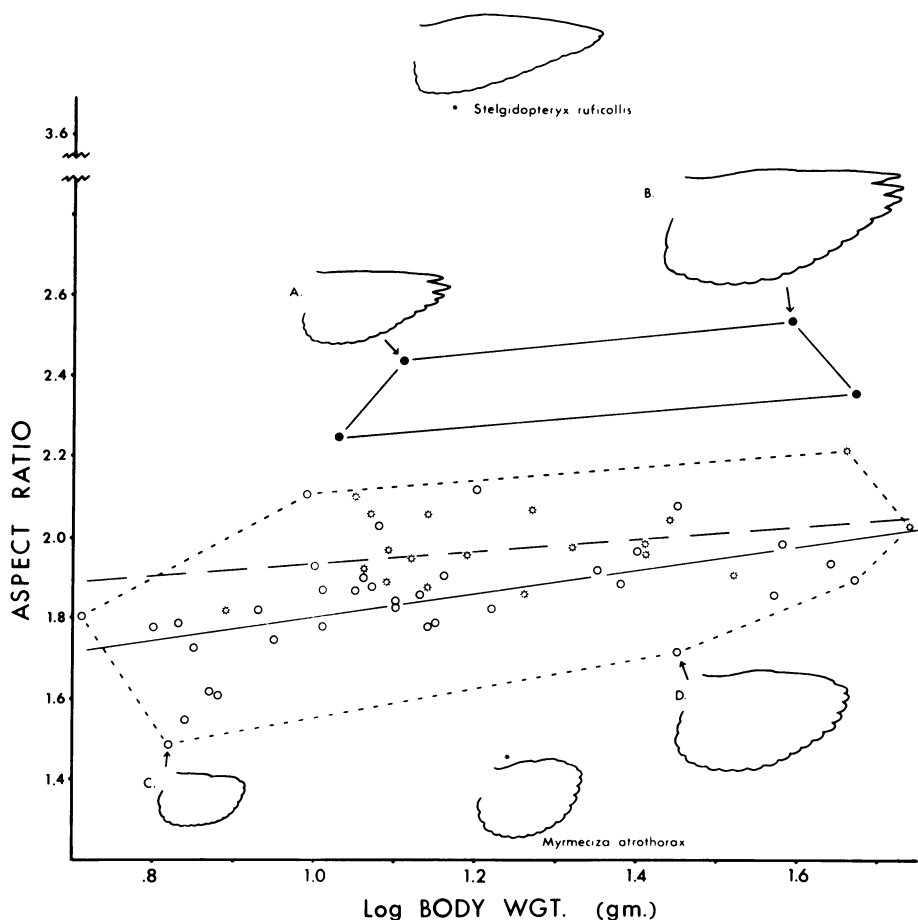


FIG. 4. Aspect ratio plotted against log body weight for some representative species of tyrant flycatchers, categorized as aerial-hawkers (closed circles, solid lines), facultative aerial-hawkers (20–80% use of aerial-hawk; open stars), and others (open circles), the latter two groups enclosed by broken lines. Regression lines are shown for facultative hawkers (dashed line) and all non-hawkers (solid line). Wing shapes illustrated: an aerial-foraging swallow (*Stelgidopteryx ruficollis*); a terrestrial formicariid (*Myrmeciza atrothorax*); tyrannids: A = *Contopus virens*, B = *Tyrannus tyrannus*, both aerial-hawkers; C = *Todirostrum cinereum*, an upward-striker; D = *Myiarchus ferox*, an outward hover-gleaning generalist.

habit that is related to the evolution of long legs and long hind claws in a number of avian orders (e.g., Engels 1940; Berger 1952; Storer 1971). Tyrannid species that habitually forage upon, or sally to, the ground have significantly longer legs than the remaining species (Fig. 6). More important, the tarsus-length versus body-weight regression shows a much steeper slope among this group. Not only do ground-foraging species exhibit longer (and thicker) tarsi than do equivalently-sized species that perch on twigs in the typical passerine style (Schaffer 1903), but the legs of the heavier-bodied species proportionately are even longer than those of the lighter-bodied ground-users.

In relative tarsus length, the “perch-and-wait” aerial-hawkers represent the opposite of ground-foragers (Figs. 5, 6). Their legs are shorter, and their allometric increase is substantially shallower than among species that habitually use the ground (note slopes of two solid lines in Fig. 6).

Once again, species that combine the two behavioral extremes are morphologically intermediate. Five species (closed triangles, Fig. 6) are aerial-hawking specialists, but either they do so largely from the ground or rock surfaces over streams (*Serpophaga cinerea*, *Sayornis*

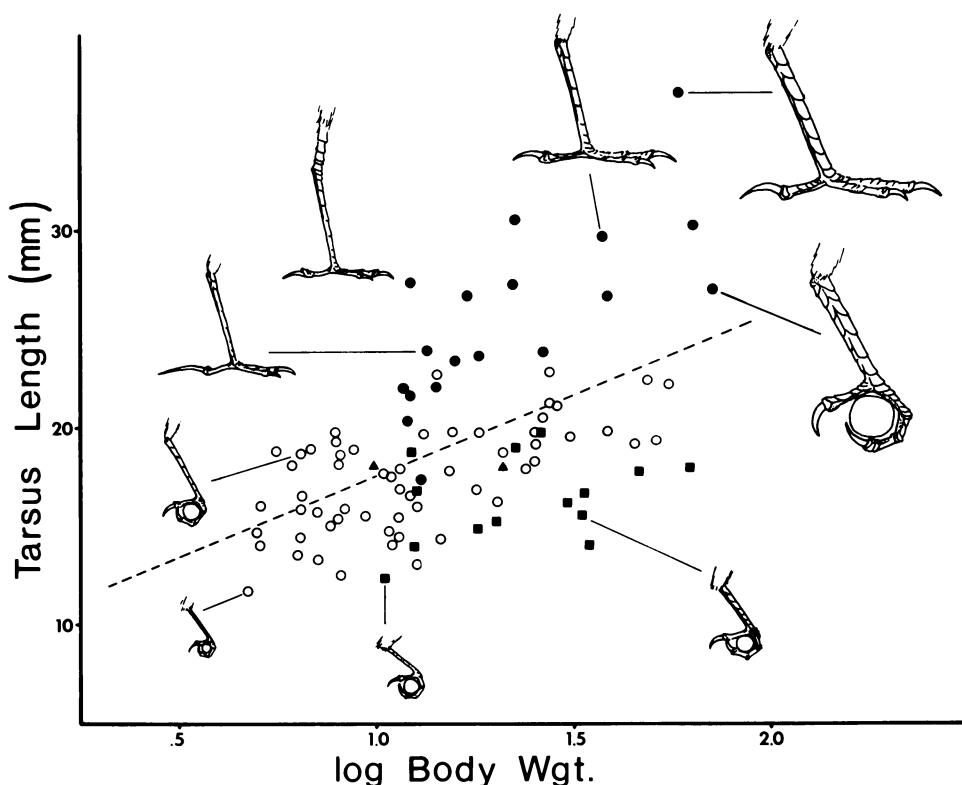


FIG. 5. Absolute tarsus length plotted against log body weight for 94 species of tyrant flycatchers. Regression line = dashed line. Ecological categories: ground-related foragers = closed circles; aerial-hawkers = closed squares; all others = open circles. Tarsi illustrated to scale, clockwise from lower left: *Myiornis ecuadatus*, *Todirostrum cinereum*, *Lessonia rufa*, *Muscigralla brevicauda*, *Machetornis rixosus*, *Agriornis montana*, *Gubernetes yetapa*, *Contopus borealis*, *Pyrrhomyias cinnamomea*.

nigricans), or they sally to the ground regularly (*Pyrocephalus rubinus*, *Knipolegus lophotes*, *Gubernetes yetapa*). The regression for tarsus-length versus body-weight among these five species has the same slope as that of ground-users, but its values fall between the lines for the two groups of behavioral specialists (Fig. 6).

In the case of intermediate behavior just described, it seems that the opposing physical demands for long legs, associated with ground-use, and for short ones, associated with aerial-hawking habits, result in tarsus lengths that approach the average for the respective body weights (Fig. 6). (In a subsequent section, I explore the extent to which this kind of morphological fine tuning exists.) What are these opposing physical demands? The functional morphology of long versus short legs among birds has received remarkably little attention for being such a clear dichotomy (but see Osterhaus 1962; Orians and Horn 1969). At present I can only speculate on the reasons for the differences. Among the ground-users, long legs presumably provide greater running speed, a higher viewing position, stronger physical support because of increased cross-sectional area, greater area for muscle attachment, and greater flexing capability during landing than would short legs. Among aerial-hawkers, short legs insure a low center of gravity upon the perch, favoring balance and stability during long, nearly motionless search periods. In addition, a shorter tarsus requires a less acute flexing angle at the heel joint to accomplish a given amount of passive flexing of the foot while perching (see Schaffer 1903). This provides a firmer hold for the perching, "sit-and-wait" aerial-hawkers than a long-legged bird could attain sitting in the same position. Both considerations would also hold for many other, ecologically similar bird groups that have unusually short tarsi (e.g., swifts, swallows, hummingbirds, kingfishers, jacamars).

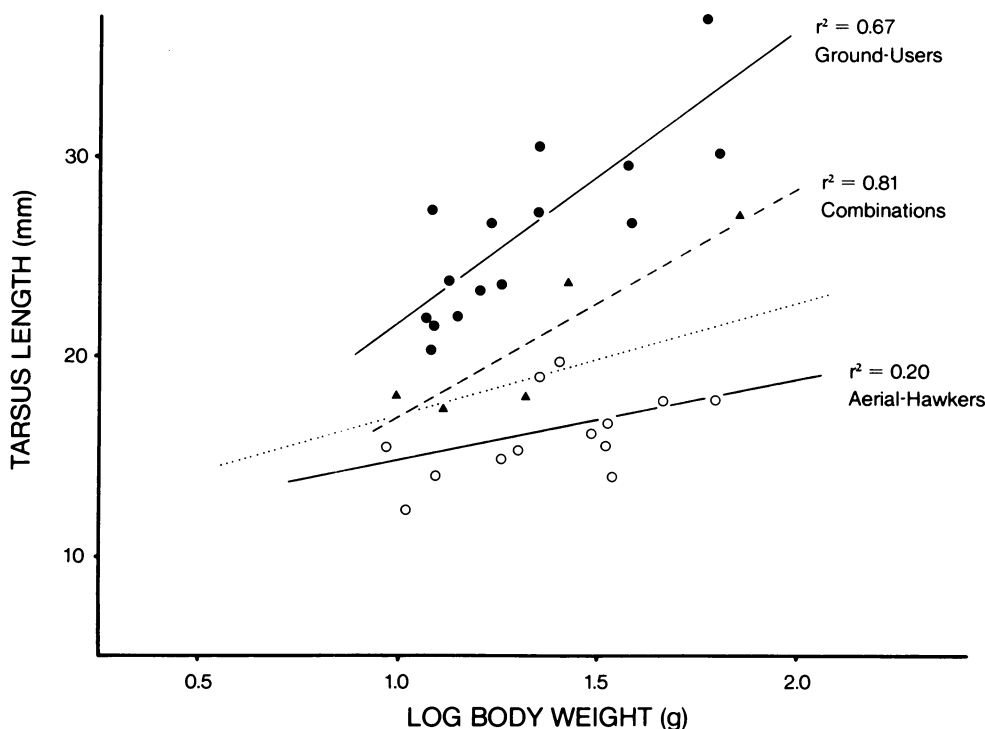


FIG. 6. Tarsus length plotted against log body weight for species in three ecological categories, showing regression lines for each group and for the family as a whole (dotted line). Ground-users = closed circles, solid line; aerial-hawkers = open circles, solid line, "combination" species, or hawkers that use the ground extensively = closed triangles, dashed line.

Upward-strikers also possess relatively long legs, especially in the smallest size classes. Because these species habitually bob, lean, and peer while searching leaf surfaces, I surmise that their long legs may afford them increased viewing area in dense vegetation, where undersurfaces often are obstructed (diagrammed in Fitzpatrick 1978). Sherry (1982) suggested in addition that the need for explosively rapid take-off during sallies selects for longer legs that provide maximum spring. Both interpretations are supported by the proportionately large muscle mass associated with the hind limbs of many upward-strikers (pers. observ.).

Two of the more bizarre adaptations for ground foraging in the family are the extended hind claw of *Lessonia rufa* and the partially scuted tibiotarsus of *Muscigralla brevicauda* (Fig. 5). Both seem related to peculiar ecological features. *Lessonia* forages with fast ground-chases and fluttering aerial pursuits on moist, boggy alpine meadows, floating mats of vegetation along Andean lake margins, and on south temperate wet grasslands. Elongated hallux claws have arisen among many ground-dwelling bird groups (e.g., longspurs, longclaws, larks, pipits). They are best developed among species that use the hind claw for support while walking on soft, wet ground or floating vegetation, as in the jacanas (Storer 1971). *Lessonia* appears to provide a tyrannid example of this adaptation. *Muscigralla*, probably the most exclusively terrestrial, cursorial tyrant flycatcher, walks and runs on the dry earth of the arid Peruvian coast. Its legs are proportionately the longest in the family, comparable to those of flycatcher species two to three times its weight (Fig. 5). These oversized legs presumably provide added height and increased running speed, both associated with the species' habit of standing atop small mounds of earth and scanning, before darting after prey along the ground. The tremendously elongated tibiotarsus of this species has been accompanied by development of scutellation above the heel joint—a unique feature in the family.

Tail form.—Unlike variation in bill, wing, and tarsus features, many of the peculiar tail modifications within the Tyrannidae have social functions, placing them outside the scope of

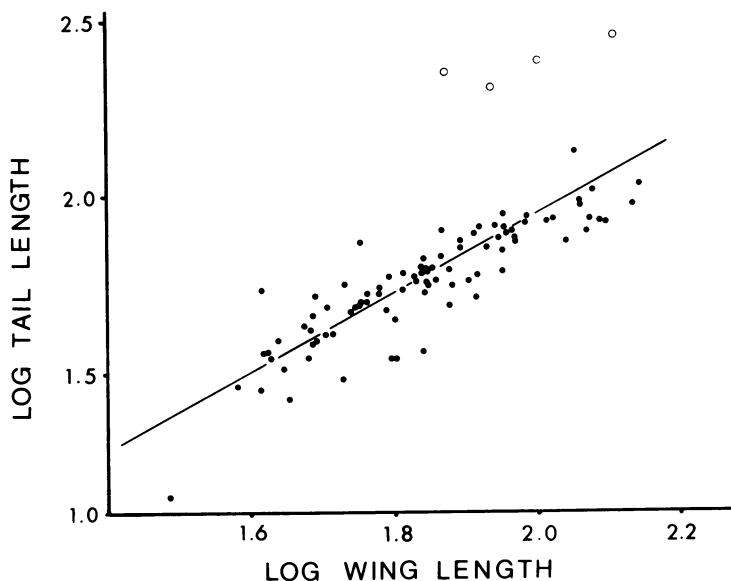


FIG. 7. Log-log plot and linear regression of tail length versus wing length in 94 species of flycatchers, including four with unusually elongated tails (open circles): *Tyrannus savana*, *Alectrurus risora*, *Gubernetes yetapa*, and *Colonia colonus*.

this paper. The typical tyrannid tail is of medium length with a small central notch. Tail length and wing length are strongly correlated (Fig. 7), and the relationship is even stronger if a few of the species with elaborate, greatly elongated tails are removed from the analysis (four open circles in Fig. 7; r^2 changes from .58 to .66). The closeness of this relationship supports the general assertion (e.g., Hartman 1961) that in most flycatchers the tail serves predominantly aerodynamic functions as in other typical passerines.

The most notable elaboration in tail form is the independent development of elongated outer tail feathers among several groups of species. This clearly represents an adaptation for maneuverability during aerial prey capture, where laterally extended outer rectrices provide a rudder against which the body can be sharply turned. Thus, aerial-hawkers show swallow-like gradations from deeply forked tails (especially in genera *Contopus*, *Pyrrhomyias*, *Hirundinea*, *Tyrannus*) to greatly exaggerated outer rectrices (*Muscipipra*, *Gubernetes*, *Tyrannus forficatus* and *savana*). In at least one genus (*Alectrurus*), containing marsh-dwelling, apparently polygynous species (Fitzpatrick, unpubl. data), this adaptation appears to have developed into a secondary sexual characteristic.

A few genera show reduced tail lengths. Most notable are *Myiornis* and *Muscigralla*. The latter species, discussed above, is so cursorial that it apparently has lost the need for the extra glide area provided by a tail of normal length. The genus *Myiornis*, which contains the smallest passerine bird (*M. ecaudatus*, Short-tailed Pygmy Tyrant, 4.5 g), uses an explosive sally for its upward-strike foraging technique, and a peculiar, hovering flight while moving amidst dense vine tangles high in the forest. Short, rounded wings provide all the lift in this form of flight (Greenewalt 1975). *Myiornis* performs no complicated aerial acrobatics, and, therefore, has little use for a typical, elongated passerine tail. Indeed, it may have lost the tail as a means of reducing drag (Sherry 1982); in these respects the genus seems to have converged upon the form and flight behavior of medium-sized beetles.

Graduated tails, in which the innermost rectrices are longest, occur in three unrelated genera: *Todirostrum* (*cinereum* species group only, Fitzpatrick 1976), *Fluvicola* (*nengeta* only), and *Stigmatura*. In all three cases the graduated rectrices are broadly tipped with white. The tail of *Todirostrum* is frequently cocked over the back during a peculiar, stereotyped, intraspecific display. *Stigmatura budyoides* apparently jerks and cocks the tail during normal foraging and in display (Wetmore 1926; Smith 1971). The combined features of conspicuous white rectrices and tail-cocking habits (both also present in *Inezia subflava*, in which the tail shows rudi-

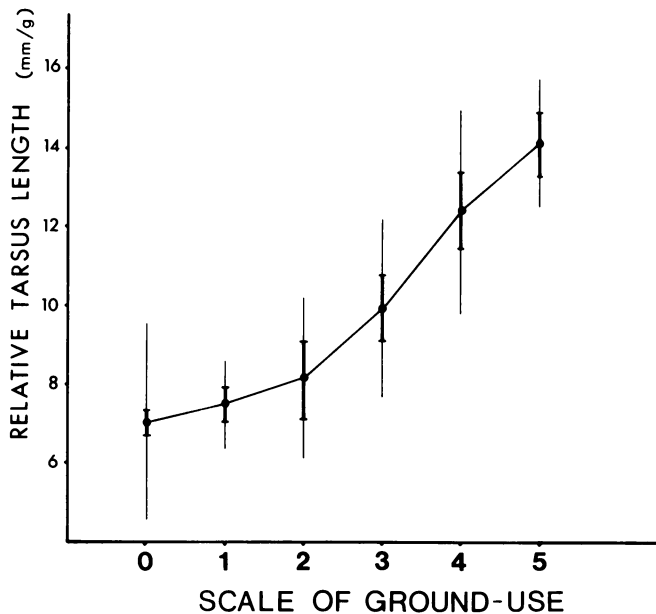


FIG. 8. Relative tarsus lengths of flycatchers using the ground to different degrees: 0 = no ground-use; 5 = exclusively terrestrial species; categories defined in text. Mean relative tarsus length (dots) plus and minus one standard error (thick bars) and one standard deviation (thin lines) are shown for species in each ground-use category. See text for method of calculating relative tarsus length.

mentary graduation) strongly suggest that graduated rectrices may have secondary social functions in the Tyrannidae.

MORPHOLOGY AS A FUNCTION OF BEHAVIOR

In the preceding section I identified groups of species representing various ecological categories and showed, in broad terms, some morphological correlates of each behavioral specialization. "Upward-strikers" have wide bills, "aerial-hawkers" have long wings, "ground-foragers" have long legs, and so on. A much more revealing question now may be asked: To what extent do external morphological features vary *continuously* between species that show a gradient in behavioral specialization? The existence of a smooth continuum, in which morphology and behavior track one another, would imply at least two points relevant to adaptive radiation. (1) Directly functional, adaptive interpretations of the morphological variation are supported if the designs of various species are shown to be fine-tuned to behavior, especially if convergence among unrelated groups is implied; (2) morphological and behavioral change can occur relatively easily, at an evolutionary pace, if a small average change in a certain behavior pattern requires only a correspondingly small change in morphology to facilitate it.

Some evidence for such a morphological continuity principle has been mentioned already, in that behaviorally intermediate species also tend to be morphologically intermediate. I examine the question more directly here, using three sample analyses in which morphological measures are plotted directly against behavioral indices.

Tarsus length versus ground-use.—Figure 5 shows that tarsus length is proportionately longest among ground-foraging flycatchers. However, even within the ground-foragers, significant variation exists. Furthermore, other species not classified as "ground-foragers" do occasionally sally to the ground. To test more critically the relationship between tarsus length and ground-use I plotted relative lengths of flycatcher tarsi against degree of ground-use (Fig. 8), separating six categories of behavior as follows:

- 0 = strictly arboreal, essentially never perches on or sallies to the ground ($n = 64$ species);
- 1 = rarely sallies to ground, no searching from ground ($n = 6$);

- 2 = 10 to 30 percent of sallies to ground, no searching from ground ($n = 4$);
- 3 = 30 to 60 percent of sallies to ground, frequently searches from ground, but uses other foraging techniques extensively ($n = 7$);
- 4 = ground-foraging specialist, 60 to 90 percent of sallies either perch-to-ground or initiated from ground, but still uses other techniques ($n = 7$);
- 5 = exclusively terrestrial and cursorial, all perches and sallies occur at the ground ($n = 4$).

Average tarsus length does vary continuously with degree of dependence upon ground-related foraging (Fig. 8). This confirms the intuitive impression that tarsus length is an evolutionarily flexible feature among tyrannids, and it even suggests a scenario through which members of a lineage may become ground-foraging specialists. The difference in tarsus length, between species in behavioral category 0 (no ground use) and those in 1 (rare, facultative use) is slight, and not significant (Student's $t = .42$; $P > 0.05$). This implies that facultative use of the ground requires no special tarsal development. Given the appropriate ecological conditions or setting, then, occasional sallies to the ground physically could be performed and even adopted as a foraging pattern, by any species. Such a behavioral shift, if it persists, would cause selection to favor those individuals with slightly longer tarsi, thus leading to gradual morphological change in those populations (cf. categories 0, 1, and 2 in Fig. 8). This, in turn, would facilitate additional reliance upon the ground-related foraging tactics. Shifts in both behavior and morphology would be gradual at this "generalized" end of the spectrum, where use of the technique still is facultative. At some point on the way up the scale of ground-use (around category 2) physical demands for morphological specialization may become stronger, causing selection to favor increasingly longer legs. True ground-foraging specialists seem to require proportionately much longer legs than do perching species (see Fig. 6). Thus, I speculate that a species that becomes a ground-foraging specialist (categories 3 and 4 in Fig. 8) may be under intense pressure to develop extremely long legs. At this point, the slope of the curve steepens, and its overall asymmetry becomes important. Possibly, complete specialization (categories 4 and 5) could lead to the evolution of such long legs that a species becomes less capable of departing from its specialized foraging mode. Its body form, now well adapted for one mode, is less adequate for other styles of foraging, rendering the specialist at a competitive disadvantage in any situation that favors more generalized behavior. This suggests that, in evolutionary terms, it may be easier for generalized species to begin the ascent up a curve toward specialization than for a specialist to descend back down the curve after nearing the top (Fig. 8.).

It is important to note that the above scenario depends upon the accuracy of the ground-use scale. The steepening curve in Figure 8 could simply result from lumping different degrees of specialization into fewer categories at the upper end of the curve. Whether the non-linearity of the curve is an artifact of the scale remains to be investigated with more detailed, quantitative study of the species involved. In any case, a morphological continuum clearly seems to hold across a variety of generalized to specialized ground-foragers.

Bill width versus upward-striking.—We have already seen that among foliage-gleaning tyrannids, upward-strikers have proportionately wider bills than do perch-gleaners and hover-gleaners (Fig. 1). To test how the tendency toward spatulate-shaped bills varies along a continuum of gleaning techniques, I plotted relative half-widths (bill width half-way from base to tip, divided by the logarithm of body weight) against a behavioral index obtained for each species by subtracting its percentages of perch-gleans and upward hover-gleans from its percentage of strikes (Fig. 9). Thus, the index for a complete perch-gleaning or upward hover-gleaning specialist is -1.0 , that for an upward-strike specialist is $+1.0$, and the index for a 50:50 generalist is 0. The "strike index" used here makes the simplifying assumption that the opposing effects of perch- or hover-gleaning versus striking combine additively. (Among other possible complications, for example, weighting each technique equally could squeeze fine ecological subdivisions closer together at the ends than at the middle of the continuum.) At least at the gross level, however, the change in morphology along the behavioral continuum is gradual and monotonic (Fig. 9). Specialized perch-gleaners and hover-gleaners have narrow bills, upward-strikers have the widest bills, and the generalists (few, in this case) are intermediate.

Once again, at a certain level of specialization the curve appears to steepen. Upward strike specialists ($\geq 80\%$ use) have proportionately much wider bills than birds at any other position along the spectrum.

Wing/tarsus ratio versus aerial-hawking.—In this example two morphological features are

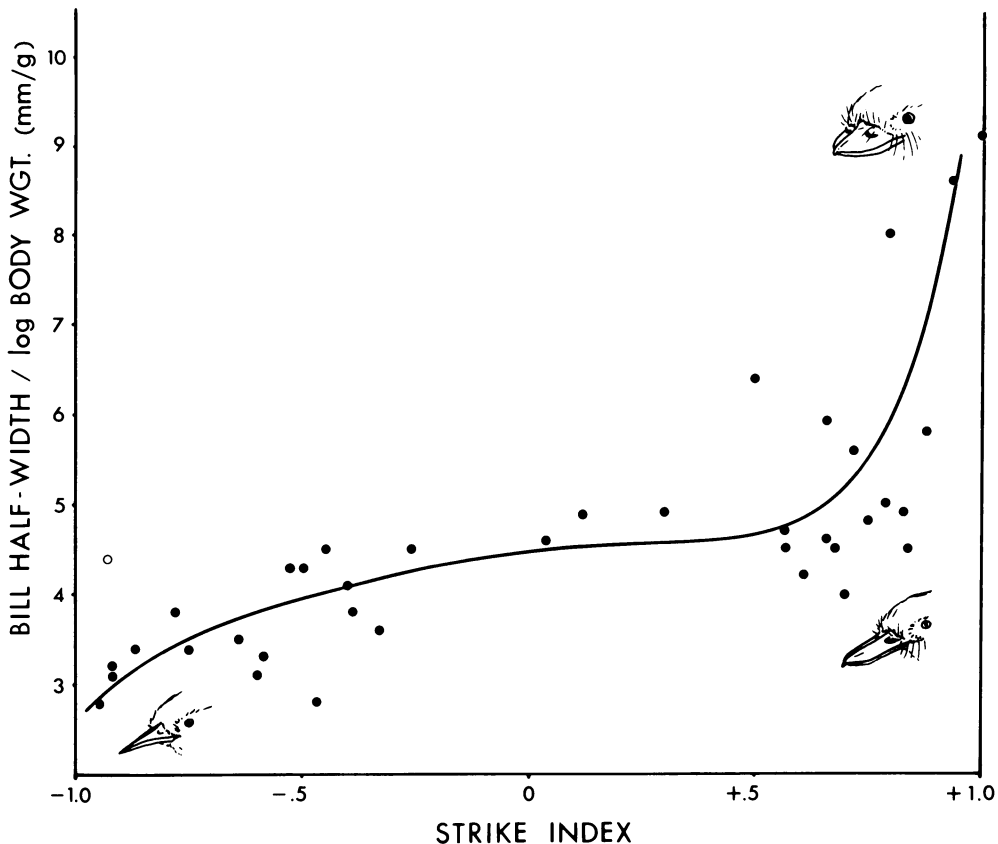


FIG. 9. Width of bill half-way from base to tip, divided by log body weight, plotted against the strike index (i.e., the proportion of use of upward-strikes, minus the summed proportions for perch-gleans and hover-gleans) for 38 foliage-gleaning flycatchers. A strike index of 0 indicates equal use of these techniques; +1.0 and -1.0 indicate pure specialists. Bill shape of one perch-gleaner (*Suiriri suiriri*, open circle) shows extreme individual variation, for unknown reasons. The value shown is at the upper extreme for the species. The line is fitted by eye. Composite sketches illustrate bill shapes of three specialized genera: *Tachuris* (left-most), *Platyrinchus* (uppermost), and *Todiostrosum* (lower right).

considered together in relation to a single, continuous behavioral variable. I have already shown (Figs. 4, 5) that aerial-hawking flycatchers possess relatively long wings and short tarsi. Here I combine these features and examine whether the ratio between wing and tarsus lengths varies continuously with degree of dependence upon aerial-hawking (Fig. 10).

As in the previous two examples, where only single characters were examined, a continuous relationship is apparent, in this case between a pair of seemingly independent characters and the use of a specialized behavioral trait. Again the data support the interpretation that long wings and short legs are adaptively favored features for aerial-hawkers. The continuum suggests that even when two characters are involved, flycatchers can evolve toward either behavioral or morphological extreme relatively easily.

Non-linearities in this relationship (Fig. 10) may occur at either end of the spectrum. Certain species (mostly upward-strikers) have proportionately shorter wings and longer tarsi than the rest, leaving them well below the central axis of the curve. For such species (black area in lower left of inset, Fig. 10), the changes in body form that would appear to adapt them to increased aerial-hawking are relatively greater than those that would be required of species closer to the central axis. This suggests that such non-users (e.g., upward-strikers) are less likely than other species to make successful ecological shifts of this sort. Extremely long wings and short tarsi of certain aerial-hawking specialists place them well above the central axis (Fig.

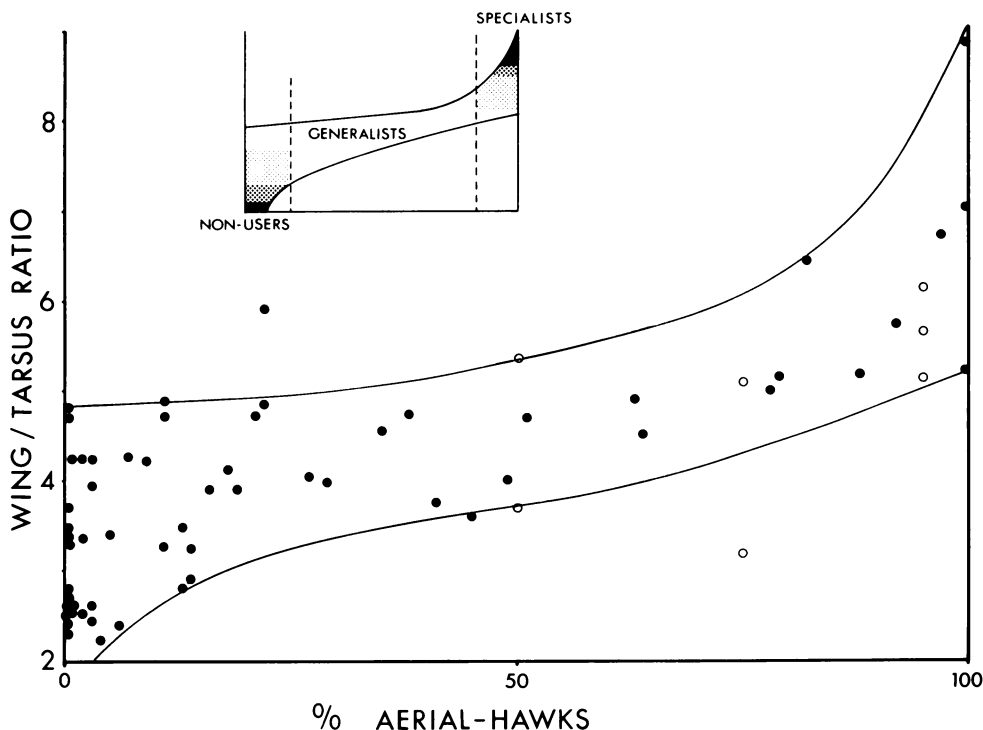


FIG. 10. Wing chord divided by tarsus length, plotted against the percent frequency of aerial-hawks in the foraging repertoire of 67 species of tyrannids. Aerial-hawking percentages are based on field data with sample sizes of at least 30 sallies (closed circles), or less (open circles). Inset schematically summarizes the pattern, emphasizing the extreme differences between the wing-tarsus ratios of certain species (shaded areas) at either end of the spectrum compared to the ratios of generalists.

10). These species also may be behaviorally more restricted than the others. The body form of *Hirundinea ferruginea*, for example (extreme upper point in Fig. 10) is so specialized for aerial-hawking that it appears unsuitable for most other kinds of capture techniques. I doubt that *Hirundinea* could shift easily to any other foraging mode without passing through a phase of much decreased efficiency, in which its behavior would become generalized while its body remained specialized.

Most species fall along the central axis of the relationship (Fig. 10). These appear morphologically more free to shift one way or the other behaviorally, without drastic change in body form. This relationship suggests that facultative aerial-hawking is a foraging technique still available to most tyrannid groups.

PATTERNS OF ADAPTIVE RADIATION

In this section I indulge in speculation about the evolution of modern flycatchers, by combining my own findings with the independently derived phylogenetic inferences made by Traylor (1977, 1979). Traylor recognized three subfamilies, which constitute the major lineages of the family. Within them are several clearly defined assemblages of related genera (summarized in Traylor and Fitzpatrick 1982). I emphasize a crucial methodological point: Traylor arrived at his systematic picture of the Tyrannidae principally by integrating the anatomical studies of Warter (1965) and Ames (1971), published data on nest forms, and his own data on plumage patterns. External structural peculiarities played only a minor role, and behavior (except nest-construction) was not involved at all. Thus, I was able to assess Traylor's proposed superstructure for the family independently, from an ecological and behavioral view. The extent to which Traylor's assemblages fit a logical, parsimonious pattern in terms of behavioral relationships is indeed striking.

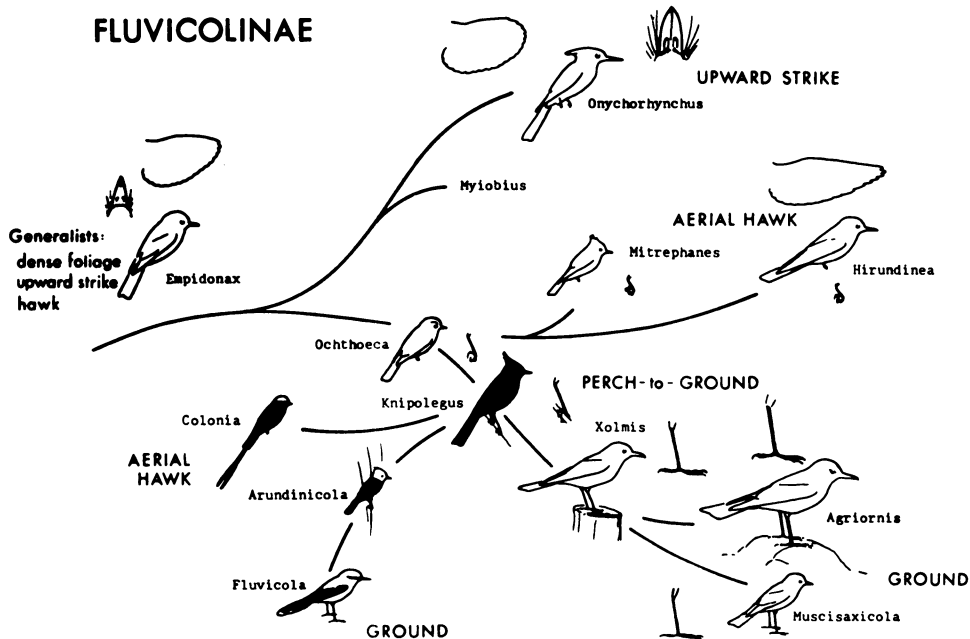


FIG. 11. The major pathways of specialization in the subfamily Fluvicolinae, following the phylogenetic groupings of Traylor (1977). Important modern-day genera that reflect generalized (lower case lettering), intermediate, and specialized (capital lettering) foraging habits are shown along hypothesized evolutionary lines of increasing specialization. Selected features of external morphology illustrate the structural trends.

Earlier (Fitzpatrick 1980) I showed that within each of the three tyrannid subfamilies occur from one to three generalized foraging modes as well as a corresponding set of one or two highly specialized modes seemingly derived from the generalized ones. In the present paper I have emphasized some conspicuous relationships between those foraging modes and certain external features of flycatchers. With these, and Traylor's (1977) lineages, as background, I speculate on a few of the pathways followed during the evolutionary radiation of the tyrant flycatchers. These speculations are based on the following observations: (1) each major lineage contains its own unique set of generalists and specialists, spanning only a certain subset of the behavioral and morphological gradations described in the preceding sections; (2) by reason of parsimony, the morphology-behavior relationships considered (Figs. 8–10) represent some of the specific pathways of evolution between generalists and specialists; (3) many of these pathways we can still see preserved among closely related species, as if certain groups (e.g., ancestors of modern genera) became successful at intermediate positions while other forms continued toward more specialized behavior and form; (4) I interpret the non-linear relationships between morphology and foraging behavior (Figs. 8–10) to suggest that evolutionary trends in general proceed more readily up a scale toward specialization, than in both directions equally. Once again, I stress that this interpretation depends upon the assumptions that the behavioral and morphological factors are scaled in biologically meaningful ways, and that decreased efficiency at a novel foraging technique hampers specialists more than generalists. This admittedly controversial point is not critical to the present discussion, however, and will be developed more fully in a subsequent paper. The important evolutionary trends within the three flycatcher subfamilies are illustrated in Figures 11, 12, and 13.

GROUND-RELATED FORAGING

Independent adaptations to terrestrial foraging have occurred in four lineages, representing at least two subfamilies and possibly all three. Smith and Vuilleumier (1971) discussed relationships and speciation patterns in the clearest case, that of the fluvicoline ground-tyrants (Fig. 11). The key transition (Fig. 11, lower right) lies in facultative perch-to-ground sallying by generalists prone to aerial-hawking in open country and forest edge (e.g., the present-day

ELAENIINAE

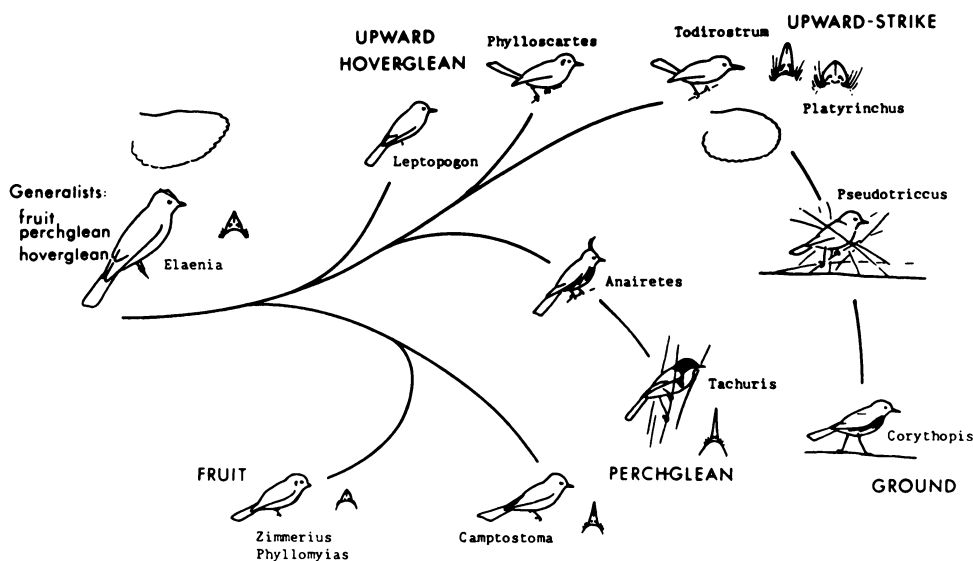


FIG. 12. The major pathways of specialization in the subfamily Elaeniinae, following the phylogenetic groupings of Traylor (1977). Schematic format as in Figure 11.

genera *Pyrocephalus*, *Sayornis*, *Ochthoeca*). Facultative perch-to-ground sallying gave rise to specialists (e.g., *Neoxolmis*, *Muscisaxicola*, *Muscigralla*). The pattern, both behavioral and morphological, seems precisely illustrated by Figure 8. Many of the intermediate positions shown in Figure 8 are represented by modern forms in this assemblage of closely related species.

A second line to terrestrial habits is illustrated by the black, sexually dimorphic fluvicolines *Knipolegus*, *Hymenops*, *Alectrurus*, *Arundinicola*, and *Fluvicola*. Most members of this group share a propensity for marsh and lake edge vegetations.

Machetornis contains one highly terrestrial species of uncertain affinities (Traylor 1977). It frequently performs perch-to-ground sallies (often from the backs of livestock), but more often walks in grassy pastures picking up ground prey as do meadowlarks (icterid genus *Sturnella*). The species shows striking similarities in plumage, voice, display, and attenuated primaries, to the kingbirds (*Tyrannus*) which are almost exclusively aerial-hawkers. I suggest that *Machetornis* may be a ground-adapted kingbird, having proceeded to its peculiar behavioral and morphological state along exactly the same route as did the fluvicolines (see Lanyon 1984 for an alternate view).

The Elaeniinae is a subfamily comprised of foliage-gleaners and generalist frugivores, with specialists in perch-gleaning and upward-striking (Fitzpatrick 1980). Here, too, a single genus of uncertain affinities has become terrestrial (*Corythopsis*; Fig. 12). In this case, however, the route presumably was not through perch-to-ground intermediates. *Corythopsis* is an upward-striker, typically sallying from the ground while walking deliberately along the forest floor. Many upward-strikers forage in extremely dense foliage near the ground, and their legs are unusually long for birds their size. Thus, they are pre-adapted for shifting entirely to the ground, where they can retain the specialized foraging technique amidst ground story vegetation of the forest floor.

FOLIAGE-GLEANERS

The most stereotyped foraging specialization among foliage-gleaners is upward-striking, a mode that carries with it numerous elaborations in body form: broad bill, short and rounded wings, long legs, and well developed rectal bristles. Upward-strike specialists are most prevalent in the Elaeniinae (Table 2, Fig. 12; see also Fitzpatrick 1980), with several genera in the

TYRANNINAE

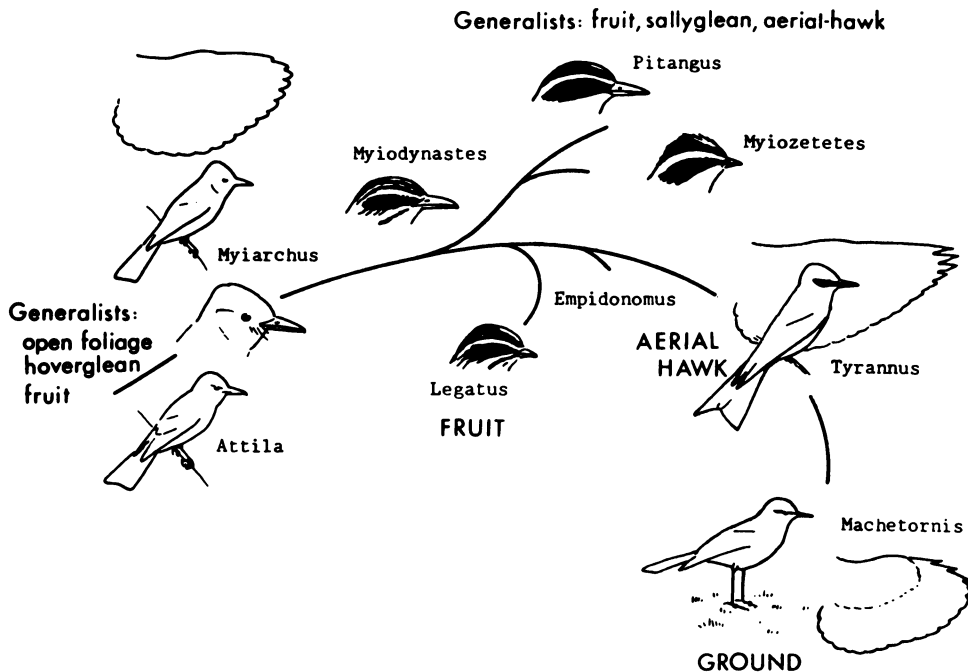


FIG. 13. The major pathways of specialization in the subfamily Tyranninae, following the phylogenetic groupings of Traylor (1977). Schematic format as in Figure 11.

Fluvicolinae and one (*Myiodynastes*) in the Tyranninae. In the transition from generalized hover-gleaning intermediates to upward-strikers a wide bill and short wings become favored as upward hover-gleaners increasingly rely on explosive sallies toward leaf undersides (Fig. 9). Sherry (1982) suggested that marked specialization in diet accompanies such a morphological shift, because the shift permits increased ability to capture fast-moving prey through surprise attack. A clear, present-day intermediate genus is *Phylloscartes* (the bristle-tyrants), an assemblage that displays considerable variation in foraging styles. Most are narrow-billed upward hover-gleaners, but a few are wider billed and use the upward-strike as often as the hover-glean.

Adaptive radiation within the huge assemblage of elaeniine upward-strikers has been remarkably conservative. This is perhaps the most stereotyped major group within the family, both in foraging behavior and in morphology. Coexistence of numerous species is accompanied by unusually fine microhabitat segregation (e.g., Slud 1964; Terborgh and Weske 1969) and unusually sharp geographic replacement between closely related species (Fitzpatrick 1976, 1981b). These observations parallel the notion that the upward-strikers are so specialized, with a unique suite of morphological and behavioral peculiarities, that they have been largely unsuccessful at evolving out of their specialty. *Corythopsis*, however, may represent a new macro-evolutionary step in this group, as proposed earlier (Fig. 12).

Besides the distinctive upward-strikers, the Elaeniinae include a homogeneous group of genera that combine the related techniques of perch-gleaning and upward hover-gleaning with varying amounts of frugivory. Small bills, associated with this combination of foraging styles, may restrict their use of aerial-hawking, a technique used regularly only by the relatively wider-billed genera *Sublegatus*, *Suiriri*, and *Elaenia*. Many elaeniine genera specialize in perch-gleaning. The only external modification associated with this speciality is the long, narrow bill (Fig. 1). In *Pseudocolaptes* and *Tachuris* this feature is extreme and is associated with

wren-like gleaning habits in tall reeds and marsh grass. Otherwise, perch-gleaners have rather generalized morphology, hence they may not be as evolutionarily constrained as are other kinds of specialists.

AERIAL-HAWKING

With only one exception known to me, all obligate aerial-hawkers belong to one of two large, independent radiations toward this "typical flycatcher" foraging mode. The exception is *Serpophaga cinerea*, which makes frequent use of aerial-hawking (see Smith 1971 for a discussion of behavior in this and related species). In both the fluvicoline and the tyrannine radiations, potential avenues of change toward aerial specialization from generalized foliage-gleaning are represented fairly closely by present-day, intermediate species.

Certain species that frequently employ aerial-hawking from enclosed perches (*Myiophobus*, *Empidonax*, *Cnemotriccus*, etc.) represent the most generalized members of Traylor's (1977) Fluvicolinae (Fig. 11; Fitzpatrick 1980). They also display early stages in morphological adaptations for aerial-hawking, having only slightly pointed wings. They have bills of medium width, associated with both hawking and upward-striking. This generalized condition could give rise to round-winged, upward-strikers (e.g., *Onychorhynchus*, *Myiobius*; affinities still uncertain), as well as obligate aerial-hawkers.

One group of fluvicolines (*Sayornis*, *Pyrocephalus*, *Knipolegus*, etc.), discussed above, represents a transition toward open country, ground-related foraging. *Colonia* is the most stereotyped aerial-hawker of this group, with long wings and tiny tarsi, reflecting this specialization.

When enclosed-perch-hawkers forage along open edges of vegetation, they shift to almost exclusive use of aerial-hawking (pers. observ.). Closely related to the near-ground-generalists just mentioned are a few genera (e.g., *Mitrephanes*, *Pyrrhomys*) that are habitual aerial-hawkers, restricting their foraging to openings and forest edge microhabitats. Their wings are relatively long and their tarsi short, in accordance with this shift. The most specialized end of this lineage consists primarily of the large genus *Contopus*, with its greatly elongated wings (Fig. 4) and notably short and weak tarsi.

I suggest that the monotypic genus *Hirundinea*, the most strikingly specialized aerial-hawker in the Tyrannidae, is a member of this group. The proportions of this problematic species are indeed extreme. It has the greatest wing-to-tarsus ratio in the entire family (Fig. 10). This should not be surprising, however, because relatively long wings combined with short tarsi characterize virtually all aerial-hawking specialists (Fig. 10). In behavior, habitat, overall plumage pattern, and even in technical aspects of voice (W. J. Smith, pers. comm.), *Hirundinea* is reminiscent of an enlarged *Pyrrhomys*, and its bill shows a similar broad base and pinched tip. In my view, the evidence indicates that *Hirundinea* represents the morphological culmination of this fluvicoline lineage of aerial-hawkers (Fig. 11).

Two groups of genera comprise Traylor's Tyranninae (Fig. 13). One is a homogeneous assemblage of hole-nesting foliage-gleaners (*Myiarchus*, *Sirystes*, *Attila*, *Casiornis*, etc.). Their generalized foraging repertoires are characterized by a predominance of outward hover-gleaning, often for very large prey, along with some frugivory and occasional aerial-hawking. The tendency for these species to perch in the open and survey the upper surfaces of vegetation, their slightly oversized bills, and the relatively long wings required for hover-gleaning, all provide behavioral and body form pre-adaptations for more habitual aerial-hawking.

The genus *Myiodynastes* (also a hole-nester, along with *Conopias*) seemingly links the former group of generalists with the remaining tyrannine genera (Fig. 13; Lanyon 1984). These remaining genera show shortened tarsi, medium to long wings, restriction to open habitats, and an array of foraging habits unparalleled in any other flycatcher group. Many of these generalists use aerial-hawking extensively, and the genus *Tyrannus* has specialized in this mode, marking the endpoint of an adaptive lineage comparable to that of the aerial-hawking fluvicolines. Species of *Tyrannus* have extremely long wings, very short tarsi, and show a gradation in tail forms from deeply notched to long and forked.

One morphological transition in the Tyranninae that is not well illustrated by present-day species is that between *Empidonax* and *Tyrannus* (Fig. 13). The former genus indeed relies heavily upon aerial-hawking technique, but does not bear a close physical resemblance to *Tyrannus*, even though a "species" originally described in the genus *Laphyctes* appears to be a hybrid between *Tyrannus melancholicus* and *Empidonax varius* (Meise 1949).

GENERAL DISCUSSION

It comes as no surprise to evolutionary biologists that the foraging behavior and the external morphology of animals are closely related. Storer (1971) presented an overview of the major evolutionary trends along these lines among birds. With few exceptions, however, examinations of radiation in major avian lineages have been largely descriptive. The anatomic variation usually is described rather thoroughly (e.g., Engels 1940; Lack 1947; Amadon 1950; Beecher 1951; Bowman 1961; Osterhaus 1962; Feduccia 1973), but the behavioral end of the story usually is left unquantified, thereby providing only half the picture. A notable exception is the landmark study of geospizine finches currently underway on the Galapagos Islands (e.g., Abbott et al. 1975, 1977; Boag and Grant 1981). In those investigations the ecological and behavioral variables are being measured and compared quantitatively with the anatomical ones. Only with this procedure can we expect to reveal more than the most superficial patterns by which evolutionary divergence takes place.

I have shown here that a general pattern of morphological adaptation is apparent within a large continental radiation of birds. In the Tyrannidae, body form varies closely with foraging mode, and the two are related through various, *continuous* functions that change gradually across most of their ranges of values. This conforms to the idea that form and function are plastic in the evolutionary sense. The two can be modified together in response to ecological pressures or opportunities.

At certain endpoints of these functions—representing nearly complete (and measurable) specialization in a single behavioral mode—drastic modifications in body form seem to accompany relatively small increments of behavioral change. In this way, physical attributes presumably allow for more effective or efficient performance of the behavioral speciality than a generalized body form would allow. Such modifications, however, may arise at the expense of evolutionary flexibility, principally because behavioral shifts by a specialist toward a more generalized foraging mode probably entail a greater reduction in efficiency than do ones coming from the opposite direction.

The best tyrannid example of possible loss in flexibility may be the upward-strike foraging mode, characterizing the broad-billed elaeniine assemblage. This mode carries with it numerous external specializations (extremely wide bill, short and rounded wing, long and slender tarsus, reduced tail). Presumably, this suite of characters makes possible the odd behavior of “surprise attack” foraging (Sherry 1982). Speciation, however, seems to have occurred largely *within* this mode once it was achieved (discussed above). Ground-foraging may be almost as limiting, for the fluvicoline ground-tyrants show almost the same degree of habitat and geographic subdivision as the elaeniine upward-strikers (Smith and Vuilleumier 1971; Fitzpatrick 1981b). Aerial-hawking also carries with it extreme morphological specialization (long wing, short tarsus, wide and triangular bill), but it can develop toward open country ground-foraging (e.g., the more primitive ground tyrants, and possibly *Machetornis*), especially among species in which the tarsus is sufficiently long to facilitate facultative use of the ground (see Fig. 8).

Directions of behavioral change are not random. In its broadest sense this observation is trivial: a woodpecker cannot begin foraging like a heron without a long, perhaps nearly prohibitive period of evolution through intermediate stages. Even within the narrow range of behavior characterizing insectivorous passerines, however, directions of change follow discrete pathways. Perch-gleaners, for example, can evolve into upward-strikers by passing through a transition stage in which upward hover-gleaning is used (Fig. 9). Sallying foliage-gleaners can become aerial-hawkers through the intermediate stage of facultative enclosed-perch hawking, a stage that favors morphological changes presumably rendering perch-gleaning and hover-gleaning more difficult. True specialists in upward-striking, ground-foraging, and even aerial-hawking may have more limited potential for changing back toward generalization, compared to the potential that generalists have for becoming specialized.

These directions of radiation, and presumably the extent to which the pathways become expressed within a given taxonomic group, depend largely upon three variables: (1) opportunities for repeated speciation and secondary contact, giving rise to ecological interactions that cause related species to diverge in behavior and morphology; (2) the degree to which competition, from outside the group and within it, restricts or directs this divergence; (3) the extent to which morphology itself constrains behavioral divergence.

In the case of the Tyrannidae, climatic and orogenic events during the Pliocene and Pleistocene of South America appear to have provided massive opportunity for repeated frag-

mentation, differentiation, and dispersal of species (Vanzolini and Williams 1970; Haffer 1974). A paucity of passerine groups on that long-isolated continent permitted the few non-oscine groups to evolve in an environment relatively free of competitors (Keast 1972). As lineages produced species that evolved toward increasing specialization, it appears today as if certain forms "settled" at intermediate stages—perhaps thereby forcing other forms to specialize further. In turn, of course, the specialists may have competitively prohibited other species or lineages from converging upon their specialities. These radiating pathways thereby might be remarkably well preserved by modern-day forms which persisted at various stages along the continua. In this view, groups like the flycatchers present us with an unusually complete picture of the pathways themselves.

Precisely how close together along pathways of adaptive radiation can related species persist? The interplay between this question and that of competition forms an important, unsolved ecological and biogeographic problem. As a group radiates, continued competition from less specialized forms (which also can proliferate through time) may reinforce any canalizing effects of morphological specialization. The persistence of intermediate species, more effective over a wider range of behavior, may itself prohibit the specialists from giving rise to species that return toward more generalized behavior and body form. The relative strengths of the morphological versus these historical and ecological constraints remain a matter of conjecture in need of further study.

I must emphasize in conclusion that the scenario just painted—the notion that the Tyrannidae contains "preserved phylogenetic lineages"—is a hypothetical one, perhaps unduly speculative. Ecological and morphological intermediacy, even among close relatives, does not necessarily imply genetic and phylogenetic intermediacy. Necessary tests for the evolutionary models and pathways discussed in the preceding section require sound phylogenetic reconstructions both within and among the various monophyletic lineages of flycatchers. Such reconstructions using various, independent characters are being developed at present. Comparisons between detailed phylogenetic reconstructions and the relationships between form and foraging behavior discussed in this paper will constitute the next major step in evaluating the adaptive radiation of flycatchers.

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