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HOW CONVERGENT IS THE AMERICAN REDSTART (*SETOPHAGA RUTICILLA*, PARULINAE) WITH FLYCATCHERS (TYRANNIDAE) IN MORPHOLOGY AND FEEDING BEHAVIOR?

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ABSTRACT.—Possible convergence between the unique aerial-feeding American Redstart (*Setophaga ruticilla*) and the tyrannid flycatchers was considered using skeleton, external morphology, substrate use, and locomotory feeding movements. The redstart is a typical paruline in the broader functional units of forelimb, hindlimb, and body axis, as well as in proportionate lengths of the main axial elements of both the forelimb and hindlimb. It retains and utilizes the advantageous features of the wood-warblers, including the capacity to hop rapidly through the vegetation. To this it has added the long and broad bill, and long rictal bristes (adaptations for aerial feeding) of the tyrannids. The wing shape remains wood-warblerlike, but it is convergent with the flycatchers in its low wing loading. The tail is long, as in the flycatchers, for better aerial control, but is spread and, apparently, used to flush insects from vegetation, as in the specialized Australo-Papuan fantails (*Rhipidura*). The redstart is a unique adaptive and ecomorphological type among north American passerines. *Received 30 March 1993, accepted 19 August 1993.*

ALTHOUGH CONVERGENT EVOLUTION is very widespread in natural systems surprisingly few attempts have been made to analyze cases in a quantitative framework. It is widely recognized that convergence is always restricted to a subset of structures or features, but it is of inherent interest to determine which structures are, and which are not, modified in response to changed demands, and just how far the changes go in the way of replicating the model.

In this paper a much quoted case of morphological and ecological convergence, that of the American Redstart (*Setophaga ruticilla*) with the tyrannid flycatchers (Sherry 1979, Bennett 1980), is explored. The redstart is the only member of the North American wood-warblers (Parulinae, Emberizidae) to be a true aerial feeder. Similarity in role and habitat use patterns with the small Least Flycatcher (*Empidonax minimus*), with which it commonly cooccurs in northeastern forests, is suggested by the marked interspecific aggression with the frequent spatial displacement of redstarts by the Least Flycatcher (Sherry 1979, Sherry and Holmes 1988).

We utilize newer methods to examine the postulated convergence between the American Redstart and North American tyrannids using internal skeleton, superficial morphology, substrate-use patterns, and locomotory feeding movements. The redstart is compared morphologically and ecologically to four other species of wood-warblers and five tyrannids with which it cooccurs in northern forests. The species were chosen both on the basis of cooccurrence and because good skeletal material was available.

METHODS

The wood-warbler species used in the study and their mean body masses (Dunning 1984) were: American Redstart, 8.1 g; Black-throated Green Warbler (*Dendroica virens*), 8.8 g; Yellow Warbler (*D. petechia*), 9.5 g; and Yellow-rumped Warbler (*D. coronata*), 12.5 g. The flycatchers (Tyrannidae) were: Least Flycatcher, 10.3 g; Great Crested Flycatcher (*Myianchus crinitus*), 33.5 g; Eastern Wood-Pewee (*Contopus virens*), 14.1 g; Eastern Phoebe (*Savornis phoebe*), 19.8 g; and Eastern Kingbird (*Tyrannus tyrannus*), 39.5 g. Thus, the flycatchers studied are significantly larger than the wood-warblers.

Morphology.—Morphological material consisted of 10 (generally unsexed) skeletons, and 15 male and 15 female museum skins of each of the 10 species. An independent data set on wing loading, aspect ratios, and associated body masses was obtained from live birds mist netted on northward migration at Prince Edward Point, Ontario, during May of 1988 and 1989. Skeletons were measured using procedures outlined by current workers in the field (Norberg 1979, Leisler and Thaler 1982, Leisler and Winkler 1985). Segments of the appendicular skeleton were measured between articulating surfaces. Lengths of the vertebral column were measured from the leading edge of the first centrum to the back (hind edge) of the last one, with the series being pressed tightly together (Hildebrand 1952). Footspan was measured as indicated by Norberg (1979:fig. 1). Lengths of individual flight feathers, that cumulatively determine wing shape, and lengths of rectrices were taken from the point at which each emerged from the skin to its tip by inserting fine calipers to the base. Standard museum techniques were followed in the measuring of skins. Bill length (maximum) is the distance from the bill-skull junction to the tip. Shape of bill measurements (length, width, depth) were taken at the back of the nostril.

The morphological data were assembled and considered in terms of adaptive complexes or functional units (Oxnard 1975, Leisler and Winkler 1985). These involved the following morphological variables: (A) *bill shape* (museum skins), bill length from back of nares to tip, and bill width and depth at back of nares; (B) *wing axis* (skeletal), lengths of humerus, ulna, carpometacarpus, phalanx 1, and phalanx 1 plus 2; (C) *flight features* (museum skins), primaries 9 to 4, secondaries 1 and 2, and outermost and innermost rectrices; (D) *body long axis* (skeletal), vertebral column (fused thoracic, lumbar, and sacral vertebrae), cervical vertebrae (total), skull length without bill, and bill length from tip to fronto-nasal hinge; (E) *leg axis* (skeletal), femur, tibiotarsus, tarsometatarsus, and midtoe (digit 3) without claw; and (F) *leg and foot dimensions* (museum skins), tarsometatarsus, midtoe, midclaw, hindtoe (hallux), footspan without claws, and footspan with claws.

The morphological data were analyzed using principal components analysis (PCA) to resolve differences between species, supplementing absolute measurements. Because many of the tyrannids were larger-bodied, the effect of size had to be removed for the PCAs. Mass data was not available for the individual skeleton and museum skins. Hence, all individual measurements were related to the cube root of the average body mass for each species, obtained from live birds netted during northward migration at Prince Edward Point, Ontario in May.

Principal components analyses were used to find the positions of individuals in morphological space, defined by "n" measurements within each of the six groups of morphologic variables defined above. All PCAs were based on the covariance matrices of the log-transformed variables. Results presented for the analyses are correlations (loadings) of morphological variables with orthogonally rotated multivariate factors (varimax rotations of the principal components) using Maclntosh Stat-View Se and Graphics (ver. 1.02, Abacus Concepts 1991).

Positions (factor scores) of individuals were ranked and the mean rank of each species calculated for any factor that showed significant among-species differences (Kruskal-Wallis test). This was to test whether any multivariate morphological measures separate the wood-warblers from the flycatchers, and where the American Redstart falls in ordination of the species along these axis. Mann-Whitney *U*-tests were used to test mean factor scores for differences between the wood-warblers and flycatchers as groups. Significance was determined at the 0.05 level.

For analysis of wing morphology (wingspan, wing width (chord), wing shape and area, aspect ratio, and wing loading), the methods and formulae of Pennycuick (1989), Norberg and Norberg (1988), and Norberg (1990) were used. The right wing of each (live) bird was flattened and extended at right angles and its outline traced on millimeter graph paper (see diagram in Pennycuick 1969). Wing areas were determined in square millimeters from the tracings using a MOP-3 Digital Image Analyzer. These data, individual and mean species indices of wing shape, aspect ratio and wing loading were calculated (see formula in papers listed above). Aspect ratio was defined as the ratio of length to maximum width of the wing. We calculated wing loading as Mg/S (Newtons/m^2), where M was mass of the bird (kg), g was acceleration due to gravity (9.81 m/s^2), and S was the area of both wings (m^2). Note that S does not include intermediate body area or tail area, which may also afford lift. Wing loadings were scaled to size of the birds by dividing by the cube root of the birds' mass (relative wing loading; see Norberg and Norberg, 1988, Pennycuick 1969, Norberg 1990).

For determining proportionate differences in lengths of major structure, the way in which many major adaptive differences are expressed, series of ratios were calculated. Comparisons were made relative to: (1) the fused vertebral column (fused thoracic, lumbar and sacral vertebrae); and (2) the tarsus. The former is regarded here as a "conservative" structure relative to which the adaptive distal components of the skeleton change. The latter is used, as needed, as an additional basis of comparison (e.g. as a measure of changes in external features like the wing). Of all univariate measures, tarsus is the best indicator of overall body size, although only within species (Rising and Somers 1989). Mann-Whitney *U*-tests were used to compare the wood-warblers and flycatchers (as groups) for significant differences (95% confidence level).

Foraging.—Foraging behavior on the species was obtained between May and August of 1988 and 1989 at Lake Opinicon and Prince Edward Point, Ontario. The methods used were slightly modified versions of those used by other investigators (Robinson and Holmes 1982, Holmes and Recher 1986, Petit et al. 1990). This involved developing data on (a) substrate used (foliage, branches, low shrubs, etc.), (b) foraging methods (sallying, feeding within substrate, hanging from substrate, or fluttering at [snatching] substrate), and (c) locomotory feeding movements (e.g. hop/flight ratios, flight distances, and angles of attack while feeding). Only foraging sequences of 20 or more were incorporated (as per Robinson and Holmes 1982). Data were gathered from no more than two individuals at

TABLE 1. Basic morphological measurements (lengths, mm) and masses (g) for selected tyrannid flycatchers and parulid wood-warblers, including the American Redstart. First six measurements on 15 male and 15 female museum specimens, and next four on 10 unsexed skeletons. Mass based on 10 to 20 live birds (both sexes) captured in mist nets, May 1989 and 1990.

Structure	Eastern Wood-Pewee	Least Flycatcher	Eastern Phoebe	Great Crested Flycatcher	Eastern Kingbird	Yellow Warbler	Yellow-rumped Warbler	Black-throated Green Warbler	American Redstart
Bill	11.4 ± 0.4	8.9 ± 0.3	12.6 ± 0.4	17.1 ± 0.9	14.9 ± 0.6	8.8 ± 0.3	9.0 ± 0.5	7.8 ± 0.2	8.4 ± 0.2
Wing	81.0 ± 3.6	62.9 ± 2.8	85.7 ± 3.0	101.7 ± 3.1	115.3 ± 4.2	61.8 ± 2.7	72.2 ± 2.6	61.9 ± 1.7	61.2 ± 2.1
Tail	63.2 ± 3.2	54.5 ± 2.2	69.8 ± 2.1	87.9 ± 3.0	83.4 ± 4.2	42.9 ± 2.0	53.3 ± 1.2	46.0 ± 1.5	54.0 ± 1.5
Tarsus	11.8 ± 0.5	14.6 ± 0.5	16.5 ± 0.5	19.2 ± 0.7	16.9 ± 0.6	17.2 ± 0.5	16.8 ± 0.7	15.3 ± 0.4	15.6 ± 0.5
Hind toe	9.3 ± 0.5	9.5 ± 0.6	11.6 ± 0.7	13.1 ± 0.7	13.1 ± 0.6	10.8 ± 0.6	10.3 ± 0.6	8.4 ± 0.4	9.2 ± 0.4
Rictal bristle	7.5 ± 1.2	7.8 ± 1.3	9.3 ± 0.8	8.9 ± 0.6	6.7 ± 1.1	3.6 ± 1.1	3.6 ± 0.9	4.2 ± 0.8	6.7 ± 0.5
Skull total	33.3 ± 0.9	29.1 ± 0.9	35.1 ± 2.1	44.6 ± 1.4	40.1 ± 1.2	27.8 ± 0.7	27.6 ± 0.9	27.0 ± 0.5	26.9 ± 0.8
Vertebrae	25.6 ± 0.5	20.7 ± 1.2	28.2 ± 2.0	34.7 ± 0.9	38.6 ± 0.6	24.0 ± 0.6	23.3 ± 1.2	21.6 ± 0.3	21.4 ± 0.5
Forelimb	59.9 ± 1.0	48.2 ± 1.6	63.2 ± 4.1	80.0 ± 2.5	83.7 ± 1.9	43.5 ± 5.1	50.4 ± 2.6	43.4 ± 0.9	42.9 ± 0.8
Hindlimb	53.2 ± 0.8	55.8 ± 1.2	63.7 ± 5.5	81.2 ± 1.2	81.6 ± 2.2	66.9 ± 2.7	64.5 ± 12.1	58.8 ± 12.5	62.4 ± 0.7
Mass	14.7 ± 0.8	10.3 ± 0.9	20.4 ± 0.8	33.9 ± 2.0	38.2 ± 2.9	9.7 ± 0.6	13.6 ± 1.2	8.7 ± 0.6	8.1 ± 0.7

any one place or time, and were collected through the season during both morning and evening feeding bouts, and over a two-year period. The feeding studies were carried out in semimature broad leaf deciduous forest with areas of edge.

Differences in distribution of angles and distances of foraging flights and distribution of foraging tactics used, between the redstart and other species, were determined using contingency-table analyses (chi-square). Four categories of flight angles were used in the analysis; we combined the two downward components because of the small numbers in these two categories. Differences between the redstart and the other species in hop, flight, and prey-attack rates were determined (Zar 1984) by small-sample, two-tailed t-tests (with critical value $P < 0.05$) modified for unequal variances when necessary.

Mean factor scores for species, based on the six morphological PCAs, were correlated with foraging behaviors to investigate whether any divergence in morphology among these species is associated with the observed foraging differences. The specific objective was to compare quantitatively the foraging behavior of the redstart to that of the other wood-warblers and the five tyrannid species, and to determine if, and to what extent, its feeding ecology and body morphology depart from those characteristic of the former in favor of those of the latter.

RESULTS

Table 1 provides data on external features, interior skeletons (lengths of fused vertebrae, total forelimb length, etc.), and body masses.

MORPHOLOGICAL COMPARISON OF FUNCTIONAL UNITS

(A) Bill shape (museum skins).—The wood-warblers and flycatchers separate significantly into two groups along factor 1 (U-test, $U_{39,50} = 1{,}868.0$, $P < 0.001$), which accounts for 55.4% of total variance and loads strongly for bill length. There is no overlap between the two groups, except that the redstart falls mostly within the flycatcher cluster (Fig. 1A). This positioning is reflected in the mean ranks of factor scores, which for the wood-warblers ranged from 7.4 through 30.2. The redstart, with a mean rank of 38.5, lies closer to the flycatcher assemblage (ranks 43.0 to 82.1). Factor 2, loading strongly for bill depth and width, accounts for 44.6% of total variance (Table 2A). Again, the groups separate out significantly along this axis ($U_{39,50} = 1{,}333.0$, $P = 0.007$); however, the separation is not distinct

(Fig. 1A). This overlap is reflected in the species mean ranks which range from 13.0 to 63.0 for the wood-warblers (redstart, 41.9) and from 12.1 to 80.6 for the flycatchers.

(B) Wing axis (skeletal).—Along factor 1, which accounts for 68.0% of the total variance and loads strongly for the humerus, ulna and carpometacarpus, the wood-warblers and flycatchers separate into two clusters (Fig. 1B, Table 2B; $U_{39,50} = 640.0$, $P < 0.001$). The species' mean ranks of 11.2 to 26.0 for the wood-warblers and 27.7 to 47.2 for the flycatchers reflect this separation. The redstart, with a mean rank of 11.5, is a typical wood-warbler. Factor 2 accounts for 32.0%, and loads strongly and positively for phalanx 1 (Table 2B). The wood-warblers and flycatchers are not statistically distinct ($U_{28,23} = 424.0$, $P = 0.106$), the wood-warblers falling in the middle of the flycatcher assemblage. The redstart are in the middle of the wood-warblers (Fig. 1B). Again, it is not aberrant.

(C) Flight features (museum skins).—Factor 1 loads strongly for secondaries 1 and 2, and primary 4, and accounts for 44.3% of total variance (Table 2C). The wood-warblers and flycatchers separate out significantly as groups ($U_{29,42} = 802$, $P = 0.024$); however, the wood-warblers, including the American Redstart, are positioned within the flycatcher assemblage (Fig. 1C). The narrow range of ranks, from 22.3 through 36.1, for the wood-warblers (redstart, 36.1), and the wider range of 10.8 through 66.5 for the flycatchers perhaps accounts for the significant difference. The two families are not statistically distinct along factor 2 ($U_{29,42} = 728.0$, $P = 0.164$), which accounts for 28.4% of the total variance and loads strongly for outer primaries 8 and 9. This is reflected in the considerable overlap of species mean factor scores and, hence, ranks between the two groups. The redstart with its long, pointed wing is a typical wood-warbler. The two groups do separate out significantly along factor 3 ($U_{29,42} = 932.0$, $P < 0.001$; Fig. 1C). This factor accounts for 27.4% of total variance and loads strongly for the innermost and outermost rectrices. Mean ranks of factor scores indicate that the redstart (rank 59.0) resembles the flycatchers (ranks 28.4 to 57.3), more closely than the remaining wood-warblers (3.5 to 15.7).

(D) Body long axis (skeletal).—Factor 1, accounting for 57.1% of total variance, loads strongly for bill and skull lengths (Table 2D). The two groups separate significantly along this axis ($U_{34,36} = 994.0$, $P < 0.001$; Fig. 1D). Rankings of the wood-warblers were from 7.4 to 30.7 for the Yellow-rumped, Yellow, and Black-throated Green Warblers, and 44.9 for the American Redstart. Thus, the redstart lies at the upper end of the wood-warbler assemblage, nearer the fly-

TABLE 2. Correlations of morphological variables with orthogonally rotated multivariate factors (F), for tyrannid flycatchers and parulid wood-warblers, including the American Redstart. Morphological groups: (A) bill shape; (B) wing axis; (C) flight features; (D) body long axis; (E) leg axis; and (F) leg and foot.

	Correlation with		
Variable	F1	F2	F3
(A) Bill shape (skins)			
Bill length	0.926	0.274	
Bill width	0.751	0.536	
Bill depth	0.331	0.932	
Percent explained	55.4	44.6	
(B) Wing axis (skeletal)			
Humerus length	0.926	0.053	
Ulna length	0.954	0.132	
Carpometacarpus length	0.862	0.371	
Phalanx 1 (of major digit)	0.106	0.970	
Phalanx 1 + 2	0.688	0.558	
Percent explained	68.0	32.0	
(C) Flight features (skins)			
Primary 9	−0.220	0.895	0.237
Primary 8	0.326	0.880	0.201
Primary 7	0.480	0.736	0.382
Primary 6	0.590	0.572	0.462
Primary 5	0.804	0.535	0.362
Primary 4	0.888	0.210	0.216
Secondary 1	0.935	0.028	0.259
Secondary 2	0.903	0.011	0.281
Outermost rectrix	0.380	0.057	0.915
Innermost rectrix	0.261	0.069	0.949
Percent explained	44.3	28.4	27.4
(D) Body long axis (skeletal)			
Bill length	0.902	0.016	
Skull length	0.913	0.315	
Cervical vertebrae	0.403	0.721	
Thoracic, lumbar and sacral vertebrae	−0.010	0.861	
Percent explained	57.1	42.9	
(E) Leg axis (skeletal)			
Femur length	0.947	−0.044	
Tibiotarsus length	0.978	−0.163	
Tarsometatarsus length	0.933	0.303	
Midtoe (digit 3) length	0.779	0.622	
Percent explained	86.8	13.2	
(F) Leg and foot dimensions (skins)			
Tarsometatarsus length	0.789	−0.008	−0.618
Midtoe (digit 3) length	0.834	0.159	−0.067
Midtoe claw length	0.255	−0.114	0.811
Hindtoe (hallux) length	0.924	−0.033	−0.012
Hindtoe claw length	0.680	0.239	−0.118
Foot span	0.864	−0.307	0.192
Foot span with claw	0.035	0.839	−0.153
Percent explained	57.5	20.1	22.4

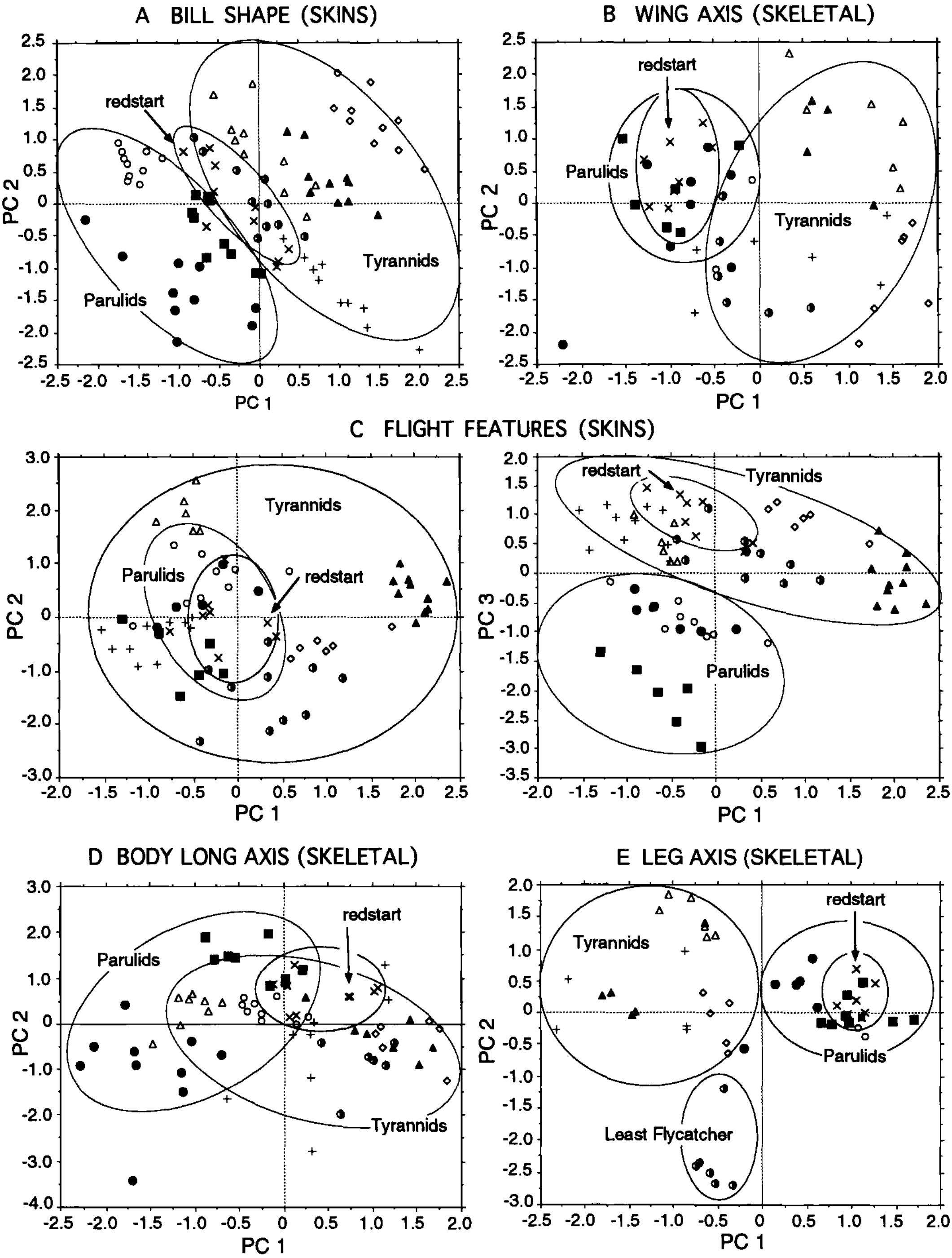

Fig. 1. Plots of factors (PCs) resulting from principal components analyses comparing American Redstart to tyrannid flycatchers and parulid wood-warblers for: (A) bill shape (skins); (B) wing axis (skeletal); (C) flight features (skins); (D) body long axis (skeletal); (E) leg axis (skeletal); and (F) leg and foot (skins).

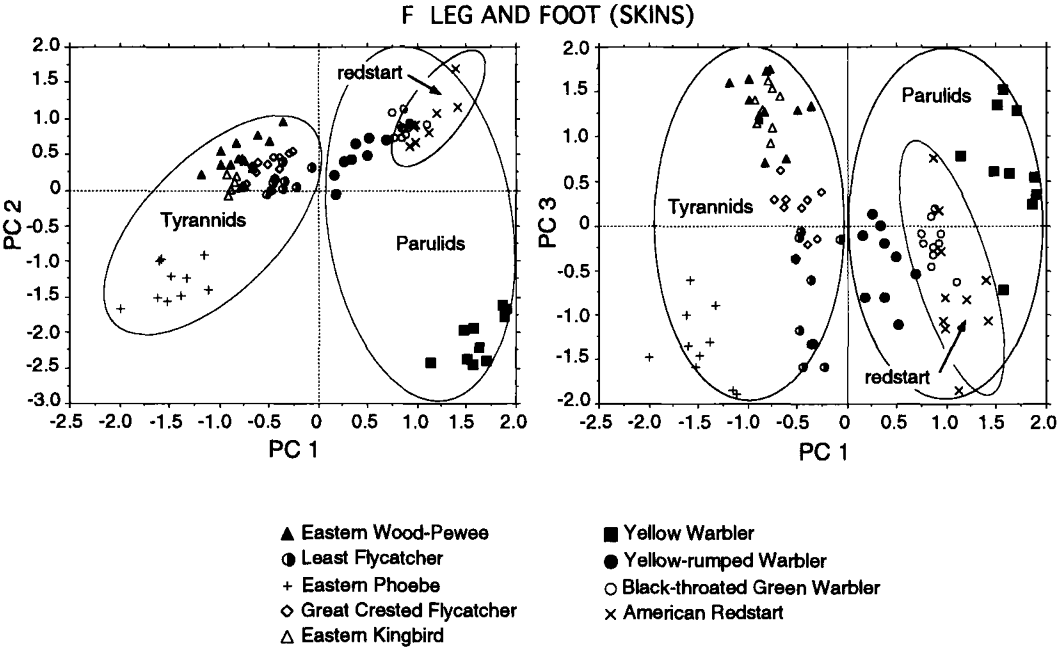

Fig. 1. Continued.

catchers, which ranked from 46.4 through 65.2. Factor 2 accounts for 42.9% of variance and loads strongly for the vertebral column (thoracic plus lumbar plus sacral vertebrae) and cervical vertebrae (Table 2D). The two groups separate significantly ($U_{34,36}$ = 937, P = 0.001), despite an overlap in positions of the Yellow-rumped Warbler and the Least Flycatcher, as shown in the plot of factor scores (Fig. 1D) and in the species mean ranks. These are from 15.3 to 67.0 for the wood-warblers and 14.2 to 43.6 for the flycatchers. The redstart has a rank of 55.0

(E) Leg axis (skeletal).—Factor 1 accounts for 86.8% of the variance, and loads most strongly for the femur, tibiotarsus and tarsometatarsus (Table 2E). The two groups separate significantly along this axis ($U_{27,26}$ = 702.0, $P < 0.001$), with the redstart falling in the middle of the wood-warbler assemblage and no overlap between the two groups (Fig. 1E), as indicated by the ranks, which ranged from 30.5 to 44.8 for the wood-warblers (redstart, 43.8) and 4.5 through 22.0 for the flycatchers. The two groups do not separate significantly along factor 2 ($U_{27,26}$ = 353.0, P = 0.972), which accounts for 13.2% of variance and loads most strongly for the midtoe (Table 2E). Rather, the wood-warblers are placed among the flycatchers. However, the wood-warblers are tightly clustered (ranks 16.3 to 33.7), with the redstart again in the middle of the wood-warbler assemblage (rank 30.5). The flycatchers are less tightly clustered, with ranks ranging from 3.5 to 50.0. The Least Flycatcher, with rank 3.5, stands apart from the other flycatchers (Fig. 1E).

(F) Leg and foot dimensions (museum skins).—Factor 1 accounts for 57.7% of total variance; loads most strongly for hindtoe, with other high loadings for midtoe, tarsus, and footspan (Table 2F). The two groups separate significantly ($U_{39,50}$ = 1950.0, $P < 0.001$) with no overlap (Fig. 1F). The range of wood-warbler ranks is from 55.0 to 84.2, and that of the flycatchers from 5.7 to 41.4. The redstart (rank 73.5) is a typical wood-warbler in leg and foot structure. Factor 2, loading strongly for footspan with claw, accounts for 20.1% of the variance (Table 2F). Along axis 2, the two families separate significantly ($U_{39,50}$ = 1,330.0, P = 0.003), as evidenced by the species mean ranks for the wood-warblers (Yellow-rumped Warbler, 54.7; Black-throated Green Warbler, 78.1) and the flycatchers (15.4 to 58.7). The Yellow Warbler, however, stands apart from the other wood-warblers with a rank of 5.6. Again, the redstart (rank 78.1) falls within the wood-warbler assemblage. Factor 3, loading

TABLE 3. Means and ranges for ratios of lengths (percents) of bill and associated structures for selected tyrannid flycatchers and parulid wood-warblers, including the American Redstart.

Structure	Eastern Wood-Pewee	Least Flycatcher	Eastern Phoebe	Great Crested Flycatcher
Bill length/skull length[a]	51.5 (47.1–55.1)	46.5 (44.4–48.5)	50.6 (47.1–55.1)	54.4 (51.9–57.3)
Bill length/tarsus length[b]	140.7 (132.0–150.4)	91.2 (86.3–96.0)	109.8 (101.1–115.8)	117.8 (110.2–124.2)
Vertebrae cervical/fused[a]	124.2 (116.0–129.8)	137.1 (128.3–150.2)	121.7 (116.0–129.8)	117.8 (114.7–120.9)
Bill width/length[b]	66.6 (61.8–70.4)	71.6 (65.9–77.0)	54.9 (51.5–62.9)	59.8 (55.3–63.7)
Bill depth/width[b]	60.1 (56.2–65.3)	59.5 (53.7–65.1)	62.4 (51.3–70.1)	68.2 (62.9–72.5)
Rictal bristle/bill width[b]	76.9 (58.1–100.0)	92.7 (63.1–111.0)	102.7 (74.8–119.2)	73.5 (72.6–74.4)

[a] Based on measurements of 10 unsexed skeletons.
[b] Based on measurements of 15 male and 15 female museum specimens.

strongly for midtoe with claw, accounts for 22.4% of the total variance (Table 2F); the two groups do not separate significantly relative to this factor ($U_{39,50}$ = 1,128.0, $P = 0.206$). There is considerable overlap between the wood-warblers (ranks 29.2 to 63.2) and the flycatchers (ranks 10.8 to 76.6).

DIFFERENCES IN PROPORTIONS OF MAJOR STRUCTURES

(G) Bill and associated feeding structures.—That the bill of the flycatchers is proportionately longer than in the wood-warblers is confirmed both when it is expressed as a ratio with total skull length or tarsus length (Table 3). The ratios confirm that the redstart has the longest, broadest, and shallowest bill of the wood-warblers. Note, however, that the Eastern Phoebe and Great Crested Flycatcher have relatively narrow bills. The redstart also is convergent with the flycatchers in rictal bristle length, with a ratio to bill width of 95.5%, which is well within the range of the flycatchers (Table 3). In relative neck length (cervicals/fused column) the wood-warblers and flycatchers show no clear-cut separation. The redstart, however, has relatively the longest neck among the wood-warblers, and the Least Flycatcher among the flycatchers.

(H) Proportional differences in forelimb and its segments.—Since in flycatchers the wing is used for feeding, it should be skeletally different from that of the wood-warblers; if the redstart is convergent with the former, its wing should be proportionately similar. The ratio of summed skeletal components to that of the fused vertebrae (Table 4) ranges from 217.1 to 233.7 in the flycatchers, and from 181.1 to 216.5 in the wood-warblers (redstart, 200.9). Thus, the former, on average, have a longer wing ($U_{50,40}$ = 73.5, $P < 0.001$). Where, within the wing, is this difference manifested? The wood-warblers as a group have a slightly longer humerus and carpometacarpus. The flycatchers, however, have

TABLE 4. Means and ranges for ratios of lengths (percents) of forelimb and flight structures for selected tyrannid flycatchers and parulid wood-warblers, including the American Redstart.

Structure	Eastern Wood-Pewee	Least Flycatcher	Eastern Phoebe	Great Crested Flycatcher
Forelimb total/vertebrae fused[a]	233.7 (226.2–242.2)	233.7 (216.2–268.6)	224.1 (213.0–242.5)	231.0 (223.6–235.5)
Wing/tarsus[b]	696.6 (648.9–741.4)	431.5 (409.1–447.4)	520.5 (482.8–546.0)	530.5 (492.6–563.2)
Tail/tarsus[b]	543.2 (500.0–591.3)	365.9 (344.2–381.6)	418.8 (396.6–434.5)	461.4 (425.1–481.3)
Humerus/forelimb total[a]	28.2 (27.7–28.9)	29.5 (28.3–30.5)	28.8 (28.0–29.3)	30.1 (29.8–30.6)
Ulna/forelimb total[a]	41 (40.4–41.7)	40.9 (40.0–41.5)	41.4 (41.2–41.7)	40.6 (40.4–41.0)
Carpometatarsus/forelimb[a]	21.1 (19.7–21.7)	19.9 (18.8–21.2)	20.6 (19.6–21.3)	20.6 (20.0–21.0)
Phalange 1/forelimb[a]	9.7 (9.0–10.3)	9.7 (8.9–10.3)	9.1 (8.6–9.8)	8.7 (8.4–8.9)
Aspect ratio[c]	1.94 ± 0.08	1.73 ± 0.06	1.76 ± 1.82	1.81 ± 0.06
Wing loading[c]	57.7 ± 2.58	74.0 ± 5.82	63.1 ± 65.0.	59.4 ± 2.56

[a] Based on measurements of 10 unsexed skeletons.
[b] Based on measurements of 15 male and 15 female museum specimens.
[c] $\bar{x}$ ± SD.

TABLE 3. Extended.

Eastern Kingbird	Yellow Warbler	Yellow-rumped Warbler	Black-throated Green Warbler	American Redstart
49.6 (47.4-53.3)	43.6 (41.9-45.2)	41.9 (39.6-44.9)	42.0 (41.3-43.6)	45.3 (43.2-46.9)
119.8 (112.6-125.0)	76.6 (70.8-82.9)	75.1 (67.6-82.9)	79.0 (75.6-82.9)	80.4 (77.7-83.3)
103.2 (98.9-109.1)	121.2 (114.0-126.1)	123.2 (117.3-129.0)	123.4 (120.3-126.1)	128.8 (123.1-133.2)
63.6 (59.6-66.7)	51.6 (48.4-54.5)	52 (45.1-58.1)	58.6 (55.8-61.8)	63.7 (58.1-69.2)
69.1 (61.2-77.4)	78.1 (70.8-86.7)	75.2 (66.0-84.4)	81.6 (79.2-86.4)	65.7 (61.1-69.1)
49.4 (35.0-67.8)	61.9 (48.3-75.4)	72.7 (45.6-92.1)	69.1 (42.3-90.5)	95.5 (92.3-98.4)

a relatively longer ulna ($U_{38,39} = 38.0, P < 0.001$). The phalanx is proportionately longer in the wood-warblers ($U_{38,38} = 55.0, P < 0.001$; Table 4). The ratio of the folded (feathered) wing to tarsus shows that it is longer in the flycatchers (Table 4).

The functional significance of these differences is unknown. Power needed to oscillate the wing (inertial power) is minimized by having the thick bones and muscles as close to the body as possible (Norberg 1981, Norberg and Rayner 1987). Hence, it might be thought that the flycatchers, that make sudden prey-pursuing leaps into the air, would have shorter humeri. Our data do not support this interpretation.

Calculation of average ratios of individual primaries relative to the longest primary shows the flycatchers to have a more rounded wing. The averages were as follows: for P9/longest, wood-warblers including the redstart (95.6%), redstart (90.3%), and flycatchers (87.1%); for P8/longest, wood-warblers (100.0%), redstart (99.8%), and flycatchers (99.7%); for S1/longest, wood-warblers (79.1%), redstart, (81.0), and flycatchers (82.0%). The data from ratios confirms the findings of the principal components analysis that in all wing skeletal structures the redstart is a typical wood-warbler.

(I) Proportionate length of tail.—The tail/tarsus ratio (Table 4) is significantly longer in the flycatchers ($U_{50,40} = 15.0, P < 0.001$). The redstart, despite having the typical long tarsus of a wood-warbler (next section), has the highest tail/tarsus ratio of the wood-warblers (346.5 compared to 250.4-317.9). This also applies to the tail/wing ratio, with: the range for flycatchers of 72.0 to 87.0; the range for wood-warblers without the redstart of 69.0 to 74.0; and the value of 88.0 for the redstart. The redstart, hence, has a disproportionately long tail.

(J) Proportionate differences within hindlimb complex.—The ratio of total hindlimb skeleton to fused vertebrae is consistently higher in the

TABLE 4. Extended.

Eastern Kingbird	Yellow Warbler	Yellow-rumped Warbler	Black-throated Green Warbler	American Redstart
217.1 (211.2-224.1)	181.1 (129.5-194.3)	216.5 (208.9-225.3)	210.6 (201.5-218.4)	200.9 (196.7-207.9)
694.4 (659.0-717.8)	369.9 (346.6-398.7)	436.3 (395.6-475.0)	411.4 (398.7-433.3)	398.8 (375.8-420.0)
499.9 (468.6-535.7)	250.4 (232.6-278.5)	317.9 (285.7-343.8)	302.4 (284.8-320.0)	346.5 (323.0-373.3)
28.7 (26.4-30.1)	31.9 (29.7-44.6)	29.7 (29.2-30.4)	29.7 (29.4-30.2)	29.6 (29.3-30.2)
40.9 (39.8-42.2)	39.7 (36.5-55.4)	38.9 (38.5-39.2)	39 (38.5-39.5)	38.7 (38.4-39.2)
20.9 (20.4-21.7)	21.1 (20.6-21.6)	21.1 (20.6-21.5)	21.1 (20.3-21.5)	20.9 (20.0-21.5)
9.5 (8.8-10.4)	10.8 (10.4-11.4)	10.4 (9.7-11.0)	10.3 (9.8-11.0)	10.8 (10.5-11.1)
2.04 ± 0.11	1.84 ± 0.09	1.86 ± 0.11	1.78 ± 0.12	1.73 ± 0.09
59.7 ± 4.28	76.5 ± 4.20	71.0 ± 7.08	70.6 ± 4.90	62.8 ± 3.80

TABLE 5. Means and ranges for ratios of lengths (percents) of hindlimb structures for selected tyrannid flycatchers and parulid wood-warblers, including the American Redstart.

Structure	Eastern Wood-Pewee	Least Flycatcher	Eastern Phoebe	Great Crested Flycatcher
Hindlimb total/ vertebrae fused[a]	207.7 (201.7–213.4)	270.0 (254.9–301.5)	225.7 (205.2–252.3)	234.4 (229.9–238.7)
Tarsus/vertebrae fused[a]	51.2 (49.4–53.2)	76.8 (71.6–86.7)	58.2 (50.4–67.2)	59.2 (56.3–60.9)
Hind toe/tarsus[b]	80.4 (75.2–84.4)	65.9 (60.4–70.0)	69.9 (64.8–75.6)	69.2 (64.3–74.2)
Femur/hindlimb total[a]	24.4 (24.1–24.8)	22.1 (21.3–23.0)	22.8 (21.4–24.6)	23.5 (23.2–23.9)
Tibia/hindlimb total[a]	36.1 (35.9–36.5)	38.6 (37.5–39.2)	36.7 (35.3–37.3)	36.6 (36.1–37.0)
Tarsus/hindlimb total[a]	24.6 (24.1–25.0)	28.5 (27.5–29.2)	25.7 (24.6–26.6)	25.3 (24.5–25.9)
Midtoe/hindlimb total[a]	14.9 (14.6–15.3)	10.9 (10.2–13.0)	14.8 (13.9–17.2)	14.6 (13.7–15.6)

[a] Based on measurements of 10 unsexed skeletons.
[b] Based on measurements of 15 male and 15 female museum specimens.

wood-warblers, which use their legs for hopping (Table 5). The ratio of tarsus to fused vertebrae shows the difference to be largely accommodated in this terminal element. Based on percentages, the femur and tibia are little different in the two groups, while the tarsus is longer in the wood-warblers (with the exception of the Least Flycatcher) and the midtoe shorter. These presumably are adaptations for hopping. The long hindtoe of the flycatchers can be linked to the use of exposed lookout perches. In all hindlimb skeletal features, the redstart is a typical wood-warbler.

WING LOADING AND ASPECT RATIO

Relative wing loading (Table 4) is lower in the aerial feeding flycatchers than the wood-warblers. In this feature, the redstart lines up with the flycatchers, and the Least Flycatcher with the wood-warblers. Wing aspect ratios are similar in the flycatchers and wood-warblers. There are consistent differences in wing shape. In the flycatchers, as noted, primary 9 is relatively shorter than in the wood-warblers. Hence, the flycatchers have a slightly more rounded wing tip. Tropical resident wood-warblers have more rounded wings than the Nearctic long-distance migrants (Keast 1980: Fig. 12).

COMPARISON OF FORAGING ECOLOGY

The contrasting ways of life of wood-warblers and flycatchers are documented in Figure 2. The typical wood-warblers feed mainly by gleaning from the foliage, and the flycatchers by taking prey in the air or snatching it from the foliage. The two groups, thus, separate almost completely in feeding behavior and use of foraging substrates. Within the groups there were minor species differences in foraging behavior and substrate use.

The redstarts obtained 40% of prey from the air, 40% by gleaning from the foliage, and 20% by snatching prey from the foliage (Fig. 2). Thus, they were intermediate between the two groups.

Feeding in the wood-warblers was largely by hopping; the flycatchers seldom if ever hopped (Fig. 3). Hop/flight ratios accordingly are much higher in the former. However, the wood-warblers, while mostly gleaning from the foliage, also made many short flights, so that flights per minute were not very different from the value recorded for the flycatchers. The redstart made many flights, particularly in July when it did proportionately more aerial feeding. Prey attack rates were twice as high in the wood-warblers that, presumably, took smaller prey items most of the time. Comparisons between the redstart and each of the other species in proportionate use of these foraging tactics showed the redstart to be significantly different from all others (chi-square test, $P < 0.001$ for all tests).

Flight distances in feeding were considerably longer in the larger-bodied flycatchers (Fig. 4). However, the small Least Flycatcher and the redstart used a wide range of flight distances. The redstart mixed a high proportion of short flights with long ones; in this feature it is significantly different from all other eight species (chi-square test, $P < 0.001$).

Flight angles during foraging (Fig. 4) show a preponderance of horizontal flights, with angled upward flights (commonly to snatch prey either in air or from foliage) being the second most common. In foraging angles, the flycatchers and wood-warblers (including the redstart)

TABLE 5. Extended.

Eastern Kingbird	Yellow Warbler	Yellow-rumped Warbler	Black-throated Green Warbler	American Redstart
211.4 (200.5–218.8)	278.7 (268.0–292.9)	277.4 (131.9–315.4)	272.8 (135.1–307.3)	292.1 (280.4–300.6)
47.8 (45.2–50.6)	74.6 (69.8–79.4)	77.4 (74.8–85.8)	83.3 (78.9–88.9)	79.1 (74.3–83.0)
78.1 (74.1–84.7)	62.9 (57.3–69.8)	61.9 (57.5–66.7)	56.4 (53.6–61.3)	59.3 (54.1–66.7)
23.1 (22.6–23.8)	20.3 (19.9–20.8)	22.6 (19.8–43.2)	22.3 (19.3–41.6)	20.2 (19.9–20.8)
36.4 (35.7–37.3)	37.4 (36.8–37.8)	37.1 (36.6–38.2)	39.0 (36.0–57.0)	36.7 (35.7–37.4)
22.6 (21.9–23.6)	26.7 (25.9–27.1)	29.5 (25.6–56.8)	32.5 (27.1–58.4)	27.1 (26.1–28.0)
17.9 (17.3–18.9)	15.6 (15.1–16.7)	16.1 (14.2–17.4)	15.4 (15.0–16.0)	16.0 (15.4–17.2)

are similar; in both, the energy-saving horizontal component was dominant.

CORRELATION OF MORPHOLOGY AND FORAGING ECOLOGY

Mean factor scores for species (for each factor of each morphological group) were tested for correlations with foraging data using the Spearman rank correlation coefficient (R) at the 95% confidence level. The first factor of the wing axis, loading strongly for the humerus, ulna, and carpometacarpus, was positively correlated with flight distance during foraging ($R = 0.833$, $P = 0.018$). This factor also was correlated negatively with foliage gleaning ($R = -0.771$, $P = 0.028$). Factor 2 for flight features, which loaded strongly for secondaries 1 and 2, was correlated with foliage gleaning ($R = 0.729$, $P < 0.05$). No correlations were found between the factor 1 scores and foraging behaviors. No correlations were found for any of the body-long-axis factors and foraging behavior. Factor 1 of the leg axis, loading strongly for femur, tibiotarsus and tarsometatarsus, was correlated with both foliage gleaning ($R = 0.979$, $P = 0.006$) and hops per minute ($R = 0.750$, $P = 0.035$). Similarly, factor 1 of the leg and foot dimensions morphological group was correlated with foliage gleaning ($R = 0.904$, $P = 0.011$) and with hops per minute ($R = 0.814$, $P = 0.021$). This factor loaded most strongly for hindtoe, and also heavily for footspan and midtoe.

DISCUSSION

The basic question posed is whether or not the American Redstart, an aberrant parulid, is structurally and ecologically convergent with the tyrannid flycatchers. There would seem to be scope for the secondary evolution of a "warbler-sized" flycatcher in that within the Nearctic tyrannid assemblage all the species are larger-bodied.

To explore the subject it has been necessary to develop a comprehensive data set on just what are the morphologies and ecologies of northern flycatchers and wood-warblers. The redstart remains structurally a parulid in most features, including the broad functional units of forelimb, hindlimb, and body long axis. In proportionate lengths of the main axial elements of both the forelimb and hindlimb, it is like other wood-warblers. It is, however, flycatcherlike in its broad bill and long rictal bristles—both of which are adaptations for aerial feeding—and in its longer tail. It has the lowest wing loading of the wood-warblers studied, approximating that of the flycatchers. In its ecology and, specifically, locomotory movements and foraging habits, it combines both wood-warbler and flycatcher features. Like the former, it gleans insect prey from the foliage and branches; like the latter, it hawks for prey in the air.

What is known about the precise function and significance of the body structures discussed here and, especially, those in which flycatchers and wood-warblers differ? The long bill of the flycatchers obviously is adaptive for aerial feeding. Bill length and the speed at which the mandibles can be closed are positively correlated (Beecher 1962); longer-billed birds, hence, should be able to capture fast moving prey more readily. The greater force exerted by a longer bill may improve the handling of larger prey (Bock 1964, Lederer 1975). The harvesting of large prey is probably important to

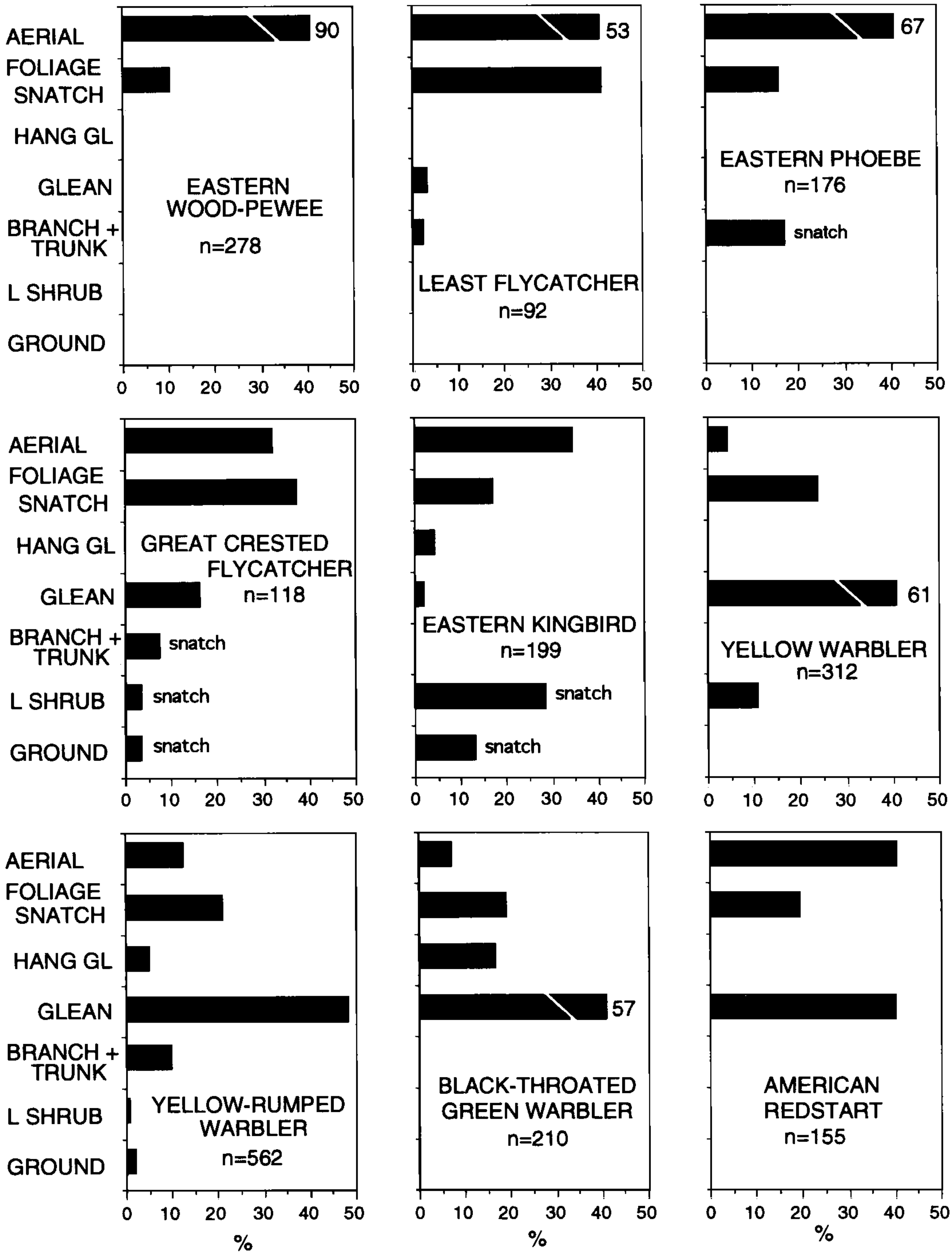

Fig. 2. Mean percent foraging substrate use and locomotory feeding movements employed while foraging. Compared for paruline wood-warblers, including the American Redstart, and tyrannid flycatchers. Categories include: aerial sallying, snatching from foliage, hang gleaning, gleaning from foliage, and obtaining prey from branches, trunk, low shrubs, and ground.

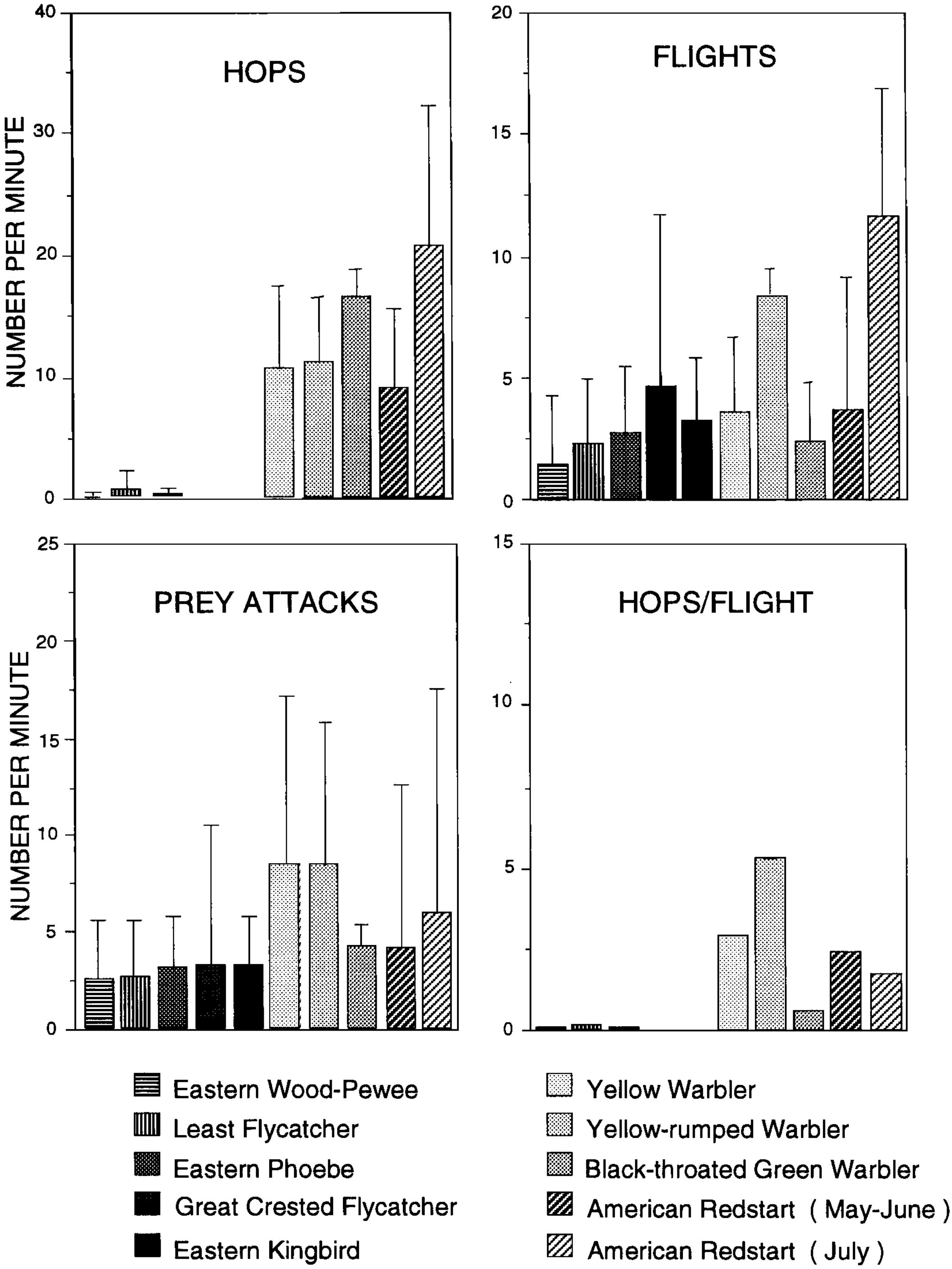

Fig. 3. Mean hop, flight, and prey attack rates per minute for tyrannid flycatchers, and paruline wood-warblers, including the American Redstart. Whisker indicates SD.

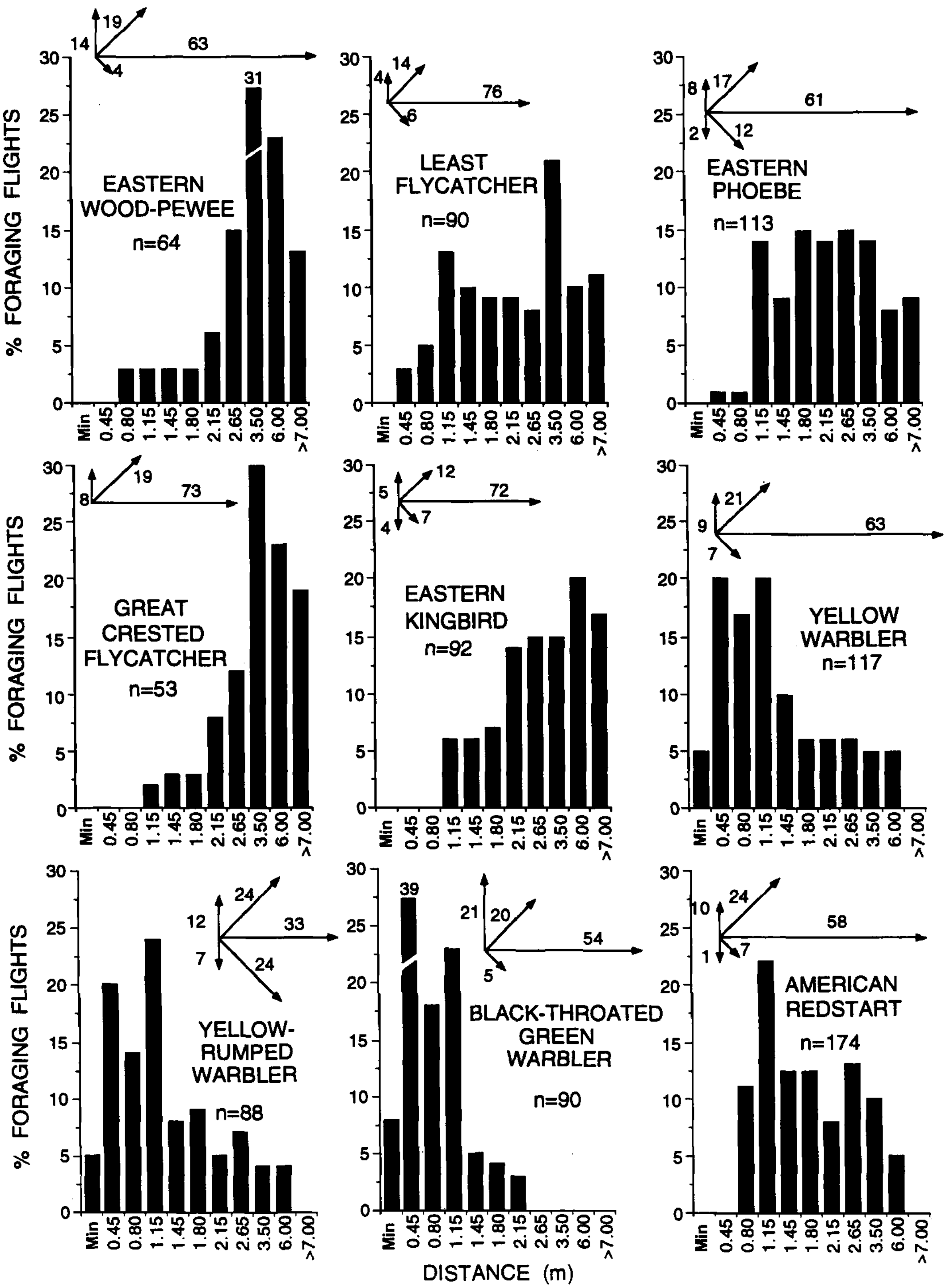

Fig. 4. Vector diagram (top of each panel) indicating percent of birds flying at given angle when foraging. Histogram (bottom of each panel) gives percent of foraging flights of a given distance. Data presented for tyrannid flycatchers and paruline wood-warblers, including the American Redstart. In histogram, labels on horizontal axis indicate lower distance limit of class represented by particular bar. Leftmost class of histogram (labeled "Min") includes very short flights (all < 0.45m). All angles and distances judged visually.

aerial feeders because of the high energetic cost of flight. A positive correlation between bill and prey size has been documented in some birds (Hespenheide 1973, Lederer 1975, Smith and Zack 1979), but this does not necessarily hold for all (Wiens and Rotenberry 1980). Finally, a larger bill favors taking prey of a wider range of sizes (Grant 1968, Herrera 1978). Bill length in the redstart is at the upper end of the wood-warbler assemblage and, in its longer bill, it is convergent with the flycatchers. However, which of the above potential advantages has influenced bill length change in the redstart, and whether it is the same as in the flycatchers, cannot be stated.

Greater gape width, long rictal bristles, and aerial feeding are positively correlated (Leisler and Winkler 1985). Rictal bristles have been variously thought to function as a funnel, effectively increasing gape width (Lederer 1972, Stettenheim 1974), to protect the eyes from food items the bird is trying to capture (Conover and Miller 1980), or as having an undefined sensory function (Stettenheim 1974). In its wide gape and long rictal bristles, the redstart is convergent on the flycatchers.

In an early essay, Savile (1957) noted that the wings of birds fell into two major categories, "elliptical" and "high speed." He noted that the former, which characterized birds feeding in confined spaces, are curved to increase negative pressure on the upper surface, and slotted to minimize terminal turbulence and produce a uniform distribution of pressure over the wing. These features combine to give high lift, control, and good maneuverability. The high-speed wing, by contrast, has a much lower camber, is tapered to a relatively slender tip, and exhibits a pronounced sweepback of the leading edge. These features reduce drag and conserve power. Later workers (Pennycuick 1969, Norberg 1979, 1981, 1986, 1987, 1990, Rayner 1988, Norberg and Rayner 1987) have related wing loading and aspect ratio to way of life. A low wing loading permits slow flight and tight turns. Slow-flying species should have broad wings and rounded tips for high maneuverability. A long wing span and high-aspect-ratio wing confers economy of effort. Hence, fast-flying species should have a pointed wing tip (Bairlein 1992).

Presumably, most of these adaptive features apply equally to flycatcher, wood-warbler, and redstart wings. The slightly more rounded wingtip of the flycatchers would be predicted from their aerial feeding habits. The wood-warblers, all long-distance migrants, are not so constrained; they can develop the long, tapering wingtip for maximum energy conservation during long-distance flights (Savile 1957, Bairlein 1992). Yet, the flycatchers also are long-distance migrants. Obviously here, then, the demands of an optimum wing morphology for feeding and migration constrain each other. See discussions of this subject in Winkler and Leisler (1992). The two tyrannids that migrate the greatest distances, the Eastern Wood-Pewee and Eastern Kingbird, which winter in Peru, have the longest wings of the series.

The redstart retains the typical parulid wing shape. Hence it, presumably, compensates for the lack of maneuverability in the wing by means of the long, mobile tail.

The tails of the birds act as elevator and stabilizers. Long tails increase longitudinal stability, and the spreading of a tail at constant base width increases stability and controls effectiveness of the longitudinal motion (Hummel 1992). However, as they tend to have a high moment of inertia, which can only be overcome by a larger wing area, there is an upper limit to how long a tail should be (Cuthill and Guilford 1990, Evans and Thomas 1992). The redstart is convergent with the flycatchers in its long tail. The redstart's tail, however, has other functions; it may be erected as a fan (Commissio 1988), pumped to expose the contrasting color pattern, and swung from side to side, apparently to flush insects (Robinson and Holmes 1982, 1984). The hemopterans and dipterans that form the bulk of the redstart's diet (Robinson and Holmes) have active predator-response mechanisms. This "flush-chase" form of aerial feeding contrasts with that of the tyrannids that sit and wait for insects on exposed lookout perches.

A specialized leg/foot morphology characterizes birds that spend much time walking, climbing, or hanging relative to generalists and aerial feeders (Norberg and Norberg 1988, Moermond and Howe 1988). The redstart is similar to the wood-warblers in its longer tarsus, which is related to the frequent use of hopping and clinging. The longer hindtoe and claws of the flycatchers are associated with their habit of perching for long periods on high exposed branches.

In summary, the American Redstart is not a wood-warbler that is evolving into a flycatcher; it is not simply a convergent form. In its morphology and ecology, the redstart combines advantageous features of both and has a range of features of its own. The redstart's features must be viewed in this light. Thus, it is irrelevent to try to estimate how "far" the redstart has evolved towards the alleged tyrannid model.

The American Redstart retains its basic paruline skeleton and all the advantages associated therewith. To these it adds features, some flycatcherlike and others unique. The bill shape and long rictal bristles match up with those of flycatchers (and aerial feeders in some other avian lineages). The redstart has not foresaken the long wingtip of the North American migratory parulines, with its energetic advantages in long flights. The redstart wing is low as in the flycatchers.

The tail is long for better control, as in the flycatchers. The tail, however, has a mobility and capacity for lateral spread suggestive of the specialist aerial-feeding *Rhipidura* fantails of the Australo-Papuan region. Like them the redstart flashes a pale-colored segment of the tail, presumably to dislodge insects from vegetation. This represents an additional feeding dimension. The habit is probably valuable in confined spaces, but less so in the wider, more open areas where the larger tyrannids feed. The American Redstart proves to be a unique adaptive type among the North American wood-warblers.

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