NICHE RELATIONSHIPS AMONG SOME DECIDUOUS FOREST FLYCATCHERS

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EXPLOITATION of a common environmental resource by several species implies overlapping niches and strongly suggests competition among the species. A variety of strategies have evolved enabling sympatric organisms to partition environmental resources effectively and thus maintain long-term normal population levels. For example, four types of *Anolis* lizards studied by Schoener (1968a) coexist with differences in body size, in choice of perching and basking sites, in selection of prey items, and in the manifestation of various degrees of sexual dimorphism. Among mammals, different food choices and slight habitat differences seem to be important features permitting coexistence among ecologically similar bats (Tamsitt, 1967) and among carnivores (Rosenzweig, 1968). Kendeigh (1945) and MacArthur (1958) reported stratal selection among sympatric warblers (Parulidae) breeding in tall coniferous forests. However, in forested communities of lower relief and in nonforested communities where vegetational stratification is much less apparent, segregation of avian species with similar niche requirements has received relatively little attention from ecologists (but see Cody, 1968; Orians and Horn, 1969), despite the increased interest in these ecological problems.

An intriguing avian feeding niche is flycatching, conventionally associated with North and Central American Tyrannidae because many of these flycatchers typically procure flying insect prey by periodic aerial sorties from stationary perches. In an earlier investigation Hespenheide (1964) made note of some interspecific competitive features between sympatric species pairs of *Tyrannus*, and further suggested intergeneric differences in habitat and nest site selection for other tyrannids. The present study on flycatchers was undertaken in a region where five species are geographically sympatric and with the objective of analyzing the separate and corporate ecologies of the species to determine the factors permitting their successful coexistence.

PROCEDURES

The Mountain Lake region (Giles County) of southwestern Virginia is characterized by open farmland with broken, heavily modified deciduous forests at elevations below 2,500 feet. Above 2,500 feet nearly continuous stretches of partially modified (by scattered timber-cutting operations and local fires) or unmodified deciduous forests are the typical climax communities. Studies of flycatchers were concentrated in the summers of 1967 and 1969 at the Mountain Lake Biological Station at 3,800 feet where a parklike, modified forest "oasis" is surrounded by a closed-canopy oak-

TABLE 1

MORPHOLOGICAL AND ECOLOGICAL DATA ON GEOGRAPHICALLY SYMPATRIC FLYCATCHERS[1]

Species	Body weight (g)	Wing length[2] (mm)	Bill size[2] (mm)	Territory size (acres)	Typical breeding habitat	Nest height and site
Tyrannus tyrannus	37.2[3]	118.7	17.6	20[4]	Farmland with scattered trees	Up to 60 feet far out on horizontal limb
Myiarchus crinitus	31.6	105.9	20.3	4–8[5]	Moderately open or closed forests and margins	10–70 feet[6] hole-nester
Sayornis phoebe	21.5	87.1	14.5	3–7[7]	Near buildings or bridges	7–14 feet on man-made structures
Contopus virens	14.0	82.5	13.3	2–11[4,5]	Deciduous forests, sometimes open	40–55 feet on horizontal limb
Empidonax minimus	10.6	64.2	10.7	<1[8]	Open deciduous forests	Ca. 20 feet in vertical forks or on horizontal limbs

[1] All data from the Mountain Lake region except as follows: [2]Ridgway (1907) exposed culmen, for males only. [3]Norris and Johnston (1958). [4]Odum and Kuenzler (1955). [5]Stewart and Robbins (1958). [6]Bent (1942). [7]Fitch (1958). [8]Davis (1959), MacQueen (1950).

chestnut or oak-association forest (Davis, 1959; Johnston, 1970). Flycatchers occurring in this region include Eastern Kingbird (*Tyrannus tyrannus*), Crested Flycatcher (*Myiarchus crinitus*), Eastern Phoebe (*Sayornis phoebe*), Eastern Wood Pewee (*Contopus virens*), and Least Flycatcher (*Empidonax minimus*).[9] A summary of their morphologic and ecologic characteristics is presented in Table 1, where a nearly perfect ordered sequence of "size" (body weight, wing length), bill length, and territory size is apparent. The sequence is *Tyrannus-Myiarchus-Sayornis-Contopus-Empidonax.*

RESULTS AND DISCUSSION

Early in the study it became apparent that *Tyrannus* really does not belong ecologically to this group for several reasons. It is not syntopic (coexistence in same habitat; cf. Rivas, 1964) with the other species because it was found in the Mountain Lake region only below 2,500 feet in the open farmland area. Probably the large territory size (ca. 20 acres) of this species is directly correlated with the more open habitat

[9] The Acadian Flycatcher (*E. virescens*) is an uncommon summer resident in the region but was not found in the study areas discussed here.

(widely scattered trees used as perches for flycatching sorties) rather than body size alone (cf. Schoener, 1968b).

The remaining four species were at least partially syntopic in portions of the deciduous forest communities at higher elevations, a situation similar to that reported by Bond (1957) for some forested communities in Wisconsin. (Even there, the distribution and occurrence of *Sayornis* was almost completely restricted to the presence of man-made structures, utilized for nesting sites, and stream borders.) Territorial relationships among these species within the deciduous forest were assessed by mapping their territories at the Mountain Lake Biological Station in June and July of 1969. Figure 1 depicts territories plus known nest sites. Overlapping territories occurred among *Myiarchus-Contopus-Empidonax* and *Myiarchus-Sayornis-Empidonax*. Frequent intraspecific conflicts (active pursuits between adjacent males, song displays) were noted, but no interspecific strife. Similarly, MacQueen (1950) and Jensen (1918) report some of these same flycatcher species coexisting with no evident conflicts.

The assertion by Hespenheide (1971) that never more than one species of small flycatcher coexists with the large Crested Flycatcher over extensive areas is not necessarily borne out by the present study. Admittedly the Mountain Lake flycatcher populations, described here and containing three syntopic flycatcher species, might be considered unique because of the modified forest habitat. But this study clearly demonstrates that large, medium, and small flycatchers can successfully coexist. Furthermore a summary of 50 randomly selected breeding bird censuses, recounted in Audubon Field Notes between 1962 and 1968, obtained in essentially mature deciduous forests from Michigan to Connecticut southward to Georgia showed the following distribution: 6 per cent contained 4 flycatcher species (*Myiarchus, Contopus, Empidonax,* and *Sayornis*), 66 per cent had 3 species (*Myiarchus, Contopus,* and an *Empidonax*), and 28 per cent had only 2 (*Myiarchus* and *Contopus* or *Empidonax*). Even though these data do not necessarily demonstrate overlapping territories and possible interspecific competitive reactions, they do strongly suggest that the "large flycatcher niche" or habitat of *Myiarchus* is frequently shared by both a small and medium-sized flycatcher.

Subtle but important habitat distinctions were detected in *Myiarchus-Contopus-Empidonax* pairs both on this study area and at adjacent deciduous forest sites. Clearly *Empidonax* reached its peak of population density on the station grounds and was virtually absent from the surrounding closed forests. *Myiarchus* and *Contopus* were equally represented in the adjacent relatively unmodified forests with their closed canopies. Thus *Empidonax* shows a preference in these modified forest communities

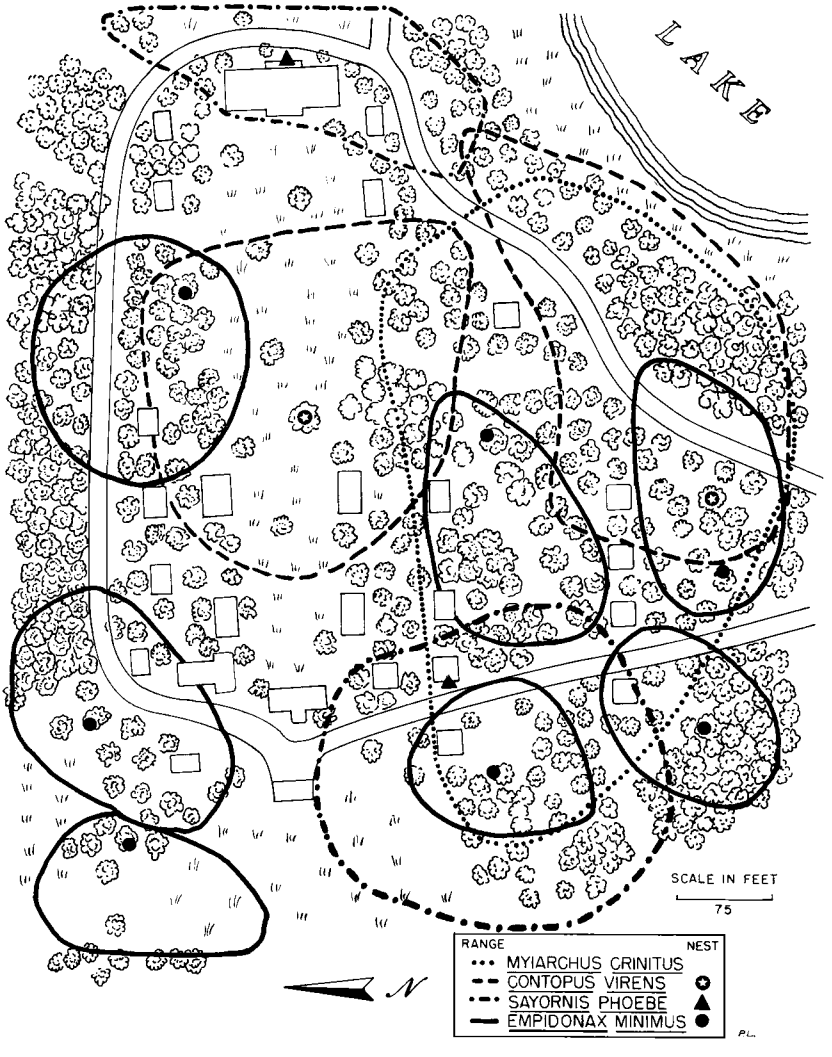

Figure 1. Occupied territories of flycatchers at the Mountain Lake Biological Station, 1969.

for areas where the subcanopy (ca. 10–40 feet) has been partially opened. Breckenridge (1956) reported for this species that "the real limiting factor was the degree of openness just beneath the forest crown." Although the present study did not include quantification of foliage density, hence a more precise measure of canopy and subcanopy openness, it was nonetheless qualitatively apparent that *Empidonax minimus* in this part

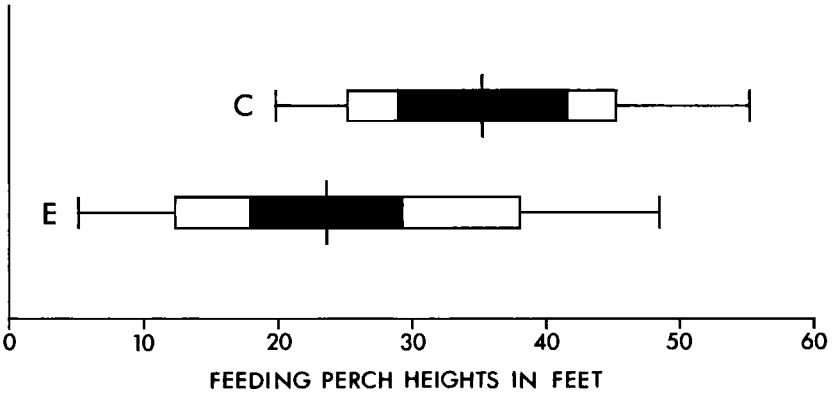

Figure 2. Feeding perches of *Empidonax minimus* (E) and *Contopus virens* (C), based on 50 hours observation of each species. Vertical center line indicates the mean, solid rectangles ± 2 SE of the mean, and the open rectangle ± 1 SD.

of Virginia's deciduous forests is a bird of less densely vegetated habitats than *Contopus* and *Myiarchus*. This finding is contradictory to the report of Hespenheide (1971) but agrees with the earlier reports of Breckenridge (1956) and Davis (1959).

Related to species' preferences for habitat structural differences were also stratal preferences for nest sites and feeding zones. Table 1 shows that *Sayornis* usually requires a man-made structure for its nest site; height is apparently relatively unimportant in this species. *Myiarchus* is peculiar among these tyrannids by being a hole-nester, and, despite its usual high feeding zone, the height of a nest hole seems to be relatively unimportant. In this study nest sites for *Empidonax* averaged about 20 feet and for *Contopus* about 50 feet. Feeding zones for the overlapping *Myiarchus-Contopus-Empidonax* group proved quite instructive. *Myiarchus* tended to feed in the forest canopy, from 50–70 or more feet, except in forest-edge situations (lakeside) where it was occasionally seen close to the ground. *Contopus* showed a distinct preference for a subcanopy feeding zone with a mean feeding height of 35 feet (Figure 2). *Empidonax*, although overlapping vertically with feeding zone and territory of *Contopus*, had a mean feeding height of 25 feet. Thus despite some overlaps, stratification of these species in the forested communities was evident, though not absolute. In even more closely related flycatcher pairs (*Elaenia martinica* and *E. flavagaster*, Crowell, 1968; *Empidonax oberholseri* and *E. wrightii*, Johnson, 1963) not only have habitat distinctions been reported in sympatric areas, but also the species tend to feed at somewhat different heights.

TABLE 2
PER CENT OCCURRENCE OF FOOD ITEMS IN EACH SPECIES SAMPLE

Taxon	*Empidonax minimus* n = 5	*Contopus virens* n = 5	*Myiarchus crinitus* n = 5
ARACHNIDA, unidentified	60	–	60
Thomicidae	20	–	–
INSECTA			
Odonata, unidentified	–	–	20
Lestidae	–	–	20
Orthoptera			
Tettigoniidae (nymphs)	–	–	20
Hemiptera, unidentified	20	–	–
Miridae	60	40	–
Coreidae (?)	20	–	–
Homoptera			
Membracidae	100	80	80
Cicadellidae	20	–	20
Cercopidae	20	–	–
Coleoptera, unidentified	60	60	20
Cerambycidae	20	40	–
Tenebrionidae	–	–	20
Chrysomelidae	–	20	–
Carabidae	–	20	–
Curculionidae	40	–	–
Mecoptera			
Panorpidae	20	–	–
Lepidoptera			
Noctuidae	–	–	60
Unidentified moths	100	40	60
Diptera, unidentified	20	40	–
Tipulidae	20	–	–
Empididae	20	40	–
Syrphidae	–	40	–
Calliphoridae	20	80	20
Rhagionidae	20	20	20
Anthomyidae	60	40	20
Drosophilidae	–	–	20
Hymenoptera, unidentified	–	–	20
Ichneumonidae	20	40	–
Braconidae	20	–	–
PLANT MATERIAL			
Amelanchier fruit	–	–	60

Field observations in the present analysis did not include quantification of feeding behavior patterns as did Crowell's investigations of *Elaenia*. It appeared that *Tyrannus, Myiarchus, Sayornis,* and *Contopus* all fed chiefly by hawking—capturing flying prey while the individual bird was in aerial pursuit. On the other hand *Empidonax* frequently fed also by hovering; that is, stationary prey was captured while the bird hovered momentarily over or under the vegetation.

Specific foods were determined here only for *Myiarchus, Contopus,* and

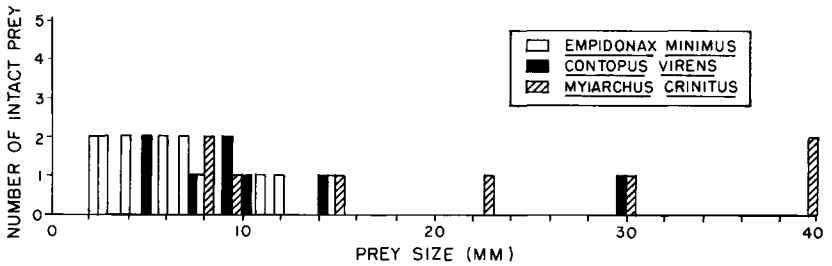

Figure 3. Size distribution of intact prey in flycatcher stomachs (five of each species).

Empidonax because these three species were most frequently syntopic not only on the station grounds, but also in some adjacent localities. From adjacent populations, five birds of each of these species were collected between 20 June and 1 July and between 17:00 and 19:00; 12 of the 15 birds were males, none of them actively feeding young. Food items identified from stomach contents are itemized in Table 2. Of notable interest here are the interspecific similarities and differences in food preferences. For example, *Empidonax* and *Contopus* shared 46 per cent of their food taxa, *Empidonax* and *Myiarchus* 28 per cent, and *Contopus* and *Myiarchus* only 25 per cent. Thus, as might be predicted on the basis of feeding zone overlap and morphologic similarities, *Empidonax* and *Contopus* were more alike in their food preferences than other interspecific comparisons in these flycatchers.

Finally, sizes of intact prey found in these stomachs confirmed these interspecific similarities and differences in food preferences. Figure 3 shows that *Empidonax* tended to feed on small prey species, *Contopus* on somewhat larger ones, and *Myiarchus* on even larger species. Thus the larger flycatcher selected large prey items, whereas the smaller flycatchers took smaller prey. It is also instructive to note the presence of fruits in *Myiarchus* stomachs, a not infrequent occurrence in this species according to Bent (1942).

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SUMMARY

A study of niche relationships among tyrannid flycatchers occupying a portion of the eastern deciduous forest showed the Eastern Kingbird

to differ from other, neighboring flycatchers in terms of body and territory sizes and preference for essentially nonforested areas. Within the forest other species were found to be at least partially syntopic—Crested Flycatcher, Eastern Phoebe, Eastern Wood Pewee, and Least Flycatcher. Among these species, all with basically flycatching habits, selection has favored interspecific differences in body size, bill size, territory size, feeding and nesting heights, choice of vegetation densities, and choice of food size, all of which are sufficient in various combinations to reduce competition and thereby permit effective partitioning of resources.

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