COMPARATIVE FEEDING BEHAVIOR OF THREE COEXISTING TYRANNID FLYCATCHERS

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Flycatching, although occasionally practiced by numerous kinds of birds, is the main feeding method in many species of tyrannid flycatchers. Flycatching is not a stereotyped behavior. Instead, there is considerable diversity in the methods evolved by its practitioners. The object of this paper is to analyze some of the spatial and temporal aspects of flycatching and to present data on this and other ways in which competition among coexisting flycatchers might be reduced.

In theory, the less overlap in the use of available resources, the better it is for the individual species. The study of related sympatric species, such as flycatchers, is of particular interest, and could supply additional evidence in support of the competitive exclusion principle (Gibb 1954, MacArthur 1958, Lack 1971). Differences in habitat use among such species may involve many factors, including the type and size of food taken, foraging height, and feeding tactics. Comparative niche relationships among other species of flycatchers have been reported in several studies (Johnson 1963; Hespenheide 1964, 1971; Crowell 1968; Smith 1966; Johnston 1971; Williamson 1971).

STUDY AREA AND METHODS

This study was conducted at the Hastings Reservation, Monterey Co., California, where three species of small flycatchers (for measurements, see Table 1) coexist in riparian woodland: the Western Flycatcher (*Empidonax difficilis*), Western Wood Pewee (*Contopus sordidulus*), and the Black Phoebe (*Sayornis nigricans*). The Western Wood Pewee also occurs on slopes with scattered trees, and the Black Phoebe frequently ventures out into grassland along fences. The three species depend for 99% of their diet on invertebrates (Beal 1912).

Because of the small breeding population involved, collecting of stomach samples to study the diet of the various flycatchers was not feasible. Instead, I used differences in foraging behavior and feeding substrate to indicate differences in habitat exploitation. For each species I recorded the estimated height of its perch and the distance flown between the perch and the prey. I also noted whether a flight was ascending, horizontal, or descending. Two methods of catching prey were distinguished: hawking and gleaning. I define hawking as the capture of a flying insect. Gleaning means the capture of an insect sitting on any kind of substrate. Frequently a bird hovered in front of a sitting insect before taking it. Such hovering flights were classified as gleaning. Gleaning from the ground occurred after a bird landed nearby (Black Phoebe) or in a passing flight (Black Phoebe, Western Flycatcher).

For each feeding sortie I recorded whether the bird returned to the perch it flew from (return flight), or whether it flew to a new perch (no-return flight). A return flight is one where a bird returns to the exact perch it flew from or to a site within a

TABLE 1

SOME MEASUREMENTS AND WEIGHTS OF THE THREE SPECIES OF FLYCATCHERS. DATA FROM RIDGWAY (1907) UNLESS OTHERWISE INDICATED

Species	N	Wing (mm)	Tail (mm)	Tarsus (mm)	Culmen (mm)	Weight[1] (g)
Sayornis nigricans semiatra	14	90.6	78.9	17.8	15.2	19.0
Contopus sordidulus sordidulus	19	84.6	62.3	13.2	13.1	14.0
Empidonax difficilis difficilis	14	64.2	54.8	16.4	11.5	11.2

[1] N = 20 (10 males and 10 females). Courtesy of Ned K. Johnson.

few cm from the original one. As all three species perched in trees in varying degrees, I arbitrarily divided the tree into seven regions: an outer shell and an inner core, each of which was divided into a lower, middle, and upper layer, and the top (Fig. 1).

Feeding tactic diversity values were calculated using the formula $FTD = \Sigma_i P_i \ln P_i$, where P_i is the proportion of the species in question using the i^{th} feeding tactic. The same formula was used to calculate substrate diversity (SD).

I recorded data throughout the day whenever one of the species was encountered: from 10 July to 8 August 1967 for the Black Phoebe, from 7 July to 11 August for the Western Wood Pewee, and from 7 July to 9 August for the Western Flycatcher. Because there were few birds, I put no restrictions on the number of observations and the length of time each bird was followed.

RESULTS

Nest site selection.—In selection of nest sites the Western Flycatcher and the Black Phoebe approached each other more closely than either species did to the Western Wood Pewee. One ledge under an overhanging roof was used by Black Phoebes in 1968, and by Western Flycatchers in 1969. Neither nest was completed, and there were no remains of the phoebe nest in 1969.

The study area contained three nests of the Black Phoebe, three of the Western Flycatcher, and at least one of the Western Wood Pewee. The territories of all three species partly overlapped. In 1969, a nest of the Black Phoebe, Western Flycatcher, and Western Kingbird (*Tyrannus verticalis*) were situated about 15 m from each other. The nest sites of Western Flycatchers on my study area were on the outside wall of a building at 1.5 m, inside a shed at 2 m, and inside a barn at 8 m. One Black Phoebe nest was on the outside wall of the same barn at 3 m, one under an overhanging roof at about 2 m, and another nest was inside a water tank at about 2.5 m. The only known nest of a Western Wood Pewee was located at about 9 m in a tree.

Egg dates.—At the Hastings Reservation, Black Phoebes normally have two clutches per year. From 1968 to 1970, first eggs in 10 early clutches appeared between 28 March and 23 April, and those of 10 second clutches

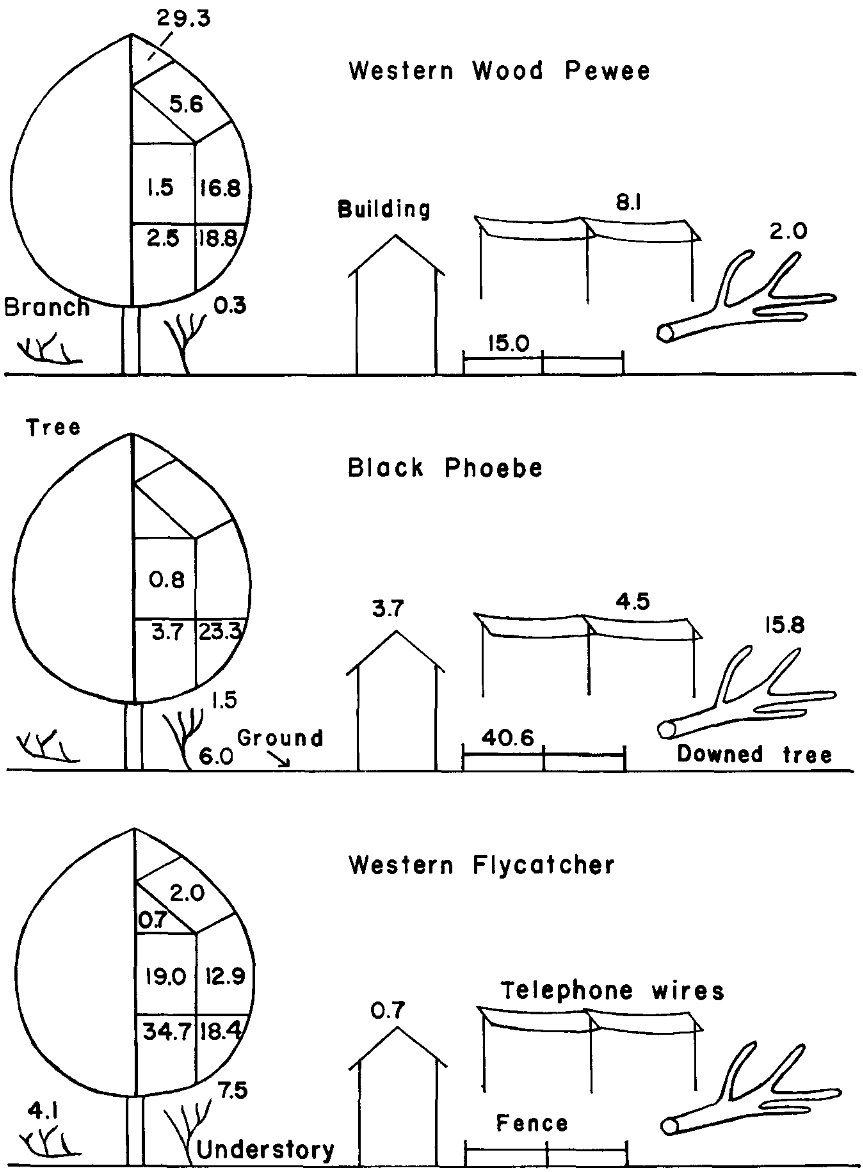

FIG. 1. Location of perches from which three species of flycatchers direct their feeding sorties, expressed as a percentage of all perches for each species.

TABLE 2

ESTIMATED HEIGHT OF PERCH AND DISTANCE OF FLIGHT TO CAPTURE PREY[1]

		Height of perch (m)			Distance of flight (m)		
Species	N	Median	Inter-quartile distance	Range	Median	Inter-quartile distance	Range
C. sordidulus	323	5.61	2.96–9.96	0.25–35	3.75	2.00–6.80	0.25–35
S. nigricans	133	1.16	0.78–2.63	0.75–10	2.04	1.21–4.58	0.25–15
E. difficilis	113	5.05	2.05–7.67	0.25–17	1.68	0.98–3.07	0.25– 8

[1] The frequency distributions of perch height and flight distance for all species were positively skewed.

between 17 May and 15 June. First clutches of four nesting Western Flycatchers were begun between 29 April and 2 May, and second clutches in two were between 25 June and 5 July. This is in agreement with data provided by Davis et al. (1963). I do not have information on the Western Wood Pewee.

Perch selection and flight distance.—The three species show clear differences in their preferred perches from which to hunt (Fig. 1). The Black Phoebe selected fences, the outer lower tree canopy, and fallen dead trees in meadows. It was the only one of the three species to perch on the ground to catch prey. About 30% of its perches were in trees. The Western Wood Pewee preferred exposed high perches, such as tree tops, the outer tree canopy, and telephone wires. Nearly 75% of its perches were in trees. The Western Flycatcher was almost entirely restricted to the middle and lower interior of trees, an area not used extensively by the other two species.

Substrate diversity indices, based on Fig. 1, in which all tree perches are lumped and treated as one, for the species were: Black Phoebe (1.51), Western Wood Pewee (0.81), and Western Flycatcher (0.48).

The median perch height of the Western Wood Pewee was not significantly different from that of the Western Flycatcher ($\chi^2 = 2.17$, $P > 0.05$, Median test in Siegel, 1956) (Table 2). These two species differed significantly ($P < 0.05$) in perch height from the Black Phoebe. Among the three species, perch height and flight distance to capture prey were not directly related.

The Western Wood Pewee flew the longest distance to capture prey (Table 3) and its median flight distance differed in this respect significantly ($P < 0.05$) from the Black Phoebe and the Western Flycatcher. The latter two did not differ significantly from each other in median flight distance ($P > 0.05$).

Foraging tactics.—All three species hawked predominantly (Table 3), and this was the only maneuver employed by the Western Wood Pewee. In

TABLE 3

FORAGING METHODS OF THREE SPECIES OF FLYCATCHERS, EXPRESSED AS A PERCENTAGE OF ALL FEEDING FLIGHTS FOR EACH SPECIES

Foraging method	*C. sordidulus* (N = 323)	*S. nigricans* (N = 133)	*E. difficilis* (N = 113)
Hawking			
in tree	3.7	0	15.0
under tree	0.3	0.8	0
among tree leaves	0.3	1.5	14.3
over grass	7.4	24.1	0.7
over ground	0	0.8	0.7
in open air[1]	87.0	49.6	29.3
Total	98.7	76.8	60.0
Gleaning			
from tree trunk	0	0	6.1
from stems, branches	0.3	0	11.6
from tree leaves	0.9	2.2	18.4
from ground	0	8.3	2.7
from grass	0	8.3	0
from buildings	0	4.5	1.4
Total	1.2	23.3	40.2

[1] Away from vegetation or ground.

contrast, the Western Flycatcher, largely confined to perching in the interior of trees, hawked slightly over half of the time. Hawking flights of the Western Wood Pewee were directed predominantly into the open air away from vegetation or the ground. The feeding tactic diversity values for the three species were: Black Phoebe (1.14), Western Wood Pewee (0.53), and Western Flycatcher (1.88). In all species returns to another perch occurred significantly more often than returns to the original perch (Table 4). This was particularly noticeable in the Western Flycatcher.

As length of flight and tendency to return to the same perch are related in the Eastern Kingbird (*Tyrannus tyrannus*) (Leck 1971), I analyzed this relationship in the three species I studied. In contrast to the Eastern Kingbird, the three species showed a unimodal distribution of flight lengths, strongly skewed toward shorter lengths. The means of the distributions lie so close to zero-flight-distance that it is meaningless to determine the relationship of short flights and return or no-return to the original perch. However, this relationship or the lack of it can be shown for long flights. To determine long flights I started at the longest flight length in each of the three frequency distributions, counting inward until I had one quarter (or

TABLE 4

TENDENCY TO RETURN TO ORIGINAL PERCH BY THREE SPECIES OF FLYCATCHERS

	Return to original perch								
	All flights				Long flights only				
Species	N	Yes %	No %	χ^2	Distance (m)	N	Yes %	No %	χ^2
C. sordidulus	323	38.1	61.9	18.36[1]	≥ 8	75	38.6	61.4	3.85
S. nigricans	133	23.3	76.7	37.90	≥ 5	33	27.0	73.0	6.81
E. difficilis	113	2.7	97.3	101.32	≥ 4	22	0.0	100.0	22.00

[1] Critical χ^2 ($P \leq 0.05$) ≥ 3.84.

less if inclusion of the next frequency brought the total over a quarter of all entries). No-return flights predominated significantly (Table 4). Considering long flights, comparison of the frequency of return and no-return flights between the Western Wood Pewee and the Black Phoebe was not significantly different ($\chi^2 = 0.85$, $P > 0.3$). The comparison between the Western Wood Pewee and the Western Flycatcher and between the latter and the Black Phoebe was significantly different ($P < 0.001$, and $P < 0.02$ respectively). I used the same procedure to assess high and low perches; again, no-return flights occurred significantly more often than return flights, regardless of perch height (Table 5). The Western Wood Pewee and the Black Phoebe do not differ significantly in the frequency of return and no-return flights from high perches ($\chi^2 = 2.19$, $P < 0.10$). Both species differ significantly in this respect from the Western Flycatcher ($P < 0.001$, and $P < 0.05$ respectively). Comparing low perches, the Western Wood Pewee differs significantly in the frequency of return and no-return flights from the Black Phoebe ($P < 0.05$) and from the Western Flycatcher ($P < 0.01$). The

TABLE 5

COMPARISON BETWEEN HIGH AND LOW PERCHES AND RETURN (R) AND NO-RETURN (NR) FLIGHTS TO THE ORIGINAL PERCH

	High perch					Low perch				
Species	Height (m)	N	R %	NR %	χ^2	Height (m)	N	R %	NR %	χ^2
C. sordidulus	≥ 11.0	76	36.8	63.2	5.26[1]	≤ 2.5	74	36.5	63.5	5.41
S. nigricans	≥ 3.5	26	19.2	80.8	9.84	≤ 0.5	29	13.8	86.2	15.21
E. difficilis	≥ 8.0	32	0.0	100.0	32.00	≤ 1.5	22	4.5	95.5	18.18

[1] Critical χ^2 ($P \leq 0.05$) ≥ 3.84.

TABLE 6

DIRECTION OF ALL FEEDING FLIGHTS, AND RELATIONSHIP BETWEEN FLIGHT LENGTH AND PERCH HEIGHT AND DESCENDING (D), HORIZONTAL (H), AND ASCENDING (A) FLIGHTS IN THREE SPECIES OF FLYCATCHERS

	Direction of all feeding flights					Long flights				Short flights			
Species	N	A %	H %	D %	(χ^2)[1]	N	A %	H %	D %	N	A %	H %	D %
C. sordidulus	323	32	17	51	13.44	75	67	17	16	76	55	22	22
S. nigricans	133	30	27	43	2.98	33	46	15	39	26	42	19	39
E. difficilis	113	47	24	29	4.66	22	41	27	32	32	25	28	77

[1] Chi square values based on ascending and descending flights only ($\chi^2 \geq 3.84$, $P \leq 0.05$).

Western Flycatcher and the Black Phoebe do not differ significantly in this respect ($\chi^2 = 0.39$, $P < 0.50$). As expected, high perches, in contrast to low ones, were associated with long flights; i.e. in *C. sordidulus* (26 high perches versus 5 low ones), in *S. nigricans* (9 and 0 [zero]), and in *E. difficilis* (7 and 3 respectively).

For each foraging flight I noted whether the birds flew upward, horizontally, or downward from the perch in pursuit of prey. All three species differed significantly in the distribution of their flight directions (pewee versus phoebe $\chi^2 = 6.10$, $P < 0.05$; pewee versus Western Flycatcher $\chi^2 = 15.75$, $P < 0.001$; phoebe versus Western Flycatcher $\chi^2 = 7.92$, $P < 0.02$). The Western Wood Pewee had significantly more descending flights than ascending flights. In the Western Flycatcher ascending flights significantly predominated, while these two flight directions did not significantly differ in the Black Phoebe (Table 6). In the Western Wood Pewee, descending flights tend to be long ones and they are associated with high perches (Table 6).

Interactions.—I saw interspecific interactions between the Black Phoebe and the Western Wood Pewee only twice. These encounters occurred in the outer lower tree canopy. In both cases the Black Phoebe was dominant. Several times these two species sat near each other on a fence wire without interacting. I saw no hostility between the Black Phoebe and the Western Flycatcher. Only once did a Western Flycatcher chase a Western Wood Pewee.

DISCUSSION

Although there must be some overlap in insect species taken, differences in the methods of feeding and preferred perch sites may be factors acting to lessen any competition between these flycatchers.

The Western Wood Pewee prefers exposed high perches on the outside of trees, it flies the longest distance, and primarily hawks by diving on its prey in the open air away from vegetation. It is the fastest flier of the three species. At the other end of the scale, the Western Flycatcher hunts in the interior of trees, where its view and path of flight is hindered by branches, hence its short flight distance. The many branches and leaves provide perches for insects, which explains the large proportion of gleaning noted for this species. The Western Flycatcher flies in quick darts and has the widest range of foraging tactics. The Black Phoebe stays close to the ground and is found primarily in the open, where it feeds by hawking over vegetation and in the open air.

The Black Phoebe shows the widest diversity of the three species in its use of different substrates, but it is intermediate in its diversity of feeding methods. Although the Western Flycatcher has a greater diversity of feeding methods than the Black Phoebe and the Western Wood Pewee, it has a very narrow substrate diversity. Of the three species the Black Phoebe appears the most versatile.

No-return flights significantly outnumbered return flights, and this was neither related to flight length, nor to perch height. Leck (1971) suggests that return flights may be associated with high prey density, in the absence of which a flycatcher might have to search and move from perch to perch. He also suggests that long flights tend to be associated with large prey items, while short flights involve small prey. Regarding the first point, frequent returns to the same perch in situations of insect abundance may not apply in flycatchers such as the Western Flycatcher, which hunt over small distances, as frequent sallies disturb the prey near the perch. Concerning the second point, I could not see the size of the insects that were caught, but it seems reasonable to expect that at larger distances proportionally more large insects are sighted than small ones. However, large insects tend to struggle when caught and preferably need to be dealt with on the nearest perch rather than the original one. I suggest that flight distance is probably not so important in determining whether a flycatcher does or does not return to its perch.

In any case, the association between long flights and no-returns is not supported by my own data nor by Leck's (1971) remarks concerning the Olive-sided Flycatcher (*Nuttallornis borealis*). A simpler explanation that applies to all five species discussed here, lies in the availability of alternative perches, to which Leck alluded, and to the species' choice of perch sites. The Western Flycatcher, inside the canopy, has plenty of perches to choose from. The Black Phoebe and the Eastern Kingbird live in the open in a habitat with ample fence rows and weed stalks. Here again, return to the perch is not necessary as others are available, but the choice is more limited than in the case of the Western Flycatcher. Lastly, the Western Wood Pewee and the Olive-sided Flycatcher use high, preferably bare perches in tree tops, and these are in limited supply.

Natural nest sites of the Black Phoebe, such as rock faces, have been greatly augmented by the vertical walls of buildings and bridges. The Western Flycatcher also uses buildings, but it needs a more or less horizontal surface on which to construct its nest. These are usually available inside and, to a lesser degree, outside buildings. Western Flycatchers also nest occasionally on ledges, and Davis et al. (1963) report one nesting above water. Along streams, where both find optimum habitat, as well as on buildings, the two species thus show potential and in some cases actual overlap in nest site selection. As nest height and foraging height in the two appear related (see also Johnston 1971), the overlap in requirements may be lessened in that their nesting cycles are neatly out of phase (pers. obs.). When the Black Phoebe has its first brood the Western Flycatcher is just beginning to lay its first clutch. This is repeated in the second brood. The periods when the young of both species are in the nest, and during which they require most food, thus do not overlap.

For eastern forests Hespenheide (1971) concludes that not more than one species of small flycatcher, such as the Eastern Wood Pewee (*Contopus virens*), coexists with the large Crested Flycatcher (*Myiarchus crinitus*). In contrast, Johnston (1971) reports overlapping territories among *M. crinitus*, *C. virens*, and *Empidonax minimus*, and among *M. crinitus*, *E. minimus*, and *Sayornis phoebe*. This apparent discrepancy probably results because Hespenheide's study was based on flycatchers living in undisturbed habitats, while Johnston apparently worked in a disturbed area rich in ecotones. The overlap among the three small species in my study is likely due to similar reasons. The broken pattern of vegetation probably provided a greater variety and abundance of insects. Johnston (1971) noted no evident conflicts among these four species, as is the case in my study with the three exceptions mentioned. The generally aggressive nature of the Western Flycatcher is reported by Williams (1942) and Davis et al. (1963), and its attack on the Western Wood Pewee may be part of that syndrome. The lack of aggression among the three species, especially between the Black Phoebe and the Western Flycatcher, suggests that their niches are well adjusted to each other.

SUMMARY

During the breeding season the territories of the Black Phoebe, Western Wood Pewee, and Western Flycatcher overlapped, and the species showed little sign of interspecific aggression. Potential competition among these flycatchers appears to be reduced by

interspecific differences in nest site selection, nest height, breeding season, foraging tactics, and the choice of perch sites. It is suggested that the Black Phoebe is the most versatile of the three species, and it is the only one to feed on the ground.

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