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NICHE CONVERGENCE IN *EMPIDONAX* FLYCATCHERS

ROBERT A. FRAKES
AND
RICHARD E. JOHNSON

ABSTRACT.—The Willow Flycatcher (*Empidonax traillii*) and Western Flycatcher (*E. difficilis*) are sympatric during the breeding season in southeastern Washington. At Kamiak Butte they occupy different habitats (the Willow Flycatcher in ninebark brush; the Western Flycatcher in Douglas fir) while at Palouse River they occupy the same habitat (floodplain forest). These species were more alike in foraging ecology when in the same habitat than when in different habitats. In floodplain forest they were very similar in their foraging ecologies, contrary to the predictions of competition theory. Food superabundance, interspecific territories, habitat differences, and limiting factors other than food are discussed as possible explanations for this situation. Interspecific competition has not, in this case, resulted in a division of the food supply.

Numerous studies on closely related, coexisting species of birds have revealed differences in food habits, foraging methods, or microhabitat which supposedly would help to divide the resources and reduce interspecific competition (e.g., Lack 1945, Gibb 1954, MacArthur 1958). However, large overlaps in foods or foraging have been reported in some cases (Lack 1946, Grant 1966, Crowell 1968, Orians and Horn 1969, Charnov et al. 1976, Baker 1977). Certain recent workers (e.g., Wiens 1977) have questioned the applicability of competition theory to animals living in variable environments. Superabundant food supplies, climatic fluctuations, effects of predation and disease, and other factors could render the assumptions of competition theory invalid. Thus, although interspecific competition has received much study, its importance in avian communities is still not clear.

The Willow Flycatcher (*Empidonax traillii*) and Western Flycatcher (*E. difficilis*) are sympatric during the breeding season in southeastern Washington. The Western Flycatcher prefers shady canyon woodlands and riparian situations, but also occurs in upland coniferous forests (Johnson 1980). The Willow Flycatcher nests in streamside vegetation and in dry upland thickets (King 1955). Both species sometimes occur along watercourses (Dawson and Bowles 1909, Sumner and Dixon 1953, pers. observ.).

At Kamiak Butte in southeastern Washington these two species are separated from each other and from other flycatchers by differences in habitat. At Palouse River they occupy the same habitat and thus are potential competitors for food. This situation presents an interesting opportunity to study the possible effects of coexistence on the foraging ecology of these two species. The purpose of this study was to examine the foraging niche of each species at both locations in order to determine if competition at Palouse River has resulted in any niche adjustments.

STUDY SITES

Kamiak Butte is approximately 19 km north of Pullman, Washington, and rises about 300 m above the surrounding prairie to an elevation of 1,060 m. Habitat types on the north slope of the butte include ninebark brush, ponderosa pine, Douglas fir, and mixtures of these basic types. Two of these were important in this study: ninebark (*Physocarpus malvaceous*) brush and Douglas fir (*Pseudotsuga menziesii*).

Dense thickets of brush have developed in certain areas where the trees have been burned or removed. The major species is ninebark but willow (*Salix* sp.), hawthorn (*Crataegus douglasii*), chokecherry (*Prunus virginiana*) and other shrubs are also present. Ponderosa pine (*Pinus ponderosa*) and quaking aspen (*Populus tremuloides*) have begun to invade in some places, but they are small and sparsely scattered. The Willow Flycatcher is the only species of flycatcher that nests in this ninebark brush habitat.

Near the top of the butte are several dense stands of Douglas fir with an understory of ninebark. The understory is reduced or absent in some places. The Western Flycatcher breeds here, placing its nest on ledges in rocky cliffs or boulders. This habitat is separated from that of the Willow Flycatcher by an extensive pine woodland where neither species breeds. Thus, although both species occur on Kamiak Butte, they occupy different habitats and do not meet.

A third habitat type, the floodplain forest, occurs in the canyon of the North Fork of the Palouse River. The section of Palouse River selected for study is located about 6 km northwest of Palouse, Washington. Black cottonwoods (*Populus trichocarpa*) are the dominant trees, forming a narrow, broken canopy along the edge of the stream. Beneath the cottonwoods there is generally a layer of small trees and shrubs such as willows, hawthorn, mountain alder (*Alnus tenuifolia*), and serviceberry (*Amelanchier alnifolia*). A few arborescent willows reach a height that is intermediate between the shrub stratum and the cottonwood canopy. In open spaces are patches of tall grass. Some scattered ponderosa pines invade the floodplain from further back on the canyon walls. The Western Flycatcher and Willow Flycatcher have adjacent territories along the river. As is the case at Kamiak Butte, Western Flycatcher territories always include rocky cliffs or boulders, which are the preferred nesting site for that species (Johnson 1980).

METHODS

Data on feeding ecology were collected by observing several breeding pairs of each species at both study sites during the breeding seasons of 1976 and 1977. Care was taken to obtain both morning and afternoon observations for each species, although most observations were made in the morning, when the birds are most active. Only those flights which were obvious foraging flights were included. The following types of information were recorded for each foraging flight observed: (1) feeding zone, (2) height of foraging perch, (3) feeding method, (4) vegetation type used as foraging perch, (5) direction and distance of foraging flight, and (6) whether or not the bird returned to the original perch. Each of these is described below.

Each habitat was arbitrarily divided into six feeding zones, three of which were defined by the three distinct layers of vegetation in the study areas: (1) an herb layer consisting of grasses or herbaceous species, usually less than one and never more than 2 m tall; (2) a brush layer, which extended from ground level to 2 to 3 m; and (3) the tree canopy, which might start as low as 3 m (usually higher) and extend to 30 m in some locations. The available air space was divided into two additional zones: (1) an open air zone, which included the space away from trees and bushes, and (2) the space directly beneath the tree canopy. The sixth feeding zone was the ground. "Feeding zone" refers to the layer or zone where a flycatcher actually captured or attempted to capture a prey item. In other words, feeding zone refers to the location of the prey rather than the location of the bird's foraging perch.

TABLE 1. Percent frequency of foraging in various feeding zones by Willow and Western flycatchers at Kamiak Butte and Palouse River, Washington.

	Kamiak Butte		Palouse River	
Feeding zone	Willow (n = 120)	Western (n = 97)	Willow (n = 98)	Western (n = 94)
Herb layer	18.3	0	14.3	2.1
Brush layer	20.8	11.3	15.3	20.2
Tree canopy	12.5	21.6	27.6	38.3
Air space under tree canopy	1.7	44.3	15.3	23.4
Open air	46.7	4.1	24.5	16.0
Ground	0	18.6	3.1[a]	0

[a] Surface of water.

We visually estimated the height of each perch from which a foraging flight was initiated. As an aid in estimating the heights of the lower perches, reference flags were placed in selected trees at 3-m intervals after the method of Beaver and Baldwin (1975). The accuracy of height estimates for many of the higher perches was checked with an Abney level.

The flycatchers in this study fed only while in flight. Two basic types of feeding flights could be distinguished: hawking and gleaning. We use these terms in the same manner as Verbeek (1975) who defined hawking as "the capture of a flying insect" and gleaning as "the capture of an insect sitting on any kind of substrate." Gleaning flights usually involve hovering near the insect before taking it. The substrate from which an insect was taken during a gleaning flight was recorded.

If the foraging perch was in a tree, the tree species was recorded. For other types of vegetation, only the general vegetative form was noted (e.g., bush, grass, herb, etc.).

Foraging flights were classified as ascending, descending, or horizontal. Distance from the original perch to the point of prey capture was estimated. Because it was difficult to estimate distances accurately, foraging flights were classified according to the following distance intervals: less than 1 m, 1–3 m, 3–6 m, 6–9 m, . . . , 15–18 m. Also, after each foraging flight, we noted whether the bird returned to the same perch or went to a different perch.

RESULTS

FEEDING ZONE

Use of the various feeding zones is shown in Table 1. At Kamiak Butte, Willow Flycatchers captured most of their prey in the open air zone, away from trees. They also used the herb and brush layers frequently. Western Flycatch-

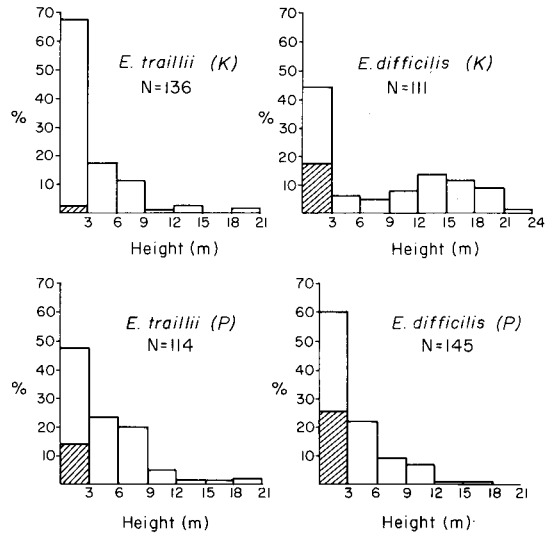

FIGURE 1. Percent foraging frequency in relation to height of foraging perch for the Willow Flycatcher (*E. traillii*) and Western Flycatcher (*E. difficilis*) at Kamiak Butte (K) and Palouse River (P). Shaded area represents foraging flights from a height of 1 m or less.

ers, on the other hand, clearly preferred the area in and under the tree canopy, although they sometimes used the brush layer and frequently gleaned insects from the ground. The difference between the two species was highly significant ($\chi^2 = 127.91$, $P < 0.001$). This difference is at least partly a function of habitat, since there are very few trees in the brush habitat of the Willow Flycatcher.

The two species were more similar in their use of feeding zones at the Palouse River study site. Both species used the tree canopy most frequently, although they also fed in the brush layer, in the open air zone, and under the tree canopy. Willow Flycatchers occasionally took insects in the herbaceous layer, where Western Flycatchers seldom foraged. Although the difference between the two species was statistically significant ($\chi^2 = 14.31$, $P < 0.01$), the amount of overlap was large (76.3%).

HEIGHT OF FORAGING PERCH

At Kamiak Butte, Willow Flycatchers foraged primarily from perches between 1 and 3 m high (Fig. 1). That height range included most of the available perches in the ninebark brush habitat. Forty-four percent of the foraging perches of Western Flycatchers at Kamiak Butte were also in the 0 to 3 m zone, and a large proportion of these were less than 1 m high. Western Flycatchers also did a considerable amount of feeding from perches between 9 and 21 m but Willow Flycatchers seldom fed at that height. The two species were significantly different in their distribution of foraging perches with respect to height at Kamiak Butte ($P < 0.001$, Kolmogorov-Smirnov test). Again, this difference may be a result of differences in habitat rather than height preference, since fewer high perches were available to the Willow Flycatcher.

Foraging perch heights of the two species were not significantly different at the Palouse River study site ($P > 0.08$, K-S test). Both species fed primarily from perches in the lower (0–3 m) level, with the number of foraging flights decreasing sharply at greater heights (Fig. 1). Willow Flycatchers fed significantly higher ($P < 0.01$) at Palouse River than at Kamiak Butte, and Western Flycatchers fed significantly lower ($P < 0.001$). Thus, the two species seemed to converge toward a common intermediate perch height where they occurred together.

TABLE 2. Percent frequency of hawking and gleaning and use of gleaning substrates by Willow and Western flycatchers at Kamiak Butte and Palouse River.

Gleaning substrates	Kamiak Butte		Palouse River	
	Willow ($n = 125$)	Western ($n = 107$)	Willow ($n = 105$)	Western ($n = 134$)
Leaves	11.2	7.5	16.2	11.2
Needles (conifers)	3.2	6.5	2.9	7.5
Tree trunk	0.8	4.7	1.0	12.7
Branches	1.6	2.8	2.9	1.5
Twigs	0	3.7	1.0	1.5
Herbs	9.6	0.9	3.8	0
Flowers	4.0	0	0	0
Grass	0	0.9	7.6	0.7
Ground	0	16.8	0	0
Water	0	0	2.9	0
Downed wood	0	2.8	0	0
Substrate uncertain	4.8	3.7	7.6	11.9
Total gleaning	35.2	50.5	45.7	47.0
Total hawking	64.8	49.5	54.3	53.0

FEEDING METHOD

The relative amounts of hawking and gleaning are shown in Table 2. At Kamiak Butte, Western Flycatchers gleaned about 50% of the time, while Willow Flycatchers gleaned only 35% of the time. The two were significantly different in this respect ($\chi^2 = 5.51$, $P < 0.025$). Western Flycatchers gleaned from a wide variety of substrates, of which the most important was the ground. Willow Flycatchers used herbaceous plants and the leaves of bushes most frequently.

At Palouse River, the Willow Flycatchers gleaned more frequently, so that there was little difference between the two species ($\chi^2 = 0.04$, $P > 0.75$). Both species gleaned frequently from leaves, and Western Flycatchers often found prey on the trunks of trees.

TABLE 3. Percent frequency of foraging from different vegetation types by Willow and Western flycatchers at Kamiak Butte and Palouse River.

Vegetation type	Kamiak Butte		Palouse River	
	Willow (n = 127)	Western (n = 106)	Willow (n = 112)	Western (n = 142)
Brush	45.7	4.7	20.5	33.8
Ponderosa pine	11.8	0	22.3	39.4
Douglas fir	0.8	88.7	0	0
Western larch	15.7	0.9	0	0
Black cottonwood	0	0	18.8	17.6
Caudate willow	0	0	19.6	0
Dead wood	22.0	5.7	8.0	7.7
Grass and herbs	3.1	0	6.3	0.7
Other	0.8	0	4.5	0.7
Total	99.9	100.0	100.0	99.9

VEGETATION TYPE USED AS FORAGING PERCH

At Kamiak Butte, Willow Flycatchers hunted primarily from species that make up what would be considered brush and dead wood (Table 3), which make up the majority of available perches in the ninebark brush habitat. Western Flycatchers, on the other hand, seldom perched in brush at Kamiak Butte, even though they often perched close to the ground where brush is abundant. They used the branches of Douglas firs almost exclusively.

At Palouse River, the two species were more alike in their selection of foraging perches. Both used brush, ponderosa pine, and cottonwoods extensively. Willow Flycatchers also used willows, grass, and herbs, categories rarely if ever used by Western Flycatchers. However, there was much overlap (69.5%) in their selection of foraging perches. Interestingly, Frakes once observed a Willow Flycatcher foraging from rocks in the middle of the river, where it appeared to be gleaning insects from the surface of the water (see Table 2).

FLIGHT DIRECTION

Foraging flights that were nearly horizontal were used most frequently by both species at both study sites (Table 4). However, at Kamiak Butte, Willow Flycatchers used more ascending than descending flights, while the reverse was true for the Western Flycatchers. The two species were significantly different in their distribution of flight directions at Kamiak Butte ($\chi^2 = 9.71$, $P < 0.01$). Ascending flights are probably correlated with low perches, and descending with high perches.

At Palouse River, they were not significantly different in flight direction ($\chi^2 = 5.16$, $P > 0.05$). Both species used more ascending than descending flights.

TABLE 4. Direction of foraging flights for Willow and Western flycatchers at Kamiak Butte and Palouse River.

Locality and species	n	Percentage		
		Ascending	Horizontal	Descending
Kamiak Butte				
Willow	134	35.8	49.3	14.9
Western	104	22.1	48.1	29.8
Palouse River				
Willow	111	27.9	54.1	18.0
Western	140	25.0	65.7	9.3

FLIGHT DISTANCE

The Willow and Western flycatchers did not differ significantly in foraging flight length at Kamiak Butte ($P > 0.6$, K-S test) or at Palouse River ($P > 0.2$, K-S test). However, both species tended to use shorter foraging flights at Palouse River than they did at Kamiak Butte (Table 5). This difference was highly significant for the Western Flycatcher ($P < 0.001$, K-S test), but not quite significant for the Willow Flycatcher ($P = 0.089$, K-S test). Over 40% of the foraging flights of both species at Palouse River were less than 1 m long.

NEW PERCH

A flycatcher's tendency to return to the original perch may indicate how much the bird moves around in its territory while hunting. This, in turn, may reflect relative prey abundance. The two species did not differ significantly at either study site in their tendency to return to the same perch. However, both returned to the same perch more often at Palouse River than at Kamiak Butte (17.4% for Willow, 21.7% for Western at Kamiak Butte; 29.7% for Willow, 31.1% for Western at Palouse River). The difference was significant for the Willow Flycatcher ($\chi^2 = 5.12$, $P < 0.025$).

DISCUSSION

The Willow Flycatcher and Western Flycatcher converge in their foraging niches when they occupy the same habitat. In almost every aspect of foraging behavior considered here, these two species are more similar at Palouse River than at Kamiak Butte: at Palouse River there seems to be little difference between them. The fact that both flycatchers change certain aspects of their foraging manner from one habitat to another suggests a flexibility in behavior. Each may alter its foraging behavior so that it is optimal for a particular habitat. When in the same habitat, the optimum would naturally be the same for both species, considering their high degree of morphological similarity. How can this be explained in terms of competition theory?

TABLE 5. Percent frequency of foraging flight lengths (distance in meters from original perch to point of prey capture) for Willow and Western flycatchers at Kamiak Butte and Palouse River.

Locality and species	n	Length					Average[a]
		<1	1–3	3–6	6–9	>9	
Kamiak Butte							
Willow	116	25.0	28.4	22.4	9.5	14.7	4.19
Western	85	15.3	40.0	27.1	11.8	5.9	3.74
Palouse River							
Willow	97	41.2	28.9	15.5	7.2	7.2	2.75
Western	88	44.3	40.9	13.6	1.1	0	1.78

[a] Calculated using midpoints of intervals.

One possible explanation is that insects may have been superabundant at the Palouse River study site. When food is plentiful, competition may be reduced or absent and differences between coexisting species might disappear (Wiens 1977). Unfortunately, we have no data on insect abundance during the period of this study, but certain aspects of the foraging flights of these birds indicate that insects may have been more abundant at Palouse River than at Kamiak Butte. Leck (1971) suggested that returning to the original perch may be associated with high prey density. When insects are more numerous, a flycatcher would not need to move around as much in search of prey and could spend more time hunting from the same perch. Both species returned to the same perch more often at Palouse River than at Kamiak Butte. Also, both used shorter foraging flights at Palouse River (Table 5). This may also imply higher prey density, since relatively more prey items could be found a short distance from the perch when insects were more abundant.

Willow and Western flycatchers probably had interspecific territories at Palouse River. No aggressive interactions between these species were observed, but the amount of overlap between their territories was small. Interspecific territoriality has been documented for other *Empidonax* species-pairs and appears to be widespread in this genus (Johnson 1980). Ashmole (1968) suggested that interspecific territoriality alone is enough to prevent two species from competing directly for food. However, as Beaver and Baldwin (1975) pointed out, flycatcher prey consists primarily of highly mobile flying insects, which can and do move freely from one territory to another. Therefore, foraging activity by a flycatcher on one territory could affect the availability of prey in adjacent territories. Even if interspecific territoriality did eliminate competition for food following territory establishment, the birds would still compete for the territories themselves. Assuming that the function of territory is to secure an adequate food supply for breeding purposes, competition for territories represents competition for food. Therefore, we are not convinced that interspecific territoriality is enough to permit coexistence, although it probably does reduce competition to some extent after territories have been established.

The fact that these two flycatchers sometimes occupy different habitats may be important. The floodplain forest may be a marginal habitat for one or both species, and the main population of each may be centered in some optimal habitat where the other species does not occur. If so, either species could maintain its population in the marginal habitat by immigration from the main population, even if it is continually being outcompeted by the other species in the marginal habitat. The Willow and Western flycatchers coexist in riparian habitats in several parts of the western United States (Dawson and Bowles 1909, Sumner and Dixon 1953), but it is not known what proportion of their populations actually overlap. Tall trees and shade seem to be requirements for the Western Flycatcher (Johnson 1980). The Willow Flycatcher, on the other hand, usually avoids trees and shade, preferring brushy rather than timbered situations, such as streamside willow and alder thickets or dry upland brush (King 1955). This difference in habitat preference probably helps to separate them in regions where they are sympatric, as it does at Kamiak Butte. Coexistence in riparian habitats may occur only in patchy situations where the trees are interspersed with open brushy spots. This is a possible explanation for their coexistence at Palouse River, considering the patchy nature of the floodplain forest habitat. In this region, the Willow Flycatcher is common in treeless streamside vegetation where the Western Flycatcher does not occur (pers. observ.).

One of the assumptions made in studies such as this is that the populations in question are limited by some resource which is in short supply. The limiting resource is usually

assumed to be food. This assumption, however, may often be invalid (Wiens 1977). Populations may be limited by other factors such as predation, disease, bad weather, etc., more often than has been thought. Two species that are virtually identical in foraging ecology and food habits could coexist indefinitely if their populations are not limited by a resource. If, as Wiens suggested, competition is an intermittent phenomenon which does not constantly act on coexisting species to cause niche separation, then we should expect to find examples like the one presented here. Our results indicate that closely related species with similar feeding ecologies can and do coexist.

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Department of Zoology, Washington State University, Pullman, Washington 99163. Present address of first author: Toxicology Program, UMC 56, Utah State University, Logan, Utah 84322. Received 12 December 1980. Final acceptance 20 February 1982.