

## RESOURCE USE BY SYMPATRIC KINGBIRDS

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**ABSTRACT.**—Resource use by Cassin's Kingbirds (*Tyrannus vociferans*) and Western Kingbirds (*T. verticalis*) was studied during the breeding season in south-eastern Arizona. The former nested predominantly in riparian creek habitat, while the latter nested in more open desert habitat. However, both species nested together where creeks flowed through open habitat. Here, they used similar nest sites, foraged in similar ways, and fed nestlings similar diets (taxonomically and by size). The nesting habits of the two species in the same habitat were more alike than those of members of the same species nesting in different habitats. Breeding success of Cassin's Kingbirds in open riparian habitat was lower than in denser riparian habitat, owing to more predation. However, we found no evidence of smaller clutch size or slower nestling growth, or more starvation in this habitat despite the lack of ecological divergence. These data indicate that competition for food is not likely to be a significant factor in maintaining the habitat separation between these two species.

Ecological studies of tyrant flycatchers have outlined differences in feeding and nesting habits between species that apparently permit them to coexist (Hespenheide 1964, 1971a; Johnson 1966; Ashmole 1968; Crowell 1968; Johnston 1971; Ohlendorf 1971, 1974; Beaver and Baldwin 1975; Verbeek 1975; Via 1979; MacKenzie and Sealy 1981). Recently, however, Frakes and Johnson (1982) showed that two closely related *Empidonax* flycatchers can coexist despite similar feeding behavior. They suggested that this could occur if competition for food were not important. In this paper we show that two species of kingbird (genus *Tyrannus*) also can coexist despite similarities in foraging behavior, nestling diet, and use of nest sites.

Since kingbirds eat flying insects that are large relative both to those eaten by other flycatchers and to what is available (Hespenheide 1971b), they should face more problems in obtaining food (Schoener 1965, 1971; Hespenheide 1971b). One would, therefore, expect that effects of competition would be most noticeable among these species. Hespenheide (1964), Smith (1966), and Ohlendorf (1974) showed that various kingbird species show substantial ecological separation, usually by differences in geographic range or macrohabitat as expected if interspecific competition for food is to be avoided. Nevertheless, they overlap ecologically in some habitats where they are sympatric.

Cassin's Kingbirds (*T. vociferans*) and Western Kingbirds (*T. verticalis*) are sympatric over a large portion of the southwestern United

States (Hespenheide 1964). They normally breed in separate habitats but coexist where tall trees are surrounded by open habitat. If habitat separation is maintained by competition, one would expect to find either ecological divergence in the habitats where both occur, or else lower breeding success of one or both species in these habitats. We gathered data on nest sites, habitat use, foraging behavior, nestling diet, timing of breeding, and breeding success of these two kingbird species where they breed alone, and where they breed together in the same habitat, in order to examine the hypothesis that each species shows ecological divergence and/or reduced breeding success in the presence of the other species, as predicted if interspecific competition is important.

### STUDY AREA

The research was carried out in June–August 1978, April–August 1979 and April–August 1980 in and around the Chiricahua Mountains of southeastern Arizona. PJB did most of the field work. The study area consisted of riparian creek valleys and desert areas that were accessible by roads, and extended from Rodeo, New Mexico, to Whitetail Creek in the northern Chiricahua Mountains. Most of the breeding kingbirds in this area were found in eleven sites where suitable nest sites were available. We grouped these eleven sites into the following four broad habitat classes: riparian forest, open riparian, dry creek wash, and desert.

Riparian forest habitat was characterized by permanently flowing creeks with essentially complete canopy cover surrounded by more

open wooded areas. Site 1 was located along East Turkey Creek near Paradise, AZ. Sycamore trees (*Platanus wrightii*) were most common along the creek with oak-juniper woodland surrounding the riparian zone. Site 2 corresponded to the Cave Creek Canyon site of Hespeneide (1964) and consisted of a dense sycamore riparian zone bordered on the south by pine-oak forest and on the north by open oak-juniper habitat.

The open riparian habitats were those where tall trees (predominantly sycamores) were interspersed with more open areas along seasonally flowing creeks. Silver Creek (site 3) was surrounded by a desert-like mountain slope to the northeast and an open oak-juniper grazed woodland to the southwest. The lower East Turkey Creek site (site 4) was bordered by a desert-like slope with some oak-juniper habitat to the east, and a flat grazed pastureland to the west. Cave Creek below Portal (site 5) was surrounded principally by thick growths of mesquite (*Prosopis juliflora*) and acacia (*Acacia greggii*).

Dry creek wash habitat was characterized by scattered small trees such as willow (*Salix* spp.) and hackberry (*Celtis reticulata*) and long dry creek beds. Sites 6 and 7 were along Whitetail Creek and were surrounded by yucca-pastureland associations, which provided many of the kingbird nest sites. Site 8 was along an unnamed creek bed, and was surrounded by desert slopes vegetated by creosote bushes (*Larrea tridentata*), century plants (*Agave* spp.), and ocotillo (*Fouquieria splendens*).

Desert habitat sites 9, 10 and 11 were along the Arizona-New Mexico border. Site 9 was an irrigated pear orchard with a few larger planted trees and abandoned fields nearby. Sites 10 and 11 were yucca patches surrounded by open desert, some mesquite shrubs, and at site 11, two houses with a few planted trees nearby. Solitary pairs of kingbirds were occasionally encountered near roads in the desert and their nests were also monitored.

Two other mountain canyons, Sulphur Draw and Horseshoe Canyon, were visited once or twice each year to obtain information on kingbird habitat distribution. The lower areas of both canyons, where kingbirds nested, were composed mostly of oak-juniper grassland.

## METHODS

We attempted to locate all nests of all breeding kingbirds in each study site. This was not always possible, owing to time constraints, but most nests were found each year. We checked nests every third afternoon for breeding status using a stepladder for desert nests and climbing trees where possible. An extendible pole with

mirror attached was used for nests as high as 14 m but we simply observed the activity of the adults at nests above that height. Data collected included date of clutch initiation, clutch size, nestling growth (for those we were able to weigh), and fledging success. In addition, we recorded nest tree species, nest tree height and nest height. Crown volumes (CrV) of nest trees were calculated in 1979 from measurements of the vertical extent (Ht) and horizontal dimensions ( $W_1$ ,  $W_2$ ) of crown vegetation using the formula:

$$\text{CrV} = \pi/6 \times \text{Ht} \times W_1 \times W_2$$

(after Sturman 1968).

We conducted mid-morning time budget studies of individual pairs of kingbirds during 1979 and 1980 for use in analyzing foraging behavior and habitat use by each species. Mated pairs of each species were selected from each of the four habitats where possible, with desert studies restricted to natural sites rather than the irrigated site (site 9). During 90–120-min observation periods, we timed all flights of each adult with stopwatches; we estimated height, length, habitat, and distance from nest for foraging flights; and we counted visits to the nest. "Perch time" between foraging flights was considered to be spent searching for insects when this time did not exceed 200 s; we considered birds to be resting if they remained perched for longer periods. The 200-s cutoff was used because longer perch times were often followed by non-foraging activity. Most foraging flights followed perch times less than 150 s long. We defined a foraging bout as that period spent foraging without engaging in any other activity, such as resting or flying to the nest. Habitat use during foraging was divided into four broad life-form categories: 1) riparian forest—insects were caught above or near groups of trees in a riparian belt; 2) open treed areas— foraging took place around isolated trees not necessarily associated with a riparian zone; 3) shrub vegetation—areas with at least 25% shrub cover but no trees; and 4) sparse vegetation—shrubs covering less than 25% of ground area, grass present or absent. We conducted time-budget observations only during sunny weather.

We obtained nestling diet information by dissecting droppings collected during nest checks and identifying insect parts to the family level, where possible. Analysis of diet overlap was done at the ordinal level owing to the difficulty of further identification of many small pieces. We sorted each sample and estimated percent volume of each insect order using a petri dish marked with 5 mm × 5 mm squares. We collected grasshoppers (family Acrididae) with sweep nets from areas where kingbirds

TABLE 1. Number of Cassin's (CK) and Western (WK) kingbird pairs by study site (all years combined).

	Elevation (m)	CK	WK
<b>Riparian forest</b>			
Site 1	1,630	10	0
Site 2	1,550	46	0
<b>Open riparian</b>			
Site 3	1,600	12	4
Site 4	1,500	16	16
Site 5	1,450	20	10
<b>Dry creek wash</b>			
Site 6	1,510	1	6
Site 7	1,450	1	18
Site 8	1,430	2	5
<b>Desert</b>			
Site 9	1,265	5	13
Site 10	1,260	0	33
Site 11	1,250	2	19
Misc.	1,300	1	22
Totals		116	146

were seen foraging while feeding nestlings, and dissected them to allow calculation of a grasshopper length vs. mandible length regression. This regression was used to estimate the size of grasshoppers fed to nestlings, as mandibles in the feces were easily measured.

We calculated rate of weight gain by nestling kingbirds using the graphical technique of Ricklefs (1967). An upper asymptote was calculated for each species, and a growth rate was then calculated for each individual nestling. Growth rates of nestlings within a nest were averaged for use in analysis.

We used Horn's information theory index (Horn 1966) to calculate overlap of resource use between and within kingbird species:

$$R_{ij} = \frac{(\sum p_{ik} + p_{jk})\ln(p_{ik} + p_{jk}) - \sum p_{ik}\ln(p_{ik}) - \sum p_{jk}\ln(p_{jk})}{2 \ln 2}$$

where  $R_{ij}$  = the overlap of population  $i$  on population  $j$  (and vice-versa) and  $p_{ik}$  = the proportion of observations of population  $i$  in category  $k$ . We chose this measure of overlap over several available in the literature because it is subject to relatively little bias when dealing with high values of overlap as in this study (see Ricklefs and Lau 1980). It is scaled from 0 (no overlap) to 1 (total overlap).

## RESULTS

### NESTING BIOLOGY

The two kingbird species differed markedly in habitat (Table 1). Riparian forests supported only Cassin's Kingbirds whereas the desert and

TABLE 2. Number of nests in each tree species by habitat for each kingbird species. All nests in three years of study are combined.

	Riparian forest	Open riparian		Dry creek wash		Desert	
	CK	CK	WK	CK	WK	CK	WK
Sycamore	49	65	31				
Oaks	15	6	1	1	1		
Junipers	5	4					
Hackberry		2	4	2	2		
Pear						5	8
Yuccas					32	1	96
Other spp.	5	2	9	1	2	4	15
Man-made	1	2	2			1	8
Totals	75	81	47	4	37	11	127

dry creek washes supported mostly Western Kingbirds. Nests of the few pairs of Cassin's Kingbirds found in the desert were in trees planted by man. The oak-juniper grassland habitat in Sulphur Draw and Horseshoe Canyon supported small numbers of Cassin's Kingbirds in each year.

In contrast to this habitat separation, each species comprised at least 25% of the nesting pairs in open riparian areas (total of 48 Cassin's and 30 Western kingbird pairs). Open riparian habitat is therefore an area where the species might compete.

Altitudinal separation of the two species was also apparent: Cassin's Kingbirds nested at higher altitudes. However, this separation appeared to reflect habitat differences rather than altitude itself (e.g., Cassin's Kingbirds were at least as numerous as Western Kingbirds in open riparian sites 4 and 5, while sites 6 and 7, at the same altitude but in dry creek washes, had mostly Western Kingbirds).

Nest placement depended on breeding habitat. In riparian habitats most nests of each species were found in sycamore trees (Table 2). However in dry creek wash and desert areas most Western Kingbirds nested in the old flower bracts of yuccas while Cassin's Kingbirds apparently avoided yuccas and built most of their nests in the few scattered trees that were available.

The relative height of the nest (nest height/tree height) for both species was virtually constant in all habitats (averages ranged from 0.73 to 0.80, Table 3) despite the great difference in physiognomy of the nest trees involved. Both height and crown volume of nest trees were much greater in the riparian areas than in the drier desert habitats. Nevertheless, the two kingbirds differed very little in height of nest tree within a habitat (Cassin's Kingbirds nested significantly higher,  $P < 0.01$ , than West-

TABLE 3. Means for characteristics of nest trees chosen by each species. Sample sizes are in brackets.

	Riparian forest	Open riparian		Dry creek wash		Desert	
	CK	CK	WK	CK	WK	CK	WK
Height of nest tree (m)	14.1 (75)	13.3 (81)	12.3 (47)	6.1 (4)	5.5 (37)	6.7 (11)	5.0 (127)
Nest height/tree height	.78 (75)	.77 (81)	.76 (47)	.74 (4)	.80 (37)	.73 (11)	.76 (127)
Crown volume (m <sup>3</sup> )	1,295 (21)	1,354 (35)	1,359 (27)	304 (2)	29 (13)	340 (5)	25 (68)

ns:  $P > 0.05$  ( $t$ -test); \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

ern Kingbirds in desert habitat but the actual height difference was small, 6.7 vs. 5.0 m). Similarly, crown volumes of nest trees in riparian areas were virtually identical for both species ( $P > 0.05$ ). However the average crown volume for Cassin's Kingbird nest trees in the drier habitats was much larger than that for Western Kingbird nest trees ( $P < 0.001$ ). Cassin's Kingbirds' avoidance of yuccas as nest sites may, therefore, be related to the almost negligible crown volume ( $< 1 \text{ m}^3$ ) of this plant.

We calculated nearest neighbor distances (NND) for all nests of both species. A frequency distribution of these distances shows that both species avoid nesting close to members of their own species (few NNDs under 60 m) but apparently do not avoid nesting close to members of the opposite species (Fig. 1). This was not always true, since on four occasions Cassin's Kingbirds prevented Western Kingbirds from nesting in the same tree by chasing them out. However, the difference in intra- and interspecific spacing of nests was highly significant for both Cassin's Kingbirds ( $t = 5.65$ ,  $P < 0.001$ ), and Western Kingbirds ( $t = 8.03$ ,  $P < 0.001$ ), with active nests of the two species found as close as 3 m apart. The net result of this difference was a doubling of kingbird density (as measured by NND or by overlap of foraging areas) in the open riparian habitat where both species were present.

Western Kingbirds began laying eggs an average of one to two weeks earlier than Cassin's Kingbirds in the study area (Table 4a). The presence of both species in open riparian areas appeared to have no effect on this difference. The range of dates when each species was feeding nestlings reflected this difference, with Western Kingbirds beginning and ending one to three weeks before Cassin's Kingbirds (Table 4b). Nevertheless, the breeding season for both species was long, with the result that the period when both species were feeding nestlings lasted about two months in each year.

The long breeding season resulted mostly from re-nesting by both species after failed nesting attempts, though some Western Kingbirds appeared to attempt second broods (adults were not banded). The overlap in breeding seasons is even more extensive when incubation periods and post-fledging periods are considered (kingbirds fed young near the nest for two or more weeks after fledging).

#### FORAGING BEHAVIOR

The two species foraged in similar ways, sallying off perches to catch flying insects and occasionally flying down to pick insects off the ground. The time spent searching or sallying did not differ statistically ( $P > 0.05$ ) between species, and both tended to increase search and sally times in the open riparian habitat (Table 5). The average distance sallied by each species was virtually identical in open riparian habitat. However, Cassin's Kingbirds sallied farther in riparian forest habitat than in open riparian habitat ( $t = 2.52$ ,  $P < 0.01$ ), while Western Kingbirds sallied a shorter distance in desert habitat than in open riparian habitat ( $t = 2.75$ ,  $P < 0.01$ ). Heights of perches used for foraging were similarly intermediate in open riparian habitat between the high perches used by Cassin's Kingbirds in riparian forest habitat and the low perches used by Western Kingbirds in desert areas. Western Kingbirds chose significantly higher perches than Cassin's Kingbirds in open riparian habitat ( $t = 3.46$ ,  $P < 0.001$ ). In general, intraspecific differences in foraging behavior between habitats were greater than any interspecific differences in behavior in open riparian habitat.

Kingbirds pursued prey at heights ranging from ground level up to 50 m. The height distribution of these foraging attempts depended on the habitat in which they nested (Table 6). Cassin's Kingbirds nesting in riparian forest foraged significantly higher than those nesting in open riparian habitat ( $t = 5.08$ ,  $P < 0.001$ ).

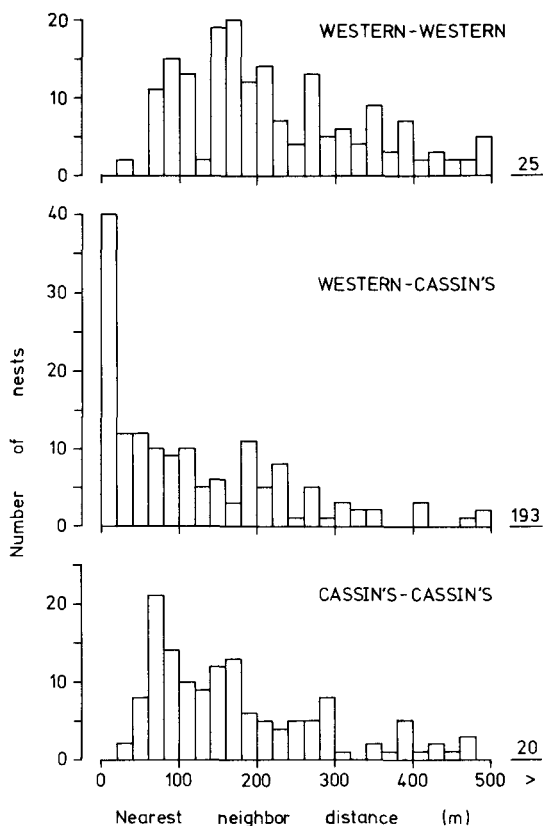


FIGURE 1. Frequency histograms of intra- and interspecific nearest-neighbor distances. Distances were measured between nests active at the same time of the season.

Similarly, Western Kingbirds nesting in open riparian habitat foraged significantly higher on average than those nesting in drier habitat ( $t = 10.24, P < 0.001$ ), where about 44% of foraging attempts were made at or below 1.5 m. The two species pursued prey at similar heights where they occurred together in open riparian habitat ( $P > 0.05$ ).

We found a similar pattern in an analysis of the vegetation types where foraging took place (Table 7). The two kingbirds overlapped widely in vegetation type in open riparian habitat, whereas populations of each differed markedly between habitats. This probably reflected the availability of vegetation types in each habitat (i.e., vegetation is sparser in the desert than in other habitats).

NESTLING DIETS

Diet information based on estimated percent volume of insect pieces in nestling feces is biased owing to differences in the digestibility of various kinds of insects. Fecal remains can nevertheless be used for comparative purposes as long as the species have similar digestive capabilities. We have assumed that this is true of nestling Cassin's and Western kingbirds.

TABLE 4. Comparison of breeding chronology between the two species. Desert habitat in this and following tables includes dry creek wash.

(a) Mean date of first egg for all nests of each species.				
	Riparian forest	Open riparian		Desert
	CK	CK	WK	WK
1978	June 16	June 20	—	June 3
1979	June 6	June 7	May 31	May 29
1980	June 13	June 15	June 7	June 5

(b) Range of dates during which each species was observed feeding nestlings.		
	Cassin's Kingbird	Western Kingbird
1978	June 9–Aug. 18	May 28–Aug. 6
1979	May 28–Aug. 20	May 19–July 28
1980	May 30–Aug. 6	May 24–July 24

Body parts that tended to be consistently present in kingbird droppings included mandibles, small pieces of elytra and exoskeleton, tarsi, leg joints, setae, pieces of wings, and compound eyes. These were often enough to identify insects to the family level. Families of insects that were common in the diet of one kingbird species were also commonly eaten by the other species. For example, we regularly found short-horned grasshoppers (Acrididae), robber flies (Asilidae), winged ants (Formicidae), and some of the bees (Apidae) in the diets of both species. Dietary overlap of the two kingbirds at the level of insect order was nearly complete in the open riparian habitat (Table 8). This diet similarity was higher than that within each species when different habitats were compared. Cassin's Kingbirds nesting in riparian forest areas tended to feed nestlings fewer grasshoppers and more flies than those nesting in open riparian areas. Western Kingbirds tended to feed nestlings more grasshoppers and fewer beetles and hymenopterans in the desert habitats than in open riparian habitat, although diet overlap was still high. The greater importance of grasshoppers in desert as compared with riparian forest was expected because the former had a greater amount of open terrain.

The size of grasshopper mandibles in feces increased but little with nestling age. This result was unexpected because nestling growth is rapid especially during the first week. One Western Kingbird nestling less than a day old that died during handling was found to have a whole grasshopper 20 mm in length plus a mydid fly 26 mm long in its stomach. Nevertheless these nestlings were fed significantly smaller grasshoppers when 0–4 days of age (4 nests, mean of 22.3 mm) than when 5–11 days old (40 nests, mean of 27.6 mm;  $t = 3.23, P < 0.01$ ). Grasshopper size data for Cassin's King-

TABLE 5. Characteristics of foraging behavior for each species by habitat (number of measurements used in calculating a mean is shown in brackets). "Search time" refers to time spent on perch between foraging flights, "sally time" is in-flight time.

	Riparian forest		Open riparian				Desert	
	CK		CK		WK		WK	
Search time (s)	42.6 (292)	ns	45.9 (155)	ns	48.8 (130)	ns	41.8 (324)	
Sally time (s)	8.1 (390)	ns	8.7 (237)	ns	7.9 (370)	ns	7.5 (792)	
Sally distance (m)	20.1 (379)	**	15.8 (226)	ns	15.4 (368)	**	12.9 (808)	
Perch height (m)	12.0 (382)	***	7.5 (225)	***	9.3 (363)	***	4.5 (791)	

ns:  $P > 0.05$  (*t*-test); \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

bird nestlings were available only for ages 5–11 days. A comparison of these data with those for Western Kingbird nestlings of the same age showed no significant difference in grasshopper size (for Cassin's: 8 nests, mean of 28.7 mm,  $P > 0.05$ ). Similarly, both kingbirds ate the same size of grasshoppers when nesting together in the open riparian habitat ( $P > 0.05$ ). Also, size did not differ intraspecifically between habitats ( $P > 0.05$ ).

#### BREEDING SUCCESS

We measured breeding success as the number of young fledged by a pair of kingbirds in a single season. This measure often included several nesting attempts by a single pair in one season. Western Kingbird nesting success did not differ between habitats (Table 9), whereas Cassin's Kingbirds were twice as successful in riparian forest as in open riparian habitat ( $\chi^2 = 8.35$ ,  $P < 0.01$ ). This difference appeared in every year of the study. Success in desert habitat was not significantly different from that in either riparian habitat ( $P > 0.05$ ), although sample size was small. The species were not significantly different ( $P > 0.05$ ) in success where they occurred together.

Approximately 50% of nest losses for both

species resulted from predation (Blancher and Robertson, unpubl.). Starvation, on the other hand, was noted in only four nests (three Western Kingbird nests, one Cassin's Kingbird nest). We examined clutch sizes and nestling growth rates as indicators of the ability of each species to gather food.

Neither kingbird differed significantly in clutch size between habitats ( $P > 0.05$ ). In open riparian habitat, Western Kingbirds had a higher average clutch size (4.0) than Cassin's Kingbirds (3.3) ( $t = 4.16$ ,  $df = 66$ ,  $P < 0.001$ ) but this was a reflection of the significant difference in clutch size for the whole study area (Western: 3.8; Cassin's: 3.4;  $t = 3.97$ ,  $df = 229$ ,  $P < 0.001$ ). The average nestling growth rates of each species were also the same between habitats ( $P > 0.05$ ), though sample sizes of Cassin's Kingbirds were small (Cassin's: asymptote = 37.4 g,  $K = 0.392$ ,  $n = 14$  nests; Western: asymptote = 32.3 g,  $K = 0.412$ ,  $n = 84$  nests).

#### DISCUSSION

The pronounced difference in habitat between Cassin's and Western kingbirds found in this study is consistent with other reports on these species (Hespenheide 1964, Smith 1966, Ohl-

TABLE 6. Height distribution of prey pursued by kingbirds (given as percentages).

	Riparian forest		Open riparian		Desert	
	CK		CK	WK	WK	
Sample size ( <i>n</i> )	390		229	380		846
Prey height (m)						
0–1.5	9.5%		23.1%	29.2%		44.4%
2–5	15.1		16.2	11.3		19.3
6–10	15.1		19.2	11.8		21.0
11–20	40.5		29.3	26.8		11.2
>20	19.7		12.2	20.8		4.0
Mean height (m)	15.0	***	10.9	ns	12.3	***

ns:  $P > 0.05$  (Mann Whitney *U*-test); \*\*\*  $P < 0.001$ .

TABLE 7. Time spent foraging (in percent) over various vegetation types in each habitat. Overlaps were calculated using Horn's (1966) information theory index.

	Riparian forest		Open riparian		Desert	
	CK	CK	WK	WK	WK	WK
Total time (s)	43,151	53,065	67,246		108,368	
Sparse vegetation	—	49.3%	39.6%		83.7%	
Shrub vegetation	14.5%	23.2	43.8		9.5	
Open treed areas	47.9	17.0	2.8		6.8	
Riparian forest	37.7	10.5	13.8		—	
Overlap ( $R_{ij}$ )		0.633	0.931		0.780	

endorf 1974). Despite this separation of most members of these two species, a few individuals of each species breed in close proximity to the other (papers listed above, Carothers et al. 1974, Goldberg 1979; Table 1). Within these zones of overlap, one would expect to find other ecological differences between the species if interspecific competition is important. We seldom observed interspecific territoriality, however, with the result that kingbird density doubled in open riparian habitat where both species occurred. One would expect competition to be especially intense in these areas, yet we found no evidence of competitive effects on clutch size or nestling growth.

These kingbirds differ but little, if at all, in habits where they breed sympatrically. Hesperheide (1964), working in essentially the same study area, and Ohlendorf (1974) found no difference in breeding chronology of the two species, although Evermann (1886) and Willett (1912) suggested that Cassin's Kingbirds nest earlier than Western Kingbirds in California. The small difference in timing of the breeding season in this study (Cassin's Kingbirds nested later than Western Kingbirds) was offset by the relatively long breeding season.

Nest sites of the two species were essentially the same in open riparian areas, agreeing with the results of Hesperheide (1964) and Goldberg (1979). Ohlendorf (1974) found that Cassin's Kingbirds nested significantly higher relative to the canopy than Western Kingbirds. He worked in western Texas, however, where kingbirds are relatively sparse and interaction between the species is less likely to be a factor in nest site selection.

Foraging behavior of the two species was also similar particularly where they nested in the same habitat. Goldberg (1979) found interspecific differences in the tendency to return to the same perch after foraging and in the take-off angle from perches, but this did not result in any difference in the height of prey taken (most prey taken by both species in her study were within 3 m of the ground). She

found that Western Kingbirds were more likely to glean insects off vegetation than Cassin's Kingbirds but this behavior was rare (0–11%) relative to insects taken in flight (59–84%) or on the ground (13–28%).

The similarity in foraging behavior is reflected in the close similarity in nestling diet. The habitat where the birds nested had a greater influence on diet than did presence of the other kingbird species. This conclusion was also reached by Ohlendorf (1974) who found that diets of the two species were more similar when considered at the same time and place than the diet of the same species at different times or places. Similar findings have been reported for other passerine birds (Dick and Rising 1965, Pulliam and Enders 1971, Maher 1979, Wiens and Rotenberry 1979, Rotenberry 1980). Even species with vastly different foraging behavior may have similar diets where food is abundant (Rosenberg et al. 1982). Hesperheide (1964) found no evidence for character displacement by bill size for the two kingbird species, except possibly in California where Cassin's Kingbirds form an isolated population.

We found that nest sites, habitat use while foraging, height of prey, and nestling diet were more similar between the two species where

TABLE 8. Estimated percent volume of insects by orders in nestling feces (values given are means; one sample includes all feces collected from one nest in one day).

	Riparian forest		Open riparian		Desert	
	CK	CK	WK	WK	WK	WK
Sample size ( $n$ )	6	7	12		42	
Orthoptera	22%	39%	40%		48%	
Coleoptera	26	23	19		13	
Hemiptera	7	6	8		10	
Hymenoptera	18	19	18		11	
Diptera	28	13	16		19	
Lepidoptera	1				<1	
Odonata					<1	
Diet overlap ( $R_{ij}$ )		0.957	0.997		0.986	

TABLE 9. Nesting success, measured as the number of fledglings produced per breeding pair in one year, by habitat and species.

	Riparian forest		Open riparian			Desert	
	CK		CK	WK	WK	CK	
No. of pairs	53		47	25	101	11	
No. fledglings	95		38	32	114	14	
Fledglings/pair	1.8	**	0.8	ns	1.1	ns	

ns:  $P > 0.05$  (G-test on the number of fledglings observed vs. the number of nesting pairs); \*\*  $P < 0.01$ .

they occurred together than between populations of a species in different habitats. This indicates that the ecology of each species is flexible and is modified by habitat but does not appear to diverge in the presence of the other species. A similar pattern was found in foraging behavior of Willow and Western flycatchers (*Empidonax traillii* and *E. difficilis*, respectively) breeding together in floodplain forest habitat, and alone in other habitats (Frakes and Johnson 1982). These results lead to several alternative hypotheses regarding competition between the species in areas of overlap: 1) populations of kingbirds are always below carrying capacity on their breeding grounds, or at least in places where they co-occur, so that food is superabundant there; 2) the availability of food varies (see Wiens 1977) and this study may have taken place during a period when food was superabundant, with the result that overlap between the kingbirds was not disadvantageous; 3) food is not superabundant but, by its nature, cannot be diminished by the birds (see Charnov et al. 1976 for discussion of non-depressible prey); 4) competition occurs but the two species do not diverge in behavior or ecology owing to the overwhelming influence of traits developed in the absence of the other species.

Differentiation of hypotheses 1, 2, and 3 requires simultaneous measurement of food supply and breeding ecology of the two species. Nevertheless, all three argue against the importance of competition for food where the two species breed sympatrically.

The fourth hypothesis predicts that reproductive success of one or both species would be reduced in areas of overlap and this would tend to maintain habitat separation of the species. Such an idea was suggested by Beaver and Baldwin (1975) as an explanation for the habitat separation of Western and Hammond's (*E. hammondi*) flycatchers. Nesting success of Cassin's Kingbirds was lower in the presence of Western Kingbirds, owing mainly to greater predation. Possibly the close nesting proximity of the two species increases predation in a density-dependent fashion (Fretwell 1972), leading most members of each species

to avoid habitats occupied by the other species. We have examined and rejected this hypothesis. We found no evidence, however, that starvation, clutch size, or nestling growth rate of either species was reduced in open riparian habitat where both species were present. Thus, it seems unlikely that the habitat separation of these two kingbirds (Hespenheide 1964, Smith 1966, Ohlendorf 1974) serves to reduce their competition for food, as has previously been implied. The observed differences in habitat use could simply have arisen during their evolution as allopatric species (Tatschl 1973), with sympatry developing more recently. The habitats that they occupy in Arizona resemble areas elsewhere where each species breeds alone (Western Kingbirds in open grasslands and riparian belts of the United States and Canada, Cassin's Kingbirds in highland valleys of Mexico; Smith 1966).

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