COMPETITIVE RELATIONSHIPS AMONG KINGBIRDS (*TYRANNUS*) IN TRANS-PECOS TEXAS

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The Western Kingbird (*Tyrannus verticalis*) and Cassin's Kingbird (*T. vociferans*) are conspicuous elements of the summer avifauna in the Trans-Pecos region of Texas. These species were selected for a study of possible competitive relationships among sympatric species because of their similarities and abundance.

The approach in this study was to examine the ways in which the resources of the area were divided among the two kingbird species. Three principal aspects were examined: utilization of different resources, using the same resources at different places, and obtaining the same resources in different ways. The Trans-Pecos is the most physiographically varied portion of Texas (Blair, 1950), and the resultant ecological diversity makes the area especially suitable for studies of this type (see Orians and Willson, 1964).

METHODS

Field work was conducted from June through August 1969 and May through August 1970, with supplemental observations in November 1970 and May 1971. Survey trips were made throughout the Trans-Pecos area to determine the geographical and ecological distribution, nesting habits, and food consumption of the kingbirds, as well as to study the habitat types of the area. More detailed studies were carried out at selected sites. Literature and museum locality records supplement the distributional data of this study. One other nesting record was obtained from the North American Nest-record Card Program.

Kingbirds were caught and then banded with colored plastic (and with aluminum Fish and Wildlife Service) leg bands. Color-banded birds were watched to learn about their daily activities, including behavior toward other flycatchers. Birds were captured with mist nets by using a stuffed Great Horned Owl (*Bubo virginianus*) as a decoy.

Specimens for food analysis were shot, weighed, and the hour of collection was usually recorded. They were then injected with 10 percent formalin to stop digestion. Digestive tracts were then used for laboratory analysis of the diet. Food items were identified, counted, and then measured by volumetric displacement. Items displacing less than 1 ml of water were measured in a 2 ml syringe graduated to 0.1 ml; volume was determinable to the nearest 0.025 ml. Larger items were measured in a 15 ml centrifuge tube. The material contained in the stomach (proventriculus and ventriculus) of an individual bird is defined here as a sample. In addition to absolute values, percent values were calculated for each measurement. The latter are considered more informative in determining similarities and differences in composition and allow comparison of unequal numbers of samples.

Botanical nomenclature follows Correll and Johnston (1970). Habitat data were analyzed by appropriate methods presented in Snedecor and Cochran (1967). Means and 95 percent confidence intervals were calculated for measurement data, and chi-square and t-test analyses were generally used to determine statistical significance.

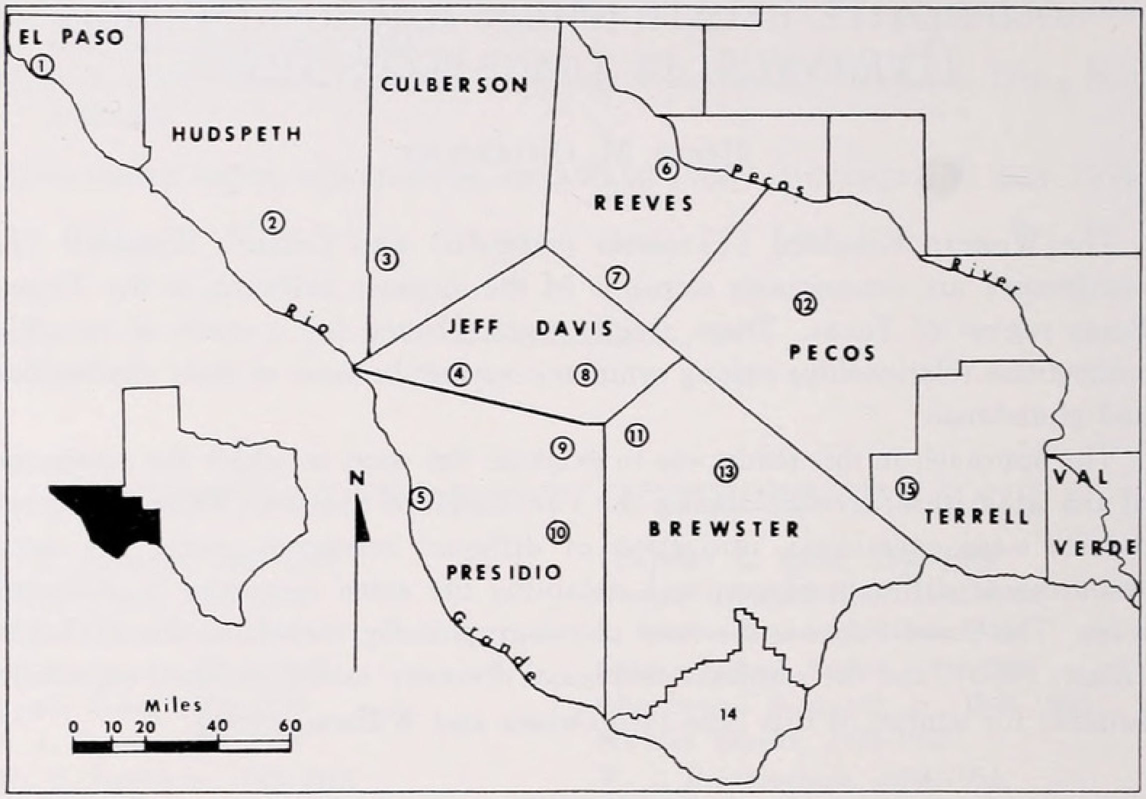

FIG. 1. Map of the Trans-Pecos region. Principal localities are indicated as follows: El Paso (1), Sierra Blanca (2), Van Horn (3), Valentine (4), Candelaria (5), Pecos (6), Balmorhea (7), Fort Davis (8), Marfa (9), Plata (10), Alpine (11), Fort Stockton (12), Marathon (13), Big Bend National Park (14) and Sanderson (15).

DESCRIPTION OF STUDY AREA

The Trans-Pecos, an area of some 32,000 square miles, encompasses a variety of habitat types, including the most arid and the highest areas of Texas. It is situated west of the Pecos River, north of the Rio Grande, and south of New Mexico (Fig. 1). Basic geologic features are an alternation of mountain ranges and alluvium-filled bolsons, with the eastern quarter of the area (Terrell, southern Pecos, and northeastern Brewster Counties) comprised of rolling to broken country known as the Stockton Plateau. Elevations range from 1,200 ft, in Terrell County, to 8,751 ft, in northwestern Culberson County.

Principal mountain areas are the Guadalupe, Davis, and Chisos ranges. The Guadalupes form an extension (about 20 mi long) into Texas of the mountainous regions of New Mexico. Their biological significance is due primarily to their great elevation rather than to the size of the area which they occupy. The Davis Mountains occupy an extensive area of Jeff Davis County, with elevations of 6,000–8,382 ft. Elevations reach 7,835 ft in the Chisos Mountains, located within Big Bend National Park (Brewster County).

Most of the region is drained by the Rio Grande, the Pecos River, and their tributaries. An extensive area in north-central Presidio, western Jeff Davis, western Culberson, and much of Hudspeth Counties has no exterior drainage, the runoff forming shallow salt lakes.

Rainfall for the Trans-Pecos region averages 12 in per year. Amounts are generally less at lower and greater at higher elevations, with a maximum of 18 in in the Davis Mountains (Orton, 1969). July, August, and September are generally the months of

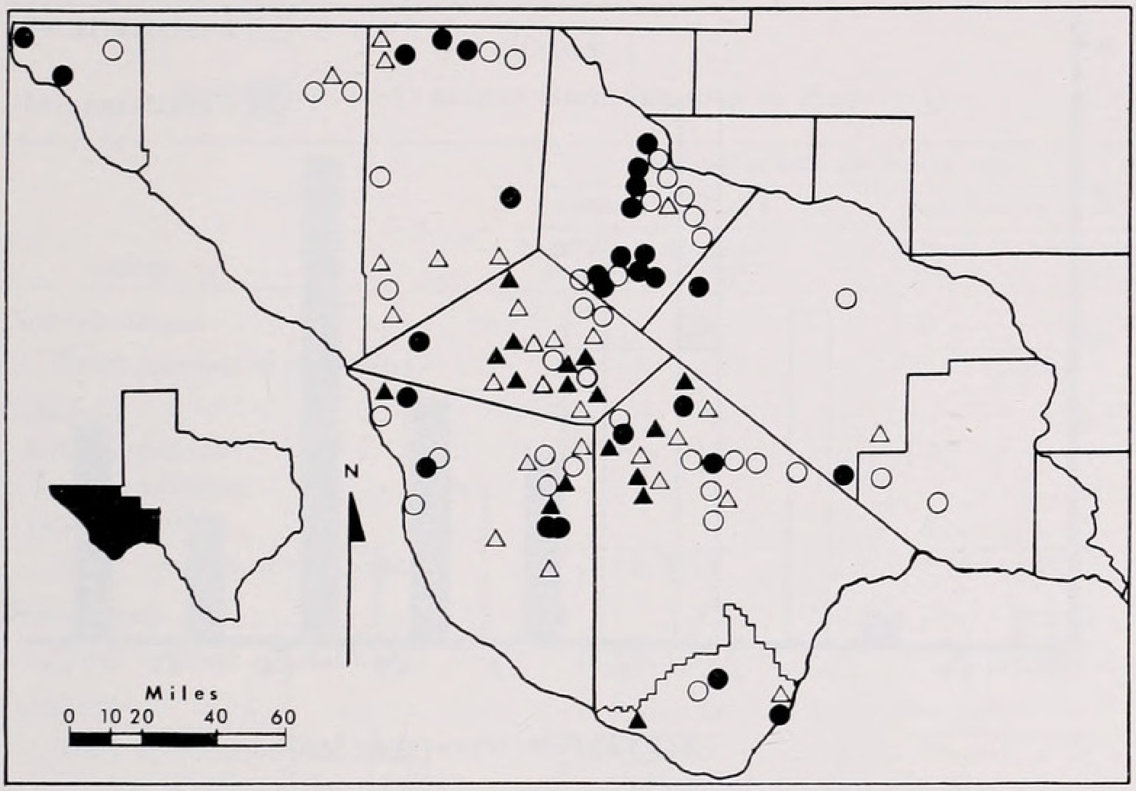

FIG. 2. Breeding distribution of *Tyrannus verticalis* and *T. vociferans* in the Trans-Pecos region. Dots are nesting and circles are summer localities for *verticalis*; solid triangles are nesting and open triangles are summer localities for *vociferans*.

greatest precipitation, although great annual and seasonal variations occur; precipitation-free periods of several months are normal (Orton, 1969). Average annual temperatures range from 58°F in the Davis Mountains to 70°F at Presidio.

The biota of the region is typical of the Chihuahuan Desert (Blair, 1950), and most of the area remains natural, modified by grazing of livestock. Considerable vertical zonation exists in vegetative types. Desert shrub is the predominating type up to 4,000 or 5,000 ft; grassland and pine-oak-juniper types occur above this elevation. Cultivated areas are generally confined to irrigated valleys, e.g. at El Paso, Presidio, Balmorhea, and near Pecos.

Desert shrub is composed primarily of creosote bush (*Larrea tridentata*), honey mesquite (*Prosopis glandulosa*), ocotillo (*Fouquieria splendens*), and acacias (*Acacia* spp.). Washes support more robust forms of these shrubs and mesophytes, such as desert willow (*Chilopsis linearis*) and baccharis (*Baccharis* spp.). Grasses are short and sparse.

Mountain grasslands occupy plains and intermontane valleys at 4,000–6,000 ft in Jeff Davis, northern Presidio, and Brewster Counties. The grasses *Bouteloua* spp., *Sporobolus* spp., *Bothriochloa* spp., and *Leptochloa dubia* are among the more important, with *Bouteloua ramosa* and *Hilaria mutica* more common in arid areas. Yuccas (*Yucca* spp.) and cholla cacti (*Opuntia* spp.) are especially common where the grasslands grade into desert shrub, although they also occur elsewhere throughout the region.

The principal woody species are at altitudes above 5,000 ft and constitute the pine-oak-juniper type. Oaks (*Quercus grisea*, *Q. emoryi*) and junipers (*Juniperus* spp.) are most common at the lower elevations. Pinyon pine (*Pinus edulis*) is abundant above 6,000 ft and replaces the oaks.

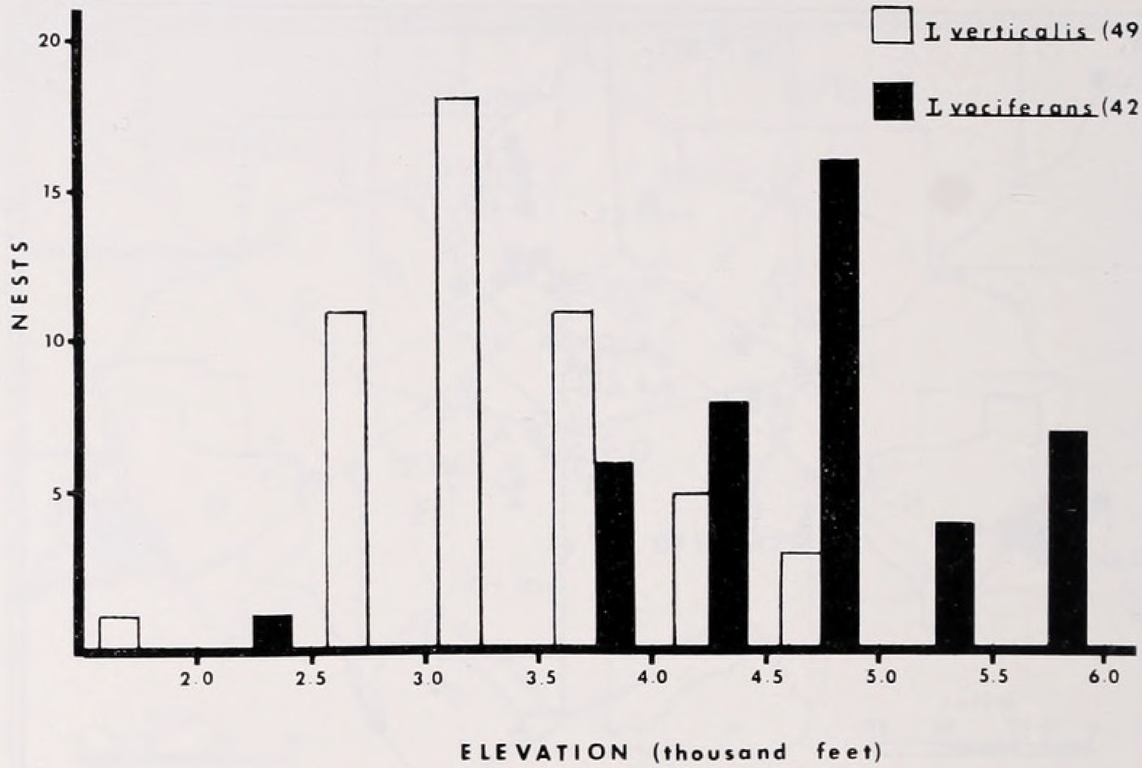

FIG. 3. Distribution of *Tyrannus* nests relative to elevation.

Riparian vegetation forms a gallery generally less than 100 ft wide in streambeds. Typical trees are cottonwoods (*Populus* spp.), willows (*Salix* spp.), ash (*Fraxinus* spp.), and walnuts (*Juglans* spp.); baccharis and willows are common shrubs.

DISTRIBUTION AND HABITAT

Both species of kingbirds are at the margins of their distributions in the Trans-Pecos region. This area represents, for this portion of their ranges, the southern breeding limit for *T. verticalis* and the eastern limit for *T. vociferans*. These are the only regularly breeding members of the genus in the area (A.O.U., 1957; and other sources). The Eastern Kingbird (*T. tyrannus*) occurs as a migrant, whereas two southern species (*T. melancholicus* and *T. crassirostris*) are rare visitors in the Big Bend area (Wauer, 1973). The breeding distribution of *T. verticalis* and *T. vociferans* in the study area is shown in Fig. 2. There they are locally common, although less abundant than reported in southeastern Arizona by Hespenheide (1964).

The kingbirds arrive in the area as early as mid-April, with nest construction commencing in early May. In general, birds remain in nesting areas from about 10 May to 10 August. Therefore, only localities at which birds were recorded in this period are considered as breeding localities. Nesting localities referred to in this paper are those at which attended nests or fledglings incapable of extended flight were found.

TABLE 1

DISTRIBUTION OF *TYRANNUS* NESTS RELATIVE TO HABITAT TYPE

Habitat	*verticalis* (n = 47) Natural site	*verticalis* (n = 47) Manmade site*	*vociferans* (n = 42) Natural site	*vociferans* (n = 42) Manmade site*
Pine-oak-juniper	–	–	2	1
Total (percent of total nests)	–		3 (7.1%)	
Grassland	–	3	–	5
Grassland-shrub	1	2	3	4
Grassland-juniper	–	1	–	2
Grassland-oak	–	–	6	2
Total (percent of total nests)	7 (14.9%)		22 (52.4%)	
Desert shrub	1	17	–	5
Total (percent of total nests)	18 (38.3%)		5 (11.9%)	
Farmland	–	19	–	–
Total (percent of total nests)	19 (40.4%)		–	
Riparian, flanked by				
Grassland	–	–	2	–
Grassland-shrub	–	–	2	–
Grassland-oak	–	–	4	–
Desert shrub	1	–	2	–
Total (percent of total nests)	1 (2.1%)		10 (23.8%)	
Suburban	–	2	–	2
Total (percent of total nests)	2 (4.3%)		2 (4.8%)	

* Nesting presumably in response to the presence of utility lines or trees associated with houses, fences, and roadside parks.

Altitudinal segregation among nesting localities of the two species is easily seen (Fig. 3), based on 49 nests of *verticalis* and 42 of *vociferans*. Forty-one (83.7 percent) of the *verticalis* nests were at elevations of less than 4,000 ft, whereas 35 (83.3 percent) of those of *vociferans* were at elevations exceeding 4,000 ft. The mean elevation of *verticalis* nests was 3,382 ± 188 ft; mean of *vociferans* was 4,735 ± 229 ft. Comparison of these means indicates that the difference is highly significant (t-test, $P < 0.01$).

Differences in altitude of nesting are associated with differences in habitat usage, based on 47 nests of *verticalis* and 42 of *vociferans* (Table 1). Thus, all kingbird nests (3) in the pine-oak-juniper habitat type were of *vociferans*, although these represented only 7.1 percent of the nests for this species. In habitats where overlap occurred, one species or the other was dominant. In grassland and riparian situations, *vociferans* was the dominant species, but *verticalis* dominated in the desert shrub and farmland areas. The construction of telephone and power lines and the planting of trees associated with houses, fence rows, and roadside parks generally favored the nesting of kingbirds. Those nests designated in various habitats as "manmade" (Table 1) were thought to be situated there only because of such human-related modifications. Distributional differences in shared habitat types (i.e. grassland, desert shrub, riparian, and suburban) are highly significant (χ^2, $P < 0.01$).

Nesting records and breeding season locality records for the two species in Jeff Davis County and the surrounding area serve to illustrate species segregation (Fig. 2). *Vociferans* predominated overwhelmingly in the pine-oak-juniper, grassland, and riparian habitats of Jeff Davis County, where elevations generally exceed 5,000 ft. *Verticalis* occurred essentially alone at elevations less than 3,500 ft in the desert shrub and farmland of adjacent Reeves County. Other portions of this area had intermediate elevations and were occupied by both species.

Post-nesting dispersal is apparent after early August. Subsequent to then, birds are more frequently observed in areas which do not afford nesting substrate, but which are used for feeding. Counts were made periodically on a route of 74.5 mi along Texas highways 17, 118, and 166 west of Fort Davis. The route transects grassland and pine-oak-juniper types, ecotones of these, and also grassland-desert shrub. Both species, but especially *vociferans*, were more abundant in August. Four trips during May through July 1969 and 1970 yielded one *verticalis* and 128 *vociferans* individuals, whereas an equal number of trips during August 1969 and 1970 yielded six *verticalis* and 511 *vociferans*. The birds utilized fences and telephone lines as feeding perches and were usually not in close proximity to any suitable nesting substrate in August.

NESTING

Kingbirds nested in a variety of sites, but nests were usually located in trees when these were available. The more frequent use (χ^2, $P < 0.05$) by *verticalis* of man-made structures is a reflection of the species' occurrence in situations where trees were fewer. Eighteen (38.3 percent) *verticalis* nests and five (11.9 percent) *vociferans* nests were located on man-made structures. Twenty-one of these nests were situated on utility poles. Thus, only 57.4 percent (27) of *verticalis* nests were in trees, compared to 78.6 percent (33) of *vociferans* nests. The most frequently used trees were cottonwoods for both of the kingbird species.

Nests of *verticalis* were generally closer to the ground. While 82.6 percent (19) of the *verticalis* nests were at heights of less than 30 ft (mean of tree

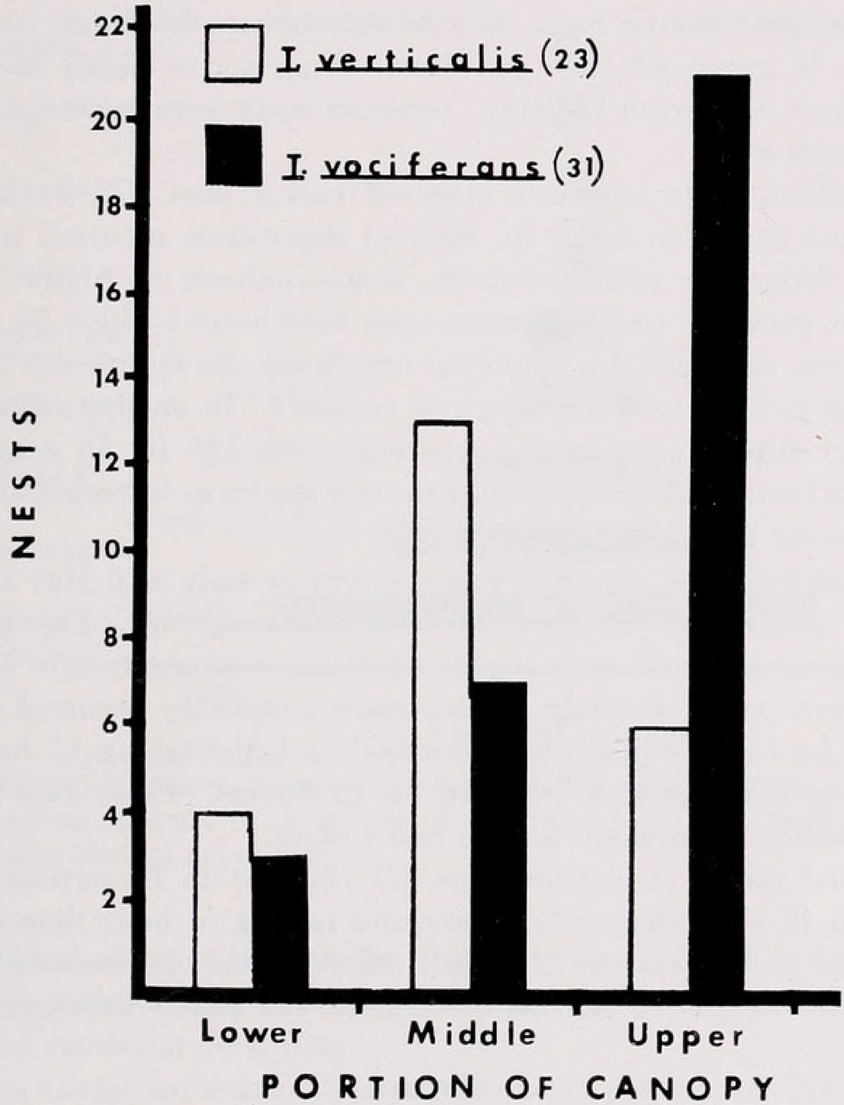

FIG. 4. Relative portion of tree canopy in which *Tyrannus* nests were located.

nests 21.0 ± 3.4 ft), only 48.4 percent (15) of the *vociferans* nests were that low (mean 29.3 ± 4.2 ft). The difference between these means is highly significant (t-test, $P < 0.01$).

Differences also existed among tree-nesting kingbirds as to the portion of the canopy (i.e. lower, middle or upper third) in which the nests were situated (Fig. 4). Whereas *verticalis* tended to nest in the middle third (56.5 percent), *vociferans* nested significantly (χ^2, $P < 0.01$) more frequently (67.7 percent) in the upper third. Hence, when nesting in trees, *verticalis* tended to nest lower than *vociferans*, regardless of tree height.

Verticalis tolerated closer spacing of nests than did *vociferans*, with nests of the former as close as 90 ft in roadside cottonwood trees west of Fort Stockton, 180 ft at Plata, and 195 ft near Balmorhea. Although these were highly modified situations, with large trees planted and maintained in desert shrub or farmland habitat types, they do demonstrate the degree of tolerance in nesting. In grassland-shrub and desert shrub not so highly modified by man (northern Culberson County), *verticalis* nests were located as close as 0.2 mi to each other.

In *vociferans*, nests were not observed nearer than 675 ft; in another instance separation was 1,650 ft. Both of these cases occurred in riparian vegetation flanked by grassland-shrub, south-southeast of Alpine. Interspecifically, i.e. *verticalis* and *vociferans*, nests were located within 35 ft of each other at Plata. Although the *vociferans* nest failed, the failure was apparently due to wind and not to the presence of *verticalis.* In another instance, east-northeast of Alpine, interspecific separation was 135 ft. In general, nests were seldom located this close, because the two species so infrequently occurred together during the breeding season.

Nest construction by *verticalis* was observed as early as 6 May and as late as 9 July, compared to 11 May and 6 July for *vociferans.* Two individuals of *verticalis* were brooding as late as 21 July; as young remain in the nest for about two weeks, nestlings of this species probably occurred as late as 5 August. An adult *verticalis* was seen feeding fledglings on 13 August, and in *vociferans* nestlings were recorded on 12 August. These data indicate a similar breeding chronology for the two species.

Means and ranges of clutches were 3.3 (1 to 5) in 14 *verticalis* and 3.3 (2 to 4) in 15 *vociferans* nests. Successful rearing of more than one brood by the same adults was not observed. However, in one instance when the first nest was lost, a second was constructed and young were raised.

FEEDING

Both kingbird species apparently fed on prey that was most readily available, although I do not have data pertaining to the abundance of prey taxa. Because of this lack, any interpretation of competition for food having existed between *verticalis* and *vociferans* is not subject to proof. However, an analysis of samples taken during the study serves to illustrate similarities and differences in the diets of the birds.

Percent occurrence (presence or absence), percent individuals (numbers of individuals), and percent volume (size of food items) are considered useful in analyzing the samples. Values less than 0.1 percent were considered "traces" and represent volumes less than 0.025 ml. Percent occurrence generally indicates the consistency in selection of a taxon. Taxa with the greater occurrence were those taken frequently, but this gives no indication of the relative number of individuals taken. Therefore, it is necessary to consider percentage of individuals. However, small types may be taken relatively often and in fairly large numbers without constituting a major portion of the diet.

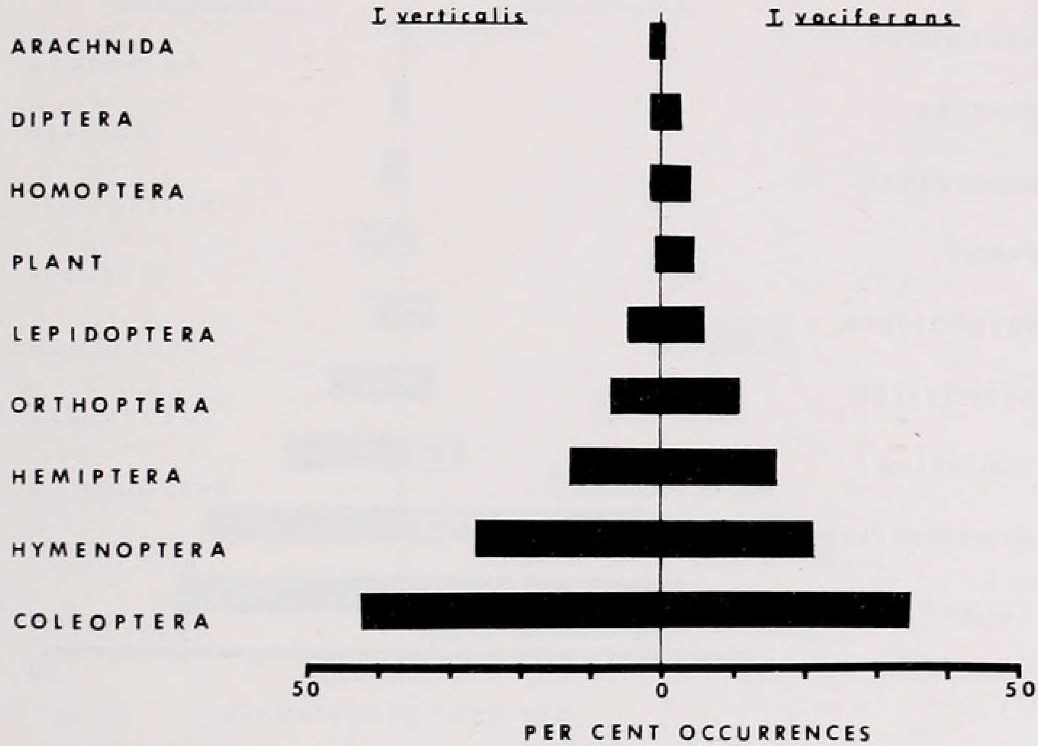

FIG. 5. Relative frequency, expressed as percent total taxon occurrences, of major prey types in *Tyrannus verticalis* (n = 48) and *T. vociferans* (n = 79) samples. Symmetry indicates similar diets of these birds.

Percent volume serves to indicate the true importance of each taxon, although this is easily influenced by the recency of consumption and rapidity of digestion for the particular food item.

All insect tissues are similar in terms of calories per ash-free gram (Slobodkin, 1961). Consequently, differential nutritive values per unit are not a factor. Although no effort was made to assess the energy expended in foraging for the various prey, it seems reasonable that the taxa representing the greatest portion of the volume constitute the most important taxa of the diet.

Analysis of food composition is based on 48 samples of *verticalis* and 79 of *vociferans*. Most food items could be identified to family. Both kingbirds were found to be principally insectivorous (97.5 percent in *verticalis*, 94.6 percent in *vociferans*), but arachnids and plant material were also consumed. The plant material in both species was comprised of fleshy fruits (Rhamnaceae) and seeds (Anacardiaceae). *Verticalis* had a mean of 4.1 ± 0.6 taxa (including plants) per sample, whereas *vociferans* had 3.8 ± 0.5 taxa. The diet of *verticalis* may be somewhat more diverse, but the difference is not significant (t-test, $P > 0.2$).

The relative occurrence of major prey types is very similar in these two species, as is reflected by the symmetry in the profiles of their diets (Fig. 5).

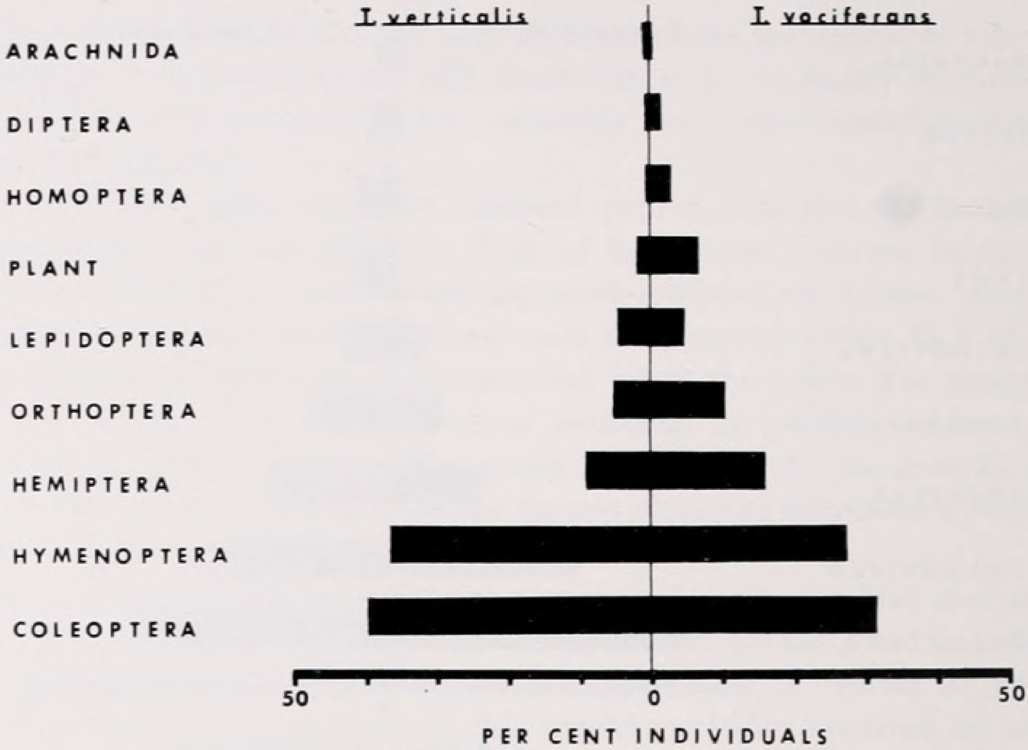

FIG. 6. Relative number of individuals, expressed as percent total individuals, of major prey types in *Tyrannus verticalis* (n = 48) and *T. vociferans* (n = 79) samples. Symmetry indicates similar diets of these birds.

The extent of overlap in diets may be expressed quantitatively by the formula of Bray and Curtis (1957), modified as: percent overlap = (2 times shared taxa) $\times$ 100/sum of taxa in *verticalis* + sum of taxa in *vociferans*.

Contrasted to the finding of complete overlap in diet based on major prey types (i.e. insect orders, arachnids, and plant material), the above calculation yields 72.7 percent overlap when based on families of prey taken. Major types are also of the same relative importance when diets are compared on the basis of the number of individuals per taxon (Fig. 6).

Some interesting differences are noted when the taxa are considered on the basis of percent volume (Fig. 7). In both kingbirds, Orthoptera (almost exclusively acridid grasshoppers) are the largest constituent of the diet, despite their relatively less frequent occurrence and fewer numbers among prey items. The greater incidence of cicadas (Homoptera) in *vociferans* is probably related to the closer association of this species to riparian situations. However, it appears that this difference is accentuated in the volume comparisons because a greater proportion of the cicadas in *verticalis* samples had undergone extensive digestion. Kingbirds (*vociferans*) were only once observed feeding a dragonfly (Odonata) to nestlings; these insects were absent from all the stomach samples.

An unusual observation of a *vociferans* took place in the grassland-shrub,

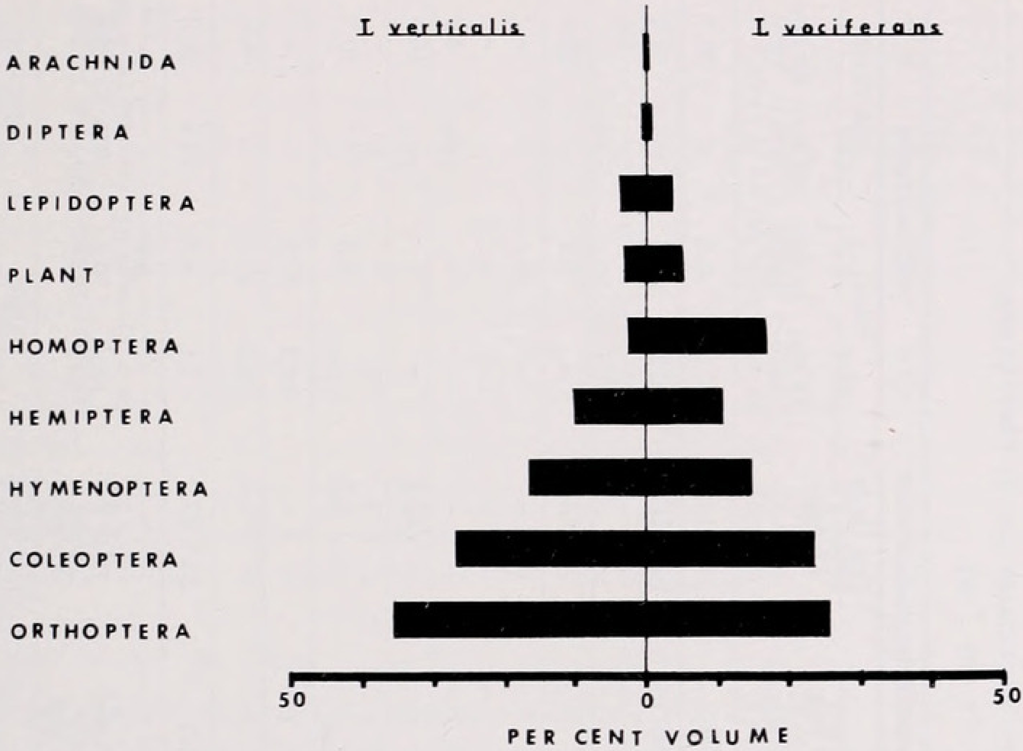

FIG. 7. Relative importance, expressed as percent total volume, of major prey types in *Tyrannus verticalis* (n = 48) and *T. vociferans* (n = 79) samples. Symmetry indicates similar diets of these birds.

west-southwest of Fort Davis, on 20 May 1970. There a bird flew down and caught a noticeably large prey item, which it abandoned as I approached. The prey was collected and later identified as a juvenile (5.5 g) harvest mouse (*Reithrodontomys* sp.). This was the only instance of predation on a vertebrate observed by me.

There were greater differences within samples of a kingbird species from the same locality on different dates and on the same date at different localities than within samples of both kingbird species at the same locality and date (Table 2). Admittedly, samples of the two species at the same locality were few, because generally they did not occur together. Even with meager data, interspecific comparisons are more appropriate than a strict seasonal analysis, because considerable bias could be introduced by the sampling methods (i.e. different times of day, habitat types, etc.). Some taxa occur regularly throughout the season (i.e. Acrididae, Reduviidae, Carabidae, Apoidea) while others are more temporal as well as local (as Dermestidae, Curculionidae, lepidopterous larvae, Formicidae).

AGONISTIC BEHAVIOR

Both species of kingbirds mobbed larger birds, including Red-tailed Hawks (*Buteo jamaicensis*), Great Horned Owls, and Common Ravens (*Corvus

TABLE 2

FOOD COMPOSITION (PERCENT OCCURRENCE) OF *TYRANNUS VERTICALIS* AND *T. VOCIFERANS*, INDICATING DIFFERENCES WITH LOCALITY AND TIME

	T. verticalis			*T. verticalis/T. vociferans*			*T. vociferans*			
	Balmorhea			Plata		Fort Davis	Plata		Ash Creek	
Prey taxa	26 May 1970 (n = 5)	9 July 1970 (n = 6)	27 Aug. 1969 (n = 5)	10 June 1970 (n = 3/ n = 4)	14 July n = 1) 1970 (n = 2/	17 Aug. 1970 (n = 1/ n = 3)	18 May 1970 (n = 7)	15 July 1970 (n = 8)	28 May 1970 (n = 3)	28 July 1969 (n = 7)
ORTHOPTERA	3.6	13.6	–	– / 7.1	20.0/ –	33.3/18.8	7.1	6.2	–	10.7
Acrididae	3.6	4.5	–	– / –	20.0/ –	33.3/18.8	7.1	6.2	–	7.1
Undetermined	–	9.1	–	– / 7.1	– / –	– / –	–	–	–	3.6
HEMIPTERA	21.5	27.2	7.2	9.1/14.2	– / –	– /18.8	–	6.3	–	28.6
Belostomatidae	–	–	–	– / 7.1	– / –	– / –	–	–	–	–
Naucoridae	–	–	–	9.1/ –	– / –	– / –	–	–	–	–
Reduviidae	3.6	4.5	3.6	– / –	– / –	– / –	–	–	–	3.6
Coreidae (*Mozena* sp.)	–	18.2	–	– / –	– / –	– /12.5	–	–	–	14.3
Corizidae	3.6	–	–	– / –	– / –	– / –	–	–	–	–
Pentatomidae	14.3	4.5	3.6	– / 7.1	– / –	– / 6.3	–	6.3	–	10.7
HOMOPTERA	–	–	–	– /14.3	– / –	– / –	14.3	37.5	–	–
Cicadidae	–	–	–	– /14.3	– / –	– / –	14.3	37.5	–	–
COLEOPTERA	49.9	18.0	64.2	54.6/49.9	20.0/ –	33.3/37.7	7.1	6.2	15.4	39.3
Cicindelidae	–	4.5	17.8	9.1/ –	– / –	– / –	–	6.2	–	–
Carabidae	14.3	4.5	21.4	– / –	– / –	– / 6.3	–	–	–	14.3
Hydrophilidae	–	–	–	18.2/ 7.1	– / –	– / –	–	–	–	–
Staphylinidae	–	–	21.4	18.2/21.4	– / –	– / 6.3	–	–	–	–
Cantharidae	–	–	–	– / –	– / –	– / 6.3	–	–	–	–
Dermestidae	7.1	–	–	– / –	– / –	– / –	–	–	–	–
Tenebrionidae (Adult)	–	4.5	–	– / –	– / –	– / –	–	–	–	–

TABLE 2 (continued)

	T. verticalis			*T. verticalis/T. vociferans*			*T. vociferans*			
	Balmorhea			Plata		Fort Davis	Plata		Ash Creek	
Prey taxa	26 May 1970 (n = 5)	9 July 1970 (n = 6)	27 Aug. 1969 (n = 5)	10 June 1970 (n = 3/ n = 4)	14 July 1970 (n = 2/ n = 1)	17 Aug. 1970 (n = 1/ n = 3)	18 May 1970 (n = 7)	15 July 1970 (n = 8)	28 May 1970 (n = 3)	28 July 1969 (n = 7)
COLEOPTERA (continued)										
Tenebrionidae (Larva)	–	–	–	– / –	– / –	– / –	–	–	7.7	–
Scarabaeidae (*Phanaeus* sp.)	3.6	–	–	– / –	– / –	33.3/12.5	–	–	–	25.0
Chrysomelidae	7.1	–	–	– /14.3	– / –	– / –	–	–	–	–
Curculionidae	17.8	4.5	–	9.1/ 7.1	20.0/ –	– / 6.3	7.1	–	–	–
Undetermined	–	–	3.6	– / –	– / –	– / –	–	–	7.7	–
LEPIDOPTERA	–	4.5	3.6	– / –	– / –	– / 6.3	–	–	15.4	–
Pieridae (Adult)	–	–	–	– / –	– / –	– / –	–	–	15.4	–
Noctuidae (Adult)	–	–	–	– / –	– / –	– / 6.3	–	–	–	–
Undetermined (Larva)	–	–	3.6	– / –	– / –	– / –	–	–	–	–
Undetermined (Adult)	–	4.5	–	– / –	– / –	– / –	–	–	–	–
DIPTERA	–	–	–	– / –	– / –	– / 6.3	7.1	–	15.4	–
HYMENOPTERA	21.4	31.7	38.6	36.4/14.2	60.0/100.0	33.3/12.5	42.9	43.8	30.8	10.7
Chalcidoidea	–	–	3.6	– / –	– / –	– / –	–	–	–	–
Scoliidae	3.6	4.5	–	– / –	– / –	– / –	–	–	7.7	–
Formicidae	–	9.1	17.8	18.2/ 7.1	40.0/100.0	– / –	–	31.3	–	10.7
Vespidae	–	4.5	3.6	– / –	– / –	– / –	–	–	–	–
Apoidea	17.8	13.6	13.6	18.2/ 7.1	20.0/ –	33.3/12.5	42.9	12.5	23.1	–
TOTAL INSECTA	96.4	95.0	100.0	100.1/99.7	100.0/100.0	99.9/100.4	78.5	100.0	77.0	89.3
SOLPUGIDA	–	–	–	– / –	– / –	– / –	–	–	7.7	–
Solpugidae	–	–	–	– / –	– / –	– / –	–	–	7.7	–
ARANEIDA	3.6	4.5	–	– / –	– / –	– / –	–	–	–	–
Thomisidae	3.6	4.5	–	– / –	– / –	– / –	–	–	–	–
SEEDS (Anacardiaceae)	–	–	–	– / –	– / –	– / –	21.4	–	15.3	10.7

corax). Such attacks were made simultaneously by the two species on an owl (and the stuffed decoy) and also on two ravens at Plata. A Boat-tailed Grackle (*Cassidix mexicanus*), which entered their nest tree, was harassed simultaneously by a *verticalis* and a Scissor-tailed Flycatcher (*Muscivora forficata*). Such aggressive behavior has obvious selective value in protecting eggs and nestlings from predation, as well as in defense against birds which might utilize the nest materials for their own nest construction.

Intraspecific territoriality in *verticalis* was frequent, especially in the birds nesting near each other at isolated localities of favorable habitat. At Plata a pair, which began nesting earlier than two others, dominated the area, excluding all other *verticalis*. One of the other two pairs eventually nested in a tree 180 ft away, but the third pair never constructed a nest—although at times the birds behaved as though they had selected a nest site.

Verticalis/vociferans interactions were observed near Plata, where a *verticalis* chased a *vociferans* from near the former's nest, but the *vociferans* returned. *Vociferans* were tolerated when they approached other *verticalis* nests; however, at a nearby locality a *verticalis* was chased by a nesting *vociferans*. The latter's nest had been partly dislodged by a strong wind the preceding evening, and earlier in the day the *verticalis* had taken nest material from it for their own construction. When not near their nests, the two species often perched within ten feet of each other and fed without interaction from the same perches.

Intergeneric aggression between *verticalis* and *Muscivora forficata* was observed on four occasions. In each instance it occurred near the nest of one of the birds, with defense manifested only in the immediate nesting area (i.e. less than 100 ft). At one such locality the birds subsequently constructed nests that were separated by a distance of only 30 ft, compared to two *verticalis* nests there separated by 195 ft. Away from their nest sites, *verticalis* and *M. forficata* were observed feeding together without aggression, and on some occasions they were perched within four ft of each other. Because of similarities in behavior and the occurrence of an intergeneric hybrid, Davis and Webster (1970) support the proposal of Smith (1966) to include *M. forficata* in the genus *Tyrannus*.

When near their nests, *verticalis* showed aggressive behavior toward a Say's Phoebe (*Sayornis saya*), a Vermilion Flycatcher (*Pyrocephalus rubinus*), and House Sparrows (*Passer domesticus*). The phoebe was attacked when as much as 20 ft away, while the other two species were allowed closer to the *verticalis* nests. An Ash-throated Flycatcher (*Myiarchus cinerascens*) was not given any apparent attention by *verticalis*, even when on two occasions it perched ten ft from their nest. Also ignored were Brown-headed Cowbirds (*Molothrus ater*), which came as close as three ft from perched kingbirds.

Intraspecific aggression by *vociferans* was observed only on two occasions. However, when near nests, *vociferans* several times attacked Cactus Wrens (*Campylorhynchus brunneicapillus*) and once each House Finches (*Carpodacus mexicanus*) and *T. verticalis*. An Orchard Oriole (*Icterus spurius*) was tolerated at five ft from a nest and a Vermilion Flycatcher at three ft. Nesting *vociferans* and *Muscivora forficata* occurred within 100 ft of each other, although the latter species tended to occur more frequently in habitats occupied by *verticalis* than by *vociferans*.

DISCUSSION AND CONCLUSIONS

Theoretically, species such as *T. verticalis* and *T. vociferans* can coexist only if each inhibits increase of its own population more than it does the other's (MacArthur, 1958). The most productive approach in studies of the ecological and other relationships of sympatric species is examination of the ways in which the resources of an area are used. Using this approach, I considered three principal aspects: utilization of different resources, of the same resources at different places, and of the same resources in different ways. If species are so different that mutual exclusion does not provide any increased access to a limited resource, interspecific aggression should, in time, decrease or disappear (Orians and Willson, 1964).

In the two breeding *Tyrannus* species in the Trans-Pecos, i.e. *verticalis* and *vociferans*, I did not find any interspecific defense of feeding areas, but such behavior was manifested in relation to nesting sites. This suggests that nesting sites are the resource most limited in supply and therefore worthy of defense. A large part of potential competition for nest sites is avoided through the distinct altitudinal segregation of the kingbirds throughout most of the region. Eighty-three percent of the *verticalis* nests were at elevations less than 4,000 ft, compared to 83 percent of those of *vociferans* at elevations in excess of 4,000 ft. None of the *verticalis* nests were at elevations greater than 4,500 ft and only one *vociferans* nest was found below 3,500 ft. This altitudinal segregation translated into difference in the habitat types used by the species. Thus, pine-oak-juniper, grassland, and riparian types were dominated by *vociferans*, whereas *verticalis* predominated in the desert shrub and farmland types.

Both species nested on man-made structures, but *verticalis* did so to a greater extent—as befits its occupancy of more open situations. Trees were preferred by both species for nesting, with *verticalis* nests lower (relatively and absolutely) than *vociferans*. This was not true in Arizona, where Hespenheide (1964) found these two species nesting in the same portions of trees. There only trees and shrubs were used and the birds were relatively more abundant than in the Trans-Pecos.

There were greater differences in the food taken by a species at a locality on different dates than by the two species at a locality on the same date. The extent of overlap in diets was 72.7 percent in families of insects and other prey taxa, but was complete in groups such as orders.

Other potential competitors of kingbirds include several species of flycatchers and non-flycatchers. The Scissor-tailed Flycatcher is biologically similar to the *Tyrannus*, occurring sympatrically with both, but more frequently with *verticalis*. An instance of interspecific aggression was observed between these two species, perhaps leading to their subsequent nesting in adjacent, rather than the same, trees. The hole-nesting Ash-throated Flycatcher occurs throughout much of the region, but it did not compete with either species in this study. Other species of flycatchers (e.g. *Sayornis* spp.) occur so infrequently that they have no obvious effect on the populations of the species studied.

Such species as the Loggerhead Shrike (*Lanius ludovicianus*) and the Mississippi Kite (*Ictinia misisippiensis*) take some of the same foods as the kingbirds but are sufficiently different otherwise in their biology that they are not obviously competitors.

SUMMARY

The kingbirds *Tyrannus verticalis* and *T. vociferans* were studied for possible competitive relationships in the Trans-Pecos region of Texas during June–August 1969 and May–August 1970, with supplemental observations in November 1970 and May 1971. The geographical and ecological distribution, nesting habits, food composition, and behavioral interactions were examined in each species.

Although the kingbirds were geographically sympatric, *verticalis* generally occupied elevations of less than 4,000 ft and *vociferans* predominated above 4,000 ft. Desert shrub and farmland were typically occupied by *verticalis*, whereas *vociferans* was more abundant in the pine-oak-juniper, grassland, and riparian habitats. Both species preferred trees as a nesting substrate, but *verticalis* often nested on man-made structures such as utility poles in open habitat where trees were not commonly found. Despite their occurrence in different habitat types, the kingbirds fed in a similar manner and had similar diets. There was no apparent interspecific defense of feeding areas, although the nest sites were defended.

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