COMPETITION AND THE GENUS *TYRANNUS*

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IN attempting to explain the great avifaunal diversity of the tropics, as well as certain distributional inequalities between tropical and temperate regions, Klopfer and MacArthur (1960, 1961) have theorized that one of the causes is a reduction of the size and an increase in the overlap of ecological niches in tropical regions. To demonstrate this they have employed the concept of character displacement (Brown and Wilson, 1956) as an index of ecological differences between competing or potentially competing sympatric species. Their data for tropical species, when compared to those of Hutchinson (1959) for temperate forms, differed in the way predicted by the hypothesis, i.e., the tropical species showed more overlap (less character displacement) than the temperate species. However, these data are only based on one class of characters and are without reference to the birds' interactions in nature. There are several other mechanisms which would not be obvious from morphological examination but which would prevent two potentially competing species from competing. Most simply, the two species may not be competing because other factors than competition limit their populations. Alternatively, Lack (1944) has suggested (1) the occupation of adjacent habitats by sympatric species or (2) the maintenance of a zone of equilibrium along a line of meeting by otherwise allopatric species as other "devices" that mitigate the effects of all-out competition at the macrohabitat level. At the level of the microhabitat, differences in physiological and behavioral, as well as morphological, characters may alleviate competition. The hypothesis of Klopfer and MacArthur thus invites comparative studies to determine the means and the extent by which competition is actually avoided in different localities.

It was recognized by Darwin that the more closely related are two species, the more likely it is that their needs are likewise similar. Sympatric congeners, because of this relation, are logical objects of studies of competition (Skutch, 1951), although Elton (1946) has pointed out the lack of necessity for systematic relationship in competition. Examination of the distributions of the six species presently included in the avian genus *Tyrannus* and known to breed regularly in North America north of Mexico shows that four of these occur in southeastern Arizona: the Cassin's Kingbird (*T. vociferans*), Western Kingbird (*T. verticalis*), Tropical Kingbird (*T. melancholicus occidentalis*), and Thick-billed Kingbird (*T. crassirostris*). In the accompanying maps (Figs. 1 and 2), prepared from various sources of distributional data (A.O.U. Check-list Committee, 1957; Blake, 1954; Cory and Hellmayr, 1927; Friedmann et al., 1957; Grinnell and Miller, 1944; Ridgway, 1907), it is seen that *melancholicus* and *crassirostris* reach the northern limits of their ranges and *verticalis* is

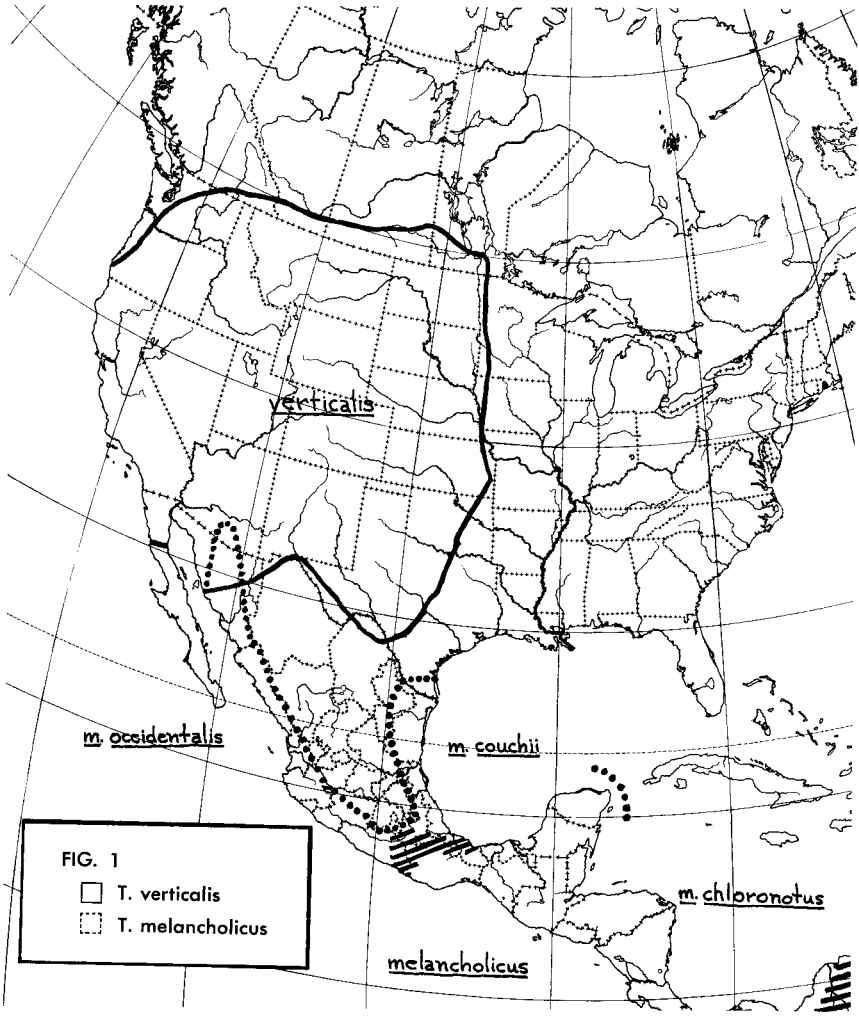

FIG. 1. Distributions of *Tyrannus verticalis* and *T. melancholicus*. Base map reproduced with permission of McKnight and McKnight Publishing Company.

on the southern limits of its range in Arizona. In terms of abundance *verticalis* and *vociferans* are common and the other two are less common (Brandt, 1951; Levy, 1959). Competition is said to exist among all four (Brandt, op. cit.; Marshall, 1957), but at present, information regarding the interrelations of these kingbirds is available only as incidental observations in studies more general in scope, e.g., those of Brandt and Marshall. Although attempts at

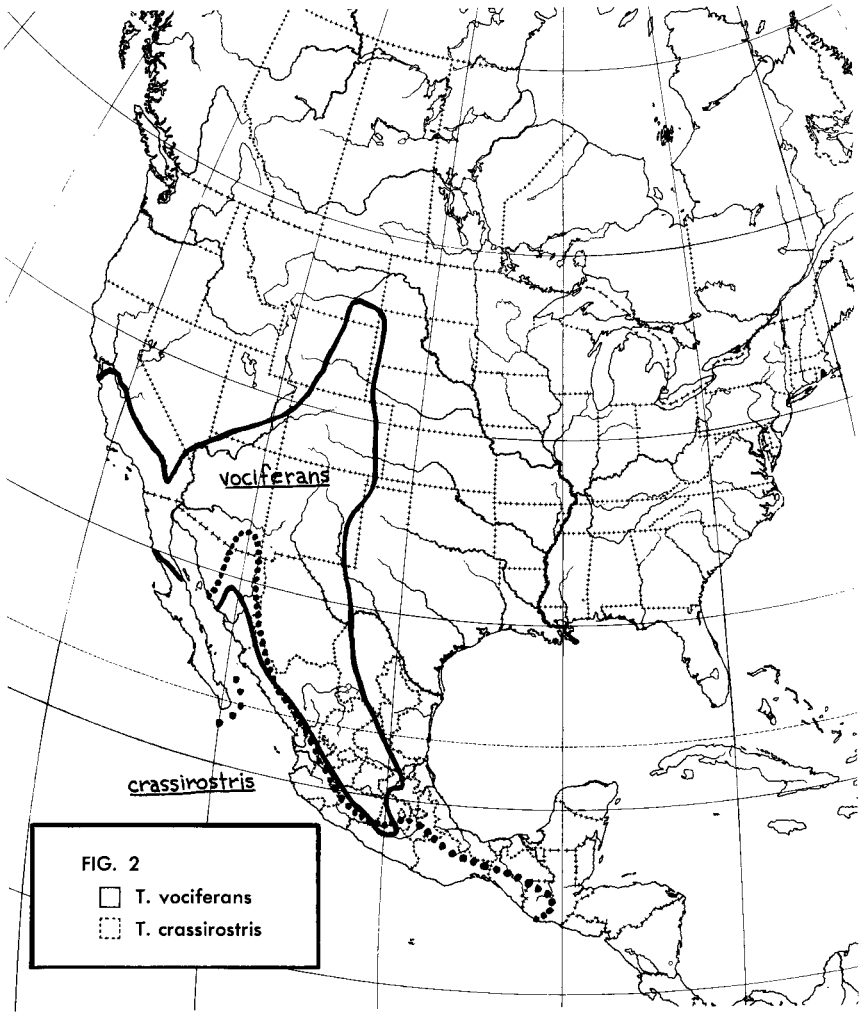

FIG. 2. Distributions of *Tyrannus vociferans* and *T. crassirostris*. Base map reproduced with permission of McKnight and McKnight Publishing Company.

ecological separation have been made, heretofore there has been no quantitative study of the problem.

DESCRIPTION OF STUDY AREA

From 1 June to 27 July 1962, extended observations of kingbirds were made at the Southwestern Research Station of the American Museum of Natural History, located in Cave Creek Canyon of Arizona's Chiricahua Mountains. Several other locations in southeastern Arizona and northern Mexico were visited.

During this period more than 120 pairs of the four kingbird species were studied to determine their breeding ecology. Most of the work centered on 100 pairs of *Tyrannus vociferans* and *T. verticalis* which bred in the vicinity of Cave Creek and along a 37-mile section of U. S. Route 80 east of the Chiricahuas.

Of the kingbird pairs in the two study areas, 53 bred near Cave Creek and were distributed along a 7-mile section of the creek from about 0.9 mile northeast of the town of Portal to about 4.4 miles west–southwest of Portal, i.e., from where the road to San Simone crosses the creek to about the upper limit of sycamores. The plant communities in the vicinity of observed nests would probably form a rough continuum from the moist, cool mountain forests to the hot, arid valley deserts were it not for locally large differences in exposure, the availability of water, or grazing pressure. The most obvious example of such a difference, frequently observed elsewhere, is Cave Creek itself. The mountain stream runs dry as the climate becomes progressively more arid downstream, but the water of the stream allows the formation of a well-defined riparian community along its path. Additionally in the case of Cave Creek Canyon, the canyon walls of 800 to 1,200 feet, which limit vegetation inside the canyon, drop steeply to the desert on the western side of the creek, and sharpen the distinction between plant community types typical of the desert and those typical of the lower slopes of the mountains. On the eastern side, the canyon walls slope somewhat more gradually to the desert over a distance of 2 miles. This slope, as one progresses toward Portal, exhibits the normal change in vegetation types that occurs as aridity increases. Since the creek continues to run along the base of this slope, there is interposed between the completely canyon and completely desert communities an area where the creek is bounded on the one side by a desert shrub community and on the other by an arid association typical of the lower mountainsides. The particular vegetation types to be found within each of three broad zones—canyon, transition, and desert—and in the riparian associations can be briefly generalized as follows:

Within the canyon there are two general types of associations: the one is characteristic of the more-exposed, south-facing slopes and is dominated by several species of oaks (*Quercus* spp.), a juniper (*Juniperus deppeana*),[1] and a century plant (*Agave palmeri*); the other is typical of the less-exposed, but rockier, north-facing slopes and is dominated by pines (*Pinus engelmannii, P. leiophylla,* and *P. edulis*) and oaks. The riparian community in this zone is almost entirely dominated by sycamores (*Platanus wrightii*), except at the canyon mouth where a few cottonwoods (*Populus fremontii*) are found. The sycamores dwindle off above 5,700 feet and are replaced primarily by large pines (*P. engelmannii*).

[1] Plant names after Kearney and Peebles (1960).

In the transition zone, to the west there are only 600 or 700 yards of rather dense oaks, juniper, and shrubs before the mesquite (*Prosopis juliflora*) community is reached. On the east the slopes change more or less gradually from pines (esp. *P. edulis*) to a mixture of oaks, juniper, and shrubs of medium height (e.g., *Arbutus arizonica*) and finally to a scattered association of juniper, oaks, and agave reminiscent of the south-facing slopes of the canyon. The riparian community broadens out at the mouth of the canyon and continues with little change to the town of Portal. Cottonwoods continue to be found among the sycamores for part of the way to Portal but are always less frequent than the sycamores.

At the town of Portal, desert shrub communities become characteristic of both sides of the riparian zone, with a change in composition from primarily mesquite to a mixture of several species, notably *Acacia constricta, Prosopis pubescens, Flourensia cernua, Atriplex cansecens,* and *Rhus microphylla.* Without the protection of the foothills the riparian zone undergoes a profound change: the sycamores become fewer, smaller, and more scattered until only a higher density of shrubs marks the riparian effect.

Away from the effect of the mountains, the desert takes a rather wide variety of forms, depending on local conditions of soil, moisture, and grazing. To sample these other desert community types, censuses were made along 36.7 miles of U. S. Route 80, from Granite Pass in the Peloncillo Mountains (Hidalgo County, New Mexico) to a bridge 5.8 miles south of Apache, Arizona, and along some of the side roads. These censuses yielded 47 kingbird pairs. Desert shrub community types exist in many combinations of species (see above, also *Mimosa biuncifera* and creosote bush, *Larrea tridentata*) or as pure stands, with mesquite and creosote bush types the most common of the latter. Washes left from the runoff of rains occasionally support either a somewhat different flora (e.g., those lined with desert willow, *Chilopsis linearis*) or more robust forms of shrubs already there, especially mesquite and acacia. Besides shrubs there are other, more open associations, including *Ephedra trifurcata–Yucca* sp. stands, various grassland types,[2] and the extremely depleted herb communities (variously composed of *Gutierrezia microcephala, Salsoli kali,* numerous annuals, etc.). Yuccas, an important nesting site for the Western Kingbird, are found irregularly in groves in most desert community types. Of the other large, but less frequent desert plant species, only the soapberry (*Sapindus saponaria*) was of any significance to kingbirds in the study.

Man's influence on the vegetation is varied but apparently is nearly always beneficial to kingbirds (see Table 1). Other than the indirect consequences of grazing by cattle, the most significant effects to both vegetation and kingbirds are the opening of the riparian association for buildings, orchards, and corrals

[2] Of *Aristida* and *Bouteloua*, e.g., see Darrow (1944).

TABLE 1
DISTRIBUTION OF NESTS

Zone	*vociferans*			*verticalis*		
	C*	D	Total	C	D	Total
Upcanyon	9		9			
Transition	27		27	8		8
Desert	2	4	6	7	43	50
Riparian	1	2	3	6	6	12
Town	1	2	3	1	9	10
Roadside					11	11
Desert					17	17
	38	4	42	15	43	58

* C = nests found in Cave Creek Canyon; D = nests found in desert census; see text.

and the planting of shade trees, orchards, and other crops in desert locations. Other, nonvegetational effects of man—again significant and beneficial—include the erection of fences, telephone wires, and assorted structures, and those miscellaneous activities which increase insect populations, especially the keeping of animals and the impoundment of water (cf Table 1).

The discussion which follows will be based primarily on the kingbirds found along Cave Creek and that portion of U. S. 80 delimited above. Other localities were visited to observe briefly either additional habitat types or different kingbird species. Of these, the most important were Guadeloupe Canyon, an arid cottonwood–sycamore canyon at the conjunction of Arizona, New Mexico, and Mexico; Sonoita Creek near Patagonia in Santa Cruz County, Arizona, and the Rio Magdelena at several points from Imuris to Terrenate, Sonora, both examples of cottonwood river bottom.

Nesting distribution of nests.—The distribution of nesting sites of the 100 kingbird pairs found in the two study areas was considered in terms of the three habitat zones described above. As seen in Table 1, abstracted from the several census maps, the greatest proportion of the Cassin's Kingbirds' nests was located in the transition zone, despite the limited amount of this type of area present. Canyon and desert localities both had nesting Cassin's Kingbirds, but these areas were clearly less preferred. The smallest numbers were in the desert and these were often associated with man's activity. The Western Kingbird was found primarily in the desert localities with a small number of pairs inhabiting the transition zone. The greater portion of the pairs of desert birds observed chose riparian or roadside and other man-created habitats in which the uniform desert community types were "interrupted," while about a third chose the more uniform desert localities.

TABLE 2
LOCATION OF NESTS

Plant type	*vociferans*	*verticalis*
Trees:	44	30
Sycamore	35	15
Cottonwood	2	10
Unrecorded	3	5
Pinus engelmannii	3	
Juniper	1	
Shrubs (*Chilopsis*, Mesquite, *Sapindus*):		11
Yucca:		17
	44*	58

* Two abandoned nests of pairs which later renested are included.

Location of nests.—The choice of the particular plant species in which a kingbird pair nested appeared to be largely dependent on the local flora. Since the riparian vegetation in most cases was composed either of sycamores or cottonwoods with few of the other species present, a bird which wished to nest in riparian communities had to nest in what was available or not nest at all. Thus, the particular plant species used is apparently of little importance (see Table 2).

On the other hand, the data suggest that what is of importance to kingbirds is the height of the nest, nest tree, or both. All of the nests of the Cassin's Kingbird were in trees. The average height of 15 nest trees whose heights were recorded was 52 feet, with a range of from 40 to 80 feet. Two of Bent's records (1942) of Cassin's Kingbirds nesting at comparatively low heights of 8 and 10 feet are therefore of interest. Another low nest attributed by Bent to a Cassin's Kingbird pair was checked with the original source (Rockwell, 1908) and was found to be incorrect, the birds being Western Kingbirds; other low nests attributed by Rockwell to Cassin's Kingbirds are subject to some doubt as he apparently had some difficulty in distinguishing the two species (op. cit.:166, lines 31 ff.). Western Kingbirds in this study area nested about equally in smaller and larger plant species, although it should be noted that they were never observed to choose a smaller species when trees were available; e.g., all nests of both kingbird species found along Cave Creek were in trees. The height of nest plants when shrubs (range 10–15.5 feet) or yuccas (range 10.5–18 feet) were roughly the same and averaged 13 feet for 12 nest sites. Only one height of a nest tree used by a Western Kingbird was recorded, there being no apparent difference from those used by Cassin's Kingbirds.

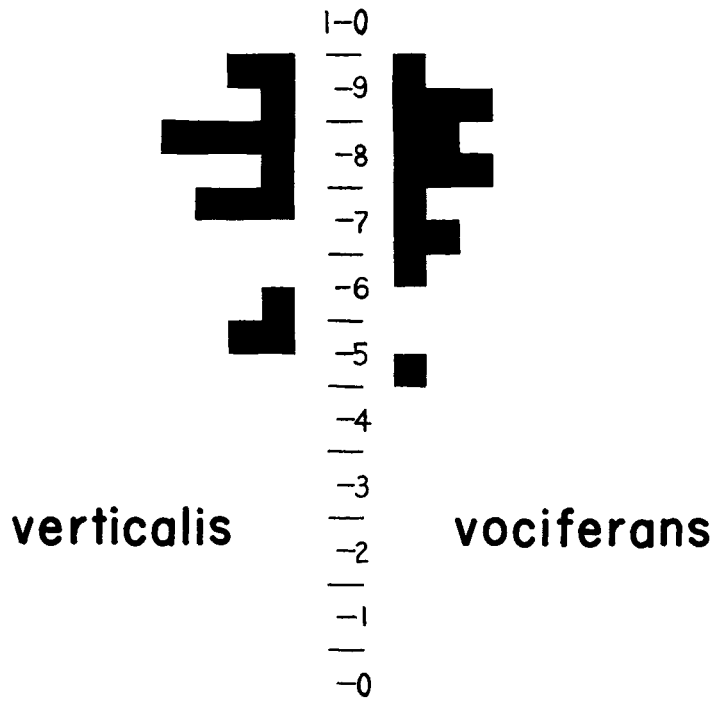

FIG. 3. Height of kingbird nests relative to that of the plant in which it was found.

While the absolute height of kingbird nests varied over a wide range (from 5.5 to 70 feet), their height relative to that of the nest plant was roughly the same for both species (see Fig. 3). Of 14 nests of the Cassin's Kingbird ranging from 22 to 70 feet high, the average relative height was 0.81, ranging from 0.47 to 0.92. Of 14 Western Kingbird nests placed at 5.5 to 50 feet high, the average was 0.76, ranging from 0.54 to 0.92. It is interesting to note that the nest with the lowest relative height was destroyed, though its likewise exceptional location in a completely dead pine may have been a more significant factor. The heights of the nests were not limited by the configuration of the nest sites since the sycamores and desert shrubs from which the data from 23 of the 28 nests were taken are branched over most of their height.

Observations of the other two kingbird species and data in the literature in-

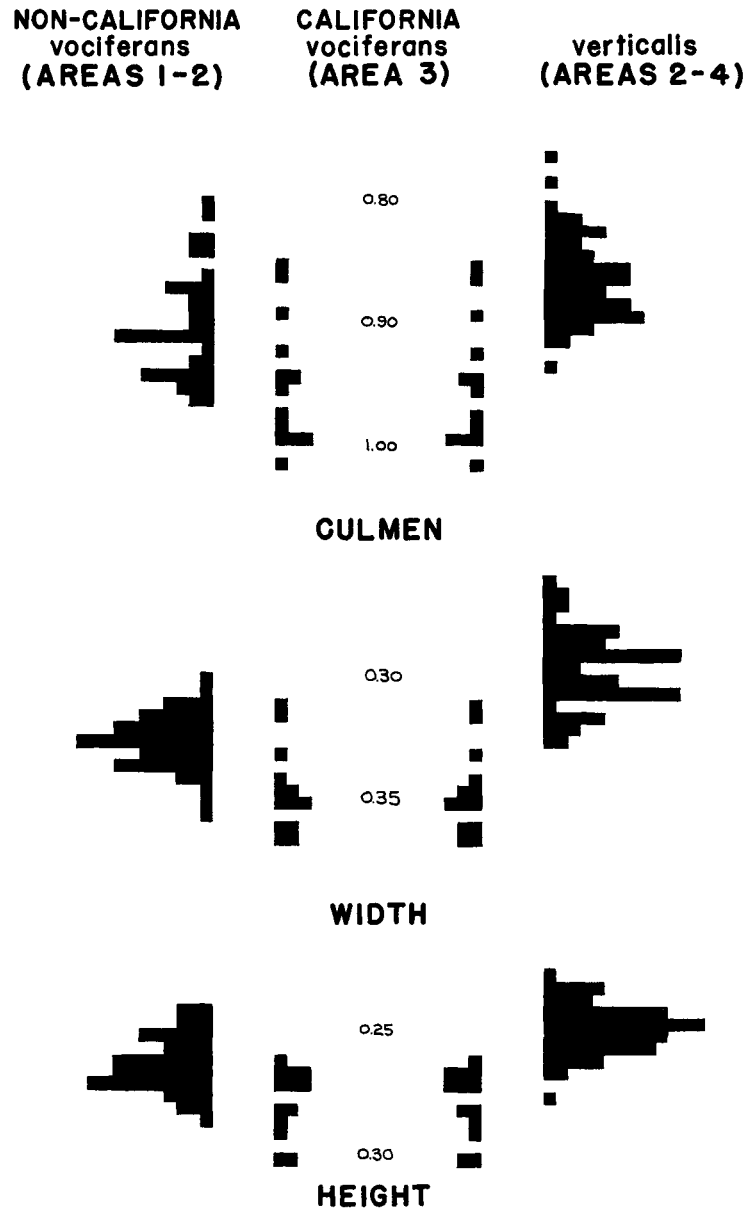

FIG. 4. Measurements of the bills of *Tyrannus vociferans* and *T. verticalis* in thousandths of an inch. There is an indication the California population of *vociferans* shows a slight character displacement in the presence of *verticalis* and in relative isolation from its own species.

dicate that their nesting habitats are roughly similar to those of the two under more intensive study. Tropical Kingbirds were observed on the Sonoita Creek in Arizona and near Imuris in Sonora, at both places in cottonwood river bottoms. Although no nests were found, reports indicate the breeding of *melancholicus* is most like that of *verticalis* in its choice of both high and low sites (Bent, op. cit.; Marshall, op. cit.; Davis, 1944). The nesting of *crassirostris*, on the other hand, is apparently most like that of *vociferans*. Observations of the Thick-billed Kingbird were made at Patagonia, Guadaloupe Canyon, and near Terrenate in Sonora. The one nest of this species observed was being built at Patagonia, 55 feet high in a 65-foot sycamore (relative height, 0.84). Comparison with reports from van Rossem (1941), Selander and Giller (1959), and Marshall (op. cit.) indicates this is typical for the species; no reports of low nests have been found.

MORPHOLOGY

In order to assess morphological limitations on feeding behavior the index of character displacement as interpreted by Hutchinson (op. cit.) and Klopfer and MacArthur (op. cit.) was employed. Measurements of 160 kingbird bills were made at the U. S. National Museum and the American Museum of Natural History. The bill was measured along three coordinates: the length of the culmen from the base of the red feather patch of the crown to the tip, the width at the anterior extent of the nostrils, and the height at the angle of the gonys. The cumulative results for *vociferans* and *verticalis* are shown in Fig. 4. To test the apparent bimodal distributions obtained initially for possible geographical variation (see Brown and Wilson, op. cit.), measurements of specimens from four different regions were graphed separately (see Fig. 5):

T. vociferans occurring alone—

(1) Mexico, not including the Baja Peninsula;

T. vociferans and *verticalis* sympatric, the populations of *vociferans* isolated—

(2) Texas to southern Arizona, north to Colorado, Utah, Wyoming, and Nevada;

(3) southern California and the Baja Peninsula;

T. verticalis occurring alone—

(4) Idaho and northern California.

These groupings of measurements showed that there was no significant intraspecies difference in the presence of the other species—which might have been expected if character displacement had occurred—except possibly in the case of the California population of *vociferans* (see Fig. 4 and Table 3) which was the only really isolated population in either species; however, the small sample allows only tentative generalization.

TABLE 3

A. AVERAGE MEASUREMENTS OF BILL DIMENSIONS OF KINGBIRDS (IN INCHES)

	Culmen	Width	Height
1. *verticalis* (59 specimens)	0.865	0.298	0.248
2. *vociferans*—non-California (51)	0.911	0.328	0.265
3. —California (13)	0.950	0.348	0.280
4. *melancholicus chloronatus* (10)	0.988	0.278	0.363
5. *occidentalis* (7)	1.016	0.278	0.378
6. *crassirostris crassirostris* (10)	1.064	0.402	0.470
7. *pompalis* (10)	1.144	0.415	0.470

B. RATIOS OF MEASUREMENTS FROM SYMPATRIC FORMS

	Culmen	Width	Height	Product
Non-California *vociferans / verticalis*	1.05	1.10	1.06	1.22
California *vociferans / verticalis*	1.10	1.17	1.14	1.47
c. crassirostris / m. occidentalis	1.05	1.44	1.24	1.87
c. pompalis / m. occidentalis	1.13	1.49	1.24	2.09

It should be noted (Table 3) that the ratios of the magnitude of the larger bill to the smaller fall well below those suggested by Hutchinson as typical for temperate sympatric species and are closer to those of Klopfer and MacArthur for tropical species. Ratios were likewise prepared (see Table 3) for *melancholicus occidentalis* and *crassirostris*, which have an extensive overlap of distribution. Interestingly, the members of *crassirostris* north of Sinaloa apparently show a marked increase in the magnitude of bill.[3] The possibility that this is a case of tropical–temperate character displacement is somewhat confused by the increase in bill size from the Central American subspecies of *melancholicus chloronatus* to *m. occidentalis*. The bills of both species are larger than those of *vociferans* and *verticalis*.

DISCUSSION OF THE DATA

Competition for space may take place at three different levels: the geographic ranges of the species, the types of communities within a given geographical area, and the particular microhabitats within a given community. Of these, the Cassin's and Western Kingbirds show significant differences in requirements in the first two. By tracing the two ranges and the zone of overlap onto heavy paper and by cutting and weighing the pieces, it was found that at the level of geographical range the zone of overlap was 63.7% for the Cassin's Kingbird and

[3] This portion of the population was named *pompalis* by Bangs and Peters (1928).

TABLE 4
DISTRIBUTION BY HABITAT

Habitat type	*vociferans*	*verticalis*
Riparian or riparian-like flanked by		
Pine and juniper–oak	9	
Pine to juniper–oak and desert	27	8
Desert only	6	22
Nonriparian—desert		28
	42	58

27.5% for the Western Kingbird with no way of assessing the population densities of the species affected in the zone of overlap as compared to others.

At the level of preference of habitat, relations are somewhat difficult to assess, owing to the difficulty of strictly delimiting a habitat. This difficulty is in turn complicated by the nesting peculiarities of the two species, i.e., nesting in one habitat while feeding in another. On the basis of the above data, it is apparent that the Cassin's Kingbird will nest in any broad habitat zone in which there are tall trees for the nest. This was emphasized most strongly by a pair of kingbirds that nested in a cottonwood about 3 miles southwest of Apache: the only other tree for perhaps a mile was a small sycamore 35 feet tall, 400 yards to the southwest. Except for two bushes and telephone wires, there was only short grass desert. The Western Kingbird, on the other hand, showed a large range in the height of the plants used for nests, but occurred only in areas where there was habitat at least as open as a desert shrub community nearby. A summary of nest distributions by habitat types is given in Table 4. "Riparian-like" habitats are those in which tall trees occurred, especially in desert locations, e.g., the town of Rodeo. It should not be inferred that a well-defined riparian association was necessary to the nesting of the Cassin's Kingbird. Large pines and junipers were used in three cases in Cave Creek Canyon on the north-facing slopes somewhat away from the creek, and the species was observed in the oak woodland in the foothills of the Santa Rita Mountains where there was no riparian community nearby. In desert riparian localities investigated by Brandt (1951:399) it was estimated there were ten pairs of Western Kingbird per Cassin's Kingbird pair in the sycamore "strands."

There is no evidence that the microhabitat of the two species is different. Although both species are highly territorial intraspecifically, interspecific territoriality apparently does not exist. Intraspecifically defended territories frequently overlapped interspecifically and one instance of Western and Cassin's Kingbirds nesting in the same tree was observed near Portal. Interestingly, it is

doubtful that the territory is actively maintained even intraspecifically in adjacent feeding habitats by pairs nesting in the riparian association, especially in view of the distances involved in feeding flights which in some observed cases approached a quarter of a mile. Chance aggressive encounters may occur, however. The generalized kingbird niche appears to be that of an overcanopy species, with the choice of feeding habitat, at least in the case of the Cassin's Kingbird, dependent only on the location of the nest. This conclusion is supported by several observations. (1) The position of the nest relative to the height of the plant in which it is placed has already been discussed. (2) The frequent location of Western Kingbird nests along roadsides, where the added height of telephone wires and fences as perches is important, is indicated in Table 1 and by the choice of several particular nest sites that would appear to be substandard were not the wires present (e.g., a census along 30.3 miles of U. S. 80 south of Rodeo, N. M., on 24 July showed 155 birds perched on wires). (3) Feeding sallies of kingbirds, in a small sample of 30 attempted captures, showed 53% attempts above the perch level, 17% at the level, and 30% below. The perch chosen in a particular foliage type was almost invariably the highest possible, or within a few feet of the highest. (4) As for the species' independence of particular plant formational types, the Cassin's Kingbird, it has been noted, fed in a full range of formational habitat types from short grass desert to riparian associations. Observations, of an upcanyon female feeding young showed that of 240 minutes, 29% was spent in the riparian zone or at the nest, 40% in pine, 25% in juniper, and 3% in either pine or juniper. The members of a pair watched for 210 minutes (female 120 minutes, male 90 minutes), feeding young at a nest on the desert edge of the riparian zone near Portal, spent 39% of the time at the nest sycamore, 59% in the desert shrub or high grass, and 4% in the riparian. The low last figure was due at least in part to another nearby and highly territorial Cassin's pair in the riparian zone. Likewise, though desert shrub communities were clearly preferred by the Western Kingbird, individuals nesting in the riparian zone were observed feeding there.

The possibility that there is a difference in the time of nesting has been suggested for the California populations of the two species of *Tyrannus* as a microhabitat difference (Evermann, 1886; Willet, 1912), but no such difference was observed in Arizona. Although stomach contents of the two kingbirds have been studied (Beal, 1912), these data are of little use because of their miscellaneous origin, and the morphological indices had to be used. In view of the large degree of spatial isolation other than in the microhabitat, it would not be surprising if there was little selection for differences in bill size, though if the larger bills of California birds are significant the amount of isolation may be important.

The effect of competitors other than congeners on food supplies or breeding spaces of the kingbird seems negligible. Of the other 11 species of flycatchers

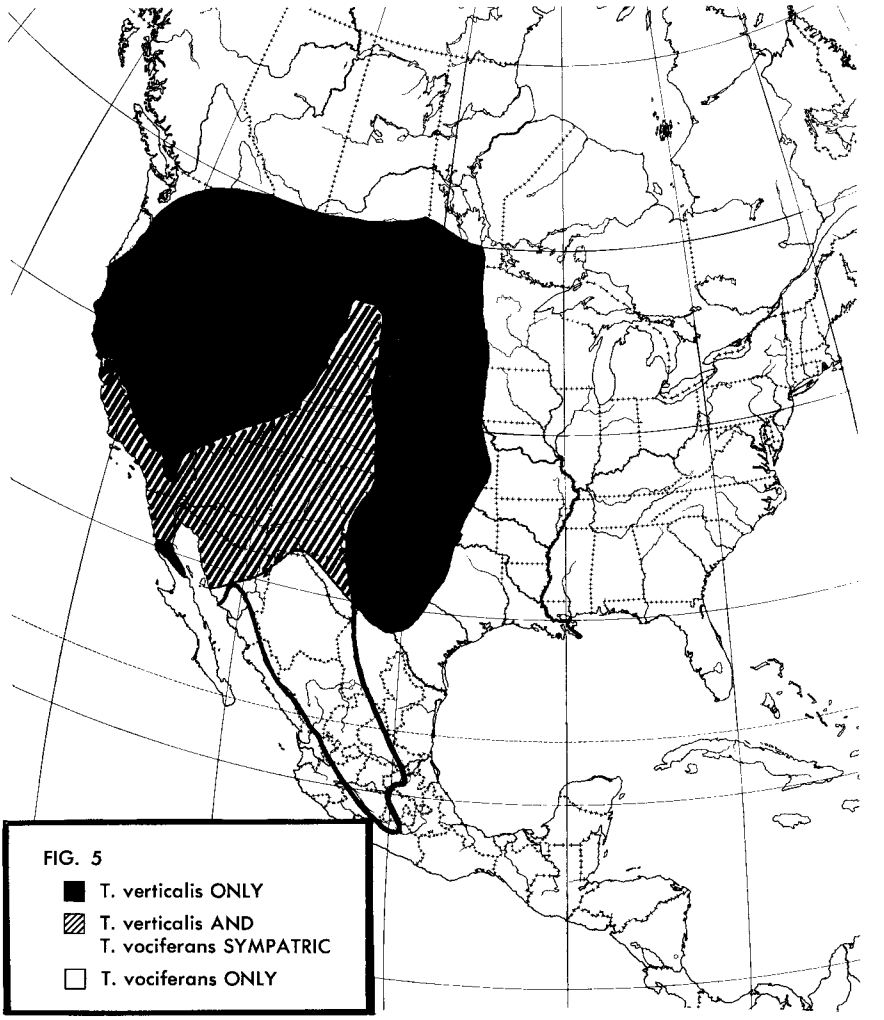

FIG. 5. The distributions of *Tyrannus vociferans* and *T. verticalis* in relation to one another. Note the relative isolation of the California population of *vociferans*. Base map reproduced with permission of McKnight and McKnight Publishing Company.

seen by me in southeastern Arizona, nine were found in association with kingbirds. Of these, four were hole-nesting species that usually tended to feed near the middle or bottom of the foliage profiles of both tall and medium-height foliage types and included the three species of *Myiarchus* and the Sulphur-bellied Flycatcher (*Myiodynastes luteiventris*). The Sulphur-bellied Flycatcher was the only one of these four seen to feed above the canopy, but the small,

peripheral nature of the species' population reduces any possible competitive significance. The Western Wood Pewee (*Contopus sordidulus*) and Beardless Flycatcher (*Camptostoma imberbe*) occurred at the middle of the higher foliage profiles, the former nesting on the top of higher horizontal limbs and feeding in and on the edge of rather dense foliage, and the latter feeding quite unlike typical flycatchers. The Black (*Sayornis nigricans*) and Say's Phoebes (*S. saya*) and the Vermilion Flycatcher (*Pyrocephalus rubinus*) were understory species along streams or in semiopen areas of tall trees and little undergrowth, nesting on man-made structures or on the tops of the lowermost branches of large trees.

There are also several possible nonflycatcher competitors. In desert localities the Loggerhead Shrike (*Lanius ludovicianus*) utilized the same perches and probably took some of the same insects as the Western Kingbird, but its preferred nesting sites and habitats were largely substandard for kingbirds. In some of the towns and riparian localities visited briefly Phainopeplas (*Phainopepla nitens*) were common, but their competitive effect on kingbirds is unknown. Raptors were always vigorously attacked by kingbirds, but there was no significant effect by either of the two parties on the other, and a Cooper's Hawk (*Accipiter cooperii*) pair nested sucessfully in a tree at the Southwestern Research Station only 100 feet from a tree that housed two broods of Cassin's Kingbirds and 250 feet from a second kingbird pair. The typical overcanopy feeders—three species of swallows and the White-throated Swift (*Aëronautes saxatilis*) occurred in the vicinity of kingbirds—tended to fly higher than kingbirds except at dawn and dusk when they frequently fed just over the treetops. Their specialized method of feeding which relies primarily on large quantities of small insects probably prevents their sharing many prey species with the kingbirds which instead rely on individual captures of large insects. Caprimulgids and the smaller, insect-eating owls are temporally isolated from competing with kingbirds.

CONCLUSIONS

At present it appears that the following factors prevent serious interspecific competition between *Tyrannus vociferans* and *T. verticalis*: (1) a high degree of spatial isolation and (2) the limiting of the populations of both species by (a) the intraspecific competition for nest sites within each species and by (b) the choice by each species of only a small part of the available habitat for nesting while feeding in all of it. *Tyrannus melancholicus* and *T. crassirostris* are virtually entirely isolated geographically from competition with *T. verticalis* and *T. vociferans*, although sympatric with each other over most of the range of *T. crassirostris*. The relations between the latter two species remain to be investigated, but indications are that they resemble the relations between the two species discussed in detail.

This study also indicates that Klopfer's and MacArthur's use of culmen lengths or similar indices to measure microhabitat differences in sympatric, congeneric species must take into account the fact that morphological similarities between related forms may be permissible where other forms of spatial isolation allow the avoidance of competition. The necessity for the examination of other, possibly variable, morphological, physiological, and behavioral characters in those species in which microhabitat delimitations occur may make a multipower index more useful, should the problem of ecological determinants of distribution be investigated more closely and on a comparative basis.

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