

THE BREEDING ECOLOGY OF TOXOSTOMA CURVIROSTRE AND
T. BENDIREI IN THE VICINITY OF TUCSON, ARIZONA

by

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The breeding ecology of Toxostoma curvirostre and
T. bendirei in the vicinity of Tucson, Arizona

by James E. Ambrose, Jr.

Introduction

It is not uncommon to find, in the lush rain forests of tropical America, closely related avian species of very similar morphology, size and habits living side by side in the same habitat. The Myiozetetes flycatchers provide a good example of this phenomenon; M. similis and M. cayennensis may be commonly found living and nesting next to one another the year around in the more open parts of the lowland forests of Panama, yet judging from appearances, one unfamiliar with them would almost certainly regard them as one species. In the temperate forests of North America, however, interspecific competition between species of essentially the same habits appears to be averted by either marked ecological differences separating species of comparable sizes, as in the Empidonax flycatchers, or by marked size differences in species occupying the same areas, as seen in the Hairy and Downy Woodpeckers (Dendrocopos). The morphologically extremely similar species of Empidonax in the western portions of the United States are segregated ecologically as follows: difficilis in moist woods, coniferous or mixed forests, canyons, and groves;

wrightii in sagebrush, pinyon, and juniper; oberholseri in mountain chaparral with a scattering of trees; hammondi high in coniferous forests; minimus in open woodlands, poplar and aspen groves, and orchards; and traillii in willow and alder thickets of low valleys, swamps, canyons, high mountain meadows, brushy bogs, and muskegs (Peterson, 1961). Dendrocopos pubescens and D. villosus, on the other hand, overlap broadly in habitat and feed on the same trees where they occur together, but the former is a decidedly smaller edition of the latter, averaging about two and a half inches shorter in length. Since villosus measures only about nine inches in total length and has a proportionately larger bill than pubescens, the approximately 29 percent differential in length indicates a significant difference in bulk.

The cases of Empidonax and Dendrocopos illustrate the embodiment in nature of the ecological hypothesis known as Gause's principle, which states that different species, when they occur together, must in some sense be occupying different niches. In its strictest sense, this principle approaches being a truism, as Hutchinson (1957) has pointed out. In practical terms, however, its implication is that organisms which live together are to a large extent favored by different parts of their environment, so that the magnitude of ecological overlap is small. This seems to hold true for a great many species, and on this basis the hypo-

thesis has become accepted by many workers in the natural sciences.

Gause's principle pertains only to those situations in which some external limiting factor exists. If two species have sufficiently similar requirements, competition ensues when the factors both need exist in limited supply, resulting in the displacement of their niches or in the elimination of one of the species (Odum, 1959).

Consideration of the number of avian species breeding in areas of disparate environmental stress and niche availability is instructive. Udvardy (1958) lists 229 species whose breeding habitat is in the forests and woodlands of North America, but tabulates only 29 which breed in the desert scrub of the same vast region and are characteristic of that habitat. In contrast, Chapman (1926) allots 406 genera and some 749 species to the humid tropical forests of Ecuador, a country whose size is one-seventieth that of North America as delimited by Udvardy! To explain this great discrepancy in number of species, Klopfer (1959) has hypothesized that tropical faunas are more diversified because natural selection has resulted in producing smaller niches in the tropics. MacArthur (1957) has set up mathematical models describing the species abundance of an area in terms of non-overlapping, overlapping, and particulate niches. Such data as are available are reported by Mac-

Arthur to resemble most closely the model for non-overlapping niches.

When compared to other ecological formations, desert scrub is seen to be relatively marginal in its ability to support life. Its limited fauna implies that community stability, as in the arctic, is precarious. Should a resource such as water become limited, therefore, drastic conditions which would make survival difficult would be expected to result. In the desert scrub, then, one would expect that mechanisms to reduce interspecific competition would be at a premium, and had conditions as drastic as those suggested already occurred, such mechanisms would surely be in plentiful evidence. Nevertheless, this does not seem to be the case. Gould (1961) found the ecological requirements of the Cardinal and Pyrrhuloxia (Cardinalis), which breed in the same area at the same time, to be very similar. Marshall (1960) found the same to be true for the Brown and Abert's Towhees (Pipilo) where they exhibit ecologic overlap, although this is a marginal and limited situation. The Curve-billed Thrasher (Toxostoma curvirostre) and Bendire's Thrasher (T. bendirei) offer another opportunity to examine the niche relationships of sympatric sibling species.

The literature concerning these thrashers not only fails to clarify their relationships, it is, rather, quite confusing in that the various authors contradict one an-

other on a great many points. Thus Gilman (1909) writes of bendirei that it is not seen during the winter months because it is then excessively retiring, but most other observers feel there is little question that most of the individuals of this species migrate southward in the fall to return in the spring (Brown, 1901; Bent, 1948; Bailey, 1928; Howell, 1916; Scott, 1886). Brandt (1951), Ligon (1961), Bailey (1928) and others report bendirei to be a very wild and wary bird, but Gilman (1909) claims that if unmolested it becomes quite tame and even enters yards to feed. Brown (1901) heard bendirei sing but once, although he collected some two hundred nests of the species. Conversely, Gilman (1909) reports frequently using the song as a means of locating the nest. To Brown (1901) it seemed that the similarity of the external nest was the only thing the two species had in common, whereas most of the other authors agree that the appearance of the nests is consistently distinctive. Howell (1916), Swarth (1914), Engels (1940), Gilman (1909), Brown (1901) and Scott (1886) report bendirei to be common or abundant, in several cases with specific reference to the Tucson area, yet it is listed in the Field Check List of Birds for that area, compiled by A.R. Phillips in 1947, as uncommon in summer and occasional in winter. Writing of curvirostre, Swarth (1920) states that cultivated lands hold little attraction for it, while Brown (1892) holds that they frequent just such places

during the winter months. Whereas most works describe the iris color of bendirei as of a lemon-yellow hue paler than the orange-yellow of that of curvirostre, Gilman (1909) will have it be orange-red. Regarding habitat, Brandt (1951) assigns bendirei to a nesting association of cactus-paloverde and curvirostre to cholla meadow. Sutton and Phillips (1942) and Phillips in Pough (1957) think bendirei to be characteristic of open farm country. Engels (1940) writes that bendirei prefers thicket margins, and Brown (1901) says it seldom leaves flat country for the "rough and barren" hills where curvirostre is found. Gilman (1909) and Swarth (1920) say that the two species occur in exactly the same areas, a statement with which many of the authors already cited seem to be in tacit agreement. Such varying reports were a further incentive to studying these birds, particularly bendirei, for the habits of this species seemed to be only vaguely known, whereas there was virtual harmony concerning the ubiquitous and conspicuous curvirostre.

Purpose

The objective of this investigation was the elucidation of the ecologies of T. curvirostre and T. bendirei, with a view to contributing some information pertinent to certain ecological generalizations, and secondarily in the hope of dissipating some of the confusion which had grown up about T. bendirei.

Acknowledgments

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Methods

Field observation and collecting of specimens for analysis of stomach contents were the principal lines of investigation used. Most of the observations were along the foothills of the Tucson Mountains to the northwest of Tucson. Although most of the 75 specimens collected were taken within the immediate neighborhood of the city, the limits of the area involved were Oracle Junction, some twenty miles to the north of Tucson; Continental, twenty-five miles to the south; Ajo Road nine miles west of the city and Wilmot cienega, about seven miles to the east. Descriptions of

the physiognomy and vegetation were taken wherever thrashers were found; 156 nest sites of curvirostre and 12 of bendirei were examined by me, and height of the base of the nest above ground was estimated. Whenever a bird was seen perched above ground, its actions or attitude, the type of perch used, and an estimate of its height were taken. To ascertain whether the environment was used differently for different purposes, or differently by one species as compared to the other, tabulations were made of the heights at which birds of both species had been noted sitting, calling and singing. At times a single bird on a perch might do all three without moving, in which case the entry was made in each category. Birds which had been flushed by the observer were not entered into this tabulation, but compiled separately. Juvenile individuals were also excluded. Student's "t" was used to test for significant differences in the various categories.

I identified seed material by reference to the seed collection in the Arizona Cooperative Wildlife Unit laboratory. Mr. Anthony Ross identified arthropod material and provided information from which I set up an analysis of probable foraging activity.

Investigations occupied irregular intervals from November 1961 to May 1963. Birds whose weights are tabulated are from the ornithological collection of the University of Arizona.

Morphology

Toxostoma curvirostre is a larger bird (Table 1) with a longer, more decurved bill, heavier proportions, a more vivid iris, and more diffuse, obtuse spotting of the chest than T. bendirei, but for all that the birds are look-alikes. Typical adults of either species may readily be distinguished by the shape of the bill, a character second only to the voice in value as a criterion for identification, but since the bill grows allometrically, it can be misleading in younger curvirostre. The shape of the chest spots, when they can be seen, is a good field mark, but wear makes the spots almost disappear in some bendirei, and some young curvirostre show little if any spotting on the chest. To change from the dull gray of the juvenile condition to the orange-yellow of the adult, the iris of curvirostre must pass through a stage closely resembling the lemon-yellow of bendirei. A young curvirostre will approximate the size and proportions of an adult bendirei. In sum, there is ample opportunity for mistaking the birds in the field, especially when there are juvenile curvirostre about.

Additional characters useful for identifying a bird in the hand are the color and form of the mandible at its base. In bendirei this is a dull brown, and viewed ventrally, the chin feathers are nearly flush with the rounded lower edges of the mandibular rami. In curvirostre the en-

Table 1

Summary of body weights as marked on specimen labels, including both sexes, but excluding juvenile specimens

	<u>T. curvirostre</u>	<u>T. bendirei</u>
Mean (grams)	82.1 ± 5.7	62.0 ± 1.4
Range (grams)	73.4 - 104.2	58.0 - 67.4
No. of specimens (N)	18	7

ture bill is black, and the chin feathers sit more deeply in the more sharply cleaved bifurcation of the rami. The differences are subtle, but I have found them constant and helpful.

Habitat

In the Tucson area, the distribution of T. curvirostre is largely dependent upon the presence of the jumping cholla, Opuntia fulgida. Of the 156 nests of this species I found, 148 (94.9 percent) were placed in plants of this species. This predilection on the part of curvirostre has long been noted, causing some to think the bird an obligate of this cactus. That this is not so is shown by the occasional nests placed in other types of plants, such as in the cane cholla (Opuntia spinosior). Furthermore, curvirostre has an extensive range, over much of which there is no cholla available. In southeastern Arizona, nonetheless, it may be said with confidence that where jumping cholla is found, there too will be curvirostre. Its only other habitat requirement is a nominal one, that of some kind of open ground on which to forage. The optimal habitat seems to be one that, while well supplied with cholla, contains a large variety of other plants. The greatest concentrations of curvirostre I found were in the broad floodplains of washes containing sahuaro (Carnegiea gigantea), ironwood (Olneya tesota), five species of Opuntia, blue and foothill

paloverdes (Cercidium floridum and C. microphyllum), mesquite (Prosopis juliflora), creosote bush (Larrea tridentata), bisnaga (Ferocactus wislizeni), desert broom (Baccharis sarothroides), bur-sage (Franseria deltoidea), graythorn (Condalia lycioides), catclaw (Acacia greggii), whitethorn (A. constricta), hackberry (Celtis), Franseria ambrosioides, and others (Fig. 1). A cholla meadow (Fig. 2), dominated almost entirely by jumping cholla, is also a choice spot for this thrasher. During the fall and winter months there seems to be a dispersion of the species beyond its normal breeding habitat, so that it becomes more conspicuous in the city and in areas lacking the protective cholla.

The factors which bendirei favors seem equally clear cut: protective shrubs in which to nest and hide, and flat or gently rolling open ground on which to forage. It nests in paloverde, mesquite, desert-thorn (Lycium), cane cholla and other vegetation, depending primarily upon what is available. Two characteristic locations are pictured: Figure 3 is an open field having all the expansiveness any bendirei could wish for, as well as a hedgerow of mesquite for hiding; Figure 4 shows an expanse of paloverde-sahuaro, presumably the climax vegetation of the area, having an understory of bur-sage or occasionally small creosote bushes, with an open pavement barely masked by the many alfilaree (Erodium cicutarium) which grow there annually. It is this vegetation which seems to have been the original habitat of

bendirei, and the foothill paloverde its normal nest site by virtue of this tree's abundance. Bur-sage is apparently low enough to make the bird feel comfortable, and large enough to conceal it while it feeds; nowhere does bendirei seem more at home than in just such a situation. It is only infrequently found where open ground is studded with bushes as large as cholla or larger creosote bushes; when on very open ground it often exhibits an understandable nervousness. Nevertheless, it has adapted very well to agrarian civilization, especially where farmers are not so efficient as to destroy the mesquite predominant in agricultural bottomlands or pluck the fields bare of every weed. T. bendirei will take up its residence in deserted lots, along roads, dikes, and railroads, wherever the shoulders are extensive enough to support its foraging.

The two species are distributed independently of one another, but over much of their range the habitat features preferred by each coincide, and then they are truly sympatric. Figure 5 portrays just such a situation, by no means an uncommon one. Whether in the valley or in the foothills, both species are found where their fairly simple requirements occur.

Table 2 shows the types of perches used by each species. The first two columns indicate the percentage use within a limited, fairly homogenous area of paloverde-

sahuaro in which both species were common. The second two columns include all observations made throughout the study. T. bendirei is seen to be avoiding the chollas in favor of trees like mesquites and paloverdes, choosing a greater variety of vegetation, and using telephone poles a good deal. T. curvirostre exhibits its usual partiality to chollas, and does not often avail itself of the high perches provided by the telephone company.

Except when roosting in the interior of cacti and other bushes, the thrashers spend most of their time foraging on the ground. In neither case are they readily visible. The notes taken when they were in evidence, perched on some bush or other object, were compiled and analyzed; the results are shown on Table 3. The differences in perch height selected by curvirostre for sitting, calling and singing are not significant. The same is true when a comparison is made of sitting and calling perches of both species. However, when one tests to find if the mean height of curvirostre singing perches is significantly lower than that of bendirei singing perches, the difference is found to be significant at the five percent level. The difference between the singing and sitting perches of bendirei are significant at the .05 percent level. This is more obvious in the field than these figures indicate, for whereas the time spent on a given perch was not considered in the computa-

Table 2

Percentage use made of different types of perches

	paloverde- sahuaro		Tucson, all areas	
	<u>T. c.</u>	<u>T. b.</u>	<u>T. c</u>	<u>T. b.</u>
jumping cholla	36.9	7.7	33.1	2.2
sahuaro	13.9	15.4	17.3	15.1
cane cholla	22.1	10.3	10.8	2.9
mesquite	3.3	2.6	5.7	13.7
foothill paloverde	8.2	15.4	5.3	11.5
ironwood	-	-	11.0	6.5
other plants	5.7	12.8	9.3	20.9
telephone poles	0.8	20.5	1.2	10.1
telephone wires	2.5	5.1	2.1	6.5
other artifacts	6.6	10.3	4.2	10.8
No. of observations	122	39	335	139

Table 3

Manner in which the vegetation is used for perching

	<u>T. curvirostre</u>	<u>T. bendirei</u>
No. of observations	338	139
Percentage cases singing	29.3	56.8
Mean ht. singing perches(ft.)	9.6 \pm 1.1	12.2 \pm 0.8
Percentage cases calling	19.2	2.9
Mean ht. calling perches(ft.)	10.7 \pm 0.9	6.3 \pm 3.5
Percentage cases sitting	51.5	40.3
Mean ht. sitting perches(ft.)	8.9 \pm 0.5	9.0 \pm 0.2

tions, the observer following an effervescent bendirei about sees a positive correlation between height of perch and length of time spent singing on it.

Birds flushed while feeding but not greatly alarmed would usually fly low, about a foot off the ground, to land on the ground some distance away. If they flew into a tree or bush, they would fly low into it, then either drop to the ground to continue foraging, fly to a more distant perch, or, particularly bendirei, would progress to the top of the tree by a series of hops up the central branches. When alarmed while singing, bendirei would often carry out the same procedure, singing all the way up, then stay on top to continue singing.

Juvenile birds were especially timorous, huddling in the middle of some low bush until a close approach would drive them thence in fright at the last minute.

Nesting

Generally, curvirostre nests from February through June, bendirei from March through June. Either may deposit later clutches, and bendirei may begin earlier, depending upon the conditions governing its return from the wintering grounds. Although some bendirei remain in the Tucson area throughout the winter, these form a small minority, and it is not until early February that the bird is seen with any

frequency. The delay occasioned by the annual journey is apparently the only factor preventing the breeding seasons of the two species from being completely coincident. As it is, there is a difference of from two weeks to a month in the initiation of nesting. In 1962, curvirostre began laying eggs on about February 3, and bendirei on about February 15 (R. S. Crossin).

As previously noted, 94.9 percent of 156 curvirostre nests were found in jumping cholla. Of the remaining eight nests, seven were in cane cholla and one in the interlaced branches of a cane cholla and a mesquite. The mean height of the nests was 4.8 ft. \pm 0.1, and the range ran from 2.5 to 8 feet. Nine of the nests examined contained one egg or young bird, nine contained two eggs and/or young, twenty-nine nests contained three eggs and/or young, and only two nests contained four eggs or young. A clutch number of three is considered normal for this species. Four eggs are unusual, and most of the smaller numbers noted are probably attributable to being noted while the clutch was as yet incomplete, or to accidents and predation.

Only twelve bendirei nests were discovered in this study, placed as follows: seven in foothill paloverde, and one each in blue paloverde, mesquite, cane cholla, desert-thorn, and in a small tamarisk (Tamarix) below a mesquite. They ranged in height from three to nine feet, with a mean

height of 5.0 ft. \pm 0.5. One nest contained one egg, three contained two eggs and/or young, and three contained three eggs or young. The normal clutch of this species, like that of the preceding, is also three eggs (Brown, 1901).

Even though curvirostre is a much more common bird than bendirei, the number of nests seen of each is no measure of relative abundance, for those of curvirostre are conspicuous even to the untrained eye, while those of bendirei are often concealed quite effectively. Figure 2 shows a curvirostre nest in the cholla to the left of center, while Figure 6 shows a foothill paloverde containing a bendirei nest.

The nest of curvirostre is, externally, a massive affair of sticks of various kinds, but always with prominent thorny twigs, especially about the rim. Where available, the particularly effective terminal branches of the whitethorn are used to supplement the formidable array of barbs of the nest cholla. Since the nests are augmented each year they are in use, some become quite bulky indeed. On the other hand, new nests may have relatively small external walls. The internal portion of the nest is a neat cup of rootlets, wiry grasses, horsehair, and other fibers. In the spring the refurbished lining is an attractive green or yellow bowl.

The nests of bendirei also have an external portion of twigs, which is usually considerably slighter than that

of curvirostre, and is sometimes only a mere suggestion of an external nest. The internal portion is a cup composed of rootlets, shredded plant fibers, lax grasses, flosses, or any other material at hand which is soft and pliable. These nests look more messy than those of curvirostre because their composition is so varied, but they are nevertheless symmetrical and well-built. There is no crown of thorns about the rim of the nest, nor are thorny twigs of the sort curvirostre so conspicuously prefers used in numbers. The bulk of the external portion of the nest tends to be made of less angular twigs than those curvirostre uses, although there is considerable variation. Use of twigs from or of the nest tree for construction of the outside of the nest helps in concealing the structure.

Table 4 shows the percentage composition of the external portions of two representative nests, one from each species, collected from the same area. The internal portion of the curvirostre nest consisted primarily of rootlets, wiry grasses, grass inflorescences and other plant material, while that of bendirei contained shredded bark and other plant fibers, grasses, rootlets, cottony floss, a two-foot string, two pieces of frayed cord, a red thread, one piece of tissue paper, a chicken feather, a quail feather, two roadrunner feathers, and one feather from the crest of a peacock.

Table 4

Percent composition by number of twigs of the external
portions of two nests

	<u>T. curvirostre</u>	<u>T. bendirei</u>
desert-thorn	50.8	5.8
creosote bush	4.1	14.2
bur-sage	11.0	20.9
whitethorn	32.7	5.3
Mormon tea (<u>Ephedra</u>)	1.4	8.0
foothill paloverde	-	43.6
sahuaro (bark)	-	2.2
total number of twigs	370	225

Although territoriality was not worked out in detail, it was obvious from observations designed for the purpose of answering that question that, where they occurred together, the territories of the two species overlapped completely, although that of two given pairs did not seem to be coincident. T. bendirei appeared to have larger territories than curvirostre, with the consequence that one bendirei territory would include portions of several curvirostre territories, but this is merely an impression for which I cannot adduce clear-cut evidence.

Behavior

T. curvirostre is a bird conspicuous in its voice and actions, generally bold and brassy, but wary when it wants to be. Its ringing double-noted whistle is probably its best-known characteristic, and its song is a clear and pleasant melody. T. bendirei, on the other hand, is a shy and elusive bird, flamboyant only when it sings, but then doing it in grand style, pouring its torrential and distinctive song from the highest perch available. Its rarely heard call notes are characterless, the more common being a mockingbird-like "chup" or "chek," though not as harsh and loud as that of Mimus, and usually delivered in volleys of two or three; the other is a quiet quizzical whistle: "quee?" Whereas curvirostre sings with fair regularity throughout the nesting season, bendirei is given to alternating pe-

riods of almost constant singing with stretches of long silence. An area in which bendirei had been heard singing plentifully, when revisited a month and a half later, was so devoid of their song or presence that it was not until after long searching that I assured myself they had not quit the area. Nevertheless, individuals of this species may be heard singing from January to June.

Both species become quite tame when accustomed to the proximity of benevolent human neighbors, and will come into yards to feed. However, bendirei is greatly affected if one comes near its nest, and will often abandon it for lengthy intervals in such a situation. Conversely, I have had curvirostre fly into a cholla a foot from my head and whistle indignantly while I inspected its nest.

Food Habits

Like most thrashers, these are primarily ground feeders, running over the desert floor to poke, peck and hammer at it, to pry up and fling aside litter upon it, and in the case of curvirostre, to vigorously dig it up. Only the bill is used as a tool in these activities, never the feet. Engels (1940) explains the differences in the feeding behavior of the species of Toxostoma, but gives the impression that bendirei does not dig, which is not so. It does indeed dig, but less powerfully, efficiently or

frequently than its congener. T. bendirei tends to dash across an area in abrupt spurts, picking and pecking here and there, although at times I have seen it make the dirt fly as it pursued some subterranean insect. T. curvirostre also feeds in this manner, but puts the emphasis on the other side of this spectrum of activity, often foraging within a rather limited area at any given time, but in a thorough fashion as it excavates holes in the desert floor two inches deep and two inches in diameter, tossing dirt and loose objects to the sides or backwards with its bill.

On two occasions bendirei was seen chasing insects on the surface, once diving headlong into a bur-sage, apparently after some flying or leaping animal. T. curvirostre was seen eating from ripe bisnaga fruit, and individuals of both species were seen perched on branches of the graythorn, plucking the fruit from the branches about them. When the sahuaro comes into bloom both species frequent the arms of the cactus, probing amongst the flowers and buds, and gorging on the pulp and seeds of the ripe fruit.

Table 5 shows the percentage composition by number of the arthropod food taken by the two species of birds. The first four columns compare only cases in which birds of the two species were collected at the same time in the same place. The second set of four columns include all specimens whose stomachs were analyzed, with the exception of one curvirostre found full of the pupae of a chalcid wasp which

Table 5

Analysis of arthropod content of stomachs
(See text for explanation)

	approx. size (mm.)	T. c.		T. b.		T. c.		T. b.	
		%	#	%	#	%	#	%	#
Arachnida									
Scorpionida	10					0.13	1		
Salticidae	5			0.4	1	0.38	3	0.54	2
aranid egg case	15	0.3	1						
Myriapoda									
Chilopoda	4					0.13	1		
Orthoptera									
<u>Arenivaga</u>	10	0.3	1			0.13	1		
Acrididae	15					0.13	1		
acridid ootheca	30-35							0.81	3
acridid ootheca	10	0.3	1			0.13	1		
Isoptera									
Kalotermitidae	4	36.9	4	8.0	2	48.23	17	25.88	3
Hemiptera									
Miridae	3	0.3	1			0.51	4		
Homoptera									
Psyllidae	3	0.3	1			0.13	1		
Neuroptera									
Myrmeleonidae	4-15	3.6	5	2.7	4	5.63	14	1.89	4
Lepidoptera									
Phalaenidae-larvae	15-24	23.1	6	11.0	3	11.91	9	12.94	5
Psychidae-larvae	8	0.3	1			0.13	1		
unidentified									
larvae	8-15	0.3	1			1.15	3	0.54	1
pupae	6	0.6	2	0.4	1	0.38	3	0.27	1
Diptera									
larvae	5					0.51	1		
puparia	8					1.28	3		
Coleoptera									
Carabidae	8	0.6	1			0.26	1		
larvae	8-15			7.2	1	0.13	1	5.12	1
Tenebrionidae	4-6	4.8	2	9.1	2	3.33	7	6.47	2
<u>Eleodes</u>	25-35	0.3	1			0.26	2		
<u>Tenebrio(?)</u>	12			0.7	1	0.51	3	0.54	1
Scarabaeidae	3					0.13	1		
<u>Oremastocheilus</u>	14					0.26	2		
scarabaeid larva	13					0.13	1		
Chrysomelidae	6	1.2	1			1.41	2		
Cerambycidae	25							0.27	1
Curculionidae	3-7	0.3	1	0.7	1	1.02	5	0.54	1
Dasytidae	3			0.4	1			0.27	1
unidentified	4-12	4.3	6	4.6	2	4.00	14	4.83	6
	20							0.27	1
Hymenoptera									
Formicidae	2-6	22.2	8	50.6	7	14.85	18	35.85	7
Mutillidae	7					0.26	1		
Andrenidae	8			2.7	1			1.89	1
Halictidae	5			0.4	1			0.27	1
Number of stomachs analyzed			14		11		37		16
Number (approx.) of arthropods		333		263		781		371	

were presumably parasitizing an insect devoured by the bird. In Table 5, "%" indicates the percentage any given type of arthropod contributed to the total arthropod diet of either thrasher. The symbol "#" indicates the number of stomachs which contained the item in question.

Since no meaningful comparison could feasibly be made between animal and vegetable material in the diet, the plant food was tabulated separately in Table 6. The difference in variety and number of seeds (or fruits) selected by the two species is striking. Most of the stomachs contained a small amount of plant debris, such as pedicels, rootlets, leaflets, and various fibers. Gravel and sand in varying amounts were also present in most of the stomachs.

Table 7 presents an attempt to gauge the foraging activity of the two birds by separating the arthropods found in the diet into groups thought to represent the levels at which they were found in the environment by the birds. Mr. Anthony Ross provided the information by which these groupings were drawn up. Percentage figures from Table 5 were then apportioned out and summed up in each category to give an estimate of the foraging pattern of each species.

Of the predominant arthropod forms, curvirostre chose considerably larger amounts of termites and ant-
lions than did bendirei, which in turn depended more heavi-

Table 6

Analysis of seed contents of stomachs

(See explanation below)

	mm.	<u>T. c.</u>	<u>T. b.</u>	<u>T. c.</u>	<u>T. b.</u>
<u>Carnegiea gigantea</u>	1	790 3	300 1	1776 10	300 1
<u>Echinocereus</u> sp.	1			545 2	
<u>Ferocactus wislizeni</u>	2	35 3		381 7	
Gramineae	1-3	76 3	10 3	290 15	15 5
unidentified seeds	1-5	4 1		232 5	
<u>Kallstroemia</u> sp.	4	1 1		161 4	
Solanaceae	2			161 3	
<u>Opuntia fulgida</u>	3			45 1	
<u>Opuntia spinosior</u>	4	25 2		41 6	
<u>Celtis pallida</u>	5	5 4		37 11	
<u>Condalia lycioides</u>	5	15 1	11 2	15 1	11 2
<u>Lesquerella gordonii</u>	1	11 1		11 1	
<u>Sorghum</u> sp.	5	9 1	2 2	64 4	2 2
<u>Chloris virgata</u>	2	3 1		3 1	
<u>Lycium</u> sp.	2	1 1		1 1	
Compositae	3	<u>1</u> 1	<u> </u>	<u>- 1</u> 1	<u> </u>
		976	323	3206	328
Number of stomachs:		14	11	37	16

The first column of figures represents approximate seed size. The next four columns are figures for birds taken at the same time and place; the last four are for all specimens. In each case the first column represents number of seeds, the second, number of stomachs containing them.

Table 7

Probable foraging activity determined from insect food

	same place, time		all specimens	
	<u>T.c.</u>	<u>T. b.</u>	<u>T.c.</u>	<u>T.b.</u>
Insects that have to be dug out:				
<u>Arenivaga</u>	0.3		0.13	
acridid ootheca	0.3		0.13	
Kalotermitidae	12.3	2.7	16.08	8.63
Myrmeleonidae	3.6	2.7	5.63	1.89
Phalaenidae	11.5	5.5	5.95	6.47
lepidopteran pupa	0.3	0.2	0.19	0.13
puparium			0.64	
carabid larva		3.6	0.06	2.56
scarabaeid larva			0.07	
coleopteran larva		0.4	0.26	0.27
Andrenidae		2.7		1.89
<u>Halictidae</u>		<u>0.4</u>		<u>0.27</u>
Est. digging :	<u>28.3</u>	<u>18.2</u>	<u>29.14</u>	<u>22.11</u>
Insects that may be scratched out with bill:				
Kalotermitidae	12.3	2.6	16.08	8.62
Phalaenidae	11.6	5.5	5.95	6.47
lepidopteran larva	0.3		1.15	0.54
lepidopteran pupa	0.3	0.2	0.19	0.14
puparium			0.64	
carabid larva		3.6	0.07	2.56
tenebrionid larva		0.7	1.02	0.54
<u>Scarabaeidae</u>			<u>0.20</u>	
Est. scratching :	<u>24.5</u>	<u>12.6</u>	<u>25.30</u>	<u>18.87</u>
Insects which spend the day under rocks:				
scorpion			0.13	
centipede			0.13	
spider eggs	0.3		1.28	
Kalotermitidae	12.3	2.7	16.08	8.63
Carabidae	0.6		0.26	
Tenebrionidae	5.1	9.8	4.10	7.01
scarabaeid larva			0.06	
<u>unidentified beetles</u>	<u>2.1</u>	<u>2.3</u>	<u>2.00</u>	<u>2.55</u>
Est. rock-flipping :	<u>20.4</u>	<u>14.8</u>	<u>24.04</u>	<u>18.19</u>

Table 7 (continued)

	Same place, time		all specimens	
	<u>T.c.</u>	<u>T.b.</u>	<u>T.c.</u>	<u>T.b.</u>
Insects that may be caught at the surface:				
Salticidae		0.4	0.38	0.54
Acrididae			0.13	0.81
Miridae	0.3		0.51	
Psyllidae	0.3		0.13	
psychid larva	0.3		0.13	
dipteran larva			0.51	
Chrysomelidae	1.2		1.41	
Cerambycidae				0.27
Curculionidae	0.3	0.7	1.02	0.54
Scarabaeidae			0.19	
Dasytidae		0.4		0.27
unidentified beetles	2.2	2.3	2.00	2.55
Formicidae	22.2	50.6	14.85	35.85
Mutillidae			0.26	
Est. surface foraging:	26.8	54.4	21.52	40.83

ly on ants and tenebrionid beetles. This differential in diet follows from the adaptations of curvirostre which make digging more effective. Of the twenty items which were not shared by the birds, fifteen occurred in only one stomach, indicating opportunism on the part of the thrashers rather than any significant difference in diet. The possibility that the relatively slight difference in size of the birds serves to impose restrictions upon their choice of foods is precluded by an examination of Table 5, which shows that curvirostre includes the most diminutive of the insects on that list in its diet, while bendirei uses the largest.

Discussion

T. curvirostre and T. bendirei exhibit only a partial degree of differentiation from one another with respect to features which separate their ecologic niches in the breeding area. It is difficult to understand how any of the more obvious differences in their use of the habitat they hold in common could be as significant in terms of competition and survival as the similarity of the food upon which they depend to live, especially in view of the fact that they do not "recognize" one another as competitors. Observation of their foraging activity precludes the possibility that the same food items are being gleaned from different levels in any but a small degree. Only in their utilization of plant material are they markedly different. It

Fig. 5

Habitat co-inhabited by Toxostoma curvirostre and T. bendirei. The vegetation includes sahuaro, foothill paloverde, jumping cholla, bur-sage, creosote bush, and cane cholla.

Fig. 6

Foothill paloverde containing a nest of T. bendirei. The nest is about halfway up the tree, just to the left of center, but is invisible in the thorny labyrinth of the paloverde.

should be noted, however, that the species better adapted for digging out subterranean animals is the one also taking more advantage of the plant material available.

The desert scrub in which these birds are sympatric is not as forbidding an environment as are true deserts; it is conceivable that food might not be a limiting factor, especially when one of the species migrates out of the area when the food supply is presumably at its lowest. Udvardy (1958) has pointed out that the North American desert regions are of relatively recent origin, and that the avian species inhabiting them are little-differentiated and imperfectly adapted members of essentially arboreal groups. Toxostoma illustrates the above proposition quite well.

All indications are that 1940 was a major turning point in the population density of bendirei, for observers before that time are of a mind in considering it a very common species in areas where it is now only rarely seen. Even though the replacement of small mesquite-bordered fields by the large, efficient farms of today probably deprived bendirei of much habitat previously available to it, the discrepancy in numbers cannot be explained by this factor alone. Brown (1901) writes of having examined some 500 nests of the species. Presumably he collected some of them himself, and others were brought to him. Brown was a busy civic leader for whom ornithology was an avocation and not a profession, yet one would be hard-pressed today to find

half that many nests were all one's time devoted to that pursuit. Today the species is not considered abundant anywhere, except locally, but Gilman (1909) could not decide which of the thrashers, all of which were numerous, predominated along the Gila River near Blackwater. Scott (1886) calls them quite common in the vicinity of Florence. Howell (1916) says that a favorite place in which to collect eggs of this species was between Ft. Lowell and Tucson. Swarth (1914) observed that it was "very abundant" in the valley of the Santa Cruz west of the Santa Rita Mountains, and common in the plains and valleys northwest of Tucson. As late as 1940, Engels (1940) stated that they occurred abundantly in the Santa Cruz Valley region. In my experience they are not uncommon locally, but are certainly not nearly as common as curvirostre, and by no means are they abundant.

Marked changes in the abundance of insects and reptiles also occurred during the 1940's, apparently correlated with changes in parts of the vegetation throughout the southwest (Charles H. Lowe, personal communication). It has been noted that bendirei is largely insectivorous; it also appears to be psychologically subordinate to curvirostre, a species with more advanced morphological adaptations concurrent with a greater range of foraging activity. T. bendirei can exist in the vicinity of human beings, but only if unmolested; curvirostre is considerably more hardy

in this respect.

A possibility suggested by all the above information is that bendirei is being crowded out of the area for two principal reasons: destruction of habitat it can utilize in the absence of curvirostre, and unsuccessful competition with curvirostre for a depleted food supply in those habitats the two species co-inhabit.

When competition occurs between two species, one is not necessarily eliminated. Given the time and opportunity, the ecological niches of the two may become displaced to allow coexistence. But if the time period in which great selective stress is operating is too short, one species will replace the other. I suggest that Toxostoma bendirei is at present being displaced from those areas in which it is sympatric with T. curvirostre.

Summary and Conclusion

It is evident that the contradictions found in the literature concerning Toxostoma curvirostre and T. bendirei are in the main only apparent and the result of fragmentary observations. The two species are distributed independently of one another, but overlap broadly in certain habitats, where they hold superimposed territories. T. curvirostre nests in the jumping cholla, Opuntia fulgida, and in the Tucson area usually occurs only with that plant during the

breeding season. T. bendirei breeds where it can find flat or gently rolling open ground on which to forage, combined with shrubs in which to nest and hide. Thus it is characteristic of paloverde-sahuaro communities and of cultivated terrain. The two species forage in essentially the same way, although curvirostre digs for more of its food than does bendirei, and takes more plant material. When the sahuaro (Carnegiea gigantea) is in bloom and fruiting, both species frequent its branches. These two thrashers use the habitat in which they occur together in somewhat different ways; this is especially marked in their choice of song perches and nest sites, and somewhat less so in their choice of nesting material. They breed at essentially the same time, although having to migrate back from a wintering ground delays bendirei in initiating its nesting cycle.

These two species show more ecologic overlap than would be supposed under the conditions in which they live. The expected mechanisms to reduce interspecific competition are only partially developed, implying recent and imperfect adaptation to the environment. What seems to be a marked decrease in the abundance of bendirei during the last two decades suggests that this species is competing unsuccessfully with curvirostre where the two occur together.

Fig. 1

The flood-plain of a wash at the base of the Tucson Mountains, in which there was a dense breeding colony of Toxostoma curvirostre. The vegetation includes ironwood, jumping cholla, sahuaro, hackberry, blue paloverde, and a large variety of smaller forms.

Fig. 2

A portion of a cholla meadow, formed by a dense stand of Opuntia fulgida, the jumping cholla. Hackberry and bur-sage may be seen in the foreground, and ironwood and sahuaro in the background. The dark mass in the cholla just to the left of center is a nest of T. curvirostre.



Fig. 3

A field frequented by a pair of Toxostoma bendirei. The male often sang from the fence posts and from the mesquite in the foreground. The surrounding trees are mostly tamarisk and mesquite.

Fig. 4

Gently undulating foothills at the eastern base of the Tucson Mountains, dominated by a paloverde-sahuarero community. In the foreground may be seen sahuaro, small creosote bushes, and bur-sage. Foothill paloverdes dot the opposite hillside. This area contained widely-spaced pairs of T. bendirei.





Literature Cited

Bailey, F. M.

1928. Birds of New Mexico (New Mexico Department of Fish and Game, Santa Fe, N. M.).

Bent, A. C.

1948. Life histories of North American birds. U. S. Nat. Mus. Bull. 195.

Brandt, H.

1951. Arizona and its bird life (The Bird Research Foundation, Cleveland, Ohio).

Brown, H.

1892. The habits and nesting of Palmer's thrasher. Zool., 3:243-248.
1901. Bendire's thrasher. Auk, 18:225-231.

Chapman, F. M.

1926. The distribution of bird life in Ecuador. Bull. American Mus. Nat. Hist. 55.

Engels, W. L.

1940. Structural adaptations in thrashers (Mimidae: genus Toxostoma) with comments on interspecific relationships. Univ. Calif. Publ. Zoo., 42:341-400.

Gilman, M. F.

1909. Among the thrashers in Arizona. Condor, 11:49-54.

Gould, P. J.

1961. Territorial relationships between Cardinals and Pyrrhuloxias. *Condor*, 63:246-256.

Howell, A. B.

1916. Some results of a winter's observations in Arizona. *Condor*, 18:209-214.

Hutchinson, G. E.

1957. Concluding Remarks. Cold Spring Harbor Symposia on Quantitative Biology, 22:415-427.

Klopfer, P. H.

1959. Environmental determinants of faunal diversity. *Amer. Naturalist*, 93(873):337-342.

Ligon, J. S.

1961. New Mexico birds and where to find them (The Univ. of New Mexico Press, Albuquerque, N. M.).

MacArthur, R. H.

1957. On the relative abundance of bird species. *Proc. Nat. Acad. Sci.*, 43(3):293-295.

Marshall, J. T., Jr.

1960. Interrelations of Abert and Brown Towhees. *Condor*, 62:49-64.

Odum, E. P.

1959. *Fundamentals of Ecology* (W. B. Saunders Co., Philadelphia, Pa.).

Peterson, R. T.

1961. A field guide to western birds (Houghton Mifflin Co., Boston, Mass.).

Pough, R. H.

1957. Audubon western bird guide (Doubleday and Co., Inc., Garden City, N. Y.).

Scott, W. E. D.

1886. On the avifauna of Pinal County, with remarks on some birds of Pima and Gila counties, Arizona. Auk, 3:249-258.

Sutton, G. M., and A. R. Phillips.

1942. June bird life of the Papago Indian reservation, Arizona. Condor, 44:57-65.

Swarth, H. S.

1914. A distributional list of the birds of Arizona. Pac. Coast Avif., 10:1-133.

1920. Birds of the Papago Saguaro national monument and the neighboring region, Arizona. Contr. from the Mus. of Vert. Zool. of the Univ. of Calif., Govt. Printing Office, Washington.

Udvardy, M. D. F.

1958. Ecological and distributional analysis of North American birds. Condor, 60:50-66.