THE COEXISTENCE OF TWO WREN SPECIES OF THE GENUS *THRYOTHORUS*

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THE ecology of closely related species of birds has been the subject of much study. It has often been found that when two such species occur sympatrically they exploit the environment differently (e.g., Hartley, 1953; MacArthur, 1958), a fact which presumably contributes to their success in coexisting. Apparent exceptions to this pattern have revealed themselves, upon closer inspection, not to be exceptions at all. The discovery of yet another apparent exception is worth reporting because it is unusual in other ways. Two sympatric species of Mexican wrens of the genus *Thryothorus* appear to respond to each other ecologically as if they were identical species, reproductively as if they were different species. The observations which indicate this unusual situation were made during the course of another project (Grant, 1965*a*). They require verification by a more thorough study which, it is hoped, may be stimulated by the following account.

THE SPECIES AND DISTRIBUTION

Observations were made of *Thryothorus s. sinaloa* (Sinaloa Wren) and *T. felix pallidus* (Happy Wren) in the months March to August 1961–1963. The two species are resident and sympatric over a large part of western Mexico. Their ranges coincide from Sonora south to Guerrero, and that of *T. felix* extends farther southward into Oaxaca. All observations were made in the zone of sympatry, mainly at Puerto Vallarta, Jalisco, and Tepic, Nayarit, but also in nearby areas in these two states. Some observations were also made of the Tres Marías Islands form of *T. felix*, which is recognized as an endemic subspecies, *T. f. lawrencii*.

MORPHOLOGY

Plumage.—In each species males and females have identical plumage. *T. felix* differs from *T. sinaloa* principally in having a bolder black-and-white face pattern, a less conspicuous, white, postocular stripe and rufous, as opposed to gray–white, underparts. These differences appear to be important in species recognition if only because on the Tres Marías Islands, where *T. sinaloa* is absent, *T. felix* has a plumage more similar to *T. sinaloa* (illustration in Grant, 1965*b*): the insular subspecies has a reduced face pattern and the underparts are white and not rufous. There are no reports in the literature of hybridization of the two species, nor was any evidence of such revealed in this study.

TABLE 1

MEASUREMENTS OF ADULT MALES COLLECTED AT TEPIC AND PUERTO VALLARTA

		T. felix	*T. sinaloa*
Wing	N	21	22
	$\bar{x} \pm 2$ SE	57.0 ± 0.58	59.1 ± 0.75
Tarsus	N	20	21
	$\bar{x} \pm 2$ SE	21.71 ± 0.24	20.90 ± 0.28
Bill length	N	20	20
	$\bar{x} \pm 2$ SE	10.78 ± 0.22	10.84 ± 0.25
Bill width	N	11	20
	$\bar{x} \pm 2$ SE	2.95 ± 0.09	2.90 ± 0.06
Bill depth	N	11	20
	$\bar{x} \pm 2$ SE	2.39 ± 0.09	2.54 ± 0.04
Fresh weight	N	6	11[1]
	$\bar{x} \pm 2$ SE	14.90 ± 0.76	17.45 ± 0.49
Weight after freezing and thawing	N	5	18
	$\bar{x} \pm 2$ SE	14.54 ± 1.12	15.33 ± 0.40

NB. Measurements made as described in Grant (1965*c*). Linear dimensions in millimeters, weights in grams.
Symbols: N = sample size. $\bar{x} \pm 2$ SE = mean ± 2 standard errors.
[1] Includes 10 individuals from Guadalajara, Jalisco.

Dimensions.—*T. sinaloa* is larger than *T. felix*, as indicated by body weight and wing length data (Table 1). However, the tarsus of *T. sinaloa* is relatively and absolutely shorter than that of *T. felix*. It might be expected that the bill lengths of the two species would differ by 10 per cent or more (cf. Hutchinson, 1959), but in fact they differ by less than 1 per cent. Differences in width and depth of bill are a little greater, but the overall difference in size and shape of the bill is quite small. The island form of *T. felix* has a bill 13 per cent longer than its mainland counterpart (Grant, 1965*c*).

ECOLOGY AND BEHAVIOR

Territoriality.—Territories of the two species were found to be more or less nonoverlapping and contiguous (Fig. 1). An observation of an individual of one species at a particular place was never followed on the next day by an observation of an individual of the other species at that place. This suggests that territoriality is interspecific as well as intraspecific. Members of the two species were observed either displaying to or chasing each other on at least three occasions at Tepic during the early part of the breeding season. In July and August (the end of the breeding season) mutual tolerance was observed. On one occasion an adult *T. sinaloa*, an adult *T. felix*, and a juvenile *T. felix* foraged on the ground for 5 minutes in a small area which varied from 1 to 2 square meters.

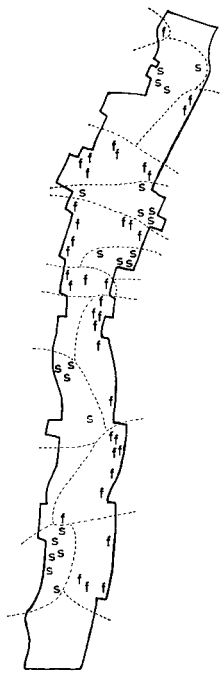

FIG. 1. Estimated territories of *T. felix* and *T. sinaloa* in a census area of 4 hectares (10 acres) ca. 9 km NW of Tepic, Nayarit. NB. The boundary of the census area is not a natural one. Total length of the area is 2,000 km, approx. Daily surveys were made 20–26 May 1963. Each bird seen or heard was recorded. Territory boundaries are estimated from observations made during and after the census period. Symbols: f = Single record of *T. felix*: s = Single record of *T. sinaloa*.

No heterospecific courtship or pairing was witnessed in this study.

Song.—The songs of four individuals of *T. sinaloa* and seven individuals of *T. felix* (a sample of more than 100) were recorded at Tepic in June 1963 with a National transistor tape recorder, and later analyzed with a Missilyzer Sound Spectrograph. Sonagrams of the songs of the two species are reproduced in Figure 2, and demonstrate the similarity in song of the two species. It was found impossible to discriminate between the two species by listening to their songs in the field. Each species sings two types of song, referred to here as type A and type B, in a variable but often alternating sequence. The introductory notes of both types of song are to some extent variable, but the later parts show constancy. There is a possibility that the terminal four notes of the type A song of *T. felix* differ from the corresponding notes in the song of *T. sinaloa*, but larger samples are required to establish this. No consistent

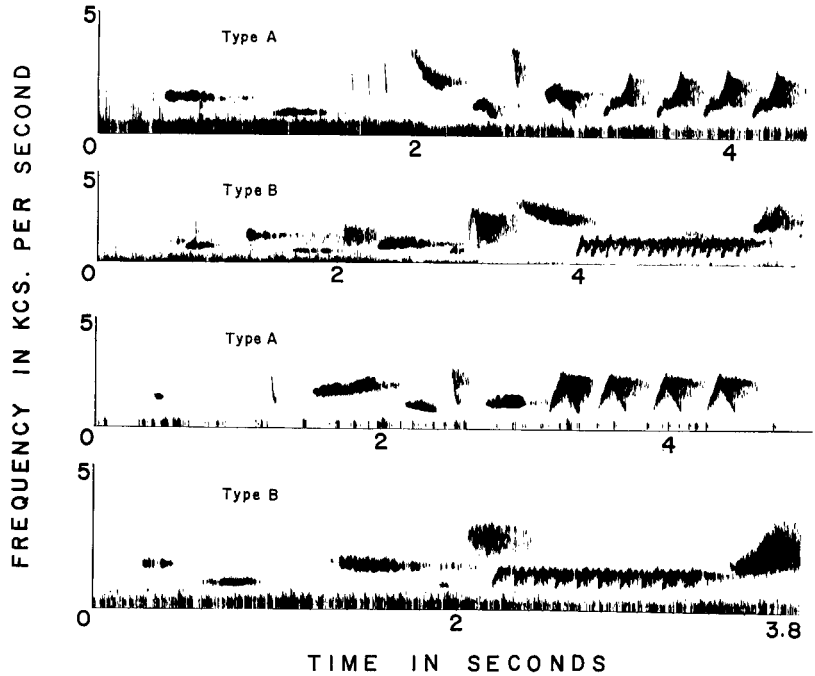

FIG. 2. Songs of *T. felix* (top two) and *T. sinaloa* (lower two) recorded at Tepic, Nayarit, June 1963.

differences between the species were found in these small samples. In passing, it is worth mentioning that the components, variation, and structure of these songs bear a strong resemblance to those of the heterogeneric Bewick's Wren (*Thryomanes bewickii*) (is this really in a different genus?), members of which have a repertoire of two to four songs (Borror, 1964). In contrast they bear little resemblance to those of the homogeneric Carolina Wren (*Thryothorus ludovicianus*) members of which may sing up to 36 different songs (Borror, 1956).

Observations revealed that songs were produced by the birds in a territorial context. Also it was sometimes found that a recording of one species played back within the territory of an individual of the same species evoked a singing response from a previously quiet individual of the other species in an adjacent territory. Both species behaved in this way. No attempt was made to standardize this procedure or to measure the results.

When two members of a pair are foraging they often vocalize alternately (antiphonally). The vocalizations of the male and female are believed to be

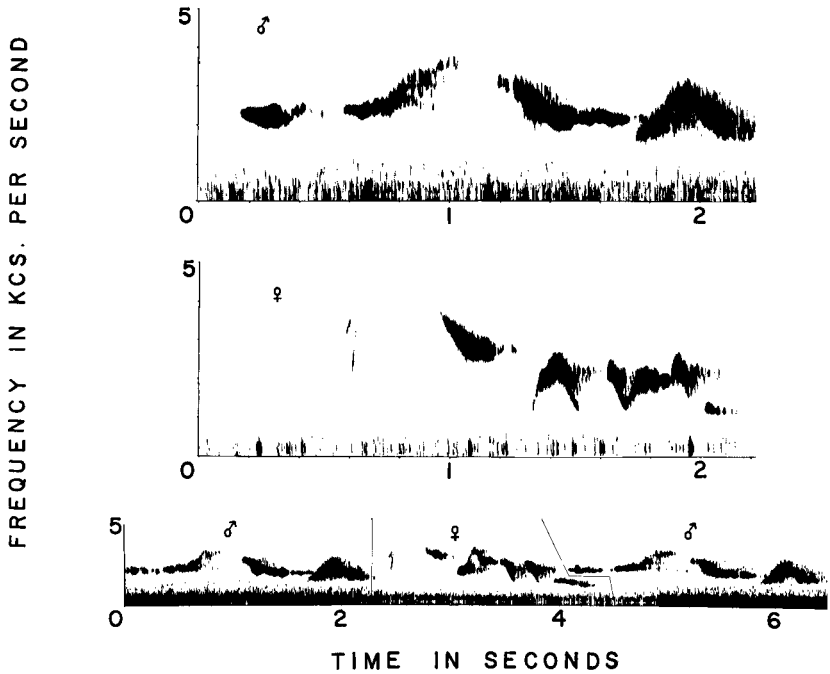

FIG. 3. Contact calls of *T. felix* recorded on María Magdalena, Tres Marías Islands, June 1963.

consistently different: the identity of the sexes was established by collecting birds previously observed and heard to sing these "contact calls." Birds which sang the territorial song were sometimes heard to change to the "male" component of the contact call, but never to the "female" component. An individual was never heard singing both components (cf. Thorpe and North, 1965). Although contact calls were not recorded from individuals of *T. sinaloa* they are almost certainly produced by them. The island form of *T. felix* was never heard to sing either type A or B of the territorial songs (in April, June, July, and August) or any other type except the contact call (Fig. 3). This is produced frequently by a single bird or a pair both before and during the breeding season. It appears to serve a communication function while the pair is foraging in undergrowth (Grant, 1965*b*); it may also serve a stimulatory function during and after courtship. Whether it has taken on an additional function in the context of territoriality on the islands or whether territoriality has been relaxed there is not known. A few observations suggest that the former is the more likely.

Habitat.—The two species occur together in the same habitat, mainly tropi-

TABLE 2

NUMBER OF SPECIMENS COLLECTED AT PUERTO VALLARTA, MAY TO AUGUST 1961

	Numbers	Per cent
T. felix	26	38.2
T. sinaloa	42	61.8
NUMBER OF PAIRS RECORDED IN A CENSUS STRIP OF 4 HECTARES (10 ACRES) AT TEPIC, MAY 1963[1]		
T. felix	8	61.6
T. sinaloa	5	38.4

[1] Six surveys on consecutive days. For further details see Grant 1966*d*.

cal deciduous forest, thorn scrub, oak–hornbeam forest, and associated vegetations. Both species occupy territories in a spectrum of habitat configurations from thick forest to isolated clumps of shrubs in a field, with *T. felix* perhaps occurring most frequently in the thicker vegetation and *T. sinaloa* most frequently in the sparser parts (cf. Selander and Giller, 1959; Zimmerman and Harry, 1951). However, no absolute difference in habitat preference between the species was detected by the author.

Observations at both Tepic and Puerto Vallarta indicated that substantially more than 50 per cent of the territories occupied by one species in one year were occupied by the same species in the following year, but that some interchange of territory occupancy did occur. *T. felix* was found in *T. sinaloa* territories of the previous year in numbers equal to *T. sinaloa* in previous *T. felix* territories. Thus, the proportions of the two species in any one region appeared to stay the same despite the changing of territories.

Numbers.—From two sources of information it appears that the two species are not numerically equal where they coexist. Specimens of the two species were collected at Puerto Vallarta in 1961 with no deliberate effort made to collect one species preferentially. Table 2 shows that here, in an area approximately 2 km square, *T. sinaloa* outnumbered *T. felix* approximately two to one. In a census of 4 hectares at Tepic in 1963 the same ratio was found, but the proportions of the two species were reversed (Table 2). As mentioned above, there was no indication that these ratios changed in the years 1961 to 1963.

Food.—More than 20 gizzards of specimens of each of the two species, collected between April and August inclusive, 1961–63, at Tepic and Puerto Vallarta, were examined. The data for *T. sinaloa* have been unfortunately lost, those for *T. felix* are presented in Table 3. In only one gizzard of an adult *T. felix* was vegetable matter found, and even then animal matter pre-

TABLE 3
CONTENTS OF 25 GIZZARDS OF *THRYOTHORUS FELIX PALLIDUS* EXPRESSED AS PER CENT OCCURRENCE IN THE SAMPLE

Coleoptera	80	Isoptera	4
Lepidoptera (larvae)	32	Diptera	4
Hemiptera	20	Lepidoptera (adult)	4
Hymenoptera	12	Fruit	4
Orthoptera	4		

dominated. From the data it can be said that at this time of the year both species feed mainly on coleopterous insects, extensively on Hemiptera and larval Lepidoptera and to a lesser extent on Araneida, Hymenoptera, Isoptera, Orthoptera, Diptera, and adult Lepidoptera. Before the date from *T. sinaloa* gizzards were lost it was determined that there were no significant differences between the species in the relative frequency of these items or in the approximate size of the food taken.

Foraging.—Observations on the foraging characteristics of the wrens were not quantified, but they did not reveal any obvious difference between the species in either the parts of the environment exploited or in the manner of exploitation. Differences, if they exist, must be small. Both species forage at a height of less than 2 meters, often on the ground: both species forage rarely in the canopy of trees, as much as 10 meters above the ground. However, since tarsus length is correlated with the nature of the perches used (Grant, 1966*a*; Selander, 1964), and since *T. sinaloa* has a shorter tarsus than *T. felix*, a difference in feeding positions may exist. On the Tres Marías Islands *T. felix* is, if anything, more terrestrial than either mainland form.

Nests.—The two species construct a nest of the same shape, that of a flask or retort bent at the base of the neck through 120–180°. The nest is built over a twig or slender branch and near its tip, and in such a way that the bowl of the flask hangs down on one side and the neck hangs down on the other. It is made of grass stems, shreds of bark, fine twigs, etc., and measures approximately 22 to 25 cm long and 10 to 12 cm in maximum height and breadth. There are slight and insignificant differences between the two species in the height and orientation of the nest (Table 4). The preferred orientation of both species is with the entrance facing north or west. Both species were found building nests within 1 meter of the nest of an aculeate hymenopteran, *Polybia occidentalis* (Oliv.) (Fig. 4). The nests were also frequently on species of acacias which are covered with highly aggressive ants of the genus *Pseudomyrmicus*. Nests were usually above open ground, water, or a bromeliad (cf. Sutton, 1948), and not close to other vegetation. In these several

TABLE 4
NEST CHARACTERISTICS

THE NUMBER OF NESTS AND THE DIRECTIONS IN WHICH THEIR ENTRANCES FACED

	N	NW	W	SW	S	SE	E	NE
T. felix	3	1	2	2	–	–	–	1
T. sinaloa	1	1	3	–	1	–	1	1

NEST HEIGHT ABOVE GROUND (IN METERS)

	N	Range	$\bar{x} \pm 2$ SE
T. felix	18	0–9	3.03 ± 0.85
T. sinaloa	9	1.3–3.5	2.62 ± 0.54

ways the two species exhibit identical adaptive defenses to the threat of nest predators.

On the mainland only one of a total of 18 nests of *T. felix* was found built upon the ground. On the Tres Marías Islands only two nests were found altogether, one on the ground and the other at half a meter above ground. That such low nesting is probably of general occurrence on the islands is suggested by the fact that old nests were frequently seen in mainland forests, conspicuously supported on the limbs of trees, but were never seen by the author on the islands, nor have they ever been recorded there by other ornithologists. Atypical ground nesting on the Tres Marías Islands has also been reported for White-tipped Dove (*Leptotila verreauxi*) (Grayson, 1871). It is presumably less hazardous on the islands than on the mainland in view of the relative lack of predators.

Breeding season.—The timing of the breeding season of the two species appears to be the same. At Tepic nest building was first observed in the second week of May. The first eggs were found in the third week of May and the first fledged young were observed in the first week of June. Some pairs of both species were found attending nests as late as July, either having started breeding late, been forced to renest, or having started a second brood. A few observations indicated that five eggs was the usual clutch size in both species. No determination of breeding success was made. *T. felix* breeds as much as 7 weeks later on the Tres Marías Islands than on the mainland, for reasons which are not completely understood (Grant, 1964, 1966*b*).

DISCUSSION

Lack of evidence of hybridization or heterospecific courtship and pairing suggests that the two species are reproductively isolated. Similarity of song

FIG. 4. Nests of *Thryothorus felix* and *Polybia occidentalis* in an acacia, about 4 km north of Puerto Vallarta, Jalisco, June 1963. The two nests are approximately one-third of a meter apart and are supported by the same complex of branches. *Polybia* nest on the left, *Thryothorus* nest on the right. The entrance to the wren's nest is on the left.

suggests that species discrimination is achieved not by song but by means of plumage, movement, and postures. The similarity of song also probably helps the maintenance of mutually exclusive territories by ensuring that in territorial defense a male will respond to the song of another male of either the same or the other species in the same way (cf. Dixon, 1961). Exclusive territories are presumably of adaptive advantage to both species in view of the apparent similarity in food requirements, as judged by observations on foraging behavior, diet, and size of bill and body.

Other ecologically similar species of wrens coexist in two ways. Either they occupy different habitats (Grinnell and Storer, 1924; Marshall, 1957), or else they occupy the same habitat but different parts of it as a result of aggressive dispersion (Brooks, 1934, 1947; Miller, 1941; Newman, 1961). It is probable, therefore, that coexistence in the same habitat with little or no interaction occurs only when ecological differences are large and the likelihood of competition minimal (Grant, 1966*c*). For instance, where *Troglodytes aedon*, *Thryomanes bewickii*, and *Thryothorus ludovicianus* occur to-

gether aggression is greatest between *T. aedon* and *T. bewickii*, intermediate between *T. bewickii* and *T. ludovicianus*, and least between *T. aedon* and *T. ludovicianus* (Sutton, 1930). In the absence of detailed knowledge of the ecology of these species the bill lengths may be taken as indicative of their food characteristics. The least compatible pair of species differ in bill length by only 8 per cent, the middle pair by 26 per cent, and the most compatible by 36 per cent (calculated from data in Ridgway, 1904). The expected correlation is thus realized.

Species in other genera display the same features. When ecological differences are small species either occupy different habitats, occupy different positions in the same habitat (MacArthur, 1958), or defend territories against each other in the same habitat (Orians and Willson, 1964). When ecological differences are substantial territories tend to be largely overlapping. For instance, the completely overlapping territories of the Cardinal (*Richmondena cardinalis*) and Pyrrhuloxia (*Pyrrhuloxia sinuata*) (Gould, 1961), species considered by Bock (1964) to be congeneric, lead one to expect a large difference in preferred food, and this is indeed likely in view of the more than 40 per cent difference in bill length (calculated from data in Ridgway, 1901). An interesting exception to the empirical rule is provided by two species of towhees (*Pipilo fuscus* and *P. aberti*) in Arizona, which sometimes occupy overlapping territories (Marshall, 1960), yet have bills of almost identical length (Davis, 1951). However, the zone of sympatry is extremely small, hence this is a limited case of coexistence. Furthermore, in this zone *P. aberti* is more confined to the woods than the other species and probably does more scratching for its food (Marshall, 1960): these differences in ecology are presumably sufficient to permit coexistence with territory overlap. It may be concluded that interspecific territorial behavior is selected for when the ecological requirements of the two species are too similar to permit them to exploit jointly the available resources (food, perches, nest sites, etc.) in the same volume of habitat without detrimental effects upon each other. The conditions under which this behavior evolves have been discussed by Johnson (1963), Orians and Willson (1964), and Wynne-Edwards (1962).

What makes *T. sinaloa* and *T. felix* unusual is that production of and response to an extremely similar complex song has also been selected for, apparently to aid the process of mutual dispersion. There is a little evidence that a similar situation exists with two species of *Pipilo* in Puebla, Mexico (Marshall, 1964). It would be interesting to know why *T. felix* is sympatric with *T. pleurostictus* in Guerrero, México, Morelos, Puebla, and Oaxaca over approximately half of the latter's range, whereas *T. sinaloa* and *T. pleurostictus* are completely allopatric. *T. pleurostictus* is larger (avg. ca. 18.5 g) than the

other two species, has a bill at least 10 per cent longer than theirs, a conspicuously spotted breast, and songs distinctly different from those of the Jalisco and Nayarit birds of *T. sinaloa* and *T. felix* (songs of *T. felix* from region of overlap with *T. pleurostictus* are not available). Since *T. pleurostictus* is so different from the other two species, why does only one member of the genus coexist with it, and why is that one *T. felix*? The large differences between *T. pleurostictus* and *T. felix* suggest that the territories of the two may overlap. It would also be interesting to know the reasons for the numerical imbalance of sympatric populations of *T. sinaloa* and *T. felix* and whether it really is constant from year to year. Since there appears to be no short supply of birds for the limited amount of space, and probably limited amount of food, here is an excellent situation for the study of interspecific competition under natural conditions.

SUMMARY

Two wren species of the genus *Thryothorus* occur sympatrically over a large part of western Mexico, and were studied in this zone of sympatry. They differ in several plumage characteristics but in most dimensions they are similar, particularly in bill length, and they are strikingly similar in their songs. Reproductively, they appear to be isolated from each other. Territories are defended against individuals of the same and the other species. It is suggested that similarity of song aids this behavior, which is of mutual benefit to the species in view of their extremely similar ecology, viz., they occupy the same habitats, forage in a similar way, feed on similar foods, build similar nests, and breed at the same time of the year. Some territories are interchanged between the species from one year to the next. The two species did not occur in equal numbers in either of two study areas, *T. felix* being about twice as abundant as *T. sinaloa* in one and about half as abundant as it in the other.

On the Tres Marías Islands only *T. felix* occurs. Here it resembles more closely *T. sinaloa* than does its mainland relative, it does not have the "territorial" song of the mainland form, and it has a bill 13 per cent longer than the mainland form. These data indicate that the presence or absence of a congener has had an influence upon the evolution of the reproductive and ecological characteristics of *T. felix*.

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