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WINTERING ECOLOGY OF THRASHERS IN SOUTHERN TEXAS

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ABSTRACT.—Three sympatric thrashers, the Brown, the Long-billed, and the Curve-billed (*Toxostoma* spp.), were studied during the winters of 1977 and 1978 in San Patricio County, Texas. The species avoided competition primarily by occupying different habitats. Brown Thrashers wintered abundantly within riparian woodlands, Long-billed Thrashers stayed mostly within shrub cover of chaparral, and Curve-billed Thrashers inhabited the more open portions of the chaparral. All three species foraged mostly on the ground and were omnivorous. The foraging behavior of Brown and Long-billed thrashers was similar (sweeping debris aside with bill) and both fed only within cover. Curve-billed Thrashers differed from the other thrashers in foraging techniques (reliance upon digging), diet, and in feeding frequently outside of shrub/tree cover.

Brown and Long-billed thrashers maintained intra- and inter-specific winter territories. Both were highly philopatric, with 27% of the color-marked Brown Thrashers and 48% of the color-marked Long-billed Thrashers returning in 1978 to their 1977 winter territories. Brown Thrashers apparently were superior competitors, mostly excluding Long-billed Thrashers from arthropod/gastropod-rich riparian habitats.

Competition may be severe between sympatric congeners. As a result of such interactions, congeners tend to replace each other abruptly between habitats or geographic regions (Lack 1971). Thrashers of the genus *Toxostoma* exemplify such segregation, with usually only one species occurring within a geographically distinct, homogeneous type of vegetation (Cody 1974). Southern Texas presents an unusual situation, though, since three thrashers, the Brown Thrasher (*T. rufum*), the Long-billed Thrasher (*T. longirostre*), and the Curve-billed Thrasher (*T. curvirostre*), are sympatric during the winter. Each of these species has broadly similar ecological needs, and all are basically omnivorous and terrestrial (Bent 1948). Curve-billed and Long-billed thrashers remain in southern Texas throughout the year, and breed in different habitats (Fischer 1980). The purpose of this study was to investigate habitat selection, behavioral interactions, foraging behavior, and food habits of wintering thrashers in order to determine their means of ecological segregation.

STUDY AREAS AND METHODS

My study was conducted from September through April 1977–1978 on the Rob and Bessie Welder Wildlife Foundation (hereafter Refuge), San Patricio County, Texas. Three study plots, 3.35 ha each, were selected: two within riparian woodland and one within dense brushland (chaparral). The vegetation of each plot was analyzed in September 1977 with 25 30.5 m-line transects (Canfield 1941). Botanical nomenclature follows Jones (1975).

The two riparian plots, Plots I and II, supported a similar vegetational cover: 209.5% and 208.8% (overlapping foliar layers), respectively. They differed greatly, however, in size, density, and species composition of the trees. Plot I was characterized by large trees, primarily sugar hackberry (*Celtis laevigata*), net-veined hackberry (*C. reticulata*), anacua (*Ehretia anacua*), and elm (*Ulmus crassiflora*) that formed a dense, closed canopy. The understory cover was light, 28.8%, and comprised mostly of colima (*Zanthoxylum fagara*). Grass and forbs formed 36.2% of the total cover.

The tree cover of Plot II was composed mostly of small, densely packed sugar and net-veined hackberry, la coma (*Bumelia celastrina*), and Texas persimmon (*Diospyros texana*). Anacua and elm were virtually absent. The understory was poorly developed, with shrubs contributing 7.6% of the cover. Grass-forb cover, 46.8%, was slightly greater than that of Plot I.

In the chaparral plot, Plot III, mesquite (*Prosopis glandulosa*) and huisache (*Acacia farnesiana*) were the only tree species recorded, although their cover was slight (8.6%). Shrubs comprised about 60% of the total cover, 168.7%, and the remainder consisted of grasses and forbs. The shrubs grew in dense, mixed thickets ("mottes") composed mostly of blackbrush acacia (*A. rigidula*), agarito (*Berberis trifoliata*), brasil (*Condalia hookeri*), colima, and granjeno (*Celtis pallida*).

I mist-netted in Plot II and Plot III in 1977–1978 and Plot I in 1978 to determine the habitat selection and site fidelity of the thrashers. Each thrasher captured was banded and marked with an individually color-coded leg-streamer. In addition, I censused thrasher populations by walking rapidly through each plot at dawn or dusk and recording the number of calling birds. Both Brown and Long-billed thrashers called vigorously for approximately 15 min during early morning and late evening.

I compared 100 foraging sites of Long-billed and Curve-billed thrashers in Plot III by measuring the diameter of the mottes in which they were foraging, and by measuring the distance to the nearest adjacent motte. Foraging behavior of 12 Brown and 7 Long-billed thrashers was quantified following Cody (1974).

With two stop-watches, I recorded the total time of the observation and the total time the bird was stationary (foraging). In addition, the total number of stops made during the feeding sequence, the estimated distance progressed, and the number of bill sweeps or pecks were recorded.

To compare thrasher diets, I collected by shotgun 37 Long-billed Thrashers (21 in October 1977, 16 in March 1978), 35 Brown Thrashers (15 in October, 20 in March), and 10 Curve-billed Thrashers (7 in October, 3 in March). Analysis of stomach contents consisted of identifying animal matter to class level and, when possible, to the order or family levels (Insecta only). I identified plant material to species when possible. Each item was counted, measured to the nearest 0.1 mm, and volume determined by measuring to the nearest 0.02 cc the displacement in a 5-cc calibrated centrifugal test-tube. For a complete list of thrasher diets, see Fischer (1979). Schoener's (1968) similarity index was used to indicate the similarity of diets between interspecific samples. This expression was calculated by the formula:

$$D = 1 - \tfrac{1}{2} \sum_{i=1}^{N} |P_{x,i} - P_{y,i}|$$

where $P_{x,i}$ and $P_{y,i}$ represent the frequency of the i^{th} category for species X and Y, respectively.

I collected 50 food availability samples in both October and early March. Each sample, located randomly, was obtained by sweeping the vegetation 25 times with a net and collecting all potential food items from 1 m^2 of ground surface. These were stored in isopropyl alcohol, and later counted, identified to class or order, and the volumetric displacement measured as described above.

I collected the following measurements from 97 Brown Thrashers, 135 Long-billed Thrashers, and 35 Curve-billed Thrashers: weight, bill length from the anterior nares to bill-tip, bill width and depth at the posterior nares, and length of the exposed culmen.

Mann-Whitney U-tests (Snedecor and Cochran 1967) were used to test samples for significant differences ($P < 0.05$).

RESULTS

HABITAT SELECTION AND FORAGING SITES

Brown Thrashers wintered abundantly within the riparian plots at densities of 7.8/ha and 8.4/ha in Plot I and Plot II, respectively. Long-billed Thrashers also occurred within these plots but in fewer numbers (0.6/ha in Plot I, 2.4/ha in Plot II). The greater density of Long-billed Thrashers in Plot II may have been related to the much denser, lower-growing vegetation, a habitat somewhat intermediate in form between the tall riparian woodlands of Plot I and the dense chaparral of Plot III.

Long-billed Thrashers were the most numerous species found in Plot III, where they had a density of 4.5/ha. Curve-billed Thrashers also wintered in this plot, though at a lesser density (0.9/ha). Brown Thrashers were present only during migration, or occasionally as wandering visitants from nearby riparian habitats.

Within riparian woodlands, Brown and Long-billed thrashers foraged at sites with well-developed overstories and rarely in open areas with no canopy cover. Both species were dispersed rather evenly throughout the plots.

In the chaparral, the foraging sites of Long-billed and Curve-billed thrashers differed. Curve-billed Thrashers foraged only in the more open portion of the chaparral where the mottes were widely scattered ($\bar{x}$ = 5.3 ± 0.2 m SE, range = 0.7–14) and small in width ($\bar{x}$ = 4.6 m ± 0.3, range = 1.0–11.0). Here, they foraged both within shrub cover and frequently in grassy openings between mottes. Long-billed Thrashers foraged in areas where the mottes were significantly ($P < 0.01$) closer together ($\bar{x}$ = 2.6 ± 0.1 m, range = 1.6–20.0) and wider ($\bar{x}$ = 8.3 ± 0.4 m, range = 1.0–6.0). Long-billed Thrashers occurred throughout Plot III from the densest thickets to and including mottes used by Curve-billed Thrashers. However, Long-billed Thrashers always remained within shrub cover as they did in riparian woodlands.

BEHAVIORAL INTERACTIONS

Both Brown and Long-billed thrashers maintained winter territories. Marked birds were sedentary and highly antagonistic towards conspecific intruders. I often saw encounters as I censused plots. Frequently, an individual was flushed repeatedly until it either circled back to the vicinity where first encountered or it was attacked and chased by another thrasher. I further tested their territorial behavior by releasing conspecifics near free-ranging thrashers. In each of ten experiments, the released bird was immediately attacked and chased from view. During and following chases, territorial Brown Thrashers often uttered a soft, low-pitched "verr" similar to that given at dawn or dusk. When one bird began calling, the territorial neighbors also began to call for five minutes or more before cessation. Long-billed Thrashers also called following an encounter, but the call normally produced, a scolding "tsuck," was different from the call given at dawn or dusk. The twilight calling bouts probably served in territorial advertisement.

In addition to intraspecific territoriality, Brown Thrashers and Long-billed Thrashers maintained interspecific territories. I witnessed naturally-occurring chases in riparian woodlands on six occasions, with the territorial birds equally divided between the two species. I also released three Brown Thrashers near Long-billed Thrashers, and

TABLE 1. Foraging characteristics of 12 Brown Thrashers and 6 Long-billed Thrashers.

	Brown	Long-billed	
	Mean ± SE (range)	Mean ± SE (range)	P[a]
Velocity (cm/min)	7.1 ± 0.8 (0.9–27.1)	7.6 ± 1.3 (0.8–16.4)	$P > 0.05$
Time stationary (%)	97.5 ± 0.1 (94.0–99.2)	97.1 ± 0.3 (90.2–99.3)	$P > 0.05$
Bill sweeps/min	43.1 ± 1.6 (27.2–82.7)	64.2 ± 2.1 (39.6–94.2)	$P < 0.01$
Foraging bout (min)	12.8 ± 1.1 (3.7–49.7)	12.5 ± 2.6 (2.7–38.6)	$P > 0.05$
Min observed	900	291	

[a] Based on Mann-Whitney statistic.

three Long-billed Thrashers near Brown Thrashers. Immediately following release, the territorial bird approached and chased the "intruding" thrasher from view, then began vocalizing. I detected no differences in the form or intensity of inter- and intraspecific territorial bouts.

I never saw agonistic encounters between Curve-billed and Long-billed thrashers, although both species were occasionally seen close together. A similar situation was observed during the breeding season when chases were recorded only after one individual neared another's nest (Fischer 1980).

Thrashers occasionally reacted aggressively toward other terrestrially foraging passerines, especially American Robins (*Turdus migratorius*), Hermit Thrushes (*Catharus guttatus*), and Cardinals (*Cardinalis cardinalis*). These interactions differed from congeneric episodes as they were limited to one or rarely two displacements; chases were never observed. Usually, a displacement was elicited when a bird of another species approached within 3 m of a foraging thrasher.

SITE FIDELITY

A total of eight (27%) of the Brown Thrashers marked in 1977 in Plots II and III were sighted or captured again in 1978. All were found in the vicinity of their initial points of capture in 1977, suggesting that returning birds use the same winter territories each year.

Long-billed Thrashers are considered a resident species in southern Texas (Oberholser 1974); however, some local movement was noted. During both years of the study, Long-billed Thrashers vanished from the Refuge in late April and did not return until September. Their reappearance coincided with the arrival of Brown Thrashers. In 1978, I recaptured 10 (48%) Long-billed Thrashers originally banded in Plots II or III in 1977. Once again, the returning birds were mist-netted from the vicinity of their 1977 winter territories. Site fidelity of Curve-billed Thrashers was not determined since none were mist-netted in 1977.

FORAGING BEHAVIOR

All three thrashers foraged mostly on the ground, although each ascended shrubs and trees in the fall to consume berries. Within cover, foraging was restricted to the ground surface that was largely covered with leaf-litter. Brown and Long-billed thrashers each displaced the litter by rapidly swinging the bill from side to side. Intermixed with this movement was occasional pecking and probing into the substrate. Most of the foraging characteristics of Brown and Long-billed thrashers were alike, with the exception of bill sweeps/minute (Table 1). Long-billed Thrashers swept or probed the leaf-litter much more rapidly than Brown Thrashers.

I did not quantify the foraging behavior of Curve-billed Thrashers as above; however, I made cursory observations of foraging birds. When searching through leaf-litter, they relied heavily upon digging and probing; sweeping of the bill was rarely employed. Within grassy, open areas Curve-billed Thrashers walked rapidly, stopping occasionally to peer at the surrounding vegetation or, infrequently, to dig. The greater reliance upon digging may be expected from comparison of bill measurements (Table 2). Curve-billed Thrashers

TABLE 2. Ratios of mean measurements of thrashers.[a]

Category	Brown–Long-billed	P[b]	Long-billed–Curve-billed	P[b]
Bill length[c]	1.03	$P < 0.01$	1.06	$P < 0.01$
Culmen length	1.04	$P < 0.01$	1.06	$P < 0.01$
Bill depth	1.03	$P < 0.01$	1.11	$P < 0.01$
Bill width	1.03	$P > 0.05$	1.10	$P < 0.01$
Body weight	1.06	$P < 0.01$	1.26	$P < 0.01$

[a] Measurements from 97 Brown Thrashers, 135 Long-billed Thrashers, and 35 Curve-billed Thrashers.
[b] Based on Mann-Whitney statistic.
[c] Bill length from anterior nares to bill tip.

TABLE 3. October and March diets of Brown, Long-billed, and Curve-billed thrashers. Within each sampling period for each species, results are presented as percent of total items (left column) and percent of total volume (right column).

Category	Brown				Long-billed				Curve-billed			
	October		March		October		March		October		March	
Animal material												
Orthoptera	3.1	9.4	0.0	0.0	3.1	15.7	0.7	0.5	10.0	3.3	0.0	0.0
Coleoptera	9.9	7.3	7.7	9.5	20.5	11.0	12.9	18.8	34.0	57.4	45.5	41.2
Hymenoptera	21.7	7.0	42.3	10.6	19.6	3.0	40.5	8.5	2.6	0.2	0.0	0.0
Other Insecta	3.8	7.5	1.7	2.5	3.1	7.6	7.5	8.8	10.7	1.4	0.0	0.0
Araneida	2.0	1.7	0.8	0.5	3.7	2.8	1.3	1.5	5.1	0.8	12.4	31.6
Diplopoda	0.9	0.3	0.5	0.4	1.2	2.8	0.0	0.0	0.0	0.0	0.0	0.0
Gastropoda	1.0	2.5	9.3	31.0	7.5	17.2	8.4	35.5	9.5	4.6	16.6	10.6
Crustacea	7.1	6.3	25.3	25.4	4.0	3.0	23.4	23.2	0.0	0.0	19.8	15.0
Chilopoda	0.3	0.1	0.3	0.3	0.3	0.1	0.4	0.4	0.0	0.0	0.0	0.0
Total animal material	49.8	42.1	87.9	80.2	63.0	63.2	95.1	97.2	72.9	67.7	94.3	98.4
Plant material												
Condalia hookeri	4.2	3.6	0.0	0.0	25.7	31.4	0.0	0.0	9.8	8.8	0.0	0.0
Celtis laevigata	7.3	34.3	4.0	4.2	1.8	4.2	0.0	0.0	6.0	21.5	2.8	0.8
Rhus toxicodendron	38.4	19.9	0.0	0.0	0.8	1.0	0.0	0.0	0.0	0.0	0.0	0.0
Diospyros texana	0.3	0.1	0.0	0.0	0.0	0.0	0.0	0.0	3.1	1.1	0.0	0.0
Other	0.0	0.0	8.1	15.6	8.7	0.2	4.9	2.8	9.0	0.9	2.9	0.8
Total plant material	50.2	57.9	12.1	19.8	37.0	36.8	4.9	2.8	28.1	32.3	5.7	1.6
Number stomachs	15		20		21		16		7		3	

have the longest and most decurved bill of the three species, perhaps a more efficient digging tool than the short and straight (or slightly decurved, Long-billed Thrasher) bills of the other thrashers (Engels 1940).

MORPHOLOGICAL COMPARISONS

One of the many potential means for reducing interspecific competition for food, if food is limiting, is the divergence of bill and/or body size (Schoener 1965, Hespenheide 1971). Hespenheide (1971) reported a strong correlation between bill and body sizes of tyrant flycatchers and the size of their insect prey. Schoener (1965) suggested that a ratio of 1.14 or more between the bill or body measurements of a small to larger species is sufficient to partition food by size rather than microhabitat. The ratios of bill and weight measurements of Brown and Long-billed thrashers differed only slightly (Table 2), with none exceeding 1.06. These thrashers would be expected to partition food resources on the basis of habitat.

FOOD HABITS AND AVAILABILITY

The three thrashers consumed a great variety of animals and berries (Table 3), in concurrence with the literature (Cottam and Knappen 1939, Bent 1948). In October, berries of brasil and hackberry were particularly important foods of each species. Insects were the second most important prey present in Brown and Long-billed thrasher diets and the primary component in Curve-billed Thrasher diets. Brown and Long-billed thrashers primarily ate grasshoppers (Acrididae) whereas Curve-billed Thrashers ate largely beetles.

In March, the diets of all three species changed greatly (Table 3). Few berries were consumed, corresponding to their much reduced availability. Insects were eaten in the same volume as before, although the most prevalent orders shifted to beetles and ants. Gastropods and crustaceans (Isopoda) were eaten in much greater quantities, and comprised over one-half of

TABLE 4. Interspecific similarity indices of Brown–Long-billed thrasher and Long-billed–Curve-billed thrasher diets in October and March.

Comparison	Similarity index			
	October		March	
	Composition	Size	Composition	Size
Brown–Long-billed	0.41	0.85	0.70	0.89
Long-billed–Curve-billed	0.17	0.70	0.36	0.63

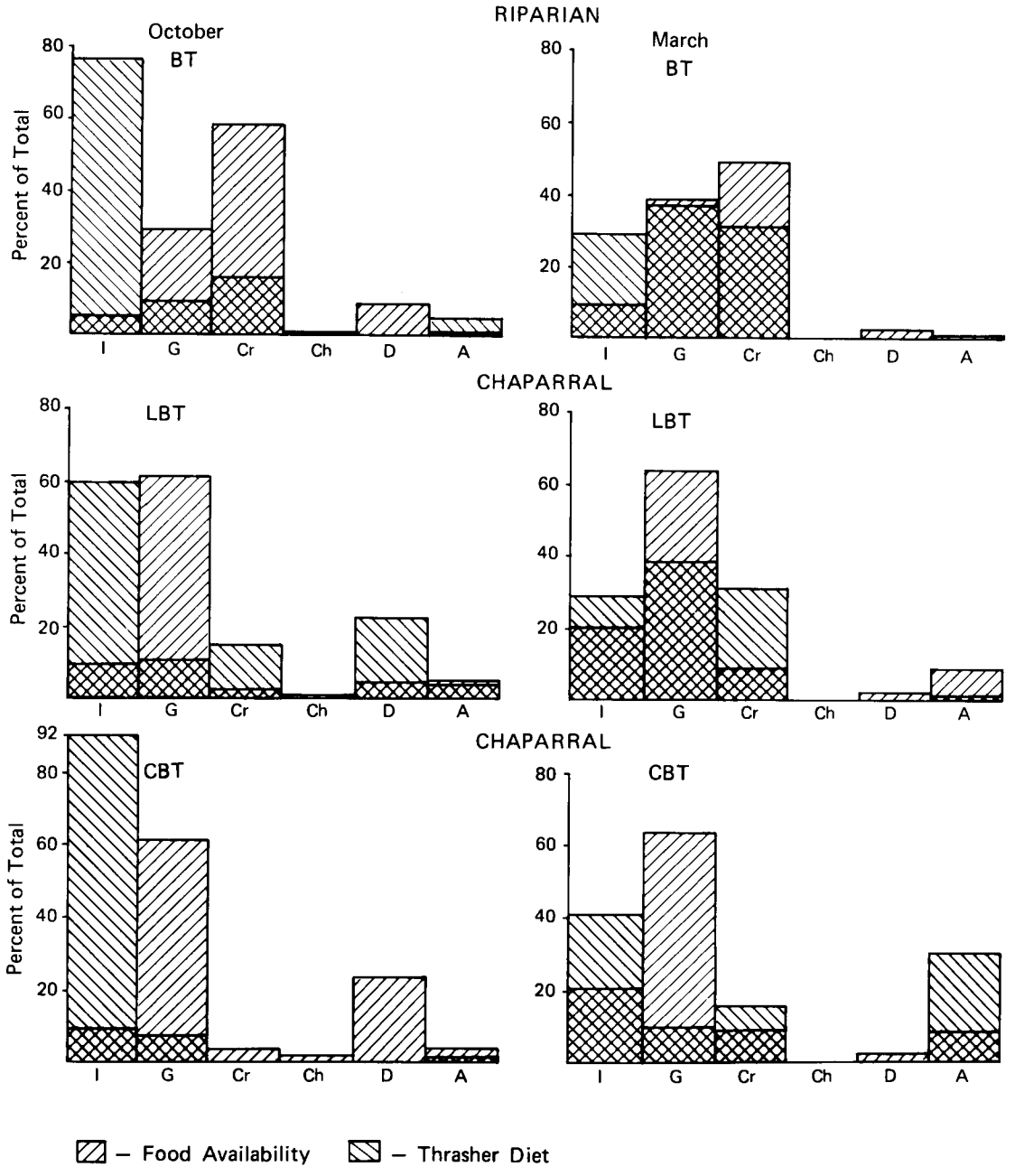

FIGURE 1. October and March diets (volume) of Brown (BT), Long-billed (LBT), and Curve-billed (CBT) thrashers in relation to food availability (volume). I = Insecta; G = Gastropoda; Cr = Crustacea; Ch = Chilopoda; D = Diplopoda; A = Arachnida.

the Brown and Long-billed thrasher diets, and one-fourth of the diet of Curve-billed Thrashers.

In both October and March, the diets of Brown and Long-billed thrashers overlapped broadly in size and taxonomic composition (Table 4), as predicted by the similar ratios of morphological comparisons. The amount of overlap varied seasonally and was the greatest in March when food resources were the least abundant. Although Long-billed and Curve-billed thrashers consumed similar-sized prey, the taxonomic composition of their diets overlapped only slightly. This difference is perhaps a reflection of the foraging site preferences discussed above.

In October, food resources (volume) were significantly ($P < 0.01$) greater in both the riparian and chaparral plots than they had been in March. In addition, food availability was 2.6 times greater in October and 5.4

times greater in March in riparian woodlands than in the chaparral (both significant, $P < 0.01$). When food availability (volume) and thrasher diets (volume) were compared (Fig. 1), certain trends became apparent. Insects were consumed more readily by all three thrashers than were animals of other classes. Millipedes (Diplopoda) were apparently avoided (they were seldom ingested), yet were present in most availability samples. Crustaceans and gastropods were minor components of the diet when alternate food sources, particularly berries, were plentiful.

DISCUSSION

Emlen (1972) censused similar habitats on the Refuge, but determined much lower densities than those that I found. In riparian woodlands he reported Brown Thrashers at densities of 0.3/ha, and Long-billed Thrashers at 0.07/ha. In chaparral, he reported a density of 0.10/ha for Long-billed Thrashers, and 0.05/ha for Curve-billed Thrashers. His very low estimates were undoubtedly the result of the furtiveness of thrashers (especially Brown and Long-billed) during most of the day. The detection of Brown and Long-billed thrashers additionally was confounded by their disruptive coloration. The use of twilight vocalizations seems to be a more accurate method of estimating populations of these birds.

Separation by habitat is clearly the most important mechanism through which Brown and Long-billed thrashers attain ecological segregation. They are similar in size and appearance, forage in a similar manner, select comparable foraging sites, and consume essentially the same foods. Where overlap occurs in riparian woodlands, interspecific territoriality is displayed.

Dietary overlap between Brown and Long-billed thrashers increased during the time of food scarcity (March). This greater overlap is in apparent accordance with foraging theory, which predicts an expansion of diets and an increase in dietary overlap as food abundance decreases (MacArthur and Pianka 1966, Schoener 1971, 1974, Pyke et al. 1977). These results differ from those of Smith et al. (1978) who determined that Darwin's ground finches (*Geospiza* sp.) diverged in their diets and took a narrower range of foods in the season of food shortage. Unlike thrashers, the sympatric finches retreated to different parts of the resource spectrum and consumed essentially different foods (Smith et al. 1978).

The habitats occupied by Brown and Long-billed thrashers on the Refuge were similar to those inhabited elsewhere (Bent 1948, Oberholser 1974). Long-billed Thrashers apparently were more restricted in their habitat occupancy on the Refuge than in the Rio Grande Valley of Texas, where Brown Thrashers are rare. There, Long-billed Thrashers occupy chaparral, but reach their greatest density in riparian woodlands (Bent 1948). These results suggest that the Brown Thrasher is a superior competitor in the region of sympatry, generally excluding the Long-billed Thrasher from the arthropod/gastropod-rich riparian woodlands.

Both Brown and Long-billed thrashers exhibited winter territoriality, a behavior reported for relatively few North American birds, including Townsend's Solitaire (*Myadestes townsendi*; Salomonson and Balda 1977), Mockingbird (*Mimus polyglottos*; Hailman 1960), Plain Titmouse (*Parus inornatus*; Dixon 1956); and Red-headed Woodpecker (*Melanerpes erythrocephalus*; Kilham 1958, Moskovits 1978). In most cases, winter territoriality is characteristic of non-migratory birds or those that spend a great proportion of the year on their wintering grounds. Both Brown and Long-billed thrashers were present on the Refuge from seven to eight months. Additionally, each subsisted in late winter largely on arthropods and gastropods, animals perhaps scarce during the weather extremes typical of south Texas winters.

Brown and Long-billed thrashers are considered members of the same taxonomic complex (Engels 1940). Their winter ranges were once probably allopatric and separated by a broad expanse of unsuitable habitat (Hubbard 1973). The landscape of southern Texas has been altered dramatically, however, during the last 300 years (Johnston 1963, Inglis 1964). Early explorers reported that grasslands were the predominant feature of the area, shrubs and trees being limited to the slopes along water courses or occasional mottes (Inglis 1964). Burning and overgrazing practices promoted shrub-invasion to the extent that most upland sites are presently characterized by chaparral. Thus, with the formation of suitable habitat, the winter ranges of Brown Thrashers, and the winter and breeding ranges of the Long-billed Thrasher probably expanded and sympatry developed.

Although both Long-billed and Curve-billed thrashers inhabited chaparral, I never saw interactions between them. Curve-billed Thrashers occupied only the more

open portions of the chaparral and, unlike Long-billed Thrashers, frequently foraged in the grassy areas between mottes. The foraging techniques and composition of the diets of Long-billed Thrashers and Curve-billed Thrashers also differed considerably. Bent (1948) and Oberholser (1974) reported that Curve-billed Thrashers prefer open brushland including pastures, and Long-billed Thrashers prefer dense brushlands. These observations suggest that sufficient divergence in behavior and microhabitat selection exists to allow ecological isolation within chaparral habitats.

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