

RELATIONSHIPS BETWEEN TWO PARTLY SYMPATRIC SPECIES OF THRUSHES (*CATHARUS*) IN MEXICO

RALPH J. RAITT AND JOHN WILLIAM HARDY

MONTANE forests of much of Mexico are occupied by two closely related species of nightingale-thrushes, *Catharus occidentalis* and *C. frantzii*. These species are so similar morphologically that they were long regarded either as one species or as two with uncertain limits and distributions. Recently Rowley and Orr (1964) and Phillips (1961, 1969) have established that the two forms are specifically distinct. Both species breed principally in humid pine-oak forests of higher elevations (above 6,000 feet); *C. occidentalis* occurs from Chihuahua south into Oaxaca; *C. frantzii* occurs from Panama north into Jalisco and San Luis Potosí. The two are sympatric in a number of mountain ranges included in the distributional overlap.

The above findings on species limits and distributional patterns were based largely on careful morphological analysis of museum specimens by the authors cited. Strong confirmatory evidence was provided by data on egg shell coloration presented by Rowley and Orr. However, little more than incidental attention was given by these workers to ecology and behavior.

The situation of sympatry of two species so similar that they were confused for one appeared to constitute an excellent subject for field research on ecological and behavioral interrelationships, especially in view of the paucity of information in the literature of the species. Studies of isolating mechanisms in sibling species of meadowlarks (*Sturnella*) by Lanyon (1956, 1957) and Szijj (1966), of *Empidonax* by Johnson (1963), of *Myiarchus* by Lanyon (1963), and of *Agelaius* by Hardy and Dickerman (1965) are among recent contributions that have dealt with understanding ecological relationships and speciation in birds. In fact, the studies of Dilger (1956a, 1956b) on more northerly representatives of the genus *Catharus* are outstanding examples of the fruitfulness of comparative field study of sympatric congeneric species.

With this background in mind we undertook to study *C. occidentalis* and *C. frantzii* in one region where they are sympatric and later to study each in a portion of its exclusive, allopatric range. The area of sympatry was Cerro San Felipe, north of the city of Oaxaca. This locality was chosen because Hardy had done considerable field work there in 1965 and knew both species to be present. We worked there together in portions of the breeding seasons of 1966 and 1967. For field work in at least roughly comparable habitats in areas of allopatry, we worked in 1967

near El Palmito, Sinaloa, on *C. occidentalis* and near San Cristóbal de las Casas, Chiapas, on *C. frantzii*.

METHODS

FIELD ITINERARY

Hardy spent the period 1–21 April 1965 in the field on Cerro San Felipe, where he and his assistants, Raymond Jillson and Juan Nava, camped at 9,000 feet in pine-oak-fir forest. The principal subject of study was the Dwarf Jay (*Cyanolyca nana*), but they did some general collecting and made ecological observations. Raitt joined the party on 19 April. This work revealed the presence of both species of *Catharus* within walking distance of the camp; it also provided important background on physiography, vegetation, and general ecology of the area.

In 1966 Hardy and Raitt, assisted by Thomas O. Boswell, spent the period 23 April to 4 May in field study of the two thrushes from a camp near to the 1965 campsite. In 1967 we worked in the field near El Palmito, Sinaloa, a few miles west of the Durango boundary at an elevation of about 6,500 feet from 24–26 April, and in the vicinity of San Cristóbal de las Casas, Chiapas, 2–4 May. From 6–13 May we worked again in the same area on Cerro San Felipe. Raitt left 13 May, but Hardy remained in the area until 16 May. Donald Caccamise assisted us in the field through 13 May, and Harold F. Mayfield accompanied us during the work in Oaxaca.

ECOLOGICAL STUDY

Hardy's study of *Cyanolyca nana* included description and analysis of the vegetation types of the area on Cerro San Felipe that will be published in detail (1970) as part of that study. They include recognition of several main variations in vegetational configuration and floristic composition, the nature and distribution of which are obviously correlated with topographic variation.

Our initial approach to the study of comparative ecology of the two thrushes was to determine whether any correlation existed between distribution of the thrush species and the distribution of the vegetation types. Cruising as much of the area as possible, we identified the individual *Catharus* encountered to species, at first by collecting specimens and by noting the color of the tip of the lower mandible when we could see it. After we determined species-characteristic differences in vocalizations, we relied on these for identification. As this initial approach yielded strong indications of habitat differences between the species, we continued it throughout the study, with increasing emphasis on vegetation types that seemed to offer possibility of co-occupancy or close juxtaposition of the two thrushes. Another source of ecological information was nest placement, and we gave special effort to finding nests, particularly in 1967.

Two stretches of riparian habitat—one occupied by each species—we censused by a combination of nest locations and mapping of territories of singing males. A limited amount of observation of foraging behavior also had some ecological implications.

We used similar ecological approaches in Sinaloa and Chiapas, searching the range of habitat types available for singing males and for nests. This was helped by playback of recorded songs and calls, especially in Chiapas.

BEHAVIORAL STUDY

In behavioral work we gave the most emphasis to vocalizations because these were virtually unknown and the close morphological similarity between the two species suggested that vocalizations might be a means of species recognition and reproductive

isolation. We tape-recorded in the field songs and principal call notes of as many individuals as possible of each species. All recordings were made at 7.5 ips, most with a Uher 4000 report recorder and Altec 684-A microphone, a few with a Nagra IIBH recorder and an Electro-Voice Soundspot directional microphone. We collected most individuals whose voices were recorded to confirm species identification; the remaining few were observed at very close range and under good light so that both of us could see definitely whether the lower mandible was dark-tipped or yellow-tipped.

Broadcasting recorded vocalizations and whistled imitations of call notes helped elicit reactions for behavioral study and for censusing. We performed a number of field experiments with alternate playbacks of vocalizations of the two species, sometimes placing a stuffed model near the recorder. The experiments are described in more detail below.

General observations on several aspects of behavior—particularly agonistic display, foraging, and nesting—were made in the course of the work on habitat occurrence and on vocalizations.

ANALYSIS OF VOCALIZATIONS

Recorded vocalizations were analyzed with sound spectrographs made on a Kay Electric Company Sona-graph, 662-A Model Recorder. In compliance with directions in the manual for the Model Recorder, tape to magnetic disc transfer was made with levels not exceeding approximately 0 decibels on the VU meter of the amplifier analyzer (-1 to +1). In analysis playback, VU readings ranged from -2 to 0 on the VU meter. The narrow Band Filter and FL-1 curve were employed. The illustrations are ink tracings of the sonographic impressions, omitting those components definitely known to be other species of birds (often trogons, *Trogon mexicanus*, and robins, *Turdus infuscatus* and *T. assimilis*), and "outdoor rumble" (wind, recorder sounds, and other known accidental inclusions).

In general the fundamental is dominant. Occasionally faint components lower than the formant frequency made deciding what to show difficult because, as Irby Davis has pointed out to us, some of these apparent components of the sound may be artifacts of recording and reproduction not actually uttered by the birds. Almost all impressions shown had additional harmonics higher than the emphasized sonic structures illustrated. Usually these showed a regular decrease in amplitude with increasing frequency and were very faint beyond the third harmonic above the formant frequency. Occasionally the harmonic just above the dominant formant frequency was weak and the next somewhat stronger. We do not here imply by their omission that they are not audible components of the sound or do not contribute to the tonal quality.

We believe that under field conditions the strength of signal, possible distortions that we failed to avoid, and problems of artifactual printing by the Sona-graph allow for our purposes their arbitrary omission. The purposes of sound analysis in this paper provide tolerances within which we believe we have operated carefully. The illustrations allow accurate visual determinations of phrase length, phrase variety, and phrase complexity, including general frequency fluctuation and structural complexity. We have avoided any comparative conclusions concerning differences in songs of individual thrushes of the same or different species or populations that would exceed the accuracy of our illustration and our use of the electronic equipment. Finally, sonograms upon which illustrations (Figures 8-15) are based are on file in the Moore Laboratory, as are the field tape recordings themselves, and for further analysis these are available to any qualified worker upon request.

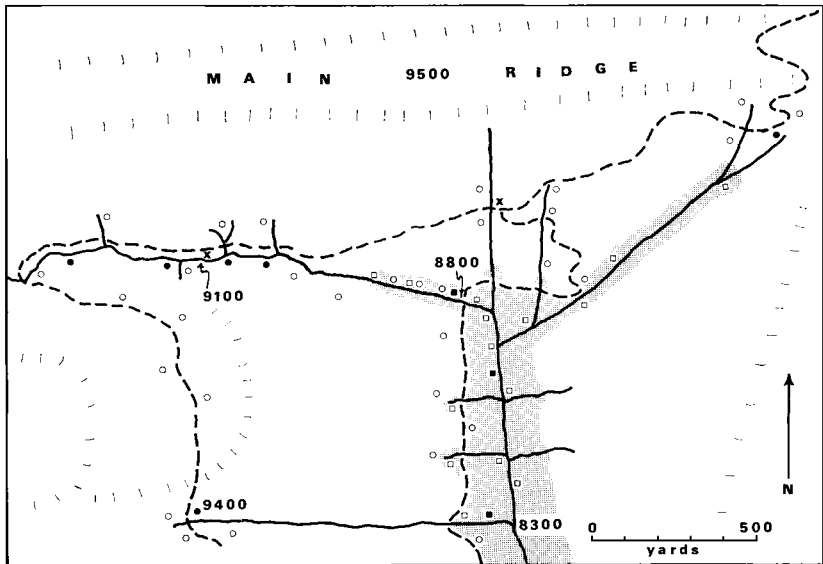


Figure 1. Map showing study area, 1965-67, Cerro San Felipe, Oaxaca. Stippling indicates dense, broad-leaved riparian forest. Solid circles, active nest sites; open circles, places of *C. occidentalis* sightings; open and closed squares, the same for *C. frantzii*; X, campsites; solid lines, streams; broken lines, roads.

RESULTS IN SYMPATRIC AREA

The results of the work on Cerro San Felipe, Oaxaca, are presented and analyzed first because they are of greatest magnitude and importance. Then the findings in the allopatric areas are discussed. Finally some overall evolutionary conclusions are drawn.

DESCRIPTION OF CERRO SAN FELIPE

Location and physiography.—The study area included somewhat more than 1 square mile of the forested south flank of one of the main ridges extending east from the peak of Cerro San Felipe. It lies approximately 10 miles north and west of the city of Oaxaca about 3 miles (5 km) east by logging road from the settlement of La Cumbre, which is located near kilometer marker #20 on the paved road between Oaxaca and Ixtlán de Juárez. This portion of the main ridge is drained by several small streams, some of them seasonal and intermittent, that lead into a main stream occupying a very deep and steep canyon or barranca at the lower, southern portion of our study area (Figure 1).

The main ridge is not broad at its summit, but it is relatively level and unbroken. Slopes in general are steep and they become increasingly

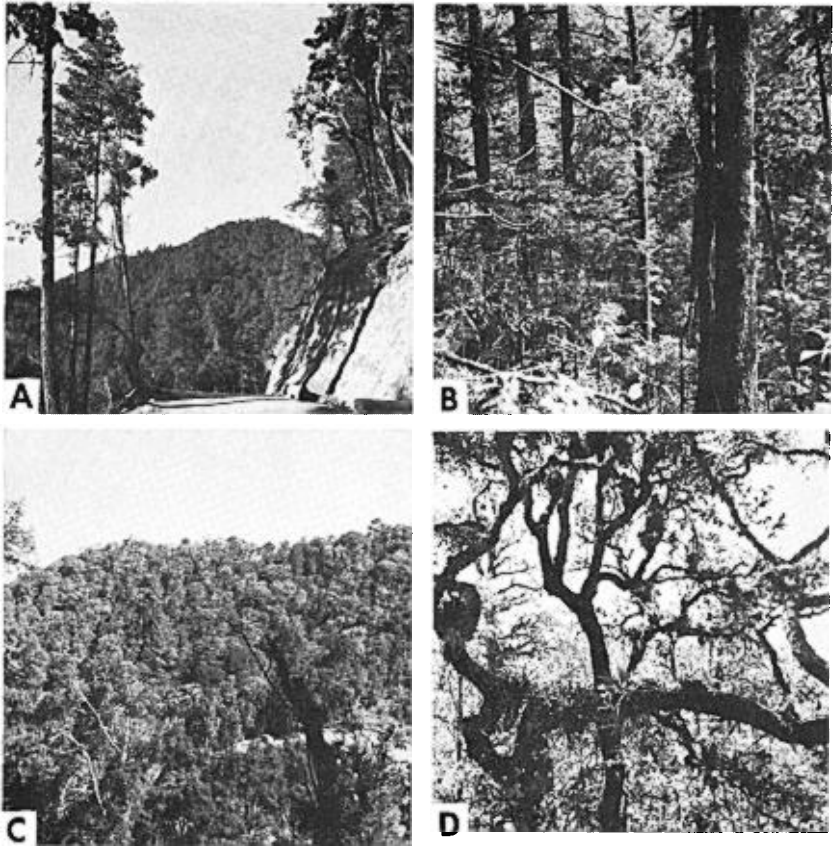


Figure 2. Vegetational aspects of Cerro San Felipe, Oaxaca. A, virtually unbroken forest; B, mesic ravine slope forest of fir, oak, and a few pines; C, dry oak woodland on xeric slopes; D, epiphyte-laden limbs of oaks.

so with decreasing elevation. Our camp sites lie at about 9,100 feet, the ridge top is a few hundred feet higher, and the bottom of the main barranca is about 8,300 feet at the point of our deepest penetration. Our work was concentrated in the vicinity of the main barranca and its principal branch, which enters from the west (apparently this branch is one of the principal drainages for the whole east side of Cerro San Felipe). We also worked some other areas intensively, especially those adjacent to the logging road.

Plant communities and aspects.—The area is covered by a forest that is virtually unbroken except where human interference has occurred, mostly within 50 feet of the logging roads (Figure 2A). Vegetation on the slopes and in the bottoms of all but a few major canyons is dominated

by various combinations of oaks, pines, and firs. It ranges from a closed, dense forest dominated by tall firs (*Abies religiosa*) and oaks (mainly *Quercus adata*) on moist sites, such as steep north-facing slopes and lower sides of deep canyons (Figure 2B), to dry woodlands of oaks (*Quercus rugosa*, *Q. laurina*) and madrone (*Arbutus xalapensis*) on exposed sites (Figure 2C), especially on the south slopes near the top of the main ridge. Most of the area is covered by a mixed pine-oak forest, with dominants including the species of other types previously described and pines (*Pinus* spp.). Understory trees in the tall dense forest include members of the same species as the dominants and some other species, especially *Litsea glaucescens*. Shrubs and other low ground cover are not dense in the forests and woodlands, but the dense forests contain a considerable accumulation of decaying fallen limbs and logs. Numerous small openings in the forest, made primarily by cutting activities described later, frequently contain dense clumps of low shrubs. Epiphytes of several groups are plentiful in the dense forests (Figure 2D).

Perennial streams are lined by riparian vegetation, usually confined to a narrow strip because the small streams so often flow through narrow canyons. This vegetation is characterized by clumps of dense tall shrubs, often overlying the streams proper, and by the presence of broad-leaved evergreen trees not found in the pine-oak-fir forests of the slopes. The most widespread of these trees is *Meliosma dentata*. In the deep barranca a number of other species occur, including alders (*Alnus* sp.) and others that we have been unable to identify. These trees in the deep barranca are tall and in places form a dense canopy (Figure 3A) with an understory of small trees (Figure 3B) also of species not found on the slopes (*Rhacoma* sp., *Parathesis* sp.). The shrubs immediately adjacent to the stream and on talus slides on the steep sides form very dense tangles. One of the commonest of these, a shrub of the pokeweed genus, *Phytolacca*, is almost confined to the vicinity of the main stream and its principal branches in the very deep and steep-sided canyons. Upper, more open canyons, especially the one through which the main stream flows in a predominately easterly direction, contain riparian shrubs and individual trees of *Meliosma dentata*, but the character of the vegetation is much more open. The shrubs are of different species and occur in small clumps, and forest trees such as oaks and firs also grow on the canyon bottom. Additional quantitative data on the vegetation will appear in Hardy's publication on the ecology of *Cyanolyca nana* (1970).

In summary the vegetation of the deep barrancas occupied by the lower portions of the principal stream is strikingly different from most of the vegetation of the sides of the canyons and ridge tops. In Figure 1 this barranca vegetation is indicated by the patterned overlay. Of course, it

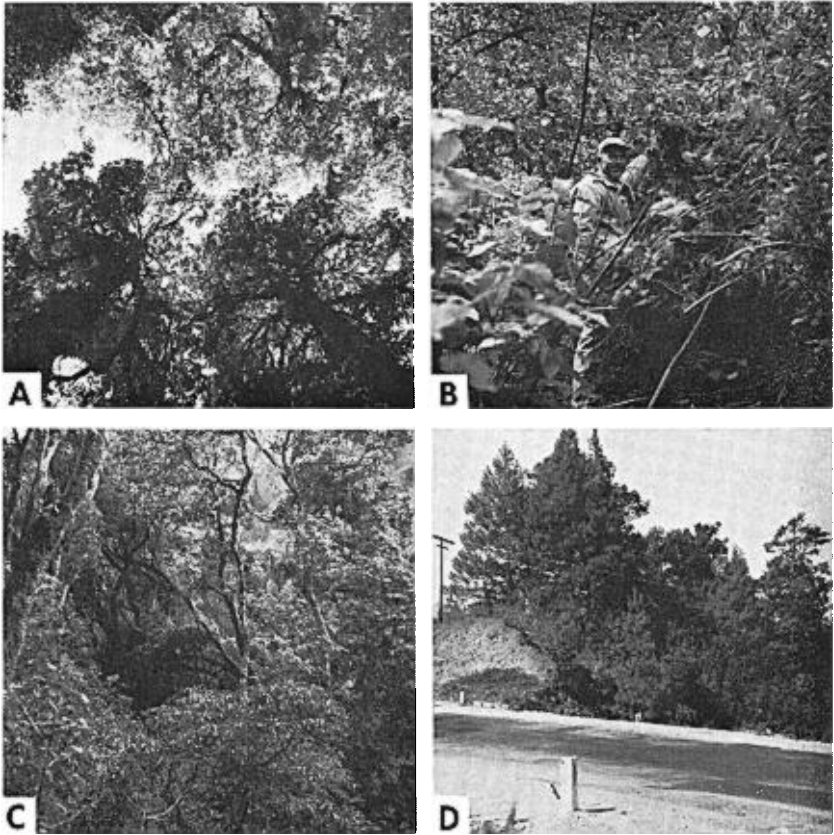


Figure 3. Vegetational aspects of study areas in Oaxaca and Chiapas. A, tall *Meliosma* trees of the deep barranca, Cerro San Felipe, Oaxaca, forming dense canopy; B, dense tree thicket under the canopy of *Meliosma* in the deep barranca of Cerro San Felipe; C, mesic dense broad-leaved forest of barranca southeast San Cristóbal de las Casas, Chiapas, site of *C. frantzii* nest; D, second growth pine-oak woodland southwest of San Cristóbal de las Casas where *C. frantzii* ground nest was discovered.

does grade into the more open riparian vegetation of the smaller, upper canyons which in turn grades into the various pine-oak-fir forests and woodlands of the slopes.

Human disturbance.—The principal land use of the area by man is for cutting timber. The entire upper area of Cerro San Felipe is managed and utilized by a paper company. Fortunately their cutting practices are selective, and most of the work is done by hand axe and saw. Although virtually the entire area is worked and the effects are widespread, the disturbance is diffuse. The most obvious effect of cutting operations is in the small draws where the logs are transported. Vegetation in many of

these draws is very open, but large areas are not denuded, and most of the forests appear virtually intact. The greatest effect of this operation is probably not in the cutting itself, but in the building of roads. These are narrow and unpaved and some are not heavily used, but road construction in the very steep topography causes artificial downslope deposit of a large amount of talus that disturbs the vegetation. In 1966 an old trail that traversed the side of the main barranca was widened and extended. Even though it is several hundred feet above the bottom, the slopes that it crosses are so steep that slides of dirt and rock pushed over the edge destroyed some of the large trees near the bottom. Considerable disturbance has occurred along the upper west-east stretch of the main stream where the main roads follows it closely. Some riparian brush and trees have been removed, especially in building turnouts from the road, and the riparian strip is thus periodically interrupted. This effect has been partially compensated for by leaving frequent piles of small branches that serve as artificial ground cover (and as favored foraging sites for *Catharus*). A few cattle are allowed to graze the area, but deliberate burning, cultivation, and indiscriminate cutting are prevented. Thus except for the immediate vicinity of roads (all of which are shown in Figure 1), the effect by humans has been restricted to a general slight opening of the forests and moderate opening and complete clearing only in occasional patches.

ECOLOGY OF THE THRUSHES

Previous studies and preliminary work.—At the beginning of intensive study in 1966, our slight previous experience and the few references to work on Cerro San Felipe by Rowley and Orr (1964), along with general a priori assumptions, led us to expect that the ecological interrelations of the two species would probably include one or a combination of three possibilities: (1) that the two species would occupy altitudinally separated but contiguous ranges on either side of a dividing line or zone within the study area, (2) that they would occupy complementary habitats in a mosaic or interdigitating pattern within the area, and (3) that they would occupy the same habitats but exploit them differently.

Ecological preferences and segregation.—Both seasons of field work showed the relationship to be predominately of the second type. All *C. frantzii* that we located were in or very near to canyon bottoms where the vegetation is of the deep barranca type. Every one of the deep canyons supporting this type of vegetation that we were able to explore contained *C. frantzii*. Forests and woodlands of the slopes, on the other hand, invariably contained *C. occidentalis*. Members of this species were heard singing or found nesting in oak woodland, in pine-oak woodlands, and in

forests of tall firs and oaks; they were also found in riparian habitats along upper, more open streams. Thus *C. occidentalis* was resident in all wooded vegetation types except the broad-leaved deep barranca type, and *C. frantzii* appeared virtually confined to this latter type. Figure 1 illustrates this distributional pattern.

This habitat difference is certainly the most obvious and almost surely the most important ecological isolating mechanism between the two species. It is apparently a strict separation, for in our many hours of observation in most vegetation types we failed to note a single exceptional "out-of-place" individual thrush. The strictness of the separation was probably best illustrated by our observations on the sides of the main barranca. The logging road that traverses the steep west slope follows a rough line of separation between obvious barranca vegetation and pine-oak-fir of the slopes. However several small draws and one larger side canyon that cross the road from above contain strips of the broad-leaved epiphyte-laden trees characteristic of the bottom, while firs, oaks, and pines descend across the road nearly to the bottom on the exposed crests of a few ridges. Normally we heard songs of *C. occidentalis* from above and those of *C. frantzii* from below as we worked this road in the evening, but on several occasions this situation was reversed as we passed either a ridge or a draw. Despite the intimate contact between the two species along this vegetational boundary, the segregation seemed to be maintained. On 19 May 1967 we saw and heard from the same spot, almost simultaneously, one individual of each species singing loudly and frequently no more than 100 feet apart, but the *C. frantzii* was on the moist bottom of the main lower side canyon under the broad-leaved canopy, the *C. occidentalis* up the slope in the open forest.

Species and habitat contacts.—Transitional habitats do occur along the course of the main tributary canyons. As indicated earlier the riparian vegetation of the upper canyons differs in character from that of the deep canyons, but the transition is not perfectly abrupt. Rather as one ascends the canyons the riparian growth narrows progressively, the canopy opens, and the broad-leaved trees and shrubs gradually drop out. One such transitional area in which we did considerable work is the lower portion of the main west-east tributary. The upper stretch of this stream, where it closely parallels the road, is relatively open and inhabited by *C. occidentalis*. The extreme lower stretch, below its crossing of the lower road, plunges into the main barranca and supports *C. frantzii*. In the intervening stretch the stream gradient and slopes of the canyon sides are variable and intermediate, and clumps of dense broad-leaved trees alternate with open stretches containing low brush on the slopes and pines, oaks, and firs near the bottom. In both 1966 and 1967 we saw and heard

members of both species along the bottom of this canyon. In 1966 we found a nest of *C. frantzii* in a *Meliosma* tree directly over the stream at the lower end of this intermediate stretch. In a mist net directly below this nest and also in one several yards upstream, we caught individuals of both species. Apparently in this intermediate situation the two species occupy overlapping foraging areas. The same is probably true in some of the other tributaries and on the edges of the deep barranca where vegetation types interdigitate in a "fine-grained" pattern. We saw no evidence of interspecific territoriality. Field experiments described later indicate that members of neither species respond to broadcast calls and songs of the other species, suggesting that defended territories might well overlap in these restricted intermediate and "edge" sites. Certainly the two species are truly sympatric in these sites, although the trenchant habitat differences keep almost all individuals of each species apart.

Ecological requirements and preferences.—In the foregoing discussion we have stressed the fidelity of *C. frantzii* to what we call the deep barranca vegetation association. The species is restricted to this association, while *C. occidentalis* occurs in virtually all other vegetation types in the area. Thus we may consider what important features the birds themselves react to in selecting their respective habitats. The deep barranca vegetation is most easily characterized floristically. Its plant species differ markedly from those of the slopes and of upper canyons, but that the birds react directly to floristic differences is doubtful. Their habitat selection probably is based on structural properties of the vegetation or other physical features of the environment. The presence of permanent flowing water is a consistent feature of *C. frantzii* habitats, but *C. occidentalis* also lives near the permanent stream of the main upper canyon and, in fact, it reaches its highest density there. Dense, tall shrubbery is another characteristic of deep barranca vegetation, although it does not occur continuously along the main stream and it does occur in areas inhabited by *C. occidentalis*. This feature may be significant, for we never saw *C. frantzii* far from such shrubbery and the species spends a great deal of time on or near the ground under dense shrub cover. A dense arboreal canopy is another characteristic of *C. frantzii* habitat, but it is neither universal nor limited to it; dense forests of firs and oaks are inhabited by *C. occidentalis*. Probably the most consistent distinguishing feature of *C. frantzii* habitats is the small amount of light that reaches the ground, and, more particularly, the fact that they remain totally shaded almost throughout the day. The dense forest habitats of *C. occidentalis* are well shaded, but all seem to receive bright, if not direct, light for an extended period each day. The habitats of *C. frantzii*, on the other hand, may receive some direct sunlight, but only for a short period at midday. The rest of the day deep shade is cast

by the high steep canyon walls, the generally heavy canopy on the canyon bottoms, the tall dense shrubs, and the tall firs and oaks growing on the lower slopes just above. Thus the essentials of the *C. frantzii* habitat are a generally shaded and moist area in which to forage and nest under a close overhead cover. *C. occidentalis* apparently has a broader range of tolerance and can live in more open, less shaded situations, even though it reaches its highest densities in the more shaded, overgrown sites.

Population densities.—Results of censuses of breeding pairs of each species in favored habitat are of interest in connection with the thrushes' general ecology. We censused approximately $\frac{1}{2}$ mile of the upper main stream and a comparable stretch of the main stream in the deep barranca by location of singing males and of nests in both 1966 and 1967. We worked the stretch of the upper canyon intensively both years, and we estimated with considerable confidence that in the slightly over $\frac{1}{2}$ mile along the road it supported five to six pairs of *C. occidentalis*. We found the nests of four of these pairs in 1967. Clumps of streamside shrubs formed the cores of the territories, and open stretches made by truck turnouts formed barriers between territories. As mentioned above, the density of thrushes in this riparian habitat is higher than in other types of vegetation. Density is probably lowest in open oak woodland with little ground cover. A similar length of the lower stream in the deep canyon supported an approximately equal number of pairs of *C. frantzii*, judging by counts of singing males and the area covered by two different singing males that we followed for considerable periods.

Foraging behavior.—We gave some attention to foraging behavior as a possible means by which the two species might achieve ecological compatibility. Unfortunately these thrushes are so shy and their coloration blends so well with their forest background that the volumes of observations on undisturbed foraging birds was not large. Both species appear to do much of their actual foraging on the ground, or on logs and rocks or in shrubs near the ground. Yet we have a definite impression that *C. frantzii* is the more ground-dwelling of the two. It sings principally from very low perches or from the substrate proper. Individuals reacting to playback or imitated calls approached us at very low level, and individuals that we flushed flew at low level to cover on the ground or within a few inches of it. On the other hand, we often saw *C. occidentalis* on perches or flying several feet above the ground. Both Skutch (1960) and Slud (1964) describe *C. frantzii* as dwelling on the ground or in low shrubs in Central America.

Morphological correlates of foraging methods.—Dilger (1956b) points out that differences in tarsal length may reflect adaptation to different forest strata and that, among northern *Catharus*, cursorial species in

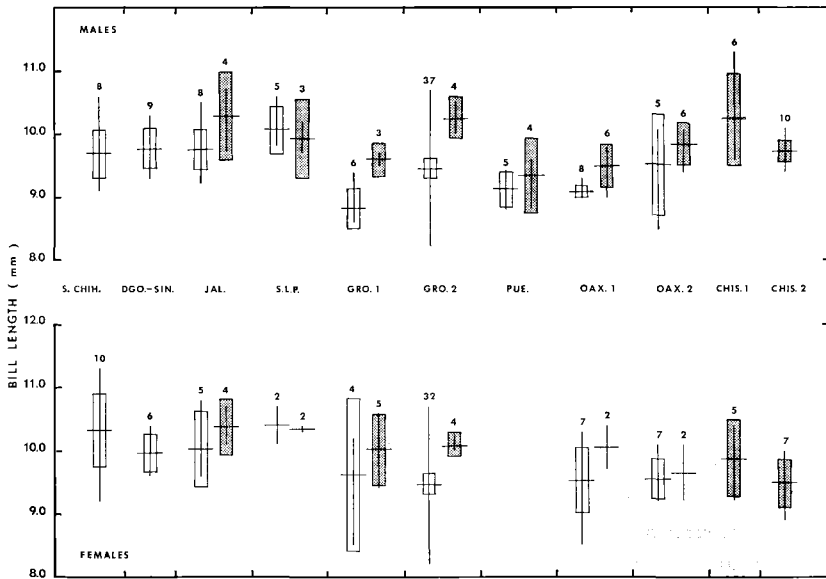


Figure 4. Analysis of bill length of *C. frantzii* and *C. occidentalis*, indicating character displacement in length in areas of sympatry. Vertical lines represent ranges of each sample, numerals indicate size of samples. Horizontal lines indicate means, and rectangles delimit plus and minus 95 per cent confidence limits. Open rectangles, *C. occidentalis*; shaded rectangles, *C. frantzii*. Localities abbreviated, left to right: southern Chihuahua, primarily Mt. Mohinora and vicinity; mountains near boundary of Durango and Sinaloa, east of Mazatlan; Jalisco; San Luis Potosi; Mt. Teotepec, Guerrero; Omilteme, Guerrero; Huauchinango, Puebla; Mt. Totontepec, Oaxaca; Cerro San Felipe, Oaxaca; San Cristóbal de las Casas, Chiapas; Volcan Tacaná, Chiapas. Bill length is from anterior end of external naris to tip.

general have longer tarsi than species of more arboreal habits. Of the two Mexican species, *C. frantzii* averages longer in tarsus at all seven sympatric localities for which we measured specimens (see Figure 4 for localities). In the Cerro San Felipe sample of males the mean length of 33.30 mm for *C. frantzii* is significantly higher than the mean of 32.34 mm for *C. occidentalis* ($t = 2.77$, 9 df, $P < 0.05$). Thus *C. frantzii* appears to be better adapted for cursorial locomotion, and morphological evidence supports our impression of their greater tendency to stay on the ground.

Differences in bill length might be expected to reflect differences in food habits. As will be discussed later, populations of *C. frantzii* tend to have longer bills than the populations of *C. occidentalis* with which they are sympatric (Figure 4). For the sample of males from Cerro San Felipe, the mean of 9.85 mm for *C. frantzii* is significantly greater than the mean of 9.52 mm for *C. occidentalis* ($t = 4.37$, 9 df, $P < 0.01$).

Nesting habits.—As possible modes of ecological isolation and also as “biological” traits of these sibling species, nesting habits are of interest. In the two seasons of field work we located seven active nests of *C. occidentalis* and two of *C. frantzii* plus several nests that were fresh but of unknown status. Of the *C. occidentalis* nests, one was on the ground, one was in a riparian shrub about 5 feet above the ground, one was at a similar height in a dense clump of willow-like composite shrubs at the edge of a clearing near the main ridge-top, and the remaining four were in trees (*Quercus* spp.) at approximate heights of 8, 12, 12, and 50 feet. Three of the latter were within 10 yards of the main upper stream. One of the nests of *C. frantzii* was in a *Meliosma* tree about 12 feet above the stream, and the other was in a small broad-leaved tree (*Rhacoma* sp.) about 5 feet above the ground under the dense canopy a few feet from the main lower tributary in the deep barranca. Two groups of fresh-appearing nests, almost certainly of *C. frantzii*, were at heights of 4 to 7 feet in dense shrubs near or over the main stream in the deep barranca (see Figure 3B). One *C. frantzii* nest found in Chiapas was on the ground. These data indicate that both species may place the nest in a variety of situations. The reports of Rowley and Orr (1964) and Rowley (1962) from various places in Mexico and of Skutch (1960) for *C. frantzii* in Central America similarly indicate a wide choice of nest sites. Certainly no difference is apparent between species in nest position, other than the differences in the habitats already described. Nest structure is also similar. Both species characteristically build a cup with a bulky outer lining, usually of moss, and a fine inner lining of dark roots, plant fibers, and sometimes hair. The descriptions and photographs by Skutch (1960) and Rowley and Orr (1964) agree with our findings for both species. Rowley and Orr (op. cit.) describe the differences in egg color and, again, our findings are in agreement for eggs from five nests of *C. occidentalis* and two of *C. frantzii*.

Phenology.—One further aspect of ecology to be considered is phenology. Our data show no evidence of difference in breeding season. In late April and early May of 1966 and in mid-May of 1967, both species were singing frequently and were territorial, as shown mainly by reaction to playback experiments. In 1966 the activity at the few nests found was principally late stages of construction and early stages of laying. During the later period of field work in 1967 we noted laying, incubation, and hatching. The single active nest of *C. frantzii* in 1967 contained two newly hatched young when it was found on 9 May. Eggs in two nests of *C. occidentalis* hatched on 10 May and 12 May, respectively. Egg and nesting data given by Rowley and Orr (1964) and Rowley (1962, 1966) agree with our findings and show no specific differences in breeding times.

BEHAVIOR AND VOCALIZATIONS

Aggressiveness and territoriality.—Differences in the two species' preferred habitats make comparative behavioral evaluation difficult. The trouble we had watching individual *C. frantzii* in the dense undergrowth at first led us to think that this species was shyer and more retiring than *C. occidentalis* and less prone to react aggressively toward territorial intrusion. We made tape recordings in both 1966 and 1967 of song sequences of both species and then played them back to elicit behavioral response. Although response at first seemed easier to evoke in *C. occidentalis*, we later concluded that habitat density often prevented our seeing the reaction of individual *C. frantzii*. Several times we happened to glimpse such approaches for a fraction of a second, and then were unable to see the bird again in the thick cover. Had we not accidentally seen the approaching bird, we would have thought there was no response. We conclude that the two species show no obvious differences in the boldness, aggressiveness, and concomitant strength of territorial assertion in the area of sympatry.

Songs of C. frantzii.—On Cerro San Felipe the song of *C. frantzii* is characterized by great phrase repertoire, melodic richness, and great variety in phrase length and frequency of dominant or formant frequencies. Tables 1 and 2 (males 3 and 4), Figures 5–7, and Figures 8–11 (phrases 1–32) illustrate the main features leading to this description. Male 3 utters one phrase (type 19) three times but otherwise is nonrepetitive in 16 phrases. Male 4 shows the greatest repetitiveness of any *C. frantzii* song sequence analyzed; 16 phrases in the 37-phrase sequence are repeats of previous phrases in the sequence. Phrase inventiveness also diminishes after the 26th phrase with an indication that it might cease altogether were the sequence extended. Figure 7 reveals the great variety in phrase length (0.4 to over 1.6 seconds).

Examination of the sonograms will show that one can easily distinguish between phrases in the sequences. Structure of many phrases is characterized by medium frequency (2–4 KHz); formants are relatively pure and sustained frequencies with motifs within phrases often around 0.5 second in length. The principal frequencies show many abrupt changes of frequency; often two clearly spaced simultaneous voices are without intervening components (or severe intermodulation effects). To the human ear the songs are clearly audible, languid, and prolonged, revealing their separate motifs, not harsh or noisy, and often pleasingly musical or harmonious and lyrical within themselves.

Songs of C. occidentalis.—In this area of sympatry the songs of *C. occidentalis* (Tables 1 and 2, Figures 5–7 and 11–12) are characterized

TABLE 1
SONG CHARACTERISTICS OF FOUR MALES OF EACH OF THE *CATHARUS* THRUSHES

Species/individual	Locality	Date	No. of song phrases	No. of song phrase types	Mean length of phrase (sec)	Length of phrase sequence (sec)	Song phrase rate	Index of phrase variety
1. <i>C. frontzii</i> NMSU	San Crist., Chiapas	4 May 1967	14	13 (48-60)	0.90	60	14/min	0.93
2. <i>C. frontzii</i> MLZ M-22	San Crist., Chiapas	2 May 1967	15	15 (33-47)	0.94	50	18/min	1.0
3. <i>C. frontzii</i> MLZ M-20	Cerro San Felipe, Oaxaca	28 April 1966	16	14 (19-32)	1.38	65	15/min	0.88
4. <i>C. frontzii</i> MLZ M-24	Cerro San Felipe, Oaxaca	10 May 1967	37	18 (1-18)	1.13	150	15/min	0.48
1. <i>C. occidentalis</i> NMSU	Cerro San Felipe, Oaxaca	12 May 1967	28	4 (1, 2, 3, 4) ^v	0.90	68	23/min	0.14
2. <i>C. occidentalis</i> MLZ M-24 (seq. 1)	Cerro San Felipe, Oaxaca	11 May 1967	16	4 (1, 2, 3, 4, 6)	0.94	90	11/min	0.25
3. <i>C. occidentalis</i> MLZ M-24 (seq. 2)	Cerro San Felipe, Oaxaca	11 May 1967	15	4 (1, 2, 3, 4)	0.86	90	11/min	0.27
4. <i>C. occidentalis</i> MLZ M-25	Cerro San Felipe, Oaxaca	12 May 1967	100	5 (1, 2, 3, 4, 5)	0.89	420	14/min	0.05

^v This phrase is a slight variant of phrase 4.

TABLE 2
ORDER OF NUMERICALLY DESIGNATED SONG PHRASES IN SONG SEQUENCES OF TABLE 1
THRUSHES¹

Individual	Order of appearance ²
<i>C. frantzii</i> 1	48-59, 52, 60
<i>C. frantzii</i> 2	33-47 (no repetitions)
<i>C. frantzii</i> 3	19-24, 19, 25-32, 19
<i>C. frantzii</i> 4	1, 2, 3, 4, 2, 5, 6, 7, 8, 4, 2, 9, 10, 8, 11, 12, 6, 13, 2, 14, 9, 15, 4, 16, 17, 6, 13, 2, 6, 4, 18, 12, 2, 13
<i>C. occidentalis</i> 1	2, 2, 1, 2, 2, 2, 1, 2, 1, 2, 1, 4 ^v , 2, 1, 3, 1, 4 ^v , 1, 2, 1, 2, 1, 2, 1, 3, 1, 2, 1
<i>C. occidentalis</i> 2	3, 1, 2, 1, 4, 6, 2, 6, 2, 3, 1, 2, 1, 6, 2, 1
<i>C. occidentalis</i> 3	1, 3, 1, 4, 1, 3, 2, 3, 1, 2, 1, 4, 3, 1, 2
<i>C. occidentalis</i> 4	3, 1, 2, 3, 1, 1, 2, 1, 4, 1, 1, 2, 3, 1, 4, 1, 2, 3, 1, 2, 1, 5, 2, 4, 1, 1, 2, 3, 1, 2, 1, 1, 2, 1, 2, 1, 3, 1, 2, 3, 1, 2, 1, 2, 1, 2, 1, 1, 2, 1, 4, 1, 2, 1, 2, 3, 1, 3, 2, 1, 3, 3, 1, 2, 3, 1, 2, 3, 1, 2, 1, 3, 2, 1, 2, 3, 1, 3, 1, 2, 1, 2, 3, 1, 2, 3, 1, 2, 3, 2, 3, 2, 1, 2, 1, 3, 2, 1, 2

¹ Refer to Figures 5-6 for graphic portrayal of variety and repetitiveness in these songs.

² Numerals in italics denote repeated phrases.

^v This phrase is a slight variant of phrase 4.

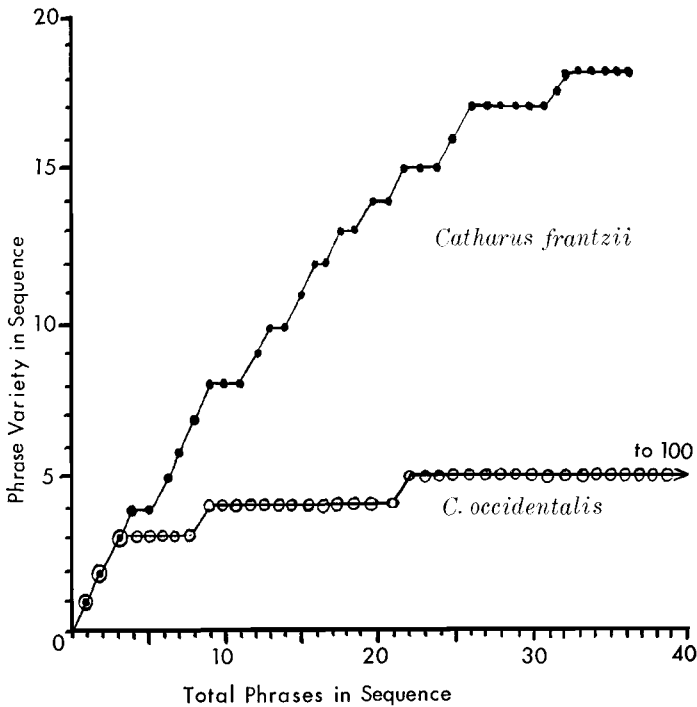


Figure 5. Comparison of variety and inventiveness in songs of *C. frantzii* male 4 and *C. occidentalis* male 4.

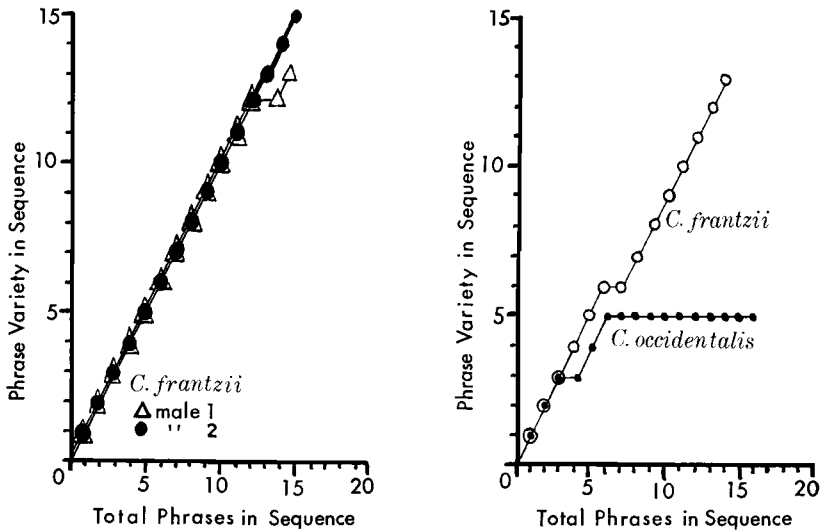


Figure 6. Comparison of variety and inventiveness in songs of (left) *C. frantzii* males 1 and 2; (right) *C. frantzii* male 3 and *C. occidentalis* male 2.

by meager phrase repertoire, close resemblance of even the spectrographically distinguishable phrase types, and squeaky or noisy sound. The lack of musical quality results from the brevity of most motifs and phrases and from the greater complexity and density of simultaneous components.

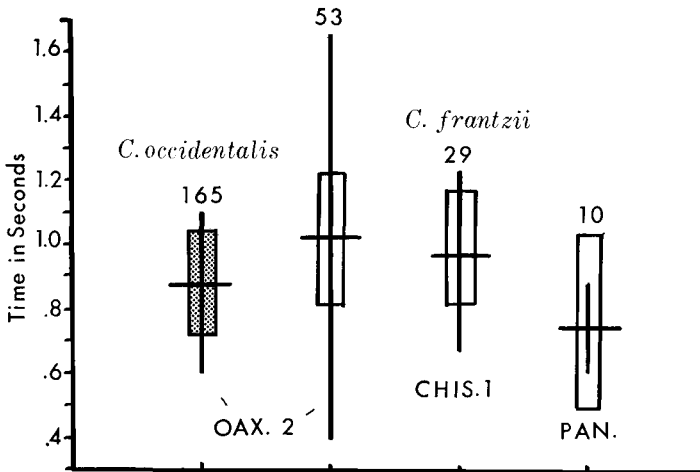


Figure 7. Statistical representation of variation in song phrase length at three localities, (left to right) Cerro San Felipe, Oaxaca; San Cristóbal de las Casas, Chiapas; and Canal Zone, Panama. See legend of Figure 4 for explanation of illustrations.

We detected only nine phrase types in all recordings of *C. occidentalis* at this locality in the 2 years. None of the four *C. occidentalis* analyzed used more than five phrase types, and all of them shared types 1-3. Note that even though the sequence of male 4 is 100 phrases long, the 22nd phrase is the last new one (type 5). All these were recorded in 1967; we recorded little adequate material of this species in 1966. The phrase types 7-9 of the 1966 bird, although similar to types 1-6, are clearly distinguishable. This suggests the possibility that more extensive recording of *C. occidentalis* might reveal more variety than is currently evident. Nevertheless it seems clear that basically *C. occidentalis* males are rather monotonous singers and that the population tends toward homogeneity in repertoire, phrase types commonly being shared by males.

Response to song playback.—In both 1966 and 1967 we performed song playback experiments with territorial thrushes of both species. In the principal experiments we carried two tape recorders, one equipped with a song sequence of *C. occidentalis* and the other with one of *C. frantzii*, each sequence being about 2 minutes in length. Entering the known territory of a given male, we tried to discover the whereabouts of the pair and to note their activities before starting the playback. First we played the sequence of the opposite species, waited approximately 2 minutes while we watched the birds' reactions, then replayed it, watched again, and then repeated the procedure playing back the song of the male's own species.

Occasionally these experiments failed to produce observable results, apparently because we were not close enough to a territorial male (either not in his territory or not close to his position in the territory at the time of the experiment), or we were unable to note the response because of dense vegetation. This was particularly true with *C. frantzii*, for we had less access to and less familiarity with the individual territories of males and the species lives in the thickest cover.

The experiments had one unequivocal result; birds never were seen to respond in any way to song or call playback of their sibling species. Also in almost all cases, males on territory (where active nests were known or strongly suspected to exist) responded by some expression of territorial behavior to playback of the song of their own species. In 1966 we conducted experiments on *C. occidentalis* in the late nest building and early egg laying stages; males in the stream side area near our camp (see far upper left portion of map, Figure 1) all responded immediately to playback of their own species' song. A description of the experiments of 3 May follows:

Experiment 1. (Note: in this first attempt we had not formulated the experimental procedure with repeated sequences and intervals for observation or rest periods outlined above.) Male and female at forest edge, near nest. Sequence of *C. frantzii*

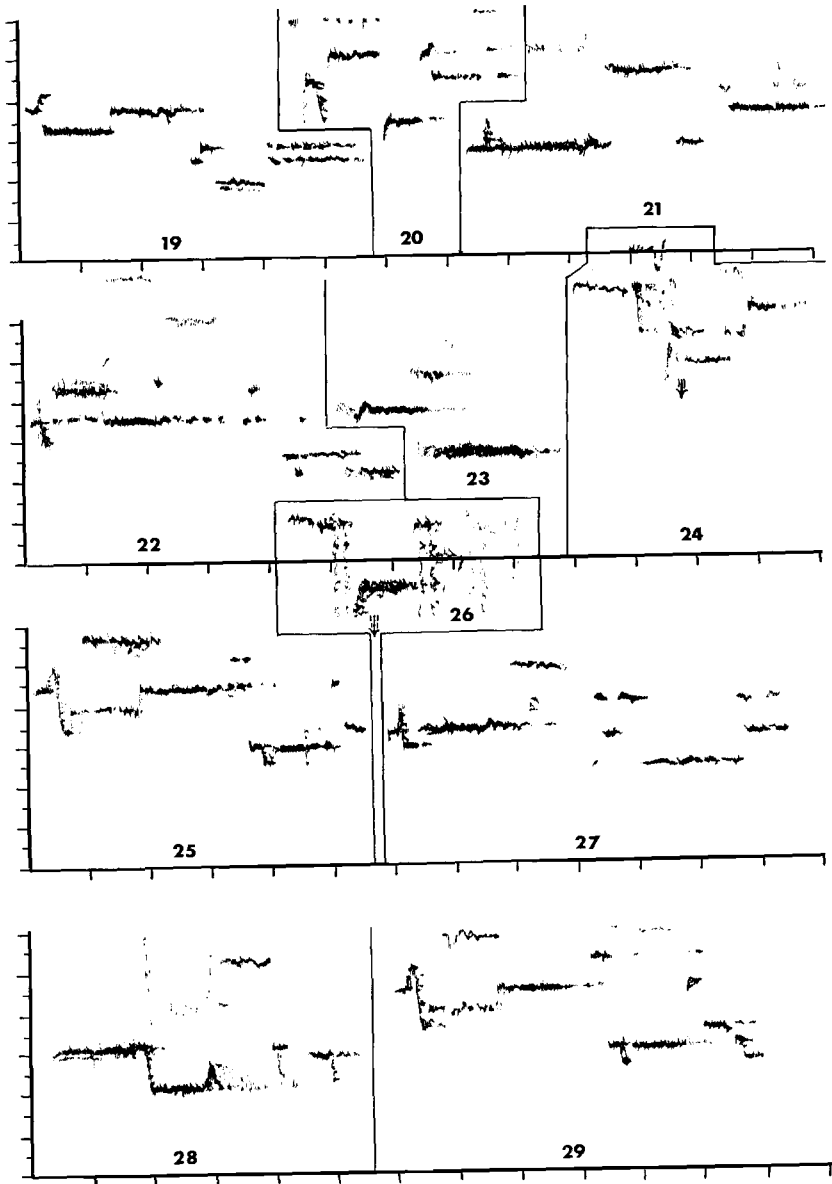


Figure 8. Songs of *C. frantzii*, male 3 (part). Song phrases shown in sonograms here and in Figures 9–15 are numerically designated as to phrase type (see column 5, Table 1). A double vertical line marks the end of one sequence and the beginning of another. Frequency in kilocycles (KHz) is demarcated on the vertical axis, at intervals of 500 Hz, 0 to 6000. (Note that some songs have components above 6 KHz; these may be measured using the scale shown). Time in seconds is demarcated on the horizontal axis at intervals of 0.2 second.

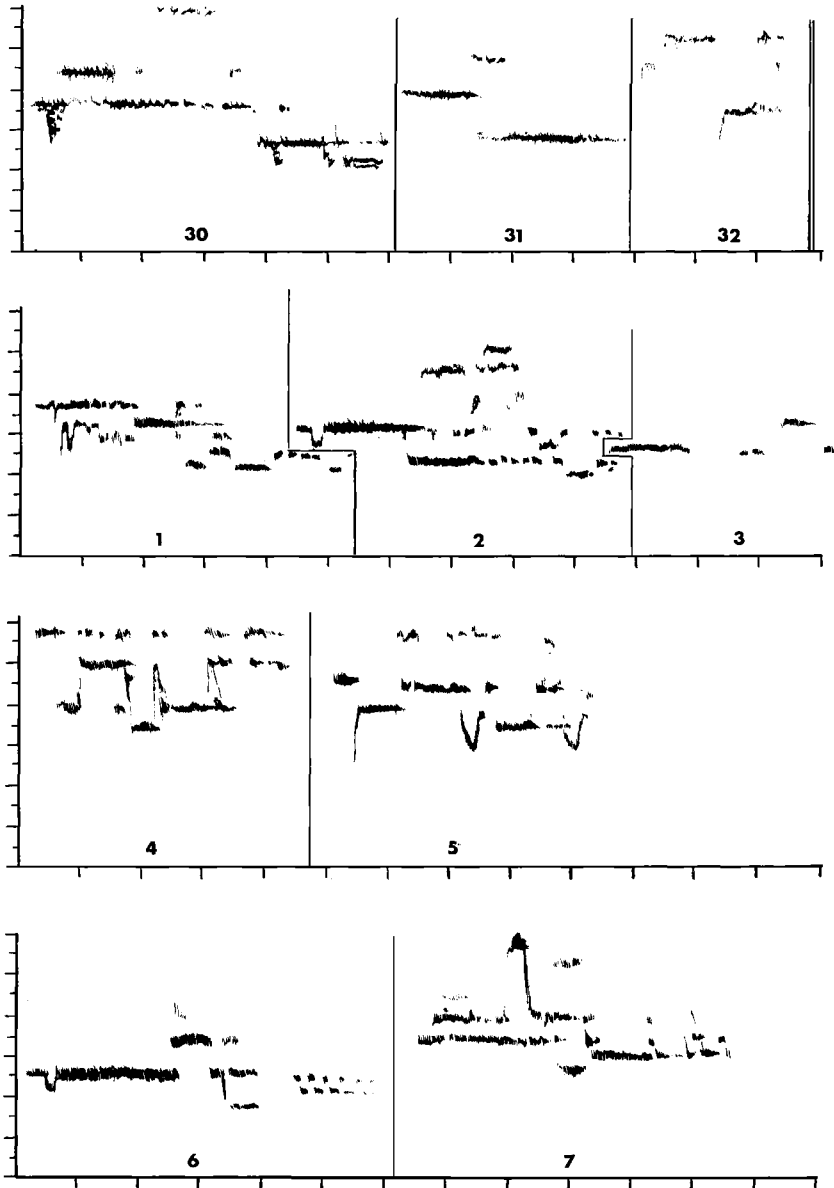


Figure 9. Songs of *C. frantzii*, male 3 (completed), male 4 (part).

song played. Female flips tail, male shows no response and is hidden from view. Sequence of *C. occidentalis* played. Male begins flying back and forth, approaches and withdraws several times, flips tail, assumes upright posture. Does not sing or approach us closely. We are not concealed from view. Sequence of *frantzii* song

played. Male continues to show inquisitiveness but ceases to fly back and forth. Perches and watches us intently.

Experiment 2. Another pair. No birds in sight. Played *C. frantzii* sequence. No response noted. Waited 2 minutes. Replayed sequence. No response noted in 2-minute interval. Played *C. occidentalis* sequence. With first phrase thrush appeared and flew back and forth. We shot the bird, a male.

Experiment 3. Two birds, probably a pair, foraging in area thought to contain nest. Played *C. frantzii* sequence. No reaction. Birds kept feeding as they randomly moved away from us. Repeated sequence. No change. Two minutes later played *C. occidentalis* sequence. One bird flies at us and up hill beyond, then back and forth, returning eventually past us as sequence continues. Probably the male. Supposed female also appears nearby. Finally a pair of birds from uphill behind us approaches to edge of clearing (road area) at place probably corresponding to territorial boundary between the two pairs. We did not collect any of these birds.

Experiments with *C. occidentalis* in 1967 are not described in detail. They took place during the incubation period in the same area of streamside territories. Again we were usually able to elicit response, but sometimes the response was delayed until we played as many as three or four repeats of the *C. occidentalis* sequence before a bird appeared. We marked the location of known nests and/or territories and performed the playbacks at these locations. Each time we also placed a stuffed model in plain view near the playback unit. In one case where a known nest was thought to be deserted (experiment 2) we were not able to attract any response, suggesting either that aggressiveness wanes in such circumstances until nest building resumes, or that the birds had left the area or been killed. In one episode the male that approached perched near the recorder and assumed a fluffed, tail down, wings drooped posture, facing the playback unit and model. In another the model and playback unit were situated at an open streamside clearing marking the boundary between two streamside territories. Upon playback, one bird from upstream and two from downstream appeared but would not emerge into the clearing.

We conclude that normal territorial response to song playback and an inanimate model is nonvocal approach, back and forth flying, and rarely assumption of fluffed, tail down, dropped wing posture. Secondly, we conclude that *C. occidentalis* makes no interspecific response to *C. frantzii* based upon song. Finally response seemed to be principally directed toward the song, not the model.

In 1966 we made three attempts to elicit response to playback of *C. frantzii* in areas we knew the species inhabited. On 28 April in the deep area of the barranca, we recorded the numerous song sequences of a male (see Tables 1-2 and Figures 11-12, phrases 19-32), and through intermittent playback of these, seemingly caused persistent singing and attentiveness to the area by the same male. On 4 May in late morning we collected the nest and one egg (another was broken in removal) of *C. frantzii*

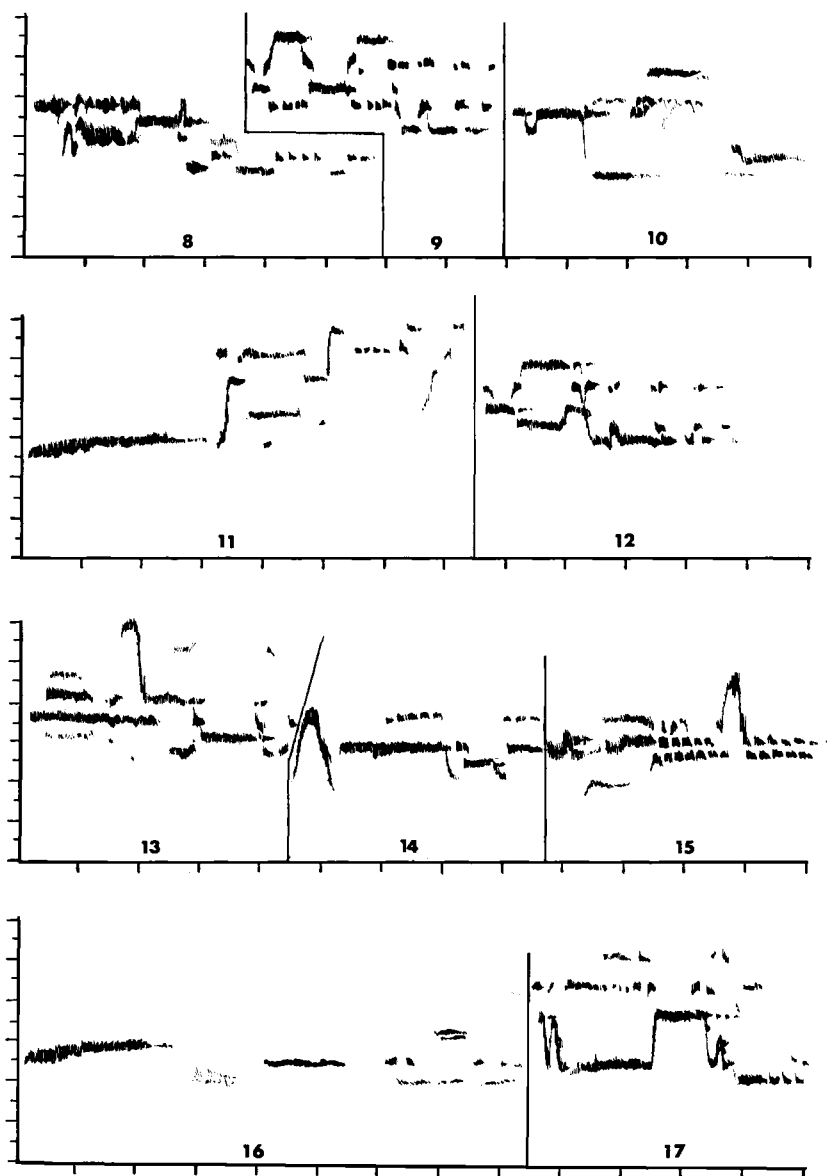


Figure 10. Songs of *C. frantzii*, male 4 (continued).

in the upper barranca. Shortly thereafter Raitt, stationed beneath the nest tree, performed experimental playback of both thrush songs in the pattern described. No response to the song of *C. occidentalis* was noted. After 1½ minutes of the first playing of the *C. frantzii* sequence, a thrush, species

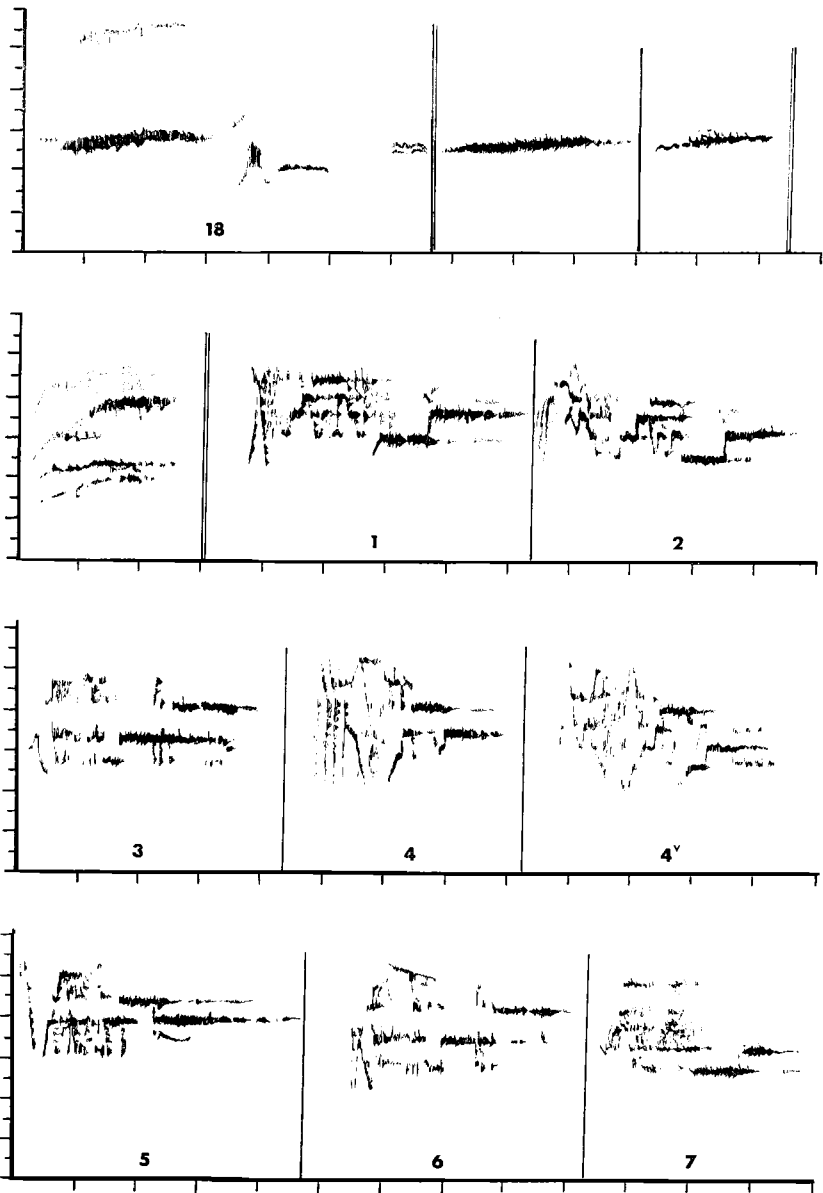


Figure 11. Line 1, songs of *C. frantzii*, male 4 (completed), and two versions of call notes of Oaxacan *C. frantzii*. Lines 2-4, call note of *C. occidentalis* and song types of Oaxacan *C. occidentalis* (part).

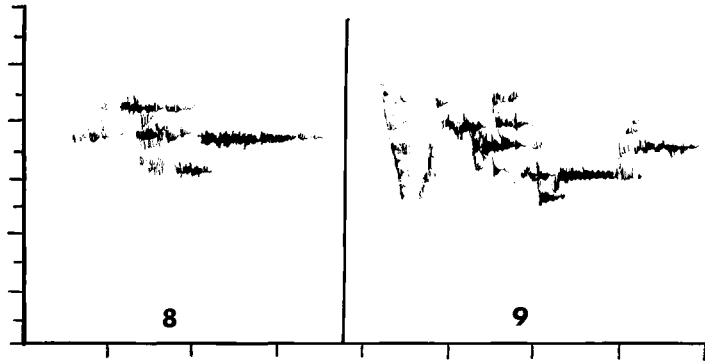


Figure 12. Song types of Oaxacan *C. occidentalis* (completed).

unknown, approached at near ground level and then disappeared quickly. Upon playing of the second sequence, a *C. frantzii* began to sing nearby, apparently in response to the playback. We had never before heard *C. frantzii* singing here, and the time of day (11:00) was unusually late for such spontaneous and persistent singing. Late in the evening of the same day farther up in the upper barranca in what we concluded in 1967 was a marginal zone of occurrence for the species, playback elicited approach of one, possibly two, thrushes to playback of the *C. frantzii* song sequence, prior to which no response was noted toward the *C. occidentalis* sequence.

On 10 May 1967 in the deep barranca we demonstrated to our satisfaction through playback experiment that *C. frantzii* is indeed as aggressive and territorial as *C. occidentalis*. We elicited strong response by one male to playbacks of *C. frantzii* song, but the difficulty of carrying equipment into the deep barranca prevented our testing response to *C. occidentalis* song. Songs of *C. frantzii* recorded in Chiapas (phrase sequences 33–47) and whistled call notes elicited calling from a territorial male that had been singing. Then the bird approached as we continued playback, and after 15 minutes began to sing from perches as near as 20 feet. After approximately 19 minutes we shot the bird but failed to retrieve it. The strong response of this bird may have been in part due to the fact that we had collected its mate 9 May. On 12 May we returned to the barranca and collected another male singing persistently at the same place where we had shot but failed to retrieve the male on 10 May. Another male collected about 20 yards upstream from that location was seen prior to being taken to be crippled in one leg and almost undoubtedly was the male shot 10 May. On 12 May it was calling but not singing; it probably had its territory usurped after being shot.

Contact call notes.—Each species had a distinctive call note in the

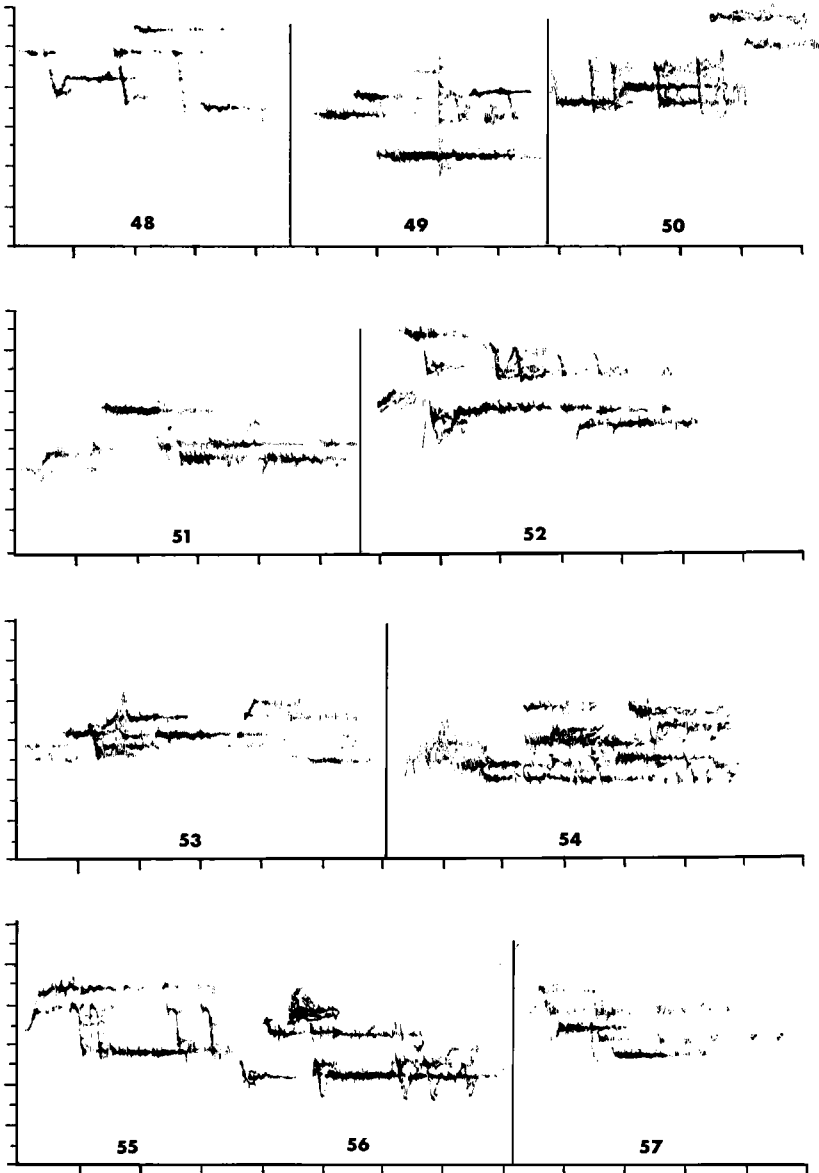


Figure 13. Song of *C. frantzii*, male 1 (part).

area of sympatry. Figure 11 shows two versions with slight differences of pitch of the call of *C. frantzii* and one of *C. occidentalis*. The call of the former is a plaintive, clear whistle, slightly rising in pitch, easily imitated by human whistling. The call of the latter is a querulous, harsh, mewling

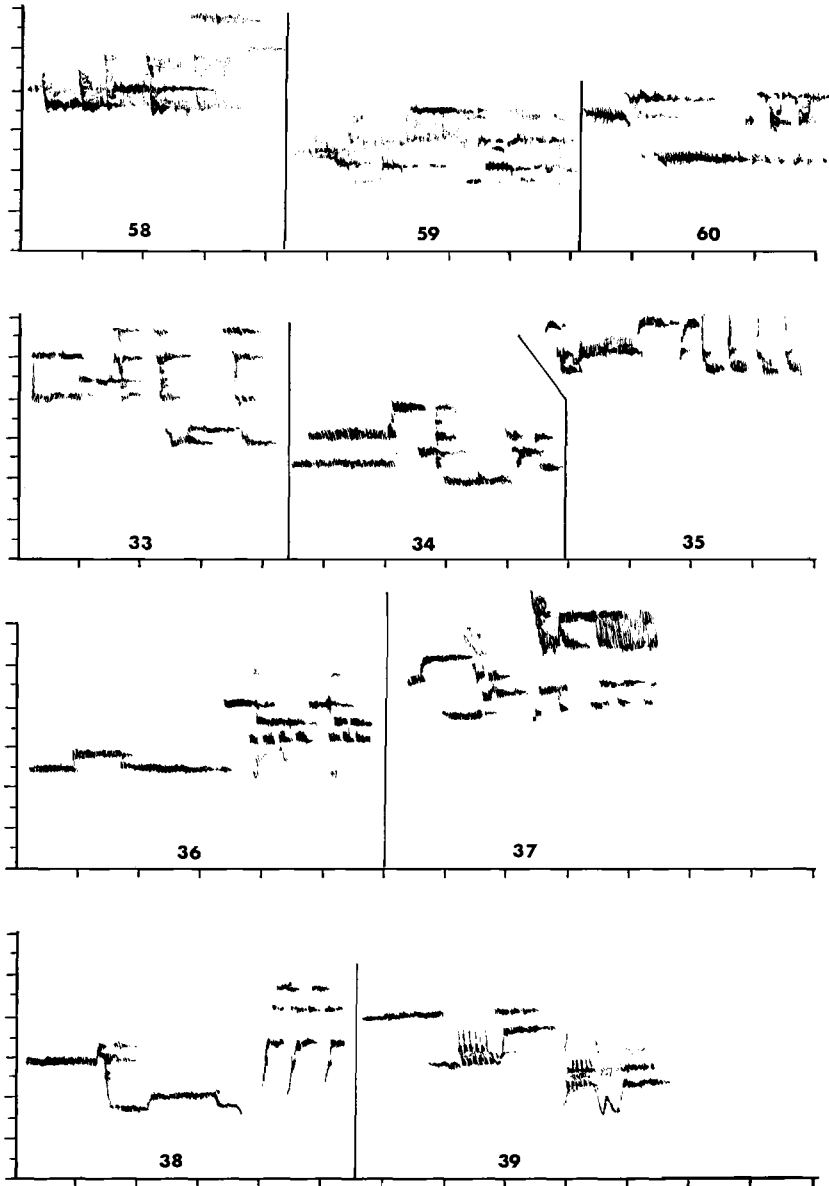


Figure 14. Songs of *C. frantzii*, male 1 (completed) and male 2 (part).

sound. It does not carry nearly so well as the clear whistle and often is given so softly that one must be within a few feet of the birds to hear it. The example shown is flexed upwardly in pitch; although this is typical, some calls are pitched uniformly, others flexed slightly downward.

Our experiments with call imitation and call playback were less formal. Both of us could accurately imitate the clear calls of Oaxacan *C. frantzii*, and we also had good loud recordings of this call. We could not imitate the call of *C. occidentalis* and our recordings of it were not strong. We believe that these calls are contact notes members of pairs use to ascertain the presence of their unseen mate nearby, for the calls do not always attract its approach. Occasionally we did elicit calling of *C. frantzii* individuals by giving the species' call note, and several times Raitt had birds approach him when he imitated the note. We did not elicit calling from *C. occidentalis*. On one occasion Hardy saw what he believed to be a foraging *C. frantzii* near the ground in the upper part of the barranca where that species occurred sporadically and was not known to breed. While watching the individual with a binocular, Hardy imitated the call note softly and immediately the foraging bird flew up slightly to a perch, flipped its tail, and directed its attention toward him. This incident suggests the possibility that, in this marginal area, the lone bird not on territory, and perhaps not in breeding condition, was surprised and stimulated by the species' call note. Its response did not include reciprocal calling or approach, and we have no evidence that either species responds to its sibling species' call.

RESULTS IN ALLOPATRIC AREAS

Findings in 1966 of habitat separation and differences in vocalizations in the zone of sympatry prompted study in 1967 of each species in a portion of its exclusive range. The objectives were to determine ecological and behavioral characteristics comparable to those determined for the two species on Cerro San Felipe in order indirectly to ascertain possible effects of interaction between the two species. For these studies we chose sites as similar as possible to the one on Cerro San Felipe in terms of types of available habitats.

SINALOA

The site selected is adjacent to and northwest of the Durango–Mazatlán highway (Mexico 40) about 1 mile west of the village of El Palmito and 2 miles west of the Durango–Sinaloa boundary. Elevations vary around 6,500 feet. Woodlands and forests of pines and oaks cover the slopes. A large, deep, steep-sided barranca to the northwest contains dense riparian growth of broad-leaved trees and shrubs, constituting a habitat comparable to that of the deep barranca on Cerro San Felipe. (See Crossin, 1967: 270 for a description of the vegetation at this location.)

Unfortunately it was not possible to determine the nesting habitat distribution of *C. occidentalis* at the time of our visit because the birds were not yet breeding. Nor were they singing or territorial—they failed to re-

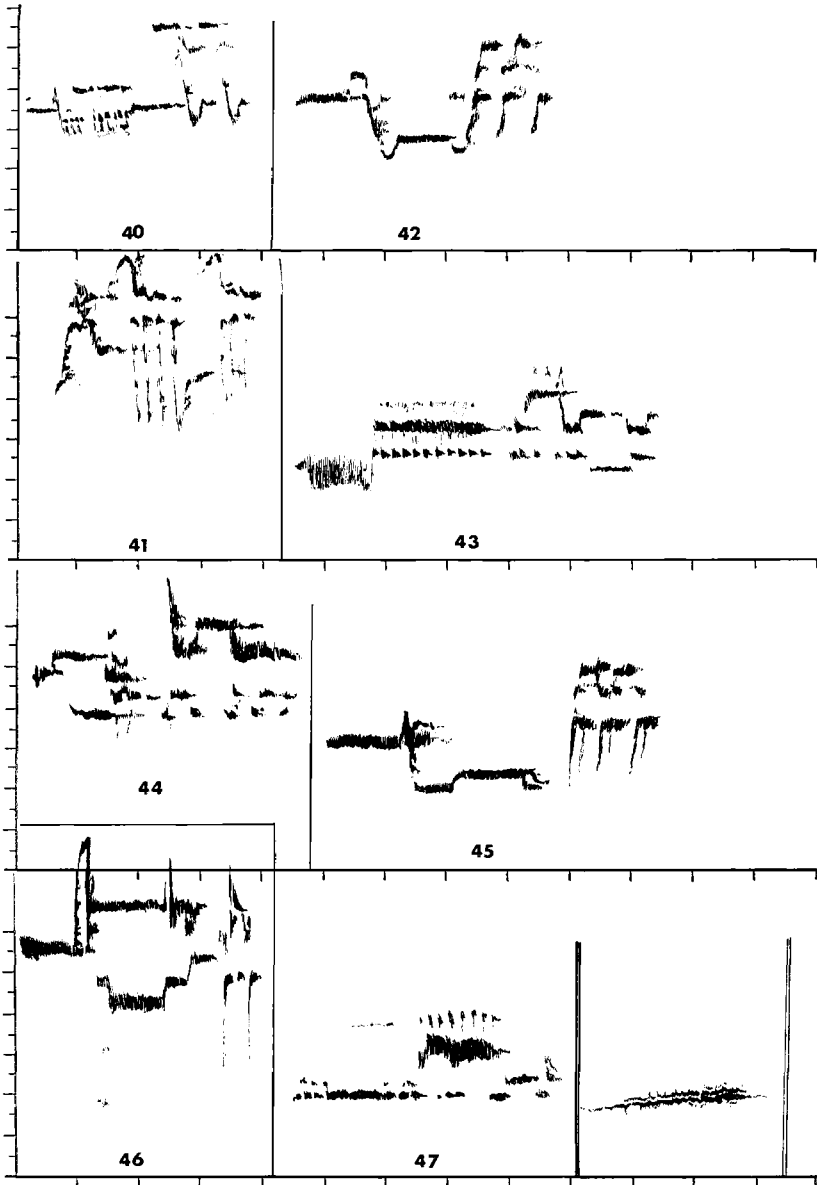


Figure 15. Songs of *C. frantzii*, male 2 (completed), and call of Chiapan *C. frantzii*.

spond to broadcast of songs and were distributed in small groups. Two collected birds had gonads of inactive appearance. Under such conditions it appeared futile to attempt our study as planned, but it is perhaps worth noting that we saw no *Catharus* in the deep barranca, although we did

not spend enough time there to confirm their absence. Richard Crossin, who spent much time in this barranca studying *Cyanocorax dickeyi*, informs us that he does not recall finding nests of *C. occidentalis* in the barranca. All the thrushes we saw were in or near the narrow strip of riparian vegetation dominated by alders along a small stream that flows eastward across the highway and past our campsite. Crossin (pers. comm.) found two nests of the thrush there in July 1964 and noted that the birds were fairly common in pine-oak woodland. In summary we can only tentatively conclude that the habitat distribution of *C. occidentalis* in this area where *C. frantzii* is absent is approximately the same as in the sympatric area. Possible differences in vocalizations cannot, of course, be discussed, as the birds in Sinaloa were not singing.

CHIAPAS

Plant communities.—In the vicinity of San Cristóbal de las Casas most of the mountainous countryside is clothed with forest or woodland of pines, oaks, and madrones (*Arbutus*). In apparently undisturbed areas members of these tree genera are found together in a relatively tall dense forest with a shrubby understory. Woodlands of oaks and madrones occur on dry sites and in logged areas, and almost pure stands of tall pines grow in some areas, probably those subject to heavy grazing. Previous field experience had led to knowledge of two barrancas that contain perennial streams and moist conditions with riparian vegetation of broad-leaved trees and shrubs. Thus the range of habitat conditions in this region, where *C. frantzii* occurs well beyond the southern limit of *C. occidentalis*, is approximately that of the study area in Oaxaca.

Our field work was concentrated in two sites, each centered around one of the aforementioned moist barrancas. Both of these lie near the main highway (Mexico 190), one 11 miles by road southeast of San Cristóbal at about 7,500 feet, the other 5 miles by road southwest of the city at about 7,800 feet. As in Oaxaca our principal method was to search these areas thoroughly to locate as many thrushes as possible, noting for each the characteristics of the habitat in which it was seen or heard. Search was facilitated by playback of a taped recording of songs and call notes of a local *C. frantzii* made on the first day of our work (a master tape of vocalizations of both species made in advance for playback in 1967 was unfortunately stolen en route).

Habitat range.—We found thrushes in both barranca areas, but saw more and heard many more in the one southwest of San Cristóbal. This difference in density is significant, for the deep barranca southeast of the city contains vegetation much more similar to that of *C. frantzii* habitat in Oaxaca. Tall broad-leaved trees and dense broad-leaved shrubs are

plentiful along this barranca (Figure 3C), whereas in the southwest area—where thrushes were more abundant—the riparian vegetation is relatively open and is comprised mainly of pines and oaks with only one small patch of alders and dense underlying shrubs.

Thus at the northeastern site we found *C. frantzii* to be less abundant in spite of what had appeared to be more favorable habitat. Playback elicited response at three separate points along approximately $\frac{1}{2}$ mile of the barranca. These birds approached us very low in the brush and gave call notes. None was seen in the open pine forest on one side of the canyon, but we collected a male with active gonads on the other side in dry pine-oak-madrone with junipers in the understory. At the other site we found *C. frantzii* in all available types of wooded or forested habitats—in broad-leaved riparian tangles, in closed riparian forest of pine and oak with only scattered ground cover, in a patch of dense, young second-growth pines and oaks mixed with *Baccharis* shrubs, in dry woodland opened by cutting, and in intact pine-oak-madrone forest. In a stretch of about 500 yards along the stream we heard three different males singing (territorial ones judging from agonistic behavior and response to broadcast). At times these birds sang from open pine-oak on the dry canyon slope.

Nesting.—Another bird sang regularly from a small patch of *Baccharis* and pine and oak saplings with just a few taller trees left after cutting. This bird seemed to remain entirely in that thicket, which was about 20 by 60 yards and bounded by open clearings and the highway. On 4 May we located this bird's nest and its mate in a moist site within the thicket (Figure 3D). It was a few inches above the ground in a grassy clump with bracken fern (*Pteridium*) providing overhead cover and contained two pale blue eggs faintly marked with pale brown. While we were at the nest both parents remained within a few yards, occasionally within a few feet, moving from branch to branch in the low shrubbery. Both were collected to verify sex and reproductive status.

Conclusion.—We conclude that the range of habitat *C. frantzii* occupies in Chiapas is definitely broader than that in Oaxaca. In fact, most of the individuals seen or heard and the single nest were in habitats typical of *C. occidentalis* in the sympatric area. Vocal characteristics and morphological characteristics of eggs and of collected specimens eliminate the possibility that we were dealing with *C. occidentalis* in these more xeric pine-oak habitats, and, of course, *C. occidentalis* has never been found south of the Isthmus of Tehuantepec (Phillips, 1969).

Behavior and vocalizations.—Male *C. frantzii* were in full song in early May 1967 near San Cristóbal de las Casas. Singing seemed most prevalent in early morning (06:00–08:00) and late evening (18:00 until darkness)

although birds sang throughout morning hours. Singing birds were obviously on territories, as the experiment discussed below demonstrates.

Song sites varied from near ground level to subcanopy, and the singers frequently changed positions while continuing to sing, often moving as much as 200 yards between song sequences. Except during experimental presentation of a mounted model thrush, males were extremely shy when in song and usually could not be approached closely. Song playback in the field ordinarily elicited persistence of singing by males, but usually not close approach or overt agonism.

Figures 13–15 and Table 1 (index of variety) reveal the great phrase variety in two males. Male 1 repeated only the fifth (type 52) phrase in his sequence. Male 2 did not repeat itself in 15 phrases. The variety shown is greater than for two males of the same species in Oaxaca (cf. Figures 8–11), but our data are too poor to show whether the difference is significant. Note in the tables and figures that the songs of these two males show wide variation in phrase length, formant frequency, and structural variety of phrases. Note that each of the 29 phrases is distinctive, the birds sharing no phrase types. As with Oaxacan males of this species, the physical characteristics make the songs clearly audible, unmonotonous, and musical. Except for weakness (low amplitude), the song of *C. frantzii* shows a remarkable resemblance to that of *Hylocichla mustelina*, the Wood Thrush of eastern North America.

We recorded very few call notes of Chiapan *C. frantzii*. Figure 15 shows their basic structure. All those recorded were very possibly uttered by the same bird or pair of birds. Note that the call has a slightly rising character and that it is two-voiced. The subordinate voice is the higher pitched one, and it lends a slight harshness or “burr” to the whistle. To approximate this call, the reader may whistle while humming simultaneously. Our observations were so few we cannot be certain that this is the species’ only contact call note, but we definitely did not hear it give any others in the 4-day period.

On 3 May 1967 we conducted an experiment that indicates the importance of song in territoriality and the nature of territorial agonism in *C. frantzii* in Chiapas. We played back song sequence 33–47 (Figures 14–15), recorded 2 May, repeatedly to the male that had given it, at the recording locality approximately 35 yards from the nest site. The Uher recorder was placed on the ground in dense second growth woodland at the base of a small tree. Two yards above the recorder a mounted *C. occidentalis* was wired to the tree in normal singing posture. After beginning the playback we retreated about 10 yards on opposite sides of the recorder and hid ourselves at ground level. We communicated with each other by portable citizen’s band 2-watt receiver-transmitters, which allowed us to keep ac-

curate track of the movements and behavior of the territorial male that responded to the playback. We played the tape almost continuously, with brief interruptions for rewind, from 07:15 to 08:45. At 07:30 we moved the model to the edge of the recorder, and at 07:45 moved up recorder and model to the model's original position.

Each time the playback started, it elicited the approach of the male. Between playbacks of the sequence we could hear him singing consistently nearby. When playback began the male always became silent and within a few moments appeared near the recorder. Usually his approach was at or near ground level. The bird usually hopped abruptly toward the recorder and then scurried away. Sometimes he flitted nervously into a low bush or tree, moved away out of sight, and then suddenly returned. At no time did he seem to respond to the model, but directed all attention to the sound. We did not see him posture, gape, or make contact with the recorder or model, nor did he show any intention movements of attack. Probably such further or stronger agonistic behavior needs more expression of reality from an interloper than our apparatus gave. For example appropriate movement by the model, call notes, interrupted singing, or other changes of singing pattern might have led to further expression of territorial hostility. The male's attention never waned during the experiment. Other thrushes in this same area attracted to playback of song under nonexperimental conditions showed similar behavior.

We conclude that *C. frantzii* is a typically territorial passerine, that song is the principal means of territorial advertisement, that singing of an interloping male elicits approach and examination response, and that further aggressiveness, if it occurs, requires more stimulus than singing coupled with the presence of a model.

DISCUSSION AND CONCLUSIONS

EVOLUTIONARY HISTORY

The outlines of the evolutionary history of these two sibling species seem reasonably clear. Their similar morphology, behavior, and ecology indicate a fairly recent evolution from a single group of interbreeding populations. According to orthodox theory as to the process of speciation in birds, a period of geographic isolation is necessary for the evolution of reproductive isolating mechanisms that constitute the sine qua non of speciation. In the case of these montane thrushes the obvious barrier that would provide such geographic isolation is the lowlands of the Isthmus of Tehuantepec. These lowlands presently mark the southern boundary of the range of *C. occidentalis*. Maldonado-Koerdell (1964) believes that the isthmus was submerged at least as recently as mid-Tertiary times but Howell (1969) has recently argued against any Tertiary water gap. However, com-

plete submergence appears unnecessary to account for a separation of original *C. frantzii-occidentalis* stock as the area is even today a formidable barrier to highland forms. At any rate a separation of a *frantzii* segment to the south from an *occidentalis* segment to the north appears certain.

The ethological and ecological differences that permit the present co-existence must have evolved during the period of geographic isolation. Apparently *C. frantzii* was able subsequently to infiltrate to the north, establishing itself within a portion of the range of *C. occidentalis* in the present geographical pattern.

REPRODUCTION AND ECOLOGICAL ISOLATION

As Mayr (1963: 66) has pointed out, in order for two groups of populations to achieve full sympatry, they must diverge sufficiently during the period of geographic isolation so that on secondary contact they fail to interbreed, and furthermore they must evolve sufficiently different ecological niches so that one does not exclude the other from its range through competition.

In the case of the two species of thrushes under discussion, reproductive isolation appears to be accomplished mainly through differences in vocalizations. We have shown in previous sections that songs and call notes both are distinct in the two species, and the playback experiments indicate that the birds themselves fail to react to the songs of the other species, treating them, in fact, as songs of an unrelated species. This stress on vocalizations as primary reproductive isolating mechanisms is in agreement with the findings of Dilger (1956a) for North American species. Dilger (1956c) postulated that the brightly colored mouthparts and eyelids of tropical *Catharus* might play a more important role. Both of these Mexican species lack brightly colored eyelids, and the bills do not differ greatly in color, but they do differ in color of the mouth lining, that of *C. occidentalis* is bright yellow, that of *C. frantzii* is orange. Possibly a display involving gaping and exposure of the open mouth at close range might serve as a source of ethological isolation. Considering both species' dark, shadowy habitats and the established distinctiveness and effectiveness of their vocalizations, the value of color of mouth lining is probably secondary in reproductive isolation. Additional study of displays used in pair formation would be of value in assessing the role of mouth color.

Ecological isolation has already been discussed in some detail. On Cerro San Felipe, at least, the principal difference is one of habitat. Published information gives little indication as to whether this same kind of habitat segregation obtains in other sympatric localities. A hint that it does lies in the fact that specimens of *C. occidentalis* outnumber those of *C. frantzii* in collections from other well-known sympatric localities such as Omil-

teme, Guerrero, for example (see Figure 4). The sort of habitat difference that we found in Oaxaca would very probably account for routine general collecting in such an area producing greater numbers of specimens of *C. occidentalis*. Unfortunately beyond this rather weak deduction we can say nothing about ecological relations in the other areas, and they certainly deserve study.

CHARACTER DISPLACEMENT AND REINFORCEMENT

The similar ecology, behavior, and morphology of these two species in Oaxaca led us to suspect the possibility of character displacement. Furthermore the strict habitat separation on Cerro San Felipe suggested the possibility of habitat displacement. Reinforcement of isolating mechanisms also suggested itself.

We approached the possibility of character displacement by measuring lengths of bill and tarsus in samples of museum specimens from both sympatric and allopatric localities. Tarsal length may be readily disposed of; *C. frantzii* tends to have longer tarsi in both sympatric and allopatric localities. Bill lengths, however, suggest a pattern of greater interspecific difference in sympatric localities. Results of preliminary statistical treatment are shown in Figure 4. Samples are small, especially if the sexes are treated separately as Figure 4 shows that they obviously should be. For this reason, we employed a single-factor analysis of variance in which the data for each sex were grouped into four categories (or treatments): allopatric *C. occidentalis*, sympatric *C. occidentalis*, sympatric *C. frantzii*, and allopatric *C. frantzii*. In determining F ratios, all other variation, both within and among localities, was assumed to be error variation. Due account was taken of differences in sample size (Steel and Torrie, 1960: 112–

TABLE 3
RESULTS OF ANALYSIS OF VARIANCE AND DUNCAN'S MULTIPLE RANGE TEST OF
VARIATION IN BILL LENGTH

Sex	F ratio	Degrees of freedom	Four groups arranged by ranked means ²			
			sympatric <i>occidentalis</i>	allopatric <i>occidentalis</i>	sympatric <i>frantzii</i>	allopatric <i>frantzii</i>
Males	8.42 ¹	3,133	sympatric <i>occidentalis</i>	allopatric <i>occidentalis</i>	sympatric <i>frantzii</i>	allopatric <i>frantzii</i>
Females	8.88 ¹	3,101	sympatric <i>occidentalis</i>	allopatric <i>frantzii</i>	sympatric <i>frantzii</i>	allopatric <i>occidentalis</i>

¹ Ratio of variance resulting from combination of species and allopatric vs. sympatric to variance assignable to all other sources. Both ratios indicate highly significant ($P = 0.01$) difference among four groups.

² Groups subtended by same line are regarded as not significantly different *inter se*; those not subtended by same line are regarded as significantly different at the 0.05 level.

114). Results of this analysis (Table 3) gave significant F values for each sex. A modified Duncan's multiple range test (Duncan, 1957) was used to determine which of the four means for each sex differed significantly from each other. The results (Table 3) indicate that sympatry itself probably has increased differences in bill length. Certainly factors other than the presence of a similar species operate to determine bill length, and statistical demonstration of significant differences does not prove cause and effect. Phillips (1969) finds just the opposite of character displacement in the geographic variation in color of these two species. Sympatric populations are more similar to each other than they are to conspecific ones from distant localities. Bill length is likely to be under a different set of selective pressures than color, and character displacement in this important feeding organ is not surprising considering the many other similarities in the two species. Thus in view of the nature of the data and the lack of other ready explanations, we conclude that selection for ecological difference has probably occurred to produce greater differences in bill length in at least some of the localities where the two species are sympatric.

The field results presented earlier also provide indications of habitat displacement. On Cerro San Felipe *C. frantzii* seems clearly to be absent from habitats that are, except for the presence of *C. occidentalis*, similar in all obvious respects to some that it occupies in Chiapas. It appears as if *C. occidentalis* competitively displaces or restricts *C. frantzii* to a narrow range of habitats and that, in this area, the character differences are insufficient to permit extensive, intimate sympatry. The mechanisms by which *C. occidentalis* effects this displacement are not known, and it may be pertinent to repeat that we saw no evidence of interspecific antagonism. We can only suppose that the postulated displacement results from some subtle or indirect interaction. Again, study in other areas of sympatry would be worthwhile in this context.

The possibility exists of character displacement in vocalizations in these thrushes. Initial examination of the sonograms of song phrases encouraged us to analyze phrase lengths statistically. Our impression was that in the area of sympatry song phrases of *C. frantzii* might be longer compared to those of *C. occidentalis* than in areas of allopatry. Figure 7 depicts the results in graphic form. Besides showing analysis of song phrases discussed and illustrated elsewhere in this paper, it includes a sample of Panamanian *C. frantzii* Irby Davis recorded for Cornell University. That sample of ten phrases was taken at random from a long sequence, which according to our timing contained no phrases longer or shorter than maximum and minimum shown. Statistically we have no grounds for inferring the existence of character displacement as suspected. The Oaxacan *C. frantzii* do show remarkable variation in phrase length compared to all

other samples, but otherwise the only tendency is toward displacement in length. Further analysis of more extensive recordings might prove fruitful.

At first we were convinced that character displacement in contact call notes occurred. The Chiapan call note of *C. frantzii* with its burred or buzzy second voice is to the ear far more like the shrill call of *C. occidentalis* than is the clear whistle of Oaxaca *C. frantzii*. Moreover in the many hours spent afield with these birds we heard no buzzy calls from the clear-noted *C. frantzii* and no clear calls from the buzzy-noted ones. Since our 1967 work in Oaxaca, however, Eugene Eisenmann has informed us (pers. comm.) that Central American *C. frantzii* gives both call types, which Raitt later verified in Costa Rica. Thus the question of character displacement in calls remains open. More recording at more times of year and further study of all populations, especially the Central American birds, with attention to influences of the sympatry of *C. frantzii* with *C. gracilirostris* or other members of the genus would probably elucidate the matter.

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SUMMARY

Two species of nightingale thrushes, *Catharus occidentalis* and *C. frantzii*, are so similar morphologically that their status as separate species has only recently become firmly established. Their ranges overlap to form a zone of sympatry that includes mountain areas of much of southern Mexico. In 1966 and 1967 we studied behavior and ecology of the two species in one sympatric locality, Cerro San Felipe, near Ciudad Oaxaca, Oaxaca. Beyond the zone of sympatry we studied *C. occidentalis* in Sinaloa and *C. frantzii* in Chiapas, both in 1967.

In the Oaxaca area the principal ecological difference is one of habitats. *C. frantzii* is restricted to dense, broad-leaved, riparian forests in deep

canyons, while *C. occidentalis* occurs in many kinds of habitats from open oak woodlands to dense, closed fir-pine-oak forest. Members of the two species encounter each other where habitats interdigitate or intergrade. In Chiapas where *C. frantzii* occurs alone, it occupies a broader range of habitats, indicating that its restriction to a special habitat in Oaxaca may be due to interaction with *C. occidentalis*. The longer tarsi of *C. frantzii* reflect its stronger preference for foraging and moving on the substrate. Bills of *C. frantzii* are longer than those of sympatric *C. occidentalis*, but bill sizes of allopatric populations are similar. This pattern is interpreted as character displacement resulting from selection pressure for ecological difference in sympatric populations.

Behavior in the two species is similar, the major differences lying in their vocalizations. Songs and call notes are easily recognized as different in the field. Analysis of sound spectrograms reveals that the songs of *C. frantzii* are more varied and less repetitious than those of *C. occidentalis*. Furthermore they show little temporal overlap in different motifs, a large proportion of clear sustained resonances, many abrupt changes in frequency, and other physical characteristics that make them subjectively pleasant to the ear. Songs of *C. occidentalis* are monotonous and non-musical because of brevity of motifs and phrases and temporal overlap of complex sound components.

Playback experiments involving alternate broadcast of recordings of the two species on territories of known occupancy showed that members of both species react aggressively to songs of their own species but fail to react to the song of the other species. We conclude that song is the principal means of species recognition and, therefore, probably also is an important means of reproductive isolation between the two sibling species.

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Department of Biology, New Mexico State University, Las Cruces, New Mexico 88001, and Moore Laboratory of Zoology, Occidental College, Los Angeles, California 90041.