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VOICE IN COMMUNICATION AND RELATIONSHIPS AMONG BROWN TOWHEES

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This paper seeks to answer two questions: (1) What is the function of each song and call in brown towhees; that is, what information does a bird communicate to its fellows vocally, or how does it regulate their behavior by its voice? (2) What evidence does voice offer for understanding relationship by descent within the closely-knit group of brown towhee species? For the first, I would extend the analysis of Quaintance (1938, 1941) to all members of the group. As to the second question, an ingenious evolutionary reconstruction, based on museum and habitat studies, has been developed by Davis (1951). Do vocal attributes agree with his scheme?

The three species of brown towhees, genus *Pipilo*, are the same size and general color and are more similar to each other than any one of them is to other ground-inhabiting finches in the same genus and in the genus *Melospiza*. Indeed, so close is their relationship that the same calls can easily be discerned in each species; although differing in timbre, similarity in form and usage proclaims them to be homologous. The Abert Towhee (*Pipilo aberti*) occupies dense riparian woodland and mesquite thickets of the Colorado River and Gila River drainages, mostly in Arizona. The Brown Towhee proper (*Pipilo fuscus*) lives in brushy margins of openings in the southwestern United States and México. The White-throated Towhee (*Pipilo albicollis*) inhabits brushy slopes, often with tree yuccas, in Puebla and Oaxaca, México. All these birds feed on the ground, mostly by scratching with both feet together; they build nests in bushes or low trees; and they are extremely sedentary, usually remaining paired for life on a permanent territory of about an acre, except that the White-collared Towhee flocks in the nonbreeding season. These are the three species. But I must treat of four forms (fig. 4) because of two distinct populations of *Pipilo fuscus* whose voices and eggs differ as much as do those of most full species of fringillines. One resides principally in California and Baja California; it may be called the California Towhee (*Pipilo fuscus crissalis*, *albigula*, and other races). The other is the Canyon Towhee (*Pipilo fuscus fuscus*, *mesoleucus*, and other races) of Arizona, New Mexico, Texas, and México.

In the distribution of brown towhees there is very little overlap of species, and such overlap as there is concerns the Canyon Towhee. It exists side-by-side with the Abert Towhee along the San Pedro River near St. David, and along the Santa Cruz River, Rillito Creek, and Sabino Creek near Tucson, all in Arizona. Its southern boundary narrowly overlaps the range of the White-throated Towhee at Tamazulapan, Oaxaca, and Tehuacán, Puebla. There is no interbreeding known among these three species which overlap; nor is there any between the two populations of *Pipilo fuscus*, separated as they are by the Gulf of California, the Colorado and Mohave deserts, and the Great Basin.

Davis' phylogeny, bringing into consideration information from paleobotany, postulates that the wide-ranging Canyon Towhee was the parent. In the Colorado River district, replacement of its early brush and woodland habitat by grassland and later

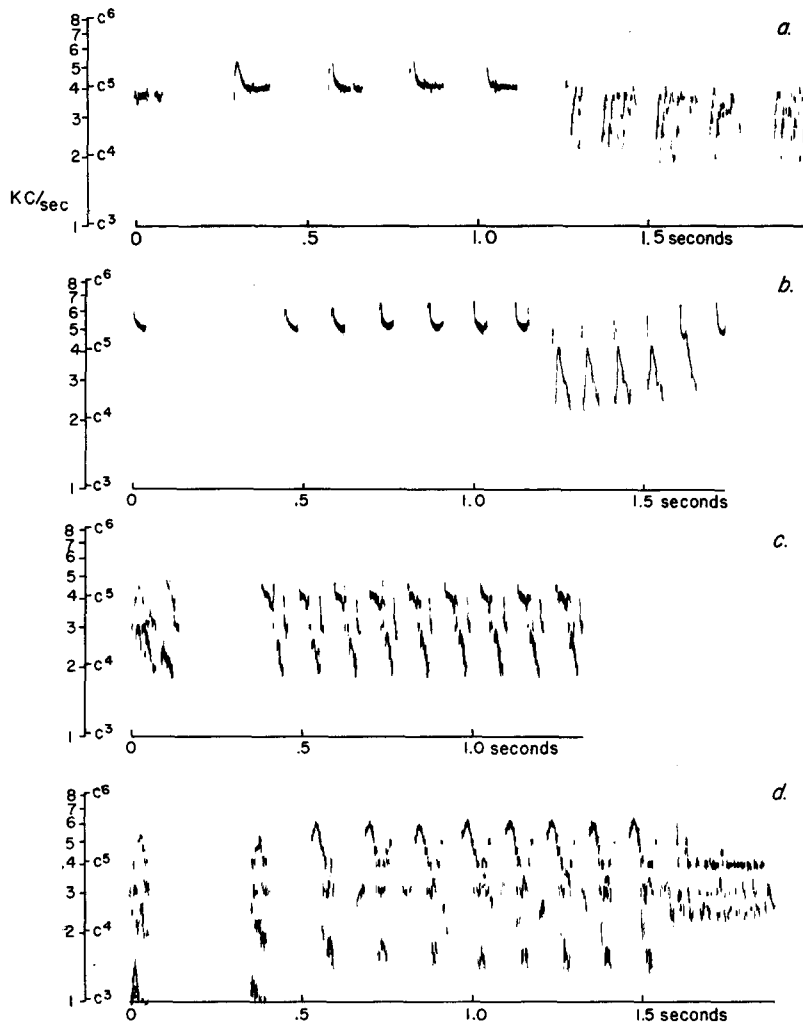


Fig. 1. Frequency-time sonagrams of brown towhee songs fitted by eye to a pitch-time scale; *a*, Abert Towhee; *b*, California Towhee; *c*, Canyon Towhee; *d*, White-throated Towhee. On the right margin of the vertical scale are indicated notes representing the third to fifth octaves above middle c^1 (256 cycles per second).

by desert, cut it in two. The western segment evolved into the California Towhee, which did not reach the level of species. As evidence of this one notes its retention of the primitive style of coloration of the Canyon Towhee in a relict population in the Cape of Baja California. This population has the behavior, voice, and eggs of the California Towhee (Marshall, 1960:63). The California Towhee then gave rise to the Abert Towhee, which pioneered into riparian woodland of the Colorado River hiatus and rapidly evolved into a full species because of isolation and a novel habitat. Meanwhile the Canyon Towhee gave rise in Oaxaca to the White-throated Towhee under conditions of habitat and isolation now obscured by man's changes. Thus the Abert Towhee is most like the California Towhee, and the White-throated Towhee most resembles the Canyon Towhee although the similarities are between undoubted full species. On the

other hand, the California Towhee in nine-tenths of its range is not much like the Canyon Towhee, although it appears to be conspecific. In an earlier paper (Marshall, 1960) confirmatory evidence was offered from behavior and voice of those forms I had studied up to that time. Now I can add experience with the White-throated Towhee plus actual graphs of the principal calls of all forms.

METHOD

In connection with banding studies of brown towhees, I used tape recordings and play-back in order to attract the birds for identification of their color bands. Eventually I taped on a Mohawk 500 most of the vocalizations of the California Towhee at San Diego, of the Abert and Canyon towhees at Tucson, and of Canyon and White-throated towhees at Tehuacán. Direct observations of response by birds to each other's calls and to play-back of their own calls were recorded in the field notebook. Later some of the calls of the Tucson birds were recorded upon the Nagra III BH. Appraisal of contrasts in timbre between species still is subjective, facilitated by hearing in close succession upon a tape recorder those which live hundreds of miles apart. Graphs of the calls were automatically scribed by the sonagraph machine. I have rendered tracings of them on a logarithmic frequency scale of musical octaves. This equalizes pitch intervals over the entire compass of the graph. For it is pitch and not frequency to which our hearing and that of the birds respond in nature, and for this reason the gross stretching apart of musical intervals in the upper part of the ordinary sonagram is absurd!

HOMOLOGOUS CALLS

1. *Song* (fig. 1).—There is a distinctive quality to the song of each of the four forms of brown towhees. That of the Abert Towhee is made up of syllables which sound like a sharp *peep*. That of the California Towhee is a sharp *chip*, that of the Canyon Towhee a musical tinkling, and that of the White-throated Towhee a coarser musical whistle. Many of the notes of the last have a timbre as in *chep* or *swee*. In form, the songs of the Abert and California towhees are the same—a vigorous and accelerating series of the ordinary calls, which often ends in a very rapid succession of notes at a lower pitch (“terminal warble”). The songs of the Canyon and White-throated towhees are similar to each other in form, usually consisting of an even succession of musical syllables, often introduced by the single call. A few of the Canyon Towhee's songs and many of those of the White-throated Towhee change tempo in the middle. The latter has a coarser song of more distinct, separated, and varied syllables.

In all four birds, the song functions in announcing that a male on a territory in the breeding season has no mate. He sings loudly through much of the day, and week after week until he disappears or until he gains a mate. Then his singing abruptly and dramatically stops. Mated male Abert and Canyon towhees did sing temporarily while I was carrying off their mates in a bag to be banded. They stopped when reunited. Other mated Canyon Towhees would sing during the day, while their females were incubating. In the course of my study at Tucson the population was steadily declining, apparently due to drought; there were no available unmated females; territories were getting larger; and I witnessed very few instances in which a singer, either of the Abert or Canyon towhee, succeeded in getting a mate. One *fuscus* there did finally in the fall get back his divorced mate of several years, who had spent the entire breeding season in nesting with the male of the neighboring territory. We must agree nevertheless with Quaintance (1938:101) that the song strongly attracts an unmated female to the territory. In the Canyon and White-throated towhees, a second function of song is terri-

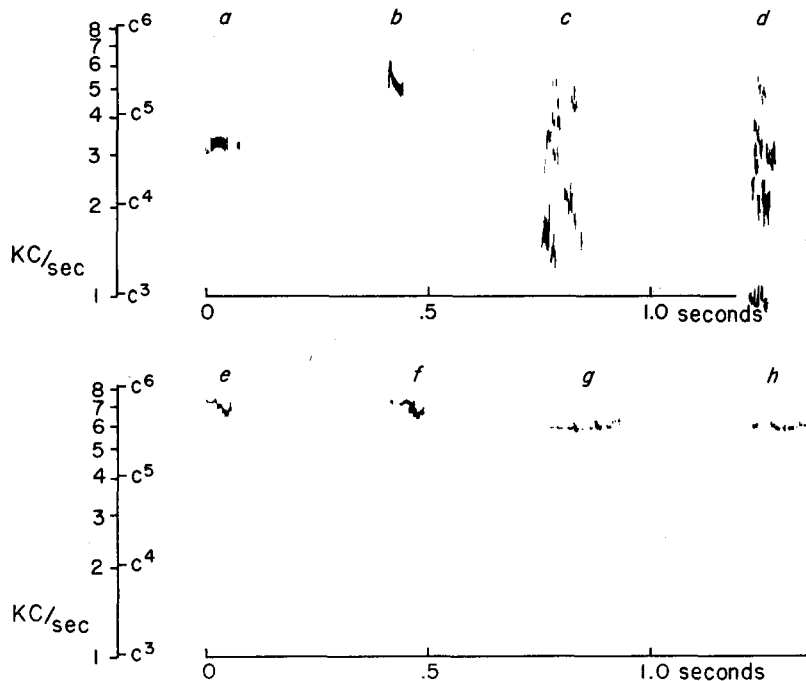


Fig. 2. Brown towhee calls: *a*, Abert Towhee; *b*, California Towhee; *c*, Canyon Towhee; *d*, White-throated Towhee. Brown towhee *seeps*: *e*, Abert Towhee; *f*, California Towhee; *g*, Canyon Towhee; *h*, White-throated Towhee.

torial advertisement by mated males at dawn during the breeding season. The male will immediately and belligerently arrive when a taped song is played in his territory, even if it is his own. A few Abert Towhees also broke into full song occasionally during their regular morning dawn calling, when this calling was at fever pitch during the period of incubation. Ordinarily, however, territorial advertisement is accomplished in a different way by both the Abert and California towhees. At the height of the breeding season there are also some territorial songs at dusk in the Canyon and White-throated species.

2. *Call* (fig. 2 *a-d*).—The ordinary calls of the Abert and California towhees are similar, high-pitched, and sharp; their distinctive vowel qualities, partly a function of higher pitch in the California Towhee, can be represented by *peep* and *chip*, respectively. In only these two species this call functions as territorial announcement by the mated male at dawn during the breeding season; he steadily repeats these piercing staccato notes while he dashes around the edge of his territory. Neighbors of the same species, as well as his own mate, are warned of the boundary over which they should not trespass. At the height of the breeding season there is also some of this calling at dusk.

The calls of the Canyon and White-throated towhees are again similar to each other; they may be represented by *shedup* (of two syllables or often shortened to one, *shedp*) and *chup*, respectively. They are of low pitch and rough quality. That of the White-throated Towhee is the coarser and more emphatic. In these two birds, the call is often used singly as a preliminary to the song. This was of great value in species recognition to me, at least, for at Tehuacán it served to bolster my identifications when it was hard

to distinguish the less monotonous *fuscus* songs from the least varied *albicollis* songs amid the babel of the dawn chorus.

In all four kinds of brown towhees this ordinary call is locative in function, especially when birds are far apart; when more intense, it signifies alarm. A bell-like peeping, given by the Abert Towhee when the observer invades the area of the nest containing young, is ventriloquistic; it is the same call, eerily modified in some slight way, which does not show up well in my recordings. A fusillade of rapid calls is uttered sometimes by the Canyon Towhee at dawn; on the only occasion that such a performance was seen, later in the day, the fusillade preceded copulation. In extreme alarm over the young, or at an owl, the Abert Towhee's voice cracks. Quaintance (1941:152) expertly defines the varied functions of this ordinary call (which he calls the *tsip* note and the *tsink* note) and intimates that differences in its rate of delivery and intensity doubtless communicate different meanings among the birds. His remarks are equally applicable to all four kinds of brown towhee.

3. *Seep* (fig. 2 *e-h*).—This is an extremely thin, yet penetrating note of very high pitch. It is the locative note *par excellence*, which has "the effect of keeping mated birds in contact when they are only a short distance apart yet are hidden from each other, as by thick shrubbery" (Quaintance, 1941:153). If one member of the pair fails to answer (usually the female), and the birds get farther and farther apart, the other's *seeps* become progressively louder, he gives every evidence of getting worried, and finally he ascends a bush and begins looking around. Wandering lone birds *seep* often and plaintively. A response could easily be the first step in pair formation. This call, so important to pairing, reveals the fundamental relationship between the two sections of *Pipilo fuscus*; it is practically the same in the California and Canyon towhees, being pure and attenuated, like the hiss of steam. It is almost imperceptibly inflected in the California Towhee. The Abert and White-throated towhees have *seeps* which are longer, louder, lower, and definitely quavering; their *seeps* are uttered in a variety of intensities, inflections and uses; the latter's is often like the *sleep* sound of a Robin (*Turdus migratorius*) taking flight.

In the Canyon Towhee, a loud *seep* uttered by a parent serves to silence the food calls of the young, at a time when danger is near. Female California Towhees sometimes utter very prolonged thin *seeps* when soliciting copulation.

4. *Squeal duet, or pair reunion duet* (fig. 3).—We return to the male mentioned earlier whom we left *seeping* and looking about for his mate who had wandered off while foraging along the ground. Suddenly both birds are in flight, covering from 30 to 100 yards, and converging upon some bush or tree which is the predetermined next stop on the forage beat of this pair. Whether or not the birds have lost contact with each other previous to the flight, it is sufficiently coordinated, perhaps by their hearing each other's wing flutter, so that the follower is in the air at least before the leader reaches the destination. In some pairs, the male usually leads; in others, it is the female. When both have arrived at the new perch, they voice a loud squeal duet, often accompanied in the nesting season by certain postures, elevated scapulars, and up-and-down movements of the head, while the birds face each other. This ritual confrontation may account for the evolution of divergent head and throat color patterns (fig. 4) so as to facilitate species recognition. In old, long-mated pairs of *fuscus* (comprising both the California and Canyon towhees) the squeal duet becomes curtailed and perfunctory—the birds are used to each other; yet in all four forms this pair reunion duet necessarily takes place dozens of times a day by way of reaffirming the attachment of the two birds for each other.

Under conditions of greater excitement, as when two pairs of the same species have

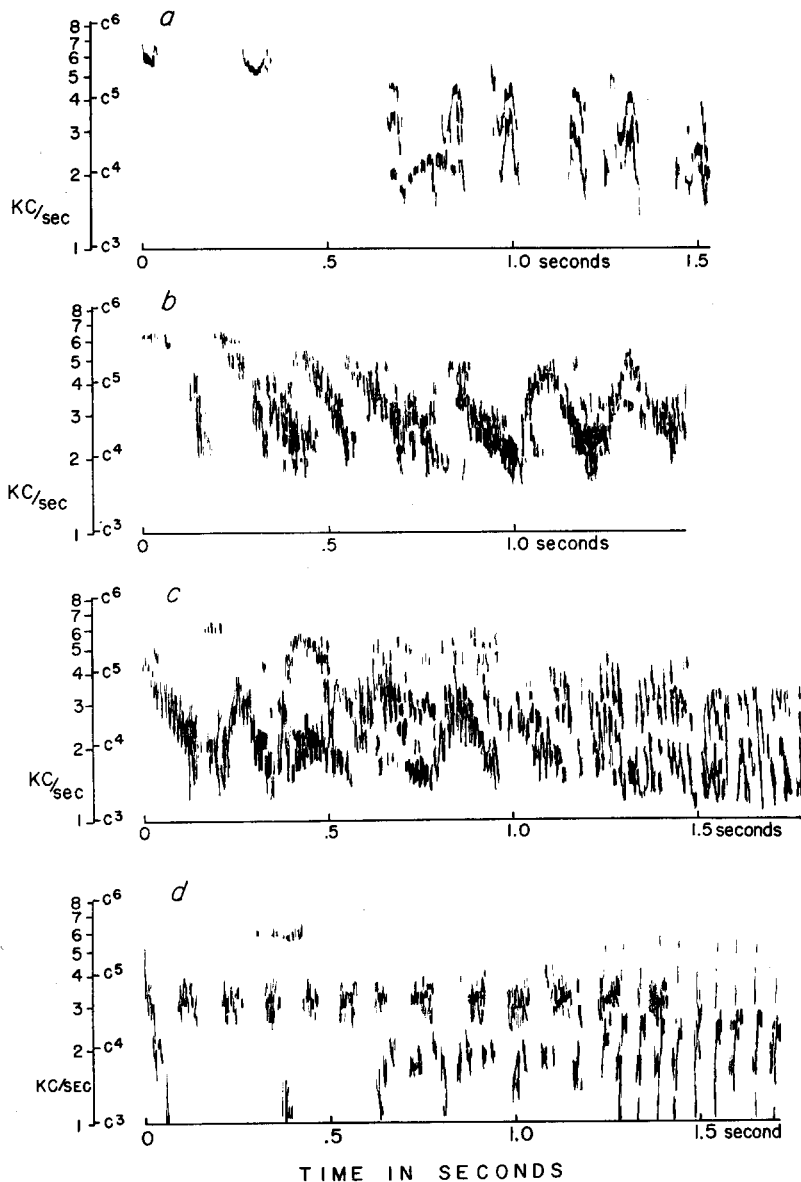


Fig. 3. Brown towhee squeal duets: *a*, Abert Towhee; *b*, California Towhee; *c*, Canyon Towhee; *d*, White-throated Towhee. It is almost impossible to record just one bird making this sound; in *b* and *c* there are at least two, in *d*, three or more.

a territorial conflict at a boundary, the duet is uttered by both pairs. Additionally, in the groups of White-throated Towhees formed during the nonbreeding period, there will be an outburst of these calls from all the birds within a dense bush, particularly at dawn. Perhaps it serves to coordinate and reaffirm the membership of the whole group and to get them all to follow the same foraging circuit.

The form of the squeal duet is similar in all brown towhees; it is a series of loud

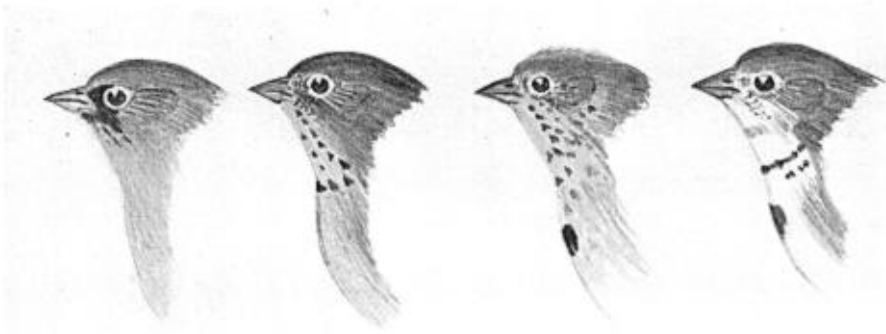


Fig. 4. Brown towhees: Left to right, Abert Towhee; California Towhee; Canyon Towhee; White-throated Towhee.

seeps (the same as the individual note described for each under call number 3 above) followed by a chatter or harsh roll. That of the Abert Towhee is more distinctly broken into separate syllables; it sounds like *sleep sleep cha-cha-cha*. The squeal duets of all the populations of *fuscus* are the same. That is, the California and Canyon towhees show no difference in this vocalization, which may be represented as *see see crrrrrrrrr*. The last long syllable is guttural and not easily resolved into separate notes, but the flutter may pulsate in intensity and pitch. In the White-throated Towhee the squeal duet consists of the usual *sleep* notes followed by a chatter made up of staccato notes delivered much more rapidly than are the comparable notes of the Abert Towhee.

These four kinds of vocalizations show the greatest difference among brown towhees and must suffice for our present comparisons. I have recorded the following rare calls in only one or two of the species, or not at all. But I expect they will eventually be found and recorded and that they will be very similar in all brown towhees.

5. *Food call*.—Fledged young, scattered through the brush, utter at intervals high-pitched, piercing notes. To the human ear, these are ventriloquistic, but each of the two parents is unerringly guided by them to the particular fledglings in its care, which are then fed. The calls are apt to increase in frequency and intensity as time lapses from the last feeding; often they become loud and continuous while the parent is actually proffering food. The food calls change considerably as the young birds grow, and I am unable to compare the species at similar stages. However, my impression is that the Abert's food call is trilling, whereas that of the Canyon Towhee is single. Fully-grown independent juvenal Abert Towhees in fall sometimes utter the food call when near the parent, at a time when they have apparently perfected the adult *seep*.

6. *Combat note*.—This is a rapid succession of guttural syllables like *cut-cut-cut* uttered while one towhee is actually fighting another. Davis (1957:155) describes them as the "snarling, throaty notes given by the attacker." I have recorded this on tape for the Abert Towhee, and I have heard it also from *fuscus*, in which it seemed similar to that of *aberti*. Davis (*loc. cit.*) describes the response of the attacked California Towhee as a decelerating series of "chink" notes—another special use of the ordinary call.

7. *Cat note*.—This is a single high-pitched chirp, uttered at regular intervals by towhees in the presence of a cat. I have heard it only in *Pipilo fuscus*, both in the California and Canyon populations, although I would expect it to be uttered by the other two species under appropriate conditions. In the few times I have heard this call, it was given by both members of the pair, and it did not attract other neighboring towhees.

8. *Nest note*.—This is a light *tic* uttered by the parent towhee when a human approaches within 25 yards or so of the nest containing young about to leave. I have heard it in the Abert and Canyon towhees.

9. *Shriek*.—This explosive cry, "the towhee squawk," is uttered by some individual brown towhees when handled, when closely pursued by a hawk, or when otherwise thoroughly frightened. I have made tape recordings of this call in all four forms of brown towhees and find no difference among them.

10. *Juvenal song*.—Soft warblings heard rarely from young California and Canyon towhees appear to be experiments at singing. They are pleasant to the human ear and are as yet not well recorded on tape.

CONSTANCY OF VOCALIZATIONS

Over the range of each form of brown towhee, the song and calls are substantially the same; they are no more distinctive in an area where two species overlap than where a form occurs alone. For instance, the voice of the Abert Towhee is the same at Yuma, Wickenburg, Mammoth, and Tucson, all in Arizona; at Tucson, Abert and Canyon towhees occur together. There are local differences in the Abert squeal duet, but all varieties are equally distinct from that of the Canyon Towhee. California Towhees sound the same at Berkeley, Los Angeles, San Diego, and the Cape of Baja California. Canyon Towhees that I have heard in New Mexico, Texas, Arizona, Sonora, and throughout the Mexican Plateau have all sounded the same (with only one exception, see below), whether or not they overlapped with *aberti* or *albicollis*. At Mitla and Tamaulapan, both in Oaxaca, and at Tehuacán, Puebla, *albicollis* have sounded the same to me, with allowances for different seasons of visits. Each vocalization then, is remarkably stereotyped, and there is little or no individual variation in any except the songs of the Canyon Towhee and the White-throated Towhee. Marler and Isaac (1960a) acquaint us with the considerable variation in the songs of the Canyon Towhee; I have picked a rather simple, though representative one in figure 1.

The White-throated Towhee's songs are even more varied. Its dawn territorial song is generally rather simple, as shown in figure 1d, but the unmated male, singing through the day, launches into considerable virtuosity. But all these songs lack a certain shrill whistled quality of the Canyon Towhee.

It will confound the students of "character displacement" therefore to learn that one Canyon Towhee at Tehuacán, Puebla, frequently sang, in addition to normal Canyon Towhee songs, utterances indistinguishable by ear from the songs of nearby White-

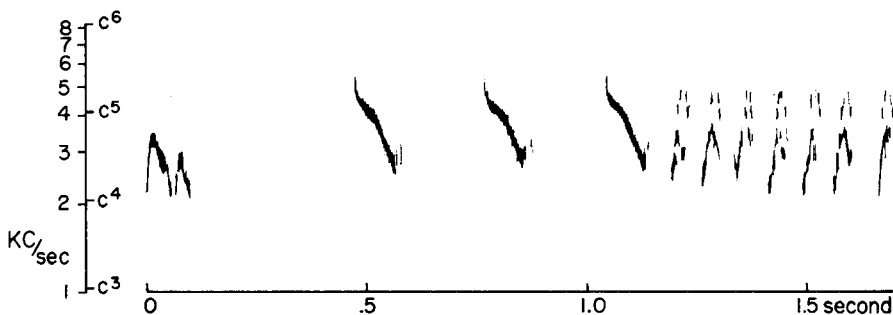


Fig. 5. Song of male *Pipilo fuscus fuscus* (Univ. Ariz. no. 4209), Tehuacán, Puebla. This Canyon Towhee's song mimics that of the White-throated Towhees adjoining his territory. He signs his name at the beginning of the song, the first syllable being the *shedp* call-note of all Canyon Towhees.

throated Towhees, except for the opening call note of *shedp* rather than *chup*! The mimicking song is shown in figure 5. This bird, at first thought to be a hybrid, was collected after several of its *fuscus*-like and *albicollis*-like songs were recorded on tape. It is preserved (no. 4209) in the collection of the University of Arizona, and it is a perfectly normal *Pipilo fuscus*. It is rather large, and in the field it was a dominating bird, terrorizing the White-throated Towhees near it. It seems to have been a veteran, who had learned some songs of its neighbors, the White-throated Towhees.

COMMENTS AND DISCUSSION

Arising out of questions and viewpoints offered by the reviewers and editors of this paper are the following comments bearing on vocal communication and evolution in the brown towhees.

1. Quaintance (1938:97) remarks that the optional "warble" ending the California Towhee's song (my fig. 1*b*) "may represent that part of an ancestral song which is gradually being lost." The ancestor is the Canyon Towhee (Davis, 1951:97-98), and there is some correspondence with rapid trill notes figured by Marler and Isaac (1960*a*: 280, fig. 7, bottom row, C2 and I1). But the quality has always seemed different to me. This excellent idea should be checked further.

2. Quaintance (1938:101) thinks that loss of a territorial function for song in the California Towhee and its relegation to mere mate-getting, is a consequence of relaxed territorial ambitions in an open habitat, where sight of the owner is sufficient warning to intruders. This conflicts with the following facts, which apply equally to the Abert Towhee: (a) The desert habitat of the ancestral Canyon Towhee is still more open, yet this bird uses song for territorial advertisement as well as for mate-getting, as do most songbirds. (b) The California Towhee has a heightened territorial aggressiveness, perhaps related to its denser populations and closer spacing of pairs than in the Canyon Towhee. It is a notorious despot and tyrant, a sample of whose fierce private wars is catalogued by Davis (1957:154-156). (c) The California Towhee has a special and dramatic manner not only of advertising its territory but of actually lining out the boundaries. This is its dawn "rounds" accompanied by the ear-splitting series of calls. The California Towhee and the Abert Towhee seem then to be highly specialized in territorial advertisement, using in that function a distinctive performance which has replaced song.

3. Two new calls reported by Childs (1948) for California Towhees in a fight with jays seem to correspond to juvenal song (used by an adult!), and the shriek ("towhee squawk").

4. The supposed occurrence of the Canyon Towhee at Mitla, Oaxaca (Davis, 1951:79) is an error due to mislabeled specimens, which adds a hundred miles of gratuitous sympatry with *P. albicollis*. The collector, Sr. Mario del Toro A., now writes me (June 18, 1964) that the type series of *Pipilo fuscus toroi* Moore was really taken at Tepeaca, Puebla.

5. Since observations of the White-throated Towhee in anything resembling natural habitat are scarce, I can add that it occurs in tropical thorn scrub, second-growth oak brush, and chaparral (interrupted by corn fields and oak woods) up to near the lowest pines in the foothills north, south, and east of Mitla, respectively. An even more "natural" environment is low dense brush with wide-spaced tree yuccas on the hills at Tehuacán, Puebla. The White-throated Towhee is abundant in this brush, even where remote from cornfields, farms and hedges. The Canyon Towhee is confined to the plowed fields there, but both species get into the agave hedges. We may conclude, therefore, that the White-throated Towhee, like the California Towhee, may have evolved

through isolation in respective regions of denser brush than is welcomed by their ancestral stock, the Canyon Towhee.

6. Parkes (1957) correctly noted a similarity in coloration of the White-throated Towhee and the Rusty-crowned Ground Sparrow, *Melozone kieneri*, especially evident in the juvenal plumage. But he deprecated the likeness of adult Canyon and White-throated towhees. New material shows that even the finest details, such as the white edge of the alula and carpus, are the same, when southern populations of the Canyon Towhee are used for comparison; that many juvenal *fuscus* are liberally streaked above and below; and that juvenal *kieneri* are usually streaked, not spotted, below.

My comparison of all juveniles and adults of all North and Middle American species and differently-colored races of *Pipilo*, *Melozone*, and *Atlapetes* permitted only these conclusions. Juveniles tend to be streaked below and above, including *Pipilo fuscus* but excluding *P. albicollis*, whose marks are broader than long. The darker an area on the adult, the denser or more coalesced are the streaks on the corresponding part of the young, with the result that streaking gives a blurry image of the adult pattern, as noted by Parkes. All these juveniles resemble their respective adults more than any other juvenile.

Melozone kieneri, so shy as to border on the mythical, is slow in yielding up its secrets, which are locked up in dense tangles of brush. To the arguments of Davis (1951:100-101; 1953:96), Sibley (1955:422), Davis (1957:164-165), Parkes (1957), and Marler and Isaac (1960a:280) may be added some concrete facts: on the above-ground nest and eggs (Rowley, 1962:268-269, fig. 11), "scratching in the manner of a Brown Towhee" and "the pair reunion (?) squeal" which "sounds for all the world like that of *Pipilo aberti*, except not as harsh" (letter from Larry L. Wolf, September 9, 1963). I confess that to me the shrill locative hiss of *Melozone kieneri* sounds like that of the Green-tailed Towhee (*Pipilo chlorurus*) and Rufous-sided Towhee (*Pipilo erythrophthalmus*), and that a black shiny bill plus addiction to densest understory brush may indicate a link between *Melozone*, *Atlapetes*, and this red-eyed section of the genus *Pipilo*. The brown towhees may be connected with some members of the heterogeneous *Aimophila*, for I have witnessed a true squeal duet in *A. ruficeps*, and both this and *A. rufescens* have the locative *see* note of *P. fuscus*, to say nothing of brown coloration, and occurrence at edges of brush. While I agree with Dr. John Davis that the ground-dwelling fringillids should be intensively studied from all standpoints of their biology before generic realignment, I think it is time to declare positively that the brown towhee group is distinct, homogeneous, and has no close relatives.

7. Marler and Isaac (1960a, b) succeed admirably in characterizing objectively the songs of the Canyon Towhee, which is their chief purpose. Concerning individual recognition, however, many of the variations shown by the sonagram (1960a:279-280, figs. 6 and 7) may be reducible audibly to a few, even granting that birds' ears are much more sensitive than man's. For instance, all 16 opening notes shown in their figure 6 probably sound exactly the same; they represent the ordinary call, *shedp* (my fig. 2c), which is so often used as an introduction for the song (my fig. 1c). An individual Canyon Towhee's repertoire, of perhaps a half-dozen syllable types, is a logical basis for individual recognition, even though several are identical with his neighbor's. (At Tucson, male Canyon Towhees often respond to each other by singing in kind.) But when a new male sings in a territory, or the owner's song is played there, the owner immediately responds aggressively. He knows by the location of the song that an intruder is there. He can keep track of his neighbors by hearing them all singing from their accustomed perches.

As to species recognition by song, what similar sounding species live in the same

area with brown towhees (1960b:443)? The answer is none for the Abert Towhee, none for the California Towhee, and at least two for the Canyon Towhee. At Tucson I have heard the song of an occasional Cardinal (*Richmondia cardinalis*) which resembled the Canyon Towhee and have recorded a song type of the latter which sounds like a Cardinal. Nevertheless, I cannot believe that these species have influenced the evolution of each others' songs. Soon the singer shifts to an unambiguous song type and the momentary perplexity is at an end. It should be remembered that these birds live permanently on small territories and that they get to know their neighbors by location, personal habits, preferred perches and forage routes. A second species which can utter songs similar to the Canyon Towhee is the White-throated Towhee. Here again, the distinctive introductory call-note in most cases eventually settles the identification.

This brings us to the evolution of distinctive voice in birds which are very closely related, namely the four forms of brown towhees. To summarize, when the White-throated Towhee evolved from the Canyon Towhee, it acquired a different timbre running through all its calls and most of its songs; as the California Towhee diverged from the Canyon Towhee, it attained a sharp call of very high pitch, suitable for territorial advertisement and also for part of the mate-getting song in a novel temporal pattern; the Abert Towhee developed to a full species from the California Towhee while its vocalizations changed in quality and lowered in pitch. Marler and Isaac have correctly picked the overall time pattern of the whole song as the least variable attribute of the Canyon Towhee's singing; it is thereby distinguished from unrelated species in its environment. But they have been reticent about asserting a forthright role for timbre and pitch in species recognition among species of immediate common ancestry.

8. At Tehuacán, Puebla, in June of 1961, Canyon and White-throated towhees kept mutually exclusive territories, with considerable fighting. I spent most of my allotted study period at Villalegría, a few kilometers north of Tehuacán, where the brush-dwelling and dominant White-throated Towhees kept the Canyon Towhees pinned down in the plowed fields. Aside from some confusion caused apparently by both species using the same song perches before it was light enough for sight identification, their voices in all calls and songs were distinguishable. Later I worked at the base of the first hill north of town, and found some confusion. There was the *fuscus* that was singing *albicollis* songs (fig. 5) that I mentioned earlier. I thought he was squiring an *albicollis* female on one day, a *fuscus* on the next. There were equivocal calls to be heard, particularly the long drawn-out squeal duets, which would start out like one species and end up like the other. I could never be sure whether one or both species, hidden in the agaves, were responsible. The population of both was dense, there was much inter-specific chasing, and *fuscus* seemed to have the aggressive upper hand. Whether or not actual hybridization occurs, this mixed population is so interesting that it deserves more study.

9. While in México, I collected the nest and eggs of the White-throated Towhee (University of Arizona collection). The nest, nine feet up in a tree yucca, is of fine stems, resembling those of the California and Canyon towhees; these three forms have a different nest from the Abert Towhee, which uses broad strips of bark. The four eggs resemble those of the Canyon Towhee in being pale and heavily marked with brown and purple, but the markings are finer and more profuse. These two forms differ from Abert and California towhees, whose eggs are pale blue with fine black dots at the large end.

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CONCLUSIONS

The vocalizations of brown towhees convey very precise information to members of the same species. This information directs pair relations, advertisement of territory, and other domestic affairs.

Remarkable correspondence in form and usage of homologous calls confirms the close relationship of brown towhees to each other. Each has a locative *seep* which with an added chatter comprises the pair reunion duet. Each has a distinctive single call-note, variously used, and which is incorporated into the song as at least a starting feature. Vocal similarities suggest that the Abert Towhee (*Pipilo aberti*) is descended from the California Towhee (*Pipilo fuscus crissalis* and races), which in turn sprang from the Canyon Towhee. Despite differences in song and call note, the California Towhee must still belong in the same species as does the Canyon Towhee (*Pipilo fuscus fuscus* and races) because of their having identical calls used in pairing. The White-throated Towhee (*Pipilo albicollis*) is closely related to the Canyon Towhee. Thus the evidence from voice agrees with the taxonomic conclusions of Davis (1951) as well as with the evidence from nests, eggs, and behavior. Voice is a valid criterion of relationship when used with other attributes, cautiously, and in a positive direction. That is, this study shows that similarities in voice go along with genetic relationship, but not the reverse: vocal differences are not necessarily correlated with remoteness of relationship.

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