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CONTENT, MEANING, AND POSSIBLE ORIGIN OF MALE SONG IN THE BROWN TOWHEE

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While making an intensive study of the San Francisco Brown Towhee, *Pipilo fuscus petulans*, I sought to define both the content and the purpose of song in this species. The song of the Brown Towhee is essentially a repetition and elaboration of its basic *chip* note. Repeated three or four times at short intervals, this *chip* or *tsip* note suddenly is given in a rapid series simulating a trill. The rhythm of the song has been likened by Hunt (Condor, vol. 24, 1922, pp. 193-203) to a golf ball which has been dropped on a hard surface and allowed to bounce until it becomes motionless.

Hunt also described endings given, in addition to the rhythmically repeated chip notes. In the Santa Lucia Mountains in California he heard one bird of a different subspecies repeatedly give an ending which sounded like the song of the Western Winter Wren. Another towhee, singing in the Botanical Gardens in Berkeley, added a trill like that of a linnnet. Hunt interpreted these endings as representing a rudimentary stage in mimicry and also as indicating evolution in the song of the species.

This spring I listened carefully to Brown Towhee songs and was surprised to find that these supposedly unusual endings were fairly common. Although varying slightly in different birds, the endings nevertheless possessed a common quality which, I believe, is unique to Brown Towhees. Further, if these figures are any indication of the frequency with which the warble-like ending is given, it would hardly be plausible to call it a matter of mimicry. I am therefore led to believe that these endings have a different significance from that given heretofore.

Of towhees which I heard singing, five different ones ended their songs with a trill or warble that might be described as linnnet-like, and four, so far as I know, did not. Of the birds that did add these endings, three were located in widely separated territories and two on neighboring territories, all on or near the University of California campus, Berkeley. The two neighboring males, used in the observations recorded here, practically always uttered the ending warble. The four birds not using it were within the area embracing the five that did. Another observer told me that in Oakland, five miles from the campus, a towhee repeatedly ended its song with these warbling notes.

Doubtless a great many, though not all, singing males use this finch-like warble or trill as an ending for their songs. In view of its not uncommon occurrence, this finch-like warble, instead of being either a mimicry or a present-day evolution of a stereotyped song, may represent that part of an ancestral song which is gradually being lost. This may be correlated, as will be suggested later, with the possibility that the song itself has become restricted in function.

In the spring of 1937, prior to the actual nesting of Brown Towhees, permanently mated males were not singing, but unmated birds were. Previously, during the nesting season of 1936, I had been impressed by the lack of a territorial song in the Brown Towhees. True, a male on sentry duty near the nest, might occasionally utter quiet

snatches which could be recognized as the towhee song, but there was never any of the loud, persistently uttered song so characteristic of unmated males.

In 1937, one of these unmated birds began singing as early as February 3 and kept it up persistently at all times of the day and even in a hard rain. At first he sang from an elevation, but as the nesting season approached, he also sang from the ground as he foraged. Three others which were first noticed singing on February 22 had probably begun earlier. Since the use of song appeared to be confined only to unmated males, it was believed that the introduction of a female to a singing, unmated male would silence its song, providing the two birds were in the same sexual rhythm.

EXPERIMENTS

Accordingly, on April 13, 1937, two experiments were made. Two captive birds which were thought to be females were introduced to two males which were singing in adjacent territories. The males had been singing from posts one hundred yards apart at Edwards Field on the University of California campus. It is not known whether they were birds-of-the-year or older birds; but one or both could have been yearlings since this habitat had only recently been created, and since it is unlikely that females of two established neighboring pairs would have been eliminated in one winter. The one at the east end of the field is hereafter referred to as the Allston male and the one at the west end as the Oxford male. These males were not banded.

The introduced birds, supposedly females, had been caught at a banding station on the campus, one nine, and one thirteen weeks previous to the above date. The females had been banded with colored celluloid bands and were marked additionally with white feathers glued on the upper side of the tail. Although they had been kept in the same cage together, they had shown no interest in each other; neither had they sung nor given the squeaking notes that mated birds utter. Since their wing measurements, ninety-three and ninety millimeters, respectively, were included in the tentative range of Brown Towhee females, it seemed plausible that this was their sex.

One of the birds to be released was taken directly to the Allston male at 7:30 a. m. This male, singing from the top of the fence, dropped to the ground at our approach; but when the captive was released, the singing male at once flew toward it and hopped in and out of the shrubbery into which the released bird had fled. Then for twenty minutes he sang lustily from the top of the fence; when disturbed by my walking toward him, he then flew to the top of the stadium to sing from there. About eight o'clock the supposed female flew out on the lawn where it at once began to forage. The male continued to sing, but with no apparent effect on the introduced bird. Presently the male flew down to the lawn and pursued the new bird, singing on the ground while it did so. The song had not been repressed by the advent of the introduced bird, for it continued unabated, with the characteristic closing warble. It should be noted, however, that when another male intrudes, singing is not the characteristic response of a male defending its territory.

Eventually, the resident bird pursued the new bird in a long, curving flight to the north edge of his territory where he paused to sing from the fence there. In a moment he flew to a cypress where the other had flown; here he chased the new bird up through the branches. The new bird then flew away and has not been seen since. Of course, the supposed female may have been a male and this may have been a territorial chase. Or, if the introduced bird were actually a female, it may not have been in the same sexual rhythm as the singing male, and hence did not elicit an adequate sexual reaction in him. (See Howard, *An introduction to the study of bird behavior*, 1929, p. 67; Allen, *Auk*, vol. 59, 1934, pp. 180-199.) In any event, the results of this experiment do not give a direct answer to the problem of what function the male song may have.

Meanwhile, the Oxford male was running beside a second unmarked bird near the boundary between its territory and that of the Allston male. After losing the bird which had been introduced to him, the Allston male sang a few songs from the fence and then seemed to become aware of the Oxford male and the strange bird with which it was running at the moment. He flew fifty yards, almost up to the other birds, and then, running to meet the Oxford male, began quivering his extended wings with great vigor. The Oxford male responded by equally vigorous quivering of extended wings. The unmarked bird which had been followed by the Allston male, and which was apparently a wandering female, stepped aside and soon flew over the fence and disappeared, but not until the two posturing males had come together in three successive violent clashes, in one of which they rose at least fifteen feet, striking with their beaks and clawing with their feet. The males then separated and returned each toward its singing post, at opposite ends of the field.

At 10:45 a. m., the second captive bird was released near the Oxford male which was singing and foraging alone on the ground. The released bird, appropriately marked with a white feather, flew above the male to the fence. The bird on the ground stopped singing, instantly alert, but it did not turn its head for a few seconds. Then it gave a few weak "tseeps" and sang faint songs as it hopped about a shrub on the ground; still it did not fly toward the other bird, although it quivered its wings once or twice. The introduced bird shortly dropped to the ground inside the fence and began to feed. It fed in one place, while the male hopped about it within a narrowing circle. The male suddenly flew at it once, but it jumped out of the way. The male then flew to the fence where he hopped, fluffed out, postured, and occasionally scratched his bill on the concrete top.

This bird began to sing loudly again about every ten seconds, alternating in utterance with the Allston male which was singing on his perch a hundred yards away. Each ended his song in the trill mentioned, but it was slightly different even in the two birds. This singing by the Oxford male in the presence of the new bird seemed in every way similar to that exhibited previously by the Allston male in the presence of the other supposed female. The Oxford male flew down about fifteen feet from the introduced bird, sang a little as he foraged and then suddenly flew at the female. There was a whirring of wings and a clicking sound as the two circled rapidly about the little cypress shrub in a sexual flight. After this they separated and foraged ten to fifteen feet apart. The male then sang occasional soft songs from the ground.

At 2:45 p. m., the same day, after the introduced female and the Oxford male had been together three and one-half hours, the male was quietly singing from the fence and the female was perched near-by. On the four succeeding days the two were together and the male was not observed to sing, but on the fifth day he had resumed singing. On the fifth day the female had apparently left of her own accord, for she was nowhere to be seen; not yet accustomed to the boundaries of the male's territory, she may have wandered beyond them. This absence of the female served the purpose of an experimental removal since the male, temporarily without his mate, resumed singing at 5:45 a. m. and was again noted singing at 2:00 p. m. The female had returned by the next day and the male song then ceased permanently. On May 12, one month after its introduction, the female was carrying straw to its nest site.

On the other hand, the Allston male, which served as a "control" bird, was still unmated. He sang vigorously for at least a full week afterward, at which time his songs began to decrease both in frequency and in completeness, as did those of other unattached males that had been singing earlier in the season. He remained in his territory

and a month later sang for at least twenty minutes at one time. His song then was incomplete, consisting of only the sharp staccato notes followed by the warbling notes; the regular towhee trill was omitted.

DISCUSSION

Howard (Territory in bird life, 1920, p. 13) early suggested that male songs serve as location notes for a female seeking a male which had a territory. Just how does the use of song in the Brown Towhee compare with that in other birds?

Of such a bird as the Reed Bunting, *Emberiza schoeniclus*, Howard says (An introduction to the study of bird behaviour, 1929, p. 35): "One would have expected that the coming of the female would have had a marked effect on the male's previous routine of behaviour. But his routine is not affected save in one important particular—the song Instead of singing with renewed vigor, he gives it up and sings but little—perhaps stops—while his neighbor, still mateless, continues." These remarks concerning some passerine birds in England, apply precisely to the Brown Towhee of California.

A similar situation exists in the Western Mockingbird. Of its advertisement song, Michener and Michener (Condor, vol. 37, 1935, p. 136) write: "We suspect that this may be, in reality, two songs, one for the purpose of advertising himself to any female that may come within hearing distance, and another to advise all males in the neighborhood that he is the owner and is ready to defend his territory. On the arrival of the mate these songs almost entirely cease." It may develop that the song of the Brown Towhee has such a dual function for birds-of-the-year, but in the present experiments mate-getting was evidently the chief need served by the singing of the unmated birds.

If the male mockingbird does not succeed in getting a mate, "his advertisement song continues with increasing fervor until late in the season when, having failed, his song ceases and he leaves his territory." It may be that the Brown Towhees differ, since the unmated Allston male practically ceased singing and yet remained in his territory.

On the other hand, song in some birds appears to have a wider use than that of securing a mate. The male Mississippi Song Sparrow sings while the female is brooding on the nest. (See Nice, Bird-Banding, vol. 1, 1930, p. 179.) The Nuttall White-crowned Sparrow, a permanently resident species, sings loudly and defends its territory during the breeding season. Song is also latent with the females (Blanchard, Condor, vol. 38, 1936, p. 147). Erickson (Univ. Calif. Publ. Zool., vol. 42, 1938, p. 269) demonstrated that the Intermediate Wren-tit proclaimed its territory by song long after it obtained a mate. Since the Brown Towhee sings only when unmated, its song is evidently of more limited use than the songs of these other species.

The situation in the Brown Towhee is of particular interest because it is one of those birds in which territoriality is of permanent duration. It is a resident bird in which there appears to be no tendency toward flocking; pairs, once mated, retain their territory indefinitely. However, no element of song enters into the territorial defense, at least in permanently established pairs, whereas in the wren-tit, for example, which also maintains permanent territories, song is used to announce the territory.

In Brown Towhees, the fact that the present-day function of the song is seemingly limited to mate-getting, may perhaps be correlated with its open type of habitat. Since the niche of the Brown Towhee includes open grassy areas where it may both see and be seen, a continuous advertisement of its presence by vocal utterance would seem to be unnecessary. If the territorial use of song were ever part of the ancestral behavior of the genus, it would not have possessed survival value in the evolving Brown

Towhee and would consequently have been eliminated. By contrast, in the Spotted Towhee, in which the habitat is chiefly brushy, the attached males sing throughout the nesting season. Therefore, in the Spotted Towhee, the utility of territorial song may account for its retention.

It is suggested that in many birds, the degree or manner in which song is used may be correlated with the type of habitat and perhaps with the social organization as well. Thus, other things being equal, birds living in dense habitats tend to have territorial song, while those such as the Brown Towhee, living in relatively open ground, tend to have the song restricted to mate-getting.

With regard to population counts, it becomes clear that in Brown Towhees counting of songs cannot be used as a census method since the use of song is restricted largely if not entirely to unmated males.

The experiments cited herein appear to have an indirect bearing on the problem of homing. The captive birds, which were both supposedly females, had been caught midway between the outdoor cages where they were held for the several weeks of their captivity, and the place of release at Edwards Field. The first towhee released, that one which soon left the field, did not reappear at either its place of origin or at its place of capture, so far as is known. However, the second bird stayed at its place of release. Had it been released at its place of capture, the awakening urge to find a mate would possibly have sent it away from home. It cannot be said therefore, that it had no homing sense or that it had been lost through captivity.

SUMMARY

The introduction of a female at the post of a singing unmated male Brown Towhee led within a very short time to the silencing of the male song, whereas the neighboring unattached male which served as the control male, continued to sing. Since permanently mated males do not sing, it would seem that the male song of the Brown Towhee has as its chief purpose the attraction and securing of a suitable mate.

With regard to the content of the song of Brown Towhees, the use of a finch-like warble as an ending appears to be moderately common, but not invariable. The fact that it does not occur in the songs of some of the birds, however, indicates a tendency toward curtailment and probable eventual loss of the warble.

Remote ancestors of the Brown Towhee may have had a territorial song which continued through the nesting season. The Brown Towhee, derived from this ancestral stock, filled a habitat niche which was relatively open and in which sight advertisement was sufficient. The territorial function of song therefore has disappeared.

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FRANK STEPHENS, PIONEER

WITH TWO ILLUSTRATIONS

By LAURENCE M. HUEY

Frank Stephens, who may well be termed one of the few truly pioneer naturalists of the Southwest, was born in Livingston County, New York, April 2, 1849, and he died in his eighty-ninth year at San Diego, California, October 5, 1937. His autobiography, written at the pressing request of the editor, which appeared in *The Condor* in 1918 (vol. 20, pp. 164-166), reflected his characteristic modesty in the brevity of its treatment of his really full and eventful life up to the date of its publication. The facts it contained will not be repeated here. The purpose of the present article is to