INTERRELATIONS OF ABERT AND BROWN TOWHEES

By JOE T. MARSHALL, JR.

INTRODUCTION

This paper summarizes observations on the relations between the Abert Towhee (*Pipilo aberti*) and the Brown Towhee ("Canyon Towhee," *P. fuscus mesoleucus*) in an environment at Tucson, Arizona, inhabited by both. Over most of their ranges these two similar species are separated into different habitats and geographic areas, so that their concurrence at Tucson provides a unique opportunity to examine competition between sibling species and to understand the behavioral differences which maintain their reproductive isolation.

Purely for convenience I should like to depart from the very commendable usage of the American Ornithologists' Union Check-list (1957), in which subspecific vernacular names are abandoned, by adhering to the name "Canyon Towhee" for the race of the Brown Towhee at Tucson, and "California Towhee" for the races in California (especially *Pipilo fuscus petulans* at Berkeley, California) with which comparisons will be made. These races are so unlike that it is well to refer to them by different names and to maintain for the group as a whole the term "brown towhees," as used by Davis (1951) to include all brown members of the genus *Pipilo*: *P. fuscus, P. aberti,* and *P. albicollis.* In the field, the Canyon Towhee is not even recognizably the same species as the populations of California; it is rather the Abert Towhee which in form, posture, voice, and abundance seems the counterpart of the birds of coastal California.

Previous works or concepts bearing importantly on our topic include the extensive nesting studies of the two species on Rillito Creek at Tucson by Bendire (1890). He found that their nests were segregated; those of the Abert Towhee were confined to the thickets of the creek bottom, and the nests of the Canyon Towhee were placed from 100 yards to a mile from the bed of this creek. Miller (1955:10) cites the two as examples of related species which have unquestionably achieved reproductive isolation in nature. Davis (*op. cit.*) has written a definitive work on the distribution, ecology and taxonomy of the entire brown towhee group, and Marshall and Johnson (in press) have summarized the life history of the Canyon Towhee.

Dawson (1954), impressed by the Abert Towhee's ability to live near the presumed limit of its tolerance in the extremely hot Imperial Valley of California, found nevertheless that it had no peculiarities of heat and water regulation; indeed it did not differ importantly from the California Towhee in those aspects of its physiology, although it made behavioral adjustments such as keeping in the shade at midday. Further investigations on the California Towhees include Quaintance's (1938, 1941) study of voice and territory, Davis' (1957) analysis of feeding behavior, and Childs' study for "Bent's Life Histories" (in press). The latter incorporates the remarkable banding results of Harold and Josephine R. Michener.

ACKNOWLEDGMENTS

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THE STUDY SITES

The study site at the San Xavier Reservation is situated in the bottomland of the Santa Cruz River, 10 miles south of Tucson. Mesquite (*Prosopis juliflora*) composes a closed woodland with an understory of gray-thorn (*Condalia lycioides*) within which are abandoned farms grown to weeds and Johnson grass. Tall mesquites and dense elders

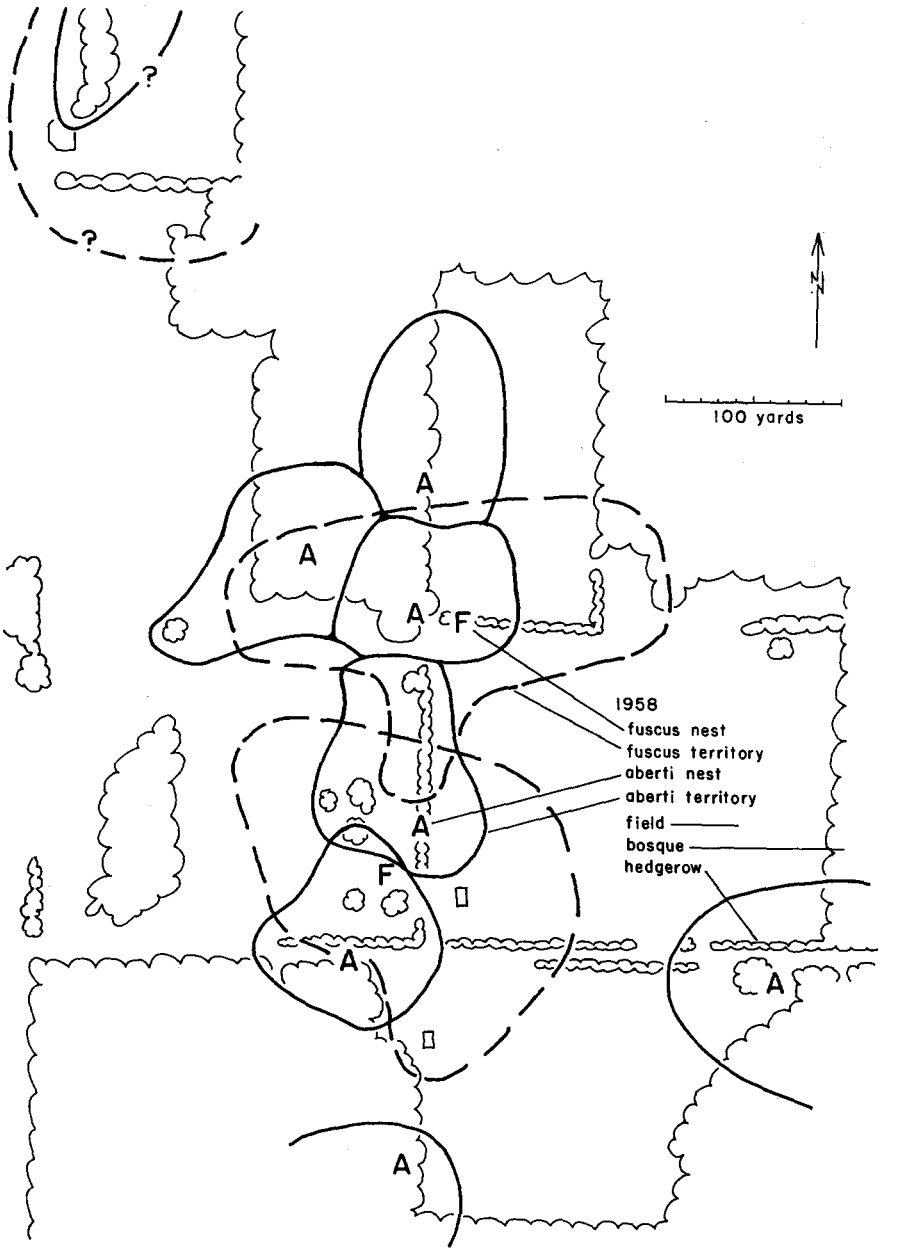

Fig. 1*a*. Territories and nests of towhees at San Xavier Reservation, 1958. There were doubtless more nesting Abert Towhees than shown.

(*Sambucus mexicana*) line the fence rows. The period of study covered at this area was 175 days from late September, 1957, to May, 1958, and late September, 1958, to May, 1959. The average time spent was 3½ hours per day. Seventy fully grown Abert Towhees and 17 Canyon Towhees were banded within 50 acres in the course of both winters. As shown in figure 1, only a few of these birds comprised the breeding populations of established pairs on territories.

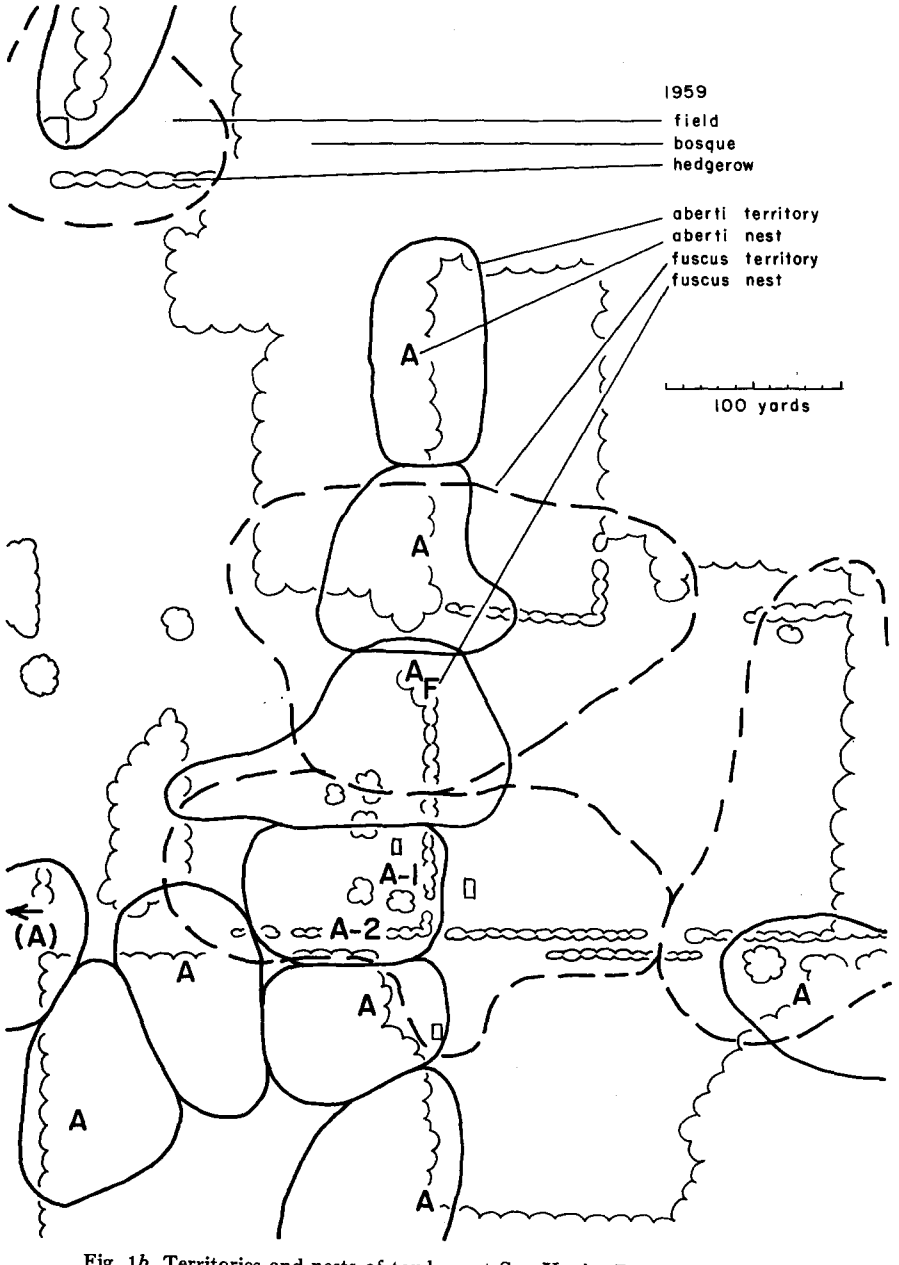

Fig. 1*b*. Territories and nests of towhees at San Xavier Reservation, 1959.

Ten miles east of Tucson, at Sabino Creek, which flows seven months of the year, tall mesquites, forming an interrupted canopy, dot the flood plain. The spaces among them are filled with weeds, sunflower patches, and catclaw acacia (*Acacia Greggii*). Along the stream and nearby are tall sycamores (*Platanus Wrightii*), ash (*Fraxinus velutina*), and elders. The flood-plain vegetation is abruptly contiguous with a contrasting desert vegetation of saguaro (*Carnegiea gigantea*), cholla (*Opuntia fulgida*), paloverde (*Cercidium microphyllum*) and creosote bush (*Larrea tridentata*). Thirty-nine days were spent observing in October, 1957, February to May and one day of June in 1958, and a day or two in March and May, 1959, at this locality, where 9 fully-grown Abert Towhees and 7 post-fledgling Canyon Towhees were banded in 23 acres. Nesting territories are shown in figure 2. There were no substantial observations for the months from June to September at either study site. A few days were devoted to study of California Towhees at the Hastings Reservation near Carmel, California, in December, 1957, and this species was also studied on the University of California campus at Berkeley in April, 1959. Because of significant behavior at dawn, observations commenced on 99 of the total of 219 days at that early hour.

METHOD

During the first winter, mist nets and Bailey traps placed under bushes were virtually selective for towhees, which were easily banded. Grain placed in gallon jars provided attraction to certain spots favorable for observations during parts of the winter. But during the winter of 1958–59, in the second year of the abandonment of the farms, a family of six peccaries moved in and raised such havoc with grain and traps that it was impossible to leave unset but baited traps in position. Other species were more vulnerable than towhees to the non-prebaited traps and their use had to be abandoned. Netting, with special nets designed for slow-flying birds, was made arduous and relatively unrewarding because of the time needed to extricate the great numbers of wintering birds of other species. Again because of the peccaries, feeders were discontinued, and grain was spread in selected areas only when it was desired to identify certain groups of individuals. Towhees were banded with United States Fish and Wildlife Service bands and with colored plastic rings. The latter were supplied by A. C. Hughes of Middlesex, England. Experience showed that it was necessary to use identical color patterns on both legs, even if it meant using four bands per bird in addition to the one aluminum band. It is not pretended that this study caused no interference with the normal life of the birds. It is sufficient now to mention that netted towhees proved wilder and harder to observe than their unbanded fellows, which necessitated studying them with a 15-power telescope while writing observations in the field notebook. Best results were obtained from a portable blind placed on top of an abandoned house, which location afforded a view of three feeding stations and of a well frequented by the birds.

The trapped or netted birds were immediately weighed, measured, banded, and released. Measurements of wing and tail, in conjunction with age differences in plumage, when compared with the data of Davis (1951), permitted a probable determination of the sex of the bird, which in most cases agreed with subsequent observations or captures in which sex was revealed by behavior, song, cloacal protuberance, or brood patch.

INTERRELATIONS IN AREA OF OVERLAP

ECOLOGIC INTERRELATIONS

Population.—At Sabino Creek the number of pairs of Abert and Canyon towhees on breeding territories (fig. 2) reflects a thin population of both species, normal for the Canyon Towhee, and subnormal for the Abert Towhee. The mesquite and riparian growth is too open and too discontinuous to permit a dense population of Abert Tow-

hees, which are limited to that growth. But the openings allow a substantial number of Canyon Towhees to share the habitat with them. The Canyon Towhees are evenly spaced in desert vegetation off to the sides of the river, and similar spacing is maintained on the flood-plain district of overlap with the Abert Towhee. The result is an occurrence of the two species there in about equal numbers. Although the Canyon Towhees fre-

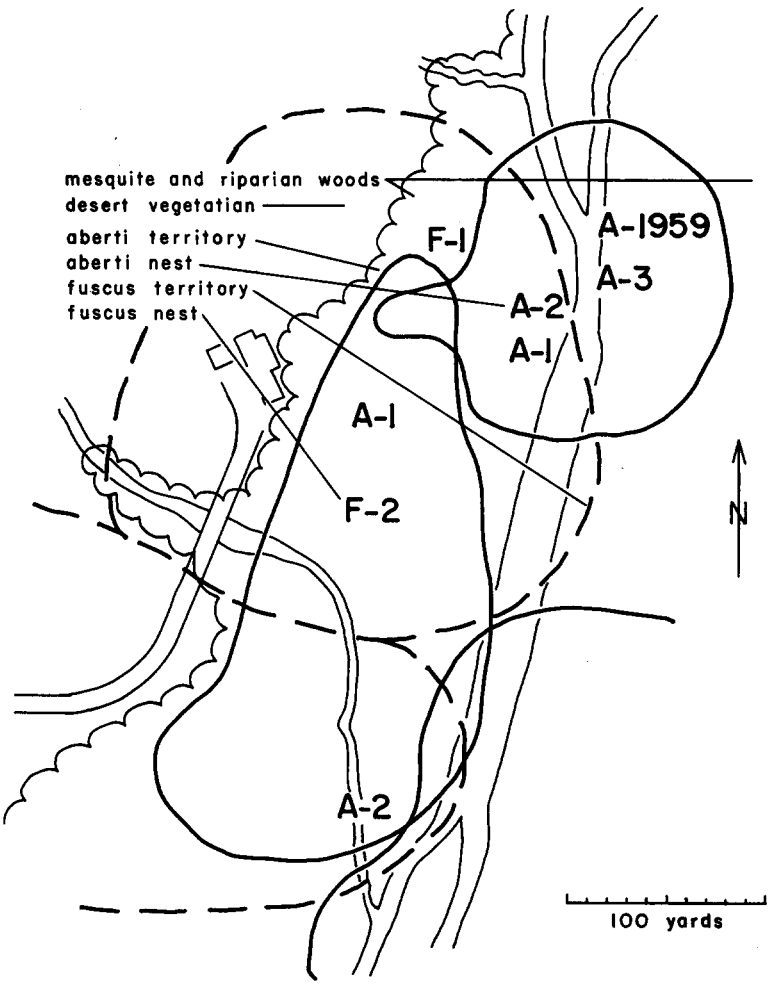

Fig. 2. Territories and nests of towhees at Sabino Creek, 1958. Scalloped line represents boundary between desert vegetation (left) and riparian or mesquite growth (right). Numerals indicate successive nests of same pair.

quently visit the desert vegetation at the sides, which the Abert Towhees never do, there is no discernible difference in their utilization of the flood-plain area itself.

At the San Xavier Reservation the closed mesquite bosque provides optimum habitat for a dense population of Abert Towhees. But the openings and farms hewn from this woodland admit a normal thin population of Canyon Towhees as well (fig. 1). Without these fields to provide necessary edge environment (between openings for foraging and bosque margin and hedgerows for hiding and nesting) the Canyon Towhee would not

exist there, nor would it be in extensive contiguity with the Abert Towhee under natural conditions except at the base of a small hill nearby (Saguarito Butte), at the side of the riverbed. Here a few pairs of Canyon Towhees on the rocky slope of cacti and paloverde confront a few Abert Towhees in the riparian and mesquite growth. Away from this butte, remnants of the original bosque margin show a gradual depression in stature of the mesquites on land gently sloping upward toward the desert. This area of mere bushes tapering into flat open hot desert is a no-man's-land for both species.

Utilization of habitat.—These considerations leave us quite unprepared for the startling fact that at the study site the two species actually overlap and utilize indiscriminately the bosque as well as the farms and hedgerows. Indeed, we should expect the Abert and Canyon towhees to cleave respectively to the bosque and farms, in line with their habitat preferences elsewhere. Actually, hundreds of locality records of marked individuals plus the summary of 165 descriptions of feeding behavior (table 1) show that both species forage in the fields and in the bosque. The only qualitative difference is that Canyon Towhees were not found in the interior of bosque beyond about 30 yards from the edge, although some pairs would cross beneath tongues of bosque 80 yards wide. Abert Towhees on the other hand can always be found far in the interior. Canyon Towhees frequently entered or fed on and around the adobe farm houses which were shunned by Abert Towhees. Since most of my observations were made along the bosque edges, ignoring a substantial number of Abert Towhees whose activities were centered in the bosque interior, the summary of feeding observations, essentially the same for both species, clearly shows that as far as the overlapping segments of the populations are concerned, the two species use the same environment in the same way. The Canyon Towhee, one of the most secretive of Arizona birds, thus finds the bosque a congenial place for secluded feeding.

Foraging method.—Table 1 shows that the Abert Towhee is proportionately more often observed scratching than is the Canyon Towhee. Although this may be a direct result of the greater ease of observing the Abert Towhee, it bears out Davis' (1957) conclusions based on structural considerations that the Abert Towhee is somewhat better adapted for scratching than is the California Towhee. Of particular interest in this connection is the Abert Towhee's propensity for "above-ground scratching." It has been seen scratching through several inches of piled leaves and twigs, and it scratches on the top of accumulations of twigs placed like collars by high water about the bases of streamside trees. One Abert Towhee may originally have been looking for nesting material while picking at the bark of a mesquite trunk eight feet above ground. But it extracted and ate a large insect and then made a thorough search of the trunk for more. During this search, while climbing about the trunk like a wren or nuthatch, it scratched several times while somehow maintaining its position, with head inclined downward, against the vertical trunk. The Abert Towhee, California Towhee, and Green-tailed Towhee are known to scratch at above-ground feeding stations, where they scatter the seed as if the scratching instinct is so inextricably wound up with feeding that it cannot be halted when inappropriate. As to bark feeding by the Abert Towhee, Brewster (1882) reports, "I have seen them hunting insects in the bark of large trees in a manner similar to that of wrens."

Outside of the study area, a pair of Abert Towhees was seen foraging in niches on the side of a 20-foot high vertical riverbank, and a pair of Canyon Towhees fed on the anthers of saguaro blossoms at the top of the tree. Such incidents though insignificant numerically, are mentioned not as anecdotes, but for the purpose of rounding out our picture of the capabilities in foraging by these birds, both rather highly specialized for feeding by picking up from the ground food which has been exposed by repeated scratch-

ing on one spot with both feet kicking simultaneously. It may be said then that the feeding of the two is essentially the same, with the more easily observed Abert Towhee showing somewhat greater versatility, more scratching, and more "above-ground feeding."

Table 1

Summary of Individual Observations of Feeding

ABERT TOWHEE (54 per cent scratch)	BOSQUE: 28 per cent (Includes dense growth at Sabino Creek)		OPEN: 72 per cent (Road, bare ground, plowed field, under bushes and weeds)	
	Scratch	Not scratch	Scratch	Not scratch
Ground, from or at				
Seeds (mostly)	12	6	34	16
Cow, horse dung	2	1	4	1
Reaching up for seeds, buds, grass shoots	....	2	....	4
Collecting caterpillars for young off weeds	....	....	....	8
Insects	1	1	....	1
In holes	....	1	....	2
Running or flying after insects	....	....	....	3
Above Ground				
Drift litter and piles of twigs	2	....	1	....
Seeds on elevated feeder and up on rock	....	....	2	1
Insects in bark of trunks and branches in trees	2	....	....	1
Insects off leaves of bush	....	....	....	1
Berries on bushes	....	1	....	....
Mesquite flower-buds in crown foliage	....	....	....	1

BROWN TOWHEE (37 per cent scratch)	BOSQUE: 26 per cent (Includes dense growth at Sabino Creek)		OPEN: 74 per cent (Road, bare ground, plowed field, under bushes and weeds)	
	Scratch	Not scratch	Scratch	Not scratch
Ground, from or at				
Seeds (mostly)	5	6	11	18
Cow, horse dung	....	....	....	1
Reaching up for seeds, buds, grass shoots	....	1	....	2
Insects	....	1	1	2
In holes	....	....	1	1
Running or flying after insects	....	1	....	....
In and on buildings and side of gully	....	....	2	....
Above Ground				
Buds of hackberry in crown foliage	....	....	....	1

BEHAVIORAL INTERRELATIONS

Interspecific contacts.—If two similar species with nearly identical feeding behavior and nesting requirements share the same habitat, it is obvious that each takes food and nesting sites which could be utilized by the other; in other words, they compete. We would expect them to recognize each other as competitors and to make behavioral adjustments, in the form of some sort of antagonism, toward each other. All the observed contacts between Abert Towhees and Canyon Towhees at the two study areas are summarized in table 2, where intraspecific and intergeneric conflicts are also indicated for comparison. These show that there is no more aggression, in the form of supplanting attacks and chases at food, between the two species of towhees than there is between them and other genera with which they do not seriously compete. The figures bear out

the persistent impression from field work that the Abert and Canyon towhees pay practically no attention to each other, in spite of feeding and nesting in the same locations. One reason for this is the singularly retiring and unobtrusive demeanor of the Canyon Towhee, which slips along silently through the dense growth of weeds, hedgerows, and bosque and scarcely comes to the attention of the Abert Towhee, let alone of the bird student!

Some of the items in table 2 require explanation. I use the term "group" for aggregations of towhees or of towhees with other seed eaters which feed on the ground. The

Table 2

Instances of Inter- and Intra-specific Contacts

a. Contacts between Abert and Canyon towhees, total 84

No conflict; together at		*Conflicts (attacker indicated by A=aberti; F=fuscus)*	
Food	33	Supplanting attack at food (winter only)	A 6 F 4
Mixed group	13	Fight (territorial?)	A 3 F 5
Same bush or tree	11		
Water	5		
Distressed fledgling	1		
Companionship?	3		

b. Hostilities among Abert Towhees, in 188 contacts

No conflict; together in		*Conflicts, same species*	
Group	31	Supplanting attack or chase from food	24
Breeding territory (two pairs or families being fed)	6	Sexual fight	8
Conflicts, other genera		Territorial squeal-duets	48
Supplanting attack at food		Territorial fights	47
Abert Towhee attacks			
Cardinal	3		
Pyrrhuloxia	5		
Green-tailed Towhee	1		
White-crowned Sparrow	5		
Abert Towhee attacked by			
Ground Dove (threat)	1		
Cardinal	1		
Threat, chase or fight elsewhere			
Abert Towhee attacks			
Cardinal	1		
Pyrrhuloxia	4		
Green-tailed Towhee	1		
White-crowned Sparrow	2		

c. Hostilities among Canyon Towhees, in 36 contacts

No conflict; together in		*Conflicts, same species*	
Group	13	Sexual fight	1
Breeding territory, families being fed	2	Competitive singing	4
Conflicts, other genera		Territorial squeal-duets	8
Supplanted at food by		Territorial fights	1–3?
Curve-billed Thrasher	1		
Cardinal	1		
Pyrrhuloxia	1		
Canyon Towhee chases or threatens elsewhere			
Cardinal	1		
House Finch	1		
Lincoln Sparrow	1		

group may consist of nearly a dozen Abert Towhees, two or three Canyon Towhees, many Cardinals (*Richmondena cardinalis*), Pyrrhuloxias (*Pyrrhuloxia sinuata*), White-crowned Sparrows (*Zonotrichia leucophrys*), Green-tailed Towhees (*Chlorura chlorura*), and Lincoln Sparrows (*Melospiza lincolnii*), with a scattering from time to time of Crissal Thrashers (*Toxostoma dorsale*), Curve-billed Thrashers (*Toxostoma curvirostre*), Rufous-sided Towhees (*Pipilo erythrophthalmus*), Rufous-winged Sparrows (*Aimophila carpalis*), and Ground Doves (*Columbigallina passerina*). Neither in the mixed assemblage nor in a pure group of Abert Towhees is there any persistent coincident direction of movement nor sign of flock organization. Supplanting attacks (see table 2) by certain dominating individuals seem to be made without reference to species, or individuals; however, further study may reveal a rudimentary "peck-order." These birds merely gather at food supplies, just as much at favored roadsides or corners of fields as at the artificial feeding stations. Generally the Cardinals and Pyrrhuloxias come first, and their loud cracking of the seeds signals other birds that food is at hand. Most of the "groups" of Canyon Towhees are trios from the winter of 1958–59; in the previous year only widely-spaced pairs were found, which rarely came into contact.

Under the dubious heading of "companionship," I refer first to an instance of a lone Canyon Towhee which joined a pair of Abert Towhees for a few minutes within the dense bosque. The second observation, on November 8, 1958, concerns a solitary individual of each species that stayed a foot or two apart and joined forces at successive foraging spots for at least a half hour; the Canyon Towhee led. Finally, on May 14, 1959, a pair of Canyon Towhees, feeding in short Bermuda grass, was joined for five minutes by a lone immature male Abert Towhee. The latter had a small territory there in habitat too open for the species, which may be the reason he could not attract a mate. His sense of ownership was evidenced by his calls and brief songs whenever other Abert Towhees passed along this hedge (from one end of the field to the other), by alarm notes uttered whenever a human observer came near the particular elder trees in which he sat, and by persistently doubling back to return to this spot when one attempted to drive him farther along the hedge. At the approach of the Canyon Towhees, with no other Abert Towhees in the vicinity, this young Abert hopped directly up to them and fed within a few inches of them, as if he were actually seeking companionship. There was plenty of other Bermuda grass in which to forage, and we may assume that he would not have come so close to the Canyon Towhees unless definitely attracted.

A juvenal Canyon Towhee which I caught after it left the nest uttered a piercing squeak which summoned up its own parents and an Abert Towhee, which "peeped" in alarm. There were three additional instances of response to calls of the opposite species. Two pertain to a lone Canyon Towhee which jumped up in a bush when I imitated the alarm note of the Abert Towhee, and which later uttered a few calls during a vociferous territorial dispute between two pairs of Abert Towhees. The third is the scattering of a group of Abert Towhees from a feeding station when a Canyon Towhee voiced alarm.

Because of their extreme rarity and importance, the actual conflicts between the two species of brown towhees will be described. The most important occurred on October 23, 1957, at the northwestern corner of the study site at San Xavier Reservation, and I quote from my field notes. "Here is a pair of *aberti* at edge bosque and one flew swiftly out to mesquite bush in field and peeped, then its mate joined it low in same bush. Meanwhile the pair of *fuscus* began to call "shedap" out there near them. Then the pair of *fuscus* was inside bosque slowly hopping after *one* of the *aberti*. The *aberti* (as far as I could tell was the only one responsible for this sound) kept up a "cut-cut-cut-cut" chatter, grating, harsh, threatening. The *fuscus* both kept up faint "shedap" calls which seemed to be their belligerent note. Of the two *fuscus* one was more aggressive, perched

higher (above the *aberti*) and followed within 6 to 8 inches of the *aberti* and actually fought the *aberti*, driving him to the ground; the other stayed at same level as *aberti* (below its mate), followed a foot or more behind, didn't peck the *aberti*, but acted exactly as if *supporting every movement of its mate*—backing it up, *literally*. The *aberti* retreated from them slowly and grudgingly—it made a more terrorizing picture than *fuscus*: all puffed up, head retracted, scapulars raised up off wings—would turn and face antagonists. Up in the bush, when the actual fight came, it was rushed from above, pecked and clapped with wings (on purpose? or just because *fuscus* fluttered?) and thus fell head down—upside-down a couple feet through bush to the ground. But it recovered and the slow progressing chase continued, down next gully, up another bush, then all three to base mesquite edge field and *aberti* sidled off N along bank and seemed to join a 2nd. . . . the two *fuscus* had done some squealing also." A half hour later, in the field, there was an outburst of calls among the same birds, then a short *cut-cut-cut* from the Abert Towhee and squeals of a Canyon Towhee as it again chased the Abert, but this was all over in a few seconds. These birds (at least the same Canyon Towhees) were subsequently banded but could not be found again for more than a year, and because it was thought they had succumbed, the study area was shifted southward. Actually, they had moved 300 yards to an irrigated farm, where at least one of the original pair of Canyon Towhees, and possibly the same Abert Towhees, were seen again on February 19, 1959. There a single Canyon Towhee flew at the pair of Abert Towhees and chased one as they arrived at a corral, whereupon the banded male Abert Towhee, suddenly stimulated to aggressiveness, chased off first the Canyon Towhee, then a Pyrrhuloxia, as he went from bush to bush and post to post of the corral in short flights, spreading his tail at each landing as he threateningly patrolled the corral area.

The remaining conflicts from the principally-studied portion of the area do not convincingly bear out any deep-seated antagonism among the birds. On December 17, 1958, a Canyon Towhee squabbled in a bush when an Abert Towhee suddenly landed there. On February 11, 1959, an Abert Towhee chased a Canyon Towhee out of a tree where it had sat preening. On April 9 a Canyon Towhee landed near what seemed to be an Abert Towhee in a tree and uttered strident territorial calls at it. Finally, on April 21, 1959, while two or three pairs of Abert Towhees and three Canyon Towhees were feeding together on seeds placed near a well, there was an attack by one of the Aberts upon the female Canyon Towhee whose territory they were in. If this was the local owner of the same Abert territory, then the antagonism had subsided by May 20 when the two pairs that "owned" this territory on behalf of the species *fuscus* and *aberti*, respectively, arrived at the well simultaneously to drink at dusk. A few minutes before there had been vicious fights there among pairs of Abert Towhees that were attempting to drink.

In view of the overwhelming abundance of records of amicable relations between the two species, it seems necessary tentatively to regard the serious conflicts among the northwestern birds as exceptional, not representative, and due to peculiar conditioning among those particular individuals. If this is actually true, then we may infer that on the whole, the two species do not sense each other as competitors.

Pair formation and reinforcement.—In view of the similarities between Abert Towhees and Canyon Towhees, what behavioral differences serve in species recognition by which appropriate matings are assured? There is of course no question that the two species are reproductively isolated in nature. Nor has there ever been observed an attempt of one species to court or to mate with the other. For an explanation we must look to minor differences in the homologous and identically-used calls and behavior patterns involved in pair formation. First, let us examine the pair bond and its maintenance,

a description of which applies equally well to both species. The actual start of a new pair bond has not been observed, and it is not likely to be seen save by a stroke of luck. The way it must happen can only be inferred from the rituals by which it is maintained and strengthened throughout the year. Pairs persist normally for the life of the mates and exist only in conjunction with the holding of a territory. All year the male shepherds the female, watching for danger, and jumping up into a bush to stand guard at the approach of a person, while she feeds unconcernedly. While thus on guard he usually anticipates her progress, and when she flies he will arrive simultaneously at her destination. There they will engage in a pair-reinforcement duet of squealing calls, often accompanied by certain exaggerated postures, during which the male usually perches higher than the female. This is the basis for sex recognition, necessary in these species which have no sexual dimorphism in coloration. When the members of a pair become separated, as they frequently do when foraging, they begin to give a locative note, a slight *seee,* and when they rejoin, they do so to the accompaniment of the "squeal duet."

Several new pairs (6 Abert, 3 Canyon) were formed before the 1959 breeding season and period of singing began; therefore we may postulate that song is not vital to pair formation and that a new pair might form at any season, but especially in early spring, as follows. A lone bird stationed on its own permanent territory (in marginal habitat for young birds) gives a *seee* call occasionally (a sign of a lone individual or one separated from its mate) and engages in a "squeal duet" with a responding bird. From their relative positions sex recognition is achieved, and if the new bird is single and of the opposite sex, a pair is in the making. The "squeal duets," very strident at first, in time taper down to very light perfunctory renditions, especially for the Canyon Towhee, as the mates become used to each other. Presumably an early stage of a new pair bond was exemplified by an immature male which moved a quarter of a mile to a new locality and was seen there squiring an unbanded mate with utmost solicitude. When I walked between them, they went in different directions. Upon rejoining (the female flew a long distance swiftly to him), the male apparently failed to recognize her and attacked her instead of performing the necessary ritual. Previously he had threatened and chased her in a tree, and it would seem that because of the newness of his pair bond he acted upon conflicting drives, each temporarily gaining ascendency: intolerance of the close approach of another bird *versus* attraction to the mate.

During the breeding season unmated males on territories (3 Abert, 3 Canyon) sang persistently. Males whose mates were carried off in cloth bags for weighing and banding (1 Abert, 1 Canyon) also sang temporarily, but singing stopped when the pair was reunited. In addition, male Canyon Towhees (two out of four pairs) sang while their mates were incubating. An Abert Towhee, whose mate was unfortunately injured in a net and had to be killed, was singing two days later (April 14). He later gained a mate for a few days (April 16–21) during which he did not sing but engaged in loud "squeal duets" with her, and finally he was found alone and singing again (April 28 to May 5). This is the only singing male in my experience that has gained a mate even temporarily, for usually there are no unattached un-landed birds left at the commencement of the breeding season, and the singers themselves may succumb (1 Canyon Towhee) possibly because of their vulnerability to predation while upon an exposed song perch. Thus song in these contexts is the male's announcement that he is on a territory and is without a mate (for the moment at least), and we may assume that as in most songbirds it is attractive to the female. A pair therefore could be formed by appropriate rituals upon the entrance of a female into such a singing male's territory.

The aspects of this hypothetical schedule of pair formation which at present are known to differ in the two species are: (1) the *seee* call, (2) the "squeal" of the pair-

reinforcement ritual, (3) the song, and (4) the coloration of the birds. This study has not yet progressed to the analysis of recorded vocalizations (which will be necessary in analyzing annectant populations of *Pipilo fuscus*) but it is hoped that in view of the simplicity of the calls of towhees, a recourse to naive syllabifications will not be condemned. The *seee* call of the Abert Towhee is quavering and inflected; that of the Canyon Towhee is even, like the similar note of the Rufous-crowned Sparrow. The "squeal" of the Abert Towhee is a laughing *seee-squeal-ha-ha-ha* or *squeal-cha-cha-cha,* whereas that of the Canyon Towhee is a more even and subdued *squeal-squeal-currrrrr.* Although the Abert Towhee's song is merely an accelerating series of its ordinary call note, *peep,* often terminating in coarse warbled phrases like the song of a Tolmie Warbler (*Oporornis tolmiei*), that of the Canyon Towhee is a pleasant musical jingle of many varieties, consisting of repeated musical notes or phrases like the songs of Oregon Juncos (*Junco oreganus*) and Cardinals. In coloration, the two species differ most noticeably about the head; the prominent whitish bill of the Abert Towhee is conspicuously set off by a surrounding mask of black feathers, and the throat and chest are concolor. The Canyon Towhee presents in front view a light face, narrow borders to the throat, and a single blackish spot on the light chest. These then are the most conspicuous differences, which effect appropriate matings; there are others of course, such as posture and proportions; mannerisms during the pairing rituals are not yet well enough known in the Canyon Towhee to permit comparisons.

AREAL INTERRELATIONS

Territory.—There are many perplexing problems concerning territoriality in these towhees which are still being investigated. For instance, in the rainy spring of 1958 there was conspicuous vocal territorial advertisement by males of both species at dawn during late winter and the spring nesting season, which began in March, whereas in the drought of 1959 there was no such advertisement, even when the largely unsuccessful nestings began in April. In the season of 1959, territorial boundaries were fought over and announced by "squeal duets" during the daytime. Perhaps the role of the "squeal duet" had been overlooked in 1958, but in that year the populations became so thin at nesting time (figs. 1*a* and 2) that there was little contact between adjacent pairs, and two pairs of Abert Towhees even raised their second broods in areas formerly held by birds which disappeared.

Territories of established pairs in each species are maintained all year. In fall and winter, however, the pairs wander over a larger area than the contracted nesting territory, and they then tolerate within what will become the nesting territory all other members of their species, which fall into the following categories: (1) roving unpaired immatures, (2) immature pairs which have established themselves in marginal habitat, (3) sedentary unpaired adults, and (4) neighboring established pairs. This system provides for thorough acquaintance with the established territory and its places for concealment and safety by a group of individuals which may be called the supernumeraries or the "floating population." They are thereby well qualified to become successful replacements for deceased members of established pairs. Six immature Abert Towhees and four immature Canyon Towhees "stepped up" into the landed class in that manner in 1959. Some of the latter, however, represented pairs on new territories.

At the onset of nesting there is no further encroachment, at least by established pairs, without serious repercussions (table 2) consisting of threatening "squeal duets" by the two opposing pairs at the mutual boundary or segment of disputed land which often leads to fighting and chasing. At least in the nesting season of 1958 and the weeks preceding it, there was vocal announcement of the territory for a few minutes at dawn by

males of established pairs, in the following manner. The Canyon Towhees would sing from high perches within or around the boundaries of their territories; each male Abert Towhee, upon awakening, would utter loud call notes (*peep*) while rushing from tree to tree around the boundary.

As shown in figures 1 and 2 the territories of Abert Towhees were smaller than those of Canyon Towhees, and at San Xavier Reservation they were "anchored" in the bosque, whereas those of Canyon Towhees centered in the fields. That is to say: a typical Abert Towhee territory consisted of bosque (or a substantial patch of trees along a hedgerow) plus the adjacent one side of a field; the larger Canyon Towhee territory, on the other hand, included the bosque edge of two or three sides of a field. Most important for our discussion, however, is the fact that the territories of the two species were superimposed upon each other and thus broadly overlapped, contrary to the exclusiveness expected among competing sibling species.

Nest placement.—The most crucial evidence that denies any interspecific areal accommodation (spacing) is the placement of nests, whose locations epitomize the fact of territorial deployment within each species. As shown in figures 1 and 2, nests are separated in accordance with advertised and defended territories, at no less than 80 yards between nests of neighboring Abert Towhees and 140 yards between those of Canyon Towhees. But they are placed entirely without reference to nests of the other species, so that simultaneously active nests of the two were as close together as 10, 25, 32, 45 and 47 yards. There was no species difference in nest sites at Sabino Creek; at San Xavier Reservation both species built in elders along hedgerows, but so far no Canyon Towhee nests have been found in the bosque. Strangely, one nest of each species at San Xavier Reservation was built in tumbleweeds hanging up against fences.

CONCLUSIONS ON INTERRELATIONS IN AREA OF OVERLAP

In limited river-bottom areas at Tucson there is habitat suitable for occupancy by resident populations of Abert and Canyon towhees. (The principal local habitat of the latter is rocky desert slopes.) The two similar species utilize this environment in the same way; the population of one is superimposed on the other with no striking ecologic, behavioral, or areal accommodations made by one species for the other. Despite the competition that would be manifest if the food supply and nesting sites became curtailed, they exist in numbers and display behavior characteristic of their occurrences alone in other environments. In fact they exist for the most part as if the other species were not there! These two sibling species of brown towhees avoid competition over the vastly greater portion of their distributional ranges by choosing entirely different habitats.

COMPARISON OF CALIFORNIA, ABERT, AND CANYON TOWHEES

Some of the better-known attributes of Abert and Canyon towhees are tentatively compared with those of the California Towhee in table 3. It is hoped that the postures and rituals of aggressive and sexual encounters will become better known for the first two, so that the comparison may be rounded out to include these fascinating aspects of behavior so easily observed in the California Towhee. Such behavior, for example, includes the sudden grasping of twigs, as symbols of nesting, by the soliciting female. Table 3 points up the remarkable similarity in voice and certain aspects of behavior and appearance between the Abert and California towhees. Behavioral evidence thus fully substantiates the conclusion of Davis (1951:98–99), based on distributional, morphologic, and paleoecologic considerations, that the Abert Towhee arose from the California Towhee, after the latter had become geographically isolated from the Canyon Towhee. Presumably the evolution of the Abert Towhee, alone in its riparian environment, was rapid (Davis, 1951:100). Differentiation was confined to those traits enhancing its re-

productive isolation from the California Towhee and those favoring its survival in the new habitat. Such changes would be the distinctive quality of the call note and the "squeal duet," the acquisition of the black facial mask, and the strong attraction to dense river-bottom woods. Other traits, in the majority, would have remained relatively unchanged, to preserve to this day the many attributes of the parent stock.

Of the three, the Canyon Towhee is set off by its thrush-like demeanor. Nowhere

Table 3

Comparisons of Brown Towhees

In brackets are equivalent terms from Quaintance (1938, 1941)

	P. aberti	*P. f. petulans*	*P. f. mesoleucus*
Proportions	Long tail	Long tail	Shorter tail
Coloration	Dark	Dark	Light
Stance on ground	Horizontal	Horizontal, tail droops, dumpy	Erect, graceful
Head feathers	Compressed	Compressed	Raised
Demeanor	Noisy, bold, but usually concealed in bosque	Noisy, bold, in open, a despot	Quiet, unobtrusive, secretive
Foraging	Long time in one spot	Long time in one spot	Keeps moving
Eggs	Pale blue, black dots at large end	Pale blue, black dots at large end	Pale, heavily marked with brown and purple
Call note	Sharp *peep*	Sharp *chip* similar to *aberti* [*tsip*]	Rough *shedup*
Function of call note	Alarm, excitement, territorial announcement at dawn	Alarm, excitement, territorial announcement at dawn	Alarm, other excitement
Song [male song]	Accelerated series of call notes ending in warble like Tolmie Warbler	Accelerated series of call notes ending in warble like Tolmie Warbler	Musical series of notes or phrases, even tempo, like junco or Cardinal
Function of song	Signifies absence or lack of mate	Signifies absence or lack of mate	Territorial announcement at dawn, or signifies absence or lack of mate
Locative note	Quavering *seee*	*Seee* with slight quaver [*tssp*]	Even *seee* like Rufous-crowned Sparrow
Alarm note near nest with young	*Tic*	?	*Tic* or *sip* like Chipping Sparrow
Pair-reinforcement duet [mate call]	*Squeal-cha-cha-cha*	*Squeal-squeal-currrrrr* [*tss' tss' tss' tsurr tsurr tsurrr*]	*Squeal-squeal-currrrrr*
Nest	Broad strips of bark	Fine stems	Fine stems
Fledglings	Move rapidly	Stationary	Stationary
Habitat	Dense riparian woods	Open ground near bushes	Open ground near bushes

in the literature has this been so well appreciated as in the excellent account by Batchelder (1885:237). A person acquainted only with the California Towhee and with the fact that it and the Canyon Towhee have the same scientific name would think his following remarks preposterous! "Here one would sometimes be seen running along and then stopping, somewhat like a Robin on an earthworm hunt. Their run really consists, however, of a series of rapid hops. There is much that is Thrush-like about their air and motions,

and if seen from behind one might almost be mistaken for a Robin, its form and attitudes are so similar, though it does not stand as upright as a Robin very often does. As a rule they kept on the ground but now and then they would get up in a bush or even in a low tree, but as soon as a Towhee saw he was attracting attention he immediately shifted his position or retired silently with a swift low flight to some safer place." Batchelder also noted the strong attachment of the birds for adobe dwellings and abandoned farm houses; he correctly ascertained their social organization and persistent pair bond.

The reader unacquainted with the conclusions of Oberholser (1919), amplified by Davis (*op. cit.*), doubtless wonders why the Canyon and California towhees are classified in the same species. The explanation lies in the occurrence on the cape of Baja California of a population morphologically similar to the Canyon Towhee, yet which intergrades northward with the California population. It will be of great interest to see if the voice and behavior of these birds from Baja California agree with the concept of relationships worked out morphologically. (Since the foregoing was written, I have found *P. f. albigula* of the Cape district to be identical in behavior and voice with the California Towhee.) Meanwhile, it is evident that the Canyon Towhee of Arizona, in common with all the populations with which it is linked by intergradation throughout México, is certainly the ecologic counterpart of the California Towhee. Like the similarity in habitat, nest construction and the details of color pattern (differing mostly in degree from the California bird), those vocal (excepting song) and behavioral traits which should be important in pair formation are similar in the two forms, in fact identical as far as I can tell in the case of the all-important "squeal duet." These are among the crucial similarities which keep open the door to interbreeding among the populations. These behavioral facts strengthen the idea developed from other evidence that the California and Canyon towhees are conspecific, although it must be admitted that it is a strain upon our species concept and that few if any other North American species possess such qualitatively different subspecies as these.

SUMMARY

Pipilo aberti and *Pipilo fuscus mesoleucus* overlap in mesquite river-bottom woodland near Tucson and utilize this wood and its edges essentially in the same way. *Pipilo aberti* is more confined to the interior of the woods than is *P. f. mesoleucus*; the former probably does more scratching for its food than the latter. There is little antagonism between the two species, their territories are superimposed, the nests can be as close together as 30 feet, and they behave as if the other species were not there. *Pipilo aberti* resembles *Pipilo fuscus* of California in most traits except those involved in pair formation and ecologic preference which traits account for its reproductive isolation. Although *P. f. mesoleucus* differs in many respects from *P. fuscus* of California, its similarity in ecology and those other behavioral and vocal traits necessary to keep open the capability of interbreeding tend to substantiate the conclusion of Oberholser and Davis that they are subspecies.

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