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### COMPARATIVE FORAGING BEHAVIOR OF THE SPOTTED AND BROWN TOWHEES

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THE Spotted and Brown towhees (*Pipilo erythrophthalmus* and *P. fuscus*) are common and widespread species in western North America. Both are mainly terrestrial, have similar body proportions, and are at present considered congeneric. In spite of their ready availability as objects for study, their foraging behavior has only been described in very general terms. Aside from Woodbury's brief paper (1933:70) on foraging by scratching in the Spotted Towhee, and the suggestions of food preferences as indicated by Beal's extensive analyses of the stomach contents of the Spotted and Brown towhees (1910:86-93), little attention has been paid to their foraging behavior. In this study both species were observed throughout the year in an effort to determine whether differences existed in their foraging behavior, and their hind limb osteology and myology were examined to see whether differences in foraging methods were reflected by differences in internal morphology. The particular subspecies of towhees with which this study is concerned are *Pipilo erythrophthalmus megalonyx* and *Pipilo fuscus crissalis*. Northern Monterey County marks the northern limits of distribution for both forms. Throughout this paper the term "Spotted Towhee" refers to the western races of the Red-eyed Towhee (*Pipilo erythrophthalmus*).

Vernacular and scientific names of plants are from Linsdale (1955).

#### ACKNOWLEDGEMENTS

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P. Hastings have contributed materially to the completion of this study.

#### MATERIALS

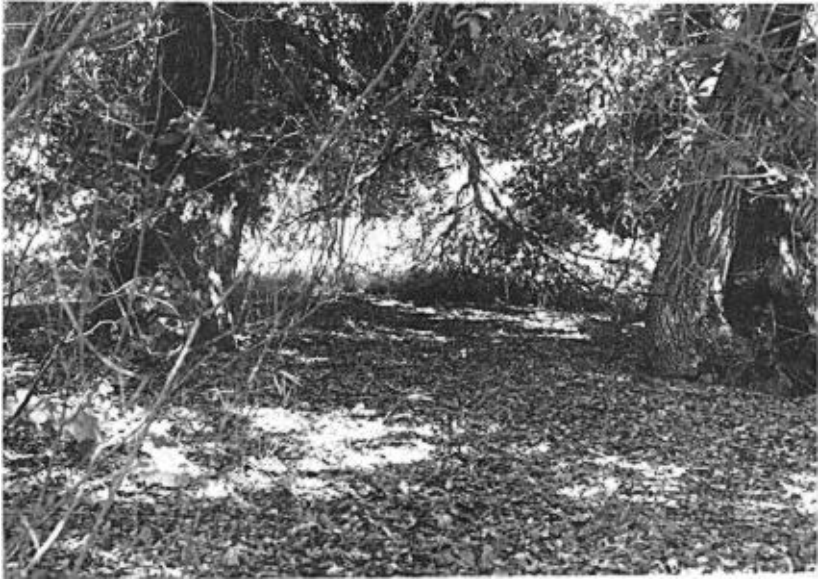
Most of the material presented is taken from my field notes, written between August 7, 1953, and February 29, 1956, at the Hastings Reservation, two and one-half miles east of Jamesburg, northern Monterey County, California. For a detailed description of this locality see Linsdale (1943: 256-260). In addition, field notes recorded by the following workers at the Hastings Reservation were used: Dana Abell, Lowell Adams, Walter W. Dalquest, Floyd E. Durham, Robert B. Finley, Jr., Henry S. Fitch, John A. Gray, Jr., Henry A. Hjersman, Robert Holdenried, Douglass H. Hubbard, Carl B. Koford, Enid A. Larson, Donald D. Linsdale, Jean M. Linsdale, Joe T. Marshall, Jr., Thane A. Riney, Charles G. Sibley, Lloyd P. Tevis, Jr., P. Quentin Tomich, Howard Twining, and Henry G. Weston, Jr.

Bi-weekly samples of Spotted Towhees were collected on neighboring ranches. Gross analysis of the stomach contents of these birds provided some information on food habits. Five Spotted and five Brown towhees were collected for dissection of hind limb musculature. Skeletons used for the analysis of hind limb osteology were in the collections of the Museum of Vertebrate Zoology.

#### FORAGING BEAT

The foraging beat of the Spotted Towhee must provide sheltered soil cover in which the birds may find their food by scratching. Spotted Towhees rarely forage in areas which are not screened from above by overhanging vegetation, and even more rarely do they search for food in bare or sparsely covered soil. Shelter may be afforded by a variety of plants but the soil cover is almost always composed of leaf litter and humus. Vegetation which supplies both overhead screening and adequate leaf litter is especially favored. In addition to overhead shelter many types of vegetation supply lateral screening as well, although this is not so important.

The vegetation in which the foraging beat lies consists of trees, large, isolated shrubs, or brush. The most important tree for foraging Spotted Towhees in this area is the coast live oak (*Quercus agrifolia*). The dense, evergreen foliage of this oak provides excellent overhead cover throughout the year, and the lowest branches often reach nearly to the ground, providing lateral screening as well. Leaf litter under live oaks is usually very heavy. In part this may result from the evergreen habit and in part from the protection of fallen



FORAGING AREAS OF THE SPOTTED TOWHEE. (Above) Nearly unbroken leaf litter beneath large Coast Live Oaks (*Quercus agrifolia*). (Below) Mixed brush, mainly Poison Oak (*Rhus diversiloba*), Coffeeberry (*Rhamnus californica*), and Snowberry (*Symphoricarpos rivularis*). The Coast Live Oaks upslope supply much leaf litter to the brushy areas below them. Photographs taken May 13 1956, at the Hastings Reservation.

leaves from wind scattering, since the lowest lateral branches act as a windbreak. Under larger, older trees the heavy layer of leaf litter and humus and the dense shade effectively suppress the growth of other plants, and the leaf litter is nearly unbroken. Such oaks represent the optimal undertree foraging sites for Spotted Towhees. (Plate 7.) Areas under blue and valley oaks (*Q. douglasii* and *Q. lobata*) are also frequently used, but less often than those under live oaks. The growth form of these trees does not afford lateral screening, the foliage is deciduous, and since the leaf litter and shade beneath them are not as deep, grasses and other plants are often present in some abundance.

In riparian situations, areas under willows (*Salix* sp.) are frequently used. These trees provide ample leaf litter, overhead screening even when leafless in winter, and in younger trees, which often form dense thickets, lateral screening as well. Although Spotted Towhees do not forage under western sycamores (*Platanus racemosa*) because the crown foliage is too high to provide adequate overhead screening, such trees may be important in adding to the leaf litter found under other riparian vegetation.

Leaf litter under large, isolated shrubs is also used. Large coffeeberry bushes (*Rhamnus californica*) are especially important in this regard. Other trees and tall shrubs less frequently used include toyon (*Photinia arbutifolia*), madroño (*Arbutus menziesii*), and blue elderberry (*Sambucus coerulea*).

A variety of types of brush provide adequate foraging sites. (Plate 7.) The two most important brush plants for towhees are poison oak (*Rhus diversiloba*) and coffeeberry. Poison oak forms dense thickets which supply some leaf litter and adequate cover even after the leaves have fallen. Since poison oak often grows near oaks, leaf litter under such thickets is often built up to adequate proportions by drifted oak leaves. Younger coffeeberry bushes form dense stands which are often utilized. Both plants frequently combine with plants of other species to form suitable foraging sites. Creambush (*Holodiscus discolor*) and snowberry (*Symphoricarpos rivularis*) are important in combination with other shrubs. California blackberry (*Rubus ursinus*) often forms dense thickets under which Spotted Towhees forage, and in addition may overgrow other shrubs such as poison oak and snowberry, affording lateral screening and contributing leaf litter as well. California wild rose (*Rosa californica*), hollyleaf redberry (*Rhamnus crocea* var. *ilicifolia*), coast ceanothus (*Ceanothus ramulosus*), common horehound (*Marrubium vulgare*), black sage (*Salvia mellifera*), and coyote brush (*Baccharis pilularis* var. *con-*

*sanguinea*) are also used to some extent. Near buildings towhees have been seen to forage under French broom (*Cytisus monspessulanus*).

Spotted Towhees were noted frequently foraging under chamise (*Adenostoma fasciculatum*) and California sagebrush (*Artemisia californica*). However, little litter is derived from the small, narrow leaves of these plants. The litter under these shrubs is derived almost entirely from the leaves of nearby trees and shrubs of other species, such leaves drifting down and becoming entrapped. Oaks are especially important in this regard. Towhees are scarce in large tracts of pure chamise and are found mainly near the edges of such stands where nearby oaks provide leaf litter. It may be that during a series of wet years adequate soil cover may build up under extensive stands of chamise and sagebrush, but at the time this study was made, after about ten years of relatively dry conditions, intrinsic soil cover was sparse.

A variety of plants has been noted as affording lateral screening. In addition to the shrubs mentioned previously, bracken (*Pteridium aquilinum* var. *pubescens*), ryegrass (*Elymus* sp.), oats (*Avena* sp.), young madroños, dragon sagewort (*Artemisia dracunculoides*), and California mugwort (*A. douglasiana*) are important in this regard.

In summary, of all the plants mentioned the oaks are definitely the most important, not only as primary foraging sites but as major contributors to the leaf litter found under other types of vegetation.

In marked contrast to the Spotted Towhee, the Brown Towhee does most of its foraging in open areas near trees or brush which can be used as shelter when danger threatens or as perches for resting and preening between foraging periods. Most of the records for natural situations involve towhees foraging in open grassland near cover. (Plate 8.) Stretches of dense, unbroken grass are unsuitable, for the birds cannot penetrate such areas. Grass must be rather open or, if dense, must be interrupted in some fashion. Well-worn animal trails, especially those of ground squirrels, deer, and rabbits are very important in modifying dense grass, since the towhees can forage along or at the edges of such trails. Height of grass does not seem as important as density, for towhees were often seen foraging along animal trails leading through tall, impenetrable stands of dry grass, especially oats of various species. In the winter, after the rains have broken down much of the once continuous cover of dense spring and summer grasses, towhees are able to forage in the interstices between clumps which are still erect. (Plate 8.) Pairs of towhees watched during the winters of 1953-54 and 1954-55 foraging

almost entirely in grassland thus broken down, were forced to abandon this area each spring after the grass had again formed a heavy cover over the winter foraging grounds. Brown Towhees forage not only in continuous grassland where sufficiently sparse or suitably modified, but on areas of bare soil, where they apparently find seeds which have fallen or been blown from nearby vegetation.

The cover adjacent to the foraging beat is variable. Some of the more important shelter plants are live, blue, and valley oaks, coffeeberry, coast ceanothus, poison oak, chamise, willows, blue elderberries, and California sage.

Brown Towhees often scratch in leaf litter under trees and brush where the terrain is relatively open. They have been seen foraging under oaks, willows, coffeeberry, poison oak, and ceanothus, and here they overlap to some extent with the Spotted Towhees. However, they seldom penetrate far into the very dense brush which is much used by Spotted Towhees. Most of the records of the two species foraging together involve them scratching in leaf litter under live oaks. In some cases leaf litter under trees may be especially important to Brown Towhees. One was noted foraging in leaf litter under a valley oak surrounded by tall, dense oat cover. This roughly circular patch of leaf litter, about 10 feet in diameter, represented an island of suitable foraging area in terrain otherwise unsuitable. The litter was much furrowed and pitted, giving evidence of heavy use.

In addition to natural situations Brown Towhees forage very frequently on roads and paths, lawns, sickled grass fire breaks, and other artificial areas. They are quick to take advantage of any disturbance to habitat which makes it suitable for foraging.

#### FORAGING METHODS

Although other methods of foraging may be used at certain times, the great bulk of the towhees' diet is obtained throughout the year by ground foraging. Their methods of finding food are similar and involve gleaning exposed food items, mainly weed seeds and insects (Beal, 1910), from the soil surface or obtaining food located by scratching in soil cover or in the upper layers of exposed soil.

In general, the nature of foraging, whether predominantly by scratching or by pecking at the surface, is determined by the nature of the terrain traversed. Where the ground is exposed or soil cover is either sparse or interrupted, foraging is mainly by pecking at the surface. Where the ground is covered by leaf litter, humus, and short grass, it is accomplished mainly by scratching. Since the

Spotted Towhee is confined almost entirely to habitat in which soil cover of some sort is present, nearly all its foraging is accomplished by vigorous scratching. Since Brown Towhees readily use several types of terrain, ranging from sheltered areas with heavy soil cover to completely exposed, bare areas, they use extensively both methods of foraging. For example, Brown Towhees foraging on roads peck at the surface when searching for food along the exposed soil of wheel tracks. However they scratch in litter which has accumulated along road edges and in road centers where leaves have drifted down and become entrapped by low-growing vegetation. Brown Towhees frequenting a dense poison oak thicket, separated from nearly continuous grassland by strips of bare earth about 10 feet wide, foraged mainly by scratching when using the leaf litter beneath the thicket or when in the grassland, but they foraged almost entirely by pecking when using the strips of bare earth adjacent to the thicket. (Plate 8.)

#### DIFFERENCES IN FORAGING BEHAVIOR

Although scratching is performed in the same general manner by the two species, there are important differences between them in detail. Spotted Towhees are noticeably more vigorous in their scratching motions. A foraging Spotted Towhee keeps the knee joint moderately flexed, the head high, and the tail held in line with the dorsum, or more frequently cocked slightly above the dorsal line. Scratching is accomplished by a sharp backward thrust of both feet simultaneously, the bird at the same time shifting its body backward so that at the end of a scratch the entire bird has been displaced from the point at which the scratch began. At the end of the backward thrust the bird recovers its original position by a short hop forward, and as it lands repeats the backward leg thrust and body shift. The wings and tail are held motionless during scratching. Sometimes the tail appears to be flicked down at the end of a scratch, but it is difficult to tell whether the bird actually depresses the tail or whether it is jarred down as the scratch ends and the bird hops forward in recovery. The strong claws dig into the soil cover, which is kicked as far as three feet to the rear, passing beneath the cocked tail and falling behind the forager. Periods of scratching are followed by a brief inspection of the newly exposed surface, the bird then pecking at bits of food, or resuming its scratching if no food has been uncovered. When one spot has been depleted of food, the towhee then moves to a new spot and resumes scratching. When a Spotted Towhee moves to a spot where the soil cover is intact, it usually scratches very vigorously five or six times in rapid succession, removing the top

layer of soil cover before pausing to search for food. Most of the food is thus found in the middle and lower layers of the soil cover or in the upper layers of the underlying soil after the cover has been removed. After the initial burst of rapid scratching, foraging proceeds in more leisurely fashion.

So strongly fixed in this species is the habit of scratching for food that individuals will sometimes scratch in trees where material has accumulated above the ground. Towhees were seen to scratch on five occasions in material in trees at heights of 4 to 15 feet, twice on the outer surfaces of wood rat houses in live oaks, and once each on an accumulation of leaves in the crotch of a blue oak, on moss growing on the horizontal section of a willow trunk, and in debris in a cavity rotted out in the trunk of a valley oak.

Two published descriptions suggest that there is some geographic variation in the manner of scratching by the Spotted Towhee. Woodbury (1933: 70), writing of *Pipilo erythrophthalmus montanus* in Zion Canyon, Utah, states that scratching is "accomplished by jumping into the air and drawing the feet backward while the upward momentum lasts. Drawing the feet backward and raking trash or leaves at the same time tends to overbalance the body forward. The bird uses several methods to hold its balance, either singly or in combination. Nearly always, the scratching motion of the feet is accompanied by a forward and upward jerk of the tail. Sometimes the wings flutter forward, and always after each scratching stroke the feet are brought forward quickly to catch the body and keep it from falling." In this method of scratching the primary displacement of the body is vertical. In the birds observed at the Hastings Reservation the leap was always forward rather than up, and the scratching motion occurred after the forward leap had been completed. The displacement of the body was always backward and forward, not up and down; the wings were not moved, and the tail was not jerked forward and upward.

Woodbury further states that "sometimes a backward movement of the body is made in jumping and the feet rake the trash while the momentum lasts. This is accompanied by a downward movement of the tail." This method of scratching, apparently used by *montanus* less frequently than the first method described by Woodbury, is invariably used by the towhees observed in this study.

A second suggestion that scratching may vary geographically is found in Dawson's statement (1923: 394): "Towhee is thoroughly at home here, and scratching for food is his job. This he pursues not by the methodical clutch and scrape of the old hen, but by a



succession of backward kicks, executed with spirit by both feet at once, and assisted by a compensatory flash of the wings." This passage seems to have been carried over almost verbatim from an earlier work, Dawson and Bowles' "The Birds of Washington," in which we find the following statement concerning scratching in the account of *Pipilo maculatus oregonus* (1909: 164): "Scratching for food is a favorite employment, and this they pursue not by the methodical clutch and scrape of the old hen, but by a succession of spirited backward kicks executed by both feet at once, and assisted by the wings." That Dawson's later statement is taken from his earlier one is very strongly indicated by the following passage from the preface to "The Birds of California" (1923: v): "inasmuch as a good deal of its [The Birds of Washington] matter was exactly descriptive of conditions obtaining in California, or at least concerned species found in California, it has been unhesitatingly used as a supplementary source-book for 'The Birds of California'." From the above it would appear that Dawson's remarks actually apply to *P. e. oregonus*, which, unlike the towhees at the Hastings Reservation, apparently uses its wings while scratching, perhaps to maintain balance.

When Spotted Towhees forage by gleaning from the surface, they maintain a nearly erect position, and the tail is kept cocked slightly above the dorsum. When food is sighted a bird must bend far forward to pick it up, since the head is carried relatively high above the ground.

Brown Towhees present a markedly different appearance when scratching. They forage from a deep crouch, the knee joint sharply flexed, the feet wide apart, and the tail either in line with the dorsum, or more frequently drooping below it. Some were seen to scratch with the tip of the tail actually touching the ground. Because of the crouched position the head is relatively close to the ground and the birds present a convex dorsal outline, the head and the tail both lower than the back. This contrasts with the concave dorsal outline presented by a scratching Spotted Towhee. The backward thrust of a Brown Towhee is noticeably less powerful and covers less distance than that of a Spotted Towhee. Because of the deep crouch this thrust has a pronounced lateral component, the feet being brought backward and away from the mid-dorsal line, whereas they are brought nearly straight back in the Spotted Towhee. Because of this, and in conjunction with the wider stance, most of the material kicked backward by a Brown Towhee passes to the rear on either side of the drooping tail.

When foraging by pecking at the surface, Brown Towhees also

work from a deep crouch with tail drooping and head held close to the ground. Thus closer inspection of the surface is achieved and the head does not have to be lowered far when food is sighted and picked up.

Three observations of juvenal Brown Towhees suggest that proficiency in foraging by scratching and pecking must be acquired through a process of learning by trial and error. One full-grown juvenile was observed foraging both by scratching and by pecking at exposed food on the soil surface. In addition to scratching in suitable areas, it kicked vigorously several times at a single dead live oak leaf lying on the ground, moving it about and twice getting its claws caught in the partly curled leaf. It then left to forage elsewhere but returned to the leaf several times, kicking it about or picking it up in its bill, holding it for several seconds and then dropping it. An adult and three juveniles were seen foraging together in a flower bed. The young birds picked off and ate the leaves of young plants. One juvenile tried to get at a leaf, one edge of which projected from under a fallen iris leaf. The bird scratched repeatedly at the thick, smooth iris leaf without penetrating it. Finally it reached down and pulled the desired leaf from under the iris. Another juvenile was noted hopping along a road and pausing frequently to pick up dead leaves, twigs, and pieces of dry grass, dropping these objects almost as soon as it had picked them up.

Both species when foraging on a slope invariably scratch facing upslope or cross-slope, and the material being removed is thus prevented from rolling back into the area being excavated. Individuals of both species sometimes change position while scratching and then continue to scratch at the same spot from the new position. Such shifts always involve 90° or 180° rotations, the bird thus scratching across the original axis or along it but facing in the opposite direction. Sometimes the new position may be maintained until the bird moves to another spot, and sometimes the bird may resume its original position after only a few scratches.

There is a difference between the two species in the manner in which they move over the ground while foraging. Considering terrestrial locomotion only, Spotted Towhees almost invariably move from one foraging spot to another by hopping, a series of hops covering distances as great as 30 feet in this fashion. Whether only one hop is made, or a series of hops, both feet are lifted and brought down simultaneously. Brown Towhees nearly always run when distances greater than 10 feet between foraging spots are involved. When Brown Towhees make a series of single hops, pausing between

them to inspect the ground for food, the feet are not moved simultaneously, but one precedes the other. Although both feet may be in the air at the same time, such single hops are in reality "step-hops," the bird taking off and landing on one foot, the other following a fraction of a second later. When a Brown Towhee takes two or more hops in succession, both feet are moved together.

Spotted Towhees appear to be much more at ease while foraging than do Brown Towhees. This is undoubtedly a result of their foraging in sheltered areas. They often forage for several minutes at a time without looking up. An observer, moving quietly, can often work to within a few feet of a foraging Spotted Towhee. Spotted Towhees, foraging toward an observer, will often approach to within a few feet before becoming aware of his presence. In contrast, Brown Towhees, spending much of their time in the open, have the habit of looking up and peering about them every few seconds.

Since Spotted Towhees spend nearly all their time under cover, they are seldom in direct sunlight and usually forage in partial or unbroken shade. The Brown Towhees, spending much time in open areas, are often exposed to direct sunlight. Like most birds, Brown Towhees are quiet during the late morning and early afternoon, especially on hot days. However, in addition to this normal avoidance of activity during periods of high temperatures, they have been seen at times to avoid carefully direct sunshine while foraging on cool days. The most extreme instance of this involved two birds foraging in the shadow of a large valley oak late in the afternoon of April 8, 1955. The weather was cool and a gentle west wind was blowing. Not only did the towhees forage in the shadow of the trunk, but they worked out along the long, thin shadows of the limbs, refusing to enter sunlit areas only a few inches away. Toward the end of the period of observation one bird worked out along a limb shadow about 20 feet long and 6 inches wide. The second bird followed about 10 feet to the rear. When the first bird reached the end of the shadow, it hopped two feet out into full sunlight and stood quietly. The second bird reached the end of the shadow, hopped out into full sunlight about one foot from the first bird, paused briefly, and then hopped three feet farther into a shaded area and resumed foraging. The first bird at once moved to the shaded area and also resumed foraging. Since towhees had been observed foraging in full sunlight on many previous occasions it may be that such elaborate efforts to remain in the shade on a cool day are related to the presence of certain food items in shaded areas. For example, certain terrestrial insects may have been present only in the shaded areas, making these areas more attractive for foraging.

Both species often call or give location notes while foraging, and foraging Spotted Towhees often sing from the ground in the period from late winter to late summer. Brown Towhees do not sing while foraging, but singing by mated males of this species is infrequent at all times.

#### PERIODS, RATES, AND GROUND COVERED IN SCRATCHING

The greater dependence on scratching by the Spotted Towhee is reflected by the fact that the three longest periods of steady scratching noted in this species were 57.5, 46, and 26 minutes, whereas the three longest periods for the Brown Towhee were 19, 18, and 17 minutes. However, there seems to be no significant difference between the two species as regards rate of scratching. During 25 timed periods aggregating 48.24 minutes, Spotted Towhees scratched an average of 34.0 times per minute, and in 5 timed periods aggregating 21.4 minutes, Brown Towhees scratched an average of 36.0 times per minute. In one period of 9.33 minutes a Spotted Towhee scratched an average of 33.7 times per minute, and in one period of 13.5 minutes a Brown Towhee scratched an average of 31.7 times per minute. Scratching rate in the Spotted Towhee ranged from 14 in 1.75 minutes (8.0 per minute) to a phenomenal 84 in 65 seconds (77.5 per minute). The great variation in scratching rate observed in the Spotted Towhee suggests that in both species this statistic depends primarily on the amount of food present per unit of material being removed.

The amount of ground covered by a bird undoubtedly depends on the denseness of the soil cover, the method of foraging used, and the amount of food present in the foraging area. A Spotted Towhee scratching steadily for 57.5 minutes covered 75 feet in one 14-minute period, with 30 feet of this being covered in 2 minutes. In another period of 11 minutes this bird confined its foraging to an area about three feet square. It is thus impossible to cite an average figure for the amount of ground covered by a foraging individual. There is some evidence which suggests that Brown Towhees that are foraging mainly by pecking range over more ground than those foraging mainly by scratching. Eleven Brown Towhees foraging by pecking covered an average of 5.8 feet per minute, the range 4 to 12.5 feet; eight birds foraging by scratching covered an average of 2.5 feet per minute, the range 0.5 to 5 feet.

#### FORAGING PITS

As a result of their foraging by scratching, both species make small pits or depressions in the soil or soil cover. Spotted Towhees dig two main types of pits. The first type is nearly circular, deepest

at the anterior end and sloping gently up to ground level posteriorly. These pits may penetrate the soil cover and reach the soil, or may be confined to the cover when it is thick. Five such pits averaged  $3.85 \times 3.7$  inches and 1.2 inches deep. The other type of depression excavated by Spotted Towhees is larger and oval rather than round. Three such pits averaged  $8.2 \times 3.5$  inches and 1.7 inches deep. The extreme in shallow scratching was accomplished by one Spotted Towhee which removed the topmost layer of mixed sycamore and live oak leaf litter over areas  $18 \times 10$  and  $8 \times 6$  inches, exposing the underlying damp litter.

Brown Towhees tend to dig somewhat shallower pits resembling the oval type of pits excavated by Spotted Towhees. Nine averaged  $8.4 \times 5.0$  inches and 0.71 inches deep.

The tendency for Spotted Towhees to dig somewhat deeper depressions than Brown Towhees is probably a reflection of the fact that the soil cover averages deeper in areas where Spotted Towhees forage. Further, the pits made by Spotted Towhees usually penetrate to the damper portions of the soil cover, where insects would presumably be more abundant. Beal (1910: 87, 89) noted that the consumption of animal food is greater in the Spotted Towhee (24 per cent of the diet as opposed to 14.26 per cent for *P. fuscus*), whereas the consumption of weed seeds, to be expected on or just below the soil surface, is greater in *fuscus* (51 per cent as opposed to 34.6 per cent for *erythrophthalmus*) (*op. cit.*: 91, 88). The differences in the depths of the pits excavated by the two species may thus be in part a reflection of interspecific differences in food preference.

#### NON-TERRESTRIAL FORAGING

Although foraging is primarily accomplished by scratching and pecking in the soil and soil cover throughout the year, from the spring through the fall both species find a considerable amount of food above ground. Foliage foraging by Spotted Towhees was observed on 31 dates falling between January 23 and December 31. Seventeen were in May, 4 in June, 3 in July, and the remaining 7 between September and January. In most instances one or more birds were noted pecking at leaves and branches, and at lichens hanging from them, but it was not possible to see what they were eating. Birds took caterpillars 6 times, beetles once, and an unidentified insect once. On 26 dates foliage foraging occurred in either live or valley oaks, and on one date each it occurred in an unidentified oak, a coffee-berry bush, a toyon, a willow, and a California blackberry bush.

Foliage foraging by Brown Towhees was noted 29 times on 19 dates

falling between February 25 and September 28. Six dates were in April, 6 in May, 1 in June, 2 in July, 2 in August, 1 in September, and 1 in February. Pecking was directed at leaves, branches, oak catkins, lichens, blades of grass, and low annuals. Only twice was the nature of the food being eaten determined, one towhee taking an insect larva and three capturing grasshoppers in a blue oak. Foliage foraging took place on grass 8 times, low annuals 5 times, blue oaks 4 times, valley oaks 4 times, live oaks twice, and once each on coast ceanothus, common horehound, chamise, a black cottonwood (*Populus trichocarpa*), an unidentified plant, and an unidentified shrub.

In the spring both species fed on the seeds, seed capsules, and bracts of miner's lettuce (*Montia perfoliata*, Table 1). The stomachs of 19 of 29 Spotted Towhees collected between April 14 and June 8, 1955, contained remains of this plant. The stomach of a Brown Towhee collected on April 15, 1955, contained seeds and pieces of seed capsule of *Montia*.

From early July to late December various fruits are prominent in the diets of the towhees. Forty-two observations were made of Spotted Towhees eating elderberries (*Sambucus coerulea*) between July 12 and September 23, and for Brown Towhees 31 observations were made between July 13 and October 15 (Table 1). Since July, August, and September are the hottest and driest months of the year at the Hastings Reservation, elderberries are probably important to both species as a source of water. Although the overlap between the periods of feeding on elderberries by the two species seems almost complete, there is some evidence that in certain years one species may start using this food source earlier than the other. Between July 26 and September 5, 1954, Spotted Towhees fed on elderberries on 12 days, of which nine fell between July 26 and August 14, and three between August 16 and September 1. Brown Towhees fed at the same bushes on 10 dates during this period. Eight fell between August 15 and September 5, with single records for August 3 and 9.

The methods of feeding on elderberries are much the same in both species. Most frequently a bird will select a perch near a cluster of berries; usually this is a branch just above or below a cluster, the forager reaching up or bending down to detach single berries. Often a towhee will perch with one foot on the stem of a cluster and the other on the cluster itself, reaching down for the fruits. Since the clusters hang from the ends of long, pliant branches a perch offering firm support is often hard to find, and a bird may move about for some time before finding a secure position from which to feed. Sometimes a towhee may be unable to find a suitable perch and give up

TABLE 1  
MONTHLY RECORDS OF FOOD ITEMS EATEN

Plant	Part eaten	Towhee	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
<i>Montia perfoliata</i>	Seeds, capsules, bracts	<i>erythro.</i> <i>fuscus</i>				10	10	3						
<i>Sambucus coerulea</i>	Berries	<i>erythro.</i> <i>fuscus</i>					14	25	3					
<i>Rhamnus californica</i>	Berries	<i>erythro.</i> <i>fuscus</i>					13	12	5	1				
<i>Rhamnus crocea</i>	Berries	<i>erythro.</i> <i>fuscus</i>						3	36	11	8	2		
								1	16	10	3	2		
							1	8	5					
								4						
<i>Rhus diversiloba</i>	Drupes	<i>erythro.</i> <i>fuscus</i>	1								1	4	1	
<i>Symphoricarpos rivularis</i>	Berries	<i>erythro.</i> <i>fuscus</i>	3								1			1
<i>Ribes divaricatum</i>	Berries	<i>erythro.</i> <i>fuscus</i>						1	3					
<i>Quercus</i> sp.	Acorns	<i>erythro.</i> <i>fuscus</i>	16	19	8	3		1			1	9	8	
			1	1	1							2	3	

its efforts to reach a cluster. Several times towhees tried to feed from an unsteady perch, lost their balance, and fell.

A second and less frequently used method is that of flying up to a cluster, taking a berry on the wing, and then dropping down to a secure perch to eat it. When foraging in this manner, a towhee will look up and eye a cluster, apparently selecting a berry. The bird then flies up to the cluster, beating its wings to maintain position, and grasps a berry in its bill. The wings are then folded, and as the bird falls it detaches the berry with a sharp twist of its head, aided by the inert weight of the falling body. The towhee then drops to a secure perch to eat the fruit. Towhees make repeated trips in this fashion, usually returning to the same feeding perch, but a Brown Towhee that made four trips to a cluster dropped down to a different perch each time. Aerial foraging is apparently used when a bird cannot find a suitable perch within reach of a cluster. Such foraging was noted twice on windy days when the terminal branches from which the clusters hung swayed to such an extent that a forager would have had considerable difficulty feeding from a stationary perch. Aerial foraging does not result from a desire to seek cover while feeding as both species often used an exposed feeding perch after getting a berry on the wing.

In eating, each berry is rolled about in the bill for several seconds before being swallowed. By thus "mouthing" a berry, the skin is broken, the seeds squeezed out, worked to the tip of the bill, and flung aside with a quick shake of the head. The skin and pulp are then swallowed. Bits of skin are often eliminated as the seeds are cast aside but only three towhees were seen consistently to discard the entire skin. Once a juvenile Brown Towhee expelled the seeds and skin of a berry and then reached down, picked up the skin, and swallowed it. Berries are sometimes swallowed whole, but they are always "mouthed" before ingestion, this apparently serving to break the skin. Brown Towhees spend less time "mouthing" and swallow whole berries more often than do Spotted Towhees. As a result they tend to eat berries at a faster rate. Three Brown Towhees averaged 7.5 seconds between berries, and 6 Spotted Towhees averaged 13.5 seconds.

Spotted Towhees ate coffeeberries (*Rhamnus californica*) between August 22 and December 24, and Brown Towhees ate them between August 26 and December 12 (Table 1). The preponderance of September records for both species suggests that coffeeberries are also an important source of water during this hot, dry month.

There is a pronounced difference between the two species in the



methods of feeding on coffeeberries. Spotted Towhees usually detach a berry, grasping it in the bill and freeing it with a combination pull and sideways shake of the head, and take it to cover to eat it. Birds may take berries to the ground under the bush from which the fruit was taken, or fly to cover with them as far as 50 feet. As judged by the remains of berries eaten by Spotted Towhees, the seeds and most of the skin are not swallowed. However, the stomach of a bird collected on October 27, 1955, contained four large pieces of the skin of a fully ripe (i.e., black) berry. Most of the berries eaten are fully ripe, although occasionally partly ripe (i.e., red) berries are taken. Since ripe berries are more easily detached than unripe ones, preference for them may result from this fact rather than from a taste preference. Spotted Towhees occasionally eat berries *in situ*, but this is rarely seen.

In sharp contrast Brown Towhees usually eat berries *in situ*. A feeding bird will work to a secure perch near a berry and then reach forward to peck at it. One or two pecks serve to slit the skin. By repeatedly pecking through this break the pulp is obtained and swallowed. The bill of a bird feeding in this manner soon becomes wet and glistening from the berry juice. Brown Towhees also prefer ripe berries, although they occasionally eat unripe ones. This may reflect a true taste preference. A Brown Towhee eating a ripe berry may detach it after a few pecks. Sometimes the berry is dropped and another chosen; several times Brown Towhees were seen to fly to cover with a berry thus detached. Infrequently they will detach a whole berry and take it to cover after the fashion of Spotted Towhees.

The interspecific difference in methods of feeding on coffeeberries reflects the basic difference in foraging behavior between the two species. Spotted Towhees, preferring to forage and feed under cover, are apparently reluctant to eat coffeeberries in the exposed situations in which they are found, whereas Brown Towhees do not require sheltered situations in which to eat this food.

Fruits of the hollyleaf redberry (*Rhamnus crocea*) were eaten by Spotted Towhees between July 25 and September 27 (Table 1). Brown Towhees ate redberry only 4 times, all in August. Both species ate these fruits *in situ*, either biting pieces from them or detaching them and discarding the seeds and sometimes the skins before swallowing them.

It is noteworthy that Spotted Towhees eat elderberries and redberry *in situ*, whereas they usually take coffeeberries to cover. The reason for this may be in the differences among the sizes of the

berries. Thirty-nine elderberries, black in color and not quite ripe, averaged 0.051 ml. in volume, and 24 blue, fully ripe berries averaged 0.083 ml. Twenty ripe redberries averaged 0.2 ml. Ten ripe coffeeberries averaged 1.3 ml. A towhee taking the three smaller kinds of berries to cover would expend considerable energy for a relatively small amount of food. As stated previously, six Spotted Towhees feeding on elderberries *in situ* took an average of 13.5 seconds to detach and eat a berry. Few data are available for the time required by a Spotted Towhee to eat a coffeeberry, for the heavy cover to which berries are taken makes observations difficult. Spotted Towhees taking coffeeberries to cover left the cover after 30, 45, and 65 seconds, and one was seen to peck at a ripe berry for 75 seconds before hopping away. It seems likely that the greater size of the coffeeberries, and the longer time taken to eat them, account for the towhees taking them to cover, as they apparently find enough food in individual berries so that foraging is relatively efficient despite the trips to cover. Since Spotted Towhees spend long periods feeding on elderberries and redberries *in situ*, the attraction of these fruits must be considerable to overcome the natural reluctance of these birds to leave cover.

Poison oak drupes were eaten only once by Spotted Towhees but were eaten 10 times by Brown Towhees (Table 1). On four occasions the birds chewed the drupes before swallowing them. Once a towhee chewed a drupe for several seconds and then dropped it. The drupe was recovered and about a third of the outer, waxy covering of the seed had been removed. It seems likely that when berries are swallowed, the waxy covering is digested and the hard seed defecated. Beal (1910) has indicated that several species of birds use this method of feeding on poison oak drupes. Other species chew off the waxy covering and discard the seed. The Brown Towhee apparently uses both methods of feeding on the drupes.

Snowberries (*Symphoricarpos rivularis*) and straggly gooseberries (*Ribes divaricatum*) were eaten by Spotted Towhees but they were not eaten by Brown Towhees (Table 1). Other fruits eaten once or twice by one or both species were hillside gooseberry (*Ribes californicum*), California blackberry, islay (*Prunus ilicifolia*), toyon, chaparral honeysuckle (*Lonicera interrupta*), manzanita (*Arctostaphylos* sp.), and madroño. Both species were seen several times moving about in dense growths of common mistletoe (*Phoradendron villosum*) but the heavy foliage prevented observers from noting whether or not the birds were actually eating berries.

In the winter acorns form a prominent part of the diet of the Spotted

Towhee (Table 1). Of 48 birds collected between January 5 and April 27, 1955, the stomachs of 27 contained acorn fragments. In eight stomachs these were the most prominent food item present. Between April 27 and October 26 only one stomach contained acorn fragments, that of a bird collected on June 8. In the fall acorns first appeared in the stomach contents on October 27, and from then on they were found frequently until collecting stopped on February 29. The available observations of Spotted Towhees eating acorns leave considerable doubt as to the ability of these birds to open the husks by themselves. Of ten observations, two involved towhees pulling acorns from their cups and carrying them to cover and three involved birds flying to cover with acorns the origins of which were unknown. A towhee was seen eating an acorn under a blue oak but the meat was exposed and had been broken into three pieces when first noted. The following observations indicate that the Spotted Towhee may depend on already opened acorns as a source of food. A Spotted Towhee was seen next to a log on which a chipmunk (*Eutamias merriami*) was eating an acorn. A second chipmunk appeared and engaged the first in a fight. The acorn fell to the ground and the towhee at once took it to cover and ate it. A Scrub Jay (*Aphelocoma coerulescens*) dropped a half-shelled acorn to the ground. Two or three birds made a rush for it but a Spotted Towhee seized it, took it to a perch, ate some of it, and then took it to several other perches. A Spotted Towhee was seen to pick out and eat meat adhering to pieces of acorn husk which had been spit out by mule deer (*Odocoileus hemionus*). A towhee under a valley oak picked up and dropped three acorns, then picked up a fourth with the basal part of the shell already removed so that the meat was exposed, flew to cover with it, and ate it. It would appear that Spotted Towhees eat many acorns which have already been opened, either by other animals or because the shell had rotted out. The two observations of towhees removing acorns from their cups and flying off with them suggests that birds may occasionally open their own. In these cases, however, the acorns may have been split or some breach may have already been made in their husks. No definitive observation is at hand of towhees pounding open whole, sound acorns.

Seven observations of Brown Towhees eating acorns fell between November 14 and March 13 (Table 1). In each case the acorns had already been opened. A Brown Towhee flew to a stump in which Acorn Woodpeckers (*Balanosphyra formicivora*) had stored several acorns. The towhee pecked at one, the bottom of which had already been broken out, until driven away by a woodpecker. One pecked

at a sprouting acorn with half the shell gone. One pecked at an acorn from which one side had apparently been removed some time before, as the exposed meat was brown. On three dates one or more towhees picked meat from pieces of husk which had been spit out by mule deer. A Brown Towhee ate pieces of an acorn which had been crushed on a road, probably by a passing car. All these observations suggest that Brown Towhees do not open acorns themselves but use already opened ones. A final observation pertains to both species of towhee. A Scrub Jay flew to a bush and shelled an acorn. A Plain Titmouse (*Parus inornatus*), a Spotted Towhee, and two Brown Towhees stayed within 4 feet of the jay as it worked, and when the jay flew the other birds followed it.

Observations of other departures from the usual ground foraging are few. A Spotted Towhee was seen to make two nearly vertical flights from the ground, each to a height of about 2 feet, as though hawking insects. Three times Spotted Towhees were seen hopping swiftly through grass, following an erratic, zig-zag course, as though pursuing grasshoppers, and one was seen to chase and eat a grasshopper. Single observations were made of Spotted Towhees eating young valley oak leaves, the blossoms of hillside gooseberry, the blossoms of California blackberry, and the seeds of black sage, all while perched in the plant involved. A brown Towhee was seen to eat two seeds of slender oat (*Avena barbata*) by leaping to them, grasping them in its bill, bending the oat plant down without breaking the stem, and removing the seeds. Another ate three vegetative buds at the stem tips of coast ceanothus. One reached up to peck at the dry flowers of vinegarweed (*Trichostema lanceolatum*), apparently obtaining the few seeds still present. Two towhees pulled at the heads of grass containing seeds. Twice towhees ate the newly grown leaves of valley oaks. Four observations were made of Brown Towhees pulling off and eating blades of newly sprouted grass. Six birds were involved. A towhee pulled off a pod of canyon clarkia (*Clarkia elegans*) and worked it about in its bill as though getting seeds. One ate a small mushroom, and one ate pieces of leaves from a common man-root (*Marah fabaceus*).

#### SPACING OF FORAGING BIRDS

The spacing of foraging birds is somewhat different in the two species, although there is considerable overlap between them in this regard. For the Spotted Towhee the great majority of records involves birds foraging in twos throughout the year. Members of foraging "pairs" kept well apart in winter, separated by distances

up to 100 feet. The wide spacing of foragers and the dense brush in which they were found made it nearly impossible to "sex" both members of such duos. Pairs, so identified by sex, were the most frequently encountered foraging groups from late February through July. During this season members of a pair often foraged close together, usually keeping 2 to 15 feet apart, a male following his mate as she moved along the foraging beat. In one case the male led the way and the female followed. When members of a pair foraged in opposite directions, becoming separated by 50 to 100 feet, one or the other would start to call after a short time. This usually, but not always, resulted in one bird flying to the other, or in the silent bird turning and foraging toward the calling bird. In winter widely separated sets of two birds rarely showed such integration of movement. Often one bird would fly from the foraging area and the other would remain. If such widely separated sets of two actually represented pairs, the pair bond must be much weaker in the winter than during the period from late winter through the summer.

Single birds, exclusive of juveniles, are often seen throughout the year. These probably represent wandering immatures, and adults which have failed to find a mate. In the fall and early winter, groups of three to six birds, foraging in the same general area, are not uncommon. The relationships of the birds in such groups are not clear. All observations of such "flocks" occurred between August and January.

In the Brown Towhee the evidence is strong that birds remain paired throughout the year, and that the pair bond is strong at all times. Pair reinforcement notes are heard in every month, and vigorous defense of apparent winter territory has been seen several times. The great majority of observations record Brown Towhees foraging in twos. Members of such "pairs" tend to forage close together throughout the year, usually keeping from 1 to 20 feet apart. Occasionally foraging birds may be separated by only a few inches, and once a bird foraging by pecking came so close to another that was foraging by scratching that the latter kicked leaves in its face, forcing it to move.

Members of presumed pairs were seen to wander apart while foraging and in some instances one member might fly to an area 100 to 150 feet away and resume foraging there. In most cases, after a short separation, one or the other would start to call steadily. Several times it was noted that when two birds were foraging together and one flew to an area some distance away, it would call steadily for a short time before leaving and again after reaching the new foraging

area. This often resulted in its partner joining it. From March through June only pairs and single birds were seen. Trios of foraging birds were seen many times from August through February. These appeared to be made up of a pair plus an unattached bird. Often two birds in such a trio foraged close together and the third some distance away. Several times the presumed pair would leave the area, the single one remaining. In other instances the single bird would fly and the pair would remain. Clashes were noted several times between pairs and single birds in such a trio. Groups of four, five, six, and seven birds were seen several times from July to February. The composition of such groups was not determined.

In summary, both species forage mainly in twos throughout the year. Partners in such duos of the Spotted Towhee forage so far apart in fall and winter, and with such little integration of movement, that it is difficult to tell whether they are truly paired or single birds. From late February through July, members of such duos forage close together and are obviously pairs on the basis of sex. At this time integration of movement between members of a pair is high. In contrast, members of duos of Brown Towhees forage close together and show a high degree of integration of movement throughout the year. Foraging and other behavior strongly suggest that such duos represent true pairs.

#### ASSOCIATED VERTEBRATES

The influence of associated vertebrates on foraging towhees is difficult to assess. As has been previously noted, the trails of ground squirrels, rabbits, and deer are important in modifying grassland so as to create suitable foraging areas for Brown Towhees. Acorn Woodpeckers, Scrub Jays, Merriam chipmunks, and mule deer are important to both species of towhees in providing opened acorns as a source of winter food. On the other hand, competition for food between towhees and other vertebrate species must occur, but without detailed analyses of their stomach contents it is not possible to determine accurately the nature and extent of such competition.

The reactions between towhees and other species of vertebrates are highly unpredictable. Under seemingly similar conditions a towhee may show antagonism toward another vertebrate, or be attacked by it, or the individuals involved may ignore each other. An outstanding example of this involved an area in which as many as five Brown Towhees and four cottontail rabbits (*Sylvilagus audubonii*) foraged in the evening. For several days no intolerance was noted, and the two species apparently ignored each other. On one

evening a towhee and a cottontail were foraging three feet apart when the rabbit suddenly rushed at the towhee and bit at it, the sound of the teeth coming together clearly audible 40 feet away.

The most frequently observed reactions of towhees toward other vertebrates fall into two main categories. First, foraging towhees may disturb, or be disturbed by other animals. Such disturbance is often mechanical. A towhee may cease foraging and make way for a passing deer or rabbit and resume foraging after the other animal has passed. Other disturbances are of a different nature. The sudden appearance of a predator may cause a Brown Towhee foraging in the open to take cover. Three Brown Towhees foraging in an open area for three-quarters of an hour flew to a nearby oak when a Red-tailed Hawk (*Buteo jamaicensis*) flew over. Brown Towhees were seen many times to take cover when Sharp-shinned and Sparrow hawks (*Accipiter striatus* and *Falco sparverius*) approached their foraging areas. The most important source of disturbance comes from the sudden calling or flight of nearby birds. The sudden scream of a Scrub Jay or the squawking of a group of Acorn Woodpeckers will often cause a towhee to interrupt its foraging and either seek cover or stand alert until satisfied that the danger has passed. Often such bursts of sound are ignored. Groups of California Quail (*Lophortyx californica*) suddenly taking flight near foraging Brown Towhees have frightened the latter into flying to cover. Towhees may disturb other birds in similar fashion. Two Brown Towhees foraging near several Oregon Juncos (*Junco oreganus*) flew from and returned to the foraging area several times, the juncos flying and returning with them each time. Repeated disturbances of this nature interfere noticeably with foraging. In one area of extensive grassland, foraging Brown Towhees used a dense poison oak thicket for cover when danger threatened. (Plate 8.) In the late afternoon this thicket also served as headquarters for a large flock of Golden-crowned Sparrows (*Zonotrichia atricapilla*) which foraged out into the surrounding grassland. Sharp-shinned Hawks often flew over the area, apparently attracted by the large numbers of small birds present. Whenever one of these predators appeared the towhees and Sparrows took cover at once. Usually, when the birds took cover no source of alarm was evident to the observer, and the birds often flew back to the foraging area after only a minute or less in cover. It appeared as though the entire group was being frightened into flight by a few nervous individuals reacting to mounting tension resulting from prolonged absence from cover. Regardless of their cause these hasty flights resulted in disrupting the late afternoon foraging of



FORAGING AREAS OF THE BROWN TOWHEE. (*Above*) Ground cover mainly of short, interrupted grass and low annuals; adjacent Coast Live Oaks and Coffeeberry provide nearby cover. (*Below*) An extensive thicket of Poison Oak bordered by bare soil, beyond which lies an extensive area of interrupted grassland. Brown Towhees foraged under the thicket, on the bare soil, and in the grassland. The nearby Valley Oak (*Quercus lobata*) supplied much leaf litter to the thicket. Photographs taken April 22 and March 16, 1956, at the Hastings Reservation.



the birds using the area. For example, on the afternoon of January 26, 1954, foraging Brown Towhees and Golden-crowns flew to cover 11 times between 3:30 and 5:41 p.m., an average of one disturbance every 12.5 minutes. Once, two towhees flew first, the sparrows following them. Another time, the sparrows flew first, a towhee flying up and joining them as they flew over. Once, the sparrows flew to cover, passing over two towhees which continued to forage. It was not possible to determine which species flew first on the other occasions. No apparent cause for these disturbances was noted by the observer during the afternoon, and after most of the flights to cover, the birds returned to the foraging area after only a few seconds. Whether or not the presence of the large flock of Golden-crowns was advantageous to the towhees is questionable. The frequent disturbance to foraging was a definite disadvantage but the presence of so many individuals to spot approaching predators was a definite advantage. However, the hawks frequenting the area may have been attracted in the first place by the large numbers of sparrows present.

Spotted Towhees are rarely subjected to the disturbances just described. Foraging under cover most of the time, they are already sheltered when disturbances occur.

The second major category of reactions between towhees and other vertebrates is that involving intolerance. There is no consistency in the behavior of foraging towhees toward any given species. In some instances the relative abundance of a competing species seems to influence the reactions of foraging towhees toward it. For example, the Fox Sparrow (*Passerella iliaca*), a winter visitant at the Hastings Reservation, forages in similar fashion to the Spotted Towhee and frequents the same types of foraging sites. Yet, no intolerance was ever displayed by either Fox Sparrows or Spotted Towhees foraging as close as one foot apart. A striking example of the apparent lack of friction between the two species was noted on March 22, 1955, at a time when male towhees were markedly aggressive toward other males of their own species. A male scratched vigorously in leaf litter. Suddenly a Fox Sparrow started to scratch in leaf litter 20 feet away, hidden from the towhee by heavy brush. The scratching sounds made by the sparrow were identical to those made by the towhee. The latter at once flew to within a few feet of the sparrow, apparently mistaking it for another towhee. After a brief inspection of the other bird the towhee at once returned to its foraging area. Although the Fox Sparrow is a definite foraging competitor of the Spotted Towhee, it is present in small numbers and is apparently

ignored. Twice Brown Towhees foraged near Fox Sparrows with neither species showing interest in the other. At another time a Brown Towhee watched quietly as two Fox Sparrows foraged and after they had left, it flew down and foraged in the area that they had been using.

Another competitor, the Golden-crowned Sparrow, is an abundant and widespread winter visitant to the Reservation. This species overlaps in foraging behavior and choice of foraging areas with both species of towhees. Golden-crowns forage in completely exposed areas, and they also scratch in leaf litter under trees and at the edges of brushy areas. They frequently forage in company with towhees, especially with Brown Towhees, usually in small flocks, but occasionally large groups numbering 25 to 75 may use a limited foraging area. Their numbers and foraging behavior make them serious competitors. Spotted Towhees were seen to attack Golden-crowns four times, and Brown Towhees attacked them six times. All attacks were directed either at single birds or at individuals which had strayed from a foraging group and had closely approached a foraging towhee. Brown Towhees surrounded by large flocks of foraging Golden-crowns usually ignored them, since an attack by one or two towhees against a large group would be ineffectual. On one occasion two towhees foraged in the midst of a large group of Golden-crowns. After two minutes one towhee ran 50 feet from the sparrows, and the other followed at once. The towhees then resumed foraging about three feet apart, well removed from the other birds. Since at least 30 sparrows were present, it seems unlikely that the towhees could have driven them away by a direct attack, and they moved to a less crowded foraging area.

Oregon Juncos were attacked three times by foraging Brown Towhees. Juncos are resident at the Reservation, but the numbers of the local population are greatly increased in winter by large groups of wintering birds. Strangely, the three attacks noted occurred on May 12, July 19, and September 23, when the numbers of juncos at the Reservation were relatively low. No close contacts were noted between juncos and foraging Spotted Towhees.

Spotted Towhees attacked Mexican Bluebirds (*Sialia mexicana*) three times, on September 21, October 1, and November 7. These dates fell within the period during which the towhees and bluebirds frequently eat coffeeberries, and the intolerance may have resulted from competition for this food. The October clash involved two towhees eating coffeeberries *in situ* unsuccessfully trying to drive five bluebirds from the same bush at which they were eating. The November clash involved a bluebird eating a coffeeberry on the

ground and a towhee perched 10 feet up in a nearby oak. The towhee suddenly flew from the tree and dived at the bluebird, passing about 6 inches above it. The bluebird flew and the towhee continued on its way. The September encounter involved two non-foraging birds, a male towhee and a male bluebird perched 6 feet apart in an oak. The towhee flew twice at the bluebird and the latter rose to meet him each time. After two brief but savage fights the two dropped to limbs about 10 feet apart, and the towhee then flew from the area. Although neither bird was foraging before the encounter, the aggressive behavior of the towhee strengthens the impression that Spotted Towhees may be intolerant of bluebirds during the coffeeberry season. During the rest of the year these species rarely come into close contact. Only one clash was noted between a Brown Towhee and a bluebird; this was on January 20 after the coffeeberries had disappeared.

Contacts between Spotted and Brown towhees were fairly frequent. On 29 occasions foraging individuals of both species were in close contact. In seven cases there were displays of intolerance. Brown Towhees were the aggressors in five cases and Spotted Towhees in two. Intolerant behavior was noted three times in May, three times in August, and once in September. May represents the peak of the nesting season for both species. In August and September the total numbers of each species are at their highest, as second brood juveniles are full-grown by that time. Competition for food must be high in the late summer and early fall. It seems significant that all cases of intolerance between the two species took place either during the nesting season or at a time of year when contacts between individuals would be unusually frequent. There are no records of intolerance from October to April. Apparently the two species are mutually tolerant from mid-fall to late spring, but some aggression may be expected during the breeding and immediate post-breeding seasons. Even during these critical periods there is no consistency in the reactions of the two species toward each other for there were eight instances of close contact between foraging individuals between May and September when no antagonism was displayed.

Miscellaneous cases of intolerance involved a Spotted Towhee attacking a Plain Titmouse (*Parus inornatus*) eating an acorn, a Spotted Towhee trying to drive a White-crowned Sparrow (*Zonotrichia leucophrys*) from a coffeeberry bush, a foraging Brown Towhee twice attacking a Mountain Quail (*Oreortyx picta*) passing by, and foraging Brown Towhees twice attacking House Finches (*Carpodacus mexicanus*).

Other contacts suggest that towhees may at times become curious

and investigate, in a deliberate and unaggressive manner, the foraging areas used by other species. A full-grown juvenal Brown Towhee, foraging 5 feet from a foraging junco, ran at the latter five times. The towhee moved slowly and deliberately, and each time, the junco flew a few feet away and resumed foraging. The impression was not one of intolerance, but merely investigation of the activities of the junco. On another occasion a Brown Towhee quietly watched a Spotted Towhee three feet away as it scratched vigorously in leaf litter. After  $1\frac{1}{2}$  minutes the Brown Towhee moved slowly toward the Spotted Towhee, paused 1 foot from it, watched it for 30 seconds, and then slowly moved toward it. When the birds were about 6 inches apart the Spotted Towhee hopped 10 feet away and resumed foraging. The Brown Towhee then moved to the pit dug out by the Spotted Towhee, eyed it for 2 or 3 seconds, and then slowly moved away, paying no further attention to the foraging bird.

#### INTRASPECIFIC INTOLERANCE

The two species of towhees diverge sharply in the amount of intolerance expressed toward others of their own species while foraging. Foraging Spotted Towhees clashed only eight times. One clash involved two males on April 12, 1955, at a time when many territorial conflicts were noted. The males came together four times, between attacks foraging as close as 2 feet apart. This foraging probably represented displacement activity. The other instances of intolerant behavior occurred in June (2), August (1), November (2), and December (2). The August case involved two birds classed as immatures by the observer, but more probably they were juveniles. One of the June cases involved competition for a restricted food source; a bird that was eating the fruits of hillside gooseberry drove away another towhee which came to the same bush. One of the November cases involved a towhee which was trying to detach an acorn; it drove away a second towhee which landed near it in the same tree.

Fifty-three clashes were noted between foraging Brown Towhees. Of these, 43 involved either adults or immatures (these indistinguishable in the field), four involved adults and juveniles, two involved immatures only, and four involved juveniles only. Of the four clashes between adults and juveniles, one occurred in June and three in July, the latter involving a pair of adults trying to drive out a juvenile. Of the four clashes involving juveniles only, one occurred in June, two in July, and one in August.

The break-down by months of the 43 attacks involving either adults or immatures shows a preponderance occurring from mid-

summer to early winter. Four attacks were noted in July, six in August, six in September, eight in October, three in November, four in December, and seven in January. From February through June there were only five clashes between foraging birds, one each in February, April, and May, two in March, and none in June. Of the 12 clashes observed in August and September, five involved birds feeding on elderberries. Two instances of intolerance involved known immatures observed on November 29, 1955. The birds had been color-banded in fresh plumage on October 13 (Red), October 15 (Orange), and October 24 (Yellow). In hand all were identified as immature on the basis of criteria outlined by Davis (1951: 3). Red and Orange were seen foraging on open ground at the rear of a house, about 35 feet apart. Red suddenly ran swiftly at Orange, covering the entire distance on foot. Orange flew into nearby brush, pursued by Red. A few minutes later Orange and Yellow were noted foraging on open ground in the yard of the house. The birds were about 2 feet apart. Orange suddenly ran about 10 feet from Yellow and resumed foraging, when Yellow suddenly ran at it. Orange flew around a corner of the house and Yellow returned to its foraging site and resumed scratching and pecking. Three minutes later Orange flew around the corner of the house, landed 6 feet from Yellow, and started to forage. After 30 seconds Yellow flew at Orange and the two then flew around the corner of the house, Yellow pursuing. All clashes were unaccompanied by any vocalization. From these observations it would appear that many of the clashes noted were actually between immatures.

The aggressive contacts previously described include only those noted between birds actually foraging and consisted of brief chases without any vocalization. They do not include the more savage attacks seen frequently in the fall and during the late winter and spring. Such attacks are usually signaled by snarling, throaty notes given by the attacker and a decelerating series of "chink" notes given by the attacked bird. This type of clash apparently represents the attempts of established birds to drive intruders from their territories. The brief, non-vocal clashes involving foraging birds apparently represent attempts to drive other birds from the immediate foraging area only.

Several attacks were observed involving duos which had been observed for lengthy periods in the same areas and were assumed to be pairs. These brief encounters resulted in some cases in the departure of the attacked bird from the foraging area, but at other times the birds resumed peaceful foraging in close proximity. In

two cases the attacker rushed at its presumed mate, drove it away, and then foraged in the exact spot where the other bird had been foraging. The most serious competition for food that a paired Brown Towhee faces is from its mate, and it may be that a bird will occasionally attack its mate if it is sufficiently hungry, or if the mate's foraging area is especially attractive.

The most savage attack noted was directed against a Brown Towhee feeding on elderberries 8 feet up. This bird was attacked by a Brown Towhee which flew at it, passing about 1 inch above it. A second Brown Towhee then flew at it, hitting it with an impact heard clearly 60 feet away. The forager was literally knocked from the bush, but returned to the cluster on which it had been feeding, and it in turn attacked and drove off a towhee which came to the bush a few minutes later.

#### HIND LIMB OSTEOLOGY

Measurements were made of the femur, tibia, and tarsus of the skeletons of 13 *Pipilo erythrophthalmus falcifer* (6 ♂♂, 7 ♀♀) and 10 *Pipilo fuscus petulans* (6 ♂♂, 4 ♀♀). Percentages of the total length of the hind limb made up by the separate elements are presented in Table 2. It is evident that in *erythrophthalmus* the femur is relatively shorter and the tarsus relatively longer. The tibia is about the same in both species. Although differences in the relative proportions of the leg bones are small, the fact that they are present in the same degree in each sex suggests that they are biologically significant. Since the Spotted Towhee moves over the ground mainly by hopping it is likely that the shortening of the femur and the lengthening of the tarsus are associated with this activity. Howell (1932: 533), describing the anatomy of saltatorial rodents, notes that "with saltatory specialization there will be progressive shortening of the

TABLE 2  
PERCENTAGES OF TOTAL HIND LIMB LENGTH

Bone	<i>Pipilo erythrophthalmus</i>			<i>Pipilo fuscus</i>		
	Sex	No.	Per cent	Sex	No.	Per cent
Femur	♂	6	25.5	♂	6	26.5
	♀	7	25.6	♀	4	26.6
Tibia	♂	6	43.3	♂	5	43.4
	♀	7	43.5	♀	3	43.5
Tarsus	♂	6	31.2	♂	6	30.1
	♀	6	30.9	♀	4	29.9

thigh, and elongation of the foot, while the length of the shank in relation to total limb length experiences a very slight reduction." The slight differences in intramembral proportions of the hind limb of the two species may be a reflection of the greater dependence on saltatory locomotion in *Pipilo erythrophthalmus*. Also, since foraging by scratching involves a forward hop following each scratch it is possible that the longer recovery hop of *erythrophthalmus* is aided by the skeletal structure of the hind limb, this accounting in part for the greater distance covered by each scratch.

### HIND LIMB MUSCULATURE

The hind limb musculature of five Spotted and five Brown towhees was examined. Fresh specimens were preserved in a fluid containing absolute methyl alcohol, formalin, distilled water, glycerine, carbolic acid, sodium carbonate, white arsenic, boracic acid, and potassium nitrate. The muscles were removed *in toto* and stored in the preserving fluid. Because of their small size volumetric analysis was not possible, and each was weighed on a Roller-Smith balance to 0.1 mg. Excess preservative was gently blotted from the muscles before weighing. A detailed description of each muscle is omitted, as Stallcup's (1954: 164-175) description of the leg muscles of *Pipilo erythrophthalmus* serves for *P. fuscus* as well. Table 3 presents the relative percentages of the total hind limb musculature of those muscles which showed marked interspecific difference. The symbol "\*" following each muscle indicates that relative percentages overlapped in only one specimen; the symbol "†" indicates that there was no overlap between the samples. The following muscles were not considered in this study: *m. iliotrochantericus medius*, *m. iliacus*,

TABLE 3  
PERCENTAGES OF TOTAL HIND LIMB MUSCULATURE

Muscle	<i>Pipilo erythrophthalmus</i>		<i>Pipilo fuscus</i>	
	Range	Mean	Range	Mean
<i>M. iliotrochantericus posticus</i> *	3.21-3.82	3.47	3.77-4.13	4.01
<i>M. piriformis, pars caudifemoralis</i> †	2.75-3.56	3.20	3.58-3.97	3.72
<i>M. iliotibialis</i> †	6.53-8.37	7.48	8.39-9.63	9.02
<i>M. femoritibialis externus &amp; medius</i> †	10.93-12.12	11.39	9.91-10.58	10.40
<i>M. tibialis anticus</i> †	6.45-7.46	7.06	5.69-6.31	5.95
<i>M. extensor digitorum longus</i> *	1.72-2.00	1.93	1.62-1.88	1.77
<i>M. flexor perforans et perforatus digiti III</i> †	2.29-2.50	2.38	2.56-2.93	2.80
<i>M. gastrocnemius</i> *	15.17-16.36	15.67	16.18-17.57	16.57
<i>M. flexor hallucis longus</i> †	5.12-5.90	5.56	3.66-4.38	4.05

\* Relative percentages overlapped in only one specimen.

† No overlap between samples.

*m. obturator externus*, *m. extensor hallucis longus*, *m. flexor hallucis brevis*, *m. abductor digiti IV*, and *m. lumbricalis*. Nomenclature follows that of Stallcup (*op. cit.*). The following accounts are of those muscles listed in Table 3.

*M. ilirotrochantericus posticus*. This is the most powerful muscle rotating the femur forward and inward. Its action tends to bring the lower leg beneath the body and causes the bird to toe in. The greater development of this muscle in *Pipilo fuscus* may account in part for the noticeable lateral component of each scratching motion. Contraction at the beginning of a scratch would cause toeing in and the feet would thus be brought not only backward but laterally as well.

*M. piriformis, pars caudifemoralis*. This muscle originates from the anteroventral edge of the pygostyle and inserts on the posterolateral surface of the femur near its proximal end. It is thus capable of two functions, acting to pull the femur posteriorly and rotate it in that direction, or to depress the tail and pull it laterally. The caudifemoralis is better developed in the Brown Towhee. This is reflected not only in relative percentages (Table 3) but in the configuration of the muscle itself. In *erythrophthalmus* the caudifemoralis is more band-like and less spindle-shaped. In *fuscus* the anterior portion of the muscle is noticeably expanded (Figure 1).

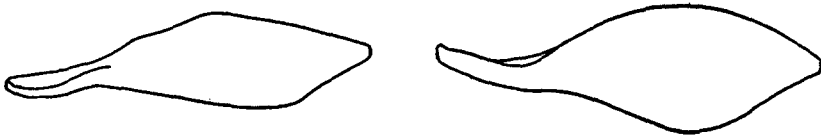


FIGURE 1. Outline drawings of *M. piriformis, pars caudifemoralis* of *Pipilo erythrophthalmus* (left) and of *P. fuscus* (right). Posterior is to the left.

As previously mentioned, the Brown Towhee forages with its tail either in line with the dorsum, or drooping below it, sometimes actually touching the ground. When running, the birds cock the tail slightly above the dorsal line. In this case, any downward pull exerted on the pygostyle by the caudifemoralis must be overbalanced by the levator muscles of the tail. However, as Fisher (1946: 666) has noted, the tendinous action of the caudifemoralis could swing the tail from side to side in a running bird, as each leg is brought forward. This would be advantageous as it would aid the bird in shifting its weight to the side of the recovering leg. It is difficult to observe lateral displacement of the tail in a running bird unless it runs directly toward or away from the observer. In the two cases in which I was directly in line with a running Brown Towhee, the lateral displacement of the tail was evident as the bird brought each leg forward. Other observations indicated no such movements of the tail, but none was satisfactory since the birds were observed from an angle. It may be that the increased development of the caudifemoralis in the Brown Towhee is an adaptation to running in this species.

Since the caudifemoralis is also capable of posterior rotation of the femur it is possible that it serves to eliminate a pigeon-toed gait. This would also be advantageous to a running bird. Fisher (*op. cit.*: 699) noted that the great development of the caudifemoralis in the Turkey Vulture (*Cathartes aura*) might account in part for the elimination of pigeon-toed gait in that species.

A noticeable peculiarity in the flight of Brown Towhees may also account for the increased development of the caudifemoralis. When a Brown Towhee makes a



short, relatively slow flight, it frequently jerks its tail downward as it flies; the Spotted Towhee does not do this. In flight the legs are folded against the body and with the femora thus held in a fixed position, contraction of the caudifemoralis is then directed against the pygostyle. Simultaneous contraction of the muscles on each side would jerk the tail downward, as lateral displacement of the tail would be cancelled out. If the femora were held in a fixed position, as in flying, they might be properly regarded as the origins of the caudifemoralis muscles during this activity. The great development of the anterior portions of these muscles in the Brown Towhee indicates that the main action is against the pygostyle, and is correlated with the Brown Towhee's habit of jerking the tail downward while in flight.

*M. iliotibialis; m. femoritibialis externus + medius.* These muscles are the most important extensors of the tibia. The *m. femoritibialis externus* and *medius*, although separate muscles, were removed and weighed as a unit, since the two are so tightly fused that it was impossible to separate them cleanly. Although the combined percentages of the iliotibialis and the two femoritibialis muscles are slightly larger in the Brown Towhee (19.42 versus 18.87), it will be seen (Table 3) that the iliotibialis is proportionally better developed in the Brown Towhee and the femoritibialis muscles better developed in the Spotted. Since the latter are the most powerful extensors of the shank, it is likely that extension of the shank is stronger in the Spotted Towhee. The iliotibialis is only accessory to the other muscles in this function. Since the iliotibialis tends to abduct the hind limb, this action may be stronger in the Brown Towhee.

*M. tibialis anticus.* This powerful flexor of the tarsus is better developed in the Spotted Towhee.

*M. extensor digitorum longus.* This muscle, extending the foretoes, is better developed in the Spotted Towhee. It was impossible for me to determine the action of the toes during hopping or scratching. If the foretoes are flexed during these activities, as seems likely, this muscle would aid in recovery. It also aids in flexion of the tarsus, another recovery action.

*M. flexor perforans et perforatus digiti III.* In both species this is the better developed of the two muscles flexing the third toe. In the Spotted Towhee the average weight of this muscle is 61.3 mg., and of *m. flexor perforatus digiti III*, 34.8 mg. The corresponding figures for the Brown Towhee are 86.1 and 42.3 mg. Further, *m. flex. perf. et perf. dig. III* exerts greater leverage, as it inserts on the second and third phalanges, whereas *m. flex. perf. dig. III* inserts on the first and second phalanges. Relative percentages of the latter muscle are nearly the same in *erythrophthalmus* and *fuscus* (1.35 and 1.38). Since *m. flex. perf. et perf. dig. III* is better developed in *fuscus*, it seems obvious that flexion of the third toe is more powerful in that species. Since this toe is the most important in cursorial locomotion, it is likely that the greater development of *m. flex. perf. et perf. dig. III* is associated with that activity.

*M. gastrocnemius.* This muscle is the most powerful extensor of the tarsus. It is better developed in *fuscus*, probably correlated with the greater dependence on running in that species.

*M. flexor hallucis longus.* This muscle, a powerful flexor of the hallux, is far better developed in the Spotted Towhee. Although *erythrophthalmus* is about 27 per cent smaller than *fuscus* as judged by fresh body weight (Table 5), *m. flex. hall. long.* actually weighs more in the Spotted Towhee. Wet weights of this muscle ranged from 135.2 to 153.8 mg. in the Spotted Towhee, averaging 142.8; they ranged from 111.6 to 134.4 in the Brown Towhee, averaging 124.2. The great development in

the Spotted Towhee is obviously correlated with the presence on the hind toe of *megalonyx* of an exceptionally long claw, longer than that of the Brown Towhee (Table 4).

#### DISCUSSION OF HIND LIMB STRUCTURE

The differences in the relative proportions of the femur and tarsus between *erythrophthalmus* and *fuscus* are undoubtedly genetic. The intramembral proportions of the hind limb of *erythrophthalmus* apparently represent an adaptation to locomotion by hopping. Since forward hopping is also involved in scratching, the proportions of the hind limb may likewise be adaptive in foraging.

Since all the differences between the muscles are quantitative, it is impossible to state whether they are genetic or merely represent hypertrophy through use. In two muscles, *m. caudifemoralis* and *m. flexor hallucis longus*, the differences may be genetic. The *caudifemoralis* is the only muscle examined that shows any difference in appearance in the two species; it is not only larger in *fuscus*, but is noticeably more expanded anteriorly than in *erythrophthalmus*. However, this expansion could be caused by increased use of the muscle to jerk the tail downward during flight. The *m. flexor hallucis longus* is not only proportionally larger but actually weighs more in the smaller species of towhee. Second, it is functionally associated with the hind claw, which is longer in the smaller species. Third, length of hind claw varies geographically in *erythrophthalmus*, and it seems likely that *m. flexor hallucis longus* would also vary geographically.

As regards the other muscles, it is impossible to determine whether or not the interspecific differences are genetic. It will be noted that the recovery muscles are better developed in *erythrophthalmus*, which has proportionally larger *m. femoritibialis externus + medius*, *m. tibialis anticus*, and *m. extensor digitorum longus*. Only one recovery muscle (*m. iliotibialis*) is better developed in *fuscus*, and it is subordinate in function to the *femoritibialis* muscles in extension of the tibia. Those muscles associated with power are better developed in *fuscus*, namely, *m. gastrocnemius* and *m. flexor perforans et perforatus digiti III*.

Well developed recovery muscles would be advantageous to a hopping bird such as *erythrophthalmus*. Strong extension of the tibia and flexion of the tarsus would provide fast recovery, during the split second that the bird is in the air, to a position that would absorb the shock of landing and allow the bird to hop again as soon as it had landed. In scratching, powerful extension of the tibia might allow for recovery from a longer scratch and greater displace-

ment of the body to the rear. The greater development of the m. iliobtibialis in *fuscus* may be associated with the tendency of that muscle to abduct the hind limb as well as extend the tarsus. This would be advantageous to a bird running over an uneven surface, as it would provide a bracing action against sudden lurches.

The better developed power muscles of *fuscus* seem to be correlated with the greater dependence on running in that species. In hopping, body weight is supported and moved by the muscles of both hind limbs, but in running the entire weight of the body must be borne and moved forward by one limb at a time. Greater development of power muscles would be advantageous in running as each leg would be able to function more efficiently in locomotion while carrying the whole weight of the body. Recovery muscles would not be so important to a running bird as one leg has a chance to recover while the other is delivering the forward thrust.

As regards the important m. flexor hallucis longus, powerful flexion of the large hind claw might play an important part in assisting the Spotted Towhee to shift its body to the rear when scratching. First, flexion of the hind claw against the surface might actually provide a backward pull, reinforcing the action of other muscles thrusting the body backward. Second, the powerfully flexed hind claw might act as a brace against which other muscles could act in the backward shift of the body. The hind claw would act in a fashion analogous to a spiked shoe, providing a fixed point against which other muscles could operate. The less vigorous scratching of the Brown Towhee might reflect the weaker development of the hind claw and m. flexor hallucis longus in that species, with consequent inability to shift the body as far to the rear at each scratch.

As mentioned previously (pages 135-136), two published descriptions of the scratching of the Spotted Towhee differ in certain details from the scratching observed by me of *P. e. megalonyx* at the Hastings Reservation. The differences in the scratching of *P. e. montanus* in Utah, as described by Woodbury (1933: 70), apparently do not result from a difference in hind claw length in that race, as the average difference in this character between seasonally comparable samples of *megalonyx* and *montanus* is not significant (Table 4), and the two races are similar in body weight (Table 5). Dawson's descriptions of scratching in the Spotted Towhee (1909: 164, 1923: 394) are apparently based on observations of *P. e. oregonus* (see pages 135-136). If this be true, as seems most likely, the use of the wings to assist scratching by that race may result from very weak development of the hind claw. Hind claw length in *oregonus* is significantly smaller

TABLE 4

HIND CLAW LENGTH OF MALE *P. erythrophthalmus*, *P. fuscus*, AND *P. aberti* (APRIL-JUNE)

<i>Subspecies</i>	<i>Number</i>	<i>Range</i>	<i>Mean</i> ± $\sigma_m$	$\sigma$
<i>erythrophthalmus</i>				
<i>megalonyx</i> (Hastings)	13	10.8-14.0	12.22±0.24	0.85
<i>montanus</i> (Utah, Colo.)	10	10.6-12.9	11.58±0.23	0.72
<i>oregonus</i> (B. C., Wash., Ore.)	10	8.5-10.1	9.51±0.18	0.58
<i>fuscus</i>				
<i>crissalis</i> (w. central Calif.)	10	9.6-10.8	10.06±0.13	0.42
<i>aberti</i>				
<i>dumeticolus</i> (Colo. Desert, Colo. R.)	10	9.6-11.7	10.56	

than in *megalonyx* (Table 4), although the latter is a slightly smaller bird (Table 5). The weakly developed hind claw of *oregonus* would probably function less efficiently in assisting the backward shift of the body during scratching. This would cause an overbalancing forward, and the flick of the wings at each scratch might well act to speed recovery to a balanced position. Further observations on scratching by *montanus* and *oregonus*, and investigation of the hind limb musculature of the two races, with special reference to *m. flexor hallucis longus*, would be worth-while.

Considering the interspecific differences between individual muscles, there can be no question that the better developed muscle is capable of more powerful action. If the quantitative differences between individual muscles do represent hypertrophy through use, rather than genetic adaptations, the situation is analogous to that in which athletes develop certain muscles for specific activities. Once developed, these special muscles are more powerful. The same may be true of the two species of towhees. It is possible that the nestlings start out with hind limb musculature that is the same in both species. Because of innate, genetically controlled behavior patterns, juvenal Spotted Towhees instinctively spend most of their time in sheltered areas, where they are forced to hop, and scratch for their food. Juvenal Brown Towhees spend a considerable amount of time foraging in the open, where they can gather food from the surface. For such

TABLE 5

WEIGHTS OF MALE *Pipilo erythrophthalmus* AND *P. fuscus*, MAY AND JUNE

	<i>Locality</i>	<i>Number</i>	<i>Range</i>	<i>Mean</i>
<i>erythrophthalmus</i>				
<i>megalonyx</i>	Hastings	13	34.0-41.2	38.45
<i>montanus</i>	Utah, Ariz.	6	34.3-39.7	38.00
<i>oregonus</i>	Oregon	4	40.2-43.3	41.80
<i>fuscus</i>				
<i>crissalis</i>	w. central Calif.	4	49.6-54.0	52.28

birds running is feasible and advantageous in escaping from danger. The different modes of life imposed on the young birds may well account for the relatively great development of certain muscles in one species, of other muscles in the other. The question of whether muscular differences are inherited or acquired will be settled only by the dissection of nestlings that have not used their hind limbs for either foraging or locomotion.

#### CONCLUSIONS

In considering posture and hind limb structure as related to both locomotion and foraging, it seems apparent that each species has achieved efficiency along certain lines at the expense of relatively inefficient performance in others. The intramembral proportions of the hind limb and the greater development of recovery muscles in the Spotted Towhee promote proficiency in hopping. This is a cumbersome method of locomotion, since at every hop a bird raises its weight through a vertical component without propelling the body forward. Energy is wasted on this vertical component, and also in absorbing the shock of landing. However, hopping is suited to the terrain in which the Spotted Towhee lives, as there are many twigs, fallen limbs, low-hanging branches, and other obstacles that would repeatedly trip up a running bird. Further, the Spotted Towhee spends nearly all its time under heavy vegetation, and rarely has to run to shelter. As noted previously, increased efficiency in hopping may promote efficiency in foraging by scratching, on which the Spotted Towhee depends almost entirely for finding food.

In *P. e. megalonyx*, at least, the great development of the hind claw and associated *m. flexor hallucis longus* appear to be adaptations that increase scratching efficiency. The more nearly erect posture of the Spotted Towhee, and its habit of cocking the tail above the dorsum, also make more vigorous scratching possible. However, the same posture is used when the birds gather food from the surface, and here efficiency is reduced, as the head is carried high, the forager cannot inspect the ground closely, and must bend forward to pick up material from the surface. Spotted Towhees, however, rarely gather food from the surface.

The greater development of power muscles in *fuscus* has promoted swift, efficient locomotion by running, feasible in the open terrain in which *fuscus* spends much of its time, and necessary as a means of reaching shelter. Since *fuscus* forages in a greater variety of terrain than does *erythrophthalmus*, we find that it does not rely mainly on either scratching for food or foraging at the surface, but

uses both methods frequently. Its foraging posture, in which the head is carried low, enables the birds to inspect the ground more closely, and they do not have to bend so far forward to pick up food. However, since they scratch from the same posture, we find that scratching is less efficient since the deep crouch reduces the ability to thrust the legs and feet backward as far or as powerfully as could be done if the posture were more nearly erect. Further, reduction of the hind claw and of *m. flexor hallucis longus* may reduce efficiency in scratching. This reduction may be of advantage in cursorial locomotion, however, as the hind toe is not used in running, and a long hind claw might strike obstructions as the foot is brought forward.

Each species appears to be well fitted for existence in the habitat which it instinctively selects. This has come about either through genetic adaptations in certain structures, through the relative development of certain structures in response to particular demands put on them, or through a combination of both.

#### TAXONOMIC IMPLICATIONS

Coues (1866: 89) first suggested that the "red-eyed" and "brown" towhees are not congeneric. The red-eyed towhees include *Pipilo ocai* and *P. erythrophthalmus*, and possibly the Green-tailed Towhee (*Chlorura chlorura*). The brown towhees include *Pipilo fuscus*, *P. aberti*, and *P. albicollis*. Davis (1951: 10, 100-101) suggested that the brown towhees might have closer affinities to the genus *Melospiza* than to the red-eyed towhees. The present study has indicated that there are definite differences between *Pipilo erythrophthalmus megalonyx* and *P. fuscus crissalis* in foraging behavior and in locomotion, and that these differences are reflected in certain aspects of hind limb osteology and myology. At first glance, this might be interpreted as biological evidence supporting the contention that the red-eyed and brown towhees are not congeneric. However, it is imperative that all species within the genus, as constituted at present, be considered, before any taxonomic significance be ascribed to the interspecific differences in foraging between *erythrophthalmus* and *fuscus*.

In surveying the brown towhees, it is apparent that *Pipilo aberti* may very well occupy a position intermediate between *fuscus* and *erythrophthalmus* as regards habitat preference, and perhaps as regards foraging behavior. Davis (*op. cit.*: 85-86) has reviewed much of the literature dealing with the habitat preferences of *aberti*. The published observations indicate that this species is very wary, and it

inhabits dense vegetation which it rarely leaves. This is suggestive of *erythrophthalmus* rather than of *fuscus*. Further, *aberti* has a somewhat longer hind claw than *Pipilo fuscus crissalis* (Table 4), although the body weights given by Davis (*op. cit.*: 7, 9) indicate that it is a somewhat smaller bird than *crissalis*. This is another approach toward *erythrophthalmus*, and it suggests that there may be a greater dependence on foraging by scratching in *aberti* than in *fuscus*. The apparent intermediacy of *aberti* between *erythrophthalmus* and *fuscus* is even more significant when it is considered that the historical evidence indicates that *aberti* was derived from the brown towhees of the Pacific Coast, of which *crissalis* is a member (*op. cit.*: 98-99). It seems obvious that biological evidence such as foraging behavior, and morphological evidence such as hind limb osteology and myology, cannot be adduced in support of any definitive treatment of the genus *Pipilo* until the range of variation of such kinds of evidence is established for the genus. Further studies are needed on the behavior and internal morphology of all species of *Pipilo*, especially of *aberti*, *albicollis*, and *ocai*, which are virtually unknown from all viewpoints except that of the museum taxonomist.

#### SUMMARY

The foraging behavior of the Spotted and Brown towhees is described. Spotted Towhees forage almost entirely under vegetation, by scratching in soil cover. Brown Towhees forage in both sheltered and open areas, gathering food either by scratching or by picking up exposed food items from the surface. Spotted Towhees scratch more vigorously than Brown Towhees, and the posture from which they forage is different.

At certain times of the year both species forage part of the time above the ground, obtaining insects and fruits.

Intraspecific intolerance of other foraging birds is much greater in the Brown Towhee.

The osteology and myology of the hind limbs of the two species were investigated. The greater dependence of the Spotted Towhee on foraging by scratching and locomotion by hopping is reflected in the intramembral proportions of the hind limb and in the greater development of certain recovery muscles. The lesser dependence of the Brown Towhee on foraging by scratching and the greater dependence on locomotion by running, are reflected in the better development of certain power muscles.

The methods of locomotion and foraging, and the structure of the

hind limb in each species, are well fitted for the habitat which each species instinctively selects.

## LITERATURE CITED

- BEAL, F. E. L. 1910. Birds of California in relation to the fruit industry. *Biol. Surv. Bull.* **34**: 1-96.
- COUES, E. 1866. List of the birds of Fort Whipple, Arizona. *Proc. Acad. Nat. Sci. Phila.*, 1866: 39-100.
- DAVIS, J. 1951. Distribution and variation of the brown towhees. *Univ. Calif. Publ. Zool.*, **52**: 1-120.
- DAWSON, W. L. 1923. The birds of California. Vol. 1. *Format De Luxe, Sunset Edition*. San Diego, Los Angeles, and San Francisco, South Moulton Company. xvii + 522 pp.
- DAWSON, W. L., and J. H. BOWLES. 1909. The birds of Washington. Vol. 1. Seattle, The Occidental Publishing Company. xv + 458 pp.
- FISHER, H. I. 1946. Adaptations and comparative anatomy of the locomotor apparatus of New World vultures. *Amer. Midl. Nat.*, **35**: 545-727.
- HOWELL, A. B. 1932. The saltatorial rodent *Dipodomys*: the functional and comparative anatomy of its muscular and osseous systems. *Proc. Amer. Acad. Arts and Sci.*, **67**: 377-536.
- LINSDALE, J. M. 1943. Work with vertebrate animals on the Hastings Natural History Reservation. *Amer. Midl. Nat.*, **30**: 254-267.
- LINSDALE, J. M. 1955. Check list of ferns and seed plants of Frances Simes Hastings Natural History Reservation. *Leaflets West. Bot.*, **7**: 201-218.
- STALLCUP, W. B. 1954. Myology and serology of the avian family Fringillidae, a taxonomic study. *Univ. Kansas Publ., Mus. Nat. Hist.*, **8**: 157-211.
- WOODBURY, A. M. 1933. The scratching of the Spurred Towhee. *Condor*, **35**: 70.
- Hastings Reservation, University of California, Carmel Valley, California, March 15, 1956.*