

ECOLOGICAL INTERACTIONS OF THE CHESTNUT-BACKED CHICKADEE FOLLOWING A RANGE EXTENSION

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Within the past 20 years, the status of the Chestnut-backed Chickadee (*Parus rufescens*) has changed from that of a rare vagrant to a common resident in the East Bay region (Alameda and Contra Costa counties) of California (Dixon, 1954 and 1960). This species also appears to be extending its range along the western side of the Sierra Nevada, where it has been reported as far south as Mariposa County, California (Curl, 1952; Mans and Chase, 1963). As this change in breeding status proceeds, *rufescens* comes into contact with potential competitors. Information on the nature of the ecological interactions of *rufescens* with these species, following contact, is an important means of evaluating hypotheses relating to the existence of open ecological niches.

In 1961 and 1962, I was able to supplement the previous investigations of Dixon (1954, 1960) on the ecological interactions between *rufescens* and the Plain Titmouse (*Parus inornatus*) in the East Bay region. In addition, data were gathered on the foraging behavior of other small insectivorous birds which occupy the same habitats as *rufescens*.

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METHODS

Most of my observations were made between March 24, 1961, and November 9, 1962, in Las Trampas Canyon, one and one-half miles northeast of Moraga, Contra Costa County, California. *Parus rufescens* was first observed at this locality in the autumn of 1956 (Campbell, 1957). The numbers and spatial relationships of *rufescens* and *inornatus* were determined along a trail 6000 feet long. The trail census technique developed by Kendeigh (1956) was employed in the course of ten early morning trips to the area in the spring of 1961, and during seven trips in 1962. Additional information was obtained by noting the position of nests and plotting the movements of individuals on a base map of the area during other trips over the trail. Six individuals of *inornatus* and four of *rufescens* were marked with color bands and followed for various periods of time.

A standard observation technique similar to that of Hartley (1953) and Gibb (1954) was employed in making a quantitative description of the foraging beat. Between March 1 and August 30, in both 1961 and 1962, 32 morning trips, totalling 91½ hours, were made over the trail. Ten trips, totalling 21½ hours of observation, were made at other seasons of the year. On each trip, I walked slowly along the trail, recording the following information for each individual when it was first encountered: (1) the location of the bird on a vegetation base map; (2) the plant species or nature of the sub-

strate and its relative size; and (3) the proximity of the bird to various structural units of the habitat, such as the canopy. Only actively foraging individuals were considered. A special effort was made to observe both silent and calling birds and to avoid recording the same individual more than once during each trip over the trail. By gathering data in this manner, the foraging beat of species can be compared because all observations were taken from the same universe (the trail). These comparisons would be biased if the two species exhibited differential conspicuousness, for the more conspicuous species would be represented by observations from a larger, and perhaps more diverse, universe. In 1961, I estimated my distance from the bird in the course of each standard observation. The mean distance at which foraging determinations were made was 45 feet (15 to 120 feet) for *rufescens* and 50 feet (15 to 120 feet) for *inornatus*. This minor difference in mean sampling distance probably does not constitute a serious error.

Variations in the frequency of various foraging maneuvers were quantitatively described by using an observation technique similar to that of MacArthur (1958). During each standard observation, whenever possible, all foraging activities were described in detail over an interval timed with a stop watch. The observation was stopped when the bird moved to another foraging zone or when my vision was obscured for more than two seconds. The length of an observation was influenced by the foliage density in different foraging zones, the distance between the observer and the bird, and the foraging tempo of the bird. In the canopy zone of coast live oaks (*Quercus agrifolia*), the mean length of observation was 23.3 seconds for *rufescens* and 27.7 seconds for *inornatus*. This slight difference is probably a result of relative differences in the foraging tempo of the two species (see beyond). Therefore, these data, presented as activity per 1000 seconds of observation, are comparable because the sampling universe with respect to the ease of observing foraging behavior was nearly the same for both species.

Standard observations were made on other small insectivorous birds whenever they were encountered. Additional observations on the flock size, nest site, and general behavior of *inornatus* and *rufescens* were made in Las Trampas Canyon and at several other localities in central California.

SPATIAL RELATIONSHIPS

Habitat.—The habitat requirements of the two species are often distinct but overlap in certain regions. The range of *inornatus* extends farther into the dry interior, where it occupies foothill woodland, piñon-juniper woodland, and mixed evergreen forest (names of major plant communities follow the classification of Munz and Keck, 1959). For the most part, the range of *rufescens* coincides with the distribution of low elevation, coastal mesic coniferous forests. However, at several localities within the "parental" range of *rufescens* (see Grinnell and Miller, 1944) the chickadees have been observed to spend a considerable amount of time foraging outside the conifer stands in adjacent clumps of mixed evergreen forest. Furthermore, there are resident populations of chickadees in Las Trampas Canyon and at the Hastings Reservation, Monterey County, California, areas where the nearest stands of conifers (with the exception of scattered small clumps of ornamentals) are over two miles away.

The vegetation pattern of Las Trampas Canyon (fig. 1) is very complex as a result of conditions prevailing on different slope exposures and past human disturbance. In relatively undisturbed areas, the xeric slopes are covered with a woodland of coast live oak which, as conditions become more mesic, grades into a mixed evergreen forest consisting of varying proportions of madrone (*Arbutus Menziesii*), California bay (*Umbellularia californica*), big-leaf maple (*Acer macrophyllum*), and coast live oak. The understory of this forest is variable, but in most places it consists of a dense stratum

of such shrubs as snowberry (*Symphoricarpos*), poison oak (*Rhus diversiloba*), blackberry (*Rubus*), and currant (*Ribes*). Disturbed areas are covered with soft chaparral,

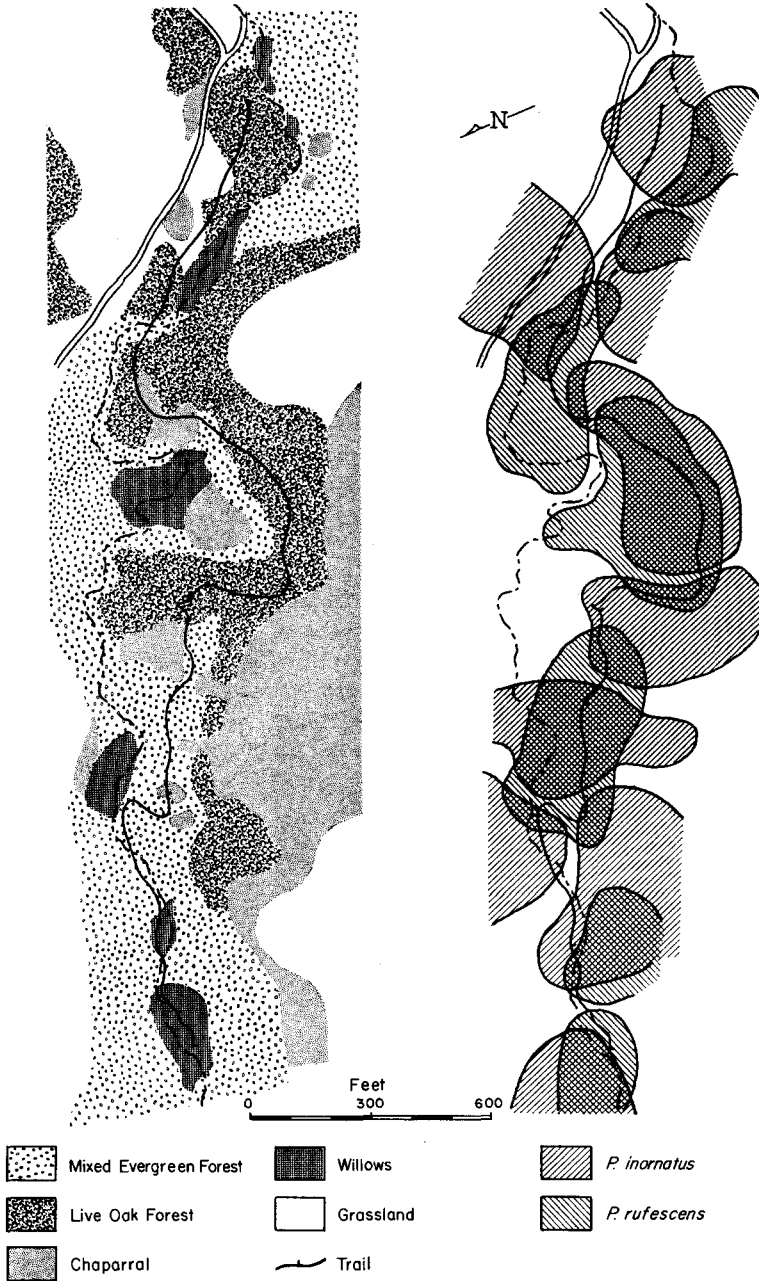


Fig. 1. Map showing the principal vegetation types (left) and core areas of *Parus rufescens* and *P. inornatus* (right) on a portion of the study area in Las Trampas Canyon. "Tick" marks on the trail represent the position of stakes, placed at 300-foot intervals. The boundaries of core areas represent the situation during April and May, 1961.

dominated by coyote brush (*Baccharis pilularis*) on dry sites, and where there are openings in the forest canopy, by a dense tangle of the same shrubs which form the forest understory. In basins along the streamcourse, where there is periodic flooding, willows (*Salix*) with an understory of soft chaparral form a distinct community.

In this canyon, the habitats of *rufescens* and *inornatus* overlap broadly (fig. 1). There is a tendency, however, for *rufescens* to restrict its activities to the mesic vegetation along the stream, while *inornatus* ranges out farther into drier situations.

Territoriality.—The boundaries drawn in figure 1 circumscribe areas over which pairs were followed on repeated occasions, and therefore delimit core areas, the areas in which the bulk of the pair's activities were centered, rather than territories. Intra-specific territoriality in *inornatus* has been described by Dixon (1956). It has been inferred that territoriality is weakly developed in *rufescens* (Dixon, 1954) on the basis of the close proximity of nests in regions of optimal habitat. In Las Trampas Canyon, I have never observed extensive trespassing by chickadees onto the core areas of adjacent pairs during the breeding season (which extends from the middle of March to the middle of June on the basis of my observations). Boundary disputes involving two pairs have been observed on three occasions in late April and early May. During such encounters, the individuals mill around within a few feet of one another; the apparent defender supplants the trespassing pair repeatedly and occasionally chases them for a short distance. A rapid series of *dee dee dee deet* calls, given in a harsh, rasping manner has been heard only in the course of these encounters. I observed one dispute for 15 minutes before the antagonists began to drift apart. On two occasions, an additional adult chickadee was tolerated on the territory while the pair was engaged in scolding a stuffed Screech Owl (*Otus asio*), placed within 15 feet of their nest.

Dixon (1954) has reported that *inornatus* and *rufescens* maintain mutually exclusive territories. In the present study, extensive overlap was found in the core areas of these two species (fig. 1). Even in the vicinity of the nest, these species tolerate the presence of one another. On one occasion, both species had nests, containing young, which were only 15 feet apart and in the same tree. These pairs were observed feeding nestlings on six different days between May 4 and 17, 1961. No interspecific aggression was observed, although the adults often passed within five feet of one another on their feeding trips. At these nests, and others, adults of both species, with dependent young, were seen foraging simultaneously in adjacent trees on the periphery of their territories. In Strawberry Canyon, one of Dixon's study areas (1954, 1960), G. E. Chaniot (MS) observed single pairs of titmice and chickadees feeding young in nests which were 60 feet apart on April 20, 1963. When the *inornatus* began to scold students near their nest, the *rufescens* were tolerated when they flew over to join in.

In the winter, members of both species often associate in mixed foraging flocks which contain a variable array of additional species. These winter flocks are loosely organized, but the two parids have been observed to move in the same direction, over distances of up to 200 yards, in a 50-minute period. Under such circumstances, the two species are often within 15 feet of one another. Aggressive encounters are rare, but occasionally an *inornatus* will supplant a *rufescens* from the foraging perch of the latter.

Foraging beat.—For purposes of analysis, I have divided the environment into arbitrary structural subunits. The canopy is the zone in which the foliage-bearing twigs are concentrated, while the subcanopy is characterized by limbs and larger branches, with very sparse foliage. These two zones grade into one another through the canopy interior, the region just inside the canopy where barren branches and twigs afford perches from which a large sector of adjacent foliage can be searched. In actual prac-

TABLE 1
FORAGING STATIONS, MARCH 1 TO AUGUST 31, 1961 AND 1962
Per cent of total observations

	<i>Parus rufescens</i> 115 observations				<i>Parus inornatus</i> 122* observations			
	Canopy	Canopy interior	Subcanopy	Total	Canopy	Canopy interior	Subcanopy	Total
Live oak	13.9	0.9	7.8	22.7	24.6	13.9	29.5	68.0
Madrone	15.6	3.5	4.3	23.4	1.6	0.8	2.5	4.9
Big-leaf maple	9.6	4.3	13.9	0.8	2.5	3.3
California bay	18.3	0.9	7.0	26.2	2.5	3.3	3.3	9.1
Willows	5.2	0.9	1.7	7.8	3.3	3.3
Other	4.3	1.7	6.0	7.4	1.6	2.5	11.5
Total	66.9	6.2	26.8	100	40.2	19.6	40.3	100

* Does not include 5 observations of *P. inornatus* foraging on the ground.

tice, these foraging stations can usually be easily recognized, particularly in the larger trees.

While there are few absolute differences in the foraging beats of these two species, there are consistent relative differences in their use of certain foraging stations (table 1). *Parus inornatus* concentrates its activity in live oaks while *P. rufescens* exhibits a more diverse choice of tree species. Dixon (1954), working in another area and using a different observation technique, found the opposite trend, with *rufescens* utilizing live oaks with greater frequency than *inornatus*. Chickadees are observed most often in the foliage-bearing zones of the tree, while titmice utilize the ground and subcanopy more frequently. This distinction is reflected by differences in the substrates where the two species find food, *rufescens* being primarily a gleaner of foliage and related substrates, while *inornatus* most often attacks woody surfaces (table 2).

TABLE 2
SUBSTRATES WHERE FOOD WAS OBTAINED, MARCH 1 TO AUGUST 31, 1961 AND 1962

	<i>Parus rufescens</i> 258 maneuvers	<i>Parus inornatus</i> 105 maneuvers
	Per cent of total foraging maneuvers	
Foliage	56.6	29.5
Flowers and buds	19.4	0.9
Fruits and seeds	1.9	9.5
Twigs and branches	14.3	42.9
Boles and limbs	7.4	13.3
Ground litter	0.4	3.8

These differences in foraging beat are maintained primarily because the species concentrate their activities in different portions of the vegetation mosaic along the trail. When the locations of all standard observations are plotted on a single map, the observations of *inornatus* tend to be grouped in stands of live oak whereas those of *rufescens* occur most frequently in the mixed evergreen forest. Nevertheless, there is a significant degree of overlap in their use of certain stands (fig. 1 and table 3).

In areas where the forest composition is relatively complex, individuals of both species were followed for prolonged periods. The length of time spent in each tree and each foraging zone was timed with a stop watch, and notes were made of the tendency of the bird to enter or avoid an adjacent tree or foraging zone. Chickadees tend to

TABLE 3
FORAGING HABITATS, MARCH 1 TO AUGUST 31, 1961 AND 1962

	<i>Parus rufescens</i> 176 observations	<i>Parus inornatus</i> 183 observations
	Per cent of total observations	
Mixed evergreen forest	72.2	33.9
Live oak forest	14.8	54.6
Chaparral	3.3	7.1
Willows	9.7	4.4

remain in the canopy by moving in a generally spiral course over the tree's periphery. Along one portion of the trail, there is an extensive live oak forest with a well developed understory of California bay, madrone, and big-leaf maple. At this location, there was a consistent tendency for *inornatus* to remain high in the live oaks while *rufescens* was always observed foraging in the understory. Where the species composition of the forest stratum was mixed, neither species exhibited an obvious avoidance to entering an adjacent tree of a particular species. Over most of the trail, the distribution of foraging height was similar for both species, although *inornatus* was observed on the ground more frequently.

FORAGING BEHAVIOR

The foraging repertoires of *inornatus* and *rufescens* are very similar. They share the ability to hang beneath twigs and from corrugations in the bark of large limbs. Aerial foraging maneuvers, such as hovering or chasing flying insects, were performed, but both species appear to be rather clumsy at them in comparison with various sylviaids, warblers, and vireos I have observed. Both *inornatus* and *rufescens* carry some prey in their bills to branches where they hold the item against the perch with the foot while dividing the prey into smaller portions with the bill. Individuals have been observed to make up to six consecutive trips, from distances of 10 feet or more, to reuse the same part of a particular branch as an "anvil." Both species hammer items which are held in the foot, but *inornatus* often exerts an additional prying action in dividing the prey, while *rufescens* regularly pulls the prey apart. Food items which require a great amount of hammering, prying or pulling are most often attacked in the autumn and winter.

TABLE 4
FORAGING BEHAVIOR, MARCH 1 TO AUGUST 31, 1961 AND 1962

	<i>Parus rufescens</i>	<i>Parus inornatus</i>
Number of standard observations	85	85
Seconds of observation	2008	2451
	Frequency of foraging maneuvers per 1000 secs. of observation	
Seconds hanging	119.0	35.1
Gleaning	124.5	40.4
Bouts of hammering	2.0	3.7
Aerial attacks	4.0	2.8
Foraging rate	130.5	46.9
Rate of visible captures	6.5	3.3

Foraging maneuvers are not employed with the same frequency by these parids. Chickadees spend more time hanging from beneath their perches and titmice devote a greater proportion of their foraging maneuvers to hammering (table 4). *Parus rufescens*

forages at over twice the rate of *P. inornatus*. Since it was not always possible to distinguish probing from the actual capture of small prey, this difference in foraging rate was checked, and substantiated, by comparing the rates at which visible prey items were obtained.

These major differences in foraging rate would suggest that *rufescens* feeds upon smaller prey items. Dixon (1960) has reported upon a single specimen of *rufescens* whose stomach contained approximately 100 small aphids. I collected two *rufescens* on April 27, 1962, within one mile of Dixon's collecting locality. Their stomachs contained the remains of 7 geometrid larvae, 4 noctuid larvae, several cicadellids, 1 aphid nymph, and 1 lycosid spider. Head-to-tail length of the intact prey varied from 1 to 21 mm., the mean being 12.6 mm. (n=12). The intact prey (n=81) taken from several specimens of *inornatus* collected in this same area in the spring of 1959, ranged from 1 to 26 mm. with a mean of 6.0 mm. (Dixon, pers. comm.). Thus these two parids are apparently capable of capturing and devouring arthropods over a broadly overlapping range of sizes. More data must be obtained before anything definite can be said about the relationship between prey size and foraging rate, because the two species may select different sized items from the same prey universe.

Throughout July, different titmice fed regularly on the achenes of the thistle, *Silybum marianum*, at three widely spaced locations along the trail. Individuals repeatedly visited the thistles, pulled out the achenes, and returned with them to the subcanopy of adjacent trees, where the fruits were hammered for about 30 seconds prior to being eaten. Although chickadees were often seen in the vicinity of these thistles, none was observed to utilize this resource.

COMPARISONS WITH SYMPATRIC SPECIES HAVING SIMILAR FORAGING BEHAVIOR

Some of the passerine species occurring in Las Trampas Canyon have foraging behaviors which resemble those of *inornatus* and *rufescens* to varying degrees. I have made standard observations on these species, but unfortunately the data are not sufficient to warrant a quantitative comparison. It is possible, however, to discuss some of the major foraging adaptations of these species.

The House Wren (*Troglodytes aedon*), Bewick Wren (*Thryomanes bewickii*), and Wrentit (*Chamaea fasciata*) concentrate their foraging activities in shrubs, brush piles, and on the ground, although they occasionally ascend into the trees where the species of *Parus* normally forage. The Wrentit is capable of performing most of the foraging maneuvers, such as hammering prey held in the foot and hanging beneath the perch, which are characteristic of the parid repertoire. The wrens obtain most of their food by simple gleaning and by probing crevices with their long, slender beaks.

The Hutton Vireo (*Vireo huttoni*), Warbling Vireo (*Vireo gilvus*), and Orange-crowned Warbler (*Vermivora celata*) have foraging beats similar to those of *Parus* but differ in their foraging technique. I have never observed these species hammer at captured prey, although vireos occasionally pull apart an object which is held against the perch with the foot. In addition to gleaning, the vireos and warblers often rush suddenly to capture arthropods at distances of over a foot from the hunting perch. These species also engage in aerial foraging maneuvers more frequently than do *inornatus* and *rufescens*. The Western Flycatcher (*Empidonax difficilis*) and the Western Wood Pewee (*Contopus sordidulus*) and, during the winter, the Ruby-crowned Kinglet (*Regulus calendula*) differ from *Parus* in their frequent use of aerial maneuvers to capture prey. The development of a foraging repertoire, which is rich in rushing and aerial components, suggests that these species are better adapted for capturing more active prey than is *Parus*.

Of all the species which share the same habitats with *Parus* in the East Bay region, the Common Bushtit (*Psaltriparus minimus*) is the only species besides *inornatus* which resembles *rufescens* closely in both the foraging beat and foraging repertoire. The bushtit, which is significantly smaller than *rufescens*, forages from June through March in highly organized intra-specific flocks (in Las Trampas Canyon, these flocks contained between 7 and 26 individuals). Throughout the year, individual bushtits move more rapidly over the foraging substrates and search for prey less thoroughly than do chickadees. Another difference is that the bushtit does not construct its nest within tree cavities as do *rufescens* and *inornatus*.

DISCUSSION

Dixon (1960) has shown that the increase in the population of *rufescens*, during the 10 years following their arrival on the Berkeley campus, has not resulted in a concomitant decrease in the population of *inornatus*. He has concluded that the two species can persist sympatrically because interspecific territoriality will prevent *rufescens* from invading the optimal habitat of the dominant *inornatus*. My observation of extensive territorial overlap suggests that niche differences must be sufficient to permit these species to occupy the same ground.

The size differences between *rufescens* and *inornatus* are of a greater magnitude than those reported for some other North American species of *Parus* which share the same habitats (Dixon, 1961). The morphological distinctiveness of the two species is further recognized by their placement in different subgenera, a distinction which is considered by some authors (Hamilton, 1959; Dixon, 1961) to denote that the forms represent different adaptive types.

Since *rufescens* has been able to invade relatively undisturbed habitats in the East Bay region without exerting a noticeable influence on the populations of resident birds with similar ecology, there is an indication that an open "chickadee" niche existed in this area prior to the range extension. In this instance, niche is defined as that set of environmental conditions or states under which a species can exist for a prolonged period (cf. Hutchinson, 1957; MacFadyen, 1957). The resources presently utilized by *rufescens* could have been shared by several resident species, but the competitive situation in the East Bay region was not such that major changes in the avifauna were necessary to accommodate a new species.

Prior to its range extension, *rufescens* already occurred sympatrically with *inornatus* in the central coast ranges of California (Grinnell and Miller, 1944). At the Jordan Ranch, near Laurel, in the Santa Cruz Mountains, I have observed the two species foraging within 150 yards of one another. In addition, all of the other species of insectivorous birds with which *rufescens* could compete in the East Bay region, are also sympatric with *rufescens* within its parental range. Therefore, we may postulate that the avifauna had already evolved the competitive adjustments necessary to accommodate a species of chickadee before *rufescens* invaded the East Bay region. It is also possible that the recent change in the breeding status of *rufescens* in this region may be a secondary invasion of an area which it formerly occupied. The discussions of Grinnell (1904) and Dixon (1954, 1961) are pertinent to an evaluation of this possibility. In either case, the existence of this unfilled niche is best interpreted as resulting from the local absence of a species from an avifauna which was already adapted or organized for its presence.

Parus inornatus and *P. rufescens* have similar foraging repertoires and utilize a similar range of feeding stations and prey sizes. There are differences, however, in the frequency with which they engage in these shared activities. These relative differences

are apparently maintained by structural modifications which permit each species to exploit the same situations, but with varying efficiencies. The more massive beak and heavier body of *inornatus* (for measurements, see Dixon, 1961) are adaptations for extracting food which is lodged in bark or otherwise surrounded by a protective covering. This advantage is reflected by the greater frequency with which *inornatus* attacks seeds, fruits, and surfaces covered with bark, and by its tendency to engage in more frequent bouts of hammering. The smaller size of *rufescens* permits it to search the foliage surrounding the terminal twigs, where it can hang beneath perches (including leaves) which offer little support. Differences in the foraging beat of the two species are correlated with these different capabilities, *inornatus* occurring most frequently in the subcanopy where woody substrates abound, and *rufescens* in the canopy. Neither species avoids entering the optimal foraging stations of the other, that is, the distinctiveness of the foraging beats is not maintained by a stereotyped behavioral response to vegetation structure. The most reasonable explanation for the observed differences in habitat utilization is that each species tends to remain longer at those stations where it can obtain food most efficiently. Hinde (1959) discusses how learning may be involved in such a behavioral response. By having the foraging behavior organized in this manner, the species can occupy niches which are sufficiently distinct to permit coexistence and yet remain versatile enough to exploit a wide range of the available resources.

SUMMARY

The Chestnut-backed Chickadee (*Parus rufescens*) has extended its range in different parts of California in the past twenty years. In Las Trampas Canyon, a locality in the East San Francisco Bay region where chickadees were first reported in 1956, the behavior of *rufescens* was compared with that of other species, especially the Plain Titmouse (*Parus inornatus*), which are possible competitors of the chickadee.

The titmice and chickadees do not presently maintain mutually exclusive territories, as was suggested in previous studies, and individuals of either species seemed tolerant of the presence of their congeners.

A quantitative method was developed to compare the foraging beats and foraging repertoires of *inornatus* and *rufescens*. These species exploit the same range of situations and are capable of performing many of the same foraging maneuvers. They differ, apparently as a result of their existing structural differences, in the frequency with which they engage in these shared activities. Niche separation is maintained by differences in the efficiency with which portions of a common range of situations can be exploited.

Since there have been no noticeable changes in the populations of birds sharing the same habitats with *rufescens* in the East Bay region, it is suggested that prior to the range extension, there was an open "chickadee" niche in this region. The existence of this unfilled niche is interpreted as resulting from the local absence of *rufescens* from an avifauna which was already adapted to accommodate this species.

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