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# SOME ECOLOGICAL RELATIONS OF CHICKADEES AND TITMICE IN CENTRAL CALIFORNIA

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Within recent years the Chestnut-backed Chickadee (*Parus rufescens*) has extended its range interiorward in the San Francisco Bay region of central California and has come to occupy areas in which the Plain Titmouse (*Parus inornatus*) previously was the sole representative of the genus *Parus*. This case is of special interest since studies of the Plain Titmouse were made at one locality prior to the influx of the chickadees (Dixon, 1949). Some of the interrelations of the two species will be considered following a review of the changes in the distribution of the chickadee.

The geographic range of *Parus rufescens barlowi*, the form concerned, was described by Grinnell and Miller (1944:304) as "Essentially, Santa Cruz faunal area; that is, narrow central coast belt south from Golden Gate and San Francisco Bay as far as Cambria, San Luis Obispo County. Eastward margin of range scarcely reaches western shore of south arm of San Francisco Bay near San Mateo and Palo Alto; in later years seen regularly in and about San Jose, where they breed (D. McLean, MS)." At the time of their writing, this chickadee was considered a vagrant in the "East Bay district." Subsequently, stocks of *Parus rufescens* became established as permanent residents in Oakland, Berkeley, and adjacent localities.

The early pattern of occurrence of this species in East Bay localities is indicated by the following published records.

Several seen at Hayward, Alameda County, December 8, 1885; one taken at Dry Creek, August 1, 1896 (Emerson, 1900).

Lone individual at Berkeley, Alameda County, "one Thanksgiving time" during the latter 1890's (Miller, 1950:34).

One individual at Berkeley, October 13 to 25, 1913 (Grinnell, 1914).

Alvarado, Alameda County, was included by Grinnell (1904:380) in a list of localities from which specimens had been examined. He pointed out (p. 374) that all records from that county were for the autumn months and suggested that they represented wandering juveniles.

Grinnell and Wythe (1927:144) listed the status of this chickadee in the area of our concern as "a rare straggler, once at Berkeley and a few times at Hayward."

A different status was ascribed to this species by Cohen (1895:157) in his report on the birds of Alameda County. He stated that "The California Chickadee prefers to breed in the most unsettled portions of the county, and is not a common bird." Cohen cited no locality records.

Further records of the occurrence of this chickadee in the area east of San Francisco Bay prior to 1938 are not known to me. On April 17, 1938, the late Henry W. Carriger observed a pair of chickadees nest-prospecting along a creek near Sunol, Alameda County. He took a set of five fresh eggs near Niles, Alameda County, on April 12, 1940, and noted nesting in the vicinity of Sunol in 1940, 1942, and 1946. I am indebted to Leroy Jensen for making Mr. Carriger's unpublished observations available.

Subsequently Chestnut-backed Chickadees spread to the northwestward. They were observed in Redwood Park, Alameda County, on July 11, 1943, according to Elwonger (1943:33). By the spring of 1945 chickadees were nesting along Wildcat Creek in Tilden Park, Contra Costa County (A. H. Miller, MS). Juvenal and adult specimens characteristic of *P. r. barlowi* were obtained by J. T. Marshall, Jr., along San Leandro Creek, Alameda County, on June 29, 1946. Marshall (MS) also saw one chickadee on the University of California campus in Berkeley on July 1, 1946. A few other observations were made on the west slope of the Berkeley Hills in subsequent years, but I know of no evidence of the nesting of chickadees in the vicinity of Berkeley prior to 1950. On May 6 of that year, Harrison Ryker and I located a nest in a California laurel (*Umbellularia*) along Strawberry Creek on the lower part of the campus of the University of California. The parents were bringing food to the nestlings. In each succeeding year, reports of various observers indicated a wider distribution of Chestnut-backed Chickadees in East Bay cities during the breeding season.

The Berkeley area, lying directly opposite the Golden Gate, long has been known as an "island" of conditions approaching those of the Transition Life-zone which is set in warmer and more arid surroundings. Grinnell (1914:29) commented upon "a marked Transition or even Boreal infusion noticeable particularly in the summer-visitant category of birds." Commenting on the occurrence of *Parus rufescens* in Berkeley, Grinnell (*op. cit.*:39) remarked as follows: "Judging from the climatic peculiarities of the immediate vicinity of Berkeley, it would appear consistent with our knowledge of geographical distribution to expect that, with the aging of our planted groves of conifers, chickadees will find conditions favorable to the establishment of permanent colonies, as with the Olive-sided Flycatcher and other boreal, and at the same time, aboreal (sic), species."

Prior to the settlement of California by the white man, vegetational discontinuities in the Santa Clara Valley possibly presented a barrier to the eastward dispersal of these tree-dwelling birds. Broek (1932:29) cited accounts of Spanish explorers of the 18th century who found that much of the floor of the valley was covered by a "park-like, grass-oak association." The spread of the chickadee into the vicinity of San Jose, as mentioned, may have been facilitated by plantings of orchards and of shade trees. The observation of Pitelka (1941) of a pair of *P. r. neglectus* in a grove at Bodega Bay, California, three-fourths of a mile from the nearest woods, suggests that continuous arboreal cover is not necessary for dispersal of this species of chickadee. Individuals may have crossed the Santa Clara Valley occasionally under primitive conditions as well as in later years. The expansion of fruit orchards in the valley, which continued during the 1920's (Broek, 1932:109), may have permitted greater numbers of chickadees to cross the Santa Clara Valley to the Diablo Range to the east. Well-wooded canyons, such as those lying alongside Sunol Ridge, provided suitable breeding habitat for this species. The expanding population of chickadees could have spread to the northwest by way of shaded slopes or riparian timber. Had a population existed there 50 or 60 years ago, as suggested by Cohen (1895) and Emerson (1900), the dispersal into the Berkeley area doubtless would have occurred much earlier than it did.

The East Bay district into which *Parus rufescens* spread is characterized by the presence of summer sea fogs (Byers, 1930). The fogs (actually a stratus cloud layer) blanket this area to varying degrees during the forenoon and effect a reduction in summer insolation. The present eastern limit of the distribution of the chickadees coincides closely with the limits of summer sea fog distribution as mapped by Byers, a relationship pointing again to a similarity in the climates of the Berkeley area and the humid coast district.

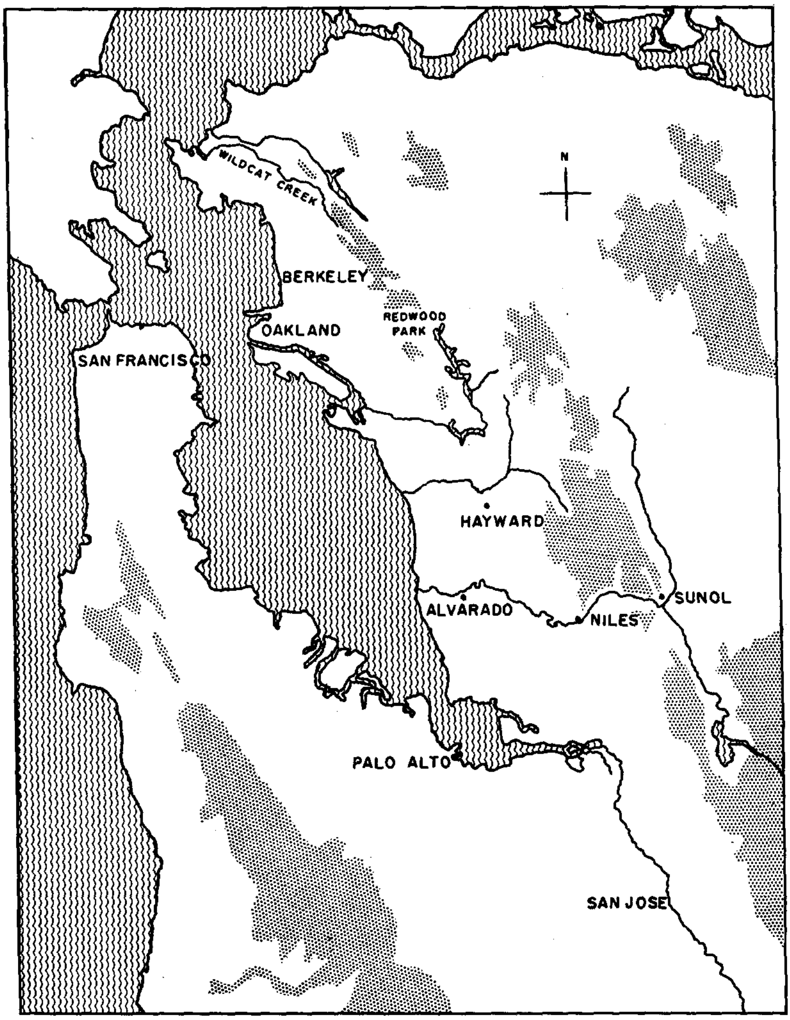

Fig. 1. Map of the San Francisco Bay region showing localities mentioned in the discussion of Chestnut-backed Chickadees. Stippling indicates areas over 1000 feet in elevation.

## THE QUESTION OF COMPETITION BETWEEN CHESTNUT-BACKED CHICKADEE AND PLAIN TITMOUSE

The entry of the Chestnut-backed Chickadee into the bird fauna of the Berkeley Hills is of interest with respect to possible interactions with its congener, the Plain Titmouse. The ranges of these two nonmigratory species are distinct for the most part, the titmouse being characteristic of drier interior localities (see Grinnell and Wythe, 1927: 143-144). Grinnell (1904:375) noted habitat segregation of the two species at Palo Alto, the chickadees frequenting planted groves of conifers and the titmice being found principally in live oak groves. He suggested that further expansion of the range of

*Parus rufescens* interiorward might be halted by food relations with other small birds, such as Wren-tits (*Chamaea fasciata*) or the Plain Titmouse.

More recently, Lack (1944) and Snow (1949) have stressed the importance of adjustments in behavior, especially feeding, if two similar forms are to coexist in the same area. Coöccupancy of an area by two species of similar ecology might provide tensions in two spheres of activity, namely feeding relations and spatial needs, especially as related to reproduction.

Table 1

Food-taking Motions of Chickadees and Titmice
November-December, 1951

*Parus rufescens*

| | Trunk | Branch | Twigs | Foliage | Fruit | Total | Per cent |
|---|---|---|---|---|---|---|---|
| Eucalyptus | 11 | 82 | 7 | 14 | 82 | 196 | 33.3 |
| Laurel | 8 | 68 | 35 | 80 | .... | 191 | 32.5 |
| Live oak | 1 | .... | 10 | 65 | .... | 76 | 12.9 |
| Other trees | 10 | 8 | 58 | 36 | 13 | 125 | 21.9 |
| Ground | .... | .... | .... | .... | .... | 0 | 0 |
| Total | 30 | 158 | 110 | 195 | 95 | 588 | 100 |
| Per cent | 5.1 | 26.9 | 18.7 | 33.1 | 16.2 | 100 | |

*Parus inornatus*

| | Trunk | Branch | Twigs | Foliage | Fruit | Total | Per cent |
|---|---|---|---|---|---|---|---|
| Eucalyptus | 14 | 17 | 17 | 2 | ... | 50 | 13.3 |
| Laurel | 7 | 3 | 5 | .... | .... | 15 | 3.9 |
| Live oak | 9 | 6 | 23 | 159 | 7 | 204 | 54.2 |
| Other trees | 5 | 11 | 14 | 20 | .... | 50 | 13.3 |
| Ground | .... | .... | .... | .... | 57 | 57 | 15.3 |
| Total | 35 | 37 | 59 | 181 | 64 | 376 | 100 |
| Per cent | 9.3 | 9.8 | 15.7 | 48.2 | 17.0 | 100 | |

*Possible overlap in foraging.*—Although the two species share acrobatic capabilities in food seeking in arboreal situations, the Plain Titmouse differs from the chickadee in size and in bill structure. The bill of the titmouse is more massive (depth of bill at nostril averages 4.8 mm. in 10 males of *P. i. inornatus*; in 10 males of *P. rufescens* it averages 3.5 mm.). This morphologic difference is reflected in the ability of the titmice to break acorns apart by repeated hammering with the bill. The titmouse is larger, 12 winter-taken males of *P. i. inornatus* (Museum of Vertebrate Zoology) averaging 16.6 grams, in contrast to 9.7 grams for 15 males of *P. rufescens* from central California.

Snow (1949) demonstrated that in Sweden each of six species of *Parus* had distinct foraging sites when occurring together in the same forest. His method of approaching the problem was to record the species of tree and the height and position in the tree for each foraging observation of each of the species of *Parus*.

A similar method of gathering data for analysis of possible overlap in feeding habits of passerine birds was suggested to me in 1948 by Dr. Frank A. Pitelka, whose advice is gratefully acknowledged. Certain data were recorded for each motion apparently made to take a food item. These included kind of tree, height in the tree of the foraging individual, and whether foraging was carried out on trunk, branches, twigs, foliage or fruit of the tree. Twigs were designated arbitrarily as those branchlets less than one-half inch in diameter.

Observations of food-taking motions were made along Wildcat Creek, Contra Costa County, California, on two days in November, 1951, and on the campus of the University of California, Berkeley, on three days in November and eight days in December, 1951. These data are presented in table 1. The principal trees at the two localities were two indigenous evergreens, the live oak (*Quercus agrifolia*) and the California laurel (*Umbellularia californica*), and introduced evergreens of the genus *Eucalyptus*. There were scattered individuals of buckeye (*Aesculus*), maple (*Acer*), and willow (*Salix*), and several species of introduced trees and shrubs. Chickadees and titmice were present concurrently in both areas. In May, 1952, observations were made on the University Campus on nine days during which time both species were feeding broods several days out of their nests (table 2).

Table 2

Food-taking Motions of Chickadees and Titmice
May, 1952

| | Trunk | Branch | Twigs | Foliage | Fruit | Total | Per cent |
|---|---|---|---|---|---|---|---|
| *Parus rufescens* | | | | | | | |
| Eucalyptus | .... | .... | .... | .... | 1 | 1 | 0.8 |
| Laurel | .... | 2 | .... | 5 | .... | 7 | 4.7 |
| Live oak | .... | 47 | 20 | 60 | 1 | 128 | 86.4 |
| Other trees | .... | .... | .... | 12 | .... | 12 | 8.1 |
| Ground | .... | .... | .... | .... | .... | 0 | 0 |
| Total | 0 | 49 | 20 | 77 | 2 | 148 | 100 |
| Per cent | 0 | 33.1 | 13.5 | 52.0 | 1.4 | 100 | |
| *Parus inornatus* | | | | | | | |
| Eucalyptus | .... | .... | 2 | 2 | 1 | 5 | 9.2 |
| Laurel | .... | .... | .... | 9 | .... | 9 | 16.6 |
| Live oak | .... | .... | .... | 19 | .... | 19 | 35.2 |
| Other trees | .... | .... | 2 | 17 | 2 | 21 | 39.0 |
| Ground | .... | .... | .... | .... | .... | 0 | 0 |
| Total | 0 | 0 | 4 | 47 | 3 | 54 | 100 |
| Per cent | 0 | 0 | 7.4 | 87.4 | 5.2 | 100 | |

No appreciable differences in feeding heights were noted and the data are not included since it is felt that they reflect merely the heights of the trees in which foraging was being done. A notable exception was the food-gathering of the Plain Titmouse on bare ground beneath the trees, an activity never observed in chickadees.

Minimal activity of arthropods would be expected during November and December so that the observations made at that time approached the condition which Crombie (1947:46) described as a high ratio of population to resources of the environment. If competition occurs, it would be expected under such conditions. Several points are revealed in a study of the data for this period (table 1). About two-thirds of the foraging time of the chickadees was spent in the aromatic eucalyptus and laurels in contrast to only one-sixth of the total time for the titmouse. The bark of the laurel trees lacks deep furrows which might harbor larger arthoropods and the bark of most eucalyptus species likewise is rather smooth. The bark of some of the species of eucalyptus sometimes peels in strips which tend to curl and afford hiding places for arthropods. Titmice have been seen searching for food in such sites. The titmice spent nearly one-half the observed time foraging on foliage of evergreen oaks. This was almost four times the percentage spent by the chickadees. Nearly one-sixth of the titmouse foraging was done on the ground, principally on the fruits of an unidentified ornamental tree. Chickadees were never observed seeking food on the ground.

Differences in techniques of obtaining food items were evident during the winter season. In addition to splitting open hard-shelled fruits with their bills, the titmice would on occasion chip away the bark of a tree with their bills, apparently exposing inactive arthropods. Chickadees in contrast were seen picking repeatedly but daintily at the bark of laurel trees or the fruits of eucalyptus as though gleaning relatively small, but numerous, food items.

Vegetable matter made up 84 per cent of the food of 39 specimens of *P. inornatus* taken in California in winter, according to Martin, Zim and Nelson (1951:140). The same authors reported that only 40 per cent of the winter food of 24 specimens of *P. rufescens* from the Pacific Coast consisted of vegetable material. Overlap between the two species in animal food taken in the winter season is only partial, judging from my observations of food-taking motions. The animal matter in the diet of the titmouse in winter may include arthropods too large or too deeply buried in furrows of the bark to be accessible to the chickadees.

It is evident from the samples for May (table 2) that both species foraged on leaf surfaces, although the sites within the trees used by the chickadees were more varied. Since most of the prey animals were in the active, feeding stage, an abundance of them in the foliage is to be expected. The chickadees spent an overwhelming percentage of their foraging time in live oaks in contrast to the several species of trees frequented by the titmice. Neither species was seen foraging on the ground at this season. Although both parids searched leaf surfaces for food for themselves and their broods and took many insect larvae, it was evident on many occasions that the titmice took larger prey items. Often these were larvae of Lepidoptera which the adults tore into strips before offering them to their offspring.

Closer comparison of the percentages of overlap than that given is not considered warranted since data on the foraging sites of other small passerines from the same habitats are not available. However, because the two parids have acrobatic foraging capabilities, which permit them to search the undersides of branches, they should be in closer competition with one another than with other small birds seeking the same kinds of foods. The considerable differences in feeding habits in winter and differences in the size of food items taken during the breeding season, as well as the disparity in size, bear out the contention of Lack (1944:274) that closely-related species of birds occurring in the same region and habitat, usually differ in feeding habits and/or in size.

*Overlap in space needs.*—Closely related species of birds living in the same locality usually occupy different habitats (Lack, *loc. cit.*), competition between the two forms thus being reduced. Substantiation for this conclusion is provided by cases in which the ecological distribution of a given species is wider in the absence of a congeneric species than it is in similar areas in which both forms are present. Svardson (1949:160) discussed some examples of this phenomenon among parids in Sweden. In districts where the Marsh Tit (*Parus palustris*) occurred, the Willow Tit (Black-capped Chickadee; *P. atricapillus*) was found chiefly in conifers. Farther north, in the absence of the Marsh Tit, the Willow Tit ranged more widely. Even though the morphologic differences between the Chestnut-backed Chickadee and Plain Titmouse are greater than those between the Willow and Marsh tits, some separation in the ecological distributions of the former may be expected. These may be inferred form the fact that the titmouse is found in drier interior localities. Conditions favoring the chickadee in the East Bay district appear to exist chiefly along stream courses in the broader canyons east of the Berkeley

Hills. Titmice are found most often in groves of live oaks on sunny slopes. On the western slope of the Berkeley Hills, the riparian habitat is discontinuous and is not extensive, due perhaps to the steep gradient in stream flow and to disturbance by man. The preferred habitats of the two parids do not therefore exist in large blocs, but are intermingled in a mosaic, so that at some localities, at least, the two species can be considered as occupying the same habitat. An exception may be cited in that groves of eucalyptus and conifers are little used by titmice but are inhabited to a considerable extent at some seasons by chickadees.

The observations reported beyond were made as opportunity permitted me to be afield in Strawberry Canyon and on the lower part of the campus of the University of California, Berkeley. The period covered is from early in 1947 until May, 1952. Some of the data on which conclusions expressed in this paper were based will be presented in a separate paper relating to a population of the Plain Titmouse.

Some competition for nest sites between chickadees and titmice might be expected, for both nest in cavities. I have not observed *rufuscens* and *inornatus* quarreling over nest sites, but I have observed antagonism at other times of the year, indicating that friction between the two is not restricted to the breeding season. Such incidents occurred with greater frequency than the occasional clashes of the titmouse with other small passerines, such as the Oregon Junco. The encounters between the two parids might be examined with reference to the concept of interspecific territorialism as discussed by Simmons (1951). He recommended (p. 407) that the use of the term be restricted to cases involving species of overlapping ecology and pointed out that definite patterns of behavior were involved. He wrote as follows: "A territory holder of one species exhibits persistent aggressive behavior to an intruding bird of a second species, showing to it some, if not all, the reactions usually forthcoming in intraspecific encounters. Aggression is related to the territory as a whole and not merely to a particular part of it." Thus disputes relating solely to nest cavities are excluded from the discussion.

Our knowledge of the pattern of territorial behavior in *Parus rufescens* is fragmentary. Bowles (1909:55) reported a nesting "colony" of chickadees in western Washington in which seven occupied nests were closely spaced in what appeared to be optimal habitat for the species. Some of the nests were no more than 50 yards apart, from which observation weak territoriality may be inferred. In the Berkeley Hills, Chestnut-backed Chickadees travel in small flocks from early June until late February. I did not note restriction of chickadees to a territory except during a brief period in spring and I saw little indication of stringent territorial patterns.

Bowles (*op. cit.*) described a song of the chickadee, similar to that of the Chipping Sparrow (*Spizella passerina*) and given only during the spring months. On one occasion I recorded this song as a series of notes of one pitch, *chip chip chi chi chi chi chip*, accelerated progressively until the last note. I have not noted the use of this song in announcement of occupancy of an area, possibly because I have had little opportunity to study *rufescens* early in the breeding cycle. However, I heard this song used on several occasions in summer and early autumn. It was uttered by chickadees pursued by other birds, usually by titmice but once by an Anna Hummingbird (*Calypte anna*), and in intraspecific encounters in late summer. This "song" may correspond to the fighting note of the Black-capped Chickadee (Odum, 1942:502).

In contrast to the chickadees, Plain Titmice in coastal California defend their territories rather vigorously against intruders of their species throughout the year (Dixon, 1949:117). The principal means of announcement of occupancy of an area is the two-syllabled "whistled" song of the male; the variety of call notes common to both sexes serve to a lesser extent. Another song of *inornatus* heard on a very few occasions is a succession of dry notes very similar to the song of *rufescens* just described. Singing is noticeable from February to May, but it may be evoked in times of stress in other seasons.

A tabulation of observed encounters between *rufescens* and *inornatus* is here presented. Some elements may be entered separately although they represent successively higher levels of response in the same encounter. For example, pursuit might follow an exchange of calls.

| | |
|---|---|
| Both species present, no antagonism evident (March 12, June 4, June 11) | 3 |
| Chickadees with brood left area when titmouse family group appeared (May 29) | 1 |
| Chickadee and titmouse exchanged call notes alternately, obviously in response to one another (March 3, May 20, May 29, June 5, Sept. 14, Oct. 13, November 13, 18, December 10) | 9 |
| Titmouse scolded chickadee while the latter was calling (May 19, August 25) | 2 |
| Titmouse sang in response to call notes of chickadee (March 12, August 25) | 2 |
| Chickadee called as titmouse sang (March 24) | 1 |
| Chickadee sang as titmouse attempted to drive it from the area (July 20, November 21) | 2 |
| Titmouse displaced chickadee from its perch (July 20, December 9) | 2 |
| Titmouse pursued chickadee, the latter taking flight (March 12, July 20, November 21) | 3 |

The responses of titmice toward chickadees included call notes and scolds, song, and pursuit—the full range in kind if not intensity of activities characteristic of intraspecific encounters. In contrast, the chickadees called and sang in quarreling with titmice but did not initiate pursuit and always gave way to their larger adversaries.

In 14 of 21 separate encounters, the friction observed between the two species was initiated by vocal contact. The general call notes, a scratchy *sicka dee dee* of *inornatus* and a wiry *zi zi zi zit* of *rufescens,* are similar in rhythm to an extent that either appears to function as a releaser to the individuals of the other species. Exchange of the closely similar (trilled) songs was not heard, although in one encounter (October 6, 1950) I was not able to determine whether the song was given by a chickadee or a titmouse. Simmons (*op. cit.*) stated that characters at the group level were important in eliciting interspecific territorial responses, citing general outline and mannerisms as most effective in the wintering oenanthid chats (avian family Turdidae) which he had studied. The quarrels between the titmice and chickadees appear clearly related to space occupancy (see beyond) but voice is the critical behavior element involved. Vocality is prominent in connection with social organization in the genus *Parus* and the basic vocal patterns appear to be retained with few modifications in many species of the genus.

Since most of the antagonism shown began with vocal exchange and since the combined populations of the two species is greatest in summer, more friction might be expected then. The aggressive responses of sedentary titmouse pairs at that season toward more mobile groups of chickadees is characteristic of the intraspecific year-around territorial defense exhibited by the titmouse. However, disputes in early spring would be more significant in relation to available space for breeding territories. A few episodes in a sequence of encounters between a pair of chickadees and an established pair of titmice was seen on the campus of the University of California in 1952. Calls were exchanged on March 3, but no further animosity was shown. On March 12, one member of a chickadee pair gave a general call to each group of whistled songs of the titmouse and was driven from the area by the titmouse shortly afterward. This action of the chickadee involved recognition of the song of the titmouse, possibly learned during interspecific combat. (A similar incident, involving different individuals, was witnessed at a locality nearly a mile away on March 24.) Subsequently, the chickadee withdrew to an adjacent portion of the campus, partly screened from the titmouse territory by a large, five-story building.

Although other incidents were not witnessed, the results are evident in the spatial separation of *inornatus* and *rufescens* in the vicinity of Berkeley in spring. Several illustrations follow:

A cavity in a eucalyptus tree alongside Wildcat Creek in Tilden Park, Contra Costa County, was used as a nest site by *rufescens* for five years, 1945–1949. From 1950 through 1952 the same cavity was used by *inornatus* (A. H. Miller, MS). In May, 1949, I observed a male *inornatus* singing in the territory to the north of the chickadee nest.

The chickadee nest which was discovered on the University of California campus on May 6, 1950 (page 114) was in an area occupied by *inornatus* in 1948 and 1951 but not in 1950.

On May 5, 1952, the pair of chickadees involved in the dispute with the titmouse on March 12 was feeding nestlings in a Cliff Swallow (*Petrochelidon pyrrhonota*) nest at the fifth story level on the north side of the Life Sciences Building, University of California. Trees were scattered and chickadees had to fly considerable distances from the nest to forage. Titmice had nested nearby in 1950, but not in 1951 or 1952, the banded occupant of the area in 1950 having moved to an adjacent territory. Titmice have nested in abandoned swallow nests on the south side of the same building repeatedly but to my knowledge have not occupied such sites on the shaded north side of the building.

The one case of nesting of chickadees in the special study area for *inornatus* was in a narrow strip of timber in a side draw of Strawberry Canyon. That draw was a part of a titmouse territory in 1947 but it never was used by titmice in the succeeding five nesting seasons.

In each of the cases cited, the territories of the two species were mutually exclusive. Some of the territories were used first by one species and then the other, pointing to the similarity in their habitat relations and again to mutual exclusion in spatial occupancy. The data of Norris (1952) suggest a territory size of not more than three acres on an average for *rufescens* in coastal pine forest. Plain Titmouse territories in live oak woodland are somewhat larger, 11 territories averaging 5.7 acres (Dixon, MS). Although the spatial needs of chickadee pairs may be less than those of titmice, the observation that the titmouse territories in Strawberry Canyon seldom contained more than one suitable nest site (Dixon, 1949:125), indicates that only under exceptional circumstances would a pair of chickadees be able to appropriate a peripheral part of a larger, titmouse territory and nest there successfully.

One might wonder from these observations if population densities of *inornatus* might not be lowered as a result of the influx of chickadees into the Berkeley Hills. In Strawberry Canyon, where conditions are favorable for titmice, presence of the chickadees has not resulted in restriction of occupancy of the area by titmice. Population data for the Plain Titmouse for a 44-acre plot are available for a six-year period, 1947–1952 (Dixon, 1949 and MS). For the first three years, chickadees did not occur on the study tract, adjacent to the university campus, during the breeding season. In later years, special effort was made to determine whether or not the chickadees could invade those parts of the canyon below the 800-foot contour during the nesting season. Breeding season densities on the study tract are listed below:

| | *P. inornatus* | *P. rufescens* |
|---|---|---|
| 1947 | 7 pairs | 0 |
| 1948 | 7 pairs + 1 male | 0 |
| 1949 | Data incomplete | 0 |
| 1950 | 6 pairs | 0 |
| 1951 | 7 pairs | 0 |
| 1952 | 9 pairs + 1 male | 1 pair |

In the year of the first chickadee nesting in the lower elevations of Strawberry Canyon, the highest known population density of titmice occurred. In the same year, due in part to a realignment of titmouse territories, three pairs of titmice in addition to the pair of chickadees nesting in the Cliff Swallow nest were found nesting in a section of the University campus which usually supported only two pairs of titmice. However, chickadees are increasing in numbers and are spreading in the area so some further adjustments may occur.

The distribution of Plain Titmouse territories in a given locality tends to be fairly constant from one year to the next because the territories are occupied throughout the year. Moreover, the maximum breeding density of the titmice for a given season usually is established before the chickadees begin seeking nest sites early in March (Dixon, MS). In all cases known to me, those chickadee pairs which nested in localities inhabited by both species selected vacated titmouse territories or sites which appeared suboptimal for titmice. However, spatial separation may be of short duration, as indicated by the following observations. After three months absence, I resumed study of the titmouse territories in Strawberry Canyon in the second week of May, 1951. During that week, chickadees were sought in the canyon but were not found. In the period from May 25 to June 4, three broods were encountered in the canyon bottom. Presumably they had nested in eucalyptus groves on the north side of the canyon above the 1000-foot level and had moved downslope seeking more adequate food sources for their fledged juveniles in the live oaks and riparian alders. At that time the titmice are feeding their own fledglings and are lax in the defense of their territories against intruders of their own species.

These observations were made at a locality where the natural habitats preferred by the two species are not distinctly separated and habitat segregation does not function to keep the two species apart. The year-around occupancy of territory by the Plain Titmouse confers a distinct advantage upon that species in its competition for space with the chickadees. Similarities in voice and mannerisms and the frequency of contacts result in interspecific tensions which, as Simmons (1951:412) pointed out, may serve to reduce competition in localities where species of similar requirements occur in the same habitat. Some of the territories in Strawberry Canyon held by titmice year after year include streamside alders and willows, a type of growth utilized by chickadees elsewhere in their range. The chickadees are excluded from such sites by the larger, permanently territorial titmice and retire to nest in planted groves not frequented by titmice, returning to the more varied native timber as soon as their nestlings are fledged. This pattern of behavior is different from that reported for this species in coastal pine forests by R. A. Norris. He stated (personal communication) that in that association, in which *P. inornatus* does not occur, family groups of chickadees appeared to remain on their territories after the young could fly. These observations suggest modification of the breeding behavior of the chickadees under certain circumstances, the adjustments made permitting them to rear their broods with a minimum of conflict with titmice.

This case is similar in some respects to that of the two species of hummingbirds studied by Pitelka (1951) in a nearby part of the Berkeley Hills. He found that the larger, permanent resident Anna Hummingbird (*Calypte anna*) kept the smaller, migratory Allen Hummingbird (*Selasphorus sasin*) from realizing occupancy of all suitable breeding sites. The smaller species usually utilized sites which were not selected by the larger form and seldom occupied territories suitable to the latter. Pitelka concluded that the breeding population densities of the smaller species would be higher in the absence of the larger competitor, a conclusion which might also be drawn from the present study. However, like the case of the larger of the two hummingbirds, the breeding densities of the titmouse (at least in favorable habitat) do not appear to be depressed. The adjustments made between the two species for the division of the available habitat do not appear to be mutual, but are unilateral as far as I can determine. The smaller form is enabled to occupy the same localities as the larger (where the preferred habitats are not distinct) by nesting in sites which are marginal for titmice and by what appears to be modification of normal breeding behavior patterns which permit it to utilize one type of area for nesting and later move to another for feeding of the fledglings.

Elsewhere in the Berkeley Hills the population balance between these two species may be more nearly equal. Dr. Alden H. Miller suggested to me that this may be the case in the lower part of Wildcat Canyon, Contra Costa County. Parts of that canyon may be cooler, as a result of shade from surrounding hills or from eucalyptus groves, and thus may be more suitable for the chickadees than are some parts of the west slope of the Berkeley Hills. The chickadee has been established in that area for a longer period and its relative numbers there at present may reflect a state of balance yet to be reached in Berkeley. In some portions of Wildcat Canyon, the woodlands are more continuous, a factor which may in some way favor the chickadees in obtaining breeding space. However, the defense of territory by established titmouse pairs at all times of the year gives that species an advantage over the chickadees in selection of breeding sites even in areas where the chickadees are well established.

## SUMMARY

Within the past 15 years the Chestnut-backed Chickadee has become established as a breeding bird in the district immediately to the east of San Francisco Bay. The interrelations of this species with its larger congener, the Plain Titmouse, are considered in the light of studies of the latter species made prior to the influx of the chickadees.

The two species differ markedly in plumage pattern and the titmouse is stouter-billed as well as larger.

The preferred habitats of the two forms are not separated sharply in some parts of the Berkeley Hills so that ecological segregation is not effected.

Study of foraging habits suggests only partial overlap in foraging sites in winter. During the period when fledglings were being fed, size of food items taken appeared to differ.

Spatial requirements during the breeding season appear similar, but the smaller form is at a disadvantage because the larger defends its territorial holdings throughout the year. In all cases studied, the breeding territories of the titmouse and chickadee were mutually exclusive. As a result of similarities in behavior and frequent contacts where both species occur in the same habitat, interspecific territorial behavior is elicited, resulting in spatial segregation during the nesting season.

Population data for the titmouse on a 44-acre tract, where conditions are favorable to that species, reveal no restriction in ecologic range or spatial holdings during the early period of establishments of the chickadee in the area.

In the face of antagonism of the larger form, the adjustments permitting the coöccupancy of the area at this stage appear to be made entirely by the smaller species. These include selection of vacated or suboptimal nesting territories and possible modification of territorial behavior patterns.

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