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## TERRITORIALITY AND SURVIVAL IN THE PLAIN TITMOUSE

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The study of territoriality in the Plain Titmouse (*Parus inornatus*) is of interest because of the extreme development of this behavior in some of its populations. Investigations of several species of the genus *Parus* (summarized by Hinde, 1952) have demonstrated that adults of most of them tend to be sedentary and that pairing for life appears to be the rule. These trends are accentuated in those populations of the Plain Titmouse that inhabit the Pacific coastal slope of California. Adults generally remain paired permanently and confine their activities to their territories, which they defend throughout the year. Family groups break up a month or so after fledging takes place, and the juveniles leave their parents' territories. First-year Plain Titmice may be associated in pairs as early as August, and paired immature birds may take up territories by early autumn. Winter flocking is not known in this species in coastal California, although it has been reported for the "gray" races inhabiting interior piñon-juniper woodland by Aiken and Warren (1914:596) and by Woodbury and Russell (1945:93).

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### METHODS

The studies reported here were made from December, 1946, to May, 1948, and, intermittently, from February, 1950, until May, 1952. Thus five of six consecutive breeding seasons are represented by some detailed observations. During the latter three years, the field work was concentrated in the spring months; trapping and banding were conducted in May and June, both in 1950 and 1951, and in October, 1951. From 1946 through 1951, 61 titmice were color-banded, 22 as adults and 39 in their first six months of life. Information on activities of individuals was obtained by sight identification of these color-banded birds and to a lesser extent by trapping at elevated trays baited with walnut meat.

The study plot was in Strawberry Canyon, adjacent to the campus of the University of California, on the west slope of the Berkeley Hills in Alameda County, California. Its area was approximately 144 acres, not 44 as stated earlier (Dixon, 1954:121). Habitat suitable for titmice consists of streamside groves of alders (*Alnus rhombifolia*) and a woodland of live oak (*Quercus agrifolia*) and California laurel (*Umbellularia*) growing in adjacent parts of the canyon bottom and in tributary "draws," especially those on the south-facing slope. In the maps (figs. 1, 2, and 3), oak-laurel woodland is indicated by diagonal lines slanting downward to the left.

### TERRITORIAL BOUNDARIES, 1947-1952

In the years from 1950 to 1952, territorial boundaries were mapped as they occurred in mid-May, whereas the limits shown for 1947 and 1948 were those existing in mid-

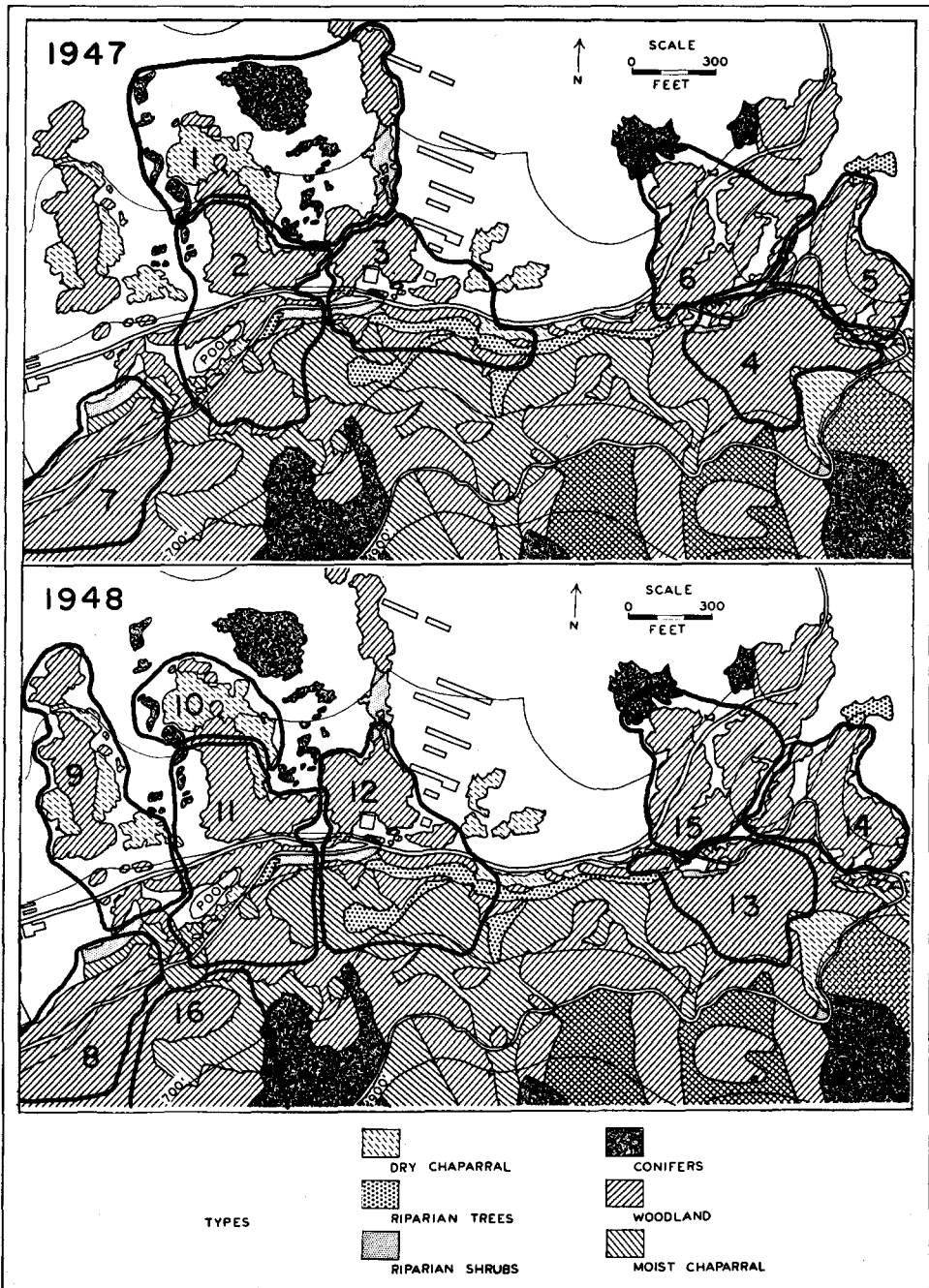


Fig. 1. Maps of territories of Plain Titmice in Strawberry Canyon, Alameda County, California, as of March 15, in 1947 and 1948.

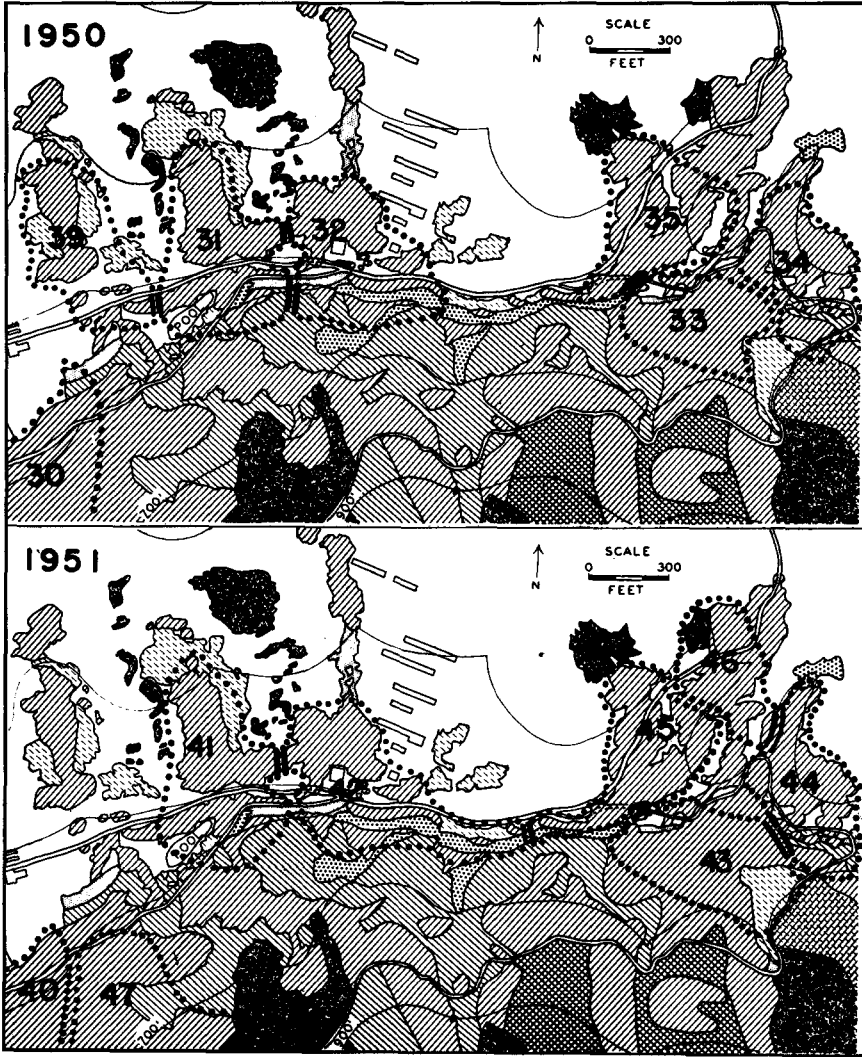


Fig. 2. Maps of territories of Plain Titmice in Strawberry Canyon as of May 15, in 1950 and 1951. Solid lines indicate those boundaries where defense actually was observed.

March. However, the boundaries fluctuated little from one season to the next, provided both members of a pair survived. In the maps for the three later years, solid lines indicate boundaries where territorial defense was witnessed, whereas borders inferred from movements of individuals and from the extent of blocs of arboreal vegetation are dotted.

Study of the maps reveals a remarkable stability of the areas occupied over the six-year period. From 1947 to 1948 (fig. 1) relatively few changes in configuration occurred. These were: (1) the addition of territory 9 to the west of 1 and 2 of 1947 (no pair was known to remain for nesting in this territory in the six years of observation); (2) the shrinkage and disappearance of territory 1 following the death of the male in January, 1948; and (3) the addition of territory 16 (between 2 and 7 of 1947), held by an unmated male. The territories were not mapped in 1949, but the outlines in 1950 did not

differ appreciably from the pattern in 1947 and 1948 (fig. 2). In 1951, two additional territories appeared, 46 (hitherto unoccupied) and 47 (comparable to 16 of 1948). These persisted in 1952 and, in addition, the transitory territory 58 and the area held by the unmated male X were occupied. Further, a pair of Chestnut-backed Chickadees (*Parus rufescens*) nested along a tributary north of territory 52. Even though the number of territories increased from six in 1950 (discounting 39) to nine in 1952 (discounting X), six territories held a fairly constant relationship throughout the six-year period. These were numbers 50, 51, 52, 53, 54, and 55 of figure 3.

*Characteristics of boundaries.*—Although no major realignment of territories was witnessed, a question arises concerning the degree to which boundary changes occurred. Before making this inquiry, we should determine the features of the habitat to which an individual titmouse responds in establishing a boundary. In this connection the terms

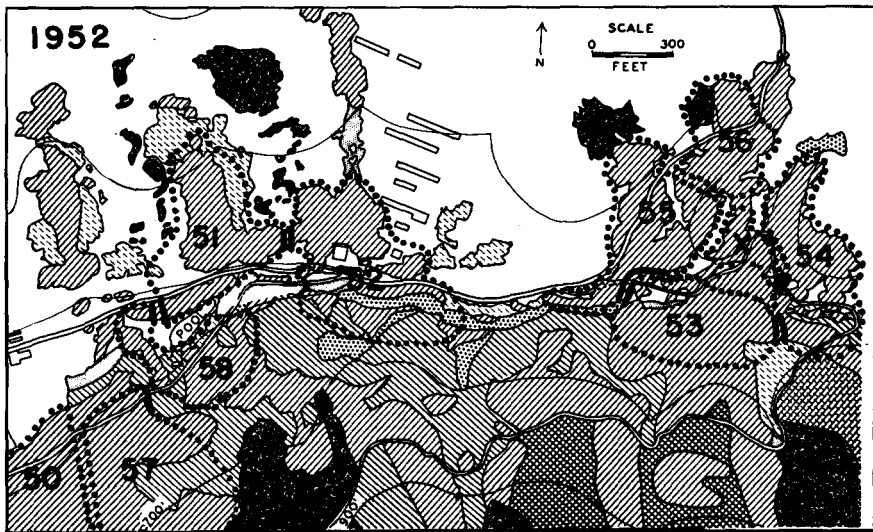


Fig. 3. Maps of territories of Plain Titmice in Strawberry Canyon as of May 15, 1952. Solid lines indicate those boundaries where defense actually was observed.

“neutral margin” (not adjoining another territory) and “defended margin” introduced by Southern and Morley (1950) may be useful. The margins of woodland usually serve as neutral, more or less permanent boundaries for these birds. As Lack (1940:307) found for the Robin (*Erithacus rubecula*) in Britain, roadways do not seem to act as barriers. However, a more extensive clearing of some riparian trees in the construction of a culvert in 1951 apparently resulted in the abandonment of the part of territory 41 south of that clearing. The area south of the culvert was occupied as territory 58 for a brief period during the following year.

Where the canopy is unbroken, a conspicuous branch or a shrub in a lower stratum may be used as a singing perch and hence becomes a boundary feature, an objective to be captured in an attempt at expansion. Parts of the boundaries between territories 1 and 2 (1947) and between 33 and 34 (1950) were of this sort. These points may be likened to the “preferred stations” about which the Great Tit (*Parus major*) is said to concentrate its activities in early spring (Hinde, 1952:50).

From the foregoing discussion it appears that characteristics and distribution of vegetation play an important role in the determination of many of the neutral territorial

boundaries of the Plain Titmouse. Of course, the boundaries must enclose an area of sufficient size to serve the needs of a pair of titmice. Although an average for 11 territories was calculated as 5.7 acres (Dixon, 1954:121), two and one-half acres probably would be close to an absolute minimum size.

The groves in the tributary gullies on the south-facing slope of Strawberry Canyon are essentially natural units of occupancy for titmice since they are partly-isolated blocs of arboreal vegetation of suitable size. If all the individuals in the canyon had been removed and repopulation allowed to take place, as in the population-removal census of Stewart and Aldrich (1951), some of these areas would have been occupied with essentially the same boundaries in effect, just as those authors found to be the case in some passerine species in coniferous forests in Maine. Other territories in the eastern part of the study area, where the woodland is more or less continuous, might have been arranged somewhat differently.

*Minor shifts in boundaries.*—Those edges of the territory which do not coincide with discontinuities of the canopy are as a rule more subject to alteration. The changes in the boundaries of a succession of territories held by M5, a male paired with a different female in each of four seasons, may indicate the usual condition of slight shifts in the margins of Plain Titmouse territories. Only about one-fourth of the margin of this male's territory bordered unwooded terrain. In 1948 the territory of M5 was expanded approximately 20 yards to the westward across a narrow glade to include the next row of trees. This encroachment on the territory of M6 apparently was made because the nest site chosen by M5's mate in 1948, a first-year female, lay very close to the western edge of the territory as it had existed in 1947 (fig. 1). By 1950, the western boundary (territory 34) had reverted to the condition of 1947, and the nest was situated on the south bank of the creek in an area not used by M5 in 1947 or 1948. Data for May, 1950, indicate a smaller territory for this male than was the case in earlier years, but this condition may have resulted from the fact that evaluation of boundaries in 1950 was made while incubation was in progress. Changes in outline of this territory appear to have been due in considerable measure to choices of nest sites by the several females.

Territorial boundaries of the Marsh Tit (*Parus palustris*), a chickadee-like species studied in England by Southern and Morley (1950:38-39), appear to have fluctuated more over a six-year period than those of the Plain Titmouse reported here. These authors attributed change in size of territory to the individuality of the owner, and they stated that older residents tended to hold larger territories than did younger birds. The only situation encountered in this study that suggested this factor of individuality occurred in territory 3, where the newly-established male M12 expanded the western portion of his territory during the late fall of 1947. This was accomplished along the margin of territory 1 defended by M1 in the spring of 1947. In March, 1948, this pair, now designated as territory 12, expanded the neutral southern boundary farther to the south than had their predecessors. Their expansion to the westward was prevented by the occupants of territory 11. This was the only instance when an attempt to enlarge holdings was noted. Such expansion by an inexperienced first-year bird may exceed the limits of area which can be defended successfully. The loss of part of the 12.5-acre domain of M1 in the fall of 1947 (fig. 1) may be explained in part on this basis. In no case, however, was an increase in size of territory with advance in age observed.

In addition to the influence of vegetational distribution, carry-over of breeding individuals from one season to the next may have an influence on the stability of territorial boundaries. The data on survival (see beyond) indicate that most of the adult titmice of this study existed on the area for more than one season. Thus, constancy of boundary would be promoted, since they are defended to some extent throughout the year.

*Observance of boundaries.*—The effects of continued occupation of an area by the same pairs may be evaluated in the light of the behavior of the birds with respect to boundaries. Unfortunately we can refer to no instance in which both members of two adjoining pairs were eliminated from the population simultaneously. However, some instances involving the disappearance of one pair are informative. The boundary between territories 11 and 12 (= 2 and 3, 1947, fig. 1) provides an example. The established pair which had occupied territory 2 in 1947 did not expand its eastern limits at the expense of the newcomer, M12, which had replaced the male of territory 3 during the fall of 1947. Moreover, his mate, F12, could not have known the boundaries from

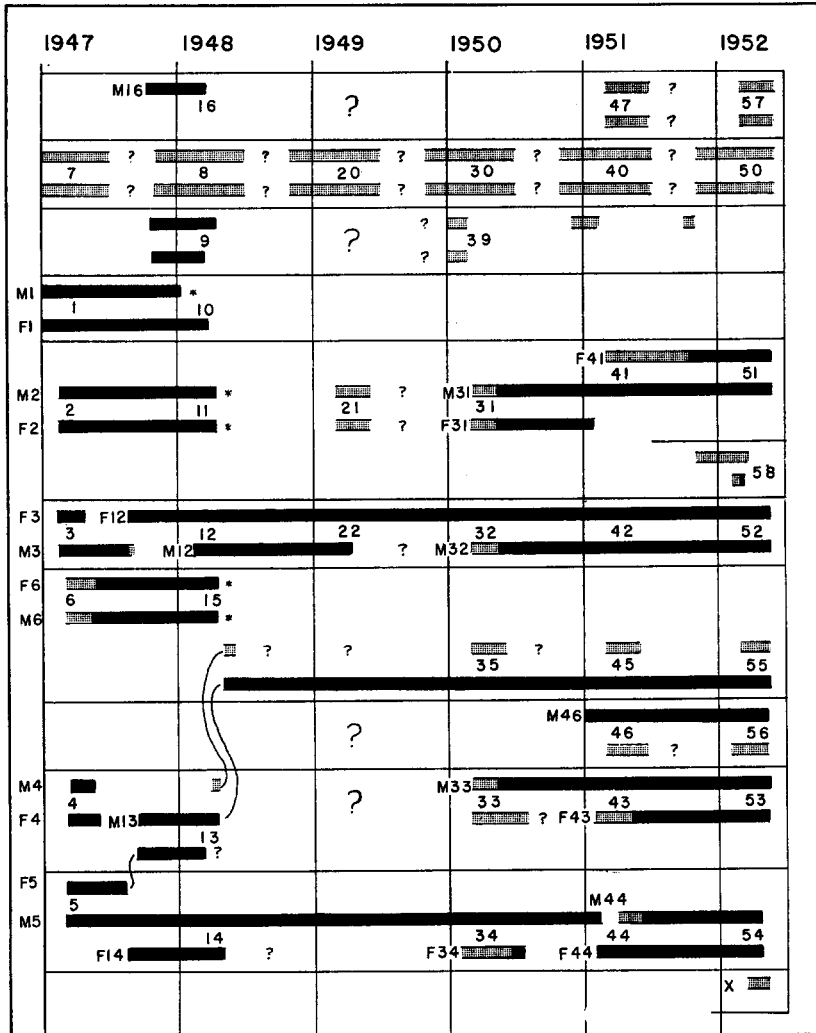


Fig. 4. Occupancy of territories by Plain Titmice, 1947–1952. Black bars indicate span of dates of tenancy of a banded individual; stippled bars, unidentified individuals. Horizontal columns represent territories shown on maps (figs. 1, 2, and 3). An asterisk indicates apparent or known removal of an individual by human agency.

the previous breeding season since she was a first-year bird. Thus she probably was not responsible for the maintenance of the boundary.

The pair of the neighboring territory (11) disappeared in April, 1948 (fig. 4). In one contest observed in April, 1949, it was evident that the pair which had occupied territory 12 in 1948 had not extended its western border at the expense of the newly-established pair. There was no natural feature to mark the boundary, which was located along a constricted "waist" of woodland connecting two more extensive tracts (fig. 1). Even though only the female of the eastern pair survived after the 1949 nesting season, the boundary remained virtually unchanged for the next three years, fluctuating over a range of not more than 20 yards. (Survival in the western pair, 21, cannot be assessed since the birds were unbanded in 1949.)

Similarly, the defended margins of territory 44 do not appear to have been altered following the disappearance of M5 early in 1951, nor did M6 enlarge his domain when territory 4 was vacated in May, 1947. Actually, trespass seldom was observed, and only one titmouse was trapped more than a few yards outside its territory. Repeated trespassing would be expected to result in learning of bait stations, and in repeated retrapping. This was known to have happened only in the case of the trespass of adjacent territories by M13 in May and June of 1950 and 1951.

Apparently the surviving pairs respect the borders as they have been established and the replacements learn them by contacts with their neighbors. Replacement following the loss of the pair of territory 12 probably occurred in the summer of 1948. Thus the gap was filled well before the period of maximum territorial response in spring. Even during that period there seems to be no pronounced tendency of Plain Titmice toward expansion of defended margins in the absence of neighbors. The opposite tendency was found in British Robins by Lack (1946:40). He stated that "when the owner of a territory disappears, the owners of the neighboring territories expand into the vacant site almost at once, and often the ground is fully occupied within twenty-four hours."

Since, in the Plain Titmouse population studied, the gaps created by the disappearance of a pair were not filled in by surrounding pairs, the survival of individuals "respecting" the boundaries would result in the maintenance of the system of population organization which was in effect. Since carry-over is considerable (see beyond), fluctuation in number of breeding pairs from one season to the next would be minimized.

As was indicated earlier, six "basic" territories remained in fairly constant relationship throughout the six breeding seasons. The increase in total population in Strawberry Canyon was achieved by the establishment of additional pairs in the previously unoccupied territories 46 and 47. Thus, the increase was effected by the occupation of greater area, the density in terms of acres per bird remaining about the same. From this observation, we might infer that territorial behavior would impose the upper limit of population density, which apparently was approached in 1952. This same conclusion was reached by Kluyver and Tinbergen (1953:283) in their study of the Great Tit in The Netherlands and it stands in contradiction to the contention of Lack (1946; 1954) that territoriality does not limit population density.

#### THE NATURE OF TERRITORIAL BEHAVIOR

During the latter part of the summer, when adult titmice are molting, their territorial activities are oriented principally toward the repelling of invading immature titmice. Singing is infrequent and there is no extensive patrolling of boundaries. During the period from August 3 through August 23, 1947, I spent a total of 35 hours in the field on 12 different days. The only times singing was heard were when an "owner"

encountered an intruder trapped on his territory (M6 versus M13, see beyond), and on one occasion following the release of an immature male from a trap. There are few contacts with neighboring pairs at this season. This territorial behavior differs from that observed in spring, which presumably is reinforced by events of the breeding cycle.

The aggressive aspect of territoriality in summer was indicated to me by several incidents including the defense of territory 6 against an intruding pair, the immature male M13 and his unidentified mate (see Dixon, 1949:117). M13 invaded the southwestern portion of M6's territory repeatedly in mid-August, 1947, being trapped there twice in three days of trapping in the period from August 17 to 21. He eventually settled in the area adjacent to the south, successfully incorporating the southwestern portion of M6's holdings into his own. Late in April, 1948, when M6 and F6 disappeared (fig. 4), M13 abandoned his own territory to claim that vacated by M6. However, M13 continued to defend the area won from M6 previously, holding it successfully for at least the next four years.

The active struggle for space recounted above differs from the passive aspects of territoriality discussed by Kluver and Tinbergen (1953:279) and stressed by Lack (1954:270). These authors cited avoidance of those areas already settled by individuals of the species as important in determining population densities. Lack (*loc. cit.*) stated that "the retreat of the new-comer is the major factor concerned" in territorial behavior. Likewise, Lehmann (1953:235), working with Bobwhite Quail (*Colinus virginianus*) in southern Texas, reported that there were certain population density levels (both breeding and winter) above which habitat improvement measures could not effect further increase. These limits were attributed to an aversion to crowding.

The authors cited above were discussing a facet of territorial behavior manifested chiefly in spring. As pointed out by Kluver and Tinbergen (for *Parus major* at that season), the less attractive habitats are accepted when the preferred ones are filled. This same phenomenon is witnessed among juveniles of *Parus inornatus* in summer and autumn as well. Both the defense by adults in summer and what may be termed "saturation avoidance" are inconspicuous and may pass unnoticed as the majority of juveniles (some of them paired) unobtrusively seek unoccupied areas. Only the more tenacious ones, such as M13, attract notice in summer.

Even in spring, mateless, first-year titmice apparently keep drifting until they find a vacancy in the population. Evidence that shifting of residence occurs among first-year birds as the breeding season approaches is provided by the abandonment of the transitory territories 9, 39, and 16, and by the replacement of deceased mates (by M44 and F41 and by the unbanded mate of M13 in 1948; see fig. 4). These movements were by individual birds, whereas at least some of the immatures seek territories in autumn as pairs (Dixon, 1949:120). At any season these wandering titmice encounter an intolerance which was found to be manifest by Chestnut-backed Chickadees as well (Dixon, 1954), in the latter case chiefly because of similarities in voice.

In spring, territorial "defense" appears to be more active than at other seasons. There is much patrolling of boundaries and formalized "clashing" with the established members of the population, the occupants of neighboring territories. The boundaries usually are changed but little as a result of these meetings, but the contests are prolonged and recur frequently, presumably because the opponents do not retreat, as an intruder which lacked a territory might be expected to do. This "defense" behavior of the Plain Titmouse is strikingly like that of the Wren-tit (*Chamaea fasciata*), a permanently-territorial inhabitant of Californian chaparral studied by Erickson (1938:263), who stated that "the general impression was not of birds continuously exerting pressure or sparring for an opening, but rather of their acceptance of the existing status."



Evidently, defense of area is not the sole function of these disputes in spring, and the application of the term "reproductive fighting" (Hinde, 1952:71) seems justified as an indication of the reinforcement of the normal tendency to defend the borders of the territories. To some extent these sham battles appear to provide social stimulation, as suggested by Darling (1952:190). Such behavior differs from the defense reaction against intruders at other times of the year and may be considered more of a ritual. This hypothesis is supported by the continued observance of boundaries by titmice rather than expansion following the disappearance of neighbors. The actual repelling of potential invaders of the territory in summer certainly is more important from the standpoint of determination of the population level. This defense of areas which have proven suitable for the needs of reproduction is effected by the established adults which clearly control the social organization of the population.

#### SURVIVAL AND REPLACEMENT

The extent to which the established individuals tend to maintain the spatial organization of the Plain Titmouse population may be judged from their survival and rate of replacement. Only six individuals were extant on the study area following the disappearance of four adults (apparently removed by target shooters) in April, 1948. Five of the remaining adults were already banded and four (F12, M12, M13, and M5) were known to be alive during the breeding season of 1949, occupying three territories (fig. 4). In 1950, three of the individuals, representing the same three territories (32, 35, 34) were still alive. As noted previously, the boundaries in 1950 did not differ markedly from those in 1948. In the breeding population of 1952, six territories were inhabited by at least one color-banded titmouse; in four of the six, one member of the pair was holding forth for at least its third season, while in each of the other two, at least one member of the pair was two years of age. In two of the territories, one occupant was nesting for the fifth season. The figures cited are based only on those individuals which were banded. If they are representative of the total population, they indicate a slow replacement rate for established adults.

For three of the years of this study it is possible to determine survival of banded adults of the previous year's breeding population. The numbers of individuals surviving were as follows:

- 1947 to 1948, 7 of 11 (excluding M1, killed accidentally in trap, January 11, 1948)
- 1950 to 1951, 5 of 8
- 1951 to 1952, 10 of 10

The total of 22 of 29 individuals persisting to breed the next year suggests an annual replacement rate of about 25 per cent.

Some additional computations can be made from the published data of Price's (1936) study of this species at Stanford University, California, from 1928 through 1933. His recovery records of adults were obtained only by retrapping in nesting boxes. Hence those pairs which chose natural cavities rather than nesting boxes for re-nesting would be lost from the record, although such disappearances did not necessarily indicate death. This assumption was supported by the fact that nest boxes deserted the season after being occupied were not appropriated by other pairs of titmice.

Although Price reported recovery of only 53 and 50 per cent of the 28 and 40 adults captured in 1931 and 1932, respectively, study of a table of mating relationships (*op. cit.*:26) suggests a higher survival rate. This table indicated pairing relationships of 38 individuals in what appear to be 14 territories. Of 20 adult titmice present in 1931, 16 (80 per cent) are known to have been present in 1932. In 1933, 19 (73 per cent) of the 26 birds trapped in 1932 re-nested in these "territories." Furthermore, the consideration

of the 38 individuals as a group shows that 27 (71 per cent) renested at least once, and 11 (28.8 per cent) renested for three or more seasons. A combination of Price's data (from a sample larger than the Strawberry Canyon population) and mine demonstrates the renesting of 57 of 75 established adults, a carry-over of 76 per cent from one breeding season to the next.

The data presented by Lack (1954:91-93) show a rather different picture of longevity for a selected group of passerine species. He reported annual adult mortality in passerines to vary from 41 to 72 per cent, and "average expectation of further life of adult" correspondingly from 1.9 to 0.9 years. Many of Lack's calculations of annual adult mortality are from age at death in a sample of banded birds; my records of Plain Titmice do not permit calculation by that method. If we accept for the present the value of 76 per cent annual adult carry-over, adult mortality in the Plain Titmouse would be 24 per cent each year. Using this figure in computing the average expectation of further life from the formula  $2 - \frac{2m}{m}$ , where  $m$  equals percentage annual mortality

(Lack, 1954:93), we obtain a value of 3.5 years. Even an apparently conservative estimate of 66 per cent survival yields a value of 2.5 years. This expectation of further life in adults of *Parus inornatus* is markedly higher than that for other passerines cited by Lack (*loc. cit.*). However, it resembles that of the sedentary, permanently-territorial Wren-tit, for which Erickson (1938:309), using the formula devised by Burkitt, calculated the "average age attained by birds that survive their first breeding season" to be 4.43 years. By way of corroboration she stated that 61 per cent of the breeding population in 1933 were three years old or older, although in a declining population adult mortality for the year amounted to 36 per cent (*op. cit.*:310). Mean longevity of Wren-tits as of March 1 was recalculated from Erickson's data as "about 3 years" by Farner (1949:73). He expressed a view that even the 2.3 years mean longevity suggested by the 36 per cent adult mortality of Erickson's sample for 1933 ascribed "an unusual longevity to such small birds."

A behavior trait shared by the Wren-tit and the Plain Titmouse is year-around territoriality. In both of these species the holding of a territory seems to confer on the established individual a decided advantage in survival. To a considerable extent this may be due to food supply. Erickson (*op. cit.*:313) presented evidence that the established individuals had a lower rate of disappearance than did the immature or non-territorial Wren-tits during the period of food shortage (November through January).

A second value of the territorial habit, the "place-conditioned dominance" (Nice, 1943:168) of the individual or pair situated in familiar surroundings, must be considered. A similar advantage might obtain among sedentary (but not necessarily territorial) individuals of other passerine species. Even though Linsdale (1949:94) noted no pronounced differences in survival between migratory and sedentary species retrapped in winter in California, inspection of his table 2 suggests a different relationship. Precise computations are not possible from his published data, but the percentage of individuals of the ground-foraging towhee species (*Pipilo fuscus* and *P. erythrophthalmus*) retrapped the fourth year is almost twice that for the migratory White-crowned Sparrow (*Zonotrichia leucophrys*).

Third, there may be a social advantage to the permanent pairing relationship. In the Wren-tit, Erickson reported (*op. cit.*:266) that "when a pair was broken up, one or both members of it disappeared entirely." Widowed males tended to remain on their territories, whereas bereft females appeared more prone to shift territory to seek a new mate. Hence, the latter probably were exposed to greater hazards in unfamiliar surroundings.

The tendency to abandon the territory did not appear so prevalent in the Plain Titmice studied, even among females. For example, before her disappearance early in 1948, the widowed female F1 remained for six weeks on the territory where she had nested the previous year. At least two other widowed female titmice (F12 twice, F44) were known to have remained in the same territory and remated, and no widowed female is known to have nested in a different location. Although these data are far from adequate, they do point to a slow rate of replacement of the established adults as a population characteristic of coastal Californian Plain Titmice.

Further evidence for the low mortality rate in adults of the Plain Titmouse and Wren-tit may be found in their reproductive rates, which are reduced correspondingly. A direct relationship of this sort was demonstrated by D. W. Snow (cited by Lack, 1954:105) for three populations of the Blue Tit (*Parus caeruleus*). Snow found a clutch size of 11.6 eggs characteristic of British populations, which had an annual adult mortality of 73 per cent, calculated on the basis of the ratio of adult to first-year specimens. At the other extreme, in the Canary Islands, adult mortality was 36 per cent and clutch size, 4.3. The Great Tit in Holland was reported as averaging 9 eggs per clutch and having an adult mortality of 49 per cent per year. Erickson (*op. cit.*:288) found that 24 Wren-tit clutches averaged 3.9 eggs, whereas the average for 62 Plain Titmouse sets was found to be 6.75 (Price, 1936:24). Judging from the mortality rates in other titmice, the 6- or 7-egg clutch indicates a mortality rate closer to 40 per cent than to the 24 per cent calculated for *inornatus*.

The Wren-tit could potentially produce two young per adult, the Plain Titmouse, three. Neither species rears a second brood as a rule. However, the tendency to renest following destruction of the first nest does not appear to be strong in the Plain Titmouse. A strong renesting tendency in *Chamaea* (Erickson, *op. cit.*:282) may counteract the smaller clutch size, for the increment to the population as a result of reproduction results in an approximate doubling in both species.

Data supporting the contention made for the Plain Titmouse come from brood counts that are admittedly meager. My counts of 13 broods averaged 5.0 fledglings per family. This figure may be low due to difficulty in accounting for all fledglings. Applying this average to the Strawberry Canyon population for three separate seasons yields the following totals:

Year	Breeding adults at fledging time	Broods	Totals Fledglings	Young plus adults
1947	14	5	25	25 + 14 = 39
1950	12	5	25	25 + 12 = 37
1951	16	?6	?30	?30 + 16 = 46
Ratio of totals				80: 42

In 1947 and in 1950, no brood was produced in territory 2 (= 32), so on a population basis, approximately two offspring are fledged per adult present. On an average, according to the data on rate of replacement of adults, only one of the four offspring produced per pair will survive to become a breeding bird the following spring.

#### DISPERSAL OF JUVENILES

The survival of established adult Plain Titmice and their territorial behavior contribute to a rigid population structure. The impact of this system strikes the juveniles soon after they achieve independence at a time of highest density of the population as a whole. In most of those passerine species which breed at one year of age, the individual is not confronted with the problem of establishment on a restricted area until the onset of the breeding season, at a time when the population density is thinned. In this respect

a Plain Titmouse's first year is compressed, at least in the populations inhabiting coastal California.

The population pressure is alleviated by the dispersal of the juveniles, which results in what Grinnell (1922:378) referred to as a "prodigal expenditure of individuals." Although Goodbody (1952) noted an "explosive" exodus of juvenal Great Tits and Blue Tits in mid-summer from the areas where they were fledged, he found 14 and 23 per cent, respectively, remaining on the 55-acre area in early September. A similar tendency toward lingering was noted among juvenal Plain Titmice in mid-August, 1947 (Dixon, 1949:128), although one juvenile is known to have left his parents' territory one month after fledging. Thus the dispersal is gradual, although none of the juveniles of *inornatus* was seen within its parents' territory by mid-summer.

The completeness of the emigration and the apparent high rate of juvenal mortality are indicated by the fact that so few juveniles ever were identified after they left the parental territories. Only four of the 35 juveniles banded while still associated with their parents on the study area in May or June in three seasons ever became members of the breeding population. These were M13, F14, F44, and M46. Two others (M14, discussed by Dixon, 1949:128, and F58) remained there but did not survive to nest. One male nested outside the area 550 yards from his birthplace; another (M16) settled unmated 800 yards from his birthplace, then abandoned his territory in March of his first year and was found dead 400 yards away when 22 months of age. These values correspond to those which Kluijver (1951:14) reported for the Great Tit in The Netherlands. He found that the majority of juveniles recovered had settled within 200 to 800 meters of their birthplaces. Price (1936:25) found only two of the 145 Plain Titmice banded as nestlings actually nesting in the area where they were reared.

This dispersal, almost certainly density-dependent, since its intensity would be increased at higher densities, is important to the species from three points of view: (a) pioneering, in the sense of Grinnell (1922), to test the suitability of terrain not currently inhabited by the species; (b) the provision of a constant but diminishing flow or pool of potential replacements for vacancies which may be created at any time of the year; and (c) dispersal of genetic traits through the population. This emigration would tend to be more pronounced and to cover greater distances during years of high survival of adults, or when the greater amount of the area was occupied, as in the locality of this study in 1952. Hence, as Miller (1947:187) has noted, the effect of dispersal of genetic traits (average number of territories crossed before settling) might differ considerably from one year to the next as a function of these several variables.

#### SUMMARY

Territorial boundaries in a population of Plain Titmice occupying a 144-acre canyon on the east side of San Francisco Bay were studied intermittently in a six-year period. The basic alignment of six occupied areas remained fairly constant throughout the six breeding seasons. This stability is attributed in part to distribution of blocs of woodland, but the tenancy of long-lived individuals is judged to have had a greater influence. Of considerable importance was the tendency toward maintenance of boundaries following disappearance of neighboring pairs rather than expansion to occupy the vacated areas.

Although most juveniles tend to avoid occupied areas in the period of summer dispersal, their intrusion is resisted actively by the established adults. At this time the established adults defend those areas which have proved suitable for occupation during the breeding season. Many of the territories on which juveniles settle in summer and autumn are abandoned as the breeding season approaches.

Patrolling of boundaries, exchange of song, and pursuit of neighbors along boundaries are conspicuous in late winter and in spring. This "defense" may serve largely to

raise the emotional level of adults in preparation for nesting, since expansion usually is not attempted.

Annual survival of about 75 per cent of the established individual Plain Titmice is indicated from the data on color-banded birds and from the band return data presented by Price. The renesting of 57 of 75 adults indicates an annual adult mortality of 24 per cent and an estimated further length of life of 3.5 years for those adults. These values are higher than those reported for most passerines, but they approach those for the Wren-tit, adults of which also defend a territory throughout the year. Correspondingly, reproductive rate is lowered and a direct causal relationship between adult survival and year-around territoriality by paired birds is inferred.

The dominance of the population by the established adults forces a density-dependent emigration of the juveniles soon after they achieve independence. This dispersal effects colonization of new areas, creates a "pool" of replacements, and contributes to gene flow.

The population of the study area experienced an increase from six to eight breeding pairs from 1950 to 1952; this was achieved through occupation of additional area, the population density in terms of acres per bird remaining essentially unchanged. This fact suggests that territorial behavior may impose an upper limit on population density.

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