

BEHAVIOR OF THE PLAIN TITMOUSE

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This study of the behavior of the Plain Titmouse (*Parus inornatus*) is based on observations of marked individuals of one population followed through an annual cycle. Particular attention has been devoted to matters of territoriality and pairing, and to a comparison of these aspects of behavior in *Parus inornatus* and other parids. A banding study of the Plain Titmouse, carried through six seasons at Palo Alto, California, by Price (1936), is the only extensive work done on this species previously. Price provides information important to an analysis of population turnover and pairing relations of individuals, but his study was carried on only during the nesting season and hence does not present a picture of the annual cycle. Most other information on *Parus inornatus* available in the literature is fragmentary.

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The study was made in Strawberry Canyon on the campus of the University of California at Berkeley between September, 1946, and May, 1948. A large part of the field work was completed in the spring of 1947. This field work was interrupted by my absence during June and July, 1947. The study area extends along Strawberry Creek for a distance of three-fourths of a mile and is about three-eighths of a mile wide; its altitude varies from 500 to 900 feet. The vegetation of the north and south slopes of the canyon differs markedly due to slope exposure. This plant cover may be classified under seven categories (see map, fig. 14). Conifers are the only exotic trees present; two genera are prominent, *Sequoia*, restricted to the shaded slopes, and *Pinus*, represented by several species. However, groves of eucalyptus are found in adjacent parts of the canyon. A major indigenous element is an evergreen woodland, dominants of which are coast live-oak (*Quercus agrifolia*) and California laurel (*Umbellularia californica*). On the south-facing slope, this formation is restricted to the side draws, the intervening ridges being grass covered (fig. 15). Two general types of brush are found in Strawberry Canyon, a more or less compact chaparral of the dry, sunny slopes dominated by coyote-brush (*Baccharis pilularis*) and poison oak (*Rhus diversiloba*), and a more broken, chiefly deciduous brush of the shaded slopes with such constituents as thimble-berry (*Rubus parviflorus*), elderberry (*Sambucus glauca*), hazel (*Corylus rostrata*), and wild lilac (*Ceanothus* sp.). Many of the shrubs of the latter association also occur as undershrubs in the oak-laurel woodland. Occasional oaks may be found scattered through the chaparral, or the woodland and chaparral formations may be mixed. Two deciduous riparian associations are distinguishable, one of shrubby growth form with willows (*Salix* sp.) and creek dogwood (*Cornus californica*) as important elements and another in which trees form small groves, usually in linear arrangement, along the stream courses. Chief species of the latter type are alder (*Alnus rhombifolia*), elderberry, and willow. A grass-herb association of numerous species is characteristic of the sunny slopes.

METHODS

After a preliminary survey, a program of color-banding was begun in November, 1946. The birds were attracted to walnut meats placed on elevated feeding trays in live-oaks; they could be retaken repeatedly in the same traps after they became accustomed to this bait. The traps were of the Potter two-cell (drop-gate) type. No attempt was made to band nesting adults or young in the nests. Titmice were banded with both

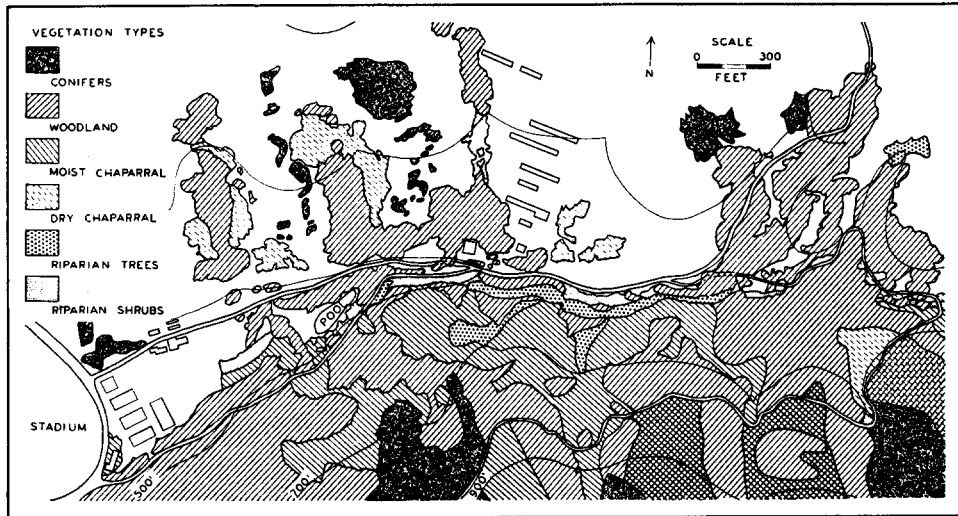


Fig. 14. Vegetation types in study area in Strawberry Canyon, Berkeley.

aluminum and colored bands, each individual receiving a distinctive combination. In subsequent discussion, males will be designated by the letter M combined with the number of the territory occupied, while females will be designated with the letter F. Sex of individuals could be determined only by observed differences in behavior during the breeding season, the chief one being the "whistled" song of the male. Titmice banded in late summer and early autumn were aged according to the method of skull examination described by Miller (1946:34).

These birds were followed subsequently and their movements and behavior recorded. Because the lower part of the canyon was readily accessible, attention was centered upon the three or four pairs of titmice there. Hence records of the birds in the upper portion of the study area are often fragmentary. However, greater attention was given these individuals in late summer and autumn.

Despite precautions on my part, the normal activity of the birds was interfered with in several ways. At times the titmice obviously were disturbed by the presence of an observer while they were foraging, and repeated trapping in some instances also disrupted their movements. Blinds were not used while nests were observed and as a result, normal patterns were interrupted. The most serious interferences were the accidental deaths of four members of the population as a direct result of trapping activities. I did not introduce nest boxes, since such a factor might influence normal population density.

HABITAT RELATIONS

Throughout its range, the Plain Titmouse is normally found in greatest abundance in the dry woodlands of small, chiefly evergreen trees characteristic of the southwest. The coastal races of this titmouse in California inhabit woodland in which oaks predominate, whereas those of the Great Basin and desert mountain ranges frequent, for the most part, piñons and junipers (Grinnell and Miller, 1944:307).

The principal habitat requirements of the Plain Titmouse can be satisfied in the woodland formation. Most tangle of these are an elevated foraging niche, nest cavities, and roost sites, either in cavities or foliage. In Strawberry Canyon, the evergreen coast live-oaks form a more or less continuous canopy of foliage which serves to protect the

foraging birds from overhead attack and from rain and wind (fig. 16). The open spacing of the trees and the general absence of foliage beneath the canopy enable the birds to detect the approach of enemies from beneath. The necessity of this foraging "cover" is suggested by the alertness of titmice while they are seeking food; they look up continually and often will pick an item such as an acorn from the foliage and carry the food to a perch offering greater visibility before consuming it. They will drop to the ground only if undergrowth is absent and then will carry the food upward to a suitable perch. Likewise, titmice are seldom seen on the outside of this dome of foliage unless it be in the uppermost branches where the view is unobstructed. The canopy is supported by a network of branchlets and twigs which afford the titmice considerable forage surface. They devote a large share of their food-gathering time to bark gleaning. Such would have to be true in large areas of deciduous blue oak (*Quercus douglasii*) woodland in winter.



Fig. 15. South-facing slope of Strawberry Canyon, March 3, 1948.
Photograph by Nathan Cohen.

While most of the food taken seems to be animal, oak and willow catkins, poison oak berries, and leaf buds have been taken. Beal (1907:69) found that the diet of this species consists of 43 per cent animal and 57 per cent vegetable material. This result was based upon examination of 76 stomachs, at least three for every month of the year. The fact that cultivated fruit and oats were found to be items of the diet suggests that some of the specimens may have been taken in agricultural areas and hence would not reflect precisely the situation to be found in the more typical haunts of this species, where, according to my observations, the percentage of animal material would be higher.

A factor which may limit the population density of this species is presence of cavities for nest sites. Mature live-oaks furnish rotted out cavities of a sort usable by titmice and to a lesser extent so do alders, willows, and elderberries, where these have trunks several inches in diameter. In the Great Basin area, old twisted juniper trunks provide cavities suitable for nesting (Grinnell and Miller, 1944:307). Johnson, Bryant, and Miller (1948:305) comment upon increased density of this species in an area where woodpecker holes in Joshua trees afforded more nest sites than were available in surrounding areas of piñon and juniper woodland. Titmice readily accept nest boxes and

have been known to nest in a variety of artificial situations. However, these conditions do not prevail over any appreciable area of the range of the species and hence are of negligible importance.

Adequate roosting cover is also necessary for the existence of this species. Natural cavities may be used; the nest site is used for this purpose by the female, in one case for a month prior to laying. Grinnell (1923*b*:176) mentions the use of cavities for roosting and notes warping of the tail feathers as an indication of fixed habits of orientation in the cavity. Huey (1927:216) mentions a case of a titmouse roosting on a twig sur-



Fig. 16. Oak-laurel woodland of south-facing slope, March 3, 1948.
Photograph by Nathan Cohen.

rounded by leaves. I have found such use of dense foliage to be more common. Cover of this sort is provided by the crown foliage of live-oaks or, on the local study area, by accumulation of dead needles in interlaced branchlets of *Pinus attenuata*. Apparently a cavity-like situation is simulated in these roosts surrounded by foliage, thus giving the birds a feeling of sufficient concealment.

ANNUAL CYCLE

Price (1936) determined that adults of this species nest in the same locality in successive seasons and, as a rule, mate with the same bird if the latter is living. He trapped titmice in their nest boxes and encountered difficulty in obtaining return records on both members of a nesting pair. Over a six-year period, 1928-1933, at Palo Alto, California, he obtained 51 records of renesting of adult titmice. In 50 of these, the individuals renested within 90 yards of their nest sites of the previous season, evidence suggesting that this renesting was within the same territory. In 33 instances the same boxes were used, and if the boxes were not occupied again, they were taken over by other species rather than by other titmice. This latter fact may indicate that these titmice used natural cavities within the territories for nesting. Of fourteen pairs, eleven remated for at least one season. If an individual lost its mate, that bird retained its territory regardless of its sex and mated the following season with a first-year bird. Of 145 nestlings banded, only two were retaken nesting in the study area.

By the close of the 1947 nesting season, I had under observation one unbanded and

six banded pairs of titmice. I followed these birds as individuals and pairs throughout the subsequent seasons. Of the banded birds which survived until the next nesting season, six of seven occupied the same small areas throughout the year. The seventh bird, a female, "divorced" her mate and moved into an adjacent, vacated territory, being supplanted by a bird of the year. The female that moved, F5, had paired with a young male by November, 1947, but disappeared in March, 1948. Price (1936:27) reported a similar case of "divorce" in which the male moved elsewhere. Of the six pairs, two remained intact, accidents or unknown circumstances claiming one or both individuals of the other adult pairs, with the exception of the "divorce" case cited. I found that the birds which had been paired in the spring of 1947 remained in close association on their territories throughout the late summer, autumn, and winter months. Continuity of pairing and occupancy of territories is shown in figure 18.

The extremely sedentary nature of titmice is shown by the fixity of habit which I have observed among the birds of the Strawberry Canyon population. For example, two male titmice utilized the same roost sites during parts of two successive winters. One individual which had roosted in a clump of pines during October and November, 1946, was identified there on January 12, 1947. He shifted his roost in March to a site nearer the nest. Observations on roosting in this territory were not made again until November 6, 1947, when this bird, M 1, was flushed from the same clump of pines seven and one-half minutes before sunset. Another male, M 2, used the lowermost bough of another pine for a roost in February and early March of 1947 and again in November and early December of 1947. Fixity of roost site may lead in turn to establishment of forage routes, for titmice commence foraging upon awakening and may continue along a definite route. Over a period of several weeks, titmice of one pair may be seen in a given part of their territory at comparable times on successive days.

In other parids, we find differing tendencies toward sedentariness. Kenrick (1940:208) found that populations of the Blue Tit (*Parus caeruleus*) in England were partly resident and partly migratory. Some of the resident individuals nested in the same area in successive seasons. Morley (1942:262) found that some individual Marsh-tits (*Parus palustris*) hold territories throughout the year in England, while others, subordinate to them, travel in flocks and establish territories in January. Van Tyne (1948:121) suggests that adults of the Tufted Titmouse (*Parus bicolor*) inhabit a restricted range throughout the year. Odum (1941a:118) suggests definite attachment of individual Black-capped Chickadees (*Parus atricapillus*) to the winter range of the flock. This appears to be an individual rather than a group response.

To summarize briefly the annual cycle, it may be stated that the Plain Titmice nest on the territories used in the fall and winter if the area selected contains a suitable nest site. Nest construction ordinarily begins in March in the San Francisco Bay region and incubation is usually underway by early April. The young birds remain in the nest for approximately three weeks after hatching. After the young leave the nest, they remain with their parents in a family flock for about a month. Subsequently they leave the area or are driven out by the adults which continue to occupy the area. I have found no indication that more than one brood per year is raised.

VOICE

Interpretation of all the shades of meaning of such highly variable call notes as the Plain Titmouse uses is virtually impossible. However many of the vocal utterances are used repeatedly in situations which are essentially similar and hence can be correlated with function. A primary division must be made distinguishing the song of the male from other call notes of the species. Nice's definition of song (1943:144), "A warning

to other males, an invitation to a female," is applicable to the Plain Titmouse. Such song is heard during sexual fighting of the male and it is given by unmated males. The song thus defined in a biological sense also has the qualities of melody which make it a song in the esthetic sense as well. This song is given also in times of unusual excitement, such as following the handling involved in trapping. Additional functions of male song in dominance relations and leadership of the brood and mate will be discussed later.

The male songs of the Plain Titmouse are of two basic types, both of clearly whistled phrases usually repeated three to five times. One of these has been described as *peter peter peter*, the accent falling on the first syllable when the song is uttered rather slowly, and on the last when singing is rapid. In either case the first syllable of each phrase is higher in pitch. This song apparently corresponds phonetically to the *peto* song of the Tufted Titmouse (*Parus bicolor*), although Bent (1946:402) quotes A. A. Saunders as stating that it is given by both sexes. A second general type of song apparently is unique to the Plain Titmouse and is heard less frequently. I have described it as *sweet sweet sweet*, each phrase a clear rich whistle of rising inflection, rarely slower in cadence so that each note sounds as though it were of two syllables *sa-weet* or *sureet*, with accent on the last syllable. The two basic types of male song seem to be used interchangeably with no detected functional differences.

A category which may be designated as sub-song actually may consist of several functional entities. One function seems to be as a dominance note similar to that described by Odum (1942a: 503). Use of a slowly-enunciated, subdued *wee-to*, somewhat like a *peter* note or a more prolonged song phrase *see-yor*, was noted accompanying aggressive behavior of males in fall and winter and also was directed by the male toward his mate. In both situations it was frequently accompanied by a pugnacious movement which forced the other bird to shift its perch. Hence this note is of an aggressive nature and may function as a substitute for a full-length song when used during combat or while the aggressor is in flight. Another call also used by the male exclusively was a series of rapidly uttered phrases which I recorded as *souey souey souey*, lower in pitch and less melodious than those described above. Another call, perhaps corresponding to the "fighting note" of the Black-capped Chickadee, is a loud emphatic *sisip* uttered by the aggressor when in pursuit of an adversary. This note appears to function in control of the female much as the song does.

Other vocal sounds of this species also fall somewhat within the category of song in its biological definition in that they serve as a warning to other individuals that a territory is occupied. Such calls which are given by members of either sex throughout the year consist of a dry scratchy *tsicka dee dee*. This rhythm is characteristic of a series of variations which differ markedly in quality. Calls of this basic type seem to correspond to what Odum (1942a:502) has called the "general call note" of the Black-capped Chickadee, and appear to function in advertisement or as an expression of self-assertion, in some cases being given without relation to evident external stimulus. A third use is to maintain or re-establish contact between birds separated while foraging. Under these routine conditions the notes are given in a matter-of-fact way; in other situations, greater emotional stress is indicated by the pitch, intensity, and rapidity with which they are uttered. Stimuli evoking this more pronounced response include presence of hawks, owls, and other enemies, or intruding titmice. Calls of similar tone may be used by a bird flushed from its roost or startled by an observer while foraging. I have noted no sex differences in the use of these notes.

Members of a pair while foraging close together frequently give soft lisping notes which may be transcribed as *sip* or *sisip*; these appear to function as location or flocking notes, corresponding to the "contact" note of the Black-capped Chickadee. Apparently

identical notes are uttered as though automatically by widowed titmice while foraging alone. A two-syllable somewhat louder *sisip* may be given by the male approaching the nest during incubation and later by both parents when approaching the nest with food. This is the only call corresponding to the "signal song" of many passerines.

Scolding notes directed toward intruders are lower in pitch and harsher than the *dee* notes of the general call and may be written as *chur durr durr*.

Alarm or fear notes are given at times when the titmouse appears to be frightened, for instance when first handled in a trap or when startled while foraging. Fear notes are high-pitched and thin and may be described phonetically as *see see see*, the notes being of one pitch only. These may be combined with scolding notes when the intruder is in view or when the bird is frightened off the roost. In addition, a screech may be given when the bird is handled, even though no pain is involved. This note, particularly characteristic of juveniles, apparently is a fear note also.

Incubating birds when disturbed at the nest give an explosive "intimidation" note which combines elements of hissing and puffing, a vocal threat which is characteristic of a number of members of the genus *Parus*, according to Bent (1946:351).

A twitter apparently indicating sexual excitement, used by birds of either sex, and the more emphatic begging notes of both females and juveniles will be discussed in connection with breeding behavior.

Odum (1942a:501) described 16 functionally different types of vocal utterances of the Black-capped Chickadee. I have failed to distinguish as many, a fact which may be due in part to the less gregarious habits of the Plain Titmouse. Odum pointed out that the variety of call notes of the chickadee seems to result from expansion of a few basic types; this statement is equally applicable to the Plain Titmouse.

MANNER OF TERRITORIAL DEFENSE

Because of its drab coloration and habit of frequenting dense foliage, the Plain Titmouse is not a conspicuous bird and indeed is difficult to locate unless its calls are heard. Since visual perception is reduced, most communication between individuals is by vocal means. The attitudes of titmice while giving advertisement calls are in keeping with other elements of their habitat relations. Rarely does a bird take a conspicuous exposed perch while making its declaration of territory, either during autumn or winter boundary disputes or during spring singing. Calling or singing takes place most frequently from a perch well protected by the canopy of foliage or by twigs of deciduous trees.

Detection of titmice intruding on territories correspondingly is most often by auditory means. I have seen a titmouse answer a general call given by a rival over 100 yards away. However, visual stimuli certainly are used at shorter distances. Action against an intruder may consist of scolds, calls, or song, often in combination with wing vibrations. Such threats frequently are sufficient to cause retreat of the trespasser. On other occasions, particularly at first contact of two individuals in establishment of a boundary, pursuit and, rarely, combat may occur. In this drab species there are no patterns to be brought into prominence, and hence associated physical expressions, such as puffing out of feathers in aggressive display, are lacking. A threatening posture in titmice appears to be an attitude of potential movement toward the intruder and may be accompanied by wing vibrations in particularly intense encounters. The pursuit which follows may be a flight toward the perched bird or to a position beside it, the objective in either case being to drive the bird from that perch. Colquhoun (1942:237) used the term "approach-threat" to describe a darting movement of one Blue Tit toward another in

establishment of dominance relations. This term will be used henceforth to designate a pugnacious movement by which one titmouse forces another to shift its perch.

THE FUNCTION OF TERRITORY

The territory concept in its broadest usage follows the definition of Noble (1939: 267): "A territory is any defended area." In further definition, "sexual and nesting territories are characterized by sexual or nesting activity, in contrast to a retreat which is occupied because it is familiar and defended because any newcomer is irritating to the resident." Noble later (p. 271) speaks of this last category as "an isolated retreat . . . defended . . . against intruders at any season." We find in the behavior of the Plain Titmouse a condition comparable to this last category. My observations suggest that in many instances the "retreat" territory is defended by both sexes. Boundary disputes involving both members of each of two pairs were more common during early spring, but were seen occasionally at other times throughout the year. However, defense of territory by only one member of a pair is not of uncommon occurrence.

On August 17, 1947, a male, M 6, was observed fighting a pair of intruding immature titmice while his mate did not take active part. He sang during his attacks on enclosed immature male, M 13. Once M 6 chased an unidentified titmouse away and returned to fight the trapped male. He left when I climbed the tree to open the other cell of the trap, but returned to fight and was trapped 13 minutes later. I removed M 6, leaving M 13 in the trap for 15 minutes, but the mate of M 6, presumably the bird which had scolded from north of the trap when I removed M 6, did not try to attack the intruding male. Despite the artificiality of this situation and the possible disturbance of M 6's mate when I removed him from the trap, there is indication of defense against both intruders rather than mere fighting between males. Similarly defense of an occupied area by the female alone has been observed, in some cases when the male was present.

These examples are typical of many instances of aggressive behavior observed in this species throughout the year. The objective seems to be maintenance of established boundaries against intruders or neighboring pairs which might attempt expansion of territory at the expense of the defender. Participation may be by the male or female or by both, depending apparently upon the external situation and internal states of the individuals concerned.

However, in addition to this year-round defense of a "retreat" territory, there is a period of more intense combat in early spring. This fighting between rival males is most conspicuous and is chiefly vocal as shown by examples cited previously. These contests in spring are characterized by the singing of one or both of the (male) principals, and, since song occurs rarely at any other season, it appears that its function differs from that of the "advertisement" calls used by birds of either sex in territorial defense throughout the year. Song then must be a means of defending some object which is of particular importance during the season at which song is a conspicuous element in male titmouse behavior. Possibly it is the female which the male seeks to defend by song. Tinbergen (1936:5) states that "the fighting before and during the formation of sexual bonds, therefore, serves to secure objects or situations which are indispensable for reproduction." The female, at this season, in addition to being a social companion on the "retreat" territory, is also an object necessary for completion of the breeding cycle. Song and fighting appear to be more intense when the female is present.

While in a majority of cases, this "sexual fighting" occurs between rival males, it may also take place between rival female titmice. Although I have never witnessed an isolated fight between two known female titmice, the occurrence of such combat is suggested in observations of other situations.

The male of territory 1 was killed on January 11, 1948. Several days afterward, the male of the adjacent territory, M 2, began trespassing and was accompanied on these visits by the widowed

female. However the mate of M 2 never crossed the territorial boundary except when accompanied by M 2 and at a time when the defending female was not present near the boundary. Observations of similar reactions between other female birds have been made.

Tinbergen (1936:3) states that female Snow Buntings fight and that they "attack almost exclusively other females. The females fight only in the presence of the males. The function of this fighting of the females, therefore, cannot be sought in defense of territory alone, for it results in securing a mate, as they do not allow another female to come near the male." Odum (1941*b*:326) cites instances of combat during the "pre-nesting" period of the Black-capped Chickadee in which "the fighting was clearly in defense of mates and not of territory since the birds involved later established territory elsewhere."

In conclusion, it appears that in the case of the Plain Titmouse, the concept of area in Noble's definition of "sexual territory" and indeed his definition of territory as defended *area* should be extended to include Tinbergen's earlier idea of ". . . objects or situations which are indispensable for reproduction." In this sedentary species, there is superimposed upon the year-around defense of an area a period of fighting not related directly to that area but toward other elements of the total situation involved in reproduction.

SIZE OF TERRITORY

Territories have been plotted essentially as they existed in early March in each of the two breeding seasons (fig. 17), and the areas measured by the use of a planimeter. Twelve territories occupied by pairs at least at the beginning of the breeding season averaged 6.3 acres in area, ranging from 3.3 (territory 5) to 12.5 (territory 1). The large size of the latter appears to be the result of scattering of the necessary vegetational elements of the environment, which in this case covered an area of 6.9 acres. These computations are subject to slight discrepancies resulting from slope which was not taken into account in measuring the plane surfaces. In the study area mapped for the 1947 season (fig. 17), approximately 43 of a total of 144 acres were occupied by titmouse territories. Size of territory was found to be constant throughout the year where both members of a pair survived.

Hutchinson and Hutchinson (1944-1947), in censusing the breeding birds near Santa Barbara, California, found the following densities of Plain Titmice in a 17-acre area consisting of 90 per cent live-oak woodland. In 1944, there was one pair; the next year, two nests; in 1946, two pairs were seen; and in 1947, three nests were found, indicating a density not unlike that found in Strawberry Canyon.

The size of territory of the Plain Titmouse may be compared to that of a number of passerine species of similar size. Odum (1941*b*:329) found for 15 territories of the Black-capped Chickadee an average of 13.2 acres, while Erickson (1938:277) found territories of the Wren-tit (*Chamaea fasciata*) in dense brush averaged 0.8 acres.

PAIR-FORMATION

Odum (1941*b*:317), in a review of the literature on the Paridae, found among birds of this family tendencies toward permanence of mating and of pair-formation prior to establishment of nesting territories. He found that pairing of Black-capped Chickadees in New York State occurred at the time of break-up of winter flocks. Although in seven of eighteen pairs studied, both members were from the same winter flock, he states (1942*a*:526) that "apparently the bond (if any) between the pair is ill-defined during the winter flocking period." He states further (1942*b*:157) that he found no evidence of divorces among banded individuals which had been mated during the previous nesting season. Gillespie (1930:121) indicates that permanent mating may occur in the Tufted

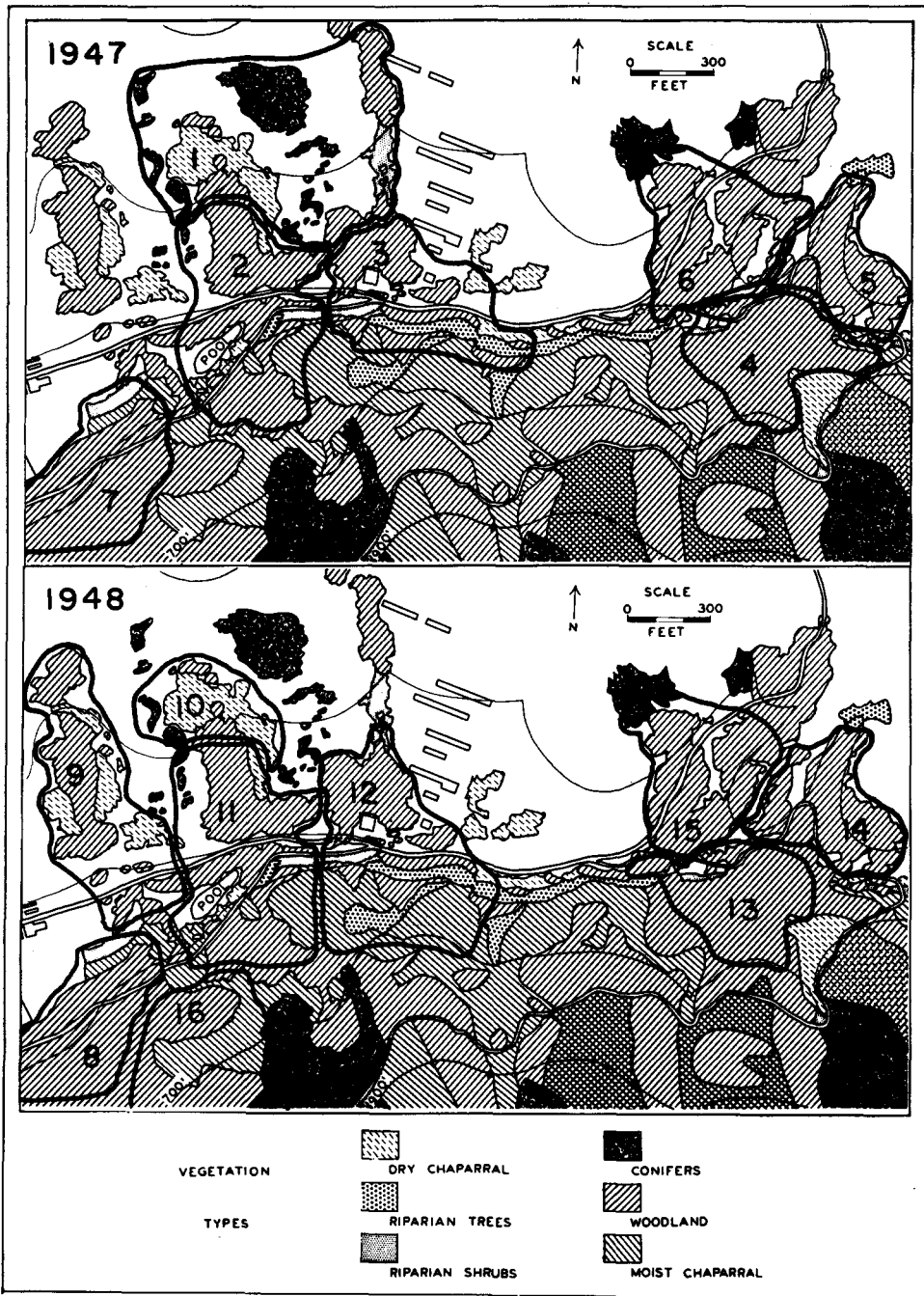


Fig. 17. Maps of territories of Plain Titmice in Strawberry Canyon as of March 15, in 1947 and 1948.

Titmouse in Pennsylvania. In speaking of winter flocks, she stated that "further manifestations of the group habit are shown in the tendency of Titmice to 'stand by' when one of their number is in difficulty. . . . when one fails to get out [of a trap] there is almost always another Titmouse near by (usually but one), calling excitedly and waiting for its comrade." Here the lone bird may be the mate.

The Plain Titmouse differs from these species in that winter flocking does not appear to be the rule. Following the break up of family groups in late summer, pair formation may occur among immature birds in a manner similar to that for the Black-capped Chickadee, insofar as it follows a flocking period and may occur without reference to territory.

On August 17, 1947, I succeeded in trapping an unbanded titmouse which was paired with a bird which I had banded on June 1, 1947, about 650 yards away. Skull examination showed the former was an immature bird. Members of another pair banded, respectively, on October 26, and November 8, 1947, were both immature birds. Grinnell (1923a:135), while collecting in Modoc County, California, on September 27, 1922, took a pair of titmice both members of which were birds of the year.

Another manner in which pair-formation may occur in the Plain Titmouse is exemplified by those cases in which widowed adult birds established on their territories remain there, later pairing with wandering young individuals. This type of pairing took place in territory 3 (see map, figure 17) prior to August 7, 1947, when the male, M 3, widowed since late April, was found paired with a female, subsequently banded F 12 and found to be immature. She was found mated with an unbanded male on that territory following M 3's (presumed) death prior to February 1, 1948.

Dominance and its relation to pair formation has been discussed by a number of workers. Noble (1939:264) distinguished two types of dominance, sexual and social, attributing them to two fundamentally different drives. He states that "the [social] dominance drive in all vertebrates is continuous, not cyclic like the sex drive. Further, the latter has a well-known hormonal basis unlike the former." Odum (1942a:521) interpreted chasing and fighting among immature chickadees in late summer and autumn flocks as "indicating that establishment of dominance is a fundamental social trait." I observed similar quarreling among immature titmice not yet paired nor established on territories.

Studies of dominance relations in winter flocks of the Black-capped Chickadee have been made by Hamerstrom (1942) and Odum (1942a). There were no opportunities for observations of dominance in the present study since the system of territories limits the numbers and extent of contacts between adult titmice of neighboring pairs. However, behavior of individual birds in such situations suggests some degree of dominance.

The male M 2 appeared to be dominant over at least two neighboring males. This opinion is based upon his penetration of the territory of one adjacent pair on several occasions and his leisurely manner of retreat when accosted by this defending male along the boundary on May 1, 1947. M 2 acted as though confident that the other bird would not attack him. In a boundary dispute three hours after this aggressive male and his mate had completed a foray fifty yards into their neighbor's territory on December 13, 1947, the defending male M 1 was not particularly aggressive. During his absence half an hour later, the aggressive male trespassed and pursued his mate, forcing her to shift her perch. This aggressive male sang little during the early spring months of 1948. In an encounter with a young male, M 9, established where there had been no titmice previously, M 2 alternated *sickadee* calls with the song of the other bird and let him initiate the attack in which the younger bird was vanquished. The fact that M 2 did not sing nor vibrate his wings as the younger bird did in a second encounter on that morning suggests that the former was more confident and not as excited as was M 9. This situation was not comparable to the defeat of an intruder within one territory, since a new boundary was being established. Another newly established male, M 12, was never seen attack-

ing M 2 on their boundary, but sang from perches several yards away from the border. On April 9, 1948, the two carried on a song battle for one and one-half hours. During this time M 2 rarely vibrated his wings and shifted his perch less frequently than did his nervous adversary. In the latter two cases, the familiarity of the established bird with the area should be considered.

A question arises as to how such dominance might be achieved. Schjelderup-Ebbe (1935:953) mentions strength, courage, and circumstances surrounding the first encounters of the individuals concerned as being the factors which determine which of two birds shall become the despot. Considering the third of these factors, it is conceivable that a situation such as the fight of a territory-defending male against a trapped intruder could give the former a "psychological" advantage over the latter, even though the meeting was not their first. The aggressive male, M 2, actually fought his neighbor, M 1, while the latter was in such a disadvantageous position on February 16, 1947. The outcome may have favored the victor on subsequent meetings. It appears, then, that social dominance is an attribute of titmice although a hierarchy is not found among adult birds because of the system of territories.

Odum (1941*b*:323) suggests that dominance may play some part in pairing of the Black-capped Chickadee. The following observation may shed some light on this in the Plain Titmouse.

After the death of M 1 in territory 1, on January 11, 1948, his mate, F 1, permitted trespassing by the neighbor male, M 2, who had dominated her on one observed occasion on December 13, 1947. Here the individuals had been known to each other for at least one year. This female remained close beside the intruding male, apparently entirely submissive as he foraged for half an hour in her territory on the morning of January 17. While the birds were concealed behind vegetation, I heard a "dominance note," preceded by a sharp note also of aggressive nature. Even after this rebuff, the female remained with the intruder and when M 2 flew toward his own territory, F 1 flew after him so quickly that the flights appeared to have been initiated simultaneously. During this period of trespass, the mate of M 2 remained in her own territory, calling to her mate at frequent intervals.

BREEDING BEHAVIOR

Because pair bonds of at least a social nature have been formed long before the onset of the breeding season, there is no need at this time for establishment of territory and attraction of a mate. There remain matters of synchronization of activities so that mating, nest construction, and rearing of young can be accomplished. As the breeding season approaches, the males apparently are in advance of the females in developmental phases of the gonad cycle, as has been shown by a number of workers on other species. An early manifestation of this advance toward breeding condition is the appearance of song in the males.

In the earliest phases of "courtship," song may be followed by an "approach-threat" directed toward the female and often accompanied by use of the "dominance note." Later the female may take flight rather than shift her perch. In such cases there ensues a pursuit, at last functionally similar to the "sexual flight" of the Reed Bunting, *Emberiza schoeniclus* (Howard, 1929:9), in which the male attempts to overtake and mate with the female, who takes flight presumably because she is not ready to copulate. The sexual flight of the Plain Titmouse differs in that flights are for very short distances, often within one tree or patch of shrubbery. Armstrong (1942:290) has suggested that such pursuit may influence metabolism and so promote ovulation. Hence what Wolfson (1942:259) has spoken of as a "behavioristic stimulus for the late and rapid development of the ovary prior to nesting" may be effected in part by this activity.

The avoidance by the female of the physical manifestations of the male's advanced condition are shown in her reaction to the approach-threat by shifting the perch and later by flight resulting in sexual chase. Such indications of disparity in readiness for

breeding are particularly evident within Plain Titmouse pairs in the San Francisco Bay region in mid-February. Males then are active in territorial disputes which are emotional level-raisers for them. A male, stimulated to a high degree at the close of an encounter with a neighbor male often will direct an approach-threat toward his mate and a sexual flight may result. The male is stimulated above a normal level by a situation often not particularly stimulating to his mate.

Such was true following a dispute on February 14, 1948, when the aggressive male M 2 flew past his mate while she was foraging and uttered a dominance note. This act was repeated a minute or so later. Again on February 23, he chased her repeatedly immediately following a dispute with another neighbor. The female had not participated in either contest. The following day, while the pair was foraging, the female discovered a cavity in the trunk of a live-oak. She perched beside the crevice, peering into it, quivering her wings and giving a twitter. The male, a few feet overhead, ignored her and the female resumed foraging within one minute. Here are several examples of lack of synchronization in the activities of one pair.

On several occasions, as in those already cited, females were observed giving what may be termed an invitational or begging display, a twitter consisting of soft, rapidly-uttered notes *sit-sit-sit*, usually accompanied by quivering of the wings. Early in the season, the external stimulus seems to be the sight of a potential nest cavity; later, the presence of the male appears to evoke the response. Where the latter seems to be the cause, the attitude clearly is invitational and the displaying bird often looks at its mate during the action. This display, involving the soft lisping twitter and wing quivering, while given by birds of either sex in times of sexual excitement, was most characteristic of the female. However, display involving wing quivering is not restricted to courtship situations alone. Both males and females were seen fluttering their wings during periods of nestling care and males occasionally did likewise prior to or during combat.

The male frequently ignores this display of the female at first, but later, as the twittering becomes more vigorous and is continued for longer periods, he may respond by feeding her. As the sporadic twitter becomes more pronounced and continuous, it resembles the chattering call notes of fledglings a day or two out of the nest. At this stage her posturing and begging notes act as releasers of the feeding behavior of the male. His feeding actions differ as the cycle advances. At first he will fly and perch beside the begging female, facing in the opposite direction, pausing only to leave what apparently is an item of food on the perch beside her. This she picks up eagerly as he leaves, and her begging ceases, at least momentarily. Later, the male will feed the female directly, apparently passing the food to her with his bill placed alongside hers. Still later, one bird may tilt its head, the food being transferred as the birds face each other. The begging of the female becomes more vigorous during the period prior to incubation and during inattentive periods, at which times her twitter is of a scolding tone. As the male approaches with food, her calls increase in intensity and she reaches toward him actively to take the food.

The frequency and intensity of this invitational display (prior to the vigorous begging of the incubation period) apparently is an index to the physiological state of the female and indicates a state of submissiveness. As the submissiveness becomes increasingly evident, aggressive behavior of the male wanes, being replaced by a more benevolent type of dominance and leadership. Here is revival and formalization of one aspect of the parent-juvenile relationship in breeding behavior. During inattentive periods of incubation, the female may be seen foraging actively until the male appears and is greeted by vigorous begging. Lack (1940:171) has pointed out the secondary value of the food contributed in a case such as this and the symbolic significance of this feeding. The function of the display is to strengthen and maintain the bonds of the pair until the

male can assume a more active role in the task of feeding the young. Earlier in the cycle it may aid in raising the level of excitation so that copulation can be effected.

Although the female appears to choose the routes at the time when nest site selection is in progress, once the site has been chosen, the male apparently assumes leadership in regulating most of the activities of the pair. This direction is effected in a large part by his use of song. In the course of foraging, the male may advance several yards and will sing almost continually until joined by his mate, after which the song ceases abruptly. The song heard most frequently in such situations is a rapid clear whistle *petur petur petur*. The same song is used by the male in leading the brood in the days following their departure from the nest. Song then appears to be a releaser inducing the juvenal birds to follow the male parent and likewise releases following behavior on the part of the female at this stage of the breeding cycle when other elements of fledgling behavior are revived. In this manner song serves as a means of the maintenance of dominance by the male. A further indication of submissiveness of the female was her answering of each song of the male with a location note or twitter.

I have observed considerable variability from one pair to the next in stage of the breeding cycle reached at a given date, in relative lengths of some phases of the cycle, and in degree of display. Such conditions could be the result of circumstances such as prolonged rivalry which might delay interest of the male in nesting activity, individual differences in aggressiveness and degree of dominance exercised over the female, and variables such as weather. This point is of interest in connection with observations on the birds in territory 13 in 1948.

In late autumn of 1947 and again on February 24 and March 7, 1948, the male, M 13, appeared to be paired with the female "divorcee," F 5, mentioned previously. His dominance seemed evident in his actions and in her apparent submissiveness when he sang. Further observations were not made until April 3 when M 13 was found with an unbanded female bird. Activities of the pair centered about the nest site used by two other individuals the previous year. The female begged occasionally and the male fed her, the feeding actions being noticeably undemonstrative and somewhat characteristic of early phases of the breeding cycle in which transfer of food is hurried and indirect. Dominance of the male seemed incomplete in comparison to the actions of other pairs. The two birds foraged following courtship feeding on April 6; then the male perched beside the cavity with food in his beak, calling, but she continued foraging independently. She did not respond to song at this time either. On a foraging excursion on April 9, he led the way back toward the nest 40 yards distant, singing *petur petur petur*. She refused to follow and he flew back and accompanied her in foraging for another seven minutes before advancing toward the nest area and inducing her to follow, again by use of song. Behavior in this situation suggests the need for gradual conditioning and the achievement of male dominance over a period of time greater than the one month interval known to have been available here. Further evidence is furnished by the fact that this pair failed to raise a brood. By May 2, the male had abandoned his territory, moving to the vacated territory 15, where he was accompanying an unbanded female, presumably the same one he was mated with most recently on territory 13.

The question of dominance is in need of clearer definition and more study. In the case of the Plain Titmouse, examination of evidence in the light of survival value may be in order. Odum (1941b:325) has stated that during the "pre-nesting" period following pair-formation in the Black-capped Chickadee, "there is nothing in the behavior of the pair to indicate which is male and which female. Neither sex seems to be the leader during feeding excursions since first one bird then the other would be observed moving ahead." Precisely the same relationships exist within a pair of Plain Titmice throughout the year. Allee (1938:196) cited evidence showing that in flocks of the domestic chicken, foraging leadership was not identical with position in the social order. In foraging of the Plain Titmouse at times other than the breeding season, it does not appear that continued leadership of one bird would carry survival value, since at that

time, both birds are equally concerned with foraging and other routine activities and perhaps each is equally capable. However, during the breeding season the concern and energies of the female are directed toward the fulfillment of other functions. Here there should be survival value in the male's guarding of the female and regulation of the activities of the pair. Moreover, Lack (1939:191) has pointed out the necessity for male dominance, since the female must assume a submissive posture in order for mating to be accomplished. Further, this dominance aids in maintaining the excitatory level necessary for completion of later phases of the nesting cycle.

Behavior of the male toward the female in early phases of the breeding cycle seems to involve dominance in that there are unilateral aggressive contacts initiated by the male. These actions of the male possibly initiate advances in the ovarian cycle of his mate, resulting in inhibition of dominant (resistance) behavior and releasing the submissiveness characteristic in later phases. Such behavior is cyclic, demonstrating differences in the expression of a sex drive which is assumed to be of equal strength in both sexes. The male's dominance in early stages, presumably caused by more advanced state of the gonad cycle, may be called "sexual dominance" since it reflects sexual state and its expression does not differ from other aggressive actions. However, it also might be considered as a revival of previously determined social dominance reinforced by sexual excitement. Certainly at other times when social dominance in this species is expressed, the level of excitement is well above normal for that season. Song is called forth occasionally by stimuli other than sexual ones. On two occasions in August and September, 1947, a young male sang upon his release after being trapped and handled. Call notes functionally the same as song have been used at various seasons in expression of social dominance. This usage suggests that the manifestation of social dominance in the Plain Titmouse is indicative of excitement and that the increase in aggressive behavior during the breeding season is an accentuated, cyclic expression of that drive.

NEST SITE SELECTION

In the latter part of February and early March in the San Francisco Bay region there is a tendency for the pairs to range widely over their territories, patrolling the peripheries and sometimes expanding these. While so doing, nest-site inspection is in progress also. Insofar as I have seen, this activity is characteristic of the female Plain Titmouse alone. Odum (1941*b*:519) found both sexes of the Black-capped Chickadee inspecting possible nest sites. Although Price (1931:41) states that cavity inspection may occur in January, the earliest date on which I have seen such activity was February 14, 1948. On February 14, 1947, the female of territory 1 roosted in a cavity in which the nest was built later. This incident may not have been related to nesting since actual building was not seen for another five weeks. However, the female may begin roosting in the nest cavity soon after it has been chosen.

Nest sites appear to be a critical factor in the distribution of nesting pairs of titmice. In 1947, I found six nests in Strawberry Canyon. The following year, two of these were used again (by two new birds in one instance), while in two other territories the birds disappeared and nestings were not completed. In the two remaining territories, other nest sites were chosen. In one of the latter areas the previous site appeared to be too damp for use. One territory, not occupied during the 1947 nesting season, was inhabited during the following fall and winter, but by mid-March the female had disappeared. Possible abandonment is suggested since I never found anything resembling a suitable cavity in this area. This situation suggests further that territories may be chosen by birds of the year without reference to nest sites. In territory 6, in 1947, the nest was not located, but the same individuals nested in the territory in 1948. They disappeared

while incubation was in progress in mid-April, and on May 2 another pair was building in the cavity. It appears on the basis of the study of this small population that there is on an average about one nest-site per territory.

NEST CONSTRUCTION

At the beginning of nest construction the activities of the pair are limited to an area around the nest and there is a sharp break in the daily activity patterns. Males often continue their sexual fighting, particularly where a pair may not be advanced far in the breeding cycle. The male attends his mate increasingly as the nesting cycle advances; he feeds her, accompanies her when she gathers nest materials, and, as a rule, shifts his roost-site to a point near the nest when she begins roosting there.

In one pair, nest site selection and building followed in close order.

On March 20, 1947, the birds of territory 2 first engaged in begging and courtship feeding on a south slope where the nest was to be located. On March 22, the birds spent the entire afternoon on the north slope near territory 1; the next morning was spent there also. The female begged almost continually during these two days. On March 25, these birds were building in a cavity on the south slope over 200 yards away. During the course of the morning the pair was occupied in nest construction. Observations were started at 7:39 and were continued for one hour and thirty-five minutes. During this time the female made thirty-nine visits to the nest, spending a total of thirty and one-half minutes inside the cavity. All nest material appeared to have been gathered within a radius of twenty-five yards. While the female was building, the male entered the nest four times and apparently fed the female while inside the cavity on two of these visits. He was not seen carrying nest materials nor have I seen other males aiding their mates in this manner, although others have reported such activity in unmarked individuals. Materials used most frequently include feathers, fur, moss, and similar soft substances.

MATING AND EGG LAYING

The only copulation witnessed during the course of this study was performed by the pair of territory 2 at 8:45 on March 27. The birds were partly screened by the foliage of an elderberry in which they were perched some 20 feet from the cavity. During the course of the mating, I heard a prolonged, continuous twitter which impressed me as coming from two birds. Both individuals left the area within two minutes after completion of the mating.

On March 29, the first date on which roosting of this pair was investigated, the female spent the night on the nest. Williams (1941:276) reported a Chestnut-backed Chickadee (*Parus rufescens*) which roosted in the nest box for six nights before she laid the first egg. On April 6, the female titmouse was incubating seven eggs. Presumably these were laid one each day commencing April 1; on my previous visits to the nest, the eggs had been covered by a layer of feathers and fur which I had mistaken for the bottom of the nest. Apparently the female does not cover the eggs with nest material during inattentive periods once incubation has begun. Odum (1941b:521) found this to be true with the Black-capped Chickadee.

The female may add to the nest in the egg laying period, bringing a feather or a leaf to the cavity, apparently a carry-over from an earlier stage of the cycle. A great deal of time is spent in foraging and little in combat, since other pairs are engaged in nesting also. Pronounced begging and courtship feeding are in evidence at this time.

The earliest date for a clutch in the San Francisco Bay region is a set of eight eggs on March 20, 1886, and the latest is a set of four eggs on May 7, 1882. The majority of pairs seem to lay during the first week of April. Clutch size is variable; Price (1936:24) found the average for 62 sets to be 6.75 eggs.

INCUBATION

Incubation appears to be the task of the female, for I have never seen the male enter a nest for more than a few seconds. Price (1936:24) found that the female alone developed a brood patch. Feeding of the incubating female by the male varies from one pair to the next. In territory 3 the male fed his mate on the nest at least half the number of times he visited the nest. On remaining occasions he called her off the nest to feed her. In this pair the male announced his approach by use of location notes, but in other pairs the male sang to call the female off the nest. This was not a special "signal song" such as is used by the Black-capped Chickadee. The male may feed the female several times in quick succession and then be absent for half an hour or more. Males sing occasionally during such inattentive periods but more frequently are silent. In some pairs I have never seen the male feed his mate on the nest. In territory 14 on April 19, 1948, the male held food in his beak continuously from 8:01 until 8:31, singing occasionally and shifting perch. The female continued to incubate and did not give the usual begging chatter in answer until ready to leave the nest at the latter time. In this instance, the male did not regulate his mate's activities. On May 2, this male entered the nest cavity to feed young there. The male often feeds the female during her inattentive periods. At the close of such periods, some males led their mates to the nest by use of song.

Attentive and inattentive periods of the female have not been worked out in great detail. Nine inattentive periods observed averaged 8.5 minutes and six attentive periods, 28.5 minutes. These agree with Odum's observations (1941b:523) of 7.8 and 24 minutes for the Black-capped Chickadee.

Information regarding length of incubation is scanty. In pair 3 in 1947, incubation rhythm was established on March 25 and the young hatched on April 9, a total of 16 days. Behavior in territory 1 indicated that the period was 16 days also (April 8-24), feeding of the young in the nest being seen on April 25. Witherby, *et al* (1938:256) state that incubation in the Coal-tit (*Parus ater*) required from 14 to 16 days, while that of most other European parids appears to be 13 to 14 days.

NESTLING CARE

The pattern of incubation rhythm changes suddenly at the time the young hatch. On a rainy morning, March 27, 1947, in territory 3, the male was singing at 6:00, continuing intermittently. The incubating female was silent until 6:32 when she scolded from the nest and then left. On April 10, presumably the day after hatching occurred, the male started singing at 5:37, six minutes before sunrise, and the female left the nest at 5:51. Both started to feed the young almost immediately. During the next two hours the male made 26 visits to the nest while the female visited the nest eight times, remaining to brood the young on six occasions for an average period of twelve minutes.

Observations were made in territory 1 from 9:45 to 11:45 on May 1, 1947, at a time when the young were about six days old. The male made six visits during the two hours, removing fecal sacs on three occasions. The female made eight visits, removing excreta twice. Brooding was not observed. At an earlier date, April 20, 1947, nestling care was observed in territory 3 for a one and one-half hour period beginning at 6:58 a.m. Here while the young were an estimated eleven days of age, brooding was observed, presumably because the hour was earlier. During this time, the male visited the nest eleven times and the female six times, remaining to brood three times for $7\frac{1}{2}$, 4 and 3 minutes, respectively. The male carried away a fecal sac once and twice was seen swallowing them, while the female carried only one away.

The trend toward more frequent visits culminates as the nestlings approach the age of departure. In territory 8 on April 26, 1948, two days before the young left the nest,

the adults (unbanded and indistinguishable) made a total of eleven visits to the nest in thirty minutes. During this period I saw no fecal sacs removed, although in territory 3, four days before departure of the young, removal of several was noted. This feeding frequency represents an average of 22 visits per hour in contrast to 17 per hour and 11.3 per hour at comparable times on the second and eleventh days, respectively. Odum (1941*b*:527) found that on the first day feedings averaged 6.5 per hour and 14.4 per hour when the chickadees were 13 days old. The male brings more food early in the nestling care period when the female spends considerable time in brooding, but later both sexes apparently share equally in bringing food.

Throughout the periods of incubation and nestling care, foraging as a rule is confined to the area close by the nest and is so increasingly as more frequent trips are made to the nest. Territorial matters are ignored for the most part, but as the nestling care period advances, the adults are more intolerant of intruders of other species. During this period, song is heard infrequently, at least near the nest. Usually some vocal announcement such as the location note, *sip*, is given as the adult approaches the nest, particularly as the young advance in development.

THE FAMILY BROOD PERIOD

Apparently the young do not leave the nest normally until they are capable of climbing up to the cavity opening; presumably by this time they are ready to fly. Mr. Joseph Connell reported seeing a brood of about five young titmice leave the nest almost simultaneously following "scolding" by an adult. The fledglings tumbled six feet to the ground and clung to the grass. On April 29, 1948, I found a nestling on the pavement beneath a maple in which titmice nested in a residential area in Berkeley. One parent perched on successively lower branches overhead, leaning as far forward as possible, swinging from side to side while looking down at the motionless fledgling and calling *see see see sickadee* anxiously. Simultaneously the male sang a clearly-whistled *sweet sweet* from trees across the street, a use of song corresponding to its function in leading of the brood. This fledgling, which was not able to fly more than a few feet, weighed 13.7 grams, approximately that of parent birds.

At least some of the young of the brood of four in territory 3 left the nest before noon on May 1, 1947. At 6:45 that evening, the widowed male led the brood to roost in a grove of live-oaks about 75 yards from the cavity. At 5:15 the next morning, he was feeding the young, leading them with a soft song *petur petur petur* to which they often answered with a location note *sip*. The male often foraged at distances up to forty yards away from the young, returning to feed them. He made apparent effort to feed all equally, periodically visiting one fledgling perched somewhat apart from others of the brood. The family group used this grove where they first roosted as a base of operations throughout the next week.

Development of the fledglings proceeded at a rapid rate. On their second day out of the nest they were inactive, remaining stationary in the foliage most of the time, waiting for the parent to feed them, but begging little. Their calls were of two types, a burry *siviva* of "chickadee" rhythm and a single note *sip* usually given in answer to the call or song of the parent. If the latter sang, the young characteristically followed him. Here we see the use of song in leadership, a use which reappears in dominance relations within the pair during the breeding season. Such conditioning appears to correspond to the process of "imprinting" described by Lorenz (1937:266) as "an acquiring process occurring only in birds and determining but one object of certain social reactions." In this case, the object is the singing male titmouse, the reaction, following his leadership.

By May 5, the fledglings foraged occasionally as though experimentally. On this

date they flew toward the male when he appeared, begging and fluttering their wings. They were noisy and restless when settling to roost, shifting perches often, but they ceased calling by 6:40 twenty-four minutes before sunset. By May 10, the calls of the young resembled those of adults more closely. On this date one immature bird was seen begging from another. The male sang less frequently, the last use of song for assembly of the brood being that following his release from the trap on May 13. The fledglings, now approximately five weeks old, clearly were foraging for themselves. On this same date the flock moved 115 yards to the west boundary of the territory where they were repulsed by the birds of territory 2. The fledglings were together on May 28, but two days later I banded one of the immature birds a quarter of a mile away. Two of the fledglings were begging from the parent on June 3 and three days later, a fight involving three titmice, presumably the adult and two young, was seen in this territory.

The parents of necessity forage within a narrow radius of their nest during the nestling care period. When the young are able to fly, the family moves to an area distant from the nest, often to a portion of the territory infrequently used. During this time, adults feeding young are so occupied that they take little notice of territorial boundaries and trespassing. The family groups in territories 5 and 6 transgressed the boundaries so frequently that I am uncertain as to the parentage of many birds banded as immatures along that boundary. Odum (1942*b*:154) cites similar overlap in two chickadee territories during the family group period. Such laxity in territorial defense may be used as evidence against the "food value" theory of territory since boundaries were ignored at this time when greatest demands on the food supply were being made. However, adults without young were seen defending their territories against wandering broods.

DISPERSAL OF JUVENILES

Dispersal of marked young individuals is a topic of considerable interest in the light of recent discussions of population genetics. In May and June, 1947, I was able to band 18 immature titmice in territories 1, 3, 5, and 6. This banding was carried on while family groups were still in flocks and is believed to have been completed prior to the influx of immature individuals from outside the study area. Return records have been obtained on seven of the eighteen birds.

One fledgling, M 14, was seen with other members of the brood on the parents' territory on May 28, 1947. Two days later, when this bird was seven weeks of age, I trapped it in an area about 450 yards upstream. This bird was recaptured here on each of the two succeeding days. By mid-August it had settled in an area 100 yards to the south, and on September 23, appeared to be paired with another immature bird (banded on the left leg only). This young male continued to occupy the same area until November 2, 1947, after which he was not seen again.

A second male, M 13, was banded on May 29, on the boundary between territories 5 and 6, and could have been of the brood of either. He settled in the western half of vacated territory 4 and appeared to be paired with F 13, a bird banded in that territory on August 19. She was killed on October 4 and later he was found paired with F 5, an adult female which had nested previously in territory 5. She was seen last on March 7, 1948, and on April 3, M 13 was seen nesting with an unbanded female. Between April 19 and May 2, he moved into the deserted territory 15 where he was attending an unbanded female engaged in nest construction. His first territory (13) was about 150 yards from the locality where he was trapped originally.

A female which may have been of the brood of territory 5 was trapped along the same boundary on May 29, 1947. She remained in the area subsequently and reared a brood in territory 14, mating with a bird which may have been her father.

Another titmouse, one of two banded in the same area with a white band on the left leg, was seen 100 yards downstream on August 10 involved in a quarrel with two other young titmice. This identification by inference shows delay in departure of an immature individual from an area adjacent

to the parental territory. This bird may have been the unidentified immature apparently paired with M 14 on September 23.

Another male, banded within territory 6 on June 1, 1947, was seen by Mr. Henry Childs on October 13, 1947, over 800 yards down the canyon. This individual was established on territory 16, although apparently unpaired when seen on March 21, 1948. This same individual was found dead on March 14, 1949, in an area 400 yards to the southwest of territory 16.

Another banded juvenile was found paired with an unbanded immature on August 10, 1947, in a residential area 600 yards from territory 1 where she was fledged. She was not seen following her mate's accidental death on August 17.

In April, 1948, a brother from the same brood was found nesting with an unbanded bird in an area 550 yards to the westward of territory 1.

This picture of dispersal of juveniles is incomplete in that not all the immatures fledged in Strawberry Canyon were banded. Among those not marked were five birds from territory 7, perhaps two from territories 5 and 6, and possibly a brood from an area a quarter of a mile northeast of territory 5, where an unbanded pair nested in 1948.

The records of the seven individuals indicate a gradual, relatively restricted dispersal of the young from the area of parent territories in this resident species. Four of these banded young birds survived to occupy territories in the canyon area during the next breeding season. These were at a mean distance of approximately 375 yards from their parents' territories in an area not uniformly habitable for titmice. Price (1936:25) banded 145 juvenal titmice but found only two nesting in a somewhat larger study area in subsequent seasons. One of these birds had travelled 700 yards and the other 1200.

It may be noted that in three of the four records of dispersal of banded juveniles to distances over 200 yards, the direction of travel was down the canyon, where continuous suitable habitat was available. Three of the birds which settled in the canyon area filled existing vacancies, that is they occupied territories where adult birds had nested the year before. The fourth bird settled in an area unoccupied the year before and, insofar as I know, was not mated. Another immature pair, presumably from outside the area, settled in territory 9, also unoccupied in 1947, but failed to nest.

At the time of dispersal of the juvenal birds in 1947, there were four vacancies in the breeding population within Strawberry Canyon proper. Two of these were filled by banded immatures, F 14 and M 13, and two by previously unbanded ones, F 12 and F 13. The death of one of the latter on October 4 opened another habitable space which was filled by the unmated adult, F 5, which had created an opening previously by leaving territory 5.

By mid-October, the banded immature birds apparently had taken up territories within the study area, had emigrated from it, or had died. Subsequently three vacancies became available in what appear to be adequate territories. The ones occurring in territory 3 in late autumn and in territory 13 in March were filled by birds not marked previously, hence presumably from outside the area. The third opening, created when the male of territory 1 was killed in January, was not filled. Trapping accidents, resulting in the deaths of a female, F 13, and the male M 1 mentioned above, created two of these vacancies, thus influencing rate of turnover in the population.

From these data it appears that while some juveniles settle on territories as early as June of their first year, others do not become established permanently until they are nearly one year old. Do titmice of the latter category keep moving until they find a suitable territory or do they settle temporarily and shift later? In seeking an answer, habitat selection may be considered, bearing in mind that the birds probably seek satisfaction only of those requirements facing them at the moment, that is, those relating to immediate survival, principally food and adequate vegetative protection while foraging and roosting. These conditions for existence in fall and winter are fewer than the more

exacting requirements of the nesting season. To be sure, preference on the part of the individual must be exercised as Grinnell (1928:441) has pointed out in the case of the Song Sparrow (*Melospiza melodia*), but wandering individuals finding all preferred areas occupied may be able to subsist in marginal habitat which in seasons of low popu-

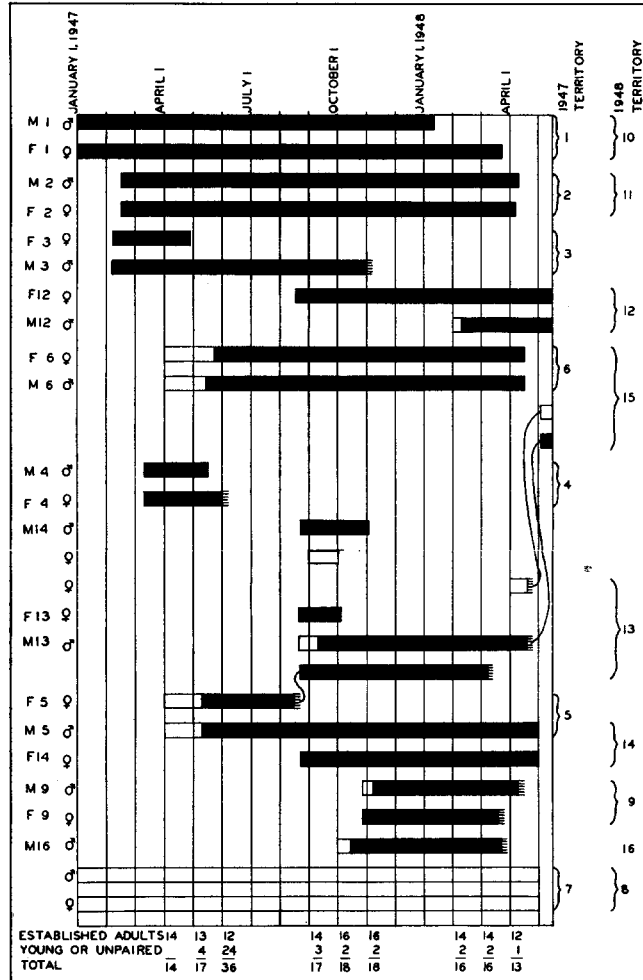


Fig. 18. Continuity of occupancy of territories of Plain Titmice in Strawberry Canyon. White bars indicate presence of unbanded birds; black bars, banded birds; incised end of bar indicates exact date of disappearance unknown. Numbers at right refer to territories plotted in figure 17.

lation pressure would harbor no titmice. Odum (1941b:330) found that nesting and feeding-resting biotopes of the Black-capped Chickadee may differ and that often two types of habitat are incorporated into one territory in order to satisfy both requirements. A similar situation developed in a territory on the campus in which the nest was located in a eucalyptus tree about 100 yards from the nearest broad-leaved trees, necessitating flights in the open on every foraging excursion.

There are in the literature a number of records of occurrence of Plain Titmice outside the breeding range of the species in late fall and winter, usually in marginal habitat. The individuals concerned presumably are birds of the year since banding studies have shown adults to be sedentary. In all probability, survival of titmice in such marginal areas would be lower than that for birds paired and established in adequate habitat. Those individuals which do survive may move back into adjacent areas suitable for nesting and fill vacancies which have opened during the winter months.

POPULATION

By April 1, 1947, the breeding population of the study area was stabilized at a density of seven pairs. Although transient unmated titmice may have passed through the canyon, I know of no resident or territory-holding unmated birds during that season. A peak population of 12 or 13 adults and about 24 juveniles was reached by June 1, after which the population declined to an estimated 16 established birds plus three unpaired individuals. By February 1, 1948, the number had decreased to seven established pairs plus two unpaired birds, dropping further to 12 plus one on April 1. Estimated population totals are shown in figure 18.

Five of the 13 birds established in the canyon on April 1, 1948, were of unknown age, being unmarked on that date or having been banded after attaining adult skull condition. Of the remaining eight, five were adults which nested in the study area in 1947, while the other three were known to be young of the preceding year. This survival of five of the twelve adults from the 1947 breeding season is only 41.6 per cent of that total. However, one individual was killed in a trap and his death possibly reduced the survival chances of his mate, thus contributing to increased turnover in the population.

If we assume that all birds new to the canyon were from broods of the previous season and use the method of Erickson (1938:310) of regarding the survival of young birds from outside the area as equivalent to that of the young birds which emigrated from that area, we find that eight birds of the 24 fledged survived. This indicates a death rate of 66 per cent among young birds fledged, in comparison to 72 per cent in the Wren-tit.

Price (1936:26) found 29 of 64 titmice banded as breeding adults during a five-year period reneating in the area in years subsequent to their banding, a return of 45.3 per cent. These results are subject to slight error in that in some cases both birds of a nesting pair were not captured. Examination of the data for each year indicates an annual replacement of slightly less than 50 per cent, suggesting that an average life expectancy of an established nesting adult would be about two years. Price banded 26 pairs of titmice, 12 of which were never recovered; pairing relations of the remaining 14 pairs are presented in a chart of permanence of mating. Examination of this table reveals records of 38 individuals representing what are apparently 14 territories. Data for 1932 and 1933 permit evaluation of vacancies in the population. In 12 territories in 1932 there were 15 individuals whose mates were known in 1931. Only three were mated with new birds in 1932. In 10 territories in 1933, there were 17 titmice whose mates of the 1932 and 1933 seasons were known; of the 17, only four were mated with new birds (excluded from this calculation is one bird which moved 200 yards to a new territory). These data present a picture of relatively slow population turnover; in twelve territories in 1933 there was a survival of 81.6 per cent of the nesting adults of the 1932 season. This figure suggesting a life expectancy of four years for an established breeding adult appears to be high; however this is based on data for one year. This population may be broken down into age classes as follows:

Age in years	Number of individuals	Per cent
6	1	4.5
5	1	4.5
4	3	13.6
3	7	32.0
2	6	27.3
1	4	18.1

Substantiation for the low annual replacement in this population is found in the fact that only 1.3 per cent of the juveniles banded there were found nesting in the area.

Miller (1947:189) pointed out that factors of population structure effecting panmixia or free interbreeding within a population are spacing of pairs and population turnover as reflected in longevity and reproductive rate. The Plain Titmouse in the area studied has a large territory relative to that of other small passerine species, averaging 150 yards (about 135 meters) in diameter in comparison to 50-80 meters for the Song Sparrow in Ohio and 50-100 meters for the Wren-tit. In the latter species, life span has been calculated at 4-5 years and reproductive rate found to be low, averaging slightly less than one bird fledged per breeding pair (Erickson, 1938:310). Survival of fledged birds was found by Erickson to be about 28 per cent; Miller estimated median distance of dispersal at 600-700 meters. While there are few figures for the Plain Titmouse available for comparison, life span appears to be shorter and reproductive rate, in terms of birds fledged, perhaps three times that of the Wren-tit, suggesting a greater rate of replacement. Records of four juveniles banded in Strawberry Canyon plus two records cited by Price (1936:25) indicate a median dispersal distance somewhat under 600 meters but essentially similar to that of the Wren-tit in absolute distance. However, the "average" Wren-tit would settle not less than six territories away from the parent territory, the titmouse, but three or four.

ROOSTING

Nature of roost sites and repetition in their use have been discussed earlier; attention at present will be focused on other aspects of roosting behavior. As other workers (Odum, 1941*b*; Williams, 1941) have found, members of the genus *Parus* usually roost singly. I found that in two instances members of two different pairs of titmice roosted as far as 50 yards apart during late autumn months. Roosting of the Plain Titmouse is not difficult to observe since the members of a pair frequently will call to one another while proceeding to their roost sites.

A special type of defense reaction was exhibited by titmice disturbed by the presence of an observer while on their way to the roost or by birds resettling for the night after having been flushed. Titmice thus alarmed often scolded while moving through the trees, and then, upon reaching a point at least within a few feet of the roost site selected, would utter a number of series of shrill notes, *see see see dee dee dee*, the later group lower in pitch. These series would decrease gradually in intensity and volume and the fading effect, which gave an impression that the bird was moving away from the observer, would be followed suddenly by complete silence. This behavior pattern was exhibited on a number of occasions by three of the four birds which were flushed from their roosts during the course of the study. This fact suggests that such a reaction may be a trait of the species as a whole. Pitelka (1940:15) found a similar "ventriloquistic" effect in the song of the Black-throated Green Warbler (*Dendroica virens*). As the male approached the nest, this song became faint, approximating a whisper which created the impression that it was coming from a distance. The adaptive value in either case seems to be prevention of exact location of the singer (or caller) by an enemy.

ALARM REACTION

A Plain Titmouse, when disturbed by an intruder, frequently will scold and go through what Allen (1943:155) has called a "pendulum" motion. This reaction consists of combined movements in which the head and body are bobbed up and down while simultaneously swayed from side to side through an arc of about 90 degrees. The fact that this alarm reaction often is executed under conditions of poor light, as by a bird flushed from its roost, or in situations in which the intruder may not be seen clearly, suggests that the pendulum action may be an outgrowth of peering.

In some cases this reaction has been performed in an "automatic" manner, as though not directed toward any stimulating object. A titmouse flushed from the roost by the cracking of a twig did a pendulum act while facing away from the intruder. In another case, I alarmed one member of a pair of titmice perched above me; this bird faced me and scolded while swaying its body from side to side. Its mate apparently did not see me but executed the same movement silently while facing in another direction. That reaction, perhaps evoked by that of the mate and not directly by my presence, appears to be what Tinbergen (1948:45) has called a "mood" or "readiness to respond to one group of functionally related motor patterns." The next move of the alarmed bird would be determined by the subsequent actions of the intruder.

A number of writers, among them Grinnell, Dixon, and Linsdale (1930:311), speak of flocking in which this species is involved: "Sometimes in winter, a pair joined in with loose aggregations of foraging birds of other species." It has been my impression that while titmice may forage in live-oaks simultaneously with flocked Bush-tits, Oregon Juncos, and accompanying Ruby-crowned Kinglets, either the other species will move on, leaving the titmice, or the latter will proceed independently after a short period of coincidental association. However, the Plain Titmice respond to the warning calls of other species, such as the "confusion chorus" of the Bush-tits.

COMPARISONS OF BEHAVIOR

In comparison with other members of the Paridae, the Plain Titmouse has a rather unusual pattern of behavior involving a sedentary existence, year-around defense of territory, permanence of pairing, and pair-formation in young birds in late summer and autumn. When analyzed, these peculiarities of behavior may be seen as tending toward extremes of traits present in winter-flocking parids. Permanence of pairing of the Tufted Titmouse has been discussed earlier and evidence of the resident status of some other parids has been presented. Odum (1941*b*:326) has described a "pre-nesting" period in the Black-capped Chickadee following pair-formation, but prior to territory establishment. During this phase of the nesting cycle, the pair isolates itself and is antagonistic to other members of the species, but in other respects is likened to a flock of two. Such behavior is characteristic of established pairs of Plain Titmice throughout the year and its survival value is apparent.

Such a pattern of behavior in the annual cycle conceivably could have had its inception in past times in the arid Southwest, in localities where suitable titmouse habitat could have been broken up to a greater degree than are the blocks of woodland on the south-facing slope of Strawberry Canyon. Here sedentariness and permanence of pairing could have had greater survival value than winter flocking for the following reasons: (1) Elements of safety involved in flock behavior would have been retained to a significant degree in the "flock of two." For this same reason, paired birds may seek a territory together in late summer. (2) Defense of territory (with its potential nest site), mate, and food supply throughout the year would insure possession of these essential elements of the breeding situation by the dominant birds. (3) Safety in familiarity of

the bird with its surroundings would be greater than that achieved by flocking birds covering a wider range.

These changes appear to be entirely compatible with the general behavior patterns characteristic of the genus *Parus* as a whole, representing accentuation of certain trends found to a lesser degree throughout the genus. Thus we see retention of conservative elements of behavior such as cavity-nesting, foraging preferences, a similar, highly developed vocabulary, and other similarities of appearance and action.

SUMMARY

A population of the Plain Titmouse, a sedentary, resident bird, was studied in Strawberry Canyon, on the west side of the Berkeley Hills in Alameda County, California, from September, 1946, until May, 1948. During this period, 35 titmice were color-banded, 18 of these as juveniles less than three weeks out of the nest.

Adult Plain Titmice, established on territories, tend to remain paired for life and defend their territories throughout the year. Defense of territory may be effected by either member of the pair and, for the most part, is vocal, being accomplished by the use of call notes which serve a function of advertisement. Calls may be accompanied by a form of attack designated here as an "approach threat." Ordinarily the Plain Titmouse does not make itself conspicuous visually, but calls or sings from a protected perch. A variable, whistled song is given by the males in spring and seems to be correlated with sexual fighting, that is, defense of the female. It also aids the male in maintaining dominance over the female at this time. Cavities for use as nest sites appear to be a critical factor in limiting population density in this species. Twelve territories averaged 6.3 acres in area.

Pair-formation occurs in a majority of cases in young birds soon after family flocks break up in early summer. This pairing may take place prior to establishment on a territory, or a wandering young bird may mate with an established, widowed adult. Replacements of the latter sort took place throughout fall and winter in the population studied. The mechanism of sex recognition in the absence of song is not known, but apparently pairing is accomplished through a period of conditioning; dominance of the male is suggested as a factor in recognition. Apparently following pair-formation a status of no dominance exists until the breeding season. The male rather clearly directs the activities of the female during incubation, and in this leadership, uses the same type of song used in leading the brood of fledglings during their first days out of the nest.

Nest site selection appears to be a function of the female alone, as is construction of the nest. She is attended by her mate in these activities. Nest site selection usually takes place by early March and construction and egg laying are completed ordinarily by the first week of April in the San Francisco Bay region. Courtship feeding occurs from the beginning of nest construction until the young are hatched. Incubation is by the female and requires approximately 14-16 days for completion. During this time she is fed by the male. The nestlings remain in the cavity for about three weeks, during which time they are fed by both parents. The family brood remains together for from three to four weeks, often centering its activities in a portion of the territory well removed from the nest. During this period, defense of territory by adults with broods is lax, in contrast to that of pairs whose nestings were not successful.

Records of dispersal were obtained for seven of the 18 young birds banded. Four of these individuals were established in the Strawberry Canyon area during the next breeding season. Median distance of dispersal of six birds of the year was slightly less than 600 meters, approximately the width of four territories. Average life expectancy of an

established adult appears to be about three years, with turnover in a population proceeding at a slow rate (chiefly from data of Price, 1936). About two-thirds of the birds fledged fail to survive until the next breeding season. Incidence of replacements in a population in winter and spring, and records of winter vagrancy suggest that such replacements are drawn from a reserve of young birds crowded into marginal habitats by population pressure.

The vocabulary of this species is quite variable; nine functionally distinct call notes are described.

The behavior patterns and annual cycle of the Plain Titmouse do not represent radical departures from those of other parids, being accentuations of trends, such as permanence of pairing, already existent in some members of the family. Modifications of certain parid traits appear to have adaptive value for the Plain Titmouse in the woodland habitats of the arid southwestern United States.

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