BIRD-BANDING

A JOURNAL OF ORNITHOLOGICAL INVESTIGATION

VOL. 48, NO. 2 SPRING 1977 PAGES 97-191

FLOCK SIZE, COMPOSITION, AND BEHAVIOR IN A POPULATION OF BUSHTITS (*Psaltriparus minimus*)

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Observations of the behavior of Bushtits (*Psaltriparus minimus*) were made by Miller (1921) and to a lesser extent by Addicott (1938). The opinion that flocks of Bushtits occupy moderately defined areas has been expressed by both of the above authors and by Swarth (1914). Addicott and Miller believed that individuals sometimes switched from one flock to another. Grinnell and Storer (1924) noted that flocks consisted of families or groups of families, but they did not state the basis for this belief. As far as I am able to ascertain, the majority of these observations were based on unmarked individuals. Addicott's work was the exception as she marked 16 birds in her study of breeding biology (pers. comm.).

This paper reports the results of a three-year study of the behavior and breeding biology of Bushtits. The data reported here pertain to (1) flock size and integrity of composition, (2) behavior during encounters between flocks, and (3) lineages within flocks. Thirteen flocks were studied on a coastal mesa approximately 470 hectares in area centered on the University of California Santa Barbara campus one mile south of Goleta, Santa Barbara County, California. The campus is surrounded by 15-20 m bluffs on three sides. North and northeast of the campus, bluffs slope abruptly to a coastal salt marsh. Along these bluffs coast live oak (*Quercus agrifolia*), toyon (*Heteromeles arbutifolia*), and poison oak (*Rhus diversiloba*) predominate. A large, flat, disturbed area produced by the excavation of the bluff for landfill is a major geographic feature on the northern edge of campus. Vegetation in this area includes coyote brush (*Baccharis pilularis*), willow (*Salix* spp.), sweet fennel (*Foeniculum vulgare*), and introduced eucalyptus (*Eucalyptus* spp.). An assortment of grasses and small annuals provide ground cover. On the eastern edge of campus the bluffs drop to an extensive sandy beach. Clusters of willow and coyote brush are present at the base of the bluffs, but they are otherwise sparsely vegetated. The southern edge of campus is dominated by a brackish lagoon surrounded on the south by two island-like sections of the mesa. These "islands" are connected to the mainland by sandbars and roadways. Coyote brush is dominant along with bush lupine (*Lupinus arboreus*). Ornamentals present along the sloping edges of the "islands" include eucalyptus, Monterey cypress (*Cupressus macrocarpa*), and acacia (*Acacia* spp.). The two major research areas were the lagoon "islands" and the disturbed flat and bluffs along the northern edge

of campus. As the study progressed, observations were made on the campus itself as well as on a number of contiguous coyote brush areas to the west.

METHODS

Adult Bushtits were captured with mist nets and color marked with plastic bands following methods used by Erickson (1938). Each bird received a unique combination of three colored plastic bands and one Fish and Wildlife Service band. Nestlings were removed from nests and banded in the same manner as soon as the tarsus was large enough. A total of 325 birds were banded.

Flocks were followed and observed at a distance to keep disturbance to a minimum. Areas of suitable habitat bordering the campus were checked twice each season for the possible emigration of marked birds from the study area. All observations were made with 7 × 35 binoculars. Data were kept on iris color (males brown, females yellow; Raitt, 1967; Ervin, 1975), age, location, and flock associates of each marked individual. Location of flocks and individuals was noted by distance and direction from prominent landmarks or plotted directly on air photos.

RESULTS

Flock Size and Composition

Flocks remained remarkably constant in size and composition during the study. Data for the composition of three flocks for the complete 1973 flocking season are presented in Figures 1-3. Age and sex data for four flocks during the 1973 season are presented in Table 1. Although data for these and other flocks for 1971, 1972, and 1974 are less complete, they are not contradictory and are not presented here to conserve space.

TABLE 1.

Age and sex distribution of banded birds in flocks A, B, C, and D during 1973

	Birds hatched in:											
	1970oe[1]		1971oe		1972oe		1972		1973oe		1973	
Flock	M	F	M	F	M	F	M	F	M	F	M	F
A	1	2	2	—	—	2	2	—	—	—	5	1
B	—	1	2	2	3	2	—	2	—	—	6	6
C	—	—	3	2	—	2	—	—	—	—	2	1
D	1	—	1	1	3	1	—	2	2	2	1	—

[1]or earlier year

Exchanges or switches of birds between flocks were noted on only two occasions even though adjacent flocks frequently came into contact. In the first instance, flock H with four marked individuals and a flock size of 15 split from the large flock B early in the 1973 flocking season (Fig. 1). After much movement around the campus,

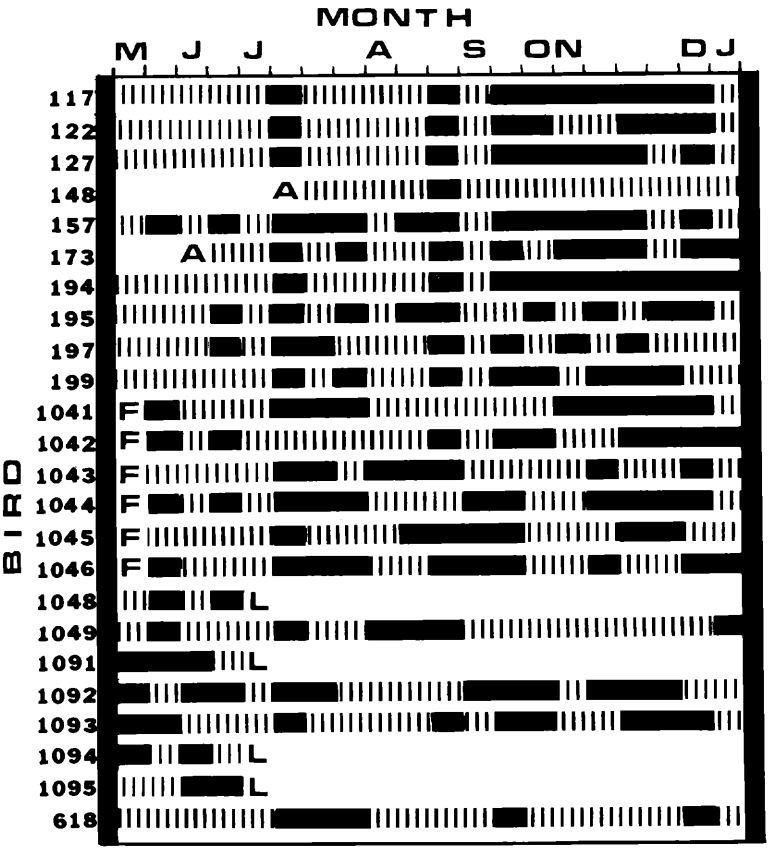

FIGURE 1. Composition of Flock B (marked birds only) during the 1973 flocking season. Months are divided by observation days. Solid black bars indicate that the individual was actually observed. Symbols in order of precedence on this and Figures 3-5 are: A = arrived in the flock on or before this day of observation, B = banded, F = fledged, L = left the flock on or before this day of observation, O = last day observed and presumed dead.

the flock settled in a peripheral area and remained there through the close of the study more than a year later. Flock B was the largest flock studied (approximately 30 birds) even after the split took place. In a second case, three marked birds from flock G, a flock that intruded into the area of flock C early in the 1973 season, switched from G to C between 18 and 30 October (Fig. 4). By 13 November both flocks had completely merged to form flock CG. Flock CG remained stable for the remainder of the 1973 flocking season and was reforming from the same mixture of individuals in the early part of the 1974 season. Counts for flock C indicated a decline in numbers from 15 to 9 birds during the two seasons before the merger. With the above 7 marked birds as exceptions, marked

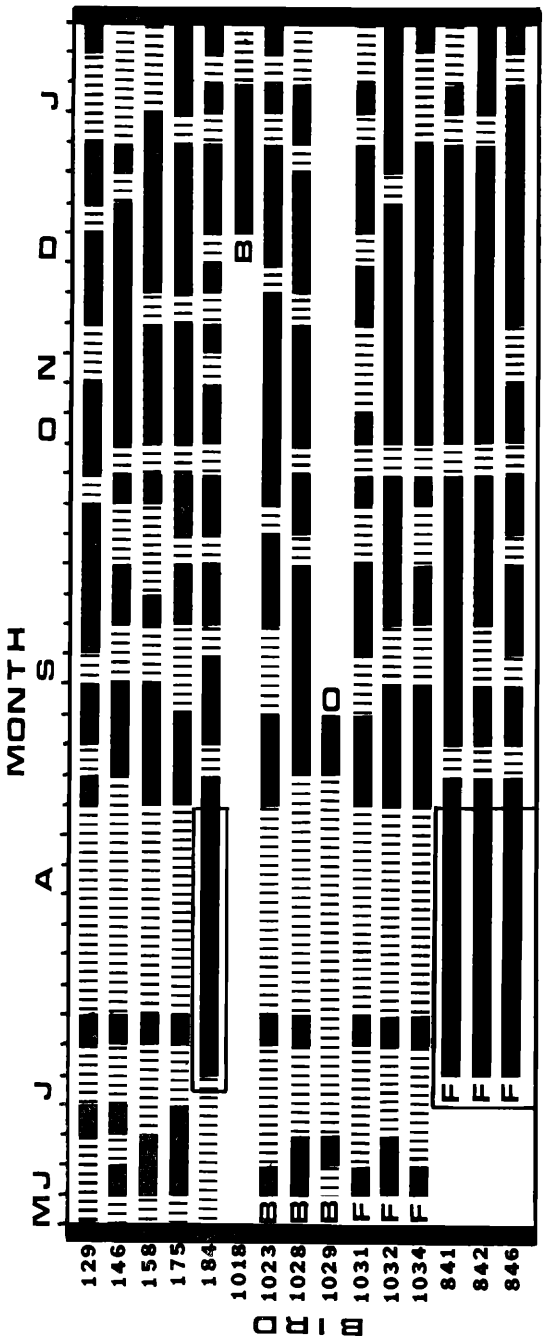

FIGURE 2. Composition of flock A during the 1973 flocking season. Enclosed boxes indicate a family group before union with other flock members. Bird 184 was the female parent of 841, 842, and 846. The male parent was not marked. See Figure 1 for explanation of additional symbols.

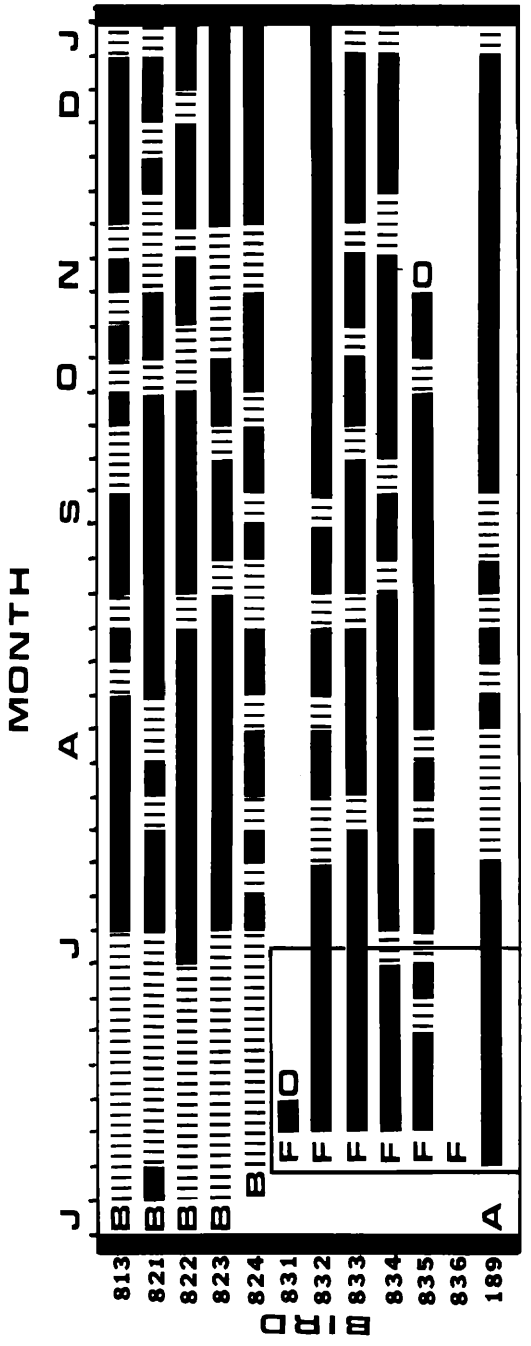

FIGURE 3. Composition of flock E during the 1973 flocking season. Enclosed boxes indicate a family group before union with other flock members. See Figure 1 for explanation of additional symbols.

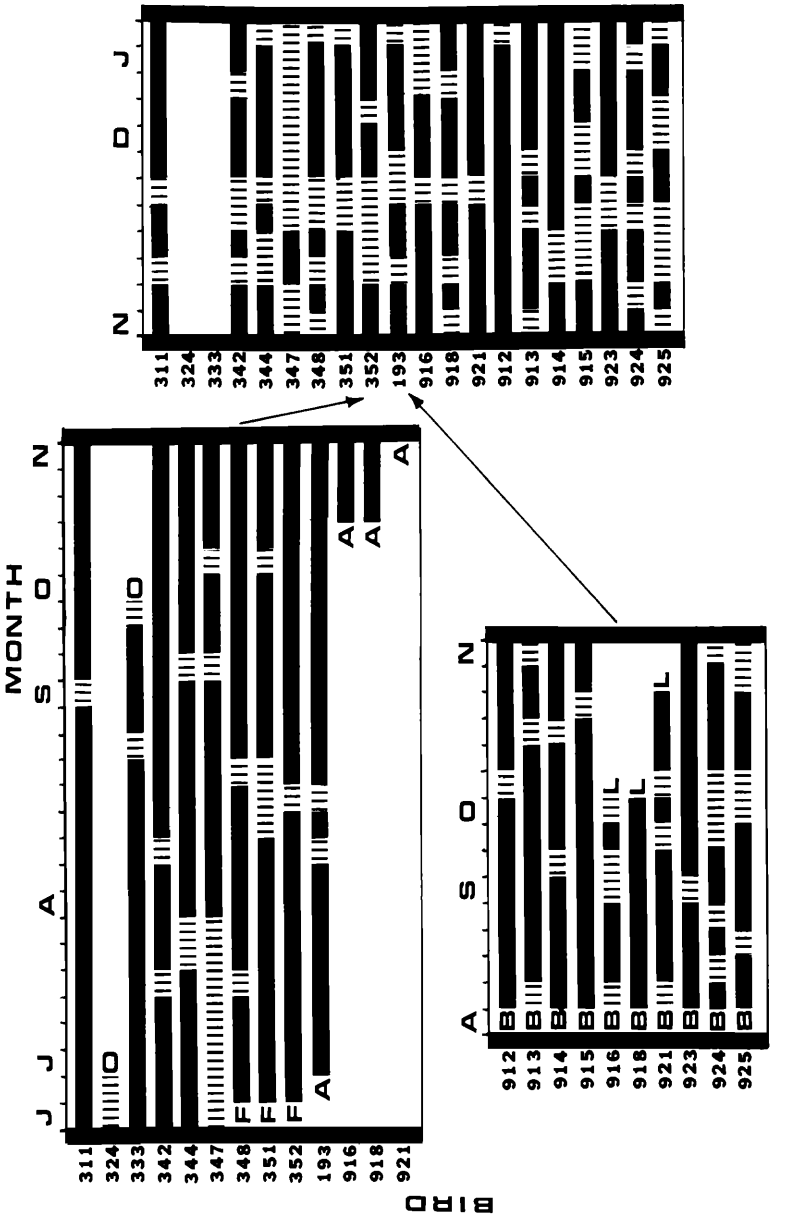

FIGURE 4. Composition of flocks C, G, and CG during the 1973 flocking season. See Figure 1 for explanation of symbols.

birds were not observed to switch flocks permanently. Of course mixtures of flocks occurred during the frequent encounters.

Observations of flock encounters provided additional evidence for the stability of flock size and composition. Members of two or more flocks came into contact daily, and on 19 such occasions the encounters were carefully documented. The following example is illustrative:

> At 13:00 on 17 December 1973, a large flock of Bushtits was located. Observation of band combinations indicated that two or more flocks were present. Occasional fights were observed and alarm notes and short trills contrasted with the usual quiet location notes. The composite group soon began to sort out into two groups. Pursuits and loud calls continued as the two groups split completely. By 13:50 one of the two groups split completely. By 13:50 one of the two groups split again. Each of the three groups was followed and the banded individuals noted. The first group consisted of 15 birds of which 10 were quickly identified. The second and third groups consisted of 12 and 11 birds of which 8 and 7 were identified respectively. The groups were flocks A, E, and D with no mixture observed.

A number of the 19 encounters were observed from before the actual contact took place through separation. Contact was complete in less than one hour and in one case six different flocks were involved. Encounters were accompanied by pursuits, fights, and loud calling and contrasted sharply with foraging behavior. Vocalizations increased in frequency and intensity as flocks approached each other. Qualitatively, males appeared more aggressive and were the only sex involved in fights. None of the 19 encounters produced any evidence for an exchange of individuals as speculated by earlier authors.

The behavior of a flock toward a single foreign individual illustrates a simplified version of a flock encounter. Two observations were made possible when I released birds near a flock other than their own. Immediately upon release and apparently upon hearing the calls of the flock, the individual moved in the direction of the flock and gave the call of a bird left behind (Grinnell, 1903). On arrival to the proximity of the flock, the bird was driven off and attempted no further approach. Males again appeared more aggressive in driving off the strange bird although both males and females exhibited agitation and increased vocalizations. In both releases the behavioral sequence was identical and both birds were later observed with their own flock.

Yearly Flock Composition

Birds were present in the same flock for 1-4 consecutive flocking seasons. Observations indicated a general tendency to return to the same flock following breeding year after year. Of 101 known breeding birds 94 nested within their respective flock areas during the entire study. As a more specific example, at the beginning of the 1973 flocking season, flock A, a completely marked flock (Fig. 2), had five banded birds from the previous year and 10 new young or newly banded birds. Birds present in 1972 but not in 1973 were presumed dead because they were not observed elsewhere by the end of the study. All of the birds of flock A breeding in early 1973 and returning to flock A during the 1973 flocking season had

nested within the flock area. The flock compositions in 1972 and 1973 were apparently the same with the exception of the addition of new young. First-year birds followed the same pattern as previously nesting adults. In 15 of 16 cases of known first-year breeding birds, the nest was located in the flock area. Young were not driven out of the area by their parents. All 16 of these first-year birds returned to their parental flock following breeding. In one case the distance from one young female's nest to her place of birth the previous year was less than five meters. The average distance moved by the 16 was 375 m. Eleven of the 16 first-year birds were males.

Seven birds moved considerable distances from their flock area to nest and were later incorporated into another flock occupying the area containing the nest site. Four of the seven are indicated by early arrivals in Figures 1, 3, and 4. One was a female known to have bred previously, and six were females of unknown age but potentially breeding for the first time. The maximum distance moved by the seven was 3,800 m. Although this may indicate a tendency for young females to move farther than young males, it is not substantiated by other available data. Distances moved for known young males averaged 432 m (SD = 275, n = 12) whereas distances moved by young females to nest averaged 204 m (SD = 177, n = 4). The sample size of young females is small and the average may be biased by undetected movements of additional young females to unstudied peripheral areas.

Flock Areas

The approximate areas of movements of flocks A-I and K for 1973 are shown in Figure 5. Overlap of areas was the rule, so

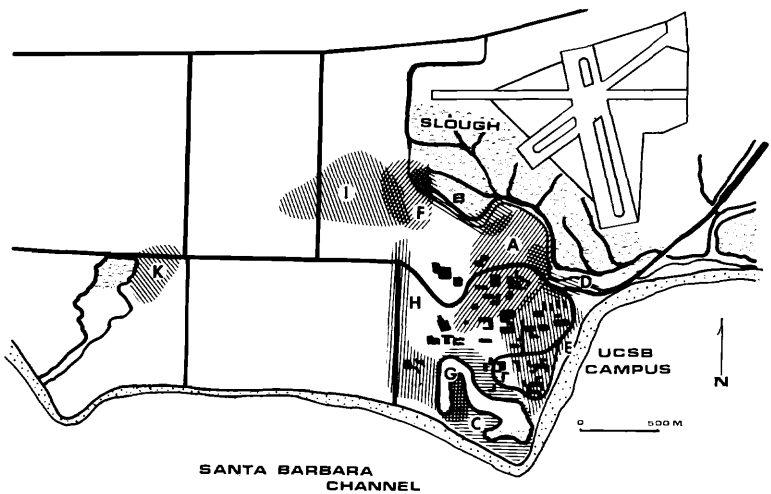

FIGURE 5. Approximate ranges of flocks A-I and K during the 1973 flocking season.

boundaries cannot be clearly shown. It appeared that defense of the area was through chance encounter because the areas were large and no regular patrol routes were established.

Family Relationships

By the end of the study the family relationships of 33 members of flocks A and E were known (Fig. 6 and 7). These relationships were at the level of parent (or grandparent)-offspring, sibling (or half sibling), uncle-aunt, cousin, and more distant relationships.

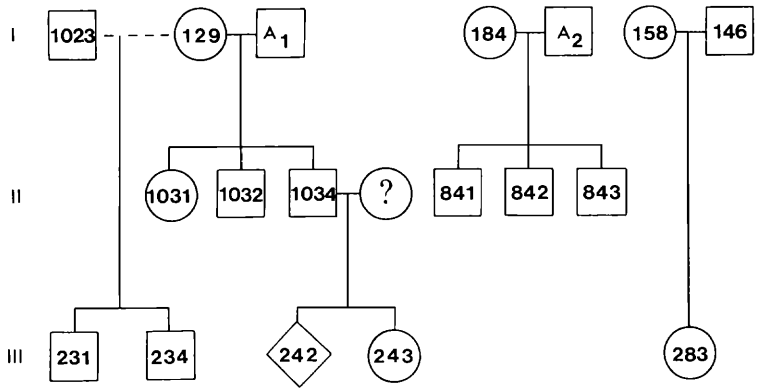

FIGURE 6. Pedigree diagram for flock A at the beginning of the 1974 flocking season. Sex symbols are as follows: square, male; circle, female; diamond, sex unknown. Horizontal rows of individuals are age classes as follows: I, birds hatched in 1972 or earlier; II, birds hatched in 1973; III, birds hatched in 1974. Unknown birds may have been of any age. Males A1 and A2 were marked with aluminum bands only. Female 129 paired with a new mate, 1023, in 1974 to produce 231 and 234.

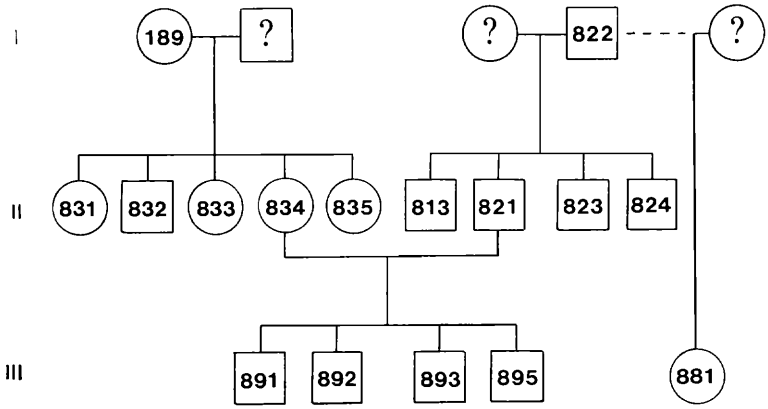

FIGURE 7. Pedigree diagram for flock E at the beginning of the 1974 flocking season. Symbols follow Figure 6. It is not known if the mate of 822 was the same bird in consecutive seasons.

Since many of the offspring remain with their parents for the first and subsequent flocking seasons, and since the composition of flocks is constant, I assume the initial birds in the study were also closely related. If this is the case, subsequent matings following loss of the original mate (as with 129 and 1023 in Fig. 6) could have been at any level of relationship. Despite this potential for inbreeding, no cases of pairings between related individuals were known in 16 pairings between birds with known pedigrees.

Pair Bonds

Six pairs of birds remained intact for consecutive breeding seasons: five pairs for two and one for three. In 11 other cases, however, mate switching from one season to the next was observed. In six of these 11 cases, mates were different from the previous season even though former mates were known to be alive. The remaining five changes (over three breeding seasons) were accounted for by the death or disappearance (and presumed death) of a member of the pair.

Multiple nests were frequently constructed in the same season by a single pair. One pair constructed or initiated five nests in the same season following successive disruption by predators. Two pairs attempted second nests immediately after successful fledging of young. Both were destroyed by predators before young could be fledged. The maximum total number of nests attempted by a single pair throughout the study (3 breeding seasons) was eight.

DISCUSSION

The tendency for flocks of nonmigratory passerines to remain relatively constant in numbers or individuals has been reported for several species. Flocks of Superb Blue Wrens (*Malurus cyaneus*; Rowley, 1965a), White-winged Choughs (*Corcorax melanorhampus*; Rowley, 1965b) Arabian Babblers (*Turdoides squamiceps*; Zahavi, 1974), and Mexican Jays (*Aphelocoma ultramarina*; Brown, 1970) reportedly contain family units that remain intact for long periods of time. Among the Paridae constancy in flock size and composition based on family units has been reported for the Long-tailed Tit (*Aegithalos caudatus*; Nakamura, 1969; Gaston, 1973) and potentially for the Cape Penduline Tit (*Anthoscopus minutus minutus*; Skead, 1959). Among the remainder of the Paridae the type of flock organization exhibited by Bushtits and Long-tailed Tits is not shown. Wallace (1941) reported that flocks of the Black-capped Chickadee (*Parus atricapillus*) occupied specific areas and that flocks were constant in composition, but were not composed of family groups. Butts (1931) noted an exchange of individuals between flocks of the same species. Odum (1942) also noted variability in flock sizes and exchanges of individuals between flocks. In the Carolina Chickadee (*Parus carolinensis*) family groups break up and juveniles form loose aggregations (Brewer, 1961). In some areas, flocks of Carolina Chickadees may have a stable range (Dixon, 1959). The European Great Tit (*Parus major*) and the Blue Tit (*Parus caeruleus*) disperse following fledging and do not

remain with their parents (Goodbody, 1952). McLaren (1975) has reported a similar behavior in Boreal Chickadees (*Parus hudsonicus*).

It is not known if the maintenance of integrity in Bushtit flocks is accomplished by visual, vocal, or other cues. Behavior of flocks during encounters and the behavior of flocks toward foreign individuals seem to indicate visual recognition, but precise supporting data are lacking.

Despite the close relationship of flock members and the cohesiveness of flocks, some movement into or out of flocks was observed. Gene flow through the Bushtit population appears to be accomplished through two or possibly three mechanisms. Genetic influx is provided by occasional flock mergers, and by the incorporation of foreign birds into a forming flock as a result of their breeding location. The incorporation of these latter individuals does not violate the general rule that foreign birds are repulsed since they are accepted at the time of initial flock formation when new young are also included. Flock mergers may be the result of an optimal flock size correlated with the ability of a flock to move as a unit through a particular habitat type and to the defense of the flock area. Divisions of flocks may occur for similar reasons. Unions or divisions of flocks may reflect adjustments of flock size to highly successful years or to seasons of high mortality. Female outbreeding is also a potential method for maintenance of genetic flux even though some young females remain with their parental flock (4 of 15 birds remaining with their parents were females). Female outbreeding has been reported in one species with similar behavior, the Superb Blue Wren (Rowley, 1965a).

Crook (1965) in his survey of social organizations noted that gregarious birds become territorial for breeding when nest sites are relatively accessible to predators are cryptic and dispersed. Bushtits follow this pattern; their nests are difficult to see and are dispersed throughout the flock area. The persistence of pair bonds and family groups through the nonbreeding season and apparent high degree of recognition of flock members contribute to flock cohesiveness and hence may be of value in exploiting locally abundant yet patchy food resources. Reformation of flocks from small family groups as a result of nest location within a common flock territory and strong individual recognition undoubtedly contributes to enhanced resource exploitation and predator defense through previous knowledge of local topography and vegetation patterns. It may be argued that Bushtit flocks never really break up, but only disperse over the flock range. A number of incidents involving interactions between nesting pairs from the same flock have been reported (Ervin, in press).

SUMMARY

A population of Bushtits was marked and followed for a three-year period on the campus of the University of California, Santa Barbara. Adults and nestlings were marked and the lineages of two flocks were partially determined.

Flocks of Bushtits remained relatively constant in size and composition throughout the nonbreeding season. Breeding individuals occupied territories within the larger flock territory and reformed with their young into the same flocks in successive years. Young were not driven out of the flock areas. Encroachment of flocks into adjacent flock territories was met with defensive behavior by resident flocks. Foreign individuals were also repulsed by flocks during the nonbreeding season. Bushtits appear to be a species dependent on flock behavior for survival during the nonbreeding season, yet dependent upon dispersal and crypticity of nests for successful breeding. It may be argued that Bushtits do not completely dispense with flocking behavior during the breeding season but only disperse throughout their flock territory.

ACKNOWLEDGMENTS

I would like to thank Mary M. Erickson, Professor Emeritus, of the University of California, Santa Barbara, for her help and inspiration through the course of this study. The late Raymond Cowles, Professor Emeritus, of the University of California at Los Angeles supplied many ideas and suggestions. Thanks are also due to Barbara DeWolfe and Stephen Rothstein for their help with numerous details. Financial assistance was provided by three grants from the Frank M. Chapman Memorial Fund.

LITERATURE CITED

Addicott, A. B. 1938. Behavior of the Bush-tit in the breeding season. *Condor*, **40**: 49-63.

Brewer, R. 1961. Comparative notes on the life history of the Carolina Chickadee. *Wilson Bull.*, **73**: 348-373.

Brown, J. L. 1970. Cooperative breeding and altruistic behavior in the Mexican Jay, *Aphelocoma ultramarina*. *Anim. Behav.*, **18**: 366-378.

Butts, W. K. 1931. A study of the Chickadee and White-breasted Nuthatch by means of marked individuals. Part II: The Chickadee (*Penthestes atricapillus atricapillus*). *Bird-Banding*, **2**: 1-26.

Crook, J. H. 1965. The adaptive significance of avian social organizations. *Symposia Zool. Soc., London*, **14**: 181-218.

Dixon, K. L. 1959. Patterns of social organization in some American titmice and chickadees. (Abstract). *Bull. Ecol. Soc. Amer.*, **40**: 46.

Erickson, M. M. 1938. Territory, annual cycle, and numbers in a population of Wren-tits (*Chamaea fasciata*). *Univ. Calif. Publ. Zool.*, **42**: 247-334.

Ervin, S. 1975. Iris coloration in young Bushtits. *Condor*, **77**: 90-91.

——— 1977. Nest appropriation and mate switching in the Bushtit. *Auk*, in press.

Gaston, A. J. 1973. The ecology and behaviour of the Long-tailed Tit. *Ibis*, **115**: 330-351.

Goodbody, I. M. 1952. The post fledging dispersal of juvenile titmice. *Br. Birds*, **45**: 279-285.

Grinnell, J. 1903. Call notes of the Bush-tit. *Condor*, **5**: 85-87.

Grinnell, J., and T. I. Storer. 1924. Animal life in the Yosemite. Berkeley, Univ. Calif. Press.

McLaren, M. A. 1975. Breeding biology of the Boreal Chickadee. *Wilson Bull.*, **87**: 344-354.

MILLER, R. C. 1921. The flock behavior of the Coast Bush-tit. *Condor*, **23**: 121-127.

NAKAMURA, T. 1969. Structure of flock range in the Long-tailed Tit, 1. Winter flock, its home range and territory. *Misc. Rep. Yamashina's Inst. Ornithol.*, **5**: 1-29.

ODUM, E. P. 1942. Annual cycle of the Black-capped Chickadee - 3. *Auk*, **59**: 499-531.

RAITT, R. J. 1967. Relationships between black-eared and plain-eared forms of Bushtits (*Psaltriparus*). *Auk*, **84**: 503-528.

ROWLEY, I. 1965a. The life history of the Superb Blue Wren, *Malurus cyaneus*. *Emu*, **64**: 251-297.

——— 1965b. White-winged Choughs. *Aust. Nat. Hist.*, **15**: 81-85.

SKEAD, C. J. 1959. A study of the Cape Penduline Tit, *Anthoscopus minutus minutus* (Shaw & Nodder). *Ostrich*, Suppl. **3**: 274-288.

SWARTH, H. S. 1914. The California forms of the genus *Psaltriparus*. *Auk*, **31**: 499-526.

WALLACE, G. J. 1941. Winter studies of color-banded chickadees. *Bird-Banding*, **12**: 49-67.

ZAHAVI, A. 1974. Communal nesting by the Arabian Babbler, A case of individual selection. *Ibis*, **116**: 84-87.

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