

## INCIDENCE AND ORIGINS OF SUPERNUMERARIES AT BUSHTIT (*PSALTRIPARUS MINIMUS*) NESTS

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**ABSTRACT.**—I studied a color-banded population of Bushtits (*Psaltriparus minimus*) in the Chiricahua Mountains of southeastern Arizona from 1986 through 1991. Overall, 37% of nests had one to four supernumerary birds, most of which were adult males. Indirect and direct evidence suggested that most supernumeraries were males that had not acquired a mate, or were failed breeders of either sex. Sex ratios were consistently skewed in favor of males, although males almost always were associated with a nest, and years in which nest loss was high had a correspondingly high incidence of multibird (>2 bird) nests. Some supernumeraries may have contributed genetically to the contents of nests they attended, either by laying eggs or by mating with the female, resulting in possible polygynous, polyandrous, and polygynandrous groups. I suggest that a primary route to multibird nests in Bushtits is via competition for existing nests and mates. Birds without nests (individuals or pairs) attempt to evict the residents and, if unsuccessful, sometimes compromise and join as helpers or additional breeders. Received 15 June 1994, accepted 27 January 1995.

COOPERATIVE BREEDING SYSTEMS are social systems in which some individuals help raise offspring that are not their own. As an excellent group within which to test hypotheses on the evolution of this behavior (Hamilton 1964, Maynard Smith 1964, Brown 1978, Emlen 1982), avian cooperative systems have been the focus of much research, especially in the last three decades (see Emlen and Vehrencamp 1983, Brown 1987, Stacey and Koenig 1990).

The Bushtit (*Psaltriparus minimus*) is one of three species of birds first described as having helpers in Skutch's (1935) landmark paper on helpers at the nest. Since then, few studies have been published on Bushtit behavior, despite a great deal of research on other cooperative breeding birds. The Bushtit's small size and furtive habits perhaps explain the reluctance of most researchers to study them. Nonetheless, many aspects of the behavior and population ecology of Bushtits make them ideal subjects for the study of cooperative breeding.

Especially interesting is the possibility that the frequency of helping behavior and the origin of helpers in Bushtits varies geographically. Skutch (1935) found that helpers were common at Bushtit nests in Guatemala (all nests he observed were attended by extra individuals).

However, it is unclear whether these birds were unmated "excess" males in the population (Skutch 1935, 1961), or juveniles from an earlier brood (Phillips et al. 1964). In contrast, studies of Bushtits in California revealed a very low incidence of helping behavior (Addicott 1938, Ervin 1974). In the Santa Barbara population, helpers either were transients or were males that had recently lost a nest (Ervin 1974, 1977). In fact, these incidents of helping behavior may have been anomalous and not an intrinsic characteristic of Bushtits (Ervin 1977).

In this paper, I describe the incidence of multibird nests (i.e. nests with more than two attendants) in a population of Bushtits in the Chiricahua Mountains of southeastern Arizona based on five years of field observations. I examine the origins of extra birds (or supernumeraries) at nests, the roles they may play at nests, and the reasons why some birds become supernumeraries. I present evidence that Chiricahua Bushtits: (1) are plural cooperative breeders (sensu Brown 1978) in that the social group contains more than one breeding female, and (2) exhibit an apparently variable mating system including occasional polygyny, polyandry, and polygynandry.

### METHODS

*Study site.*—The study site is in the Cave Creek basin of the Chiricahua Mountains (31°52' N, 109°15' W), about 7 km from Portal, Arizona. It is a gently sloping,

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xeric area cut by two deep gorges, each containing permanent streams. Elevations range from 1,700 to 1,800 m. The predominant vegetation is open oak woodland grading into pine-oak woodland (see Whittaker and Niering 1965, Sloane 1992). The weather generally is arid and hot, with an average annual precipitation of 506 mm and an average temperature of 12.5°C at the Southwestern Research Station (ca. 2 km from study site). Bushtits breed during the drier months (March through July) between the region's two rainy periods (December to March and July to September).

In 1986 only, the study site of 600 × 600 m contained a grid marked by a system of flags spaced 50 m apart. A few nests outside of this area also were studied. From 1987 through 1990, I monitored a larger, ungridded study area of approximately 4 km<sup>2</sup>. In these years, the size of the study site was dictated by the size and shape of the home ranges of the two main breeding flocks (Greenhouse Trail [GT] and Winn Falls Lookout [WF]; 15–30 adults each) plus the peripheral portions of all six breeding flocks that were immediate neighbors of the main flocks. Because the search area was smaller in 1986, only portions of the two main breeding flocks were monitored in that year. I defined a flock as a group of birds, individuals of which associate with (i.e. were observed with) one another periodically and do not associate with members of other flocks. Because Bushtit breeding flocks may coalesce into larger winter flocks during the non-breeding season, I use "breeding flock" to refer only to the exclusive associations maintained throughout the breeding season.

*Subjects.*—From 1986 through 1990, I caught and color-banded 607 nestling, juvenile (i.e. birds hatched earlier in season), and adult Bushtits. All birds were banded with a unique combination of three colored leg bands and a U.S. Fish and Wildlife Service aluminum band. On average, 80% of adult Bushtits within the study area were banded throughout the 1987–1990 breeding seasons. By the end of each breeding season, almost all adults and fledglings were banded in the two main study flocks, and a large proportion of peripheral birds was banded as well. Nestlings were banded at 10 to 12 days of age (see Sloane 1992).

Birds were aged by the length and shape of the 10th primary (Phillips et al. 1964, Pyle et al. 1987). All adults hatched in the previous season are referred to as second-year (SY) birds. Birds banded as adults are referred to as after-hatching-year (AHY) birds. I added a year to these ages in each year following (third-year [TY] and after-second-year [ASY], respectively). Adults and older juveniles were sexed by eye color (Raith 1967, Ervin 1975).

*Procedures.*—In all years except 1986 (when I arrived in mid-April), I was present during the entire breeding season. Bushtits began building nests in early March and fledged most final nests by late July.

Thus, I was able to observe birds in their breeding flocks early in the season and watch the initiation of pairing and nesting behavior. In addition, I was able to observe fledgling groups coalesce and flocks extend their home ranges as the breeding season came to a close.

Maximum home ranges of breeding flocks were estimated by delineating (on an aerial photograph) the outermost locations of flock members after nest building had begun and before all nests in a flock had fledged, connecting these locations with lines, and then counting the number of 50 × 50 m quadrats contained within the resulting polygon. A quadrat was included only if at least half of it was contained within the polygon.

I found 200 active Bushtit nests from 1986 through 1990. Of these, 47 were found in the building stage and observed for the entire nesting cycle (building and feeding). After the young left these nests observations continued on the resulting fledgling groups. An additional 30 nests found in the building stage were observed at least until the nestlings were of banding age (10 to 12 days). The remainder (123) were found either in the nestling (feeding) stage or the building stage, but the nests were destroyed before the eggs hatched. Nests were monitored often enough to determine accurately the timing of nest loss, to identify attendants (because of nest-ownership changes and competition; see Results), and to determine the stage of the nest (building, incubating, or feeding).

I conducted 2,111 nest watches from 1986 to 1989. Nest watches varied in length from 10 min to 4 h; almost all exceeded 30 min. Each nest was monitored for at least 30 min on alternate days. This schedule was adequate for determining stage in the nesting cycle, estimating feeding rates, identifying all birds at the nest, and observing competition and nest-ownership changes. A comparison of 1986 data indicated that feeding rates estimated from the first 30 min sampled versus those from longer samples (up to 4 h) were not significantly different (paired *t*-test, *n* = 43 pairs, *P* = 0.10). Feeding rates were high (i.e. from 6 to 96 feeding visits/h). In 1990, nests were watched only long enough and often enough to determine stage and to estimate number of attendants.

During each nest watch, an effort was made to determine the identity of visitors and attendants without compromising the other information taken (such as feeding rate). An "attendant" was defined as an individual observed: (1) entering nests with food or nesting material and exiting without the items; (2) placing nesting material on the outside of nests; and/or (3) feeding fledglings. This was in contrast to a "visitor," who came into the nest area or entered the nest but did not engage in nesting activity. Any behavioral interactions observed among Bushtits in the nest area also were described. In addition to nest

watches, nests were observed periodically when unusual activity was suspected, or when a nest was encountered during a routine search of the area. Fledgling groups were observed, when possible, for 1 h both on the day of fledging and again within two weeks after fledging. When fledgling groups were encountered, all birds within the group were located, and feeding individuals were identified.

A nest or fledgling group was classified according to the number of birds attending, using only nest watches of at least 20 min in duration. Fledgling watches had to be long enough to identify all members (0.5 to 1 h). The number of birds attending during a particular watch was defined as the number of clearly identified different birds attending. A supernumerary was defined as any attendant (juvenile or adult) other than the original pair at the nest. A "multibird nest" was defined as any nest with more than one attendant of either sex and of any age (i.e. an addition of at least one supernumerary to the original breeding pair). In cases where the supernumeraries could not be distinguished from the original breeder(s), the nest was referred to as a multibird nest, but no particular individual at the nest was classified as a supernumerary. If a nest was identified as having three or more birds attending for at least one nest watch, it was classified as a multibird nest at that stage. A nest had to be watched at least twice during a stage to be classified at that stage. It is possible that some nests with temporary supernumeraries (i.e. attended only once or twice) incorrectly were placed in the same category as nests with continuously present supernumeraries. Conversely, the number of attendants probably was underestimated for nests that were not watched for extended periods of time (particularly in 1990, and to some extent in 1989). Thus, the total number of multibird nests recorded may be an underestimate.

Origins of supernumeraries were determined by histories of banded individuals joining at nests. In addition, I used adult sex ratios to evaluate whether supernumeraries involved excess males in the population. Sex ratios were determined by counting and sexing all breeding and nonbreeding adults in the population throughout the breeding season. The proportion of failed nests was used to estimate the number of failed breeders in the population. Failed nests were those that did not produce fledglings; most were destroyed by predators. I did not include nest "takeovers" as failed nests, although takeovers did produce displaced breeders (see Results).

An effort was made to locate the victims of nest loss (failed breeders) immediately following the loss to determine their activity and location. Because it became apparent that supernumeraries could be breeders at the nests they attended (see Results), I attempted to determine potential genetic contributions to nests. I examined the nest contents for the

number of eggs and the number of nestlings at banding age. In addition, I observed adults attending nests during egg laying for evidence of courtship and/or opportunities for copulations.

## RESULTS

*Flocking behavior and nest initiation.*—Before nest completion in early April, Bushtits foraged and roosted in loose flocks of 15 to 30 adults. Flocks had large foraging home ranges (ca. 100 ha) that overlapped extensively with the home ranges of other flocks, particularly at the beginning and near the end of the breeding season. Aggression among members of different flocks was rare, and mild when it did occur. In 9 of 16 flock encounters (flocks in same place at same time) observed in 1986, I saw no interactions of any kind. In the remaining seven encounters, I observed only a few short chases. In the very beginning and at the end of the breeding season, several breeding flocks coalesced temporarily into one flock, especially at dusk, and roosted at night in the same general area, although not in the same trees.

Early in the breeding season, pairs within breeding flocks established small, weakly defended territories around nest trees. Defense involved short chases and occasional physical contact, but was not consistent. For example, an individual repelled on one occasion might be tolerated by the breeding pair during the next, only to be rejected again a few hours or days later. In addition, only some intruding flock members were repelled. "Nesting home ranges" (defined by outermost locations of all flock nests) were contained within and were smaller (ca. 32 ha) than foraging home ranges. Unlike foraging ranges, nesting home ranges did not overlap among flocks.

Nest-building behavior was erratic, being common on sunny days (even when cold) and rare when overcast. During overcast days, Bushtits foraged in mixed-species flocks or with other members of their breeding flock. Although pairs were mildly aggressive towards other flock members in the immediate vicinity of their nest tree during the building stage, all individuals in a flock moved freely within the flock's foraging range, visited other nests, and frequently aggregated into small subgroups throughout the breeding season.

*Incidence of supernumeraries.*—The number of

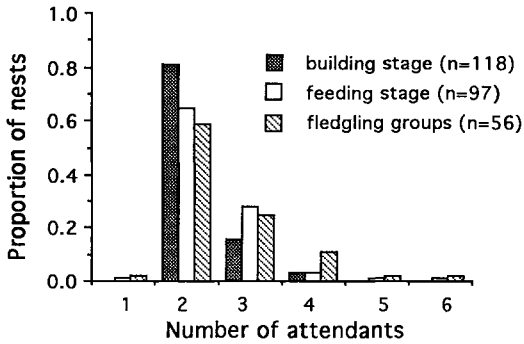


FIG. 1. Proportion of nesting groups with one to six attendants (including primary attendants and supernumeraries) separated by stage of nesting cycle.

individuals attending nests could be positively determined in 97 feeding-stage nests that also met the minimum criteria for number of active nest watches. Thirty-four (35%) of these nests had more than two attendants, with one nest having six concurrent attendants. Overall, 39% (22/56) of fledgling groups had more than two attendants (Fig. 1). The percentage of nests with supernumeraries during the feeding stage varied considerably among years, ranging from a low of 15% in 1989 to a high of 57% in 1987.

Birds began attending nests at all stages, but those in the feeding stage had, on average, more attendants than did nests in the building stage. Only 19% (22/118) of nests in the building stage had more than two attendants. The number of birds attending nests increased with the stage of the nest for nests found at any stage ( $\chi^2 = 6.8$ ,  $P = 0.011$ ; Fig. 1). Nests established relatively late (as estimated by hatching dates) had no more attendants than did earlier nests in either the building or the feeding stage (Figs. 2A and B). These results suggest that the overall increase in the number of attendants with nesting stage was not due merely to the time of year, but possibly to an accumulation of birds at existing nests over time. However, there was no significant change in the percentage of nests with more than two attendants from building to feeding stages for nests that were watched continuously through all stages ( $\chi^2 = 1.7$ ,  $n = 77$ ,  $P = 0.21$ ), which conflicts with the above interpretation.

*Identities and roles of supernumeraries.*—Of the 36 supernumeraries for which age was determined, 32 (89%) were adults and only 4 (11%) were juveniles. No juvenile supernumeraries

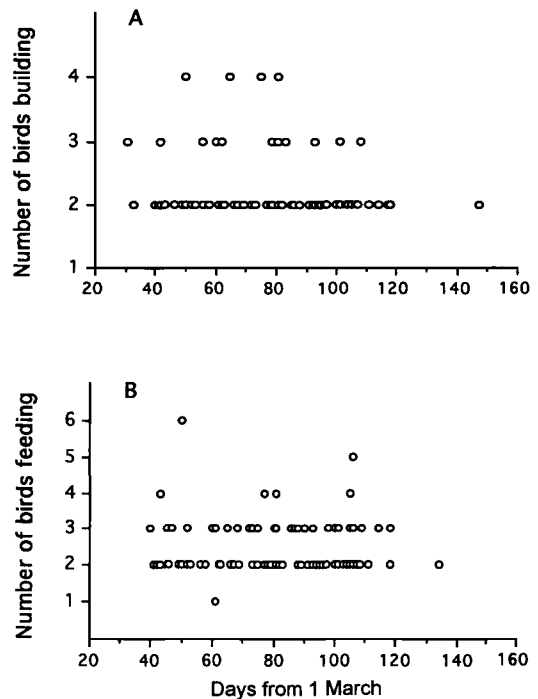


FIG. 2. Relationship between hatching date and number of nest attendants during (A) nest construction ( $n = 82$ ) and (B) the nestling period ( $n = 98$ ). All years combined.

were present in 1987 or in 1990. All four juveniles recorded as supernumeraries first associated with a breeding attempt during the nestling or fledgling stage.

Of the 42 supernumeraries observed feeding (i.e. provisioning) at nests, 34 (81%) were males and 8 (19%) were females. Some supernumeraries were observed feeding or building only once or twice, whereas others were observed at every nest watch, attending the nestlings consistently until they were independent. Only one individual was present at a nest frequently during the building and incubation stage without becoming involved in either activity. This male, however, fed the young in the nest and continued to feed them after they fledged.

At a minimum of 12 nests, supernumeraries joined either before or during egg laying and may have become breeders. At two of these nests, courtship behavior (consisting of fluttering chases and vocalizations around the nest) was observed between all opposite-sex members of the group. In six others, all combinations of opposite-sex birds were seen in isolated pairs

during egg laying, providing opportunities for supernumeraries to copulate. Finally, at three nests with two attendant females, more eggs or nestlings were in the nest than would be expected for one female: (1) one nest contained 10 nestlings; (2) one nest contained six nestlings, three unhatched eggs, and one nestling skeleton; and (3) one nest contained six nestlings and four unhatched eggs.

In 17 other cases, however, supernumeraries probably were nonbreeding attendants, because they joined at a nest after egg laying was completed (13/17), or they were juveniles from earlier nests (4/17). For all other nests with supernumeraries, the timing of joining was unknown, and the genetic contribution of the attendants could not be determined. Some of these birds may have joined at nests before egg laying and, thus, would have had the opportunity to contribute genetically to the nest they attended. Also, even nonattending adults may have contributed genetically to the contents of a nest. Both females and males may contribute when the female member of a pair lays eggs in a neighboring nest (egg-dumping). Two times I observed what appeared to be egg-dumping behavior, although in neither case could I verify this by counting eggs before and after the event. On the first occasion, a breeding male and female visited a neighboring nest in the absence of the owners. Both birds entered the nest briefly and then exited. The female then re-entered the nest and remained for 6 min while her mate perched in the nest tree, looking about constantly. Both birds left the area before the nest owners returned. In another case, a pair that had been evicted from their nest visited a neighboring nest from the same flock. The female entered the nest and remained for about 10 min while her mate waited outside. This time, however, the resident male returned, and the two males fought violently for several minutes around the nest tree and in the nest before the intruding pair left the area.

*Origins of supernumeraries.*—The origin of supernumeraries was known in 19 of 49 cases; all were members of the same breeding flock as the resident pair. Supernumeraries consisted of juveniles (4/19), unmated males (3/19), and failed breeders of either sex (12/19). In two cases, juveniles unambiguously fed full siblings (see Sloane 1992). In another case, a juvenile male clearly was not the offspring of all of the birds he helped because he attended at two late nest-

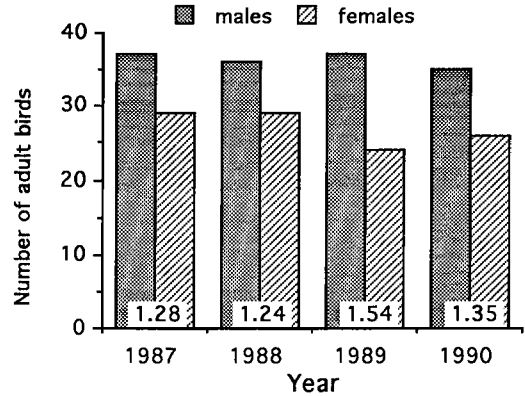


FIG. 3. Number of males and females observed routinely on study area, 1987 to 1990. Annual sex ratios (males: females) shown at bottom of bars.

ing efforts with different sets of parents (Sloane 1992). Because his origin was unknown, he may have been helping his parent(s) at one of the nests, but not at both. All adult supernumeraries for which histories were ascertained either were failed breeders or previously unmated males.

Several other lines of evidence support the hypothesis that some supernumeraries were excess males. First, the adult sex ratio, both on the entire study area and within flocks, was consistently skewed in favor of males (Figs. 3 and 4). Second, most supernumeraries were adult males, and these birds sometimes were associated with a breeding effort from its inception. Finally, very early in the breeding season, multibird building efforts, in most cases, involved more than two adult males (Fig. 5). When three years (1987 to 1989) were compared, however, the sex ratios (males:females; 1.28, 1.24, and 1.54, respectively) and proportion of multibird nests (38%, 24%, and 32%, respectively) were not correlated.

Some unpaired males took no active role in nest attendance. For example, XYYG and XBRR were two males hatched in 1987 that remained unmated and unattached to any nests for the bulk of the 1988 season. XYYG never had a nest and eventually became associated with a large fledgling group in his flock, occasionally feeding the fledglings. XBRR finally nested with an unbanded female late in the season.

The hypothesis that failed breeders also are an important source of supernumeraries was supported as well. There was a significant pos-

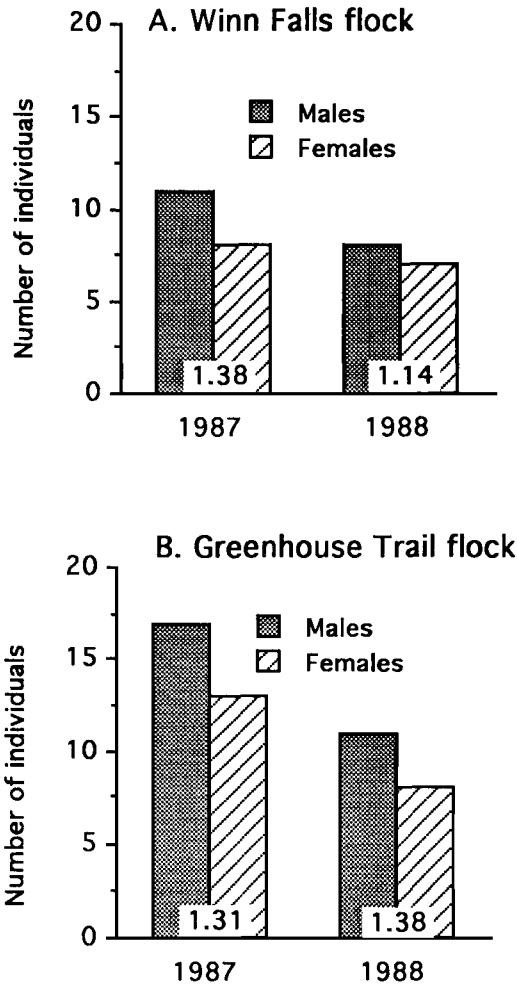


FIG. 4. Number of males and females observed in two main study flocks, 1987 and 1988. Sex ratios (males: females) shown at bottom of bars.

itive relationship between yearly nest loss and yearly proportion of multibird nests ( $F = 528.0$ ,  $P = 0.028$ ; Fig. 6). In 1987, the WF flock had a low proportion of nest loss (19%) and no nests with supernumeraries; however, the GT flock had a higher proportion of nest loss (62%) and 22% multibird nests. In the same year, ownership changes occurred at 25% of the GT nests (see below).

*Behavior of failed breeders.*—Not all breeders became supernumeraries immediately following a failed breeding attempt. Failed breeders engaged in several different behaviors soon after a nest failure (Fig. 7). Some immediately built new nests within the nesting home range

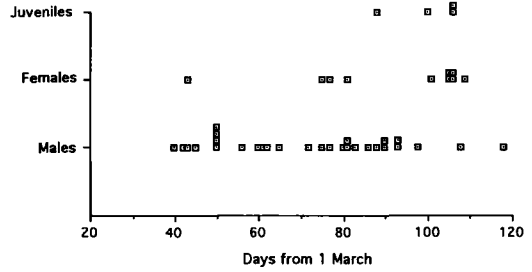


FIG. 5. Frequency distribution of hatching dates at nests attended by juveniles, adult males, and adult females ( $n = 42$  birds, 1987 to 1990).

of their breeding flock. Pairs were more likely to do this than single individuals, because the latter had to find a mate before building a new nest. Others engaged in aggressive behaviors (noisy chases and physical contact) at a neighboring nest. One result of this aggression was the eviction of the resident pair from their nest (a takeover or ownership change). The second result of aggression was joining at the nest. Joining was sometimes preceded by aggression (competition) directed by the potential supernumerary toward the resident birds.

The following example illustrates the full range of outcomes experienced by failed breeders. This pair encountered four nest failures in one breeding season and exhibited all of the behavioral options at least once:

X-RR (SY female) and YPYX (ASY male) found building at NT78 (nest 78) on 20 March 1988. During building stage, they were frequently seen foraging with GXYW (SY female) and XPPL (ASY male), who were building at NT84 nearby. Between 4 and 10 April, NT78 was destroyed by predators. On 12 April, YPYX was observed aggressively chasing, hitting, and

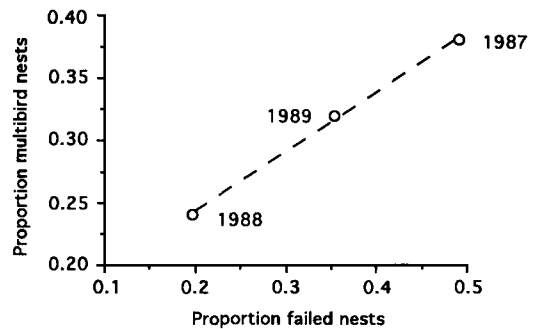


FIG. 6. Relationship between frequency of nest failures and multibird nests, 1987 to 1989.

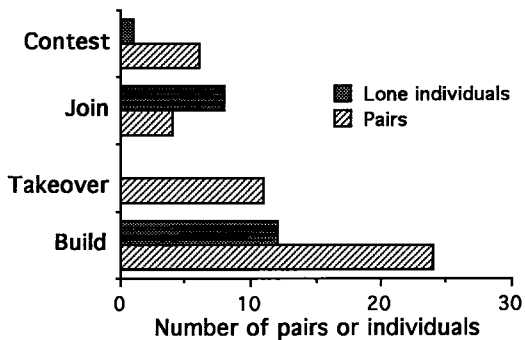


FIG. 7. Frequency of different behaviors exhibited by individuals and pairs after nest failure. "Contest" (engage aggressively with neighbors before building new nest, taking over, or joining); "join" (join resident pair); "takeover" (evict residents); and "build" (build new nest).

closely following unbanded male who, along with an unbanded female, was current resident of NT79, located about half-way between NT84 and NT73. During the interaction, which lasted at least 25 min, YPYX frequently visited nest itself (which was in building stage), and was seen entering twice. Unbanded male wing-fluttered towards YPYX frequently (a submissive behavior), and unbanded female remained in area foraging. X-RR was not around. On 18 April (during egg laying), X-RR observed foraging near NT79 with flock of about 8 Bushtits.

On 24 April, YPYX was building at NT84. At subsequent nest watches, X-RR also was observed. GXYW and XPPL not seen near nest again and apparently were usurped.

On 29 April, XPPL and GXYW found building at NT73. Nest had been object of three ownership changes earlier in season. GXYW was involved in one of these changes, at that time paired with an unbanded male. Nest was abandoned by yet another pair between 20–30 March in very unfinished state; it was merely a loose sack of spider-web with no shape and many large holes.

NT84 destroyed by predators in incubation stage on 11 May. On 13 May both YPYX and X-RR found building new nest (NT97) located between NT84 and NT73. This nest was visited by unbanded male on several occasions. Nest was destroyed by predators or nest material thieves (a Solitary Vireo [*Vireo solitarius*] was observed on three occasions to remove nesting material from nest) on 23 May, possibly in incubation stage.

Contents of NT73 hatched on 18 May. Initially, only XPPL and GXYW fed at nest. On 24 May, however, YPYX, X-RR, XPPL, and GXYW were observed feeding nestlings. These four continued to so until 3 June,

TABLE 1. Nest ownership changes, total visits, and competitive visits to Bushtit nests in the construction stage, 1987 and 1988. Numbers in parentheses are proportions of total nest watches during which birds visited, or competitive interactions were observed.

Variable	1987	1988
No. of building stage nests	44	47
Proportion of nests depredated	0.49	0.23
Total no. of nest watches	500	410
No. nest watches with visitation	64 (0.128)	50 (0.123)
No. nest watches with competition	25 (0.050)	9 (0.022)
No. ownership changes	14	7

when nest destroyed by predators. Three of six nestlings fledged successfully during this predation event, and all four adults continued to feed fledglings.

On 11 June, YPYX and X-RR found building another nest, NT110, very near NT73. It was destroyed by predators or abandoned on about 14 June. X-RR and YPYX did not attempt another nest, nor were they observed engaged in competition at any of the few existing nests.

In summary, X-RR and YPYX attempted to build their own new nest after only one of their four nest failures, and this occurred after they competed for an existing nearby nest. After the first nest failure, they successfully evicted a resident pair and, later, they joined that same pair at their feeding nest. Their final failed nest (NT110) probably was destroyed too late in the season for the pair to renest.

When a nest was lost, other active flock nests became objects of increased visitation and competition by the failed breeder(s). This aggression apparently resulted either in ownership changes or temporary or permanent joinings. Compared with 1988, ownership changes and visitations with aggressive interactions were more common in 1987, when nest loss was relatively high (Table 1). One nest takeover could result in a "domino effect" of nest-ownership changes in that evicted birds themselves attempted to replace the residents at neighboring nests (Fig. 8). The amount of aggression and competition around nests after a nest failure probably was greatly underestimated because birds were not always located immediately after a nest failure, nor were nests watched continuously.

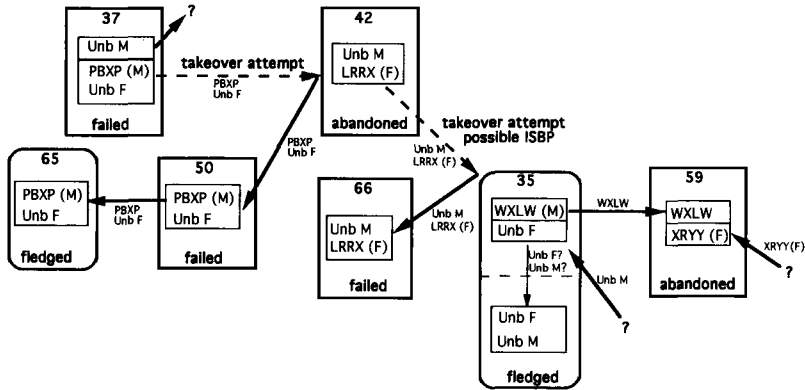


FIG. 8. Cascade of nest events following destruction of nest 37 by a hailstorm. Each box represents a nest; attendants are identified within. Arrows denote movements of birds; dashed arrows are unsuccessful takeover attempts. Ownership changes represented by arrows within box (nest 35). WXLW's move from nest 35 to nest 59 occurred only five days before eggs hatched at nest 35, making his contribution to nest 35 feasible. Unbanded male at nest 35 joined early enough to have contributed as well. ISBP = intraspecific brood parasitism; M = male; F = female, Unb = unbanded; ? = origin unknown.

## DISCUSSION

*Incidence and origins of supernumeraries.*—In contrast to Bushtits studied in California (e.g. Addicott 1938, Ervin 1974), those in the Chiricahua Mountains of Arizona frequently had supernumeraries at their nests, with variation in the proportion of multibird nests among years and among flocks. Some of the supernumeraries appeared to be nonbreeding helpers; they arrived after the eggs were laid and fed nestlings that could not have been their own direct descendants. In addition to being cooperative, Bushtits were plural breeders (sensu Brown 1987), living in large flocks with many concurrently breeding females. In his study of Bushtits in Santa Barbara, California, Ervin (1977) defined flocks as breeding-season family units (i.e. singular breeders), although he recognized the possibility that Bushtits retained some larger flock structure throughout the year. In the Chiricahuas, this multifamily flock structure was pronounced throughout the season and produced a situation in which helping by siblings and individuals other than immediate relatives could occur easily.

Nest supernumeraries came from all the possible sources proposed in earlier studies. Juveniles from an earlier brood, an origin suggested by Phillips et al. (1964), sometimes returned to care for their younger siblings, but this behavior was extremely rare and appeared to occur

only when the young being fed were exceptionally hungry. This occurred once when a female's mate disappeared (forcing her to feed her second brood alone) and twice when a fledgling either was injured or otherwise unable to fly and keep up with its nest mates. More commonly, supernumeraries were adults (pairs, lone males, and lone females) that joined neighboring nests after their own nests had failed, a route similar to that proposed by Ervin (1977). Notably, my study population is the first in which females were observed behaving in a supernumerary capacity. In previous studies of Bushtits, all supernumeraries have been males.

Excess adult males in the population also appeared to be an important source for supernumeraries, an origin first suggested for Bushtits in Guatemala (Skutch 1935, 1961). In the Chiricahua population, adult males made up a high proportion (78%) of supernumeraries, and the population sex ratio was consistently male-biased. In almost all cases, these excess males were attendants at nests. A male-biased sex ratio is to be expected, because in Bushtits (as in most cooperatively breeding birds) females are the dispersing sex and probably experience greater mortality. In contrast to my findings, Ervin's (1974) study population was slightly female-biased (i.e. 53% females), perhaps accounting for differences in the frequency of supernumeraries in the two populations.

*Evidence of genetic contribution.*—Bushtits in the



Chiricahua Mountains did not exhibit a simple breeder/nonbreeding-helper dichotomy. Some of the supernumeraries may have contributed genetically to the nest contents. If so, then they would have been feeding their own offspring in addition to those of the resident pair, making Bushtits cooperative breeders in the joint-nesting category. Breeding units at such nests could be termed polygynous, polyandrous, or polygynandrous, and examples of all such combinations were present in this population. This may be one reason that supernumeraries do not always join existing nests uncontested—their presence could lower the proportional egg contribution of the original residents.

The evidence for genetic contributions by supernumerary females was especially striking at nests attended by more than two adult females. In all cases, nests contained >7 eggs, whereas nests attended by only one female never contained more than 6 eggs. Because nests with only male supernumeraries never exhibited a similar increase in clutch size, the larger numbers of eggs almost certainly resulted from contributions by both females, rather than from single, well-fed females laying enlarged clutch sizes.

The evidence for genetic contributions by males was less direct given that few copulations were observed. All four of the copulations I observed involved a mated pair and occurred near the nest. However, all attendant males that joined before egg laying were seen alone with the resident female during the egg-laying stage, and there did not appear to be any mate-guarding behavior by either male. In fact, it was often impossible to distinguish by behavior the supernumerary males at a nest. Once I observed two different males courting the same female. Two males initially may pair with a female in a polyandrous trio, without any apparent agonism between males. In these cases, the term supernumerary is a misnomer because both males may mate with the female and care for the offspring.

Additional opportunities for extrapair genetic contributions exist within the Bushtit social structure. Chiricahua Bushtits are plural breeders. Breeding flocks, containing many breeding pairs, remain cohesive such that individuals interact freely throughout the breeding season. Thus, males and females from different nests are in close proximity even during the egg-laying period, providing opportunities for extra-

pair copulations to occur uncontested. An extremely fluid social structure also provides the opportunity for intraspecific brood parasitism ("egg dumping"); members of the flock frequently visit other nests. With egg dumping (observed twice in this study), a female and her mate both may contribute to another nest. All of the behaviors listed above suggest that parentage at nests could be multiple, involving all attendants at a nest and even some nonattendants within the same flock. Despite the potential for extrapair copulations, results of DNA fingerprinting thus far suggest that Bushtits retain monogamous associations (Bruce et al. 1996, Sloane et al. unpubl. data).

*Multiple routes to multibird nests.*—There are several routes to multibird nests in the Bushtit, with each class of supernumerary (juvenile, unmated male, and failed breeder) responding to different stimuli and constraints (see Fig. 9). Juveniles that are not capable of contributing to a nest genetically may join simply in response to the begging sounds of unusually hungry nestlings or fledglings (all observed cases of juvenile helping involved unusual circumstances in which nestlings or fledglings were not receiving enough food and begged unusually loudly and persistently). Because, in most cases, juveniles were feeding siblings, there may be selection for the expression of this behavior via indirect benefits, but only when the potential cost of not helping, or the stimulus to help, is great enough.

Among Bushtits in the Chiricahuas, the most common route to multibird nests appears to be via competition for existing nests and/or mates by adults currently without a nest. Under this scenario, adults without a nest (either because they lost one or were unable to obtain a mate early in the season) first attempt to evict the current owners (or owner of same sex) of a neighboring nest in an aggressive attempt to take over the nest completely. Agonistic interactions at neighboring nests after a nest failure had three potential results. First, complete ownership changes occurred in which the residents were replaced by the intruders. Second, the residents remained at the nest after successfully repelling the competitors. Finally, the intruder(s) and the residents coexisted and shared the nesting effort, temporarily or permanently. Thus, a multibird nest sometimes is the result of a compromise between the competitor(s) and the resident(s); i.e. neither "wins."

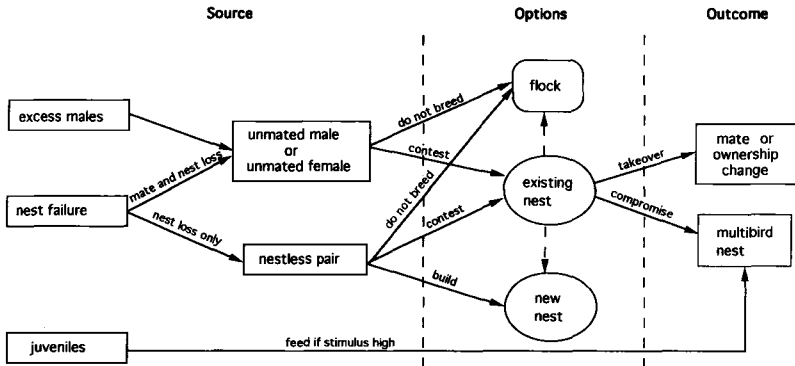


FIG. 9. Potential pathways to multibird nests in Bushtits.

*Costs and benefits of nest-sharing.*—Potential costs are involved in sharing a nest, both for the residents and the interlopers. First and foremost, there is the obvious cost of shared parentage. For example, two males sharing a nest and one female will each produce, on average, one-half the number of fertilized eggs that they would have produced alone, assuming the female produces the same number of eggs as she would have with one mate. Even a female or a pair laying a complete clutch in a shared nest (as seen in several nests with more than one breeding female) may not fledge as many offspring, because in these shared nests the ages of offspring were asynchronous and the nestlings probably competed more unevenly with each other for food. In fact, some of the nests with more than two laying females contained both unhatched eggs and the remains of nestlings that may have died of starvation due to competition with an unusually high number of nest mates. Finally, multibird nests had a greater probability of predation and were less likely to produce fledglings, possibly due to increased noise and activity at the nest (Sloane 1992).

Given the potential costs of sharing a nest, why do birds without nests contest at existing neighboring nests instead of simply building a new nest of their own? Contesting and compromising may be the best choices given the two alternatives—rebuilding or not breeding at all. Rebuilding may not be the best option because Bushtit nests probably are exceptionally costly to build (they are relatively large, are built primarily with spider webs, and are heavily lined with a thick layer of soft feathers). As a result, nest construction requires substantial

time and effort (up to 53 days; Addicott 1938). Failed breeders may find a takeover less energetically costly and even be willing to share the nest if the takeover is unsuccessful. Similarly, unmated males (and unmated females later in season) face the prospect of not producing any offspring if they do not contest or join. This is especially true for unmated males because it is unlikely that they will find an unattached female given the male-biased sex ratio in the Chiricahuas. For these same reasons, the resident birds may be reluctant to relinquish a nest (mate) and so may be willing to compromise rather than abandon only to have to seek out a new nest and/or mate of their own.

In addition, residents may benefit by having supernumeraries at their nests. First, I have evidence that nestlings in nests with supernumeraries are more likely to survive extreme, unseasonable cold (10-day-old nestlings attended by supernumeraries survived a cold spell in late May while nestlings of the same age at three nests without supernumeraries died). Second, pairs with supernumeraries renested earlier and decreased their own feeding rate at the nest, perhaps increasing their subsequent survival (unpubl. data). It is not clear whether allowing supernumeraries to join a nest confers a net benefit or a net cost to the residents.

Advantages to individuals of joining may be the anticipation or knowledge of direct genetic contribution, either in the future or in the past, tipping the balance in favor of joining in spite of its obvious costs. As long as birds join before eggs are laid, they have the opportunity to contribute directly after joining. However, birds also may make a direct genetic contribution pre-

ceding the joining event and prefer to join, or be willing to compromise as joiners, at those nests. These would be nests where the resident female had copulated with an extrapair male, or nests that a female or pair had parasitized earlier. However, adults sometimes join nests even when it appears that they have not made a genetic contribution. Two explanations may account for the presence of these supernumeraries. For example, supernumeraries could contribute to or take over the succeeding nest and/or mate (as in Pied Kingfishers [*Ceryle rudis*]; Reyer 1986), thus eventually deriving direct benefits. At one nest, a male replaced another during the incubation stage and helped raise the first male's offspring (in the absence of the parental male) before later raising a clutch of his own with the same female in the first male's nest (Bruce et al. 1996). Alternatively, supernumeraries simply may be responding to the stimulus of begging nestlings as suggested by Ervin (1977). In aviaries, Bushtits in the appropriate physiological state (i.e. feeding fledglings when captured) will feed even adults when the fledglings are removed (Sloane 1992). Bushtits do not engage in courtship feeding and have never been observed feeding adults in the wild.

Even with a potential net cost of joining, the advantages to Bushtits of retaining a cohesive flock throughout the season may compensate for the possible disadvantages of frequent contact and subsequent competition during the breeding season. For example, during the breeding season, individuals frequently forage together and huddle for warmth during inclement weather. In addition, as fledglings become independent they form flocks of juveniles, leaving their parents free to begin a second nest.

*Variation in incidence of supernumeraries.*—Geographic differences in the frequency and identity of supernumeraries appear to exist among Bushtit populations. Supernumeraries were frequent in southern populations (Skutch 1935) and less frequent in the north (Addicott 1938, Ervin 1974). My population, falling geographically between the others, exhibited variable (but not rare) occurrences of multibird nests. Failed breeders were the only source of extra birds in California (Addicott 1938, Ervin 1974), whereas excess males were the primary source in Guatemala (Skutch 1935). In my study, both sources were important. These differences may merely reflect differences in sample sizes, observation techniques, and duration of observations. Skutch

(1935), for example, studied a population in which birds were not individually identifiable and, in Addicott's (1938) study, only a few birds (16) were marked. In both studies, the number of nests observed was small (3 and ca. 15, respectively). Annual or among-nest variation in these populations, especially in the frequency of supernumeraries, could have gone undetected. Ervin's (1974) study, which was longer (three years) and involved color-banded birds, emphasized flock structure and composition, not nesting behavior. Even so, he observed nest ownership and mate changes during the breeding season but was unable to determine the source of these changes (Ervin 1977). My study encompassed six breeding seasons, >200 nests, and >600 banded individuals, allowing me to detect variation among years and nests. The variation that I found (both year-to-year and flock-to-flock) makes it clear that long-term studies are necessary to assess accurately the range of possible behaviors in the Bushtit and in other species with complex social systems. The intricacies of social structure in Bushtits likely would not be apparent unless nests were watched frequently, for long periods of time, and over several years.

It also is possible that geographic differences in the incidence and origin of supernumeraries reflect population differences, either genetic or facultative behavioral responses to differences in ecology and demography. Proximate factors such as sex ratio, rates of nest failure, and population density could affect the number of multibird nests and the identities and roles of supernumeraries. For example, if birds are single-brooded in a particular year (such as in 1987), then helpers clearly cannot be juveniles from previous nests. Similarly, whether male supernumeraries are common may depend on demographic events, such as high mortality of females during dispersal leading to an excess of males. In the relatively mild climate of the California coast, mortality of dispersing females may be lower than in the mountainous regions of Arizona or Guatemala, resulting in a sex ratio that is not male-biased. Finally, nest-predation rates will influence directly the number of failed breeders and, thus, the amount of competition and subsequent nest takeovers and joinings. In my study, the positive relationship between predation rates and incidence of multibird nests lends support to this hypothesis. However, the population studied by Ervin (1974) experienced

high nest predation (61%), but exhibited a low rate of multibird nests (0.6%). Geographic variation in social structure in response to proximate factors has been documented in other cooperative species of birds including Acorn Woodpeckers (*Melanerpes formicivorus*; Koenig and Stacey 1990) and Galapagos Mockingbirds (*Nesomimus* spp.; Curry 1989, Curry and Grant 1990).

*Comparison with other avian cooperative systems.*—Plural breeding units occur in several other species of cooperative breeders, including White-fronted Bee-eaters (*Merops bullockoides*; Emlen 1981, 1990), Mexican Jays (*Aphelocoma ultramarina*; Brown and Brown 1990), and Galapagos Mockingbirds (*Nesomimus parvulus*; Curry 1988a). Cooperation and plurality within a cohesive flock reach an extreme form in the San Blas Jay (*Cyanocorax sanblasianus*; Hardy et al. 1981) in which all members of a flock, breeders and nonbreeders, feed offspring in several concurrent nests. Plurality in Bushtits is not so extreme. Although flock members frequently visit other nests, helping by adults that had their own active nests occurred on only two occasions (unpubl. data). Nonetheless, the occurrence of plural cooperative breeding in the Bushtit is significant, potentially affecting the costs and benefits of alternative reproductive behaviors. Failed breeders within plural cooperative groups are presented with options not available to those in singular breeding units, including the opportunity for intraspecific brood parasitism and competition over several existing nests.

Juvenile Bushtits were observed in a supernumerary capacity only on rare occasions; juvenile helpers also are rare in other cooperative species (Brown 1987). One notable exception is the Common Moorhen (*Gallinula chloropus*; Leonard et al. 1989). As in Bushtits (Sloane 1992), juvenile moorhens exhibit variation in the amount of help given to younger siblings that is correlated with benefit/cost ratio for the helpers—juveniles are more apt to help when the nestlings are exceptionally hungry and/or when excess food is available, making the cost of not helping high (siblings could die) and the actual cost to the helper low (food was easy to procure; Eden 1987, Sloane 1992). Although juvenile helping was rare in my population of Bushtits, the behavior did occur. This illustrates an important aspect of Bushtit social behavior; juveniles have the capacity to direct parental

behaviors at offspring that are not their own and do so if the conditions are appropriate. In many other species in which fledglings are retained and come into contact with a second brood, the opportunity to feed siblings exists, but juveniles do not take advantage of it.

The retention of males on their natal territories and the dispersal and associated mortality of females result in a male-biased sex ratio that appears to be a major factor in the development of multibird nests in Chiricahua Bushtits. This characteristic is common to many other species of cooperative breeders (e.g. Florida Scrub-Jay [*Aphelocoma coerulescens*]; Woolfenden and Fitzpatrick 1984). The only options available to unmated males are to not breed at all, or to join at a nest and help offspring that are not direct descendants. The potential advantages of the latter can be: (1) helping to raise related offspring, thus increasing fitness indirectly; or (2) helping in order to reap future direct benefits. For example, male helpers may take over the nest and mate with the female in subsequent nesting attempts (Reyer 1986, Bruce et al. 1996). In Bushtits, an additional possibility exists; supernumeraries may contribute genetically to the contents of the nest, thus benefiting directly and immediately.

Failed breeders that become helpers are not rare in other species of cooperative breeders. For example, White-fronted Bee-eaters whose nests have failed sometimes remain in the group and help at neighboring nests (Emlen 1990). Similarly, male Galapagos Mockingbirds whose nests fail may revert to helper status, particularly if they have the opportunity to help relatives (Curry 1988a). Although this behavior is limited to males in the Galapagos Mockingbird, in my study both male and female Bushtits behaved as supernumeraries. In the Long-tailed Tit (*Aegithalos caudatus*), a species closely related to the Bushtit and with an apparently similar social structure, females whose nests have failed often leave their mates (and the flock in which they breed) and return to their natal flock to help their parents (Glenn 1985, C. M. Perrins pers. comm.). Among female Bushtits, I never observed failed breeders returning to their natal flock, even when they had parents breeding in a neighboring flock.

Polygamous associations and variable mating systems occur in several other cooperative breeders, including Acorn Woodpeckers (Mumme et al. 1988), Dunnocks (*Prunella mod-*

ularis; Davies 1992), and Galapagos Mockingbirds (Curry 1988b). Like Dunnocks, Bushtits may have monogamous, polygamous, or polygynandrous associations during the mating season. In Dunnocks the variation arises from competition among individuals for foraging areas and mates (Davies 1985), whereas in Bushtits it appears to arise via competition for nests. Like Bushtits, Acorn Woodpeckers have nonbreeding helpers and joint-nesting adults, but polygamous groups arise primarily from the retention of young birds on natal territories (Koenig and Mumme 1987).

Overall, the Bushtit social system appears most similar to that of the White-fronted Bee-eater (Emlen 1981, 1990). White-fronted Bee-eater clans appear to be functionally very similar to Bushtit flocks, although bee-eaters nest colonially and Bushtits do not. White-fronted Bee-eater clans consist of close kin (Emlen and Wrege 1988), whereas in Bushtits, males remain in their natal flocks and females apparently disperse only short distances, probably resulting in a high degree of relatedness within flocks (Ervin 1974, Sloane 1992). Most importantly, the helper status of an individual White-fronted Bee-eater is transitory as it is in Bushtits, with no distinct "helper class." Helpers can be juveniles (rare) or failed breeders of either sex. Furthermore, in both White-fronted Bee-eaters and Bushtits, opportunities for extrapair copulations and egg dumping exist (and have been documented in White-fronted Bee-eaters [Emlen and Wrege 1986]). However, in White-fronted Bee-eaters the presence of supernumeraries increases fledging success at nests (Emlen 1990), whereas it is not clear whether the presence of supernumeraries at Bushtit nests results in a net cost or benefit to the resident pair (Sloane 1992).

Information available on the Long-tailed Tit, which is a common species in the Old World, indicates that it has a social structure similar to that of the Bushtit (which is the only New World representative of the same family, Aegithalidae). Long-tailed Tits live in large flocks year-round and have adult supernumeraries (often failed breeders) at some nests (Gaston 1973, Glenn 1985). Similarity in behavior between these two species is not surprising given their close phylogenetic relationship and their similarities in diet, body size, habitat, and nest structure. It is tempting to speculate that this Old World species may be responding to nest losses in a manner not unlike Bushtits, resulting

in a similar social system for many of the same reasons.

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