

THE BEHAVIOR AND REPRODUCTIVE SUCCESS OF THE BLUE-GRAY GNATCATCHER

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Despite its broad distribution and relative abundance, the Blue-gray Gnatcatcher, *Poliophtila caerulea*, has never been the subject of an extended behavioral investigation. Our knowledge of this species, best summarized in Bent (1949), is based upon short-term observations at a few nests and isolated notes on other aspects of behavior. Nice (1932) has written the most extensive paper on the biology of the gnatcatcher (in the following text, "gnatcatcher" refers only to *Poliophtila caerulea*) that is based upon original observations. Our information on the biology of other *Poliophtila* spp. is even more fragmentary.

While studying the niche exploitation pattern of the gnatcatcher, I had an opportunity to follow its general behavior closely on the breeding grounds in California and the winter quarters in Arizona. The following behavioral observations are being published here because they relate to subjects of greatest interest to ornithologists. My material on the habitat requirements and foraging ecology of the gnatcatcher appears elsewhere (Root 1967).

METHODS

I observed breeding gnatcatchers during 1959–1961, and 1963 at the Hastings Natural History Reservation, Monterey County, California. The most thorough observations were made in 1963 when I followed the population from the arrival of the first birds in March until breeding activities ended in late August. My principal study area, where I spent more than 1200 hours, was 56.1 acres (22.7 hectares) in extent and contained large stands of oak woodland and chaparral. Twelve pairs of gnatcatchers occurred on this plot in 1963. Additional observations were made in a variety of vegetation types at other localities in central California.

Our best field data on passerine behavior have often come from extended observations at a few well-situated nests. In this study I have tried instead to follow the complete

spectrum of activities for a representative sample of breeding pairs. I visited each of the territories on the study plot two or three times daily except for short periods when I was away. On at least one of these daily visits, I followed a member of the pair for about 20 minutes, recording its movements and encounters with other gnatcatchers on a map of the area. I stayed with the bird for a longer period when it was engaged in an unfamiliar activity.

A special effort was made to find all of the nests on the study plot; every extant nest and fledgling brood was observed at least once a day. It was usually possible to link the successive nests of each pair together, because gnatcatchers normally re-use material from their own previous nests (discussed below). Most of the later nests were found by following pairs which were dismantling abandoned nests. Four adults were captured by using the predator-decoy method (Root and Yarrow 1967). These, together with nestlings from three broods, were marked with color bands and followed throughout much of the 1963 breeding season. On the basis of the almost daily sightings of each bird, the succession of nests, and the behavior of the banded individuals, it was possible to piece together complete biographies for six breeding pairs during the 1963 season.

Each of the gnatcatcher's behaviors was described in my notes until I was completely familiar with the details and variability of its performance. The principal behaviors were then classified and noted whenever they were observed. These data gave a rough measure of the relative frequency of various behaviors. Many of my observations were made in the oak woodland where the openness of the vegetation afforded clear visibility. After a few weeks the birds became accustomed to my presence and permitted me to observe their undisturbed activities from as close as 15 feet.

Each nest and group of fledglings was observed for at least 10 minutes daily, and sometimes for periods of over an hour. I have consulted the detailed nest records kept at the Reservation by John A. Gray, Jr., Robert Holdenreid, and Charles G. Sibley to fill out my account of behavior at the nest. In addition, the field notes of John Davis, Jean M. Linsdale, and others were used to document the seasonal occurrence of gnatcatchers at the Hastings Reservation.

The winter behavior of the Blue-gray Gnatcatcher and the Black-tailed Gnatcatcher, *P. melanura*, was studied on three trips, totaling 24 days of observation, during 1962 and 1963. Most of the winter studies were carried out on the floodplain of the Colorado River near Yuma, Arizona, and at three localities near Tucson, Arizona (for a more detailed description of my study areas, see Root 1967).

RESULTS

TERRITORIALITY

Immediately after arriving on the breeding grounds, each male gnatcatcher begins to defend a territory. At the Reservation, the first males have been sighted as early as 24 February and as late as 30 March. During the spring of 1963 a period of over a month elapsed between the arrival of the first resident male on 6 March and the establishment of the last territory on 18 April. This lack of synchrony in territory establishment appears to be related to temporal differences in the abundance of foliage anthropods on different territories (Root 1967).

All of the gnatcatcher's courtship, nesting, and foraging activities occur within the boundaries of the territory. The territory is defended by the males and sometimes by the female against all conspecific individuals. Adult females and juveniles are tolerated on the territory when they join the resident pair in harassing a predator (below). On three occasions, however, pairs were seen to leave their nest vulnerable to the predator's attack in order to drive an adult male, apparently attracted by the pair's mobbing calls, from the territory.

I was able to determine the complete boundary of nine territories with reasonable accuracy by following the males for prolonged periods in the early morning and afternoon. The movements and territorial encounters of these males over a period of at least four successive days were plotted on a base map. This map furnished the basis for drawing approximate boundaries which were then

checked by making further observations. The areas of these territories were estimated by drawing the final boundaries on an aerial photograph (which had been taken especially to facilitate accurate mapping at the Reservation) and tracing the outlines with a planimeter. Between 28 April and 5 May 1963, a period when territorial boundaries are well defined and relatively stable, these territories were found to average 4.6 (2.2-7.4) acres or 1.8 (0.9-3.0) hectares in extent.

Before the beginning of a nest and during the period when eggs are being laid, the male, often accompanied by the female, patrols the periphery of the territory frequently. Once nesting is underway, the male's patrolling activity is most pronounced during the half hour period that follows sunrise. While patrolling, the male gives an advertising song which consists of a variable array of from four to eight short sibilant phrases (e.g., *spee spuu spee speet*). The advertising song of the gnatcatcher is not as loud as that given by most other passerine birds living at the Reservation.

When another male or pair is encountered along a boundary, the males approach each other and engage in an intense series of vocalizations and posturing. The outcome of 62 border incidents was observed in this study. Upon first recognizing an alien individual, the male usually assumes a tail-spread posture: the tail is fanned to its fullest extent, displaying the white outer rectrices which are partially concealed by black rectrices under most circumstances. The tail is held horizontally to the long axis of the body and wagged from side to side. Often the males engage in short undulating flights during which the spread tail is displayed. The advertising song is given frequently during boundary disputes, but the most characteristic vocalization given in these encounters is a slow series of emphatic *peeew* calls which are accented on the first syllable.

When disputing males meet on a well-marked boundary, they move parallel to one another with a distance of 40 to 150 feet separating them. Along poorly defined boundaries, the territory is defended in a more vigorous fashion. The males approach to within 30 feet of one another and continue to give the tail-spread display and the advertising song or *peeew* calls. In addition, one of the males may occasionally assume an upright posture: the closed tail is depressed below the long axis of the body and the feathers of the lower dorsum and flanks are raised. Whispered

vocalizations, including the long rambling series of warbles, whistles, and calls which are commonly assumed to function as the gnatcatcher's "song" (Bent 1949) are sometimes given. Since the upright posture and whispered vocalizations are associated with courtship activities (below), their occurrence in boundary disputes may be elicited by the presence of an opponent's mate.

In the most intense disputes, one male flies directly at the other male. If this second male retreats, it is chased as far as 70 feet, the pursuer snapping repeatedly with its beak at the fleeing male. Frequently, the second male flies up to meet its opponent in midair. In this event, the males, their breasts nearly touching, ascend in a vertical flight as high as 40 feet above the ground, all the while snapping at each other with their beaks. On six occasions, the disputants were observed to fall to the ground where they remained locked in combat for several seconds before ascending again in the vertical flight. The combatants break apart at the apex of these vertical flights and a short chase ensues. Between bouts of fighting, the displaying males actively search for food. Any large prey item which they capture is held conspicuously in the tip of the beak for several seconds before it is devoured.

The female usually takes a less active part in territory defense than does the male. During a dispute, the female normally gives *peeew* calls while remaining about 15 feet behind her displaying mate. On one occasion when a pair trespassed deeply into another territory, the two females fell to the ground where they remained locked in combat for several seconds while the males displayed to each other a few feet away. When the female is alone and encounters a trespasser, she usually assumes the tail-spread posture and gives *peeew* calls. On three occasions, the defending female attempted to chase the alien male until she was joined by her own mate.

A characteristic feature of territorial behavior in the gnatcatcher is the high frequency with which boundary encounters result in actual combat (fig. 1). Territory defense is most intense during the period immediately following the arrival of males. Once nesting is underway, the boundaries become relatively stable, and from late April through June I have repeatedly observed gnatcatchers that respected an undefended boundary. The boundaries are patrolled infrequently and only the areas surrounding the nest and favored foraging sites are regularly

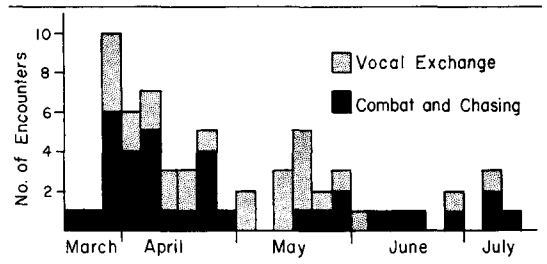


FIGURE 1. The frequency of territorial defense in the Blue-gray Gnatcatcher during 1963. Each column represents a period of 5 days.

defended. Those disputes involving combat that occur late in the season are associated with the shifts in territory boundaries which often accompany renesting activity. Starting in late May, there is a gradual decrease in territorial behavior.

PAIR FORMATION AND COURTSHIP

The pair bond was already complete when the three males which established territories in chaparral were first discovered during my daily rounds of the study area in March, 1963. The bond in these pairs must have been formed before their arrival at the Reservation or, most likely, within the 24-hour period following the male's settlement. In the oak woodlands, there was a delay between the male's establishment of a territory and the formation of a pair bond, although unattached females were seen drifting through the study area during this period.

Following their arrival unmated males frequently inspect potential nest sites on the territory. During these inspections, the male crouches in a tree fork, similar in configuration to those in which nests are found, and turns at least 180 degrees while looking at the surroundings. On two occasions, I had an opportunity to observe the sequence of events that immediately follows the arrival of a female on the territory. In both cases, I had been following a single male for several minutes before he encountered a recently formed pair on the territory boundary. In each instance, the female followed the unmated male onto his territory for a short period before she returned to her original mate. The male responded to the female's presence by perching near her in the upright posture (described above) and singing an elaborate whispered song which contained a variable array of warbles, whistles, and calls. The female then followed the male to a few potential nest sites in which the male perched

for several seconds in the upright posture and continued giving the whispered vocalizations.

Before the beginning of a nest and following the destruction of a nest, the female is frequently seen following her mate. When the female lags behind, the male returns to sing and posture near her. The male shows several nests sites to the female by perching in suitable forks and giving the whispered vocalizations. The female then crouches in these same forks and, while treading with her feet, turns around and examines the surroundings closely. Many of the behavioral components in this nest-inspection display are the same as those employed in nest building. The female may inspect forks that are not shown to her by the male. Later the pair focuses its attention on two or three prospective nest sites, where they trade places in the fork repeatedly and exchange token nest materials. Following the beginning of nest construction, the male continues occasionally to give the upright posture and whispered vocalizations when the female is near the nest.

During early April, females which subsequently disappeared were seen on four occasions to follow a male and inspect nest sites with him for periods of more than an hour. These observations suggest that at least some females examine different territories before they settle in an area and begin breeding.

Other displays that probably function in courtship and maintenance of the pair bond are occasionally seen throughout the spring and early summer. These include a head flagging display, in which the bird faces its mate and wags its head from side to side with the beak partially opened; and begging, in which the bird crouches, cocks the tail slightly upward, and quivers the wings in front of the mate. The male sometimes reacts aggressively toward the female by bill snapping and chasing her for a short distance. Throughout the year, both members of the pair exchange *speee* calls while they are foraging near one another.

During the period just before the beginning of the autumn migration, some adults are still traveling together in pairs while others seem to be alone. On 23 August, two pairs, which were without broods, were each followed for 20 minutes. When these birds were shot, they were found to be midway through the post-nuptial molt. The testes of the males were less than 1 mm in length.

NEST ARCHITECTURE

The nest is built by both members of the pair (Nice 1932). Both sexes are capable of per-

Date:	April 24	25	26	27	28	29
Weather:	●	● /	●	◐	○	○
°F =	48°	47°	44°	53°	64°	64°
No. of visits						
♀	0.5	0	0	5.0	6.0	6.5
♂	2.0	0	0	8.0	2.0	10.5
Σ	2.5	0	0	13.0	8.0	17.0
Secs. at Nest						
♀	2	0	0	38	110	191
♂	26	0	0	64	25	114
Σ	28	0	0	102	135	305

FIGURE 2. The relationship between weather conditions and nest building tempo during 15 minute intervals. The data were taken at the same time each day at two nests where construction began on 22 April 1963. Degree of cloud cover is represented by the darkening of the circles, rainfall by the diagonal lines.

forming all of the nest-building activities, although there is an indication (table 1 and casual observations) that the female does most of the final arranging of materials when the nest is near completion. The labor of building at nests before the fledging of the first brood is shared about equally between the sexes; during short observation periods at 18 different nests, males made 40 trips to the nest while females made 47 trips (also see fig. 2). Following the fledging of a brood, the males do most of the construction on the subsequent nest; in the course of observations at seven such nests, males made 28 trips as compared with only 6 trips by females. The frequency and length of bouts of construction decreases during overcast or rainy weather (fig. 2).

The nest cup is built of dry grasses and plant fibers which are arranged roughly in a swirl, with the finer materials being situated toward the interior. Often the twigs and small branches that form a part of the nest site are incorporated into the cup. The nest is lined with plant down and with feathers from several species of birds. The exterior is ornamented with crustose lichens affixed to strands of spider web and placed in the outer portions of the cup. This ornamentation serves to camouflage the nest under most circumstances, as the bark of the deciduous oaks (chiefly, *Quercus Douglasii*), where most nests are found at the Reservation, is usually covered with the same species of lichens. The orna-

mentation does not always closely match the surroundings of the nest, however, and nests that are placed in chamise (*Adenostoma fasciculatum*) or small oaks having a sparse lichen covering are often quite conspicuous. Chamberlin (1901) reports that pieces of burnt bark were used in place of lichens in an area that had recently been burned over. A nest that had no external ornamentation was found in a desert willow (*Chilopsis linearis*) wash at the Joshua Tree National Monument in southern California (Miller and Stebbins 1964).

The nest is anchored in place by "fingers" of spider web that extend as much as 15 mm from the cup to where they are attached to the bark of the supporting branches. The materials are so arranged as to lend a degree of elasticity to the nest. Before egg-laying and again on the day of fledging, measurements were made of a nest that produced five young. During this period, the inside diameter at the rim increased from 40 to 56 mm, the outside diameter increased from 57 to 68 mm, and the depth of the cup decreased from 37 to 32 mm.

Gnatcatchers gather nest materials at distances as much as 250 feet from the nest site. In obtaining these materials, the birds must frequently engage in activities for which they appear to be poorly adapted. Gnatcatchers have been observed having obvious difficulty in tugging dead grasses free of tangled vegetation and in maintaining their perch on a tree trunk while prying lichens from the bark. The inability of the gnatcatcher to hold an object with the foot while pulling at it with the beak would appear to be a major hindrance in gathering nest material.

When a nest site is abandoned, the gnatcatchers frequently tear the old nest apart and re-use the building materials in a new nest. This nest-moving behavior has been reported from widely scattered localities throughout the breeding range (Lloyd 1932; Hargrave 1933; Murray 1934). Of the 42 nests that I found in 1963, 23 were known to contain material from a previous nest. A banded female re-used building materials in six consecutive nests, and on one occasion moved the bulk of a complete nest to a new site which was over 500 feet away. Materials are taken from nests that are abandoned following fledging of the young as well as those that are deserted during the construction and incubation periods. Three nests that were overrun with the mesostigmatic mite *Ornithonyssus sylviarum* were not moved, even though the pair re-nested within a distance of only 150 feet. I

found no evidence to suggest that pairs re-use building materials from nests other than their own. Two pairs were observed to re-use materials from two of their former nests in the construction of a new nest.

Both members of the pair dismantle old nests. The birds always perch outside the nest cup while tearing it apart. While a major portion of a new nest may come from a previous nest, it always contains some new material.

The re-use of nest materials that are accumulated in the first nest probably reduces the amount of effort required to build subsequent nests. The building period, the interval between the beginning of construction and the laying of the first egg, averaged 13.6 (12–15) days at five nests where only new materials were used, and 4.8 (3–6) days at five nests where building materials were drawn from a previous nest. Since all five of the new nests were built immediately following arrival in the spring, some of the differences in the length of the building period may be related to differences in the reproductive condition of the birds.

While building the nest, the gnatcatchers always stand in the center of the supporting fork or cup. During the first or platform stage of construction, the birds attach a loose accumulation of plant materials to the nest fork with spider silk. At this time, the builders frequently lean down to place silk on the bark below the fork. When the platform is only a few millimeters high, lichens are placed on the exterior by wiping the beak along the platform's edge, where the lichens adhere to the "sticky" spider silk that covers the outer margins. Thus the nest is camouflaged from its very beginning. When there is a deep accumulation of material in the nest fork, the gnatcatchers begin an additional series of building activities. After dropping material onto the platform, the birds push their breasts into the mass and while treading with their feet, turn through an arc of as great as 180 degrees. This serves to push up the walls of the nest. Once there is a shallow depression in the platform, some materials are arranged around the rim by poking up and down with the partially opened beak while turning around. After the walls of the cup are a few centimeters high, the rim is stroked with the underside of the beak, neck, and tail while the bird is engaged in foot treading. The ornamentation of the exterior and some lining are added throughout the construction period. As the nest nears completion, the gnatcatchers

TABLE 1. The relationship between completeness of the nest and building tempo.^a

Stage	Time	No. of visits			Secs. at nest		
		♀	♂	Σ	♀	♂	Σ
New platform	12:15	6	7	13	66	63	129
Shallow depression	10:50	7	10	17	146	126	272
Low cup	11:15	2	0	2	65	0	65
Full cup	11:40	7	0	7	118	0	118

^a Data gathered during 20-minute observation periods at each nest on 1 May 1963 when the sky was clear and the temperature was 65°F. Nest stages are described in the text.

spend longer periods at the nest (table 1) arranging materials.

Because of its adhesiveness (Eisner et al. 1964), spider silk appears to be an essential ingredient of the nest. In addition to the uses described above, spider silk binds the other materials into an elastic mass that can be shaped by the simple treading and stroking movements.

Both members of the pair give a few calls when approaching or leaving the nest. This conspicuous behavior made it easy for me to find nests during the construction period. Occasionally, the gnatcatchers exchange building materials with each other near the nest.

EGG LAYING AND INCUBATION

Of the 20 complete clutches examined in this study, 2 contained 3 eggs, 11 contained 4 eggs, and 7 contained 5 eggs. At three nests, it was found that one egg is laid on each consecutive day, probably in the early morning.

The incubation period, reckoned from the date when the last egg was laid to the date when the last egg hatched, was 15 days at two nests.

On all nine territories for which I had sufficient data, both members of the pair engaged in incubation. During short visits made in the morning to 20 different nests, the male was incubating on 30 occasions and the female on 70 occasions. There was no obvious difference in the incubation pattern of those pairs that had previously fledged a brood. At a nest watched by Sibley (field notes) in the late afternoon, the male incubated for 128 minutes and the female incubated for only 48 minutes. During this period, the birds sat continuously on the nest for an average of 25.1 (7.5-54.5) minutes. Similar incubation patterns at nests in Oklahoma and Ohio have been described by Nice (1932).

Incubation occurs sporadically on the first day following completion of the clutch, but on subsequent days the eggs are rarely left un-

covered for more than a few minutes. Both members of the pair call to their mates occasionally while sitting on the nest. Following the exchange of several calls, they frequently trade places on the nest, although birds that have been silent for several minutes are also relieved from incubation.

DEVELOPMENT OF YOUNG AND PARENTAL CARE

I was able to follow the complete development of the nestlings from the day of hatching to the day of fledging at only two nests. The young remained 12 days in one nest and 13 days in the other. The post-hatching development in these broods was as follows:

First day, the nestlings are naked and their eyes are closed. When the edge of the nest is tapped, they frequently raise their heads and open their beaks in a gaping response. The mouth lining is bright yellow with two black spots on the tongue.

Second day, the developing flight feathers are evident as short pinfeathers.

Third day, the developing pinfeathers of the body tracts become evident.

Fifth day, the eyes are opened to narrow slits when the nestlings are gaping and remain closed the rest of the time.

Sixth and seventh days, the flight feathers and feathers of the body tracts erupt at the tips of the feather sheaths.

Eighth day, the eyes remain open most of the time.

Ninth day, the nestlings give *peet* calls from the nest when the adults are nearby.

Tenth and eleventh days, the nestlings begin to stand up while stretching their wings and preening their flight feathers.

Twelfth day, the nestlings climb onto the nest rim and nearby branches while stretching and preening, after which they return to the nest.

The nestlings are brooded during the daytime until at least the eighth day after hatching. Brooding occurs most frequently on the first two days following hatching. Nice (1932) observed a steady decline with increasing age of the nestlings in the per cent of the time spent brooding at two nests in Oklahoma. The females do most of the brooding, although males occasionally sit on the nest for a short period. The male brings food to the brooding female, which she then feeds to the nestlings, or occasionally eats herself. The female mandibulates large prey items which the male brings for several seconds before feeding them to the young. When the sun is high and shining directly upon the nestlings, one of the adults frequently shades the nest by standing on the rim with the wings partially opened.

The adults carry the fecal sacs that are produced by the nestlings at least 30 feet from the nest before dropping them. When a fecal

TABLE 2. Number of feeding trips made to nests containing nestlings of different ages.^a

Nest	Approx. age of nestlings in days	Date	Observation period	Trips during 2 hours		
				♀	♂	Σ
1	3	27 May	09:15-11:15	17	23	40
			14:00-16:00	20	12	32
	4	28 May	09:15-11:15	14	24	38
			14:00-16:00	14	25	39
2	12	22 May	14:40-16:40	0 ^b	67	67

^a There were five nestlings in both nests.

^b Female present on territory.

sac falls out of the nest, it is retrieved and carried away. On occasion, the adults eat the fecal sacs or feed them to the nestlings.

Food is occasionally brought to the nestlings from distances as much as 500 feet from the nest, but most of the adults' foraging activities are concentrated within a radius of about 200 feet around the nest. The adults immobilize all large prey that they obtain for the young by beating it against a perch. The prey is carried to the nest in the tip of the beak and usually placed head first into the nestling's mouth. If a nestling has difficulty in swallowing the item, the adult removes the prey and repositions it in the nestling's mouth. Sometimes prey that is taken from the nestling is beaten and mandibulated by the adults before it is again fed to the young. Near the nest, the female occasionally begs the male for food, which she immediately feeds to the nestlings.

Prolonged observations at nests show that younger broods are fed less frequently (table 2, and Nice 1932) and that, while the highest feeding rates usually occur during the morning, the feeding tempo does not vary greatly throughout the day (tables 2 and 3).

Nestlings of the Brown-headed Cowbird (*Molothrus ater*), which is a brood parasite of the gnatcatcher, are fed at a rate similar to that of a normal brood. On 7 July, a single cowbird which fledged three days later was fed 12 times by the male and 15 times by the female between 08:55 and 09:55. Two fledgling cowbirds fed singly by separate pairs of

gnatcatchers averaged 28.0 g in body weight, while the total weight of five gnatcatcher fledglings, the maximum size of a normal brood, was 29.3 g.

During the four days before fledging, the male made 39.1 per cent of the total feeding trips reported in table 3. At 15 other nests, where short-term observations were made, the males made 29.4 per cent ($n = 136$) of the feeding trips to first broods and 53.4 per cent ($n = 131$) of the feeding trips to second broods. The male's feeding rate appears to be adjustable, however; when the female is brooding the young nestlings at these early nests, the male brings most of the food. As a result of this adaptability, the male may be able to increase his role in feeding the brood in the event of a severe food shortage. Such a response has been observed in the Blue Tit (*Parus caeruleus*) in which a male nearly doubled his feeding rate at the nest after his mate disappeared (Arnold and Arnold 1952).

The fledging of a brood usually takes less than a day. At one nest, the first fledgling left at 10:14 on 30 June, the second at 05:24 on 1 July, and the remaining two at 06:28 on 1 July. At three other nests, all four or five nestlings fledged within an 18-hour period between my visits to the nest. On one occasion, at least three young left a nest during a 20-minute period when the adults were harassing a stuffed Screech Owl (*Otus asio*) which I had placed about 30 feet from the nest. The adults do not seem excited when a fledgling leaves the nest.

The post-fledging development of three broods that were observed in 1963 was as follows:

First day, the fledglings are capable of flying distances of at least 20 feet at a time. They frequently fall or flap their wings in an effort to maintain balance when landing. It may be that the aerial maneuvers, which are so characteristic of the gnatcatcher's foraging repertoire, develop from these initial balancing movements. As a result of a tendency for the fledglings to follow the adults, the brood usually remains close together. They spend most of the time perched quietly in dense foliage where they engage in frequent bouts of preening. The fledglings

TABLE 3. Number of feeding trips to a nest during two hour periods at different times of day.^a

Observation period	Dates											
	27 June			28 June			29 June			30 June		
	♀	♂	Σ	♀	♂	Σ	♀	♂	Σ	♀	♂	Σ
05:15-07:15	31	29	60	38	27	65	45	23	68	52	27	79
09:15-11:15	35	27	62	25	20	45	62	24	86	47	23	70
13:15-15:15	21	23	44	29	18	47	28	7	35	16	27	43

^a Observations were made at one nest containing four advanced nestlings. The first fledgling left the nest at 10:14 on 30 June, while the other three remained until the morning of 1 July.

TABLE 4. The number of times an individual fledgling is fed in relationship to the individual fed immediately preceding.^a

Individuals	Follows					
	A	B	C	D	E	
Precedes	A	17	5	1	3	1
	B	2	9	2	4	1
	C	2	1	11	1	1
	D	4	2	1	15	4
	E	2	1	1	3	11
Totals	27	18	16	26	18	

^a This brood had fledged the previous day. The observations were made by Sibley (field notes) between 08:22 and 11:52 on 23 May 1938.

do not forage for themselves, but instead, they beg food from the adults by quivering their wings, gaping, and giving a short series of *peet* calls.

Second day, the fledglings have less difficulty in moving from perch to perch, but still remain perched in one place for periods of longer than 30 minutes. Often two or three members of the brood will perch so close together that they touch each other.

By the fourth day, the fledglings are noticeably more active in hopping about and in following the adults for short distances. Bill wiping is first seen on this day.

Fifth day, the young begin to peck at leaves and twigs near their perch. This pecking does not seem to be directed at anything in particular, as one fledgling was seen to peck at its foot and at the same leaf on repeated occasions over a 10-minute period. Another fledgling recovered a perch from which it had slipped by executing a hovering maneuver similar to that employed by the adults (Root 1967).

By the ninth day, the fledglings are obtaining some of their own food by gleaning.

By the thirteenth day, the young are capable of performing all of the foraging maneuvers that are characteristic of the adult repertoire. Still, the fledglings obtain the bulk of their food from the adults. The brood is still highly gregarious and follows the adults constantly.

By the sixteenth day, the young are striking out on their own frequently, but they are still fed occasionally by the adults until at least the nineteenth day after fledging.

Independent juveniles are occasionally heard to give a whispered rendition of a highly variable sequence of calls, which may be termed a "sub-song."

Sibley (field notes) found that the adults tend to feed the same individual fledgling several times in succession (table 4). His data, gathered on the day following fledging, show that a brood of five young was fed a total of 105 times in a 3½-hour period, or 30 times per hour. I found that a brood of four fledglings was fed at least 42 times in an hour on their fifth day out of the nest. A fledgling cowbird was fed 28 times by a female gnatcatcher during a 25-minute period.

The role of the sexes in feeding fledglings

changes markedly between the first and second broods. During short periods of observation on eight different groups of fledglings, the males made only 9.4 per cent ($n = 53$) of the feeding trips to first broods, and 84.4 per cent ($n = 66$) of the trips to second broods. The possible reasons for the sharp decline in the female's attentiveness in feeding the late brood are unknown.

In late August, two adult males and a female, collected while feeding fledglings, were midway through the postnuptial molt.

MAINTENANCE BEHAVIOR

Preening was rarely observed, probably because birds engaging in this activity are relatively inconspicuous. During the five bouts of preening that I observed closely, the birds remained silent while perching for a few minutes on an exposed twig in the direct sunlight. Between intervals of preening the body plumage, the birds probe the rump and base of the tail by reaching back over the closed wing. The ventral surface at the base of the tail is rotated upward and preened over the wing. The wing is partially opened and extended to permit preening of the inner surface.

The head was scratched by placing the leg over the partially extended wing on the six occasions when this activity was clearly observed. The beak and the feathers at its base are frequently rubbed against the perch.

During July and August conditions are very dry at the Reservation and the only free-standing water occurs at a few isolated pools. Gnatcatchers were never observed to visit these pools. Dust bathing and anting were never observed.

The maneuvers employed in capturing and manipulating food are described elsewhere (Root 1967).

INTERSPECIFIC AGGRESSION

The gnatcatcher responds aggressively toward most vertebrates which venture to within about 20 feet of its nest. If the intruder is a small, nonpredatory species, the adult gnatcatchers attempt to drive it away with bill-snapping and aerial attacks. Most species respond immediately to the attack by fleeing, in which case the gnatcatchers chase them for a short distance. The following species were chased away from the vicinity of the nest by gnatcatchers (number of encounters in parentheses):

- Western Fence Lizard, *Sceloporus occidentalis* (2)
- Black-chinned Hummingbird, *Archilochus alexandri* (1)
- Nuttall Woodpecker, *Dendrocopos nuttallii* (1)

- *Western Flycatcher, *Empidonax difficilis* (1)
- *Western Wood Pewee, *Contopus sordidulus* (1)
- *Plain Titmouse, *Parus inornatus* (11)
- Wrentit, *Chamaea fasciata* (1)
- House Wren, *Troglodytes aedon* (11)
- Bewick Wren, *Thryomanes bewickii* (4)
- *Western Bluebird, *Sialia mexicana* (2)
- Hutton Vireo, *Vireo huttoni* (4)
- Solitary Vireo, *Vireo solitarius* (1)
- Orange-crowned Warbler, *Vermivora celata* (1)
- Black-headed Grosbeak, *Pheucticus melanocephalus* (1)
- Lazuli Bunting, *Passerina amoena* (1)
- Lesser Goldfinch, *Spinus psaltria* (4)
- Lawrence Goldfinch, *Spinus lawrencei* (1)
- Spotted Towhee, *Pipilo erythrophthalmus* (1)
- Brown Towhee, *Pipilo fuscus* (1)
- Oregon Junco, *Junco oreganus* (4)
- Chipping Sparrow, *Spizella passerina* (2)
- Merriam Chipmunk, *Eutamias merriami* (2)

The asterisk designates those species that are known to supplant the gnatcatcher away from its nest.

The above list includes several species whose food habits are similar to those of the gnatcatcher, suggesting that interspecific aggression around the nest might function to create some degree of hyperdispersion with species that are potential competitors. Also included in the list are species which are dominant to the gnatcatchers in encounters that occur at a distance from any nest. The gnatcatcher is particularly hostile toward the House Wren, attacking this species at distances of over 40 feet from the nest during all stages of the nesting cycle. The House Wren is known to steal building materials and eggs from the nests of other small birds (Bent 1948). The number of encounters with the other species is roughly proportional to their abundance on the study area.

Throughout the breeding season, the gnatcatcher responds to any large predator which it encounters on the territory by engaging in a characteristic harassment display. This display was observed under optimal conditions on several occasions when I placed either a stuffed Screech Owl (*Otus asio*) or a Horned Owl (*Bubo virginianus*) near the nest.

When the predator is first recognized from the nest, the gnatcatcher leaves silently and flies a short distance away. It then approaches the predator and starts to give a rapid series of *bhew* calls. The *bhew* calls resemble the *peeew* calls which are given during territorial disputes, but differ in being more emphatic, in the increased tempo that the calls are delivered, and in the longer duration of the series. In apparent response to the *bhew* calls, the first gnatcatcher is joined by its mate within a short period. In addition, gray squir-

rels (*Sciurus griseus*) and several species of birds approach to join the gnatcatchers in harassing the predator. The gnatcatcher holds the tail slightly above the horizontal, often partially spread, and wags it from side to side. Gradually they move to within 5 to 10 feet of the predator and begin to fly at its head from various directions. In the most intense encounters, gnatcatchers hover above the predator and dive repeatedly at its head. Frequently the gnatcatchers strike the predator with their beaks. Owls are harassed throughout the breeding season, but the most intense encounters occur when the gnatcatchers have a nest or fledglings. After a stuffed owl is removed, the pair continues to give *bhew* calls and to examine the spot where the owl was placed at frequent intervals for a period of from 5 to 10 minutes.

Under natural conditions, the following species were harassed by gnatcatchers at the Hastings Reservation (number of encounters in parentheses):

- rattlesnake, *Crotalus* sp. (1)
- Cooper's Hawk, *Accipiter cooperii* (4)
- Barn Owl, *Tyto alba* (1)
- Screech Owl, *Otus asio* (1)
- Pygmy Owl, *Glaucidium gnoma* (4)
- Scrub Jay, *Aphelocoma coerulescens* (78)
- Yellow-billed Magpie, *Pica nuttalli* (2)
- Western Bluebird fledgling, *Sialia mexicana* (1)

The Scrub Jay, which is a relatively common bird at the Hastings Reservation, is a serious predator on the eggs and young of small birds, such as the gnatcatcher, which build open nests (Bent 1946). Gnatcatchers which do not have nests or dependent young either ignore or harass jays only mildly. When gnatcatchers are aware of Scrub Jays within a radius of about 150 feet from a nest or brood, the adults fly over to begin their attack. The harassment display against jays is usually effective: the jays appear to be obviously distracted and often leave the territory within a short period. Gnatcatchers have been seen to follow jays for distances of over 100 yards and for periods of longer than 10 minutes. Nestlings crouch in the nest when the adults are harassing a jay nearby, while fledglings quickly scatter when a jay approaches them. Juvenile gnatcatchers usually ignore the Scrub Jays which they encounter on their own, but they are attracted to the scene where adults are mobbing a predator.

The harassment display is not always effective. Sibley (field notes) observed six Yellow-billed Magpies ripping apart a gnatcatcher nest and eating the eggs while the adults dove repeatedly at the predators' heads. Once the

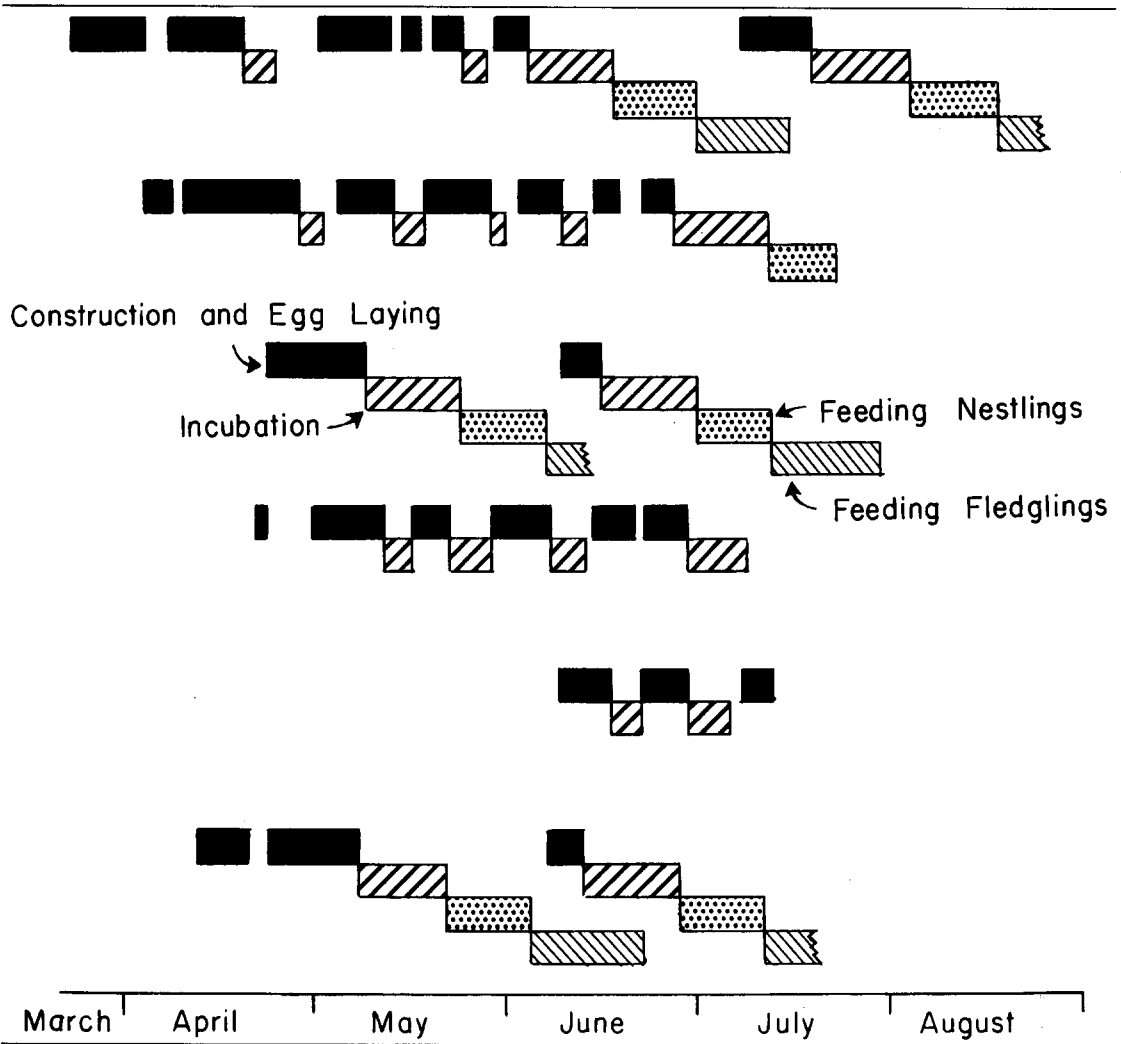


FIGURE 3. The seasonal distribution of various reproductive activities by six pairs of Blue-gray Gnatcatchers during 1963.

nest was destroyed, the gnatcatchers' harassing activity subsided quickly.

A pair of gnatcatchers has been observed to harass a female cowbird during the breeding season (Blincoe 1923). In the foothills of the Sierra Nevada, a pair of gnatcatchers which were feeding nestlings harassed a Loggerhead Shrike, *Lanius ludovicianus* (Myers 1907). Cooper's Hawks and a stuffed Sharpshinned Hawk (*Accipiter striatus*) were harassed when they were discovered on a perch. Gnatcatchers responded to accipitrine hawks flying nearby, however, by giving strident alarm calls and fleeing to a dense clump of foliage where they remained silent until after the hawk had left the area.

A Western Bluebird fledgling which could not fly well enough to flee when a pair of gnatcatchers tried to drive it from the nest

tree was harassed almost continuously for more than two hours by one or the other of the adults. Since bluebirds are not normally harassed, this observation suggests that an intruder's behavior may be as important as its color or configuration in eliciting the mobbing response.

REPRODUCTIVE SUCCESS

Of the 12 pairs of gnatcatchers that remained on the study area throughout most of the 1963 breeding season, five were unsuccessful in raising a brood to fledging age, three succeeded in raising one brood, and four succeeded in raising two broods. The seasonal pattern of reproductive effort for six of these pairs is presented in figure 3; I found every nest of these pairs that persisted for more than two days. Two color-banded females

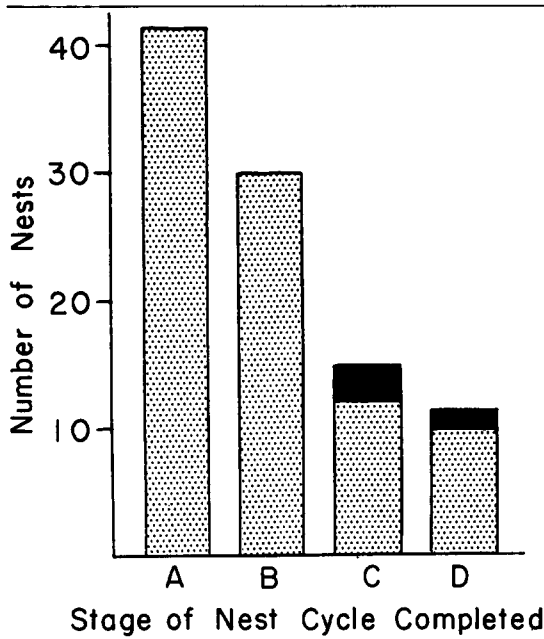


FIGURE 4. The stages of the nesting cycle successfully completed in 42 nesting attempts during 1963. Only nests that were first found during the early stages of construction are considered. The stages are defined as follows: A. Construction of the cup completed. B. Incubation begun. C. Eggs hatched. D. Fledglings left. The black portion of the histograms refers to nests known to contain young Brown-headed Cowbirds.

were each observed to construct seven nests during a single breeding season. Construction of a new nest may begin as early as the day following the fledging of the first brood and in at least one instance, the fledglings of the first brood were fed by the adults throughout most of the incubation period on a second clutch.

My data on reproductive success (fig. 4) are presented in terms of the stages of the nesting cycle which each nest completes. A nest was considered to be successful if all or only a part of the original clutch succeeded in completing a stage of development. Ornithologists usually calculate reproductive success in terms of the number of eggs which successfully complete each stage. Since gnatcatchers frequently desert their nests and there is a high rate of nest predation, I followed the fate of each individual in only those few nests which I could examine without disturbing the nest site. Gnatcatchers fledged from 24.4 per cent of the nests which reached an advanced stage of construction in 1963 (fig. 4). Nolan (1963) found that the average nest success, calculated in the same manner as the figure above, of six species of birds which

build open, elevated nests was 19.3 per cent (10.0–33.3 per cent) in a deciduous scrub biotope in Indiana. Thus the gnatcatcher's reproductive success seems to fall within the normal range of variation for birds which nest in similar situations. The greatest losses (63.4 per cent) occurred during the egg-laying and incubation stages, while there was only a 26.7 per cent loss during the period when nestlings (both gnatcatchers and cowbirds included) were present.

The exact cause for the failure of a nest was known in only a few cases. Nonetheless, indirect evidence suggests that predation on the eggs was the major mortality factor. Several nests were found where part or all of the clutch was missing and the nest lining was torn up (when gnatcatchers dismantle an old nest, material is always removed from the outside first). Cowbirds, which were first seen at the Hastings Reservation in 1959, also contribute heavily to nest losses. Six of the 22 broods found in this study consisted of a single cowbird nestling. One brood of four gnatcatcher nestlings which hatched eight days previously were found dead in a nest which was heavily infested with the mesostigmatic mite *Ornithonyssus sylviarum*. The stomachs of these nestlings were filled with partially digested food, and there was no evidence of internal parasites or attack by a predator.

In late May and early June of 1961, there was a population outbreak of the tent caterpillar, *Malacosoma constricta* (Lasiocampidae), at the Hastings Reservation. The late-instar larvae of this moth, which are not eaten by the gnatcatchers (Root 1966), completely defoliated the oaks on a large portion of the study area. I made a thorough search of the defoliated area between 11 June and 15 June, and was able to find only three gnatcatcher nests, all of them in late stages of construction or early incubation. Other pairs on the area did not seem to be engaged in any reproductive activity. This situation suggests that the decrease in food supply, which must have accompanied the defoliation of the trees, resulted in a general failure of the nesting activity normally underway at this season (Root 1967).

BEHAVIOR IN WINTER

During the winter gnatcatchers are frequently seen foraging together in what appear to be pairs. On 13 different occasions, involving at least seven different "pairs," two birds remained within six yards (sometimes much closer) of one another for more than five

minutes. Within a 45-minute period, two gnatcatchers moved a distance of over 150 yards together, exchanging frequent *speee* calls as they progressed. I frequently noted that the color of the lower dorsum of one bird was duller in comparison with that of its partner. Both individuals in two such "pairs" were shot; in each case the gnatcatcher with the dull plumage proved to be a female while the brighter specimen was a male. These plumage differences are very subtle and are not always obvious in museum specimens. On 29 January, a gnatcatcher gave a whispered song, which was indistinguishable from the courtship song, eight times during a 20-minute period. This bird was alone and had not yet achieved the male's characteristic nuptial plumage. The close association between the sexes during the winter is of interest, since the late arrivals, and possibly the early arrivals, on the breeding grounds are not paired.

The social bond between wintering gnatcatchers is not strict, however. On eight occasions, single individuals were followed for more than 15 minutes. Once two birds which had been foraging together separated and remained apart (two observers involved) for at least 35 minutes.

Gnatcatchers appear to remain on home ranges during the winter. I have been able, with the help of other observers, to follow the movements of the same individuals almost continuously for as long as three hours in vegetation dominated by saguaro (*Carnegiea gigantea*) and palo verde (*Cercidium microphyllum*) at Sabino Canyon and the San Xavier Reservation, both near Tucson, Arizona. I returned to these same spots at different times of day throughout a period of a week and found that it was possible to circumscribe the areas within which gnatcatchers occurred. I estimate that the gnatcatcher's home range in this biotope is at least 22 acres, which is larger than the normal breeding territory at the Hastings Reservation. In an isolated screw-bean (*Prosopis pubescens*) woodland near Yuma, Arizona, at least nine gnatcatchers (eight specimens taken) were found within an area of 22 acres. At this locality, the birds were spaced out, often as obvious pairs, and each individual seemed to restrict its movements to an area of about three acres or less. Territorial defense of the winter home range was never observed. On two other occasions, three gnatcatchers foraged within 15 yards of each other for a few minutes without engaging in any aggressive behavior.

In Arizona, the gnatcatcher is frequently seen foraging with Verdins (*Auriparus flaviceps*), Black-tailed Gnatcatchers (*Polioptila melanura*), and Ruby-crowned Kinglets (*Regulus calendula*) during the winter months. This association between *P. caerulea* and *P. melanura* is particularly interesting, since the two species possess similar morphological adaptations and foraging repertoires, and would therefore be expected to be strong competitors for food. These two species were seen foraging within 10 yards, twice within three yards, of one another on eight occasions without displaying any aggression toward each other. In two instances, the birds were followed for long enough to determine that there is obvious cohesion, a tendency for two birds to travel in the same direction together, between the two species. On 20 December, a pair of *P. melanura* and a single *P. caerulea* remained within 15 yards of each other while moving over 120 yards together during a period of 23 minutes. At the end of this observation, the male *P. melanura* began to give a series of five-parted vocalizations and then flew about five yards to supplant the *P. caerulea* from its perch. Soon after this encounter the two species slowly drifted apart. A male *P. melanura*, which was previously silent, was seen to supplant a *P. caerulea* on one other occasion.

The gnatcatchers which were collected at Yuma during the winter had moderate to heavy accumulations of fat. The mean body weight of 10 winter specimens was 5.6 (5.0–6.1) g, while the average weight of 13 adults which were collected at the Hastings Reservation in July and August was 5.7 (5.4–6.0) g.

DISCUSSION

TERRITORIALITY

Territoriality is often considered to function as a form of contest competition (Nicholson 1957) giving dominant individuals exclusive access to a supply of limited requisites which is sufficient for survival and reproduction. For birds, the supplies of food and suitable nest sites are frequently held to be the most critical requisites. That most gnatcatcher territories contained an abundance of nest sites is indicated by the construction of as many as seven nests in different locations within the boundaries of a small territory during a single breeding season. Similarly, the food supply on the territories seemed to be more than adequate. Breeding gnatcatchers normally made their greatest demands on the available food supply when the adults

were feeding young (Root 1967). During this same period, the adults' foraging area became restricted to a portion of the territory surrounding the nest and much of the area used earlier was poorly defended. Such contractions in the size of the utilized territory during the nestling stage have been reported for a variety of bird species (e.g., Odum and Kuenzler 1955; Stefanski 1967). The simplest inference suggested by these observations is that the territory boundaries defended at the beginning of each nesting attempt usually enclose a surplus of food and nest sites. This simple interpretation, however, is static and fails to account for important changes in the gnatcatcher's habitat requirements.

Defense during the period of territory establishment (March-April) appears to set the gnatcatcher density for the remainder of the breeding season. After late April, no new territories were established although pairs moved off the study area and were replaced by pairs from adjacent areas. Within this relatively stable population, the defense of "oversized" territories provided sufficient space for the gnatcatchers to alter their utilization of habitats in several adaptive ways.

The abundance of food in the immediate vicinity of the nest becomes progressively more important as the nestlings mature. It seems unlikely that the adults could deliver small arthropods to the older nestlings at the observed rates (tables 2 and 3) and also forage regularly in distant portions of the territory; this may also be true for other small insectivorous species. As a result, nests are best located where food is extremely abundant. At the Hastings Reservation gnatcatchers apparently responded to a seasonal succession in the abundance of foliage arthropods in different habitats through an almost continuous realignment of territory boundaries (Root 1967). Thus in March and early April, chaparral and live oaks were the preferred foraging habitats. When the supply of available arthropods in these habitats began to decline in late April, there was a gradual shift in territory boundaries that resulted in most pairs having greater access to the adjacent deciduous oak woodland where food was more abundant. The large size of the initial territories facilitated this shift by permitting nests to be relocated in the new optimal habitat on areas that the original defenders visited infrequently.

The large territories also provided ample access to special habitats that were used for only short periods. Thus the same, small,

dense stands of chaparral and live oaks were utilized alternately by fledglings from the adjacent territories on their first few days away from the nest (Root 1967). Similarly, the adults from as many as three territories shared the same chaparral stand (which had been defended as a single territory in March) during their postnuptial molt in August.

Finally, the "oversized" territories may function as a reserve against exceptional years when food is temporarily in short supply. When the oaks were defoliated by tent caterpillars in 1961 (above), the abundance of gnatcatcher prey must have been greatly reduced (Root 1966). At this time, the density of adult gnatcatchers in the vicinity of the study area appeared to be normal but most breeding activity had been halted and much of the foraging was centered in the isolated stands of chaparral and live oaks that had escaped defoliation. When the deciduous oaks began to develop new foliage, the gnatcatchers were able to resume nesting soon after.

These observations lead me to suggest that territory size in the gnatcatcher is "ultimately" related (Lack 1954, 1966) to the supply of limited resources. The apparent surplus of such requisites at any one time does not negate this interpretation. The gnatcatcher's utilization of different habitats in the vicinity of its territory is flexible, changing in response to seasonal and yearly variation in the dispersion of limited resources and according to the varied requirements associated with different stages in its life history. If the territory size was just sufficient to contain the requisites used over a short period, the population could become so crowded that many individuals would be restricted to small areas, unable to meet their requirements as local conditions varied.

Compared with other species that defend territories of similar size, the gnatcatcher's territorial behavior seems to be less conspicuous and "ritualized." The gnatcatcher's advertising calls are soft (to the human ear) and the males rarely display from exposed song perches. As a result, the frequent patrolling observed during territory establishment may be necessary to hold a large area. Such reliance on patrolling is probably related to the shifting pattern of habitat utilization; as pairs become occupied with nests, their dominance over little-used portions of the territory is reduced by their infrequent visits. These areas can then be occupied with little opposition by adjacent pairs.

The prominence of territory in the gnat-

catcher's breeding ecology is reflected in the courtship and predator mobbing behavior. Thus the females' activities immediately after arriving on the breeding ground suggest that they are assessing the qualities of the territories as much as those of the males. On all three occasions when an alien male attempted to join mobs harassing a predator near the nest of another pair, territory defense by the residents took precedence over further aggression toward the predator. This observation requires further verification, perhaps by the presentation of models at mobs formed around predator decoys.

NESTING POTENTIAL

Pairs of gnatcatchers can complete as many as seven nests in a season (fig. 3). Adaptations that increase the number of nesting attempts, and thus the chances of leaving successful progeny, have obvious advantage to a species that experiences such a high level of nest loss (fig. 4). The selective pressures involved are reflected in 1963, (an apparently normal year) when five of the twelve pairs on the study area were unable to raise a brood to fledging age.

The gnatcatcher's prolonged nesting season at the Hastings Reservation (late March to late August) is the principal factor that permits pairs to build several nests. Within this long season, the reproductive potential is further increased by behavioral adaptations that serve to compress the time interval between successive nests.

The re-use of building materials from former nests appears to decrease the time spent in constructing later nests. As suggested by Weston (*in* Bent 1949) and McCabe (1963), the original nest probably serves as a cache for critical building materials that are difficult to obtain late in the season. Dead grasses, used extensively in the nest cup, may be more difficult, or dangerous, for gnatcatchers to obtain from the ground after the new grass cover has achieved its maximum growth in May. Similarly, the re-use of building materials reduces the need to gather such items as spider web which require much time despite their availability throughout the breeding season. Finally, moving nest material permits pairs to establish new nests rapidly when they lay claim to new territory (above) that is temporarily vacant.

The lack of marked sexual specialization in parental and nest building behavior increases both the responsiveness and efficiency of the adults' breeding activities. Both mem-

bers of the pair share about equally in constructing the first nest when all of the materials must be gathered fresh (none has been cached in a previous nest) and adverse weather causes frequent delays (fig. 2). The nestlings of the first brood are fed mainly by the female while the male continues to defend the contracted territory. After the first brood fledges, the female continues to do most of the feeding, leaving the male free to build the bulk of the new nest. The male can begin this nest as early as the day after the first brood fledges. The male then takes a more nearly equal role in feeding the nestlings of the second brood; this may be correlated with the summer decline in the abundance of foliage arthropods (Root 1967). The interchangeable roles of the parents is the major factor that enables gnatcatchers to care for two successive broods at the same time (fig. 3). Judging from the length of the breeding season (fig. 3), it may be possible sometimes for pairs to raise three successful broods a year at the Hastings Reservation.

SUMMARY

The behavior of the Blue-gray Gnatcatcher was observed during four breeding seasons at the Hastings Reservation, in coastal California, and on the wintering grounds in southern Arizona. The breeding season data are based on short, daily observations on each of the pairs nesting in a 56.1-acre study plot containing oak woodland and chaparral.

Both sexes are present when the first territories are established at the Reservation; the extreme dates for first arrivals are 24 February and 30 March. Within a season, a period of over a month can elapse between the arrival of the first residents and establishment of the last territory. In the spring, territories average 4.6 acres. Territory defense is not highly ritualized; the males patrol the territory boundaries frequently and close encounters involving vigorous displays and combat are common.

During courtship, females follow the males and inspect potential nest sites where many displays are performed. Newly arrived females consort briefly with different males.

Both members of the pair build the first nest although the female does most of the final arranging of materials. Nest building is curtailed during rainy, overcast weather. As early as the first day after a brood is fledged, the male starts a new nest on which he does the bulk of the construction. The nest cup, from its earliest stage of construction, is orna-

mented with lichens. These lichens make the nest more conspicuous in certain situations. Spider silk, perhaps because of its adhesive properties, is used extensively in the nest. Pairs usually move the materials from their own abandoned nests to new building sites that may be as far as 500 feet away. Materials are not moved from nests that have been overrun by the mite *Ornithonyssus sylviarum*.

The incubation period is 15 days and the nestling period is 12–13 days. During the last days in the nest, broods may be fed as often as 43 times an hour with the most active parent visiting the nest about once every two minutes for extended periods. Fledglings are dependent upon the adults for most of their food until about the 16th day after leaving the nest. While both parents feed young throughout the season, the females assume the most active role with early broods, the males with fledglings of late broods.

Adults chase most small vertebrates (at least 22 species) that approach their nest and engage in the intense harassment of predators encountered on any part of the territory.

During 1963, young fledged from 24.4 per cent of 42 nests that were first found during the construction stage. Banded pairs made as many as seven nesting attempts during the breeding season (late March to late August). Some pairs were unsuccessful in raising a brood to fledging age while others succeeded in raising two broods. The greatest loss of nests occurred during the egg-laying and incubation periods. Probably predation by Scrub Jays is the major factor responsible for nest loss. A heavy infestation of the mite *O. sylviarum* was apparently responsible for the death of one entire brood of nestlings. Six of 22 gnatcatcher broods consisted of a single Brown-headed Cowbird. During 1961, all nests apparently failed after a population outbreak of tent caterpillars that defoliated the oaks.

During the winter in Arizona, gnatcatchers seem to remain on home ranges and often travel as "pairs." Frequently they forage in close association with the Black-tailed Gnatcatcher; this is of interest because the two species have very similar niche requirements and should be strong competitors.

Viewed on a short-term basis, gnatcatcher territories apparently contain a surplus of limiting requisites. The probable function of the "over-sized" territory is to provide sufficient space for the birds to alter their pattern of habitat utilization in response to temporal changes in the dispersion of food and

cover. Thus territory size may be ultimately related to the availability of resources. Territoriality is a dominant activity that influences many other aspects of the gnatcatcher's behavior.

The re-use of nest material and the interchangeable roles of the parents can be interpreted as adaptations that increase nesting potential and the population's responsiveness to environmental change.

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LITERATURE CITED

- ARNOLD, G. A., AND M. A. ARNOLD. 1952. The nesting of a pair of Blue Tits. *Brit. Birds* 14: 175–180.
- BENT, A. C. 1946. Life histories of North American jays, crows, and titmice. *U. S. Natl. Mus., Bull.* 191.
- BENT, A. C. 1948. Life histories of North American nuthatches, wrens, thrashers, and their allies. *U. S. Natl. Mus., Bull.* 195.
- BENT, A. C. 1949. Life histories of North American thrushes, kinglets, and their allies. *U. S. Natl. Mus., Bull.* 196.
- BLINCOE, B. J. 1923. Gnatcatchers attacked cowbird. *Bird-Lore* 25:253–254.
- CHAMBERLIN, C. 1901. Some architectural traits of the Western Gnatcatcher. *Condor* 3:33–36.
- EISNER, T., R. ALSOP, AND G. ETTERS HANK. 1964. Adhesiveness of spider silk. *Science* 146:1058–1061.
- HARGRAVE, L. L. 1933. The Western Gnatcatcher also moves its nest. *Wilson Bull.* 45:30–31.
- LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford. 343 & viii pp.
- LACK, D. 1966. Population studies of birds. Clarendon Press, Oxford. 341 & v pp.
- LLOYD, C. K. 1932. The Blue-gray Gnatcatcher moves its nest. *Wilson Bull.* 44:185.
- MCCABE, R. A. 1963. Renesting of the Alder Flycatcher. *Proc. XIII Intern. Ornithol. Congr., Ithaca*, p. 319–328.
- MILLER, A. H., AND R. C. STEBBINS. 1964. The lives of desert animals in Joshua Tree National Monument. *Univ. of Calif. Press, Berkeley*. 452 & vi pp.

- MURRAY, J. J. 1934. The Blue-gray Gnatcatcher moving its nest. *Wilson Bull.* 46:128.
- MYERS, H. W. 1907. Nesting ways of the Western Gnatcatcher. *Condor* 9:48-51.
- NICE, M. M. 1932. Observations on the nesting of the Blue-gray Gnatcatcher. *Condor* 34:18-22.
- NICHOLSON, A. J. 1957. The self-adjustment of populations to change. *Cold Springs Harbor Symp. Quant. Biol.* 22:153-173.
- NOLAN, V., JR. 1963. Reproductive success of birds in a deciduous scrub habitat. *Ecology* 44:305-313.
- ODUM, E. P., AND E. J. KUENZLER. 1955. Measurement of territory and home range size in birds. *Auk* 72:128-137.
- ROOT, R. B. 1966. The avian response to a population outbreak of the tent caterpillar, *Malacosoma constrictum* (Stretch). *Pan-Pacific Entomol.* 42:48-53.
- ROOT, R. B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. *Ecol. Monogr.* 37:317-350.
- ROOT, R. B., AND R. M. YARROW. 1967. A predator-decoy method for capturing insectivorous birds. *Auk* 84:423-424.
- STEFANSKI, R. A. 1967. Utilization of the breeding territory in the Black-capped Chickadee. *Condor* 69:259-267.

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