

The Niche Exploitation Pattern of the Blue-Gray Gnatcatcher

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THE NICHE EXPLOITATION PATTERN OF THE BLUE-GRAY GNATCATCHER¹

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INTRODUCTION

The niche concept remains one of the most confusing, and yet important, topics in ecology. Traditionally the concept refers to the functional role, particularly in trophic interactions, of a species within a community. There has been little agreement, however, on what factors adequately define this functional role; in describing niches, various authors have chosen to stress different features of a species' diet, natural enemies, microhabitat, and periods of seasonal or diurnal activity. Much of the misunderstanding between ecologists concerning the competitive exclusion principle and the existence of "vacant" niches can be traced to this ambiguity (see reviews by Udvary, 1957; Hardin, 1960; and DeBach, 1966).

In 1957, Hutchinson and Macfadyen, writing independently, defined the niche in a new and different way. Both authors cast the niche in terms of the range and combination of environmental conditions that permit a species to exist indefinitely. In other words, the niche is seen as an abstract "space" in the environment which some species must be able to exploit successfully for an extended period. While the Hutchinson-Macfadyen concept is no more helpful than the "role" concept in providing an operational definition for the niche, it serves to direct our attention to new types of investigation. For instance, the same species may occur in several different habitats

or cope with a changing set of conditions within a single habitat. Through a comparative investigation, one may hope to discover features common to these several environments. By this process, one may peel away all but the most critical features, leaving a core of limiting factors that defines the fundamental niche of a particular species. This approach has been attempted in the present study.

The niche may be thought of as composed of several dimensions (Hutchinson, 1957), each corresponding to some requisite for a species. Organisms are usually adapted to exploit only a portion of the requisites that are available in any environment. When the characteristics of these requisites are plotted on a continuous scale (e.g., prey size, position of the habitat in a vegetation continuum), the species exhibits a characteristic "exploitation curve" (Fig. 1). The exploitation curves for all requisites combine to form the species' "exploitation pattern". The shape of the exploitation curve will be determined by the interplay of several selective forces. The population will often respond to interspecific competition by becoming more efficient, through the evolution of specializations, in exploiting a more restricted range of requisites. Intraspecific competition will oppose this tendency toward greater specialization by causing the population to exploit the environment in a more generalized manner, thereby capturing a larger niche space (Svärdson, 1949). Finally, the relative stability of the environment will influence the exploitation pattern (Klopfer, 1962). Species which occupy habitats that fluctuate widely in their suitability for existence must

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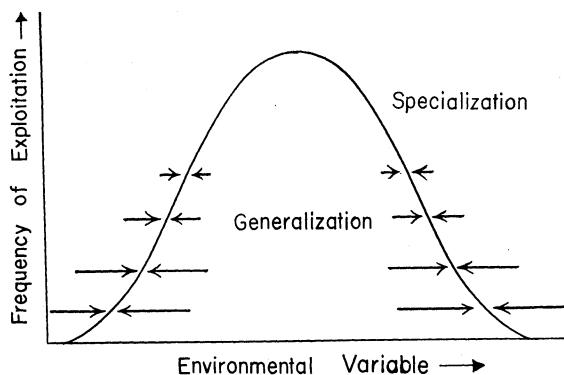


FIG. 1. A hypothetical exploitation curve of a population with respect to one dimension of the niche. The arrows show how selective forces which promote greater specialization or generalization influence the shape of the curve.

either remain highly generalized or possess adaptations, such as the ability to migrate or to become dormant, that permit the population to survive when its specialized requirements fail.

The central theme of this paper is the manner in which the exploitative behavior of the Blue-gray Gnatcatcher (*Polioptila caerulea*) is organized to achieve optimal adaptation in a changing environment.

The gnatcatcher* is a small bird, weighing about 5.8 gm, which feeds exclusively upon arthropods. During the breeding season this species is sexually dimorphic, the male having black feathers in the loral region and a more brightly colored dorsum. The genus *Polioptila* has been divided into nine New World species (Paynter, 1964) which breed allopatrically or in different habitats. Situations where members of the genus come into marginal contact with one another have been described by Brodkorb (1944), Paynter (1955), and Miller and Stebbins (1964). Mayr and Amadon (1951) have placed the genus in the Sylviinae, a subfamily which has undergone its most extensive adaptive radiation in the Old World. The breeding range of *P. caerulea* occupies a major portion of the continental United States and extends southward into Guatemala. The fragmentary literature on the gnatcatcher's breeding behavior is summarized in Bent (1949), Nice (1932), and Root (*In press*). During the winter, the northern populations migrate to the southern United States and Mexico. The food supply and habitat requirements of the species vary on a geographical, seasonal, and yearly basis. By describing the gnatcatcher's behavioral response to these environmental variations and to the increased energy demands associated with raising young, I have attempted to discover how the interplay between specialization and generalization influences the exploitation pattern of a single species.

*Throughout this paper, "gnatcatcher" is used only to designate the species *Polioptila caerulea*.

STUDY AREAS

The principal study area was located on the Hastings Natural History Reservation, situated at the northern end of the Santa Lucia Mountains, in Monterey County, California. The broad-sclerophyll vegetation and physical conditions of the surrounding region have been described by Cooper (1922), Shreve (1927a and 1927b), and Linsdale (1943). Intensive observations were made on a plot which was 56.1 acres (22.7 hectares) in extent and varying from 1700 to 2150 feet in elevation. The study plot was so oriented as to include several plant associations which in this region form a vegetation complex that is expressed variably according to slope exposure (Fig. 6). The vegetation of the generally north-facing slopes consists of a deciduous oak woodland (*Quercus Douglasii* H. & A. with some *Q. lobata* Nee and hybrid oaks). In some areas, these trees develop a spreading life-form and occur in open stands, while more extensive areas are dominated by an oak scrub consisting of small (8 to 24 ft. tall) deciduous oaks (Fig. 2). White (1966) has thoroughly described the deciduous oak stands in this region. The field layer of the oak woodland consists of grasses and forbs characteristic of the California annual type (Heady, 1958). Coast live oaks (*Q. agrifolia* Nee) occur in draws and on the shaded lower slopes. The south-facing slopes are covered with a chaparral which is dominated by chamise (*Adenostoma fasciculatum* H. & A.) on the drier sites (Fig. 3) and buckbrush (*Ceanothus cuneatus* (Hook.) Nutt.) in more mesic situations.

Additional observations were made at the Hastings Reservation in canyons where a mesophytic forest consisting of varying proportions of live oaks, broadleaf maple (*Acer macrophyllum* Pursh.), madrone (*Arbutus Menziesii* pursh.), bay (*Umbellularia californica* (H.A.) Nutt.), and willows (*Salix* spp.) occur.

A wintering concentration of gnatcatchers was studied in a 22 acre woodland of screw-bean (*Prosopis pubescens* Benth.) on the flood-plain of the Colorado River, 2 miles northeast of Yuma, Arizona. A dense layer of naturalized tamarisk (*Tamarix* sp.) and arrowweed (*Pluchea sericea* (Nutt.) Cov.) forms the understory in this association.

The foraging behavior of wintering gnatcatchers was compared with that of their resident congener, the Blacktailed Gnatcatcher (*P. melanura*), at two desert localities near Tucson, Arizona: at about 3000 ft. elevation on the south slope of the Santa Catalina Mountains in Lower Sabino and Lower Bear Canyons, and along the Santa Cruz River on the San Xavier Indian Reservation. An association which is characterized by the presence of saguaro (*Carnegiea gigantea* (Engelm.) Britt. & Rose) and palo verde (*Cercidium microphyllum* (Torr.) Rose & Johnston) covers the rocky slopes at these localities (Fig. 4). In local areas within this vegetation type, bur-sage (*Franseria deltoidea* Torr.), cholla and prickly-pear (*Opuntia* spp.), and ocotillo (*Fouquieria splendens*



FIG. 2. Deciduous oak scrub-woodland at the Hastings Reservation, Monterey County, California.

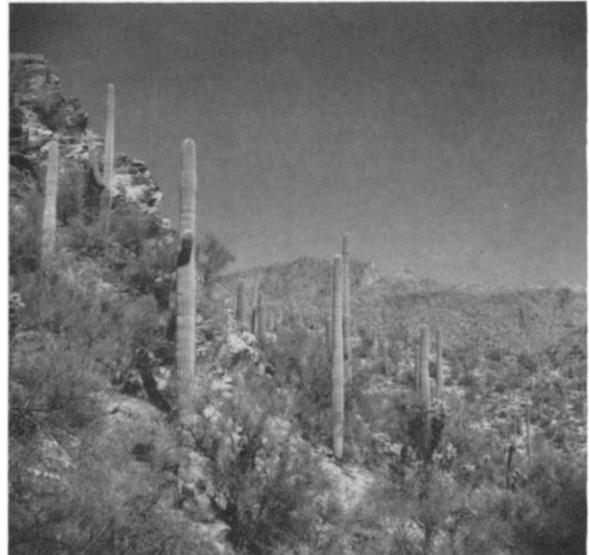


FIG. 4. Saguaro-palo verde plant association in Lower Sabino Canyon near Tucson, Arizona.



FIG. 3. Chaparral dominated by chamise (*Adenostoma fasciculatum* H. & A.) at the Hastings Reservation.

Engelm.) are common. The saguaro-palo verde vegetation, also called Sonoran desert scrub, and its associated physical conditions in the Tucson region have been described by Shreve (1915) and Whittaker and Niering (1965). A mesquite (*Prosopis juliflora* (Sw.) DC.) woodland, often with an understory of gray-thorn (*Condalia lycooides* (Gray) Weberb.) and tumbleweeds, occurs on benches at the base of the rocky slopes. The most extensive stands of mesquite woodland were studied on the San Xavier Reservation. Fremont cottonwoods (*Populus Fremontii* Wats.) and willows (*Salix* spp.) form a timbered belt along the stream-course at these localities.

Additional observations of shorter duration were made of *P. melanura* at several localities in the Col-

orado and Sonoran deserts of southern California and Arizona.

METHODS AND MATERIALS

A total of 1197 hours were spent observing gnatcatchers on their breeding territories at the Hastings Reservation during the following periods: June 14-August 23, 1959; June 8-July 17, 1960; and March 4-August 8, 1963. Additional observation periods, totalling 25 days in the field, were spent during the early spring and late summer. Studies on the winter behavior of *caerulea* and *melanura* were carried out on three field trips to the Southwestern deserts in the winters of 1962 and 1963.

A thorough knowledge of the gnatcatcher's general behavior and life history was required before suitable field methods for study of the exploitation pattern could be developed. This knowledge was acquired by making extensive, daily observations on a few representative territories. Many of the quantitative methods were designed specifically to take advantage of certain behavioral traits discovered during this phase of the investigation. Furthermore, the life history observations provided a general background without which any discussion of niche exploitation patterns would have little meaning. Unfortunately, because of limitations on the length of manuscripts, these natural history data cannot be included here. The critical reader will have to consult my dissertation (Root, 1964b) and a paper now in press for a full description of territorial and courtship displays, interspecific aggression, nest building behavior, parental care, development of the young, reproductive success, and social behavior on the wintering grounds.

The pattern of territory establishment and the subsequent shifts in territorial boundaries were determined while walking over the entire study plot two or three times daily. Whenever an individual was en-

countered, it was followed for about 20 min, and all of its movements, aggressive encounters with other gnatcatchers, and the location of nests were plotted on a base map of the area. On the basis of these repeated sightings of each bird, it was possible to follow the biography of most of the breeding pairs on the study area throughout the 1963 breeding season. While there may have been some undetected replacements among unmarked birds, observations could always be related to a particular territory during the nesting cycle. This was accomplished by following each bird back to its nest at least once a day. The gnatcatcher's habit of reusing nest material from its own previous nests made it possible to link the successive nesting attempts of each pair together: for each new nest, it was only necessary to follow the birds back to their previous nest. Four adults were marked with color bands and followed throughout most of the 1963 breeding season. Owl-decoys and tape recordings of the predator mobbing call were used to lure these birds into mist nets (see Root and Yarrow, 1967, for a complete description of the procedure). Nestlings from three broods were also marked with color bands.

A quantitative description of the foraging beat was made by using a standard observation technique (Root, 1964a). During each trip to the study plot, I visited each territory in a sequence which varied from trip to trip. When an actively foraging bird was encountered, the following information was recorded: (i) the individual observed, (ii) the time of day, (iii) the habitat, (iv) the bird's location within its territory, (v) the plant species or nature of the substrate and its relative size, (vi) the bird's height above ground, (vii) the bird's proximity to various structural units of the habitat, such as the canopy, and (viii) the relative size of the perches used. Only one observation was made while an individual remained on the same substrate and no more than three consecutive observations, always separated by intervals of more than two min, were made on the same individual. When a pair was feeding young, observation was restricted to the parents' foraging activities after it had fed the brood. This procedure assured that only individuals which were actively seeking food, and not merely bringing food to the brood, would be considered. It also permitted estimation of the rate at which the different members of the pair fed the young. Care was taken to avoid disturbing the bird in any way. By gathering data in this manner, it was possible to detect variations in the foraging beat which are associated with different seasons, different times of day, and different stages in the nesting cycle.

There are two possible sources of error which may be encountered with this technique. First, the males may be more conspicuous because of their singing activities and they may forage in certain stations more frequently because of their proximity to singing perches. This was not a serious problem in the present study because both members of the pair regularly

give call notes while they are foraging and male gnatcatchers do not often engage in prolonged singing bouts from high or exposed singing perches. Secondly, the birds may be less conspicuous at certain foraging stations because of variations in the density of foliage found in different habitats. For this reason, all comparisons of the foraging beat were based upon observations taken in the oak woodlands where the open nature of the vegetation afforded good visibility at all levels of the habitat.

The foraging tactics, expressed as the frequency that various foraging maneuvers are employed, were described by using a technique developed by MacArthur (1958) and Root (1964a). During each standard observation, all foraging activities were recorded over an interval time with a stop watch. Special note was made of (a) the exact places where food was found, (b) the relative size and type of the prey whenever possible, and (c) the sequence of activities which occurred between the bird's first obvious recognition of the prey and either the escape or the ingestion of the prey. An observation was stopped either when the bird moved to another foraging zone or when my vision was obscured for more than two seconds. From these timed observations, it was possible to determine the rate that gnatcatchers performed various foraging activities under different conditions. Since all of the data compared in this manner were based upon observations made in the oak woodland there was little chance for errors resulting from differential observability to enter the comparisons. Similar observations were made on other small species of insectivorous birds when they were encountered on the study area.

Some readers may be surprised by the short runs of the timed observations as compared with the period of time spent on the territories. This difference reflects the extreme difficulty of obtaining critical observations of these insectivorous birds. It was usually necessary to approach to within 30 ft of a bird in order to be assured of seeing all of the important behaviors. To accomplish this feat without disturbing the bird usually required "taming" an individual by following it daily for a week or more.

The food supply was sampled by taking 40 sweeps with a heavy insect net at regular intervals in each of the foraging stations that gnatcatchers were known to use most frequently. The opening of the beating net was 12 inches in diameter. Sweeping was always done in the early afternoon on sunny days when the wind velocity was low. Each sample contained sweeps taken in several different locations on the study plot. The contents of the net were dumped into large polyethylene bags where the arthropods were inactivated with a small amount of chloroform (Chemsak, 1957). The sweeping technique tends to sample selectively for those types of arthropods which station themselves in exposed situations. In the present study, however, the sweep samples are considered to give an adequate representation of the birds' food supply because studies of the foraging tactics showed that

these same types of arthropods are those which are most accessible to the gnatecatchers. The number of arthropods taken in 40 sweeps will depend, to a large extent, upon the foliage density of the different plant species examined. Therefore, the comparisons made in this investigation are based upon the prey density over a constant distance. In contrast, Dixon (1962), working on the same Hastings Reservation study plot, presents data on the volume of arthropods found in 100 gm of dry foliage. These two indices consider different components of prey availability. Variations in foliage density are incorporated into the former index, so that the data reflect the changes in prey density experienced by a bird in traveling over equal portions of the habitat. Dixon's measure presents changes in prey density as experienced in searching a constant weight (or roughly, a constant surface-area) of foliage.

The sweeps were all taken at heights of between 4 and 9 ft above the ground. I believe that the arthropods found at these heights are fairly representative of the situation throughout the entire depth of the tree canopy. In the oak woodland, because of the openness of the vegetation, the microclimatic conditions appear to be relatively uniform over the peripheral foliage of each tree. No height or shade preferences could be detected for several species of membracids, a family which forms an important part of the gnatecatcher's diet, in Minnesota and Oklahoma (Dennis, 1964).

All of the arthropods in the sweep samples were carefully sorted and preserved in 70% ethanol within a few hours after the collection was completed.

The samples were then separated further according to either family or order and each distinguishable group within these categories was given a numerical designation. Throughout this paper all references to arthropod taxa follow the nomenclature of Brues *et al.* (1954) or Borror and DeLong (1960). In addition, the length from the anterior of the head to the tip of the abdomen was measured for each specimen.

Bird specimens were collected near the Hastings Reservation and on the wintering grounds in vegetation-types which closely resembled those on the study areas. The stomachs were preserved in 70% ethanol and their contents examined under a dissecting microscope at a later date. The diet was determined in the following manner: all relatively intact prey were identified to family (to species for many of the most common items) and their length from the frons to the tip of the abdomen was recorded. Then the numbers of prey represented as fragments were estimated by counting the number of some highly sclerotized and distinctive structure, such as the right forelegs. In most cases, it was possible to identify the fragments to the family level. When the diet is compared for the same group of birds on the basis of intact prey and intact prey plus fragments (Table 1), it is obvious that certain types of food are over-represented as fragments. For this reason, all quantitative comparisons of the diet were based upon only the intact

TABLE 1. Comparison of the diet of the Blue-gray Gnatcatcher as determined by different methods. Based upon 13 specimens taken near Yuma, Arizona.

Taxon	Composition of the diet in percent of the total number of prey	
	Intact Prey n=53	Intact Prey + fragments n=271
Homoptera.....	43.4	22.9
Heteroptera.....	1.9	0.7
Lepidoptera.....	3.8	0.7
Diptera.....	1.9	1.8
Coleoptera.....	28.3	62.2
Hymenoptera.....	7.5	6.6
Araneida.....	9.4	4.4
Other.....	3.8	0.7

prey items. In many cases this procedure yielded samples which were too small to warrant detailed analysis.

Detailed notes on the behavior, nest sites, and habitat of the Blue-gray Gnatcatcher and other small insectivorous birds were taken throughout this investigation. In addition to my own observations, the field notes written by the following workers at the Hastings Natural History Reservation were used: John Davis, John A. Gray, Jr., Robert Holdenreid, Jean M. Linsdale, Joe T. Marshall, Jr., Thane A. Riney, Charles G. Sibley, Lloyd P. Tevis, Jr., and P. Quentin Tomich.

HABITAT REQUIREMENTS

GEOGRAPHIC VARIATION IN BREEDING HABITATS

The habitats occupied by the gnatecatcher vary in different parts of the breeding range. Throughout the following discussion of habitat requirements, all references to plant formation-types (e.g., woodland) follow the classification of Dansereau (1958).

In the southeastern United States the gnatecatcher reaches its greatest abundance in forested river bottoms and upland pine woods with an understory of oaks, and occurs less frequently in a wide variety of other wooded habitats (Weston in Bent, 1949; Smith, 1954; Sprunt, 1954; Burleigh, 1958). On the edge of the temperate deciduous forest region in Indiana, Illinois, and Kansas, the gnatecatcher inhabits open scrub and woodlands as well as the mesic forests (Goss, 1891; Webster, 1959; Nolan, 1963; G. E. Chaniot, pers. comm.). At the northern edge of its breeding range in Michigan, New York, and New England the gnatecatcher exhibits a marked preference for the tall trees of the closed canopy forests which occur along river flood-plains (Eaton, 1914; Forbush, 1929; Weston in Bent, 1949; and personal observations).

On the Yucatan Peninsula and adjacent Isla Cozumel, tropical populations inhabit a low scrub habitat during the breeding season (Paynter, 1955).

The habitats of the gnatecatcher in the western United States and adjacent Mexico have been sum-

marized by Grinnell and Miller (1944), Miller (1951), and Marshall (1957 and MS). Throughout the West, the gnatcatcher is a common breeding bird in the oak and pinyon-juniper woodlands of the Upper Sonoran Zone. The species also occurs regularly in the open chaparral which normally borders stands of these woodland types. Less commonly, gnatcatchers are found in the willows, sycamores (*Platanus*), and cottonwoods along stream courses in regions dominated by woodland and chaparral. The broad-leaved "canyon" forest of California is only a marginal habitat for the gnatcatcher. These canyon forests structurally resemble the flood plain forests of the East more closely than do the oak woodlands.

HABITAT OCCUPANCY IN THE CALIFORNIA COAST RANGE

In the South Coast Ranges of California, different vegetation types intermingle forming a mosaic of habitats. This situation has permitted me to compare the gnatcatcher's occurrence in stands of vegetation having different characteristics. During the peak of the breeding season in May and June, I have searched for gnatcatchers in several habitats in Monterey and Contra Costa counties.

Breeding territories were found which were completely contained within extensive stands of oak woodland. As a result of past disturbance and differences in site conditions, these woodlands are highly variable. A single woodland territory of the gnatcatcher may therefore contain varying proportions of live oak woodland, mixed live oak-deciduous oak woodland, dense deciduous oak scrub, and open stands of mature deciduous oaks. Gnatcatchers forage in all of these variants of the woodland habitat. Those territories which contain large areas of open woodland (e.g., territory 8 in Fig. 6) tend to be larger, suggesting that territory size is related to the amount of tree foliage present.

One breeding pair of gnatcatchers was located in an extensive stand (over 100 acres) of chaparral. These birds, which were never observed within 100 yds of the adjacent oak woodland, centered their activity in a gulch which had escaped fire damage for several years. In contrast to the surrounding chaparral, the buck brush and chamise shrubs of this gulch were much larger, some of them reaching a height of 9 ft. so that the vegetation resembled oak scrub in many respects. Gnatcatchers were absent in extensive stands of chaparral having a lower stature, except in those areas where oak woodlands were immediately adjacent. Several territories were found which contained both oak woodland and chaparral (Fig. 6). While foraging, the pairs on these territories crossed the boundary between the very different plant formations (cf. Figs. 2 and 3) several times daily.

I made 6 census trips, over a trail which was 2 miles long, in canyon forest and riparian woodland at the Hastings Reservation. The one pair which was located in these habitats, was found in an open stand of willows along a stream where field observers have

been reporting gnatcatchers since 1939. This pair made frequent foraging trips into the chaparral and oak woodland which grew within a 100 yd radius of the willows.

Gnatcatchers are absent from the live oak woodlands in the fog belt along the Pacific Coast just 14 miles west of the Hastings Reservation.

SEASONAL CHANGE IN THE VEGETATION

The breeding habitats of the gnatcatcher undergo several important changes during the period when these birds are present at the Hastings Reservation. Throughout this investigation, I kept records of seasonal changes in the life-form characteristics of those plant species which were important foraging posts for gnatcatchers. The temperature and rainfall records taken at the Hastings Reservation between October, 1962, and October, 1963, are summarized in Fig. 5. The following is a summary of the major phenological events in the vegetation during this period.

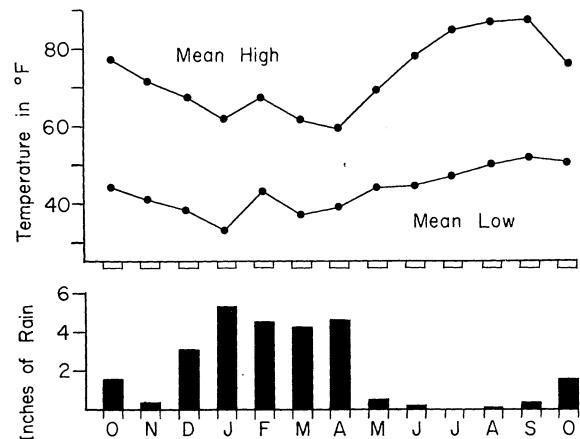


FIG. 5. The rainfall and mean air temperatures recorded at the Hastings Reservation weather station during 1962 and 1963.

The deciduous oaks were stripped bare of foliage following the first frosts and winter storms in late November and December. The opening of the leaf buds began in the middle of March and reached a peak in the last week of March and the first week in April. Growth of the leaves continued throughout April and by May 10 the development of the foliage was complete. The live oaks have evergreen foliage. The development of new leaves and flowers started in early April and reached a peak in late April and early May.

Buck brush, which has evergreen foliage, was in full bloom throughout March and early April, with some of the flowers persisting until late May. The growth period of chamise, which also has evergreen foliage, was somewhat later; the development of new foliage and flowers began in May, reached a peak in June, and continued in July.

The grasses started their annual growth following the first rains in autumn, but did not reach a peak in

productivity until the warm and rainy weather of March and April. By late May, growth of the grasses and most herbs had stopped and the field layer began to take on the golden tan color which is characteristic of the summer drought period.

Seasonal changes in the behavior of the gnatcatchers and the availability of their prey (discussed below) are correlated with these phenological events.

SEASONAL SHIFTS IN HABITAT OCCUPANCY

Gnatcatchers respond to seasonal changes in their environment by utilizing different portions of the vegetation mosaic. This response was studied by tracing the territory boundary of each pair at frequent intervals. The following account summarizes the major changes in the population's utilization of habitats during the 1963 breeding season. The sequence of each male's arrival from the wintering grounds (represented by consecutive numbers) and the configuration of his foraging area at three different periods are presented in Fig. 6.

Pair 1 arrived on March 6 and for a period of ten days they roamed widely through the habitats included within the foraging areas of pairs 1 and 3 in Fig. 6a. The bulk of this pair's foraging activity, however, was centered in a large patch of buck brush. Pair 2 established a territory on March 12 in an area which included a large stand of chamise. Territory 3 was settled on March 18 in an area held earlier by pair 1 and containing about equal proportions of buck brush chaparral, live oak woodland, and deciduous oak woodland. Compared with the territories that were settled later, these first three territories shared some common features. In each case, the female was found following the male on the first day that I was aware of their presence. These pairs occasionally entered the barren deciduous woodland to patrol their territory boundary, but spent most of the time in vegetation dominated by evergreen plants. I found two established pairs in the stand of chaparral occupied by pair 1 in 1963 (Fig. 6a) on March 21, 1964, when gnatcatchers were absent from the rest of the study area. Other naturalists at the Hastings Reservation have noted that territories were established in the chaparral prior to being settled in the deciduous oak woodland during the springs of 1938 (Linsdale, MS), 1946 (Riney, MS; Tevis, MS), and 1948 (Tomich, MS).

Territories 4-7 were established by single males between March 25 and March 30. These four territories contained mostly deciduous oak woodland, but the males defended "corridors" to clumps of evergreen vegetation (Fig. 6a) where the birds foraged for long periods during the early morning and late evening. Such enclaves of evergreen foliage were the sites of regular territorial disputes between adjacent males. Females were occasionally seen consorting with males 4-7, but a definite pair bond was not established on these territories until April 1. Territories 8-12, which also contained large proportions of deciduous oak woodland (Fig. 6b), were settled between April 1

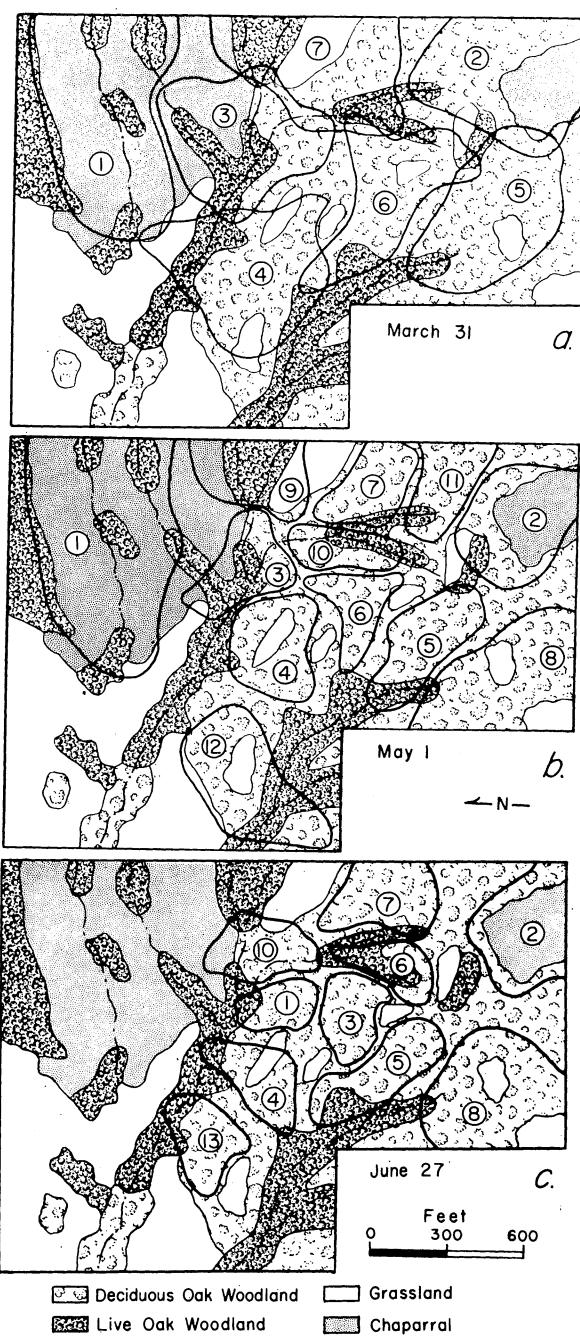


FIG. 6. The vegetation pattern on a portion of the study area at the Hastings Reservation. Each map presents the configuration of the foraging areas (solid lines) of the Blue-gray Gnatcatchers on a different day during 1963. The numbers refer to the pair designations used in the text.

and April 18. By April 28, the pair bond was completed and the first nests were underway on all territories except 6, where the male remained unmated until June 9 (Fig. 19).

After the failure of 4 nests, pair 1 (female banded)

left their territory in the chaparral and moved their

nest to a new location (Fig. 6c) in the oak woodland on May 18. The chaparral on territory 1, which was the first habitat settled in the spring, was not used by adult gnatcatchers again until July 6.

The configuration of the foraging areas on June 27 is given in Fig. 6c. During this period, the gnatcatchers centered their activity in the deciduous oak woodland with the exception of the members of pair 2, who spent most of the time foraging in chamise. On June 24, pairs 9 and 11 had abandoned nests which were in the early incubation stage. These adults wandered about their territories for two days before they disappeared from the study area. Their abandoned nests were never dismantled. Pair 12 moved their nest to a new location that was off the study area on May 2. The area formerly held by pair 12 remained vacant until May 30, when pair 13, whose previous history was unknown, settled there.

During the first or second day after fledging, the young of the first broods (see Fig. 19 for dates of fledging) followed their parents to clumps of chaparral or live oaks. On 5 occasions, the territory boundary was obviously extended during this period to encompass a larger proportion of chaparral or live oak woodland. The broods remained within these habitats until at least the sixth day after leaving the nest and returned to these same locations frequently throughout the fledgling period. The adults associated with these fledglings (except pair 2) returned to the deciduous oak woodland portions of the territory to build their next nests. Since the adults usually forage close to the brood, the shift in habitats between the nestling and fledgling states serves to alternate the pair's feeding activity on different portions of the territory. On territories 1 and 5, the fledglings of both broods were taken to the same stand of evergreen vegetation by the adults. Because of the shifting of the territorial boundaries at different stages of the breeding cycle, the same stands of vegetation could be used by the fledglings of adjacent pairs at different times. For instance, the live oak woodland in the draw just north of territory 1 in Fig. 6c was used by the first brood of pair 1 from July 6-July 15, by the second brood of pair 4 from July 18-July 23, and by the second brood of pair 1 from August 18-August 23.

In late June, independent juveniles, identified by their relatively shorter beaks and the yellow coloration of the commissural point, started to drift into areas that were not occupied by breeding adults. For instance, on July 17, 18, 27, and August 23, juveniles were seen foraging in the riparian woodland beside the bunkhouse where I was living. Gnatcatchers were never observed near the bunkhouse at other times of the year.

By August 7 all of the gnatcatchers on the study area (except pair 1 which were still feeding nestlings) had left the deciduous oak woodland. Adults were seen frequently in chaparral and adjacent live oak woodlands on the Hastings Reservation throughout August. On August 23, I shot 3 adult males, 2 adult females, and 2 fledglings within the stand of

chaparral that had formed the core of territory 1 in March (Fig. 6a). I observed a similar shift in habitat occupancy from deciduous oak woodland to stands of evergreen vegetation during August, 1959.

NEST SITES

The inspection of potential nest sites is a prominent activity of both members of the pair immediately following their arrival on the breeding grounds (Root, *in press*). This behavior would suggest that the presence of suitable nest sites is an important factor in the gnatcatcher's assessment of the habitat. With this possibility in mind, I made detailed descriptions of each nest site in an attempt to discover if all nests shared some of the same characteristics.

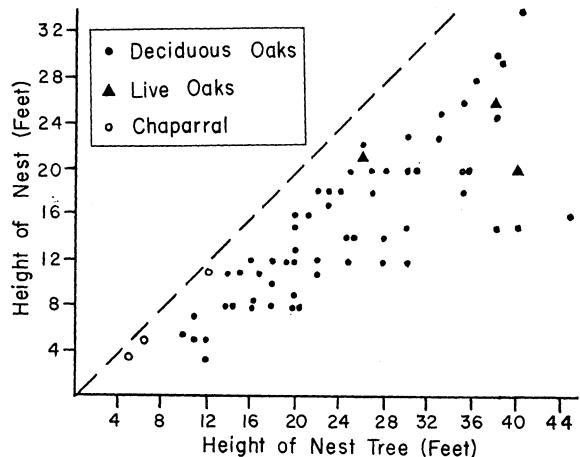


FIG. 7. The relationship between nest height and the height of the nest tree.

The height at which nests were placed above the ground is related to the height of the nest tree (Fig. 7). All three of the nests placed in chaparral were situated near the top of the shrub. Nests that were built in oaks were always placed at least three feet below the top of the tree. Pair 1 built 7 nests whose heights ranged from 11 to 26 ft above the ground.

Of the 64 gnatcatcher nests found at the Hastings Reservation, 90.6% were placed in deciduous oaks. Two of the three live oaks which were used had been partially defoliated by tent caterpillars so that they superficially resembled deciduous oaks. Pair 2 built both of their nests in chamise shrubs despite the presence of several deciduous oaks in their territory. During the period when pair 1 was centered in chaparral (Fig. 6), they built two nests in live oaks, one nest in a buck brush shrub, and one nest in one of the three deciduous oaks on the territory. In the foothills of the Sierra Nevada (Tuolumne County, California), gnatcatchers have been reported to build nests in pine and alder trees (Chamberlin, 1901). Since the members of a pair are known to build nests in a variety of plant species and at different heights above the ground, these features would not seem to be critical factors in the selection of nest sites.

Nests were placed in a variety of situations with

respect to the proximity of screening foliage. Two successful nests, one in a chamise shrub and the other in a dead portion of a deciduous oak, were almost constantly exposed to the sun's rays. Several nests were built against a tree trunk in the zone of sparse foliage below the woodland canopy while other nests were surrounded by dense sprigs of foliage. Gnatcatcher nests seem to be concealed mainly through the resemblance of their exteriors to the bark surfaces of the nest forks. This type of concealment might explain why some successful nests can be built in exposed sites. Following the defoliation of the oak woodland by tent caterpillars in 1961, however, the three nests I found were placed in oaks which had advanced further in the redevelopment of foliage than other trees on the territory.

The positioning of gnatcatcher nests in a variety of sites has been illustrated by Chamberlin (1901) and Nickell (1956). Of the 64 nests discovered in this study, 28 were placed in vertical forks formed against a trunk or vertical limb at a point where two or three upright branches or twigs emerged; 24 were built in vertical "Y-shaped" forks formed by the bifurcation of large branches; 10 were saddled between upright branches or twigs on horizontal limbs; and two were built within dense tangles of twigs at a point where two separate branching systems became intermeshed. In the eastern United States, gnatcatcher nests are usually placed on horizontal supports (Nickell, 1956), while vertical forks are used most frequently at the Hastings Reservation. This geographic variation in nest placement is probably a response to differences in the growth-form of the trees growing in different gnatcatcher habitats.

Careful measurements at 10 nests revealed that the configuration of the nest fork can be quite variable. The only necessary requirements the nest fork must possess seem to be a surface that supports the base of the nest and two or three elements (e.g., twigs) which are so spaced as to provide a site for the attachment of opposite sectors of the nest wall. In light of the wide latitude of characteristics that acceptable nest sites possess, it is interesting that some nest forks are used more than once in a single breeding season. The same vertical fork was used by pair 3 (female banded) for the first nest (April 4-April 10) and the fourth nest (May 21-June 1). This same fork was also used in June, 1961. The second nest (April 11-May 2) of pair 3 and the sixth nest (June 22-July 7) of pair 10 were placed in another vertical fork. In each case where a fork was re-used, all the material from the previous nest had been removed in the intervening period.

I did not observe any obvious seasonal changes in the nest site characteristics of the gnatcatcher (cf., Horvath, 1964, on the Rufous Hummingbird, *Selasphorus rufus*).

FORAGING BEAT

Quantitative studies of the foraging beat were made in the oak woodland where the open structure of the

vegetation permitted me to observe the gnatcatchers' activity in all portions of the habitat. In the following figures and tables, "self-maintenance" is used to refer to pairs which had either nests in the incubation stage or no nests at all. Standard observations for pairs that were engaged in nest construction are not included as it would be easy to confuse the gathering of nest material with actual foraging behavior.

The proportion of the standard observations made on various foraging substrates within the oak woodland are given in Table 2. During March and April, when the deciduous oaks are barren or in the process of developing new foliage, live oaks were used more frequently than at other times. When an individual was followed for an extended period, it was obvious that the bird entered each tree, regardless of the species, that was encountered along the foraging route, i.e., gnatcatchers did not exhibit any avoidance toward entering a particular kind of tree. The seasonal differences in the frequency that different substrates were used then must result from the length of time the birds spent at each foraging station. The tendency for gnatcatchers to concentrate their activity within clumps of evergreen vegetation during March and April was discussed above. In addition, on the borders between stands of live oaks and deciduous oaks, gnatcatchers were observed to linger in the live oaks. On March 30, a male remained in a live oak for four minutes, in an adjacent deciduous oak of comparable size for only 11 secs, and then flew to another live oak. My field notes contain several references to the extreme rapidity with which gnatcatchers moved from perch to perch while foraging in barren deciduous oaks at this season.

During July, fledglings spent more time in the live oak woodlands than in June, when most broods were led to stands of chaparral. These events are reflected in the increased utilization of live oak canopy during the late summer by adults with young (Table 2).

I have divided the woodland habitat into three arbitrary structural subunits. The foliage zone is where the leaves, twigs, and small branches grow at the periphery of the crown. The subcanopy is the zone surrounding the trunks where limbs and large branches occur and foliage is sparse. Individuals were classified as foraging in the herb layer whenever their feeding maneuvers were directed at the ground or herbaceous plants.

Most of the foraging activity is concentrated in the foliage (Table 2). The gnatcatchers exhibit a greater tendency to enter the subcanopy of deciduous oaks during March and April when the foliage is sparse. Birds which were feeding young did more foraging in the herb layer. This shift in foraging beat is further expressed in the higher frequency that pairs with young used low hunting perches (Fig. 8). Adults with young seemed to be searching for grasshoppers and other large insects while foraging on or near the ground. Grasshoppers were brought to the nestlings on nearly 20% of the 704 feeding trips observed at one nest in late June. Only one grasshopper was

TABLE 2. The foraging beat of the Blue-gray Gnatcatcher in oak woodland. The data are expressed as the percent of the standard observations made during each sampling period.

Breeding Status	Sampling Period	n	Deciduous oaks		Live oaks		Herb layer
			foliage	subcanopy	foliage	subcanopy	
Self-maintenance	Mar. 6-May 9	160	64.9	12.5	20.7	1.2	0.7
	May 10-Jun. 16	168	78.6	6.5	10.7	4.2	0.0
	Jun. 26-Jul. 26	141	87.9	6.5	2.8	0.0	2.8
Feeding young	May 10-Jun. 16	109	71.6	7.3	8.3	0.0	12.8
	Jun. 26-Jul. 27	148	58.1	6.1	18.8	2.1	14.9

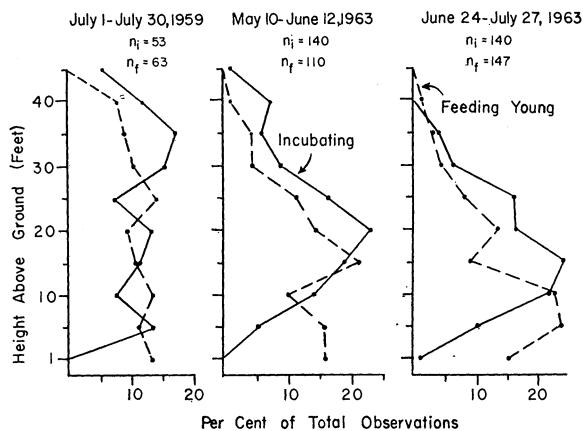


FIG. 8. The height distribution of foraging activities by Blue-gray Gnatcatchers. The sample sizes for birds that were incubating and feeding young are given as n_i and n_f respectively.

found in the stomachs of adult gnatcatchers, although these insects were common in the areas where birds were collected. Beal (1907) reports that three times as many grasshoppers are fed to nestling House Wrens (*Troglodytes aedon*) as are consumed by adults.

Other than the tendency for pairs with young to forage near the ground, feeding activity was not restricted to any particular level of the foliage zone (Fig. 8). This absence of stratification in the foraging beat is correlated with the wide vertical distribution of foliage in the open woodland habitat. Scrub oaks grow in dense stands where most of the foliage is concentrated in the upper portion of the trees. In open stands, the oaks assume a spreading form with the foliage being more evenly distributed. Gnatcatchers that were engaged in self-maintenance activities tended to forage more frequently in the upper third of scrub oaks than they did in the spreading trees (Table 3). This suggests that the density of the foliage may influence the levels at which foraging takes place. This effect is seen further by comparing the profiles of foraging heights for 1959 and 1963 (Fig. 8). The 1959 data were gathered on a portion of the study area where the woodlands are more open. The more even distribution of foraging levels taken by adults with young (Table 3) reflects their tendency to move toward the herb layer.

The frequency that various types of perches were employed is presented in Table 4. The approximate diameters of the perches are as follows: twigs, less than 1 cm; branches, 1 to 4 cm; and limbs, larger than 4 cm. Gnatcatchers remained on twigs and branches during 98.5% of the standard observations. When foraging in the subcanopy, small diameter perches were used most frequently even though they were uncommon in this zone by comparison with the situation in the foliage zone. Usually horizontal twigs are used, but vertical twigs, particularly when foraging in the very top of the trees, were used without any obvious difficulty. On those rare occasions when twigs and branches were not used, the birds usually perched on the upper surfaces of horizontal or diagonal limbs. Gnatcatchers were observed on upright trunks or limbs on only nine occasions (includes birds gathering nest material). The fissures in the bark on trunks furnished footholds which the gnatcatchers utilized with difficulty as evidenced in their frequent use of the wings to perform balancing maneuvers. The birds did not remain on these vertical surfaces for more than about four seconds. Despite their obvious ineptness in using vertical substrates, gnatcatchers were observed twice perching on trunks with their heads downward in the manner of nut-hatches (*Sitta* spp.). In contrast to hole-nesting birds, such as wrens or titmice, foraging gnatcatchers were never observed to enter cavities in the trunks or limbs.

Between forays into the herb layer, gnatcatchers used raised, woody perches at the base of trees or on fallen branches. In addition to the types of perch mentioned in Table 4 gnatcatchers used grass culms on eight occasions and tree leaves on five occasions. The birds remained on these pliant perches for only a few seconds and fluttered their wings constantly to maintain balance.

Because of the density of the shrubbery, it was not possible to make standard observations of the foraging beat in chaparral. It was obvious, however, that gnatcatchers spent a greater amount of time in the subcanopy while foraging in chaparral than they did in the oak woodland. The sparsity of the herb layer in chaparral and the greater density of twigs in the shrub subcanopy may account for this difference. To exploit the shrub canopy with its numerous up-

TABLE 3. Levels of the oak foliage zone used by foraging Blue-gray Gnatcatchers. The data are expressed as the percent of the standard observations (n).

Breeding status	Scrub Oaks				Spreading Oaks			
	n	top	middle	bottom	n	top	middle	bottom
Self-maintenance.....	175	72.0	20.6	7.4	130	54.6	39.2	6.2
Feeding young.....	166	42.2	26.5	31.3	87	46.0	34.5	19.5

TABLE 4. The hunting perches of the Blue-gray Gnatcatcher in different foraging stations. The data are expressed as the percent of the standard observations (n = 726).

	twigs and branches	limbs and boles
Canopy.....	84.8	0.0
Subcanopy.....	8.4	1.1
Herb layer.....	5.3	0.4
Totals.....	98.5	1.5

right branches, the gnatcatchers frequently used vertical twigs and leaves as perches.

While gnatcatchers usually move rapidly over a wide portion of their territory, they sometimes restrict their foraging activity to a small area in response to certain conditions. When the sun was low on the horizon, gnatcatchers, often in association with other species of foliage-gleaning insectivorous birds, were found foraging on sun-lit banks of foliage which bordered large openings. As the sun rose in the sky, the gnatcatchers moved away from these openings, but throughout the mid-morning and late afternoon, they continued to forage mostly on the sunny side of the trees. Adults which were feeding fledglings have been observed to return to the same bank of foliage on as many as ten consecutive foraging trips while their young were perched several yards away. No obvious fixation on a particular sector of the territory was observed in adults that were feeding nestlings.

WINTERING GROUNDS

Gnatcatchers have not been observed at the Hastings Reservation during the winter: the extreme dates for their occurrence are February 24 and October 2. A sparse wintering population occurs outside the breeding range on the California coast (Grinnell and Miller, 1944). At Carmel, 22 miles northwest of the Hastings Reservation, only one or two gnatcatchers are found each winter, usually in stands of riparian willows or coastal chaparral (L. O. Williams, pers. comm.).

The study areas in Arizona were near the northern edge of the winter range. The habitats in Sabino and Bear Canyons may be marginal situations. At least 6 gnatcatchers inhabited these localities during early December, 1962, but the species was absent from these canyons in late January, 1963, after a spell of uncommonly cold weather. The birds remained at the

San Xavier Reservation and Yuma localities throughout the winter.

In the Sonoran Desert, gnatcatchers were absent from canyons which did not contain a belt of timber along a stream. The birds were often found foraging in saguaro-palo verde vegetation over 300 yds from the nearest wooded stream. On the two occasions when gnatcatchers were followed before sunrise, however, the birds remained in the timber until the sun struck the rim of the canyon before moving rapidly up-slope to forage in the sun-lit desert. Possibly the timber provides roosting sites for wintering gnatcatchers.

Plants with a "typical" shrub or tree life-form, such as palo verde, mesquite, screw-bean, bur-sage, catclaw (*Acacia Greggii* Gray), willows, and cottonwoods were commonly used as foraging posts. Gnatcatchers were never observed to forage in cacti, such as saguaro, cholla, and prickly-pear which were abundant in the winter habitats near Tucson.

As on the breeding grounds, the wintering gnatcatchers forage most frequently in the foliage zone. Since many of the desert shrubs have a low growth form (e.g., bur-sage), the birds often forage within three feet of the ground. On seven occasions, gnatcatchers were observed hopping on the ground for short periods (less than 12 sec). Probably wintering gnatcatchers have better access to the ground in desert regions because of the low stature of the woody vegetation and the sparsity of the herb layer.

Little is known about the habitat requirements of the gnatcatcher in the southern part of its winter range. In Colima, Mexico, Schaldach (1963) reported that wintering gnatcatchers are common in tall palm plantations, arid thorn scrub on the coastal plain, and dense thorn forests in the interior.

FORAGING TACTICS

FORAGING REPERTOIRE

When searching for food, gnatcatchers normally hopped rhythmically from perch to perch, remaining only momentarily in one location. One adult changed its perch 80 times during 120 sec of observation. Still hunting, where the bird remains on the same perch for more than five seconds while carefully searching the distant surroundings, was rarely observed. The major components of movement were tangential or vertical when searching the sides of trees and radial when foraging on the tops, reflecting the gnatcatchers' tendency to remain in the foliage zone.

At each perch, the head was rapidly cocked from

side to side as the bird surveyed its surroundings. Such jerky movements of the head are characteristic of species utilizing the rapid peering method of locating prey (Grinnell, 1921). Substrates slightly below the perch were examined by leaning forward while fluttering the wings. The terminal sprigs of foliage were inspected while hovering nearby in mid-air. Adults with young made frequent aerial surveys of the herb layer during which they flew more than 15 ft from the nearest hunting perch. During these surveys, the spikes of tall grasses, especially *Elymus glaucus* Buckl., were examined carefully while the gnatcatcher hovered a short distance away. Gnatcatchers were seen to hang beneath a perch in the manner of parids (Root, 1964a) only six times; in each case the gnatcatchers remained in this position for only about one second.

Gnatcatchers did not attack every insect which they encountered. The late instar larvae of the tent caterpillar, *Malacosoma constricta*, were avoided. Often flying insects were attacked a few seconds after another (usually a dipteran or hymenopteran) had approached the bird much more closely.

While foraging, the tail is held slightly above the long axis of the body and wagged steadily from side to side. Usually the tail is closed. During July and August, 1959 and 1963, however, gnatcatchers with fledglings often foraged with their tails completely spread. These adults frequently opened and closed the tail rapidly so that the white outer rectrices were displayed with a "flashing" effect. These tail movements did not serve in any obvious communicative function, as the birds were often alone when they were performed. Since wood warblers which have contrasting tail patterns and engage in aerial feeding, e.g., *Setophaga ruticilla*, also forage with the tail spread, (Ficken and Ficken, 1962; Ficken, 1962) it may be that such movements function to flush insects from the foliage. Andrew (1956) found that insectivorous birds flick their tails more frequently than do herbivorous birds. He interprets such tail movements as "ritualised intention movements" which function mainly to make an individual conspicuous, especially before flying, to conspecific individuals. I would suggest that, in addition, some tail movements have a functional role in the foraging repertoire.

The behavior employed in attacking prey is built up from a variety of component maneuvers, each combination being adapted to the particular set of circumstances under which the prey was found. Nearly stationary prey encountered within easy reach of the perch was captured by simple gleaning. Objects below the perch were picked up by leaning forward while maintaining balance by cocking the tail above the back. Stationary prey, recognized at a greater distance from the perch, was taken by rushing and hovering. In a rush, the bird flies directly to another perch, using the momentum of landing to lunge forward in striking the prey. During a hover maneuver, the gnatcatcher remains aloft while attacking prey which is not flying (MacArthur, 1958). Frequently

the feet were brought into contact with the foliage, which perhaps served to provide orientation and stability while hovering momentarily in the same spot. Hovering was employed when prey was located where perches were not available, such as on the undersides of leaves and at the extreme periphery of the canopy. Chestnut-backed Chickadees (*Parus rufescens*) attack prey found in similar situations by hanging beneath the perch (Root, 1964a). Stationary prey was seized in the tip of the beak following a sudden forward thrust of the head. Occasionally an audible snapping of the beak was heard when resting prey was captured.

On five occasions, the same prey individual was attacked with different maneuvers in rapid succession. In one case, involving a hemipteran which rested on the petiole of an oak leaf, the gnatcatcher first attempted to reach the bug by stretching upward from a perch below, then tried to lean downward from a perch above the petiole, and finally captured the insect in a hovering attack.

Hawking maneuvers were employed to capture prey which was flying or falling through the air. Prey which dropped from the foliage as the bird approached was usually pursued by tumbling, a maneuver in which the bird falls with its body held upright and the beak directed downward. Lateral movements, twisting, and bill snapping, audible at about 20 ft, coincided with periods when the fall was checked by fluttering the wings. Occasionally the bird descended to the ground in this manner, where it engaged in intense searching for a few seconds. Tumbling accounts for about 23% of all hawking attacks (Fig. 9).

Flying insects were attacked in direct aerial chases. These attacks were launched ahead of the bird at angles from the perch which varied from steep dives to ascensions which were nearly vertical (Fig. 9). When gnatcatchers overtook prey that was flying away from them the capture was accomplished by simply snapping up the insect. When the flight line of the prey approached or crossed that of the bird, however, the gnatcatchers swung into an upright position at the point of interception. Occasionally, it was necessary for the bird to engage in frantic "barrel rolls" and tumbles, each accompanied by an audible bill snap, before grasping the prey. Extremely active insects, such as large diptera, were sometimes attacked repeatedly during prolonged chases which lasted as long as two minutes. Gnatcatchers rarely returned to their original perch after hawking.

The audible snapping of the beak seems to be associated with the capture of more active prey.

A comparison of the distances that gnatcatchers flew to make hovering and hawking attacks (Table 5), gives an indication of how the searching radius for stationary and flying prey varied. These data are necessarily crude, but I believe that the figures circumscribe the normal searching radius of the gnatcatcher. Hawking pursuits of over 20 ft were observed but these are not included in Table 5 as it was

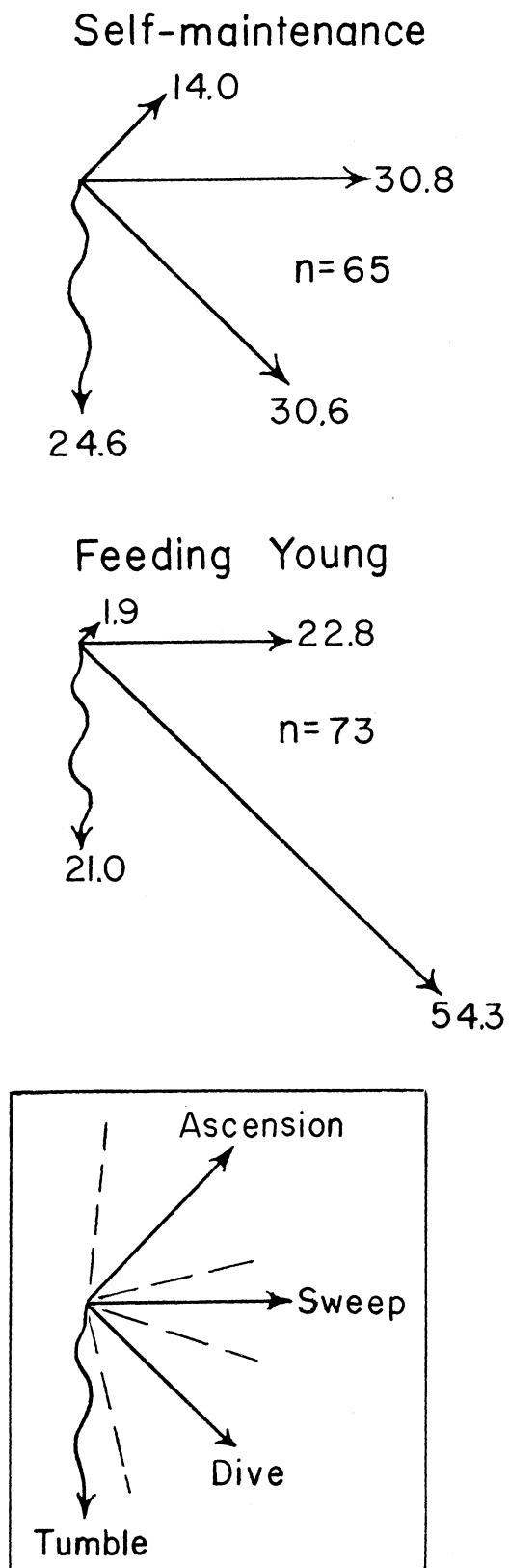


FIG. 9. The percent of the hawking attacks directed into different sectors around the hunting perch.

obvious that the bird was overtaking a rapidly fleeing insect.

Prey which was less than about 6 mm in length (reckoned by comparison with the length of the bird's beak) was swallowed or fed to young directly after it was captured. Larger and more active prey were subdued before they were devoured. The gnatcatcher's handling of such prey was observed closely on 42 occasions. Usually the prey was carried in the tip of the beak to a nearby perch which slanted upward at a shallow angle. Here the gnatcatcher assumed a wide stance across the perch, turned the body so as to face along the downward slope of the perch, and slapped or rubbed the prey against the perch at a point outside and below the feet. The Orange-crowned Warbler, *Vermivora celata*, assumes the same posture while battering large prey. This downward stance may facilitate the retrieval of prey that is dropped. Gnatcatchers frequently dropped large prey; on three occasions an insect was dropped three times before it was finally eaten. Prey that was dropped was always retrieved before it had fallen more than four feet below the perch. The feet were never used to grasp the prey or to hold it against the perch. On one occasion, an adult had obvious difficulty in maintaining its balance while pecking at something on its foot.

All types of large prey were mandibulated and battered against the perch while held in the tip of the beak. Often the battering movements produced a soft tapping sound. In addition, large insect larvae were grasped near one end, while the long end was slapped against the perch. The birds often shifted their grasp from one end of the larvae to the other by holding the beak in an elevated position and mandibulating across to the new hold. Adult lepidopterans were often rubbed against the perch so that the wings became frayed and sometimes portions of the wings dropped off. Prey was battered continuously for periods of up to 205 sec before it was eaten. The prey was swallowed whole except in those cases where portions of the wings had been rubbed off. Commonly the base of the beak was rubbed against the perch after a large insect was devoured.

The complete foraging repertoire was employed by gnatcatchers on both the wintering and breeding grounds. While the vegetation structure, climatic conditions, and availability of prey varied in the different habitats, the foraging maneuvers were always executed in the same manner.

TACTICAL RESPONSE

The foraging tactics of any species are defined by the relative frequency that various foraging maneuvers are employed. By comparing the gnatcatchers' tactics in different sets of timed observations, I was able to determine how the foraging behavior of this species responded to seasonal changes in the food supply and to the increased energy demands associated with feeding young. This discussion of foraging tactics is based upon samples (Table 6) which

TABLE 5. The estimated distances that Blue-gray Gnatcatchers attacked prey with different capture maneuvers.

	Hovering		Hawking	
	n	mean (range)	n	mean (range)
Self-maintenance.....	101	6.8 (1-36) inches	59	31.5 (2-96) inches
Feeding young.....	110	9.4 (2-48) inches	74	39.9 (4-132) inches

TABLE 6. The size and characteristics of samples used in computing foraging tactics.

Sampling period	Self-Maintenance			Feeding Young		
	No. of timed observations	Seconds of observations	Number of individuals observed	No. of timed observations	Seconds of observation	Number of individuals observed
March 6-March 30.....	70	2024	10			
April 4-May 9.....	79	2069	16			
May 10-June 16.....	161	5571	12	112	3473	12
June 26-July 27.....	141	5360	13	149	4353	12

TABLE 7. The foraging intensity of the Blue-gray Gnatcatcher during 1963.

	Maneuvers /500 sec. of observation		Visible captures /500 sec. of observation	
	Self-Maintenance	Feeding Young	Self-Maintenance	Feeding Young
	$\bar{X} \pm 2 S. E.$	$\bar{X} \pm 2 S. E.$	$\bar{X} \pm 2 S. E.$	$\bar{X} \pm 2 S. E.$
March 6-March 30.....	19.5 \pm 2.9		1.5 \pm 0.8	
April 4-May 9.....	16.4 \pm 4.4		1.0 \pm 1.4	
May 10-June 16.....	12.6 \pm 2.2	20.0 \pm 2.1	1.2 \pm 0.9	4.3 \pm 2.1
June 26-July 27.....	10.8 \pm 1.8	27.2 \pm 2.6	2.3 \pm 0.9	6.0 \pm 1.3

were obtained in the oak woodland habitat on the Hastings Reservation study plot.

The foraging intensity (Table 7) was obtained by adding the frequencies that the three major classes of attack maneuvers (gleaning, hovering, and hawking) were performed in a unit length of observation. It was not always possible to distinguish actual attacking maneuvers from instances when the beak was thrust near to the foliage while merely searching for prey. For this reason, the rate birds captured prey that was visible to the observer is also included in Table 7. Gnatcatchers caught prey which was not visible to an observer; adults frequently fed fledglings directly after attack maneuvers that appeared to be unsuccessful.

At all seasons of the year, adults encountered away from a nest were almost always engaged at foraging. There were significant differences, however, in the intensity at which these birds fed (Table 7). The frequency of attack maneuvers performed by birds that were engaged in self-maintenance activities differed between sampling periods (significant at the 0.01 level by the Kurskal-Wallis one-way analysis of variance).

Within each sampling period, the foraging intensity of adults that were feeding young was higher than the self-maintenance level (both the frequency of attack maneuvers and visible captures were significantly different at the 0.05 level by the Mann-Whit-

ney U test). This intensification in foraging represents an adaptive response to the added burden placed upon the adults by the energy demands of the brood. The increase in the foraging intensity, however, probably does not bear a direct relationship to the food requirements of the brood. Each member of the pair is able to increase the proportion of the time it spends foraging because the hatching and subsequent development of the nestlings releases the adults from incubation and brooding duties. In addition, the brood may be fed different types of prey than are consumed by the adults (see below).

There is agreement between the feeding rate at nests and the increase in the rate at which visible captures were made by adults with young. At a nest observed in late June, the female brought food to older nestlings at an average rate of once every two or three minutes (Root, *in press*). During this period, adults with young found additional visible prey at a rate of about once every 2 min (calculated from Table 7). This relationship is probably spurious, however, since the data on foraging intensity do not include the activity of adults during periods when they were away from the brood, preening, etc., while such lapses in activity are included in the data on feeding rates at nests.

During March, when the foliage was only partially developed on the deciduous oaks, gnatcatchers di-

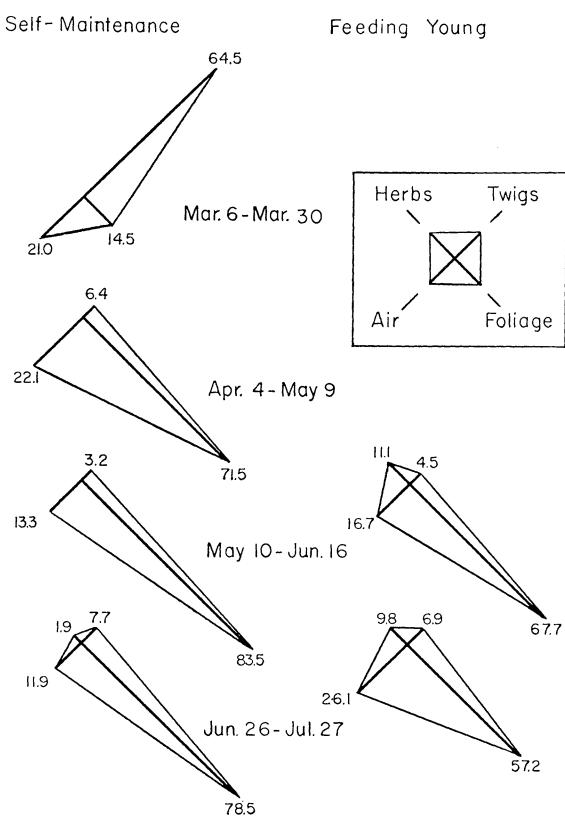


FIG. 10. The substrates where the Blue-gray Gnatcatcher obtained food. The length of the arms in each set of coordinates represents the frequency that each substrate was attacked as a percent of the total number of attacks.

rected most of their attacks at twigs and branches (Fig. 10). Once the development of the leaves was complete, however, most of the prey was obtained from the tree foliage. The tendency of adults with young to shift their foraging beat toward the herb layer (Table 2 and Fig. 8) was reflected in the higher rate at which these same individuals actually found prey on the herbs.

Some of the variations in the population's foraging tactics are presented in Fig. 11. Within each sampling period, adults with young engaged in hawking and hovering maneuvers more frequently than did the adults that were without young. As a response to the brood's increased demands on the foraging success of the adults, this shift in the foraging tactics probably reflects a tendency for adults with young to attack prey in a greater diversity of situations. For instance, prey that was flushed from the foliage by the bird's approach or previous attacks was chased more frequently by adults with young during the late spring and summer (Table 8). The increased proportion of attacks on insects that were flushed may be related to the frequently observed tail-flashing behavior of adults that were feeding young.

During late June and July, there was a slight but consistent increase in the frequency of hawking ma-

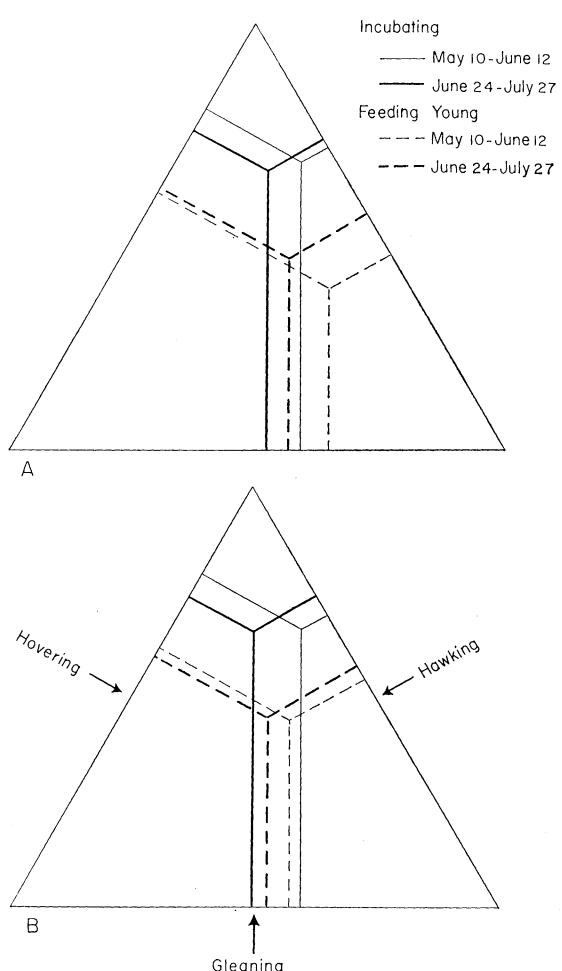


FIG. 11. Variations in the foraging tactics of the Blue-gray Gnatcatcher. The length of the arms in each of the coordinates represents the frequency that each maneuver was performed as a percent of the total number of attacks. The foraging tactics for the oak woodland habitat as a unit are presented in A., while the foraging tactics in the canopy zone of the deciduous oaks are presented in B.

neuvers performed by adults which were engaged in self-maintenance activities as well as those which were feeding young. Since the climatic conditions and the foliage characteristics of the oak canopy were relatively constant from May through July, this seasonal change in the tactical response probably was related to changes in the characteristics of the available prey.

There was little individual variation in the tactics employed by adults with young during the same season (Table 9). This suggests that most members of the population possess similar foraging capabilities.

DIET AND PREY AVAILABILITY

The gnatcatcher's diet was completely restricted to arthropods. (appendix). The three instances when plant fragments were found in the stomachs probably represent cases where plant material was acci-

TABLE 8. The proportion of attack maneuvers directed at prey which was flushed from the foliage.

Sampling period	Self-Maintenance		Feeding Young	
	Total attacks (n)	Attacks at flushed prey (percent)	Total attacks (n)	Attacks at flushed prey (percent)
March 6-May 9.....	190	9.5		
May 10-June 16.....	146	0.7	137	5.1
June 26-July 27.....	122	0.8	215	6.0

TABLE 9. Variation in exploitation patterns of individual Blue-gray Gnatcatchers feeding dependent young in oak woodland. The data are presented as the number of foraging maneuvers per 500 secs. of observation.

Individual*	Secs. of Observation	Foraging Intensity	Tactical Response			Location of Prey		
			glean	hover	hawk	foliage	bark	herbs
♀ 1.....	736	25.8	10.9	10.2	4.7	15.5	0.7	4.8
♀ 4.....	758	25.6	13.8	5.9	5.9	13.1	3.3	5.9
♀ 5.....	605	28.1	8.3	14.0	5.8	16.5	1.7	4.1
♀ 7.....	729	24.0	13.7	6.2	4.1	17.1	1.4	4.1
♀ 12.....	1096	21.9	5.9	13.7	2.3	13.7	1.4	4.5
♂ 5.....	707	26.1	9.2	9.9	7.0	15.6	0.7	2.8
♂ 12.....	850	20.0	10.0	7.1	2.9	13.5	1.2	2.4

*Numbers refer to the territory designations in Fig. 11.

TABLE 10. The percent of the stomachs in which major categories of prey occurred.

	Monterey County, California			Yuma, Arizona
	June-August 1959	March-May 1963	June-August 1963	December and January 1963
Homoptera.....	100.0	56.5	100.0	53.8
Heteroptera.....	10.0	39.1	26.7	7.7
Coleoptera.....	80.0	78.2	40.0	92.3
Lepidoptera.....	25.0	47.8	6.7	15.4
Diptera.....	50.0	17.4	20.0	23.1
Hymenoptera.....	80.0	47.8	60.0	15.4
Araneae.....	50.0	26.1	26.7	53.8
Other.....	15.0	13.0	13.3	7.7
n.....	20	23	15	13

dentially ingested with the normal prey. At least 70 different families of arthropods, however, were represented in the diet, reflecting the gnatcatcher's capacity for exploiting a wide variety of situations. Because of the diverse diet, it was often necessary to lump the samples of prey into higher taxonomic units before attempting to draw comparisons. The analysis of diet is based upon the total number of prey individuals, since each item represents a successful attack maneuver and thereby provides a better index to the gnatcatcher's exploitation pattern than such measures as percent volume or weight. The percent of the stomachs in which prey taxa were found is presented (Table 10) as a check upon the importance of each food type to the diet of the entire population: percent occurrence reduces the bias resulting from a few birds feeding upon a concentration of "abnormal" prey.

The behavior of arthropods known to be important prey species of the gnatcatcher was noted throughout the study. Membracid, cicadellid, and mirid bugs, and chrysomelid and mylabrid beetles were usually found on the foliage and small twigs of the trees. Curculionid beetles, ants, and spiders were found on the larger branches as well as in the foliage zone. These insects rarely flushed when approached suddenly. When these winged insects were tapped with a pencil, they either moved to the other side of their perch, or sprang into the air and after falling a few inches, either alit in the foliage below or flew off on a horizontal course. Hemipteran nymphs simply dropped from their perch when struck with a pencil, while ants and spiders fled along the twigs and branches. Depending upon the situation in which such prey was found, gnatcatchers could easily attack these arthropods with gleaning, rushing, or hovering maneuvers.

If the prey was able to escape the initial attack, subsequent tumbling or hawking maneuvers could be employed. Thus the foraging beat and the foraging repertoire of the gnatcatcher are clearly related to the preferred habitats and escape reactions of the major types of prey found in the diet.

The taxonomic composition and the size distribution of the foliage arthropod fauna varied on a seasonal and yearly basis (Figs. 12-14). At the Hastings Reservation, the gnatcatchers foraged at the stations where the foliage arthropod samples were taken during 76.9 to 89.7% of the standard observations (Table

2). The composition of the gnatcatcher's diet also varied in time and space, but these changes in food habits were not related in any simple way to the observed changes in the foliage arthropod fauna. Such differences in the distribution of prey in the diet and in the environment can be a result of either the predator actively selecting prey from the food that is available or of discrepancies between the sampled food resource and that which was available to the predator. Availability is difficult to assess, for it requires more than a measurement of the food within the predator's preferred foraging beat. Because of distasteful char-

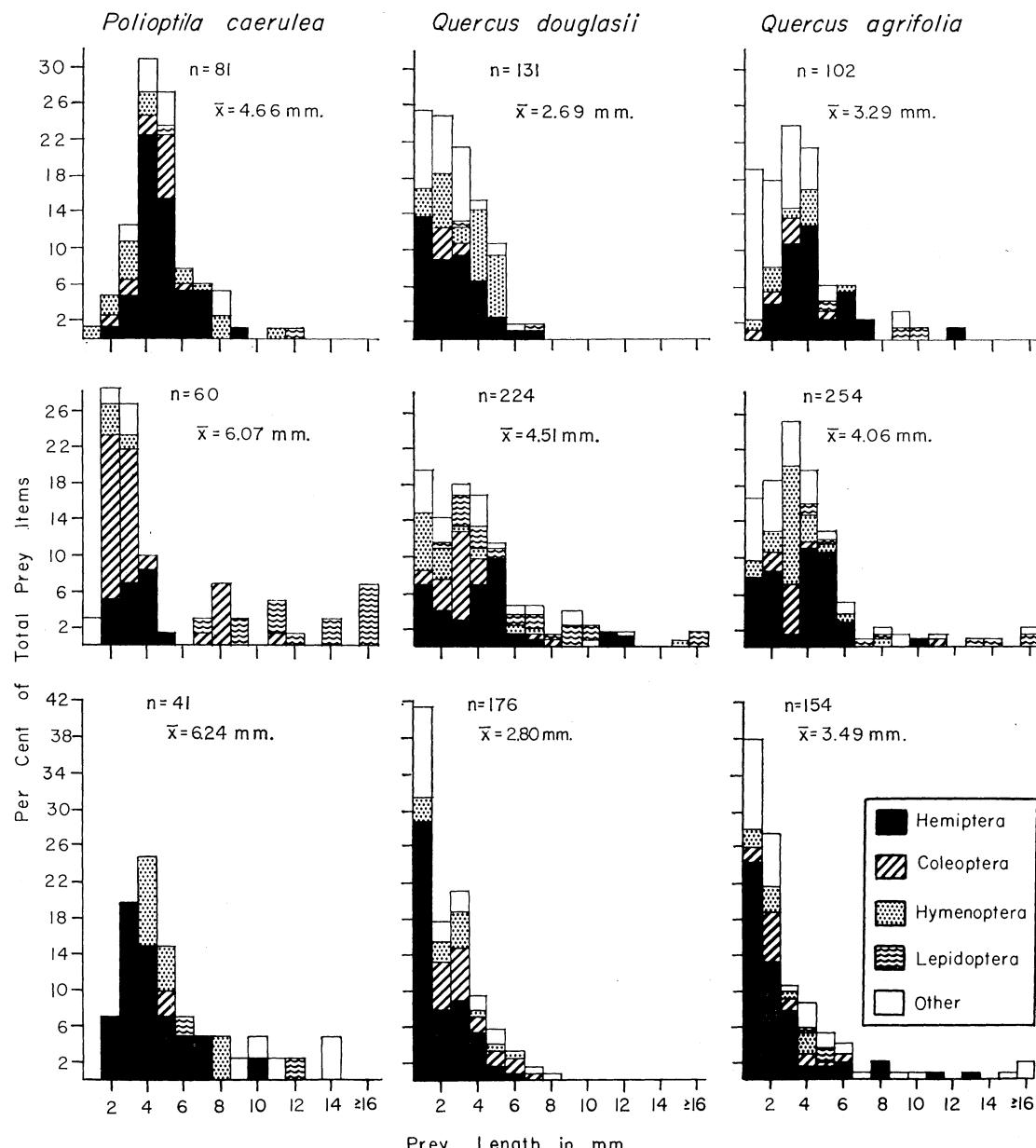


FIG. 12. The size distribution of arthropods in the stomachs of the Blue-gray Gnatcatcher and in the foliage of the deciduous blue oak (*Q. Douglasii*) and the coast live oak (*Q. agrifolia*). The three graphs at the top present the combined samples taken during June-August, 1959; the middle three, March-May, 1963; and the bottom three, June-August, 1963.

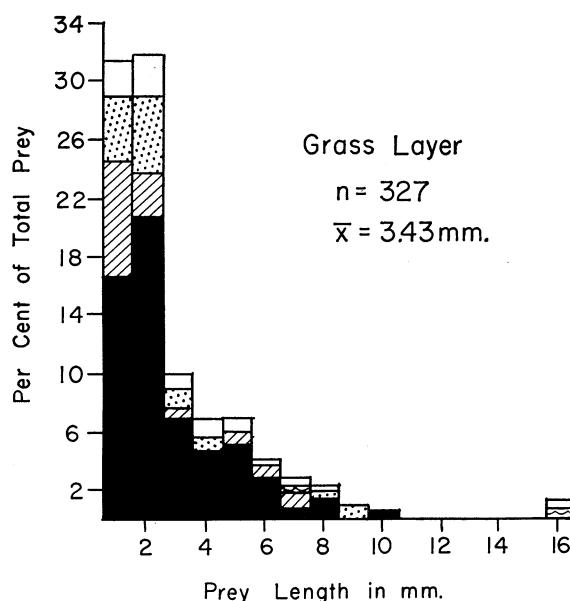


FIG. 13. The size distribution of arthropods in the grass layer of oak woodland. The samples were collected during June-August, 1963. The designation for arthropod taxa are the same as those in Fig. 12.

acteristics, certain types of prey may be avoided completely, e.g., the late instar larvae of the tent caterpillar, *M. constricta* (Root, 1966). For this reason, *M. constricta* larvae were not included in the size distributions of foliage arthropods (Fig. 12). In addition, subtle structural, physiological, and behavioral limitations may prevent the predator from consuming large quantities of certain classes of prey (Tinbergen, 1960). In large part, the avian predator's diet is influenced by a tendency to concentrate on those kinds of prey which the bird can find and ingest most efficiently (see Gibb, 1958 and 1962).

The average length of the prey that was taken by gnatcatchers was always longer than the average length of the arthropods that were present in the preferred foraging stations (Fig. 12-14). The size distribution of prey in the diet at different seasons was relatively stable in comparison with the taxonomic composition of the diet. During the winter, however, when only small arthropods were present in the environment, the mean length of the prey in the diet was also reduced. The mean length of prey in the stomachs of eight dependent young that were shot in June and July, 1963, was 8.86 mm. Since the food of adults shot during this period was somewhat smaller, there is reason to believe that gnatcatchers with young forage selectively for even larger prey.

The major differences between the size distributions of arthropods in the diet and in the environment occurred within the smaller size categories. Gnatcatchers were capable of eating arthropods which were less than 1 mm in length and yet they did so infrequently. This suggests that small prey were "overlooked" because their energy yield was too low to warrant the effort involved in their pursuit. The

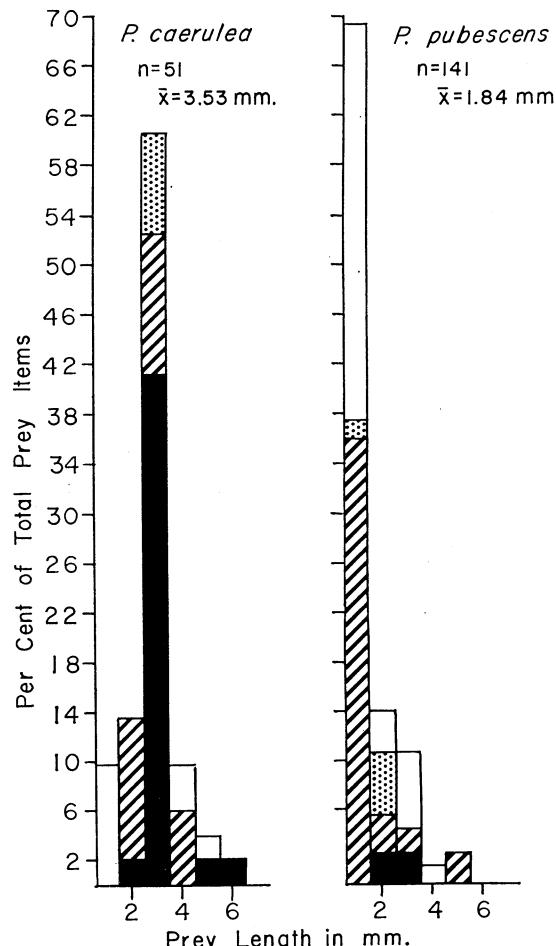


FIG. 14. The size distribution of arthropods in the stomachs of the Blue-gray Gnatcatchers and in the foliage of the screw-bean (*P. pubescens*) near Yuma, Arizona. The graphs present data from combined samples gathered in January and December, 1963. The designations for arthropod taxa are the same as those in Fig. 12.

rarity of items in the diet which exceeded 10 mm in length reflects the scarcity of such prey in the environment. Thus it appears that the distribution of prey lengths in the diet results from a dynamic adjustment between the selection of prey which exceeds a suboptimal size and the degree of scarcity of large prey in the environment.

The upper limit on prey size was probably determined by the bird's inability to dispatch and ingest large insects. Larger prey were dropped frequently and took longer to subdue (above). On two occasions, gnatcatchers were observed to have obvious difficulty in swallowing large adult lepidoptera: the prey was dropped and reoriented in the beak a few times before ingestion was accomplished. On three occasions, similar difficulties were observed in the swallowing of lepidopterous larvae that exceeded about 18 mm in length (reckoned by comparison with the length of the beak). After swallowing large prey, the birds remained on the perch for about a minute where they

TABLE 11. Changes in relative abundance of certain types of prey in the diet and in the foliage of deciduous oaks and live oaks at the Hastings Reservation. The data are presented as the percent of the total number of individuals (n) in each sample.

	Gnat-catchers	Deciduous Oaks	Live Oaks
June-August, 1959			
Membracidae.....	30.7	4.6	5.9
Cicadellidae.....	13.6	16.0	2.9
Miridae.....	4.9	4.6	7.7
Lepidopterous larvae.....	4.9	1.5	0.9
Other.....	45.9	73.3	82.6
n.....	81	131	102
March-May, 1963			
Membracidae.....	3.3	6.7	2.4
Cicadellidae.....	3.3	5.8	4.7
Miridae.....	31.7	14.7	24.4
Lepidopterous larvae.....	18.3	18.3	3.9
Other.....	43.4	54.5	64.6
n.....	60	224	254
June-August, 1963			
Membracidae.....	34.1	1.7	6.4
Cicadellidae.....	19.5	23.3	21.1
Miridae.....	4.9	1.1	1.9
Lepidopterous larvae.....	2.4	4.5	1.9
Other.....	39.1	69.4	68.7
n.....	41	176	156

alternated between wiping the base of the beak against the perch and pointing the beak upward while turning the head from side to side. Large prey which nestlings were unable to swallow was eaten by the adults on three occasions.

Closer agreement was seen between the gnatcatcher's foraging response and changes in the abundance of certain types of prey (Table 11). All of the prey individuals included in Table 11 exceeded 2.5 mm in length and possessed characteristics which made them vulnerable to attack by gnatcatchers (above). Mirids and lepidopterous larvae formed a large part of the diet during the spring when these groups were relatively abundant in the foliage. During the summer, membracids and cicadellids became more important in the diet. The higher degree of predation on cicadellids was associated with an increase in the relative abundance of these insects in the environment. The increased proportion of membracids in the summer diet could not be explained on this basis, however. Perhaps gnatcatchers were feeding selectively on the membracids, particularly *Platycotis* spp. and *Stictocephala* sp. which are stout-bodied and exceed 5 mm in length, in response to a seasonal decline in the abundance of large lepidopterous larvae.

THE FOLIAGE-GLEANING GUILD

GUILD CONCEPT

Data were gathered on the exploitation patterns of birds that regularly fed on foliage arthropods in the oak woodlands at the Hastings Reservation. These

species are local members of the "foliage-gleaning guild." A *guild* is defined as a group of species that exploit the same class of environmental resources in a similar way. This term groups together species, without regard to taxonomic position, that overlap significantly in their niche requirements. The guild has a position comparable in the classification of exploitation patterns to the genus in phylogenetic schemes.

As with the genus in taxonomy, the limits that circumscribe the membership of any guild must be somewhat arbitrary. To be considered a member of the foliage-gleaning guild in the oak woodland, the major portion of a bird species' diet had to consist of arthropods obtained from the foliage zone of oaks. As a result, birds that occasionally use the foliage zone were excluded even though they may have exerted some influence on the guild's food supply. A species can be a member of more than one guild. For instance, the Plain Titmouse, *Parus inornatus*, while belonging to the foliage-gleaning guild with respect to its foraging habits, is also a member of the hole-nesting guild by virtue of its nest-site requirements.

According to the competitive exclusion principle (Hardin, 1960), there must be some minimal difference in the exploitation patterns of sympatric species. Even if this principle was incorrect, it is obvious that interspecific competition has deleterious effects and that natural selection would tend to favor divergence which reduces the intensity of competition. Most studies of interspecific competition have considered only sympatric members of the same genus on the assumption that species with close taxonomic relationship tend to be the strongest competitors. The work of Brian (1952, 1955) on ants, Hartley (1948) and Maitland (1965) on fish, and Pitelka (1951) on birds, to mention but a few, has demonstrated, however, that intergeneric competition can also be an important factor. One advantage of the guild concept is that it focuses attention on all sympatric species involved in a competitive interaction, regardless of their taxonomic relationship.

The guild concept has additional use. As mentioned earlier, the term *niche* is used in reference to two quite distinct concepts: the functional role or "occupation" of a species in a community and the set of conditions that permit a species to exist in a particular biotope. This combination of concepts under a single term has led to controversies over the interpretation of data presented to refute the generality of the competitive exclusion principle (cf., Ross 1957, 1958; Savage, 1958). If we restrict our definition of niche to the latter (Hutchinson-Macfadyen) concept, such arguments could be resolved by recognizing that groups of species having very similar ecological roles within a community are members of the same guild, not occupants of the same niche.

Finally, the guild concept may be useful in the comparative study of communities. It is usually impractical to consider at once all species living in a biotope, so ecologists must restrict their analyses to

particular taxonomic groups. This procedure frequently obscures the functional relationships within the communities, because species performing several different unrelated roles are considered together. The same guild may be represented in several different communities and can thus serve as the basis for comparing species diversity, degree of character difference, biomass, etc. in different biotopes. In using the guild in these comparisons, we are dealing with a functional or ecological category—one that has been molded by adaptation to the same class of resources and by competition between its local members. Functional classifications based upon "feeding groups" have been used by Salt (1953, 1957) and Turpaeva (1957) in their comparative analyses of natural communities.

The term, guild, has appeared once before in the ecological literature as a translation of "Genossenschaften" in the English edition (1903) of Schimper's "Pflanzengeographie auf physiologischer Grundlage." It was used there to refer to four groups of plants that are dependent upon other plants for their existence—lianes, epiphytes, saprophytes, and parasites. This usage of guild has not become established and can be considered obsolete or "archaic." I am using the word guild in a new sense because it seems to be the most evocative and succinct term for groups of species having similar exploitation patterns.

MEMBERSHIP AT THE HASTINGS RESERVATION

During the breeding season the foliage-gleaning guild in the oak woodlands at the Hastings Reservation includes the Warbling Vireo (*Vireo gilvus*), Hutton's Vireo (*Vireo huttoni*), Orange-crowned Warbler (*Vermivora celata*), Plain Titmouse (*Parus inornatus*), and the gnatcatcher. The titmouse just barely meets the criteria used to delimit the guild, because a large portion of its diet consists of plant material and arthropods living on bark. Occasionally other foliage-gleaning species such as the Common Bushtit (*Psaltriparus minimus*), Black-throated Gray Warbler (*Dendroica nigrescens*), and Yellow Warbler (*Dendroica petechia*) were encountered in the oak woodland adjacent to large stands of chaparral or riparian forest. The House Wren (*Troglodytes aedon*), Bewick's Wren (*Thryomanes bewickii*), Scrub Jay (*Aphelocoma coerulescens*), Oregon Junco (*Junco oreganus*), and Chipping Sparrow (*Spizella passerina*) occasionally foraged for arthropods in the oak foliage but obtained most of their food from the subcanopy or ground.

The Western Flycatcher (*Empidonax difficilis*) is an important avian insectivore in the oak woodland, but its foraging behavior differs greatly from that of the foliage-gleaners. Like other flycatchers, *E. difficilis* hunts by searching a large area from a "sentinel" position on an exposed perch. Most prey is taken in long sweeping aerial attacks on flying insects or arthropods that alight momentarily on the foliage. This concentration on active insects is reflected in the high

proportion of Hymenoptera and Diptera found in the diet (Beal, 1910).

The Warbling Vireos, Orange-crowned Warblers, and gnatcatchers leave the Hastings Reservation in the winter. The resident members of the guild are joined by the Ruby-crowned Kinglet (*Regulus calendula*) and Audubon's Warbler (*Dendroica auduboni*) at this season. During the winter the foliage-gleaning birds range over a wider variety of vegetation types and are less restricted to the foliage zone of trees than during the summer. The resident species begin nesting somewhat earlier than the migrants. A pair of titmice began a nest on 21 February 1963 and I found a Hutton's Vireo nest on 20 March 1963. To the north, in Sonoma County, the last species has been reported to begin nesting in early March (Bent, 1950).

The species diversity of gleaners in the oak woodlands reaches a peak in late March and throughout April when transient species and winter visitants overlap in their presence at the Reservation with the breeding members of the guild.

The following discussion considers the niche relations of guild members during the breeding season. Only quantitative data on individuals engaged in self-maintenance foraging during March-August are reported. Qualitative statements about these species are based upon several additional observations that were made at Las Trampas Canyon, Contra Costa County (Root, 1964a) and other localities in central California.

FORAGING BEAT

There were 4 pairs of Warbling Vireos, 2 pairs of Hutton's Vireos, 4 pairs of Orange-crowned Warblers, and 7 pairs of Plain Titmice during the 1963 breeding season on the portion of the study area shown in Fig. 6. The territories of the two vireo species were centered in clumps of evergreen oaks along the draws, while some of the gnatcatcher and titmouse territories extended out onto the ridges and contained almost pure stands of deciduous oak woodland. The Orange-crowned Warblers were found on slopes where there was a well developed shrub layer beneath the oak canopy. Nevertheless, all of the species regularly utilized both deciduous and live oaks.

All of the guild members forage most often in the foliage zone of oaks, but differ in their restriction to this station (Table 12). Hutton's Vireo frequently perches in the subcanopy, but directs most of its attacks "outward" at arthropods in the foliage zone. The titmouse is able to exploit a greater variety of stations within the oak woodland than the other species. Often it is found foraging on the large limbs and trunks in the subcanopy or on open ground (Root, 1964a). During the winter, when the abundance of arthropods drops sharply in the foliage zone of deciduous oaks (Fig. 19), this species is the only guild member to forage regularly in stands of barren trees. My data on the Orange-crowned War-

TABLE 12. The foraging beat of members of the oak foliage-gleaning guild at the Hastings Reservation. The data are expressed as the percent of standard observations.

	n	Tree zones		Herb layer
		foliage	sub-canopy	
<i>Polioptila caerulea</i>	309	90.0	8.6	1.4
<i>Vireo gilvus</i>	80	90.0	10.0	0.0
<i>Vireo huttoni</i>	60	65.0	33.3	1.7
<i>Vermivora celata</i>	113	84.9	9.7	5.4
<i>Parus inornatus</i>	140	48.6	41.4	10.0

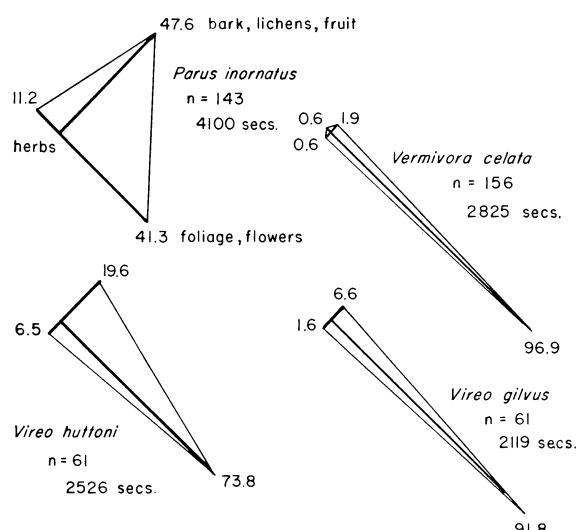


FIG. 15. The substrates where members of the foliage-gleaning guild obtained food in oak woodland. The coordinates are explained in Fig. 10. The length of the timed observations used in computing foraging tactics is given below the total number of maneuvers (n).

bler may be somewhat biased in favor of tree foraging. Occasionally, these birds were observed using twig perches at the base of shrubs and small oaks while foraging on insects in the herb layer. Because of the dense shrub canopy on parts of warbler territories and the relative silence of birds foraging at these lower levels, I may have missed some of their activities. By following the individuals for periods of 30 min or longer, I found that this error is probably minor.

FORAGING MANEUVERS

With the exception of the Plain Titmouse, the guild members all capture most of their prey on oak foliage (Fig. 15). Both Hutton's Vireo and the Plain Titmouse frequently obtain food from bark surfaces, but during the breeding season most of these attacks are directed at twigs in the foliage zone. The frequencies of basic foraging maneuvers employed by guild members are presented in Fig. 16. These basic maneuvers are defined as follows:

maneuver	position of prey	position of bird
glean	resting on substrate	standing on perch
hover	resting on substrate	in the air
hawk	in the air	in the air

The two vireo species have a similar foraging "style." They remain on a perch for a longer period than the other species before moving rapidly to another vantage point a few feet away. They also seem to search for prey at a greater distance from the perch, often directing attacks at insects 3 ft or more away. Their frequent use of hovering attacks may be related to the wide search radius, because it is probably difficult to alight near prey that is seen at a distance. These hovers differ somewhat from those of the gnatecatcher. Frequently gnatecatchers remain stationary in midair (in hummingbird fashion) while grasping the prey and then fall back to a perch. Vireos do this on occasion, but usually strike the prey while passing by in rapid flight. When extracting prey from dense terminal sprigs of foliage, vireos often grasp the leaves in their feet and hang upside down for a moment. Gnatecatchers normally employ hovering maneuvers to attack prey in this situation. Large prey are mandibulated and battered against the perch by both vireo species. In addition, they occasionally hold large insects against the perch with their foot while tearing them into smaller portions with the beak.

Foraging Orange-crowned Warblers move rapidly from perch to perch as they probe into clusters of leaves with their beaks. Under the best observation conditions it could be seen that many of these probes did not involve the capture of prey: the beak is thrust methodically into places where prey is likely to be found as part of the normal searching routine. Since it was often impossible to distinguish such searching probes from those used in capturing prey, my estimate of foraging intensity for the warblers (Fig. 16) is undoubtedly too high. In contrast with the vireos and gnatecatcher, these warblers employ aerial attacks infrequently. On the other hand, they characteristically stretch, lean, or even hang momentarily from the perch to peek at nearby foliage. Hovering and hawking maneuvers are executed in a manner similar to those of the gnatecatcher. Large insects are mandibulated or battered against the perch.

Plain Titmice are capable of extracting concealed prey from a variety of situations that cannot be exploited by other species in the guild. The titmice often pull apart leaf galls, flowers, curled dead leaves, and lichens with their beaks to expose arthropods. They also hammer apart acorns and other fruits, and pry bark from branches to obtain food. Frequently objects are held down with one foot while the beak is used to tear them apart. In order to compare the foraging tactics of titmice with the other species (Fig. 16), it is necessary to distinguish pecking used to extract prey from that employed in actual capture. As a result, I have reported bouts of pecks at the same object as one gleaning maneuver. The infre-

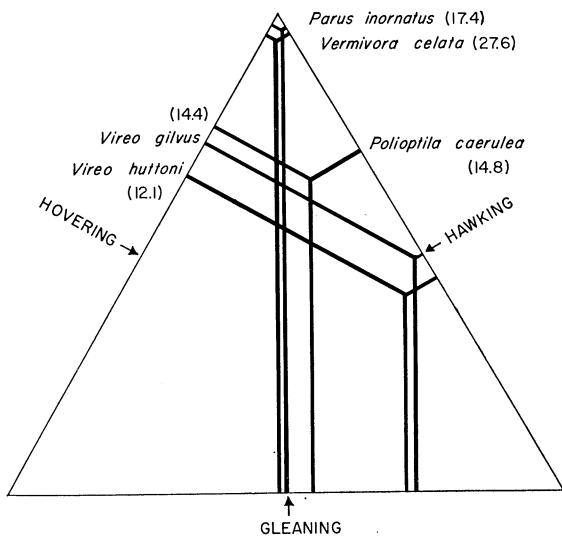


FIG. 16. The foraging tactics of members of the foliage-gleaning guild in oak woodland. The coordinates are explained in Fig. 11. The numbers following each species express its foraging intensity as the number of attack maneuvers/500 sec of observation.

quent hovering and hawking attacks performed by titmice consist of a "clumsy" lunge at nearby prey. Insects at the bottom of terminal foliage clumps or on the underside of twigs are usually captured in hovering maneuvers by the vireos and gnatcatcher. Titmice attack prey in these situations while hanging upside down from a perch. During the 4100 sec of standard observation for this species, the birds hung from perches 30 times (for an estimated total of 120 sec) and remained in an upside position for as long as 15 sec.

DIET

Data on the arthropods in the diets of guild members are summarized in Fig. 17 and Table 13. Only stomachs of birds collected in oak woodland near the Hastings Reservation during the breeding season were examined. Both intact prey and arthropod fragments are included in Table 13. Counting of fragments tends to overestimate taxa with thick exoskeletons, such as the Coleoptera (see Table 1), and therefore fragments could not be used above to compare the frequency of taxa in the gnatcatcher's diet with the abundance of prey on the foliage. By including the fragments in Table 13, however, a more complete impression of relative differences in the diets of guild members can be gained than would be possible if I had counted only the few intact prey that are available.

All of the guild members captured prey within a similar range of sizes, but the two vireo species and the Orange-crowned Warblers tended to capture large caterpillars more frequently than the other species. Hemiptera were a significant item in all diets; the same common species of cicadellids and membracids were eaten to some extent by all of the guild members.

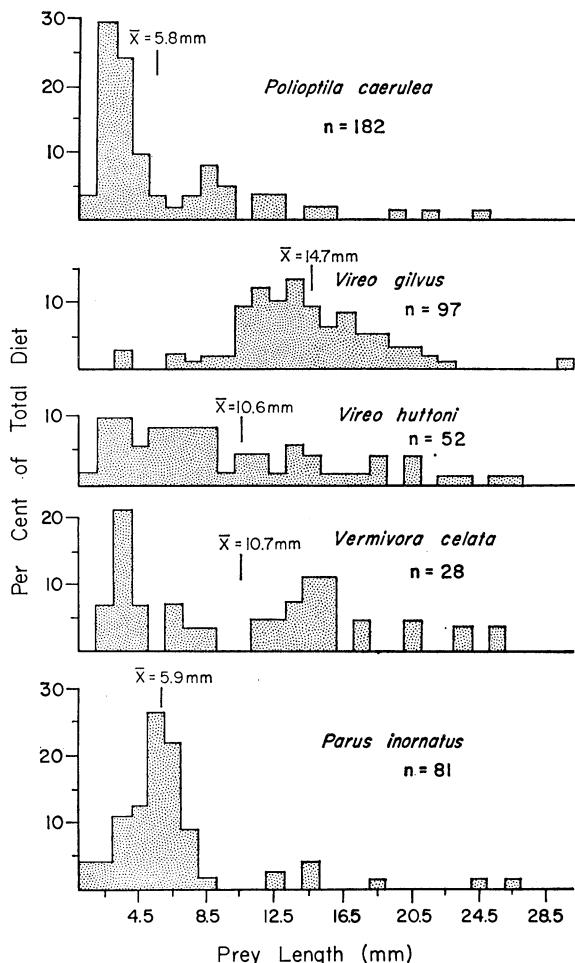


FIG. 17. Size distribution of intact prey in the stomachs of foliage-gleaning birds. Based on birds collected in oak woodland near the Hastings Reservation.

Only the titmice regularly fed upon plant material: seeds and plant fragments were found in 13 of the 16 stomachs examined.

MORPHOLOGICAL ADAPTATIONS

Studies on the functional anatomy of birds have shown that the structure of the beak is closely related to a species' foraging behavior (Engels, 1940; Bowman, 1961; and others). The guild members display a spectrum of bill types (Fig. 18) which, in turn, correspond to gross differences in their foraging tactics and diet. Species that are primarily gleaners (e.g., Orange-crowned Warbler) possess narrow thin-tipped beaks, while aerial foragers, such as the Western Flycatcher (included with guild members in Fig. 18 for comparison), have the base of the beak dorsoventrally compressed. The relatively massive beak of the Plain Titmouse is probably linked to its extensive use of the bill in hammering apart hard objects. By comparison, gnatcatchers seem to exploit two different foraging modes: gleaning arthropods from the foliage is expressed in the sharp tip of the

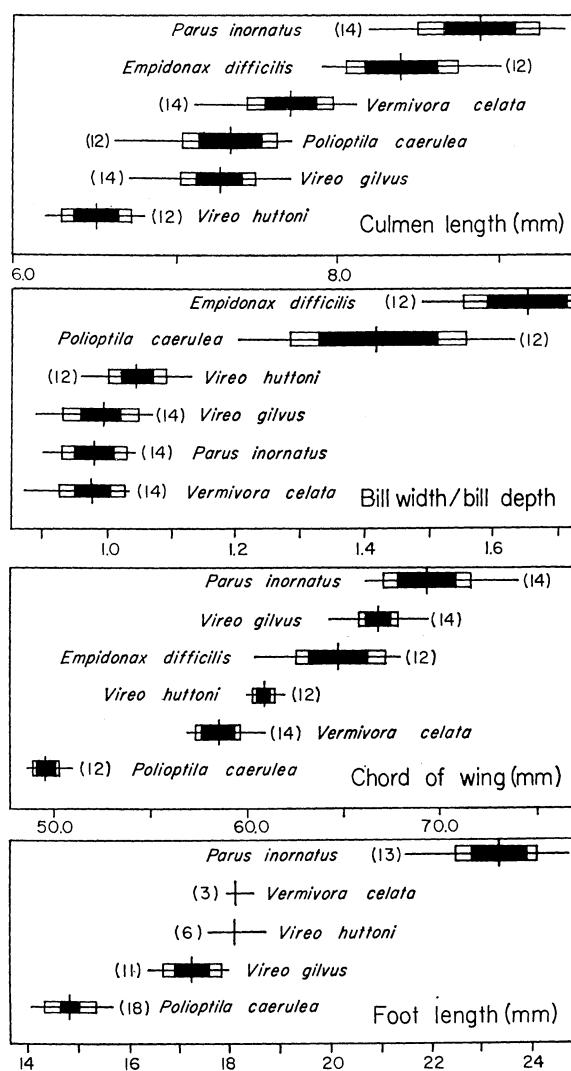


FIG. 18. Morphological variation in the birds of the foliage-gleaning guild. The horizontal lines represent the observed ranges; the rectangles mark one standard deviation on either side of the mean, with the solid portion indicating the 95% confidence limit for the mean. Only male specimens collected during the breeding season, in the Central Coast Range of California were measured. The bill measurements were made with the anterior margin of the nostril as a reference point. Foot length was measured on specially prepared specimens from the end of the hallux to the tip of the middle toe (excluding the claws).

beak, while the compressed base of the bill represents an adaptation for aerial foraging.

These comparisons serve to emphasize that the shape of the beak derives from a mosaic of adaptations suited to a particular set of foraging maneuvers. For this reason the foraging tactics must be considered when selecting dimensions for use in comparing morphological differences between potential competitors. The use of differences only in culmen length to estimate degree of niche overlap in birds (Hutchin-

son, 1959, Klopfer and MacArthur, 1961, and Schoener, 1965) may be inappropriate because the more "active" dimension segregating species would probably be beak width among aerial foragers and beak depth in fruit or seed eaters. In the foliage-gleaning guild, those species that overlap significantly in culmen length have the base of the beak compressed to different degrees (Fig. 18).

Schoener (1965) has shown that there is less difference in beak length between small sympatric birds, particularly in insectivorous families, than between large species. He suggests that this is because the large food morsels captured by large birds are less abundant than small prey. In addition, the larger birds probably have greater energy requirements. As a result, large species can tolerate less overlap than smaller birds that are feeding upon the more abundant small prey. The data on the foliage-gleaning guild supports Schoener's hypothesis in part.

The size distribution of arthropods in the tree foliage (Fig. 12) shows that large insects are relatively less abundant. The weights of guild members (based on breeding males taken near the Reservation) were as follows:

	n	mean wt. in gm
<i>Polioptila caerulea</i>	14	5.7
<i>Vermivora celata</i>	6	9.3
<i>Vireo huttoni</i>	9	11.2
<i>Vireo gilvus</i>	10	11.3
<i>Parus inornatus</i>	13	17.8

These size differences are also reflected in the measurements for the chord of the wing (Fig. 18). The character differences in the series of mean bill lengths (Fig. 18) are as follows:

Species	ϕ
<i>Vireo huttoni</i>	1.12
<i>Vireo gilvus</i>	1.01
<i>Polioptila caerulea</i>	1.05
<i>Vermivora celata</i>	1.15
<i>Parus inornatus</i>	

where ϕ is the ratio of the larger to the smaller measurement (Hutchinson and MacArthur, 1959; Hutchinson, 1959). Thus we see that a character difference greater than 1.14 (used by Schoener to identify the "transition zone") separates only the largest species, the titmouse, from the other guild members.

An implicit assumption in Schoener's hypothesis is that beak size (within the same avian family) is directly related to the size of the preferred prey. The two species of *Vireo* appear to fit this assumption (cf., Figs. 17 and 18). For the guild as a whole, however, there is no correlation between bill length and the mean size of prey. Furthermore, while there seem to be specific differences in preferred food size, there is almost complete overlap in the size range of prey

TABLE 13. Arthropods in the diets of foliage-gleaning birds. The data are expressed as the percent of total prey individuals (n) that could be identified.

	<i>Polioptila caerulea</i>	<i>Vireo gilvus</i>	<i>Vireo huttoni</i>	<i>Vermivora celata</i>	<i>Parus inornatus</i>
Hemiptera.....	36.0	10.3	11.9	47.8	13.2
Coleoptera.....	32.3	15.0	29.8	6.5	55.3
Lepidoptera.....	7.1	62.0	24.6	37.0	6.5
Hymenoptera.....	13.8	6.6	22.4	4.3	10.2
Other.....	10.8	6.1	11.2	4.3	14.8
n.....	287	213	134	46	81

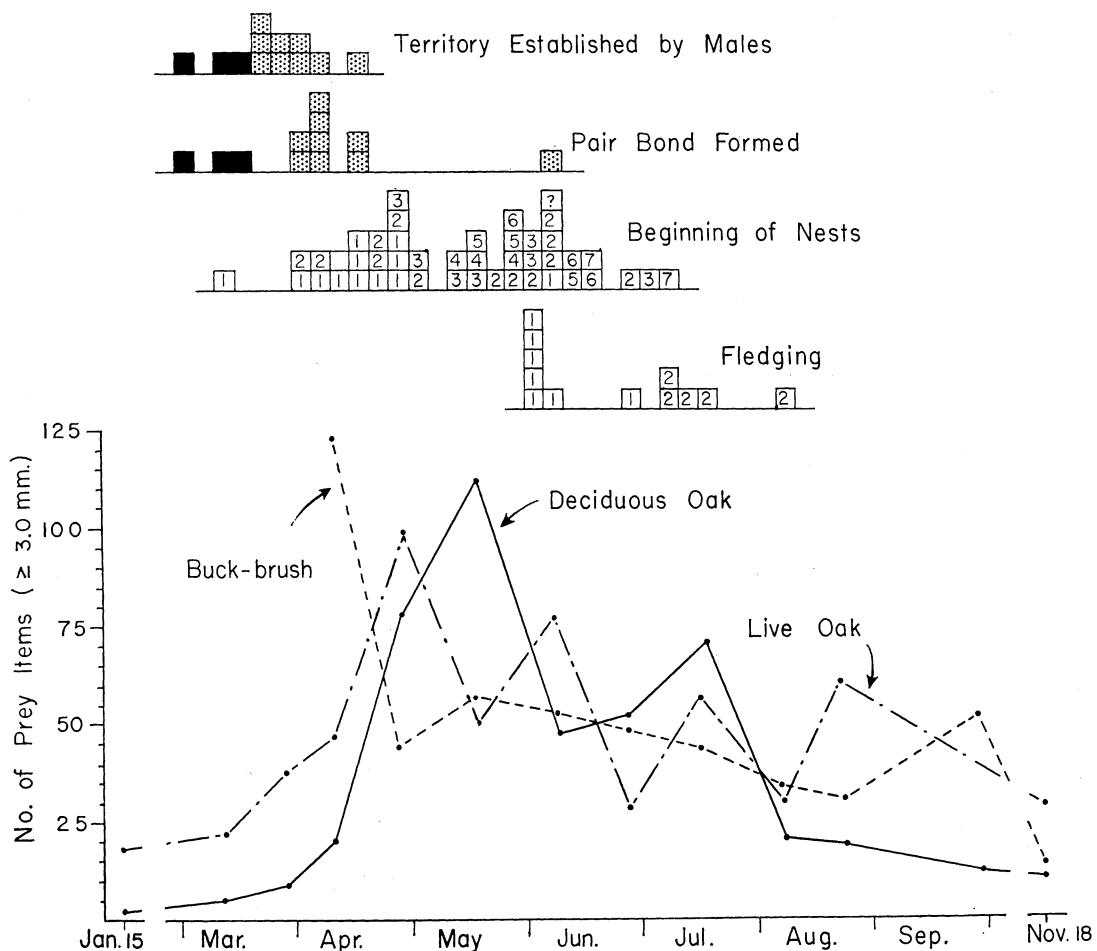


FIG. 19. Seasonal changes in the breeding activities of the Blue-gray Gnatcatcher and the abundance of foliage arthropods at the Hastings Reservation during 1963. In the two histograms at the top, the black squares refer to territories which were centered in chaparral and the stippled squares refer to territories in oak woodland. The numbers in the histogram labeled "beginning of nests" refer to the position that each nest occupied in the sequence of nests built by each pair. In the bottom histogram, the numbers designate whether the fledglings were from the first or second successful brood of the season. The points on the graph of prey abundance present the number of arthropods collected in 40 sweeps with a beating net.

captured by the guild members (Fig. 17). Thus it would appear that the shape of the food abundance curve (Fig. 12) restricts selective foraging for prey of different sizes, even in the titmouse, with its relatively large character differences. Partitioning of the guild's food supply is not based upon a single factor,

such as prey size, but instead, involves the simultaneous action of differences in "preferred" foraging beat, foraging maneuvers, and diet.

Those guild members that spent most of the time in the foliage zone (Table 12) where small diameter perches abound, have smaller feet than the titmouse

(Fig. 18) which frequently forages from limbs and boles.

ADAPTIVE RESPONSES TO CHANGES IN THE FOOD SUPPLY

The importance of the food supply as a limiting factor of avian populations is well established (Lack, 1954 and 1966, presents extensive reviews). In the temperate and arctic latitudes, and perhaps in the tropics as well, the composition and quantity of this critical resource vary on a seasonal, yearly, and geographical basis. Birds inhabiting such regions must possess adaptations for exploiting the variable food supply. Changes in the abundance of foliage arthropods and the timing of important events in the breeding cycle of the gnatcatchers are summarized in Fig. 19. Since the purpose of Fig. 19 is to compare the foraging conditions at different seasons and in different habitats, only arthropods within the optimal range of prey size for the gnatcatcher (3.0 mm in length and longer) are considered. The following is an account of the gnatcatcher's adaptive responses to these changes in the food supply.

HABITAT SELECTION

The importance of the structural configuration of the vegetation and the topography of the region as determinants of habitat occupancy has been well studied (Lack, 1933, 1949; Svärdson, 1949; MacArthur, MacArthur, and Preer, 1962; Klopfer, 1963; and Weeker, 1963). Indeed, the theories of Lack and Svärdson attempt to explain the habitat selection process almost completely upon the bird's recognition of such structural features of the environment. Both authors point out, however, that structural cues are proximate factors (i.e., "releasers" of the behavioral mechanism) and that ultimate factors, those concerned with survival value, must act through natural selection to delimit the spectrum of cues used by a species in habitat selection. The gnatcatcher's pattern of territory establishment provides an interesting contrast to previous work, in that ultimate factors seem to be directly involved in the habitat selection process.

In other species of migratory birds the "optimal" habitats are selected out first by the early arrivals (Svärdson, 1949). Male gnatcatchers, following their arrival in March and early April, wander over a large area which permits them to assess the favorability of different habitats. Not all habitats within the area are visited. At the Hastings Reservation, gnatcatchers were rarely observed in the broadleaved canyon forest, even though this habitat appeared to offer ideal foraging conditions for this species. The first territories which are defended encompass large areas of chaparral or live oak woodland (Fig. 6). The height and spacing of the dominant plant species in these two vegetation types are quite different: there is a greater similarity in outward structural configuration between the live oak woodland and the deciduous oak woodland, the latter not being attractive to gnatcatchers at this season. Apparently something in ad-

dition to these structural cues is involved in the habitat selection process.

The deciduous oak woodlands did not become attractive to gnatcatchers until after the chaparral and live oak habitats were saturated by the early arrivals. Since the deciduous oaks were almost devoid of leaves during this period, the possibility exists that foliage density provides cues eliciting habitat settlement. This possibility could not be evaluated thoroughly in this study because foliage density is clearly related to other important factors, such as the abundance of foliage arthropods, in most field situations. An experimental procedure, such as a comparison of territory establishment between plots where the prey populations had been reduced with insecticides and untreated plots, would be necessary to separate foliage density from other cues that might be involved in habitat selection. Nevertheless, indirect evidence leads me to believe that foliage density is relatively unimportant as a proximate cue for recognition of optimal habitat, at least with the gnatcatcher. In August, when the foliage characteristics of the oak woodlands and chaparral are little changed from their condition in May and June, the gnatcatchers leave the deciduous oak habitats and return to the chaparral and adjacent live oaks. In addition, the western subspecies of the gnatcatcher leaves the evergreen vegetation of California during the winter and migrates to desert habitats where the foliage is relatively sparse.

Nest site characteristics might also provide the gnatcatcher with important cues for the selection of breeding habitats. The inspection of potential nest sites is a dominant activity of both sexes during the period of territory establishment and pair formation (Root, *in press*). While inspecting nest sites, the gnatcatchers examine the immediate surroundings intently, suggesting that a critical assessment of the habitat is taking place at this time. Klopfer (1962) and Weeker (1963) have suggested that early experiences with the environment may influence an individual's subsequent selection of habitats. Since the surroundings of the nest are the first features of the breeding habitat that each nestling perceives, it would not be surprising if these characteristics were important in habitat recognition. Sargent (1965), experimenting with caged Zebra Finches, has shown that rearing and previous nesting experiences have some effect upon the birds' choice of nesting materials and nest "habitats." Individual gnatcatchers build consecutive nests in very different situations, however. A banded female (from Pair 1) built nests in deciduous oaks, live oaks, and a buck brush shrub; in shaded and unshaded locations; and on vertical and horizontal nest forks. I have thus been unable to discover a feature of the nest fork or its surroundings which appears to limit the individual's choice of habitats.

Differences in the food supply of the habitats in which gnatcatchers occur during the period of territory establishment appears to be the principle variable that can account for the differences in the attractiveness of the habitats. The first territories which are

defended include large areas of chaparral and live oak woodland, habitats containing the greatest abundance of foliage arthropods at this season (Fig. 6 and 19). Formation of the pair bond is also related to differences in the food supply. The initial assessment of the habitats by the males is continued by the females during the period when they are consorting with different unmated males (Root, *in press*). The pair bond does not appear to become established until after the abundance of arthropods in the dominant trees and shrubs on the territory exceeds some minimum amount (about 15 large arthropods in 40 sweeps of the foliage).

Svärdson (1949) has proposed that habitat selection by birds is not "released" by any single factor in the environment, but instead, that several environmental stimuli, which can be combined in various ways, reach a "sum" that is sufficient to elicit territory establishment. The habitat selection process of the gnatcatcher seems to be organized in a similar manner. I would suggest that the process takes place in two stages. First, responses which are innate or learned early in life, delimit the general region and the spectrum of habitats within a given region to which the gnatcatchers return in the spring. After their arrival, the second stage begins. While wandering over a series of acceptable habitats, the birds are able to assess the food supply (and perhaps the availability of nest sites) in different areas. Finally, territories are established in those areas which provide the most suitable combination of requisites for survival of both the adults and the young.

Thus the same characteristics of the environment serve as both proximate and ultimate factors in the final stages of the gnatcatcher's selection of breeding habitats. The continued assessment of the environmental requisites during the period prior to the beginning of the first nests assures that the population's initial breeding effort will be concentrated in the most favorable habitats. In years when there is a late spring or some regional catastrophe reduces the favorability of a habitat, the gnatcatchers are able to change their normal pattern of habitat occupancy in accordance with these changes. The gnatcatcher's pattern of territory establishment seems to support Klopfer's expectation (1963) that the habitat selection process of Temperate Zone birds will be so organized as to permit the species to respond opportunistically to such changes in its environment.

CHANGES IN TERRITORY CONFIGURATION

Adult gnatcatchers defend a territory which contains the necessary requisites (e.g., food, shelter, and nest sites) for their own survival and rearing young. Territoriality of this sort promotes a "contest" type of intraspecific competition (Nicholson, 1957). The initial contest for territories appears to have a direct influence on the size of the breeding populations. Of the 12 original males that set up territories on the

study area in March and April, 1963, two subsequently moved from the area. These vacancies were filled by two pairs from other areas. The breeding habitats appear to be nearly "saturated" following the period of territory establishment, with each pair claiming an area which contains adequate supplies of the requisites required for successful breeding.

In the weeks that follow the initial settlement of the breeding area, however, there is a reversal in the abundance of food between the habitats encompassed within the original territories. The configuration of the territory boundaries shifts in accordance with these seasonal changes in the dispersion of optimal food resources (Fig. 6). Between May and July, when the abundance of foliage arthropods in the deciduous oaks is high (Fig. 19), nesting activity is focused in the deciduous oak woodlands. As the food supply of the deciduous oaks declines in August, the gnatcatchers move back into the chaparral and live oaks.

Throughout the breeding season, the territorial boundaries are extended to include the dense clumps of evergreen vegetation to which fledglings are led by the adults. Such areas may provide the vulnerable fledglings with a refuge from predators.

An interrelated series of behavioral adaptations facilitates the shifting of territorial boundaries in response to the gnatcatcher's changing demands on its environment, and to the seasonal changes in conditions prevailing in different habitats. During periods when the adults are making frequent trips to the nest with building materials and food for the nestlings, the males can patrol the perimeter of the territories only infrequently. As a result, the pair's most active defense of the territory becomes compressed into a relatively small area around the nest. Adjacent pairs which have lost their attachment to a nest, either through the failure of a nest or the fledging of a brood, are able to move into these vacant areas while the original holder is occupied elsewhere with nesting activities.

The fluid territorial organization of the gnatcatcher is promoted by a lack of synchrony in the nesting cycle of adjacent pairs. The prolonged period over which the birds arrive on the breeding area and begin nesting (Fig. 19) produces asynchronous cycles early in the season. The timing of territory establishment is itself related to changing conditions in the various habitats. In addition, nest predators, through their spotty destruction of nests, interrupt the breeding cycle at different times (Root, *in press*). Since the ability to change the configuration of territories offers obvious advantages for the gnatcatcher, the lack of synchrony has beneficial effects. In this regard, the gnatcatcher differs from those species (cited in Wynne-Edwards, 1962) whose breeding cycles are closely synchronized, apparently in response to seasonal peaks in their food supply. The gnatcatcher's diverse diet, its ability to successively exploit different habitats, and its prolonged breeding season, reduce the necessity for highly synchronous breeding.

CHANGES IN FORAGING BEHAVIOR

Both the abundance and the species composition of the foliage arthropods vary in time and space (Figs. 12-14, Table 11). To exploit such a variable food supply, the gnatcatchers must possess a versatile foraging behavior that can respond quickly to sudden changes in prey availability. Accordingly, the gnatcatcher's capacity to alter its foraging beat, foraging maneuvers, and diet at different seasons has been demonstrated (Figs. 8, 10-12, and 14).

The high species diversity of the arthropod fauna, coupled with the gnatcatcher's selective predation on it, makes it difficult to establish an exact correspondence between changes in the availability of different kinds of prey and changes in the foraging behavior (see section on diet for further discussion of this point). One clear relationship emerges from these data, however. In all of the situations studied, gnatcatchers concentrated their foraging efforts on those arthropods which, by virtue of their large size, high abundance, or sedentary behavior, could be exploited most efficiently. Such opportunistic feeding behavior seems to be characteristic of most true predators: similar trends in prey selection have been observed in gastropods (Paine, 1963), robberflies (Powell and Stage, 1962), fish (Nilsson, 1955; Brooks and Dodson, 1965), and other species of birds (Gibb and Betts, 1963).

ADAPTIVE RESPONSES TO THE BROOD'S FOOD REQUIREMENTS

The energy requirement of the dependent young exerts heavy demands upon the foraging abilities of the adults. Broods of advanced nestlings and young fledglings were fed by the most attentive parent about once every 2-4 min (for further details on the rates at which broods were fed and seasonal changes in the parental roles of both sexes, see Root, *in press*). In addition, the normal self-maintenance energy requirements of the adults must be elevated somewhat by their frantic activity in feeding the young. Thus the interval of about 22 days, when the brood is completely dependent upon the adults for food, obviously constitutes a critical time in the gnatcatcher's utilization of its food supply.

In addition to their adaptive responses to seasonal and spatial changes in the food supply (discussed above), adult gnatcatchers also possess several behavioral adaptations that are primarily related to the increased energy requirements of the brood. While the time and energy budgets (Orians, 1964) were not studied directly, it is obvious that the adult's release from incubation and brooding permits the pair-unit to devote progressively greater proportions of time to foraging as the food requirements of the developing brood increase.

The young gnatcatchers are fed larger arthropods, on the average, than are consumed by the adults. Since large preys are less abundant, their capture requires that pairs with young must search a greater volume of the habitat. This is accomplished by an ob-

vious increase in the searching velocity, the number of hunting perches assumed per unit time, by adults with young.

The foraging intensity of the adults increases significantly when they are feeding young (Table 7). The rate at which prey is captured in an interval of time spent foraging is thereby increased. This intensification of the foraging activity is accompanied by shifts in the bird's tactical response. The adults with dependent young capture a greater proportion of their prey in aerial attacks (Fig. 11) and in the pursuit of prey that has been flushed from the foliage (Table 8). Such changes in the foraging tactics reflect a tendency for adults to engage in more strenuous maneuvers in order to capture highly active prey. In comparison, adults which are engaged in self-maintenance activities appear to conserve energy by pursuing mainly those arthropods that can be captured with less effort.

Adults with dependent young also increase their exploitation of arthropods in the herb layer. There is a suggestion that by shifting to the herb layer, these adults are able to capture larger prey, e.g., grasshoppers, than would be possible within the foliage zone. Since the availability of suitable hunting perches is low in the herb layer, it is often necessary for the gnatcatchers to engage in long hovering flights or to flutter constantly while searching from a pliant or upright perch while foraging at this level. Thus it would appear that exploitation of the herb layer requires a greater expenditure of energy than does foraging in the foliage zone of trees.

These tactical responses of adults with young are expressed by exploiting the more peripheral portions of the foraging niche. The magnitude of this niche broadening can be estimated by a comparison of diversity indices for various components of the exploitation pattern. The index, $H = -\sum p_i \log_e p_i$, where p_i is the proportion of all behaviors represented by behavior i , was calculated for this purpose (Table 14). The properties of this widely used index have been discussed by MacArthur and MacArthur (1961), MacArthur (1964), Whittaker (1965), and Pielou (1966). Both R. T. Paine (*in litt.*) and L. C. Cole (pers. comm.) have pointed out that to compare H values validly, one must assume that the situation is thoroughly sampled and that further effort will not change the p_i s. I found that trial calculations for 50 consecutive maneuvers give fairly consistent results within each sampling category (the difference between extreme H values from 5 such samples was 0.152). This implies that any bias due to sample size is negligible in Table 14 where the H values are calculated for even longer runs of 125 consecutive maneuvers.

Within each sampling period, the adults with young exhibited a greater foraging diversity, both with respect to the substrates where prey was obtained and in the maneuvers employed in capturing prey, than those engaged in self-maintenance activities (Table 14). In each case, the increased diversity was accomplished by foraging outside of the gnatcatcher "adap-

tive mode": only by performing maneuvers, made strenuous by the lack of primary adaptations, were the adults able to exploit a wider spectrum of resources. Gnatcatchers engaged in self-maintenance foraging employed the same repertoire as those with young, but performed the strenuous maneuvers infrequently. Thus the broadening of the niche during the period of the brood's dependency was produced by a flattening of the exploitation curves (Fig. 1) and not by any important expansion in the limits of the niche.

This response of increasing the foraging diversity to meet the increased energy requirements of the brood may be a common adaptation among birds. Evans (1964) found that nestlings of three sparrow species were fed a more diverse array of prey life-forms from a wider variety of microhabitats than were eaten by the adults. Similarly Kuroda (1963) demonstrated that the foraging behavior of adult Grey Starlings (*Sturnus cineraceus*) became less selective when the normal brood size was experimentally increased.

Orians (1961), Verbeek (1964), and Verner (1965) have shown how the amount of time budgeted by a species to various activities is related to variations in the energy requirements. The changes in the foraging behavior of gnatcatchers with dependent young, however, demonstrate that several additional factors are involved in the response to increasing energy requirements. As a result of the increase in foraging intensity, the selection of larger prey, and the more frequent performance of strenuous maneuvers, the expenditure and capture of energy are very different for a unit of foraging time spent by a bird which is feeding young and one which is engaged solely in self-maintenance.

ORGANIZATION OF THE EXPLOITATION PATTERN

The food supply of the gnatcatcher has been shown to vary widely in time and space. To exploit this resource efficiently, the gnatcatcher's foraging behavior must be plastic enough to respond to variations in the food supply while remaining specialized enough to avoid intense interspecific competition. Put another way, the species must be sufficiently specialized as to compensate for what has been termed the "jack of all trades" principle (MacArthur and MacArthur, 1961) and yet not so specialized that efficiency and survival are reduced in seeking out highly restricted conditions in a diverse and changing environment. The following discussion considers the manner in which the gnatcatcher's exploitation pattern is adapted to meet these conflicting requirements. The terminology and conceptual scheme employed in this discussion have already been considered in the introduction to this paper.

Each dimension of the gnatcatcher's niche is bounded by indistinct limits which are apparently imposed by the birds' inability to exploit the peripheral situations efficiently. Morphological adaptations, considered here in their broadest sense as including

modifications of the external features, physiological abilities, and configurations of "neural pathways," are the factors that most likely set these boundaries. Within each set of limits the gnatcatchers are able to alter their behavior in response to changes in the environment. This is accomplished by varying the frequency with which different "adaptive mode" activities are performed. Thus the gnatcatchers changed from chaparral to oak woodland habitats during the late spring (Fig. 6), from twig to foliage insects following bud-burst (Fig. 10), from small arthropods in the winter to larger prey in the summer (Figs. 12 and 14), and from mirids and lepidopterous larvae in March-May to membracids and cicadellids during June-August (Table 11).

The niche dimensions of the birds studied by Crowell (1962) seem to be limited in the same manner as those of the gnatcatcher. Crowell contrasted the foraging behavior of populations living on the mainland with populations of the same species living under conditions of reduced interspecific competition on Bermuda. Morphological divergence between the respective mainland and Bermudian populations was only slight. The exploitation curves of the birds on Bermuda had different modes, but these always fell within the range of activities observed on the mainland. The results suggest that the niches of these species are circumscribed by limits that are conservative and morphologically determined.

The exploitation pattern of a population can be formed by the interplay of two adaptive strategies: either the population can be morphologically variable, so that each individual is restricted to a portion of the total niche, or all of the individuals may possess a similar range of capabilities (cf. Klopfer, 1962; Levins, 1963; and Van Valen, 1965). In most cases, exploitation patterns are probably based upon a mixture of these two extremes. The difference in the foraging behavior of sexually dimorphic birds reviewed by Selander (1966) are representative of a strategy stressing morphological variation. The gnatcatcher seems to emphasize the alternative strategy. Different individuals performed the same maneuvers and obtained food from the same substrates with similar frequencies (Table 9). The observed differences probably reflect the small sample size and the opportunistic response of individuals to the local conditions on their territories. Furthermore, several individuals (not cited in Table 9) from both the winter and breeding grounds were observed to perform the entire foraging repertoire. The limits of the exploitation pattern therefore appear to be similar for all members of a gnatcatcher population.

Gnatcatchers are capable of performing all of the basic foraging maneuvers employed by other members of the foliage-gleaning guild except using the foot to hold prey. Furthermore, they capture prey from all of the major arthropod taxa, and over a similar size range to that exploited by the other insectivorous birds. The gnatcatchers, however, engage in some of these activities (e.g., climbing trunks,

TABLE 14. Indices of foraging diversity (H) of the Blue-gray Gnatcatcher. H is Shannon's measure for diversity (see the text for a description of its calculation and properties). The values for H are based on samples of 125 consecutive capture maneuvers in each category. The substrates where prey was obtained are classified as tree foliage, bark, herbs, and air; the capture maneuvers as gleans, hovers, hawks, and tumbles.

	Diversity of Substrates		Diversity of Maneuvers	
	Self-maintenance	Feeding Young	Self-maintenance	Feeding Young
May 10-June 16.....	0.542	1.006	0.804	1.133
June 24-July 27.....	0.729	1.142	0.923	1.214

hanging beneath perches, or consuming large caterpillars) only on rare occasions, and then with obvious difficulty. The exploitation patterns of other foliage-gleaning birds are expressed in a similar fashion. Thus the niche limits of the guild members appear to overlap broadly, with the major separation between species being achieved through differences in their efficiency in performing the basic maneuvers common to all.

Hinde (1958) has proposed that birds learn to exploit the prey which they can obtain most efficiently. This conclusion has been substantiated in laboratory preference experiments on finches (Kear, 1962). Further support for this hypothesis is found in Hess's (1964) demonstration that the normal pecking preference of newly-hatched chicks can be altered by providing food rewards for different stimulus objects. These results suggest one means by which species can avoid intense interspecific competition while exploiting niches which overlap. When a particular type of prey becomes superabundant, several species that are not highly adapted for its capture can exploit this resource with relative ease. As the food supplies dwindle, the exploitation patterns can contract, with each species concentrating on those situations for which they are best adapted. Thus the exploitation curves of guild members would be expected to alternate between overlap and discreteness in response to seasonal changes in prey availability. Such pulsations in accordance with changes in the food supply have been observed in the feeding behavior of birds (Lack, 1946; Gibb, 1954) and fish (Nilsson, 1960; Lindstrom and Nilsson, 1962) which have similar exploitation patterns.

The members of the foliage-gleaning guild each exhibited a characteristic mixture of preferences in foraging beat, feeding maneuvers, and diet that may be shifted in response to changes in food availability. In this manner, the guild members are apparently able to exploit niches sufficiently distinct to permit co-existence, and yet broad enough to meet the demands of a changing environment. Thus the niche relations in the foliage-gleaning guild fit well with the predictions of other authors; the niche limits are broad, and therefore overlapping, because the environment is highly variable (Klopfer, 1962); and the species are separated by "fine-grained" differences because their prey is small relative to the size of the consumer (MacArthur and Levins, 1964).

Since structural modifications are correlated with these differences in foraging preference, it would appear that a distinctive morphology is an important prerequisite for guild membership. The prevalence of character displacement in closely related sympatric species (Brown and Wilson, 1956; Schoener, 1965) supports this conclusion. The relationship between character displacement and the degree of niche overlap has been considered by Hutchinson (1959), Klopfer and MacArthur (1961) and Klopfer (1962). Their conclusions are based entirely upon differences in one dimension of the trophic apparatus. The results of this investigation, however, demonstrate that consideration of only one morphological feature can yield ambiguous results; two guild members may compensate for a low character difference in one feature by divergence in another (Fig. 18).

The various specializations that limit the gnatcatcher's exploitation pattern are integrated in such a manner that the bird will encounter a large number of foraging situations as it moves through the habitat. Such an arrangement results in what has been termed a "convex" exploitation pattern (MacArthur and MacArthur, 1961). The gnatcatcher's foraging beat is restricted by its inability to use perches that are either pliant or of large diameter. As a result, the birds usually forage in the foliage zone of trees and shrubs where suitable perches abound. A variety of plant species within a given habitat provides perches of suitable size and density for foraging gnatcatchers. The birds are thereby able to enter the foliage zone of most of the plants they encounter while traveling at any level above the herb stratum. Gnatcatchers tend to linger in certain species of trees at different seasons, and in sunlit banks of foliage when the sun is low on the horizon. It seems likely that this results from the bird's "velocity" being reduced by favorable foraging conditions.

The foraging tactics seem to be closely related to the gnatcatcher's relative restriction to the foliage zone. The repertoire is rich in aerial and rushing maneuvers that allow them to capture the small, active insects common amidst the foliage.

The gnatcatcher's diet is limited mainly by the sizes of prey which can be captured efficiently: the energy return from extremely small prey is too low to warrant the effort, and large prey are either too difficult to capture or cannot be swallowed. Prey with effective concealment and escape reactions, and those which

are distasteful, are not found in the diet. This still leaves a wide variety of arthropod species whose characteristics are acceptable to gnatcatchers. By having the feeding specializations related to the size and behavioral attributes of the prey, rather than its taxonomic relationships, the gnatcatcher is probably more likely to encounter suitable food in different habitats and at different seasons.

The exploitation patterns of other species of the foliage-gleaning guild are limited in other ways. The Plain Titmouse, for instance, is better able to use a much greater variety of hunting perches. This permits the tits to respond to changes in the dispersion of their food supply by shifting between the foliage zone, the subcanopy, and the ground. On the other hand, the titmice appear to be more highly restricted to the oak woodland habitats at the Hastings Reservation. Similarly, the foraging maneuvers that can be performed easily are less diverse, but the tits are able to exploit plant foods as well as arthropods. Restriction in one dimension of the niche seems to be compensated by increased breadth in another. As a result of such adjustments, it is impossible to judge whether one species is more broadly adapted than another without considering the complete exploitation pattern.

The general organization of the exploitation patterns among the birds of the foliage-gleaning guild is basically similar, although the specific features of the pattern are integrated in different ways. All are able to respond opportunistically to changes in the environment within broad limits, apparently determined by morphological adaptations. Furthermore, the limiting specializations are primarily related to structural features of the habitat and to behavioral and size characteristics of the prey. In this way the birds are less influenced by the spatial and temporal changes that have been observed in the availability of particular prey taxa or the abundance of arthropods associated with particular plant species. Thus the exploitation patterns of foliage-gleaning birds are so organized that each species can remain optimally adapted to the greatest possible variety of opportunities.

SUMMARY

The food supply and habitat of the Blue-gray Gnatcatcher, a small insectivorous bird, vary widely in space and time. This paper considers the manner in which the gnatcatcher's niche exploitation pattern is organized to achieve optimal adaptation to the conflicting demands of a changing environment.

The behavior of the gnatcatcher was studied at the Hastings Reservation in the Central Coast Ranges of California during the breeding season, and at three localities in the deserts of Arizona during the winter. More than 1200 hours were spent in actual observation during three different field seasons. Field observation techniques were developed to quantify changes in the gnatcatcher's foraging beat, feeding tactics, food supply, and diet. Similar data were gathered

on other species of sympatric insectivorous birds. In addition, the pattern of habitat occupancy, nest site requirements, and general natural history of the gnatcatcher were studied.

In the early spring gnatcatcher territories are established in chaparral and live oak woodland, where foliage arthropods are abundant. Deciduous oak woodland is not settled until later when the insects living there have begun to increase. Habitat selection by the gnatcatcher can be only partially "released" by structural characteristics of the vegetation: habitats that differ greatly in physiognomy are occupied while some vegetation-types having a similar structure are left vacant. Thus it appears that the abundance of such critical requisites as food and nest sites is directly involved in the habitat selection process.

Gnatcatchers are able to shift their territory boundaries in accordance with seasonal changes in the dispersion of optimal food resources among the various subhabitats. The constriction of the territory during the nest construction and nestling stages of the reproductive cycle leaves vacant areas that may then be colonized by other pairs. The fluid organization of territories is promoted by a lack of synchrony in the nesting cycle of adjacent pairs. As a result, different broods are able to share certain areas well suited for young fledglings by using them at different times.

At their preferred foraging stations, gnatcatchers select the larger and more vulnerable prey. The diet and foraging beat shift in accordance with seasonal changes in the availability of prey.

The energy requirements of the dependent young exert heavy demands upon the foraging abilities of the adults. Pairs fed broods of older nestlings and young fledglings as often as 43 times per hour. Compared with birds engaged in self-maintenance feeding, the food gathered by adults with young was increased by their: (i) devoting a greater proportion of time to foraging, (ii) increasing the foraging intensity, i.e., the frequency of attack maneuvers per unit of foraging time, (iii) increasing the diversity of the foraging tactics and foraging beat, and (iv) capturing larger prey. In meeting the demands of the brood, the adults foraged outside their normal "adaptive mode," a response that probably requires a large expenditure of maintenance energy. The bearing of this result upon the interpretation of "time and energy budgets" is discussed. It appears that the abundance of food is an especially critical requisite during the brief period when the brood is completely dependent upon the adults for sustenance.

A new unit, the ecological "guild," is proposed for groups of species that exploit the same class of environmental resources in a similar way. The utility of the guild concept is discussed. Members of the foliage-gleaning guild, to which the gnatcatcher belongs, overlap in their foraging repertoires, foraging beats, and diets. It appears that niche segregation within the guild is maintained by differences in the efficiency with which portions of a common range of

situations can be exploited. These different efficiencies are reinforced by morphological differences.

The exploitation pattern of the gnatcatcher is expressed opportunistically within limits that are largely set by morphology. The limiting specializations are related to structural features of the habitat and to behavioral and size characteristics of the prey; these are factors that tend to change less in space and time than do other features of the environment.

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APPENDIX

The Diet of the Blue-gray Gnatcatcher

The following is a list of all the food items, each identified to the family level, which were recovered from the stomachs of gnateatchers. The numbers in parentheses refer to the total number of individuals, based upon both intact specimens and fragments, of a particular family in the diet.

Orthoptera

Gryllidae (1)

Corrodentia

Myopsocidae (3)

Thysanoptera

Pholeothripidae (3)

Hemiptera

Homoptera

Membracidae (138)

Cercopidae (55)

Cicadellidae (85)

Areopodidae (1)

Fulgoridae (11)

Psyllidae (1)

Chermidae (5)

Heteroptera

Anthocoridae (1)

Miridae (64)

Reduviidae (4)

Corizidae (7)

Cydnidae (2)

Pentatomidae (1)

Neuroptera

Raphidiidae (1)

Chrysopidae (5)

Lepidoptera

Arctiidae (1)

Phalaenidae (19)

Geometridae (12)

Pyralidae (3)

Tortricidae (1)

Diptera

Tipulidae (5)

Ceratopogonidae (2)

Mycetophilidae (5)

Sciariidae (1)

Aeroceridae (1)

Phoridae (1)

Trypetidae (1)

Geomyzidae (1)

Agromyzidae (1)

Drosophilidae (1)

Ephydriidae (1)

Chloropidae (1)

Tachinidae (7)

Calliphoridae (1)

Anthomyiidae (5)

Hymenoptera	Ostomidae (2)
Argidae (2)	Elateridae (1)
Cephidae (1)	Coccinellidae (4)
Ichneumonidae (15)	Mordellidae (6)
Braconidae (2)	Pythidae (5)
Mymaridae (1)	Anobiidae (24)
Eulophidae (1)	Bostrichidae (1)
Thysanidae (1)	Chrysomelidae (84)
Encyrtidae (5)	Mylabridae (121)
Torymidae (1)	Curculionidae (83)
Pteromalidae (17)	Scolytidae (1)
Cynipidae (7)	
Chrysitidae (1)	Araneae
Formicidae (38)	Linyphiidae (3)
Sphecidae (11)	Lycosidae (33)
Coleoptera	Salticidae (4)
Histeridae (1)	
Staphylinidae (10)	Acarina
Dermestidae (1)	Tetranychidae (3)

*Plant material in three stomachs