BEHAVIORAL ADAPTATIONS RELATED TO WATER RETENTION IN THE BLACK-TAILED GNATCATCHER (*POLIOPTILA MELANURA*)

by

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ABSTRACT

During the summer of 1966, a field study was conducted in an attempt to find evidence of behavioral adaptations to the desert environment in Black-tailed Gnatcatchers (Polioptila melanura). Many phases of its life history were studied. Behavioral modifications were found to be most pronounced during periods of summer heat, and generally involved avoidance of direct sunlight and a reduction of activity during hot periods. Foraging was maintained throughout the day in the summer, though with reduced intensity at high ambient temperatures. Maintenance of foraging throughout the day in the summer may be necessary to replace water lost in evaporative cooling and normal respiration. This species apparently does not utilize free water; metabolic water and the body fluids of arthropods are the primary sources of water.

INTRODUCTION

A bird that lives in a hot, desert environment is faced with several unique problems; the most obvious is the scarcity of free water. A species can combat this problem by limiting its range in the desert to areas where free water is available, by obtaining water from its food, or by living on metabolic water. Excess water loss may be curtailed by hyperthermic (heat storing) mechanisms, reduction of activity during hot periods, and confining activities to the coolest part of the environment.

Several species appear to have the ability to live on oxidative or metabolic water for many days in captivity. The Zebra Finch (*Taeniopygia castanotis*), the Budgerygah (*Melopsittacus undulatus*), and some races of the Savannah Sparrow (*Passerculus sandwichensis beldingi* and *P. s. rostratus*) are able to survive on a diet of dry seeds under laboratory conditions. It is unlikely that any small bird under natural conditions can survive solely on metabolic water (Bartholomew and Cade, 1963).

Most birds undoubtedly obtain their water needs by drinking, or consuming foods high in preformed water, or both. Those species that do not visit water sources daily during the hottest parts of the year are primarily insectivorous, or they feed on succulent vegetation, or both. Many species that do eat succulent plants or insects will also drink free water if it is available (e.g., Mockingbirds, Curve-billed Thrashers, Ash-throated Flycatchers, and House Finches).

The Black-throated Sparrow (*Amphispiza bilineata*) shows a seasonal dependence on surface water (Smyth and Bartholomew, 1966). During the dry season Black-throated Sparrows drink water frequently even at cool ambient temperatures. During the dry season insects and succulent plants are not so readily available and Black-throated Sparrows feed entirely on seeds. Whenever insects and green plants are available, Black-throated Sparrows do not visit open water sources.

In addition to obtaining adequate water, desert birds are faced with the problem of keeping their body temperature within safe limits. Birds in general have slightly higher body temperatures than do mammals. Thus birds may have some advantage over mammals as diurnal desert inhabitants in their favored position for heat transfer with a warm environment.

No desert birds are known to have higher body temperatures than nondesert birds, nor are they known to have greater tolerance to elevated body temperatures. If desert birds were able to tolerate higher body temperatures than nondesert ones, they could reach a more favorable position for heat transfer with the environment. The latter would be facilitated by a greater ability to store heat and cool the body without losing water. This ability has not been demonstrated and apparently birds cannot tolerate body temperatures over 46 C for any length of time (Dawson and Schmidt-Nielsen, 1964).

The size of an organism makes a great deal of difference in the rate at which it gains or loses heat. At an ambient temperature of 45 C, for example, a small warbler-sized bird would have to initiate cooling mechanisms before a quail sized bird. The same reasoning holds for all heat absorbing objects (Schmidt-Nielsen, 1964); accordingly, pebbles heat up much faster than large boulders. This phenomenon is due to the great disparity in surface area to volume ratio, with the small object or animal having a much greater surface area in proportion to its volume. The surface area in such cases is the important factor since heat transfer is a surface phenomenon. The over all situation in living organisms is somewhat complicated by the fact that a portion of the heat gained arises via metabolic processes. Thus, a bird living in a hot climate must contend with two sources of heat; that produced metabolically and that present in the environment.

With these ideas in mind, I decided the Black-tailed Gnatcatcher (Polioptila melanura) would be a suitable species to examine for evidence of behavioral adaptations to the desert environment. The species is a resident desert dweller and is typically found in washes cutting through stands of creosotebush. It is seldom found in riparian or irrigated areas (Phillips, Marshall, Monson, 1964), and its range in the United States is restricted to the Lower Sonoran Life-zone (Fig. 1). The Black-tailed Gnatcatcher is primarily insectivorous but also occasionally eats vegetable matter (Bent, 1949). Not only is the Black-tailed Gnatcatcher a desert inhabitant, it is also one of our smallest passerines, and has an average weight of about five grams. In spite of its small size and choice of habitat, the Black-tailed Gnatcatcher seldom, if ever, takes free water (Gubanich, 1966). Insects upon which this species feeds must provide water.

In view of the Black-tailed Gnatcatcher's habitat preference and size, it is obviously faced with a serious problem of maintaining a physiologically adequate water balance. Intimately related to this problem is that of thermoregulation. Assuming that Black-tailed Gnatcatchers fit the general avian pattern in lacking unique physiological adaptations to the desert environment (Schmidt-Nielsen, 1964), I thought that the key to this species' ability to survive in the desert may revolve around its behavioral modifications. As a result of a summer's work in the field and numerous trips during the cool months, I will present evidence that the Black-tailed Gnatcatcher relies on effective utilization of microhabitats to survive in the desert.

Figure 1. The geographic distribution of the Black-tailed Gnatcatcher in the United States and Mexico.

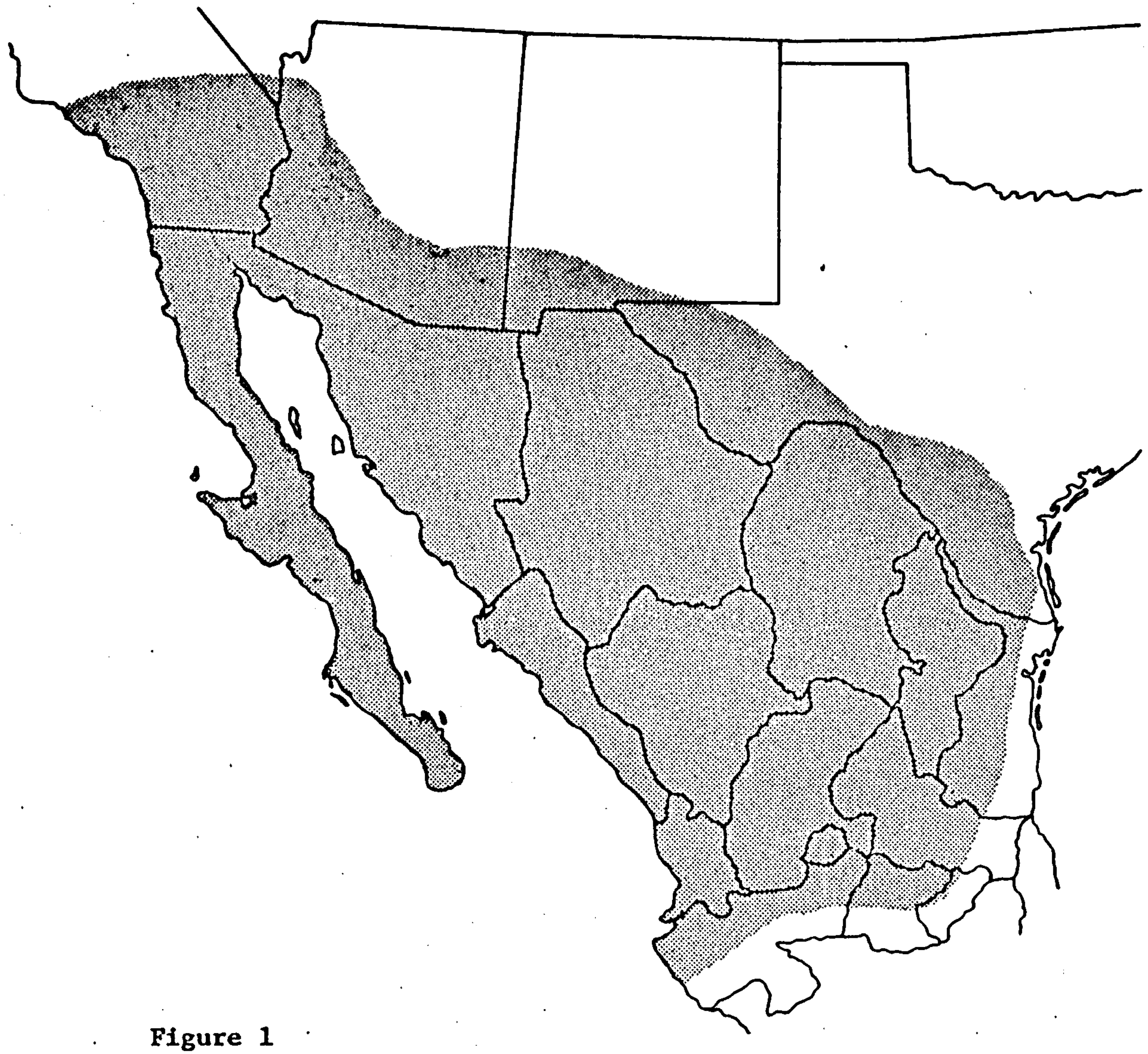


Figure 1

THE STUDY AREA

Most of my research was done in an area seven miles south and seven miles east of Tucson, Arizona (0.8 miles north of the U. S. Highway 80, Wilmot Road Junction). The elevation in the study area is approximately 2750 feet above sea level.

Topographically, the area is quite flat. It is cut by Wilmot Road in a north-south direction, and two prominent washes cut through the area in an east-west direction. The larger of the two washes (a man-made drainage ditch) drains to the west from Wilmot Road and the smaller runs west toward Wilmot Road. A large patch of bare ground separates the small wash from the rest of the study area. The small wash (5 to 10 feet across and 3 to 4 feet deep) supports a luxuriant stand of mixed hackberry and mesquite.

The flora of the area is typical of the Lower Sonoran Life-zone. The dominant plants include mesquite (*Prosopis juliflora*), desert hackberry (*Celtus pallida*), catclaw (*Acacia greggi*) creosote-bush (*Larrea divaricata*), paloverde (*Cercidium sp.*), and several types of cacti. The most common cacti are the chollas and prickley pears (*Opuntia sp.*); barrel cacti (*Echinocactus sp.*) are also present.

The northern edge of the study area is bounded by a creosote-bush flat that extends north to Davis-Monthan Air Force Base, a short distance away. The southern edge of the study area is a mosaic of creosotebush, mesquite and cholla that extends from the study area across U. S. 80. The east and west boundaries of the study area were set at approximately 200 yards on either side of Wilmot Road. The entire area comprises about 150 acres.

In addition to the area described above, I also spent some time in the foothills of the Santa Catalina Mountains north of Tucson. In particular, I worked in lower Pima Canyon, lower Sabino Canyon, and on the Bajada in the vicinity of North Campbell Avenue. I have also spent some time west of Tucson in the Tucson Mountain foothills and in the Sahuaro National Monument northwest of Tucson.

METHODS AND MATERIALS

This thesis is a report based on approximately 500 hours in the field. Of this 500 hours, 254 hours were spent in my study area actually watching individual Black-tailed Gnatcatchers or pairs of gnatcatchers (hereafter in this thesis, reference to gnatcatchers implies Black-tailed Gnatcatchers). In addition, I used about 150 hours looking for and observing Black-tailed Gnatcatchers in other areas. I also spent about 30 hours trying to mist-net gnatcatchers and another 40 to 50 hours watching a waterhole near the study area. Much unrecorded time was also spent searching for new nests.

Mist nets were used to capture gnatcatchers and at least one member of each pair in my study area was banded with color celluloid bands. Fish and Wildlife Service bands were also affixed to the color banded birds. Banding the gnatcatchers was one of my most perplexing problems. The birds easily went through nets of one and one-half inch mesh and frequently escaped from nets of one inch mesh. The gnatcatchers also became very net wary after several attempts to capture them. Once the birds were banded they tended to be easier to catch again, as their bands frequently fouled the net, but the problem of net awareness made recaptures difficult.

As data were collected in the field they were entered directly into my field notebook or recorded on special data sheets. Sun-shade foraging data were obtained by using a wrist watch to record total observation time and a stopwatch to record the amount of time the gnatcatchers spent foraging in bright sunlight. I did not consider a bird to be in the sun unless its entire body (tail excluded) was exposed to direct sunlight. At the termination of a reading, both total observed time and the total time of sun exposure were recorded on the data sheets. Normally I did not use optical aids while taking sun-shade foraging data. It was easy to get close enough to the gnatcatchers to eliminate the need for binoculars. Further, it was virtually impossible to check the wrist watch, start or stop the stopwatch and record data while looking through binoculars. With binoculars, I frequently lost sight of the birds while trying to carry out these operations simultaneously.

Collection of information on nest building activities, incubation periods, and nestling feedings was aided by a 20 power spotting scope. Most of these data were gathered from positions within 20 feet of a nest. The spotting scope was also used during waterhole observations, and in an attempt to gather foraging efficiency data. The spotting scope proved to be too cumbersome to be of much value in the latter case.

I recorded temperatures about three feet from the ground at hourly intervals from a Centigrade mercury thermometer (range 0-50 C), accurate to 0.2 degrees. Sun temperature recordings were made from the thermometer hung on a dead twig in the direct sunlight, shade temperatures were obtained with the thermometer hanging in the deep shade of a tree or bush. All readings were made after the thermometer had been in place for one minute.

Relative humidity data were obtained from the Davis-Monthan Air Force Base weather station. This weather station is 3.6 miles NNW of the study area but I believe there may have been a moderate disparity between humidity at Davis-Monthan and humidity in the study area. This disparity may have been especially important after the summer rainy season started because of the heavy plant growth and ground cover in the study area. This cover would tend to allow water to evaporate more slowly, thereby keeping the humidity high for a longer period. Also, there was probably a greater influence on humidity via plant transpiration in the study area.

NESTING ADAPTATIONS

If a species survives and exploits a given environment, it must be adapted in some manner to that environment. A basic provision of species survival is reproduction. Thus, if a species is to survive and reproduce in a given environment, one might expect that species to show unique physiological and/or behavioral adaptations that have survival value in that environment.

The Black-tailed Gnatcatcher would be expected to show adaptations to its environment regarding reproduction. It has been suggested that the domed nest of some African Weaver birds (Ploceidae) has evolved to protect nestlings and adult birds from intense solar radiation and inclement weather (Collias and Collias, 1964). This may also be the case in certain North American desert species such as the Verdin (*Auriparus flaviceps*) and the Cactus Wren (*Campylorhynchus brunneicapillus*). The Black-tailed Gnatcatcher does not build a domed nest but it does build its nest in a shaded site. Each of the 11 completed gnatcatcher nests I observed during my study was placed in a tree or shrub in such a position that shade prevented exposure of the inner nest lining to direct sunlight. Three other nests that were abandoned before completion were exposed to the afternoon sun.

All 11 nests in which eggs were laid were built in the fork of two or more branches, and were situated under a canopy of small leaf-bearing twigs or under a large branch. Egg-containing nests were also well shielded on all sides. One nest in the Sahuaro National Monument northwest of Tucson was built in the center of a clump of mistletoe at the top of a paloverde tree. This latter nest was well shaded and camouflaged.

Not only does the Black-tailed Gnatcatcher tend to build its nest in well shaded positions, it also tends to utilize species of trees and shrubs that afford the greatest shade and camouflage. Of the 14 nests I observed, six were in desert hackberry (Celtus pallida), six were in mesquite (Prosopus juliflora), and two were in paloverde (Cercidium sp.). The mesquite and desert hackberry probably provide more shade than paloverde because of their comparatively heavy growth of larger leaves. The paloverde is a spinescent tree with much reduced leaves, which may not give total day long shade to nests. Only two of the nests I observed were built in paloverde, and one of these was deep in a clump of mistletoe. The second nest observed in a paloverde was destroyed shortly after the first egg was laid.

Nest construction took two to four days in four nests that I found on the first day of building. The nest of the Black-tailed Gnatcatcher is a very neat compact structure, about 1.25 inches to 2.0 inches in height. The inside diameter of the nest is 1.0 to 1.5 inches, the outside diameter 2.0 to 2.25 inches, and the depth ranges from 1.0 to 1.5 inches. All nests that I found were grayish in color and made of fine plant fibers and grasses, bits of bark, cattle or horse hair, feathers and spider webs. These materials were neatly interwoven and small twigs were incorporated into the outer portion of each nest and helped to anchor it more securely. None of the nests I found were damaged by the heavy winds and rain of summer thunderstorms.

The adult birds share the nest building responsibilities. During three hours of nest building on the morning of 14 May the male of pair #1 made 37 trips to the nest. But he spent only 488 seconds actually incorporating materials into the nest. During the same period, the female of pair #1 made 29 trips but spent 1210 seconds incorporating materials into the nest. The female incorporated all of the materials which she collected as well as some of the construction materials brought to the nest by the male.

On the morning of 16 May, pair #2 began construction of their second nest. This nest was constructed using materials from their first nest which was abandoned before completion. During a two hour period the male made 62 trips to the new nest and spent 1326 seconds incorporating materials into the nest. The female, during the same period, made 35 trips and spent 1089 seconds incorporating materials into the nest.

By using the materials from an earlier nest, pair #2 undoubtedly saved time and energy. In 97 trips in two hours this pair constructed a larger portion of their nest than did pair #1 in 66 trips over a three hour period. This reuse of nesting materials may be of decided advantage to birds living under stress conditions, though in these examples the mornings were clear and cool (20 C to 26 C). On the two occasions that I saw birds utilizing old nests as a source of materials, the new nests were within 100 feet of the old nests. If the birds had to transport materials a greater distance, the energy saved may not be significant. Pair #1 built three nests, though not in sequence, that were within 100 feet of each other without utilizing the old nests as a source of construction materials.

Nest building activities appear to be more vigorous in the early morning hours. The two examples just cited occurred between 0630 and 1000. I observed the construction of two other nests during the afternoon and the pace was much slower (Table 1). The important factor in this case, however, is probably the temperature rather than the time of day.

The 14 nests observed in this study ranged from 2 to 14 feet above the ground. In areas of relatively low vegetation, the nests were closer to the ground; in areas of higher vegetation, nests were higher. Thus nest height appeared to be related to the availability of tall trees and shrubs. It is possible that a nest situated close to the ground over bare soil would be exposed to intense heat re-radiating from the soil, I have at times measured ground exposed temperatures in excess of 55 C. It is also possible that a nest built too close to the ground would be more apt to be lost to predators than one built higher.

The Black-tailed Gnatcatchers in my study area showed a tendency to build their nests toward the periphery of shrubs or trees as opposed to the centers. A number of factors could be responsible for this tendency: suitable anchorage, shade availability, concealment,

Table 1. A comparison of the number of trips made in search of nesting materials to time of day and sun exposed temperature. Time at nest indicates the total number of seconds spent at the nest during each series of trips.

Pair No. and Sex	Nest No.	Time of Day	Temperature C	No. of Trips	Time at Nest
1 Male	1	0630	20-26	37	488
		to			
1 Female	1	0930	"	29	1210
2 Male	2	0730	22-24	62	1326
		to			
2 Female	2	0930	"	35	1089
1 Male	2	1530	38	9	181
		to			
1 Female	2	1700	"	7	210
1 Male	4	1430	41-39	10	101
		to			
1 Female	4	1630	"	13	84

and ease of entrance and exit are a few possibilities. I suggest that nests in such peripheral situations may be in better positions to benefit from the shade afforded by overhanging twigs and branches. Also, peripherally placed nests may benefit more from cooling breezes than nests placed deep in a dense hackberry, for example. Table 2 summarizes nesting in this study relative to the points just discussed.

Table 2. A summary of nesting in Black-tailed Gnatcatchers observed in this study relative to nest position, distance from ground, distance from preceeding nests, and height of plant utilized (nc = not completed).

Pair No.	Nest No.	Position	Dist. from Ground in Feet	Ht. of Plant in Feet	Dist. from Prec. Nest in Yards	Fate of Nest
1	1	Top	6	7	-	eggs
"	2	Periph.	5.5	10	100	eggs
"	3	Top	10	12	60	eggs
"	4	Top	12	13	15	no eggs ?
"	5	Top	6	6	30	abandoned
"	6	Periph.	9	15	110	eggs
2	1	Periph.	3	7	-	nc
"	2	Periph.	2	4	20	eggs
"	3	Top	5	6	30	eggs
"	4	Periph.	3	8	60	eggs
3	1	Periph.	6	9	-	eggs
4	1	Periph.	2	5	-	eggs
"	2	Periph.	4	8	50	nc
5	1	Top	14	16	-	eggs

DURATION OF THE PAIR BOND

On 3 March, 1966, Robert D. Ohmart and I banded a female Black-tailed Gnatcatcher. On subsequent trips to the study area I was able to locate this banded bird and her mate. Although I was never able to band the male, I think that I was dealing with the same male throughout the study. Throughout the spring months I never saw any stray gnatcatchers in the study area. Had this female taken another mate prior to breeding, I suspect they would have moved to another area, or I would have had more than one breeding pair on this 50 acre portion of the study area.

On 8 July, 1966, I banded both members of pair #2. This pair was then incubating eggs in their fourth nest. After this nest was abandoned on 14 July, no attempt was made to start a fifth nest. During the remainder of the summer I was usually able to locate this pair along a small wash in the southeast section of the study area. Following 22 September, 1966, I was not able to locate this pair again.

Bent (1949) states that Black-tailed Gnatcatchers do not return to previously used nesting areas. The three pairs that bred in my study area during the summer of 1966 did eventually leave the area following a period of wandering. Following cessation of nesting activities all three pairs wandered about the study area and eventually disappeared between 1 August (pair #3) and 23 December (female of pair #1). At present (April 1967), there are at least two pairs of gnatcatchers in the study area but none of the birds is an individual that I banded in 1966.

The pair bond in this species may be of longer duration than the nesting season. All of the gnatcatchers that bred in my study area were in pairs for some time before and after nesting. The idea of a long pair bond in Black-tailed Gnatcatchers is also supported by a common field experience with this species; gnatcatchers are almost always seen in pairs. I would estimate that 80 percent or more of the gnatcatchers I have seen in the field occurred in pairs. I have seen solitary Black-tailed Gnatcatchers or more than two only a few times. Most observations of single gnatcatchers I have made occurred during the non-breeding season (September through March). Some of these observations may have been of Blue-gray Gnatcatchers (Poliopoptila caerula), which are present in the Lower Sonoran Life-zone during these months. On one occasion I saw a family group of Black-tailed Gnatcatchers in which two adult birds were feeding three young.

I doubt that the long pair bond and the pre- and post-nuptial wanderings are advantageous in preserving water or regulating body temperature. I feel that the wandering exhibited by the birds in my study area simply reflect the absence of a breeding stimulus. Maintenance of a yearlong pair bond would tend to eliminate searching for and courting a mate in the spring, but weather conditions are not severe enough in the spring to warrant placing any thermoregulatory or water retentive implications on such activities.

TERRITORIALITY AND INTERSPECIFIC BEHAVIOR

During the nest building period male Black-tailed Gnatcatchers were frequently noted calling from exposed branches within 50 yards of the nest tree or shrub. The males would fly from perch to perch, calling three to six times from each perch. Since I never observed such behavior on the part of the females, I think such displays by the males serve a territorial function.

Territorial announcement by male gnatcatchers appears to be influenced by the prevailing weather conditions and the time of day. I have recorded 13 instances of this type behavior between 0630 and 1000 hours, but only one on a clear, hot afternoon. Twice I recorded such a display on cloudy afternoons.

After the nests were completed and eggs were laid, territorial calling ceased. I did not see any attempts by either member of a pair to defend the boundaries defined by male perch calling. Black-tailed Gnatcatchers observed in this study defended only the nest tree or shrub and those trees and shrubs immediately adjacent to it.

Both male and female Black-tailed Gnatcatchers attempted to exclude most larger birds from the vicinity of the nest. Curve-billed Thrashers (*Toxostoma curvirostra*), Brown Towhees (*Pipilo fuscus*), and Cactus Wrens (*Campylorhynchus brunneicapillus*), for example, were not tolerated in the nest tree or shrub or those adjacent to it. Smaller species such as Verdins (*Auriparus flaviceps*) and

Lucy's Warblers (<u>Vermivora luciae</u>) were allowed to approach within eight to ten feet of the nest before being driven off. Most of the larger birds tended to ignore the vigorous dive bombing attacks of the gnatcatchers, but the smaller intruders moved quickly away.

Only one attack by a gnatcatcher resulted in actual contact with the intruding individual. On this occasion a Mockingbird (<u>Mimus polyglottos</u>) flew into the nest tree and landed within a few inches of the gnatcatcher's nest. The male gnatcatcher immediately attacked the startled Mockingbird from behind and struck it in the back with his feet and bill. In other encounters with intruding species the gnatcatchers merely flew close to the intruder's head.

During the course of this study I observed conflicts between gnatcatchers only once. On 30 June, a gnatcatcher appeared in a paloverde tree adjacent to the fourth nest of pair #1. This stray gnatcatcher may have been a Blue-gray Gnatcatcher, a female Black-tailed Gnatcatcher or a young bird of either species. Regardless of its true identity the intruder was immediately attacked by both members of the nesting pair. The dispute ended in a matter of seconds but it was vigorous while it lasted. Apparently most small birds except others of the same species are allowed to approach quite close to the gnatcatcher's nest before being driven off. The intruding bird in this case was actually farther from the nest than were many species of larger birds when they were attacked. See Table 3 for a summary of species that were attacked.

Table 3. Reaction of Black-tailed Gnatcatchers to intruding birds. Figures indicate number of encounters.

Intruder	Attacked in Nest, Tree or Shrub	Attacked in Adjacent Trees or Shrubs or on the Ground
Ash-throated Flycatcher	1	0
Verdin	3	0
Cactus Wren	21	24
Mockingbird	9	3
Curve-billed Thrasher	1	3
Gnatcatcher (unidentified)	0	1
Lucy's Warbler	1	0
Brown-headed Cowbird	1	0
Pyrrhuloxia	1	0
House Finch	0	0
Brown Towhee	0	2
Rufous-wing Sparrow	0	0
Black-throated Sparrow	1	0

During this study I did not observe any aggressive behavior by Black-tailed Gnatcatchers in areas remote from the nest tree. They did not show any attempt to maintain the boundaries defined by male perch calling during nest building. The nests of pair #2 were about 350 yards south of the nesting area utilized by pair #1, and the single nest of pair #3 was about 300 yards west of the same area. The boundaries defined by male perch calling, in all three pairs, were less than 200 feet from the nest in any direction. Perhaps if more Black-tailed Gnatcatchers had been nesting closer together, the boundaries evidently defined by male perch calling would have been maintained.

Relative to water retention and thermoregulation, a small territory could have definite advantages over a large one in this species. Defense of a large area could increase the energy requirements of a pair of gnatcatchers, especially the male. By defending an area with a 20 or 30 foot radius around its nest, a pair of gnatcatchers could eliminate unnecessary energy expenditures.

COWBIRD PARASITISM

Every accessible gnatcatcher nest (eight nests) in the main study area was parasitized by Brown-headed Cowbirds (Molothrus ater). One nest was in such a position that I was unable to determine the number or type of eggs that were laid. The only eggs that were hatched in any of the nine nests in which incubation took place were cowbird eggs.

On two occasions I removed two cowbird eggs from a gnatcatcher's nest (pair #2, nest #2; pair #3, nest #1). Within two days new cowbird eggs were found in the nest and gnatcatcher eggs were missing. By the end of one week following the deposition of the first egg, gnatcatcher nests often contained only cowbird eggs.

In four parasitized nests the incubation period exceeded the 12 day incubation period (Nice, 1953) for Brown-headed Cowbirds (Table 4). Apparent extension of cowbird incubation periods in these instances may have been due to a continual replacement of older cowbird eggs with new ones. Cowbird eggs are extremely similar in appearance to gnatcatcher eggs; they are slightly larger but colored very much the same. It appears that cowbirds laying eggs in gnatcatcher nests often removed previously laid cowbird eggs. Black-tailed Gnatcatchers abandoned their nests following 16 or more days of fruitless incubation.

Table 4. Summary of Brown-headed Cowbird parasitism of Black-tailed Gnatcatchers nesting in the main study area. Figures for egg numbers represent the total known number of eggs laid in a given nest. Extended incubation periods (over 12 days for cowbirds and 14 for gnatcatchers) are probably due to a continual replacement of old eggs by new eggs (see text).

Pr. #	Nest #	No. of days following nest completion that first cowbird eggs were laid	# Cowbird eggs	# Gnatcatcher eggs	# Gnatcatcher eggs removed by Cowbirds	# of eggs hatched	Incubation in days
1	1	2	1	3	3	0	9
1	2	1	2	0	0	0	3
1	3	4	3	1	1	0	16
1	4	?	?	?	?	0	2
1	5	nest not comp.	-	-	-	-	-
1	6	1	3	1?	?	2(Cowbird)	17
2	1	nest not comp.	-	-	-	-	-
2	2	2	4(2 removed)	4	4	0	17
2	3	3	3	1	1	0	less than 10
2	4	2?	2	3	3	0	19+
3	1	3	5(2 removed)	4	4	0	18

FORAGING BEHAVIOR

Foraging is probably one of the single most important activities in which a bird engages. The accumulation of energy is prerequisite to all activities and this energy can come only from the food a bird consumes. Thus before a bird can expend energy in any phase of its life cycle, it must have stored energy or have a ready supply of food that can be converted to energy. In the case of the Black-tailed Gnatcatcher, food sources must not only provide energy but they must also provide water.

The attainment of food is, therefore, a very basic aspect in the life of any bird species. Behavioral adaptations to a hot dry climate would be expected to be manifested in the foraging behavior of desert species. I intend to show that this is the case in the Black-tailed Gnatcatcher.

The Black-tailed Gnatcatcher is a very active species and spends most of the daylight hours in search of food. In contrast, most larger birds restrict their foraging activities to the morning and late afternoon hours, especially in the summer. The Black-tailed Gnatcatcher seldom forages on the ground; most of its foraging occurs in the peripheral branches of trees or shrubs.

Black-tailed Gnatcatchers are insectivorous. In one series of 60 stomachs, less than two percent of the contents proved to be vegetable matter, although one stomach in this series contained over 90 percent vegetable matter (Bent, 1949). During the course of my study I never observed Black-tailed Gnatcatchers taking vegetable matter.

The arthropods upon which gnatcatchers feed are usually very small. Even while using a 20 power spotting scope at close range I was seldom able to see the actual food items that were captured. Occasionally, I was able to observe gnatcatchers preying upon small insects and spiders.

I was able to determine the types of food being fed to nestling Brown-headed Cowbirds (Molothrus ater) by pair #1. Pair #1 hatched two cowbird eggs, one on 30 July, and one on 31 July. By using the spotting scope at close range, I was able to see most of the objects given to the young cowbirds (Table 5). Most of the larger food items (spiders and geometrid moth larvae) were brought to the nestling cowbirds, but I did see the adult birds eating these large arthropods more frequently than I had earlier in the summer.

During early August, following the first summer rains, insects were very abundant. During this period I frequently observed gnatcatchers, including pair #1, take large arthropods. The gnatcatchers appeared to maintain their customary foraging habits, taking moth larvae and larger spiders whenever such food items were encountered. This inclination of Black-tailed Gnatcatchers to take larger food items to their nestlings is probably indicative of an increased abundance of larger arthropod forms at this time of the year.

Table 5. Types of food brought to two nestling Brown-headed Cowbirds by pair #1. Data represent 10 hours of observations on the afternoons of 1, 2, and 5 August.

Food Type	Percent of Total	Number of Individuals
Geometrid Moth Larvae (Inch Worms)	40.9	67
Spiders	26.2	43
Beetles (True Bugs)	2.4	4
Locusts	3.1	5
Moths	0.6	1
Unidentified	26.8	44
TOTAL	100.0	164

Daily foraging areas vary in size during the year. In the winter and spring months, Black-tailed Gnatcatchers forage over a much larger area than during the nesting season. Pair #1, for example, utilized an area of approximately 12 acres for foraging prior to nesting. After the onset of nesting, the size of the foraging area was reduced to two acres. Hensley (1954) states that nesting Black-tailed Gnatcatchers near Ajo, Arizona, maintain a territory of about 2.3 acres. Since nesting birds in my study defended a territory with a radius of about 30 feet around the nest tree, perhaps the figure indicated by Hensley refers to the foraging area which was quite similar (2.0 ± acres to 2.3 acres) in my study.

As the temperature rises there is a very definite change in the foraging behavior of Black-tailed Gnatcatchers. During the cool morning hours, the birds spend nearly half of their foraging time in bright sunlight. As the sun exposed temperature rises above 35 C, foraging in open sunlight decreases markedly (Fig. 2). Concomitant with a decrease in foraging in open situations, there is a definite drop in the intensity of the foraging activity. Foraging does not cease entirely during hot periods, only the degree of activity associated with it.

Two factors relative to temperature must be examined in explaining these changes in foraging behavior. The sun exposed temperature is of primary importance in limiting the amount of time a Black-tailed Gnatcatcher forages in open sunlight. Secondly, the

Figure 2. The percent of total recorded observation time Black-tailed Gnatcatchers spent foraging in bright sunlight. The columns each represent the time spent foraging in the sun in different temperature blocks (e.g. 35 C to 40 C). This figure is presented in condensed tabular form in Table 6.

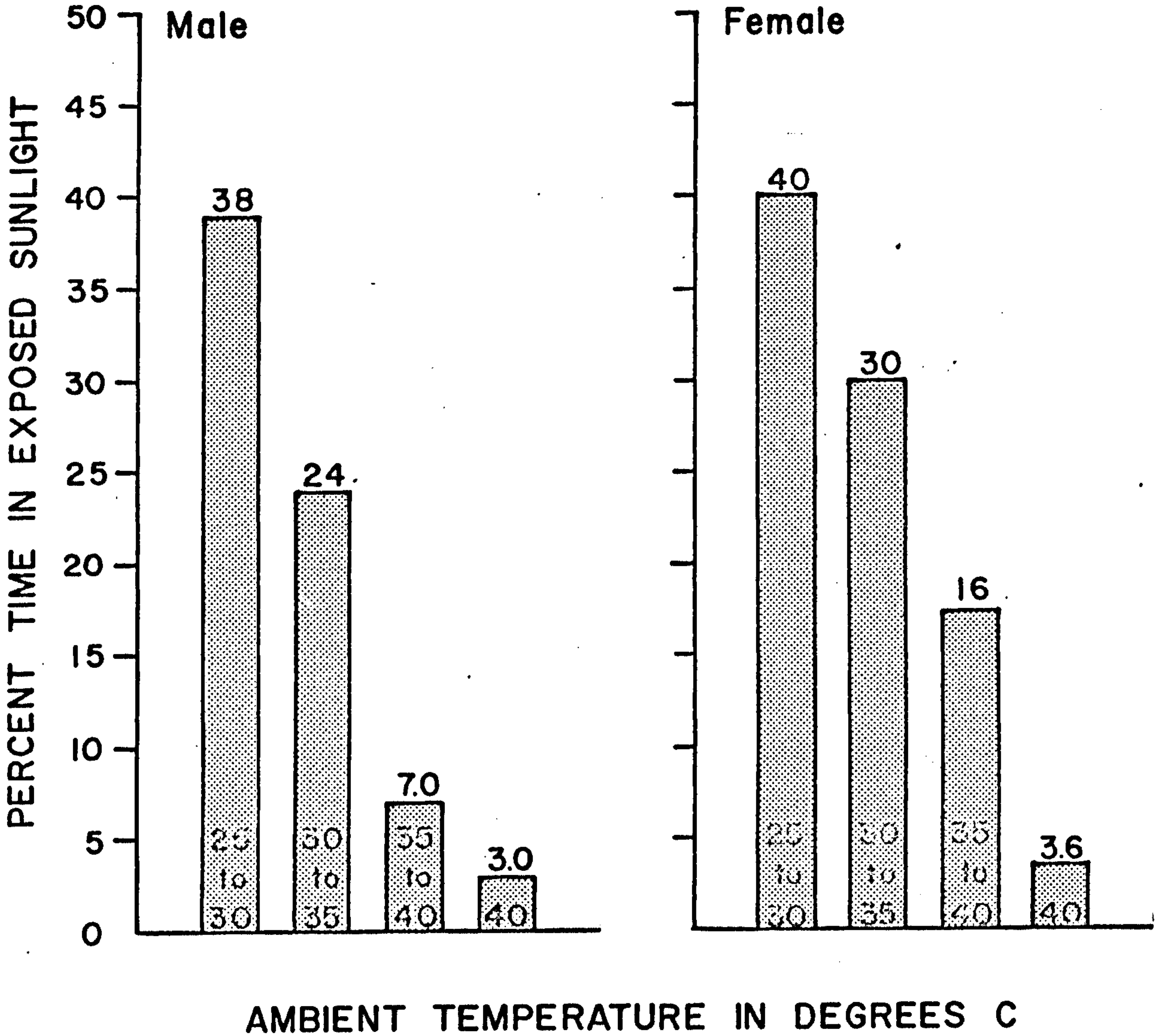

Male
Female
PERCENT TIME IN EXPOSED SUNLIGHT
0
5
10
15
20
25
30
35
40
45
50
38
24
7.0
3.0
40
30
16
3.6
25 to 30
30 to 35
35 to 40
40
AMBIENT TEMPERATURE IN DEGREES C

Figure 2

Table 6. Total observation time on Black-tailed Gnatcatchers and the percent of that total spent foraging in bright sunlight (obs. = total observation time for that temperature block in seconds; sun = amount of time in seconds Black-tailed Gnatcatchers were observed foraging in bright sunlight; % = percent of total observation time spent in bright sunlight).

	Males	Females
25-30 C		
obs.	5730	5757
sun	2177	2303
%	30.0	40.0
30-35 C		
obs.	5519	6700
sun	1324	2010
%	23.9	30.0
35-40 C		
obs.	6665	5919
sun	472	947
%	7.0	15.9
over 40 C		
obs.	4757	4066
sun	142	122
%	2.9	3.0

shade temperature rises along with the sun exposed temperature, this temperature increase is reflected in decreased foraging intensity.

On hot afternoons when the sun exposed temperatures exceeded 40 C, shade temperatures were usually above 35 C. During such periods foraging behavior was typified by slow, diliberate searching. The gnatcatchers often sat quietly in deep shade and looked about for insects. When an insect or spider was sighted the bird would move from its perch to make the capture. When sun exposed and shade temperatures were less than 35 C, foraging behavior was typified by very active, almost exuberant searching for food, in contrast with the subdued activity at higher temperatures.

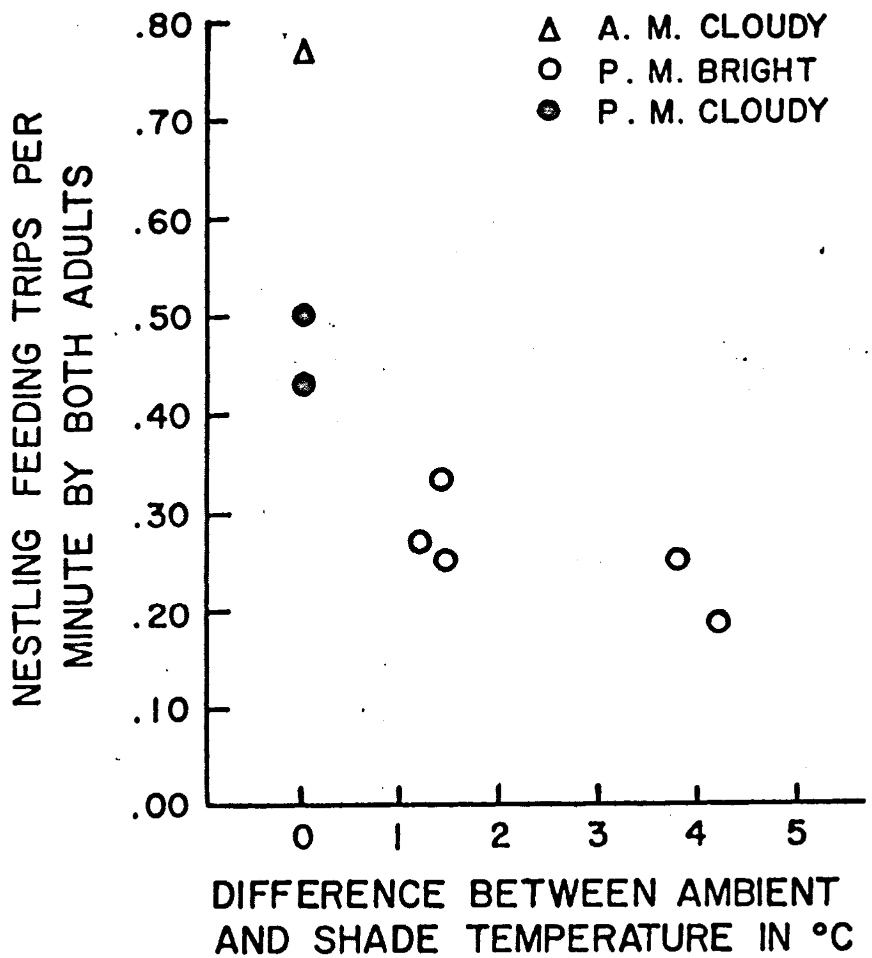
I think that the patterns of foraging behavior that I have described are directly related to temperature. I have seen Black-tailed Gnatcatchers foraging vigorously on hot afternoons but the tendency is definitely towards reduced activity. I have also observed gnatcatchers foraging actively in open situations on cool, cloudy afternoons. This latter situation leads me to believe that time of day is not the important factor in determining foraging activity. If decreased afternoon activity is a time of day response, I would not expect gnatcatchers to forage actively on cool, cloudy afternoons.

While eggs were being incubated, foraging by both adults continued throughout the day. This was accomplished by alternating foraging trips and incubating periods. While one bird incubated the eggs, the other foraged nearby. After a variable period of 15 to 40 minutes the incubating bird began calling; the foraging bird returned to the nest and traded places with the incubating bird. When temperatures were high, the foraging bird usually stayed in the nest tree or one adjacent to it. I frequently observed incubating gnatcatchers catching insects from the nest. Thus, even while incubating eggs, gnatcatchers continue to replenish energy and water.

Nestling feeding trips were also influenced by rising environmental temperatures. The number of nestling feeding trips per unit of time would reflect changes in foraging behavior since adult birds had to catch food for the young as well as forage for themselves. One would expect a decrease in the number of feeding trips made to a nest by adult birds concomitant with a decrease in foraging activity. During hot afternoon periods, the number of nestling feeding trips per minute shows a definite decrease over the number of trips made during the cool morning hours. On cloudy, cool afternoons, the number of feeding trips increased compared to the number made on hot, clear afternoons (Fig. 3).

During the cool months gnatcatchers continue to forage actively throughout the afternoon. If reduced afternoon foraging activity that is so evident during the summer months was a time of day response, a similar decrease in activity would be expected during the cooler months. Perhaps maintenance of foraging activity at this time of the year is related to food availability and shorter day length. Even if true, this does not explain active foraging on cool afternoons during the summer. Further, arthropods do not disappear during the winter. Many insects and small spiders may be found then on leaves and twigs.

Figure 3. The influence of temperature on nestling feeding trips per minute by adult Black-tailed Gnatcatchers feeding two Brown-headed Cowbird young. Exposed sun temperatures (= ambient here) were over 39 C when these data were collected. Data represent 10 hours of afternoon observations on 1, 3, and 5 August, 1966.



A. M. CLOUDY
P. M. BRIGHT
P. M. CLOUDY
NESTLING FEEDING TRIPS PER MINUTE BY BOTH ADULTS
.80
.70
.60
.50
.40
.30
.20
.10
.00
0
1
2
3
4
5
DIFFERENCE BETWEEN AMBIENT AND SHADE TEMPERATURE IN °C

Figure 3

DISCUSSION AND CONCLUSIONS

An inverse relationship exists between body weight and respiratory water loss in birds. Larger birds lose proportionately less water at moderate ambient temperatures than do small ones. According to data presented by Bartholomew and Cade (1963) a 10 g House Wren (Troglodytes aedon) loses about 36 percent of its body weight per day at 25 C. A 145 g California Quail (Lophortyx californicus) loses about 5 percent of its body weight in evaporative water loss per day at 25 C.

Specific data on evaporative water losses are not available for the Black-tailed Gnatcatcher. Assuming this species fits this general pattern of water loss, it could lose 35 to 40 percent or more of its body weight per day at 25 C. Since it seldom, if ever, takes free water (Gubanich, 1966), water that is lost during respiration must come either from the body fluids of insects or from metabolic water. I feel that foraging throughout the day by this species is necessary to maintain a favorable water balance.

It is highly improbable that metabolic water production would be of significance in offsetting respiratory water loss in a five or six gram bird (Dawson and Schmidt-Nielsen, 1964, Bartholomew and Cade, 1963). If a five gram Black-tailed Gnatcatcher lost a conservative 35 percent (1.75 g) of its body weight per day at 25 C, it would have to consume and oxidize the caloric equivalent of 3.12 g of carbohydrates per day to offset this loss via oxidative water production. It is unlikely that a Black-tailed Gnatcatcher could consume enough insects per day to provide this amount of carbohydrate. Bartholomew and Dawson (1953) have shown that metabolic water production could offset only about five percent of the daily evaporative water loss in a 10 g House Wren.

Black-tailed Gnatcatchers do not appear to utilize free water, even in areas where standing surface water is readily available. Gubanich (1966) reports seeing Black-tailed Gnatcatchers daily at a waterhole on the Cabeza Prieta Game Range in Southern Arizona but never saw the birds drink. During the summer of 1966, rain puddles were frequently present in my study area but I never saw gnatcatchers drinking from them. Waterhole observations I made during the summer of 1966 did not include the Black-tailed Gnatcatcher as a drinking species. Thus, replacement of water lost across the respiratory surfaces must come primarily from the body fluids of arthropods, augmented by slight metabolic water production.

Utilizing insects as a sole source of water should not put any osmotic strains on Black-tailed Gnatcatchers. The high concentrations of amino acids in the hemolymph of insects, 50 to 100 times those in the blood of mammals (Duval, Portier and Courtois, 1928), should pose no problems of osmoregulation. High concentrations of amino acids in hemolymph are associated with low salt concentrations and the nitrogen released in the metabolism of these amino acids can be removed as uric acid with little loss of water (Dawson and Schmidt-Nielsen, 1964). Metabolism of these amino acids also results in the formation of metabolic water.

Temperature regulation, in addition to maintaining a physiologically adequate water balance, is a major problem for birds living in desert regions. The two problems are very much interrelated since a large amount of heat can be dissipated by evaporation of water across the respiratory surfaces (Dawson, 1954 and 1958). As the ambient temperature rises the amount of water lost via evaporative cooling increases. A fourfold increase in evaporative water loss occurs between ambient temperatures of 33 C and 40 C in the Cardinal (*Richmondena cardinalis*) (Dawson, 1958). A similar increase in evaporative water loss has been shown in Brown Towhees (*Pipilo fuscus*) and Abert's Towhees (*P. aberti*) (Dawson, 1954).

In most birds that have been studied, panting begins at body temperatures between 42.5 C and 43.5 C (Dawson and Schmidt-Nielsen, 1964). The increased respiratory rate associated with panting results in an increase in metabolic heat production. The heat dissipated by evaporative cooling at ambient temperatures of 40 C or more is less than the heat produced by panting (Bartholomew, Hudson and Howell, 1962, Dawson, 1954). At ambient temperatures of 40 C or more, the amount of heat dissipated by transfer is much reduced. This reduction of heat dissipation by transfer coupled with an excess of metabolic heat indicates that heat is stored at high ambient temperatures. Concomitant with heat storage, a rise in body temperature occurs. A number of species that inhabit hot areas have been shown to tolerate increases in body temperature of 2 C to 4 C without ill effects (Bartholomew and Dawson, 1958, Dawson, 1958 and others).

Evaporative cooling during periods of panting thus appears to retard but not prevent a rise in body temperature. The storage of heat (hyperthermia) tends to put the bird in a more favorable position for heat transfer with the environment, and, at the same time, reduces the amount of water lost in temperature regulation (Dawson and Schmidt-Nielsen, 1964, Chew, 1961).

I have observed panting in Black-tailed Gnatcatchers in a number of cases under different conditions. Nest building gnatcatchers were often observed panting, even on cool (26 C sun exposed temperature) mornings. Male gnatcatchers panted for as long as seven minutes after chasing Cactus Wrens from the vicinity of the gnatcatcher's nest. The latter example occurred before 0700, and the sun exposed temperature was only 24 C.

The adult birds of pair #1 panted almost continually while trying to feed two Brown-headed Cowbird young, especially after the shade temperatures exceeded 30 C. This case represents a situation in which Black-tailed Gnatcatchers were visibly stressed and repeatedly panting. After feeding the nestling cowbirds, the gnatcatcher would often stand on the rim of the nest or a nearby twig and cool himself. Cooling behavior during such periods consisted of panting or gaping and spreading the wings and legs slightly. The gnatcatcher exhibiting such behavior oriented himself such that he was facing into any breeze that was blowing. Behavior of the preceding type may be indicative of a hyperthermic mechanism in which cooling by transfer augments evaporative cooling and reduces the amount of water lost via evaporative cooling. Such cooling mechanisms have been suggested as existing in California Quail and Gambel's Quail (L. gambeli) (Bartholomew and Dawson, 1958). If spread-wing behavior is indicative of such a mechanism in the Black-tailed Gnatcatcher, transfer would probably take place across the lightly feathered areas under the wings.

Vigorous activity causes a marked increase in body temperature. At moderate ambient temperatures (23 C) 40 g Brown Towhees show a rise in body temperature of 2 C within five minutes during periods of activity (Dawson, 1954). Reduction of activity during hot periods of the day has been observed in a number of species including Brown Towhees and Abert's Towhees (Dawson, 1954), Cactus Wrens (Anderson and Anderson, 1963) and Black-throated Sparrows (Smyth and Bartholomew, 1966). Chew (1961) states that such reduction of activity is required to prevent peak body temperature from arising prior to peak environmental temperature.

The reduction in foraging activity in Black-tailed Gnatcatchers, and other species of desert birds previously mentioned, is probably due to high environmental temperatures. By reducing foraging activity during hot periods, gnatcatchers avoid the addition of excess metabolic heat to the environmental heat load. When activity must continue during the heat of the day, periods of activity are alternated with periods of panting and spread-wing cooling behavior.

Increased humidity has been shown to greatly alter the ability of fowl and pigeons to prevent a rapid rise in body temperature (Randall, 1943). This phenomenon is due to the moisture carrying capacities of moist air versus dry air. At a given temperature, dry air is capable of picking up more water vapor than moist air. At an ambient temperature of 40 C, a bird ventilating its respiratory tract with dry air will lose more moisture, and hence more heat, than a bird in moist air.

I have not detected any significant changes in sun-shade foraging behavior or foraging intensity in Black-tailed Gnatcatchers that could be attributed to increases in relative humidity. During the course of this study, relative humidities rarely exceeded 50 percent. When relative humidity did exceed 50 percent, it was always in the morning and in conjunction with low environmental temperatures. Under such conditions a small bird like the Black-tailed Gnatcatcher would probably lose enough heat by conduction to offset excess metabolic heat incurred through foraging activity. Further, high humidity would not reduce the efficiency of evaporative cooling greatly unless the ambient temperature equalled or exceeded the bird's body temperature with relative humidity over 90 percent (King and Farner, 1964).

In Southern Arizona, the Black-tailed Gnatcatcher is a resident species in the Lower Sonoran Life-zone. Black-tailed Gnatcatchers do not regularly take free water, even in areas where standing water is available. Both water and energy are derived from arthropod prey. Nesting adaptations to a hot environment are illustrated primarily in the position of the nest. Completed nests observed in this study were placed on the periphery of a shrub or tree in well concealed and shaded positions. Foraging in exposed areas decreased markedly when sun exposed temperatures exceeded 35 C. The degree of activity associated with foraging, even in shady areas, also decreased markedly as the shade temperatures approached 35 C. High relative humidity was always associated with low environmental temperatures; no stress situations or changes in behavior could be associated with high relative humidity. Changes in behavior and heat stress situations were noted only during periods of high environmental temperature and low relative humidities, or during periods of unusual activity at cool temperatures.

Thus the Black-tailed Gnatcatcher is able, through behavioral modifications, to exploit successfully the desert environment. The possible existence of hyperthermic mechanisms, indicated by panting, coupled with minimal sun exposure and reduced activity during hot periods are the principal avenues along which water retention and temperature regulation are facilitated. Continuation of foraging throughout the day, though with greatly reduced intensity during hot periods, insures a continual replenishment of water lost in evaporative cooling and respiration.

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