THE BREEDING ECOLOGY OF THE BLACK-THROATED
SPARROW IN SOUTHERN NEW MEXICO

MICHAEL CARL DELESANTRO

N M S U

THE BREEDING ECOLOGY OF THE BLACK-THROATED SPARROW

IN SOUTHERN NEW MEXICO

BY

MICHAEL CARL DELESANTRO, B.S.

A Thesis submitted to the Graduate School

in partial fulfillment of the requirements

for the Degree

Master of Science

Major Subject: Biology
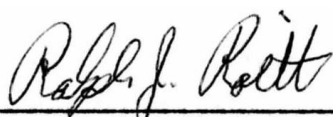
New Mexico State University

Las Cruces, New Mexico

October 1978

"The Breeding Ecology of the Black-throated Sparrow in Southern New Mexico," a thesis prepared by Michael Carl Delesantro in partial fulfillment of the requirements for the degree, Master of Science, has been approved and accepted by the following:

_____
Dean of the Graduate School

_____
Chairman of the Examining Committee

November 28, 1978
Date

Committee in charge:

    Dr. Ralph J. Raitt, Chairman

    Dr. William A. Dick-Peddie Dr.

    Walter G. Whitford

    Dr. Charles A. Davis

ACKNOWLEDGMENTS

VITA

June 8, 1954 - Born at Atlantic City, New Jersey

1975 - B.S., Rutgers University, New Brunswick

1976-1978 - Teaching Assistant, Department of Biology,

New Mexico State University

PROFESSIONAL AND HONORARY SOCIETIES

New Mexico Ornithological Society

Cooper Ornithological Society

Wilson Ornithological Society

FIELDS OF STUDY

Major Field: Biology

Studies in Avian Ecology

Dr. Ralph J. Raitt

ABSTRACT

THE BREEDING ECOLOGY OF THE BLACK-THROATED SPARROW IN

SOUTHERN NEW MEXICO

BY

MICHAEL CARL DELESANTRO, B.S.

Master of Science in Biology New

Mexico State University Las

Cruces, New Mexico, 1978 Dr.

Ralph J. Raitt, Chairman

The winter flocking behavior and breeding ecology of the Black-throated Sparrow (Amphispiza bilineata) were studied on 80 ha of creosotebush (Larrea divaricata) desertscrub, 40 km north of Las Cruces, Doña Ana County, New Mexico, from November 1976 through September 1977. The objective of the study was to examine the ecology of this abundant, but little studied, species and relate these data to its success in its harsh desert habitats.

Black-throated Sparrows fed exclusively on the ground in winter flocks and tended to concentrate their efforts in arroyos where seeds may have been deposited by wind and water. Pairing apparently took place in flocks prior to establishment of territory.

Territory establishment and defense were not different from those reported for many other species of territorial passerines. Territories

of 14 males ranged in size from 0.89 ha to 2.36 ha with a mean of 1.61 ha. Territory was largest at initial establishment and decreased in size to its smallest when adults were feeding young. Once the young were out of the nest, the entire original area was used but defense appeared limited to the area around the young. These changes suggest that territory has not evolved as a means of securing food in Black-throats since during the critical nestling and fledging periods the large original area was not defended.

Territories were established in areas with greater than average cover of creosotebush and grasses. Territory vegetation parameters were not correlated with aspects of sparrow breeding ecology, perhaps due to the small sample size.

Fifty-two nests were found. Nests were located in their nest plant with a non-random orientation toward the east-northeast with respect to the plant canopy. This provided early morning solar warming and shade and shelter from the afternoon sun and prevailing southwesterly winds.

The initiation of egg-laying took place in two distinct peaks; first in early May and again, following the start of summer rains, in July. Clutch size varied from 2-4 eggs with a mean of 2.6. The female alone incubated the eggs which hatched in 12-13 days. Hatching success was 49.1% and fledging success was 31.7%. The nestling period lasted eight-nine days. Nest success was 25%. Predation was the major source of nesting mortality. It is suggested that the large territory of these birds is an adaptation for reducing nest predation. Success was greater in late season nests, perhaps due to greater dispersion of nests.

Foods of nestlings were apparently gathered opportunistically.
Adults continued to forage for young even at temperatures of 38.5°C or greater. Foraging was done mostly in creosotebush, especially after the summer rains.

Physiological and behavioral responses to deserts are discussed. It is suggested that four aspects of the ecology of Black-throated Sparrows are primarily responsible for its success in arid habitats: a) efficient physiological adaptations to desert environments, b) opportunism in foraging, c) fine-grained use of its habitat, and d) large territory to reduce predation through dispersion of nests.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The Black-throated Sparrow, _Amphispiza bilineata_, is a common and conspicuous species in a variety of arid habitats in the southwestern United States and northern Mexico (Scott 1887, Montgomery 1905, Bailey 1928, Miller 1955, Gullion et al. 1959). In some habitats it is the only recorded breeding bird (Small 1974), and it occurs even on the floor of Death Valley (Wauer 1962). Despite its abundance throughout much of its range, little is known of its ecology, or of the adaptations that allow it successfully to breed in its harsh and unpredictable desert habitats.

Undoubtedly, part of its success is due to its physiological adaptations to water, heat and ionic stress (Smyth and Bartholomew 1966, Gordon 1968, Johnson and Ohmart 1973). In addition, it is the only species in southern New Mexico known regularly to use creosotebush (_Larrea divaricata_) as a nest site (Raitt and Maze 1968), giving it an advantage in habitats dominated by this shrub. Also of interest is the large territory of this small bird. Heckenlively (1970) estimated it as 120-150 m in diameter, but reports by Dixon (1959), Raitt and Maze (1968), Gustafson (1975), and Stamp (1978) give breeding densities for this species that suggest a larger territory. Generally, as aridity increases resources become more unpredictable in time and space (Noy-Meir 1974, Weins 1976). If bird territories in desert habitats have evolved to enclose resources, then their size should be positively correlated with aridity (Wiens 1976).

In recent years, investigators have begun to examine desert avifaunas and individual species in detail (Raitt and Maze 1968, Ohmart 1973, Tomoff 1974, Austin 1976, 1977, 1978, Austin and Ricklefs 1977). The

1

Black-throated Sparrow is an excellent subject for such a study.   Knowledge of the ways in which this species copes with the desert certainly will be useful in analyses of desert adaptations and avian community structure in the arid Southwest.

STUDY AREA

Winter flocking behavior and breeding of Black-throated Sparrows were studied from 28 November 1976 through 10 September 1977, on approximately 80 ha of creosotebush desert scrub, 40 km north of Las Cruces, Doña Ana County, New Mexico (32°, 30'N; 106°, 45'W).

Climate of the region is characterized by maximum temperatures of about 42°C in July, with minimum temperatures in January, and mean annual precipitation of about 228 mm, most of which falls in local summer thundershowers from July through September (Raitt and Pimm 1976).

The study site is part of a sloping alluvial fan, or bajada, at an elevation of about 1300 m, at the base of Mount Summerford in the Doña Ana Mountains. The northern half of the site was a validation site of the International Biological Program desert biome study, coordinated by Walter G. Whitford, at New Mexico State University, Las Cruces, N.M. Vegetation of the northern half of the site was described by Whitford (1972) as typical Chihuahuan desert scrub with 23% cover of creosotebush, 1% cover each of mesquite (Prosopis gladulosa) and tarbush (Flourensia cernua), and less than 1% cover each of snakeweed (Gutierrezia sarothrae), mariola (Parthenium incanum), and Yucca spp. In addition, two perennial grasses, bush muhly (Muhlenbergia porteri) and fluff grass (Erioneuron pulchellum), account for about 0.5% cover each. The northern half of the site is highly dissected by numerous small intermittent water courses, or arroyos, and is bisected by a large arroyo draining toward grasslands to the north. Vegetation of arroyos in the region was described by Raitt and Maze (1968). Small, or minor, arroyos typically contain plants of similar species to those of the flats or mesas, but of larger stature and density. Large, or major arroyos contain, in addition, such plants

3

as apache plume (Fallugia paradoxa), brickelbush (Brickellia laciniata), desert willow (Chilopsis linearis), and hackberry (Celtis reticulata). Apache plume and desert willow form dense thickets in the major arroyo on the site.

The southern half of the site differs from the northern in having a more homogeneous appearance, due to being less dissected by arroyos, a higher cover of mesquite (4%), more uniformly large and evenly dispersed creosotebush, and little or no grass cover. There are no large arroyos on this half of the site.

The northwest and northeast of the site are bordered by grassy areas. To the west, grama grasses (Bouteloua spp.) descend from the slopes of Mount Summerford and intermix with scrub vegetation, while to the east is a/small, isolated area of fluff grass and scattered shrubs. Other sides of the site are bordered by scrub vegetation of similar composition to that of the site. Two gravel roads delimit the east and west edges of the site.

Approximately 30 ha of the site had been subdivided into a 100 by 100 m grid by I.B.P. workers. I extended this grid to encompass 80 ha and mapped the area, showing drainages and roadways, at a scale of 1 mm = 2 m, using aerial photographs (Fig. 1).

During the months of March and April, 23 adult sparrows were mist netted, weighed, and marked with plastic colored leg bands and aluminum U.S. Fish and Wildlife Service bands. Seven of these were netted from flocks. The remainder were captured by using a stuffed model of a Black-throated Sparrow and broadcasting tape recorded songs. When territorial sparrows responded to the model or songs, they were flushed into the nets.

The movements of 12 of these birds were recorded on the maps, and territories of 14 males were mapped using territory-flush methods of Wiens (1973). Territory boundaries established by this method were verified by playing tape recordings of sparrow songs at the mapped limits and observing the reactions of the pair, similar to the methods of Patterson and Petrinovich (1978). This method provided close initial correlations with the flush method and was used to check for changes in territory during the breeding season of selected males.

Nests were located by systematic search of the site throughout the breeding season. The orientation of nests with respect to the center of the nest plant canopy was recorded to the nearest of eight principal compass directions (N, NE, E, etc.). Behavior of adults at the nest was observed from a blind at 12 nests, often from within 3 m of the nest. Food brought to the young

Figure 1.   Map of the study site showing drainages, territory boundaries

and nest locations; roads are indicated by the double solid line, major arroyos by the

doubled dashed line, minor arroyos by the single solid line, territories by the dot-dashed

line, nests active at time of territory mapping by a square, and other nests by the large
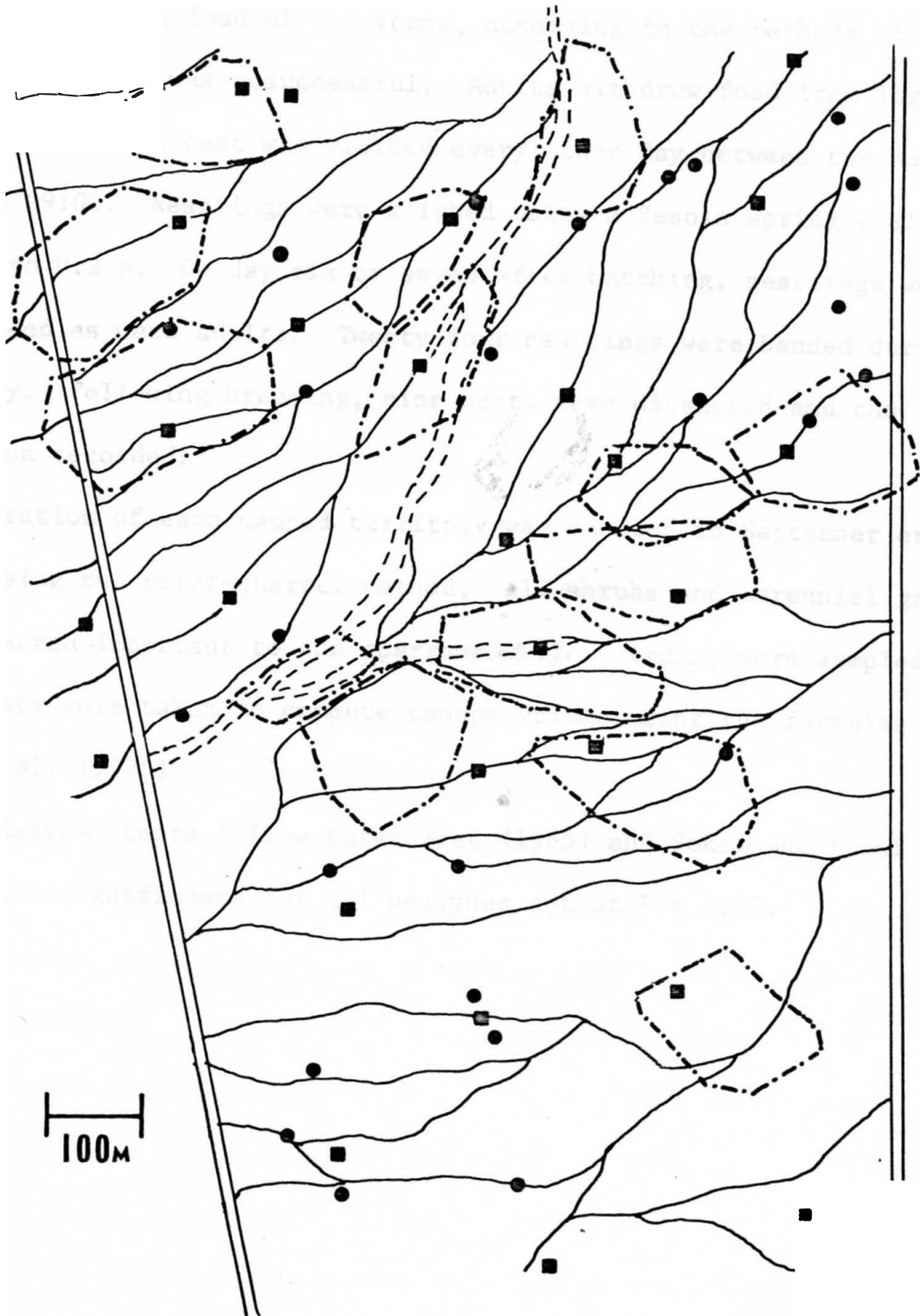
dot.

FIGURE   1

usually could be easily identified from this distance. I also observed nests from a distance with a 20x spotting scope. I attempted to use neck ligatures to sample food of the young, according to the methods of Orians (1966), but was unsuccessful. Adults withdrew food from ligatured young. Each active nest was visited every other day between the hours of 06:00 and 09:00. Nestlings were weighed using a Pesola spring scale accurate to 0.2 g. On day six or seven after hatching, nestlings were color-banded as were adults. Twenty-four nestlings were banded during this study. Following breeding, nine nests were dissected and the composition recorded.

Vegetation of each mapped territory was sampled in September or October using the point-quarter method. All shrubs and perennial grass species deemed important to the sparrows while breeding were sampled. Measurements were taken to compute canopy volume using the formulae of Ludwig et al. (1975).

Statistical tests follow Batschelet (1965) and Sokal and Rohlf (1969), with significance for all analyses set at $P = 0.05$.

WINTER FLOCKING

During the months of September through February, Black-throated Sparrows occurred in single species or mixed species flocks of 5-200 birds. Mixed species flocks, including White-crowned Sparrows (_Zonotrichia_ leucophrys), Brewer Sparrows (_Spizella breweri_), Junco spp. and Sage Sparrows (_Amphispiza belli_), were more common later in the winter. These flocks were seldom found on the bajadas in open scrub, but rather were concentrated in arroyos and areas with grass cover. Arroyos are areas where seeds may be deposited by wind and water and where there is greater vegetation cover. These factors tend, in turn, to concentrate the birds.

Black-throated Sparrows fed exclusively on the ground in the winter months. Individuals remained within 2-3 m of conspecifics. Consequently, flock movements were usually well coordinated. In mixed flocks, however, Black-throats tended to fragment off by themselves and remained more or less separate from members of other species.

Few interactions were noted during the fall and early winter. By February, however, displacements and aerial chases of short duration were quite frequent, and on warm days, while the birds were still in flocks, singing was heard.

By mid-February, the first pairs of birds were seen separate from flocks. It is not known precisely when pairing takes place. In many species pairing takes place on territory (Davis 1955), but birds here were paired prior to establishing territory and it is reasonable to assume that pairing took place while the birds were still in flocks. This pairing prior to the onset of warmer weather appears advantageous in facilitating the initiation of breeding. Also important in this regard, perhaps, is

the fact that Black-throats do not undergo a spring molt (Oberholser 1974).

Although the Black-throat is a permanent resident in this region, it is likely that different birds are present on the site in winter than in summer. It is known that Black-throated Sparrows are partially migratory (Bent 1968). Late winter is apparently a time of substantial movement. None of the birds banded from flocks were found on the site after the start of breeding, indicating that flock movements were quite extensive. However, 12 of the 16 birds banded by using the model and tape recordings were later found on territories.

TERRITORY

During the early stages of territory establishment, immediately
after pairing, pairs often joined flocks that moved through their territory and
remained with them until the edge of the territory was reached. At this time males
began to sing vigorously from certain song perches, usually atop <u>Yucca</u> or mesquite,
and chases were common. Before or after a chase, the aggressor male often
displayed from a perch by turning toward the intruder, lowering the wing tips,
raising and fanning the tail, and pointing the bill skyward, thus exposing the
black throat feathers. This exposing of the throat appeared to be an important
signal in aggressive interactions. Also important in these encounters
is a series of rapid descending notes (Heckenlively 1970). Songfests, in which
two, or in one case, three males perched nearby and sang at a territory boundary,
were noted several times, as reported by Robins
(1971a) for the Henslow Sparrow (<u>Passerherbulus henslowii).</u> Territory
establishment and defense involved song, chases and, in some cases, fights and did
not appear to be different from that reported for other species of territorial
passerines (Stenger 1958, Tompa 1962, Weeden 1965, Stefanski 1967, Welch 1975). It
did not appear that accoustical communication had an increased importance over
visual display in territory defense as postulated by Heckenlively (1967, 1970).

One aspect of territory in Black-throated Sparrows is different from that of
many small passerines. Both sexes appeared to respond equally
to intrusions and usually they responded together, until nesting was under way.

Territory size, as determined by initial mapping and subsequent tape playback with the model, was largest at initiation, prior to the start of nesting. Fourteen territories ranged in size from 0.89 to 2.36 ha (mean = 1.61 ha). Once nesting had begun and during the egg-laying and incubation stages, territory defense was limited to a smaller, inexactly defined area around the nest.

After the eggs had hatched, little or no response to the tape and model could be elicited, suggesting that territory defense was at its minimum at this time. Once the young were out of the nest, the entire original defended area, and often more was used. However, at this time defense appeared to be more of the young than of the territory. Thus, adults with young were tolerated within another pair's boundaries and territory was not rigidly defined at this time. Changes in territory such as these have been reported for many species. Those of the Savanna Sparrow (Passerculus sandwichensis) described by Welch (1975) most closely parallel those of the Black-throated Sparrow.

During late June, when most early nests were already complete, aggressive encounters increased, as some birds that had lost earlier nests reestablished their territories. At this time territory boundaries changed slightly for these birds.

Many unsuccessful pairs did not attempt second nests, and no successful pair is known to have attempted a second brood. The lack of territorial activity left large open spaces between defended areas. In fact, at no time was the entire area filled with territories. There were always buffer zones left undefended between some territories.

I estimated 36 breeding pairs on the site at the start of nesting.

birds were very secretive about their breeding, and territory mapping

ived to be difficult. The rapid turnover of nests and relatively rapid

ablishment of territory and shift into breeding also contributed to

ficulty of territory mapping.

The northern half of the site was more densely populated and

ounted for two-thirds of all nests and adults. The southern half of

site was characterized by large areas devoid of birds.

The mean territory size in this study agrees well with territory

2s of small desert birds determined by Hensley (1954) in Arizona, but

_arger than those of other sparrows as summarized by Potter (1972),

i the exception of the Tree Sparrow (Spizella arboreas), which nests

undra-scrub.

The territory of Black-throated Sparrows is an all purpose territory

e A of Nice 1941). With the exception of when young are followed off

territory, all activities associated with breeding occur on the territory.

The limits of eight of the 14 territories mapped in May were closely

correlated with landmarks, such as roads or arroyos. It seems likely
that these features of the habitat birds. Territories tended to be oval in
shape.

In addition to their use as boundaries, arroyos were areas of refuge
.for young and less often, adults. In several instances young were found
hiding in dense arroyo vegetation while the adults foraged in adjacent

When chased, adults took refuge in the concealing arroyo vegetation

Still, only five of 14 territories included large areas of arroyo

vegetation, and only one was dominated by it. However, where major arroyo vegetation was found, because of its tendency to occur in large clumps, it exerted an influence on analyses of vegetation greater than its proportion of the territory. The one territory dominated by major arroyo vegetation was established by a male that did not obtain a mate until early July, and then had to expand his territory into adjacent previously undefended scrub to include the nest built by the female.

All other territories were dominated by creosotebush scrub. Table 1 summarizes vegetation comparisons between the site and territories. Shrub density, cover, and volume measurements were highly variable, as were estimates of grass cover. The means of these values, however, were consistently greater than the overall site values reported by Whitford (1972), indicating that these birds were apparently selecting the more densely covered areas of the site, (t-test, % cover: P < .01). Ten of the territories also had grass cover in excess of the overall site mean of about 1%. All 10 of these were located on the northern half of the site. Therefore, it appears that denser than average vegetation and greater than average grass cover are important site requirements for sparrow territories. Sparrows also appeared to avoid areas with large trees, such as major arroyos.

If these factors are considered in light of the differences in territory density on the north and south halves of the site, it can be seen that the lower density of the south is due to a combination of the lack of arroyos, the lack of grass cover, and the fact that the creosote-bush scrub was less dense, though individual plants were larger.

TABLE 1. Comparison of mean % cover of vegetation on Black-throated Sparrow territories and on the study site as a whole.

Plant species	Territories[a]	Site[b]
Larrea divaricata	33.8	23.7
Prosopis glandulosa	2.9	1.0
Gutierrezia sarothrae	1.5	0.6
Flourensia cernua	1.7	1.0
Yucca spp.	0.5	0.6
Riparian plants	0.3	0.2
Grasses	2.6	1.0

[a]The atypical major arroyo territory was excluded.

[b]Data from Whitford (1972).

I performed simple linear regressions and multiple regressions of vegetation parameters, including volumes per hectare of individual species, total volume per hectare, cover and density per hectare per species, total cover and density per hectare, dominance of shrubs, and importance values of each species, with parameters of territory and breeding ecology, including territory size, breeding success, and clutch size. Territory size, breeding success, or clutch size were not correlated with any measure of vegetation or combination of measures. Tests for breeding success were clouded by the high percent of nests lost and the low number of territories sampled.

The lack of correlation might be due to small sample size but might also be due to the fact that territory size was related to some other environmental factor such as the availability of food or some characteristic of individual birds, such as differences in hormone levels.

NESTS AND NEST BUILDING

Nests were placed on the territory apparently at random. Of 52 nests built by 38 pairs, 29 were placed in areas of mesa vegetation, 21 were in minor arroyos, and two were in major arroyos. Table 2 shows the choice of nest plants on the site. Black-throated Sparrows make extensive use of creosotebush as a nest substrate and are apparently the only bird to do this (Raitt and Maze 1968). Large spindly bushes are not used, but rather the smaller, more fully leafed plants are chosen. Since the south of the site is characterized by larger creosotebush, a lack of suitably vegetated nest sites may be partly responsible for the lower nesting density on this half of the site. Also of interest is the use of snakeweed and creosote-snakeweed combinations early in the season. This dense small half-shrub alone or in combination with creosotebush was apparently preferred by many birds since its use as a nest plant was greater than its proportion in the community (χ^2; P < .01). The combination of creosotebush for support and snakeweed for cover was important.

Mean nest height was 29.2 cm (range: 10.2–76.2), and mean height of nest plant was 87.5 cm (range: 50.8–228.6). These values are within the range of those found by Raitt and Maze (1968).

Figure 2 shows nest orientation with respect to the center of the nest plant. Orientation was non-random with a heavy preference for northerly and easterly components (Rayleigh's statistic: mean direction = 76.7 degrees, P < .01). This orientation was best to provide early morning solar warming and maximum shade and shelter from afternoon sun and prevailing southwesterly winds. However, in many cases shading was incomplete and the female had to compensate by shading the nest in midday.

TABLE 2. Plant species used as nest sites by Black-throated Sparrows.

Plant species	Number of nests
Larrea divaricata	29
L. divaricata and Gutierrezia sarothrae	9
G. sarothrae	5
Flourensia cernua	4
Prosopis glandulosa	2
F. cernua and G. sarothrae	1
Dalea formosa	1
Condalia lycoides	1
Total	52

Figure 2. Orientation of 39 Black-throated Sparrow nests with respect to the center of the support plant canopy. The arrow indicates the significant mean direction (Rayleigh's test, P < .01). Thirteen other nests were located at the center of the plant canopy.
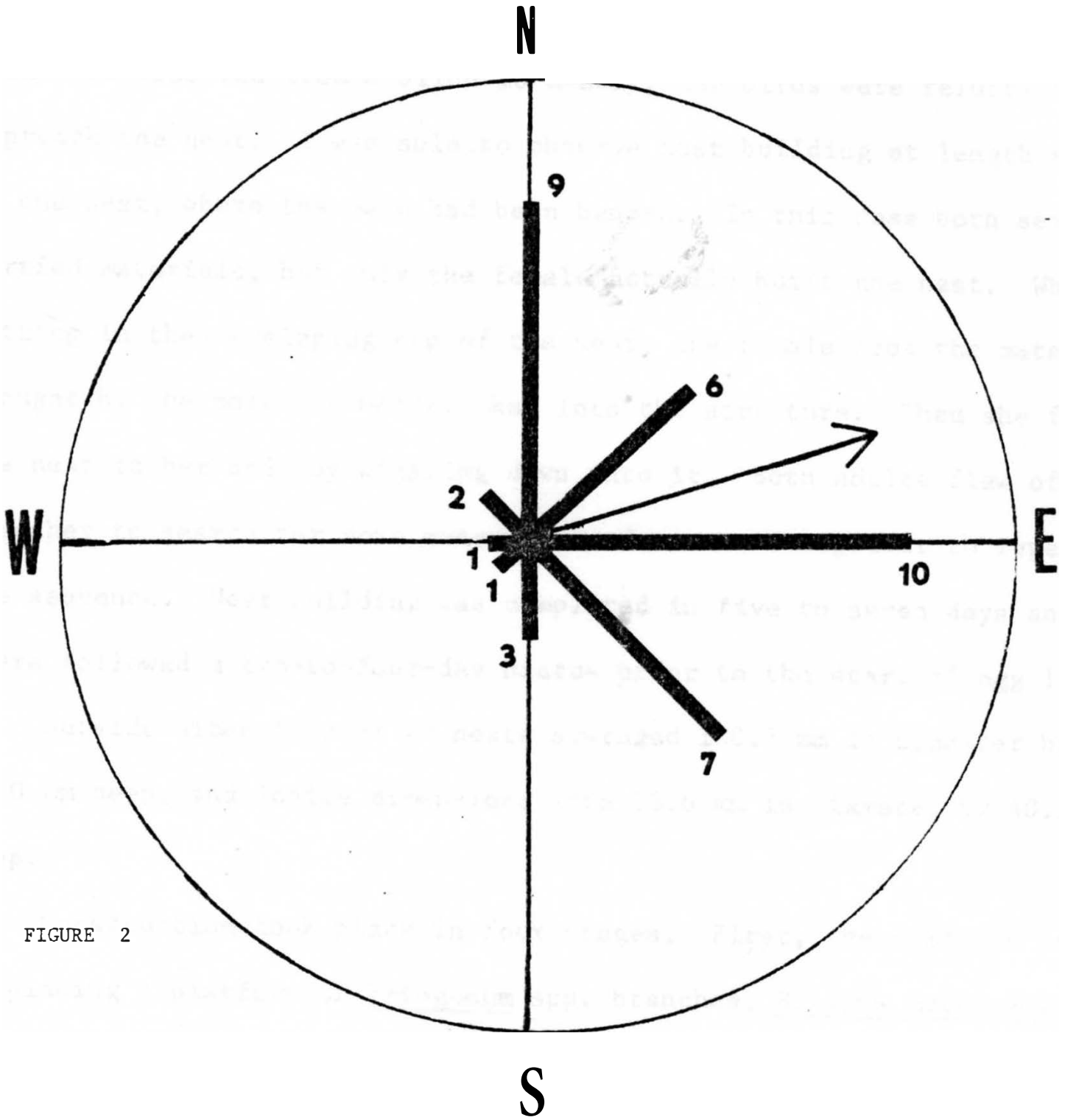
FIGURE 2

Similar non-random nest orientation has been found in the Cactus Wren
(Campylorhynchus brunneicapillus) and the Verdin (Auriparus flaviceps)
(Austin 1974, 1976).

Black-throats are very secretive during nest building. I never
saw a bird carrying nest materials except when I was observing at a nest.
Even when observed from a blind 10 m away, the birds were reluctant to
approach the nest. I was able to observe nest building at length only
at one nest, where the male had been banded. In this case both sexes
carried materials, but only the female actually built the nest. While
sitting in the developing cup of the nest, the female took the materials
brought by the male and worked them into the structure. Then she formed
the nest to her body by wiggling down into it. Both adults flew off
together to search for more materials and returned together to repeat
the sequence. Nest building was completed in five to seven days and
there followed a two-to-four-day hiatus prior to the start of egg laying.

Outside dimensions of 27 nests averaged 100.7 mm in diameter by
81.0 mm deep, and inside dimensions were 53.6 mm in diameter by 40.3 mm
deep.

Construction took place in four stages. First, the nest was begun
by placing a platform of Eriogonum spp. branches, Baileya multiradiata
and Lepidium sp. stems, and coarse grasses in a fork of the nest plant
that had at least three supports. Next, an outer shell of Yucca fibers,
coarse grasses and plant stems was built up from the platform. Third, an
inner shell of fine Yucca fibers, grasses, especially Muhlenbergia porteri,
and fine branchlets of Eriogonum and Lepidium were formed into the bowl.

Finally, this was lined with very fine _Muhlenbergia, Perezia nana_, and _Erioneuron_ inflorescences and tufts of rabbit fur. All of the early nests examined also contained porcupine (_Erethizon dorsatum_) hair.

Figure 3 shows the sequence of initiation of laying for 35 nests in which the start of laying could be determined by counting back from hatching or fledging dates if necessary. The figure shows a pronounced trough in June that is a bit misleading. While this was the time of fewest nest starts, five nests started between 23 May and 27 June failed before exact dates could be determined.

Eggs were laid one per day until the clutch was complete. Thirty-six eggs were measured to the nearest 0.5 mm using outside calipers. Eggs were short-oval, white and unmarked, and averaged 18 mm by 13.3 mm (range: 17-20.5 by 12.5-14.5). Eight fresh eggs averaged 2.07 g (range: 1.8-2.3).

Incubation was accomplished by the female alone. During incubation the female sat very tightly and often had to be pushed off to examine the nest. The presence of a distraction display in this species also was noted. A female that I flushed from the nest from a distance of about 1 m, dropped to the ground a few feet away and began running slowly with the wing tips dragging on the ground as if injured, giving loud chips. She took refuge in a small arroyo and began scolding me as I checked the nest.

Eggs hatched in 12 to 13 days from the time the last egg of the clutch was laid. Hatching was synchronous in all but one case. In that case, one egg hatched a day later than the two others in the clutch.

Forty nests were considered to have contained complete clutches. These nests had 104 eggs for a mean clutch size of 2.6 eggs (range: 2-4). Twenty-two nests had three eggs, 17 had two eggs, and one had four.

Figure 3. Initiation of egg-laying of Black-throated Sparrows tabulated on a weekly basis: 35 nests were able to be dated. Five other nests were found between 27 May and 14 June that could not be dated. The short vertical lines indicate major rainfall dates of the season.
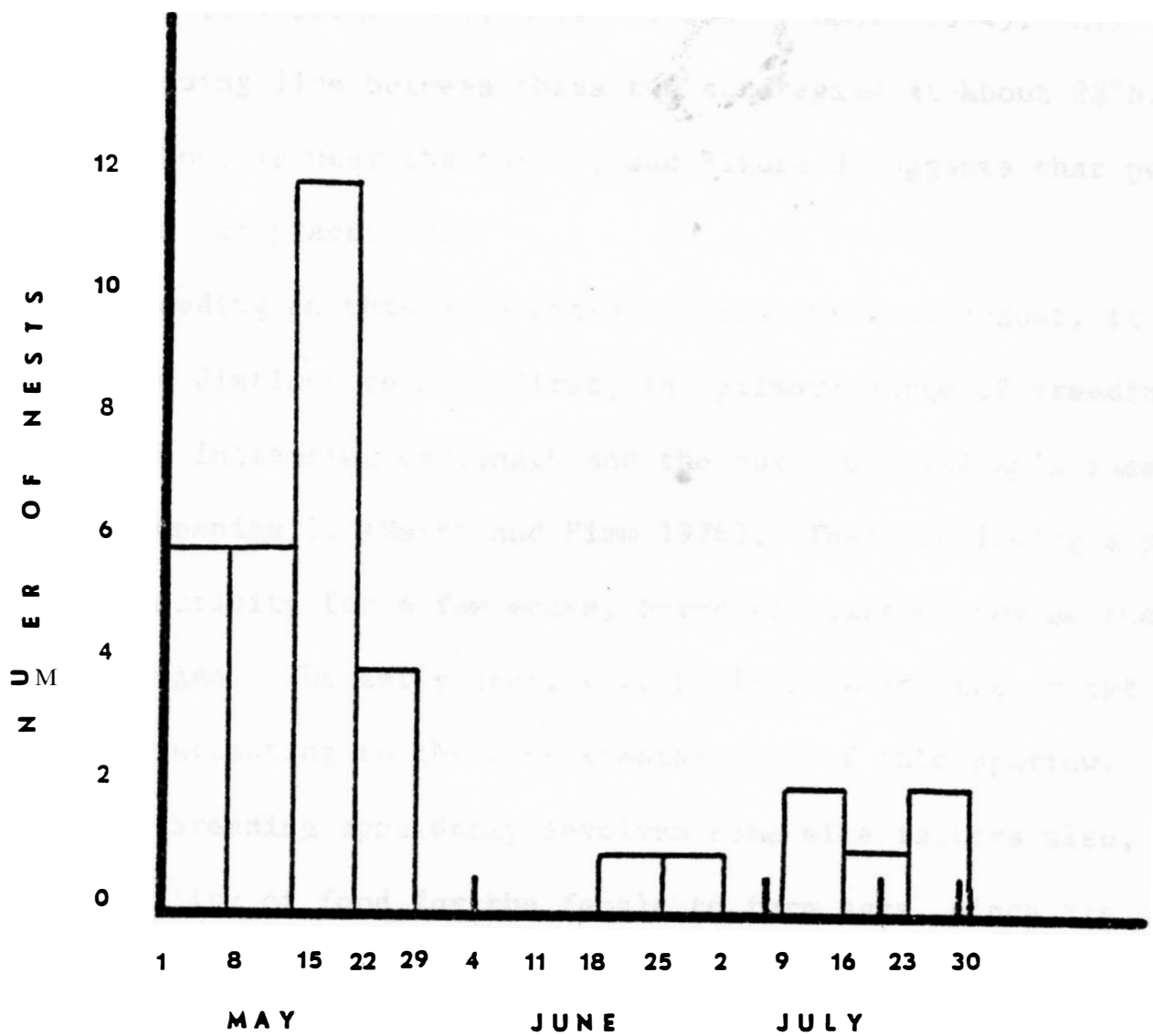
24

FIGURE   3

Twelve other nests were found after their contents had been altered or removed by Brown-headed Cowbirds (Molothrus ater) or predators. Only nests with complete clutches were considered in analysis of individual mortality.

The Black-throated Sparrow apparently breeds in response to photo-period in this region, and is perhaps more rain-stimulated elsewhere to the south and west (Miller 1958, Marshall 1963, Tomoff 1974). Miller placed the dividing line between these two strategies at about 28°N. This region, then, is near the border, and Figure 3 suggests that perhaps both strategies are practiced.

Though breeding on this site extended from April to August, it appeared in two distinct peaks. First, the primary surge of breeding took place with increasing daylength and the burst of available insect life that accompanies it (Raitt and Pimm 1976). Then, following a period of relative inactivity for a few weeks, breeding started anew as the summer rains began. The early nesting took place during the driest part of the season, attesting to the desert-adaptation of this sparrow.

Timing of breeding apparently involves some site factors also, such as the availability of food for the female to form eggs, since areas as near as 40 km were in very different stages of breeding. On this site birds were feeding nestlings with a few fledglings out of the nest, while on the site of Raitt and Maze (1968) 40 km to the south, birds were already in large flocks, a stage not reached on this site for about two weeks.

Table 3 presents sources of mortality tabulated by individual and nest. Hatching success was 49.1%. Overall egg success was 31.7%, and success of nests was 25%. Predation accounted for 60.8% of all losses of eggs and 65.4% of all nest losses. Cowbirds were responsible for the loss of 19.2% of all eggs and 17.3% of all nests.

The Black-throated Sparrow's response to cowbird brood parasitism was nearly always promptly to desert the nest and, in most cases, rebuild. This defense caused loss of time and energy, but was effective, since no cowbirds fledged from sparrow nests. In only one case was the cowbird egg incubated to hatching, but the nestling and those of the sparrow were eaten by a predator. Probably of more importance in defense against brood parasitism was the extreme secrecy in nest building that undoubtedly allowed most nests to avoid being parasitized. Stealth is the most efficient means of dealing with parasitism (Payne 1977). Cowbirds were a major source of loss only for early nests. Late nests were not parasitized as heavily. Percent nest success was higher late in the season, at least in part due to this relative lack of parasitism. Nests begun prior to mid June were 22.7% successful, while those begun after that date had 37.5% success (G-Test, P < .01).

Three-egg clutches were 31.8% successful while two-egg clutches had 35.3% success. Three-egg clutches had a greater hatching success but were more heavily preyed on than two-egg clutches.

Success was much lower than that of eight species studied by Hensley (1954) and lower than most species reviewed by Nice (1957), though no data on desert species were presented by her. However, success rates for

TABLE 3. Fates of individuals and nests of Black-throated Sparrows.

	Individuals[a]	Nests[b]
Unsuccessful		
Predation		
Egg stage	26	13
Nestling stage	19	9
Total	45	22
Desertion (after laying)		
Cowbird caused	20	9
Human caused	4	
Total	24	11
Desertion (before laying)		4
Infertility or embryonic death	2	
Unknown causes		2
Successful	33	13
Totals	104	52

[a]Based on the 40 nests containing complete clutches.

[b]Based on all 52 nests found.

certain species, notably the Field Sparrow (Spizella pusilla), are
consistently reported low also (Nice 1957, Best 1978). The Black-throat
nests very close to the ground in most cases and is subject to the
greater mortality usually found in ground nesting species (Ricklefs 1969).

Predation is probably the single most important selective agent
in breeding of these sparrows. It is likely then that a means of reducing
it would be evolved. The large territory of this small bird may be this
means. Overdispersion of nests through territoriality reduces predation
(Lack 1966, 1968). The greater success of later nests might thus be
attributed to the greater dispersion of nests and consequent lower
predation.

NESTLING GROWTH, NESTLING FOOD, FLEDGING

At hatching, young were sparsely covered with white down. In two days this down turned a light gray and remained that color until replaced by the contour and flight feathers.

Using the methods of Ricklefs (1967), nestling growth is best fitted by the logistic equation of the following form: $W = 12.2/1 + e^{-.554 (t)}$, where 12.2 is the asymptote, W is weight, .554 is the weight gain constant K, and t is age after hatching (Fig. 4). Young leave the nest at about 91% of adult weight and obtain full adult weight within two weeks. There was no difference in growth rates of nestlings in broods of different sizes or between early and late broods. The growth parameters fall well within the range of values reported by Ricklefs (1968) for temperate zone sparrows of similar size. There appears to be nothing unusual about the growth of this species in this habitat.

Both adults participated approximately equally in the feeding of the young. The male made more trips than the female while she was brooding, but the female made more trips later. The male began feeding from the first day after hatching, in contrast to males of Henslow Sparrow (Robins 1971b), which do not begin feeding until day three or four. The female alone brooded and shaded the nest from the sun. Feeding trips reached their maximum number per hour on day six or seven. The range of trips by both adults was 0-14 per hour, with a mean on the day of peak feeding of 6.1 trips per hour. The overall number of trips per hour throughout the nestling period was 4.1. Table 4 lists foods brought to nine nests in 21 hours of observation. Adults often brought several small items at a time to the nest and fed these to one or two young. Larger items, such

Figure 4. Black-throated Sparrow nestling growth curve. The horizontal line is the mean of daily weights, the box the standard deviation, the vertical line the range of observations, and the number at the top of the range the sample size.
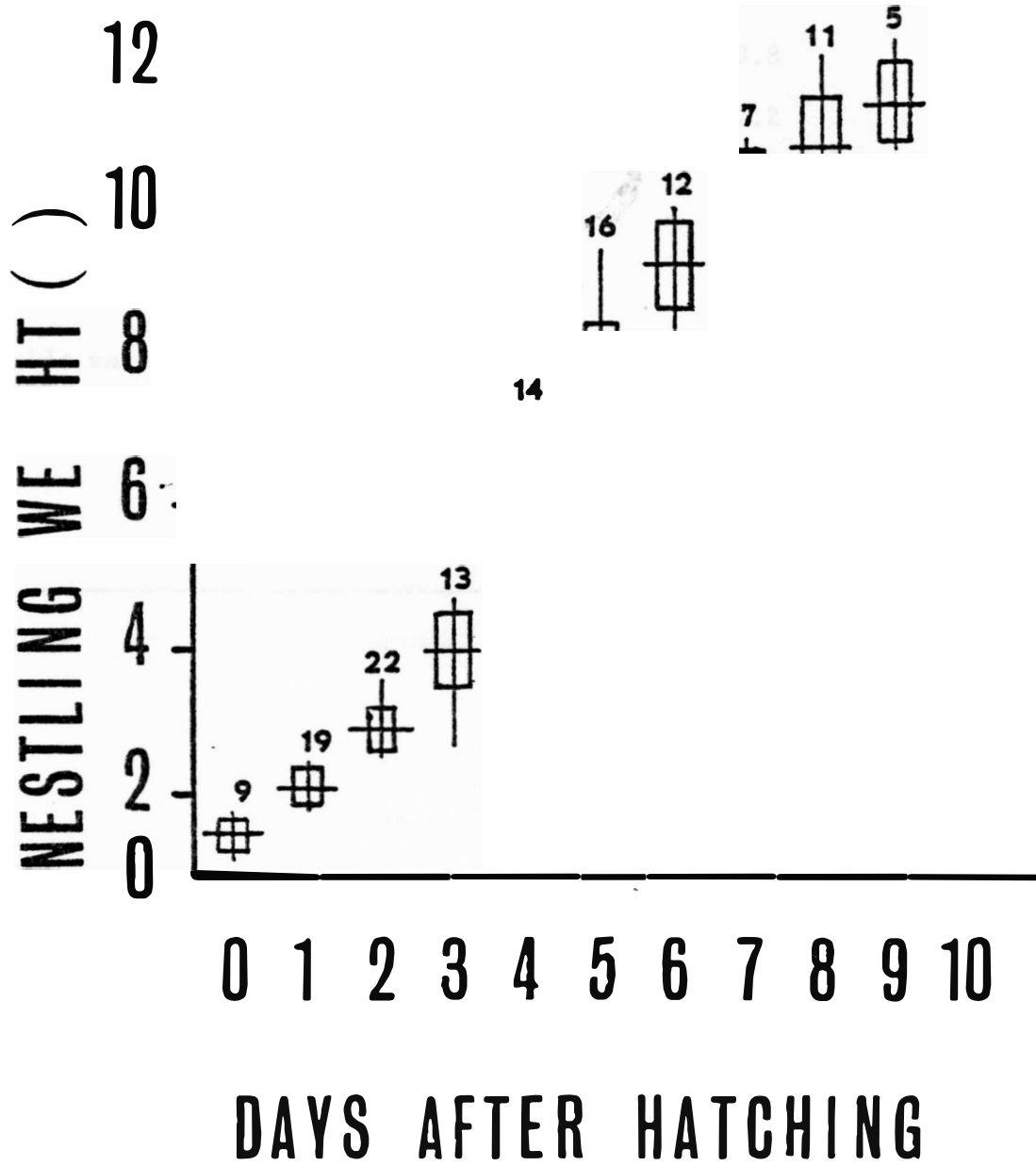
FIGURE 4

TABLE 4. Foods of nestling Black-throated Sparrows as percentages of the number of items brought.[a]

Insects

Lepidoptera (larvae)	36.6
Orthoptera	28.8
Coleoptera (larvae)	7.2
Isoptera	4.8
Hymenoptera	1.7
Other unidentified arthropods	14.4
Vegetable material	0.3
Unidentified items	6.2
	100.0

[a]N = 391.

as grasshoppers or beetle grubs, were mashed up before being fed. There was no distinct slow period in midday when feeding trips were markedly reduced, as reported by Best (1977) for Field Sparrows. Instead, adults continued to forage apparently unabated and fed young even with ambient temperatures of about 38.5°C. One pair made six trips during a 30-minute period from 12:45-13:15 when the temperature was just over 35°C. Smyth and Bartholomew (1966) reported Black-throats foraging at temperatures up to 40°C.

Early in the season Lepidoptera (Geometridae) larvae were the main food brought and these remained important throughout the season. Orthopteran nymphs and adults increased in importance as the season progressed and were most common after the summer rains. Isoptera and Hymenoptera (mainly ant brood) were fed only after the rains. In one instance an adult brought a fruit of the nightshade (Solanum elaeagnifolium) and, after several attempts, fed it to one nestling.

Black-throated Sparrows are apparently opportunistic in foraging for their young. They bring those insects that are in greatest abundance, shifting prey as the season progresses. Foraging for nestling food took place within a relatively restricted area of about 50 m in diameter around the nest. In no case was the full territory used at this stage of nesting. Creosotebush scrub was used extensively for foraging throughout the season. Most of the time adults foraged in or under Larrea or in taller grasses. Arroyos were generally not used as foraging areas even though nests were located in them. Following the onset of rains, adults at late nests foraged by foliage gleaning in Larrea or Prosopis more than on the ground. Tomoff (1974) reported the opportunistic use of creosotebush, following the emergence of insects after summer rains, by Black-throats

and other birds that usually were not foliage gleaners. Black-throats
in this region made the shift from ground foraging to foliage gleaning
earlier, when small insects were abundant from March to May. This is
reflected in the stomach contents of adult sparrows from a similar
creosotebush scrub area south of the site analyzed by B. Burger (unpub-
lished ms.).[1] In the fall and winter the diet was mostly seeds. In
March, as insects began to become available, but before nesting was
under way, seeds became less important. Insects increased in importance
to about 85% by weight of all adult food following the onset of rains in
July. Best (1977) and Robins (1971b) reported similar nestling diets in
other opportunistic sparrow species.

Young left the nest eight or nine days after hatching, before they
were able to fly. Within two or three days they were able to fly
sufficiently well to keep up with the adults. Once out of the nest,
foraging shifted back to the ground. Grassy areas were used extensively
by adults with young, concomitant with the return to ground foraging.
Adults continued to feed the young for at least two weeks, and family
groups remained together until the resumption of flocking in July and
August. Most birds were in flocks while the later nests were still
active.

The first young to fledge left the nest on 24 May. The last young
left the nest on 12 August. Thirty-three fledged from 13 nests for a
mean fledging rate of 2.5 per successful nest.

[1]Data on file, NMSU Department of Biology.

DISCUSSION

In recent years investigators have been increasingly intrigued by the adaptations of birds of the deserts of North America. Yet, few species have been studied in detail. One notable omission is that of the Black-throated Sparrow. While the physiology of this species has been adequately reported (Smyth and Bartholomew 1966, Gordon 1968, Johnson and Ohmart 1973), information is lacking on other aspects of its ecology that relate to its adaptations to its desert habitats.

Heat and Water Stress

Miller (1963) stated that birds in general are preadapted to deserts, through high body temperatures, tolerance of hyperthermia, low-water uric acid wastes, mobility, insectivory, and behavior, and that few truly desert-adapted birds are known. Small physiological differences would be enough to allow birds to survive in the desert. Since Miller's time many workers have presented their findings on desert birds. The Verdin survives in the desert without any apparent physiological adaptations (Goldstein 1974), by behavior (Austin, 1976, 1977) and by modification of its habitat through the use of its domed nest as protection from environmental extremes (Moore 1965, Austin 1976). The Cactus Wren likewise builds a protective nest and orients it to ameliorate its environment, relying on behavior to avoid extremes (Austin 1974).

Several species of quail (Callipepla squamata, Lophortyx gambelli, L. californicus) were shown to tolerate high temperatures through hyperthermia and by seeking shade during hot weather (Henderson 1971, Bartholomew and Dawson 1958). Other species shown to have special

36

adaptations to the desert are the Poor-will (Phalaenoptilus nuttallii) (Bartholomew et al. 1962) and the Roadrunner (Geococcyx californianus) (Ohmart 1973).

The Black-throated Sparrow, however, is the only bird of its size or smaller that has been shown to be truly desert-adapted. Smyth and Bartholomew (1966) found that the Black-throat could survive on a dry seed diet and called this species the best adapted of all the seed eaters to desert life. They found that it was able to excrete extremely concentrated urine and drink salt water. Furthermore, it remained active at temperatures up to 40°C. Gordon (1968) noted that Black-throats were able to significantly reduce respiratory water loss when deprived of water. Johnson and Ohmart (1973) attributed this efficiency and ability to tolerate water stress to the fact that Black-throats have kidneys containing two to three times as many medullary lobules, and these lobules are longer and more curved than those of most other finch species.

Unpredictability of Resources vs. Predation

Noy-Meir (1974) and Wiens (1974) state that as precipitation decreases, patchiness of resources increases. In deserts then, a high degree of patchiness and unpredictability is expected. As resources become more patchily distributed, the area needed to enclose an adequate supply becomes greater (Wiens 1976). Thus, desert birds should possess large territories, and do (Hensley 1954, Wiens 1974). In some species the resource of importance is nest sites. In the Verdin, for example, density is low in creosotebush scrub because there are few suitable nest plants (Raitt and Maze 1968). The Black-throated Sparrow, however, uses the habitat in a much more fine-grained way and some resource other

than nest site is responsible for its large territory. The territory of Black-throated Sparrows, because they are more fine-grained, is smaller than that of many desert birds of equal size. Food does not appear to be the defended resource since during the nestling stage the area used for food gathering was much smaller than that defended earlier. Similarly, during the critical fledgling stage, though the entire territory was used, it was the area in the vicinity of the young that was actively defended. Adults with young were not chased if they encroached on other sparrows' territory at this time.

In light of the high predation rate and consequent low success, it may be that space is the defended commodity for its aid in reducing predation (Lack 1966, 1968). Nest spacing of 150 m or more was not uncommon on this site. Greater success later in the season may have been due to factors other than the greater dispersion of nests, such as relative freedom from cowbird parasitism or greater supplies of food after the onset of rains, but food was not thought to be limiting at any time.

It would be valuable to know how territory size changes with changes in breeding density on the site. Certainly, a more thorough study of the problem of resource patchiness and territory size must be conducted for all desert birds before the reasons for the large territory can be determined.

Opportunism and Flexibility of Foraging

Another adaptation to patchiness and unpredictability is opportunistic omnivory, feeding on whatever happens to be most abundant at the time. This is apparently widespread in finches in nestling diets (Robins 1971b,

Best 1977) and in the change from seed eating in winter to insectivory in the breeding season. Concurrent with their generalist feeding habits, Black-throated Sparrows are at an advantage in foraging in creosotebush scrub habitats because they make extensive use of this shrub, in contrast to most species.

Opportunism in breeding also is advantageous in desert habitats and suppression of breeding in some seasons would be useful (Noy-meir 1974). R. Raitt (personal communication) informs me that he has evidence that Black-throats may not breed in very dry years, presumably because their insect foods do not occur without the rains.

Conclusions

The overall breeding ecology of the Black-throated Sparrow is not very different from that of many species studied. There are, however, slight differences in at least four aspects that are apparently enough to allow this bird to be among the most abundant of all desert birds in the Chihuahuan Desert and presumably elsewhere.

First, is its exceptional physiological adaptation to the extremes of desert environment.

Next, is its opportunistic foraging.

Third, its fine-grained use of habitat allows it to avoid the restrictions placed on other species by a lack of suitable vegetation, such as that of arroyos.

Last, large territories and consequent increased nest dispersion serve to reduce the otherwise extreme losses to high predation.

LITERATURE CITED

Austin, G. T. 1974. Nesting success of the Cactus Wren in relation to nest orientation. Condor 76:216-217.

Austin, G. T. 1976. Behavioral adaptations of the Verdin to the desert. Auk 93:245-262.

Austin, G. T. 1977. Production and survival of the Verdin. Wilson Bull. 89:572-582.

Austin, G. T. 1978. Daily time budget of the postnesting Verdin. Auk 95:247-251.

Austin, G. T. and R. E. Ricklefs. 1977. Growth and development of the Rufous-winged Sparrow (Aimophila carpalis). Condor 79:37-50.

Bailey, F. M. 1928. The birds of New Mexico. New Mexico Department of Game and Fish, Albuquerque, New Mexico.

Bartholomew, G. A. and W. R. Dawson. 1958. Body temperatures in California and Gambel's Quail. Auk 75:150-156.

Bartholomew, G. A., J. W. Hudson and T. R. Howell. 1962. Body temperature, oxygen consumption, evaporative water loss, and heart rate in the Poor-will. Condor 64:117-125.

Batschelet, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. AIBS, Washington, D.C.

Bent, A. C. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. Part 2. Dover Publications, Inc., New York.

Best, L. B. 1977. Nestling biology of the Field Sparrow. Auk 94:308-319.

Best, L. B. 1978. Field Sparrow reproductive·success and nesting ecology. Auk 95:9-22.

Davis, D. E. 1955. Breeding biology of birds, in A. Wolfson (ed.), Recent studies in avian biology. University of Illinois, Urbana.

Dixon, K. L. 1959. Ecological and distributional relations of desert scrub birds of western Texas. Condor 61:397-409.

Goldstein, R. B. 1974. Relations of metabolism to ambient temperature in the Verdin. Condor 76:116-119.

Gordon, M. S. 1968. Animal function: principles and adaptations. Macmillan Co., New York.

Gullion, G. W., W. M. Pulich and F. G. Evenden. 1959. Notes on the occurrence of birds in southern Nevada. Condor 61:278-297.

Gustafson, J. R. 1975. A Sage Sparrow egg in a Black-throated Sparrow nest. Auk 92:805-806.

Heckenlively, D. B. 1967. Role of song in territoriality of Black-throated Sparrows. Condor 69:429-430.

Heckenlively, D. B. 1970. Song in a population of Black-throated Sparrows. Condor 72:24-36.

Henderson, C. W. 1971. Comparative temperature and moisture responses in Gambel and Scaled Quail. Condor 73:430-436.

Hensley, M. M. 1954. Ecological relations of the breeding bird population of the desert biome in Arizona. Ecol. Monog. 24:185-207.

Johnson, O. W. and R. D. Ohmart. 1973. The renal medulla and water economy in Vesper Sparrows (Poecetes gramineus). Comp. Biochem. Physiol. 44A:655-661.

Lack, D. 1966. Population studies of birds. Oxford University Press, London.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen and Co., London.

Ludwig, J. A., J. F. Reynolds and P. D. Whitson. 1975. Size-biomass relationships of several Chihuahuan Desert shrubs. Am. Midl. Nat. 94:451-461.

Marshall, J. T. Jr. 1963. Rainy season nesting in Arizona. Proc. 13th Intern. Ornithol. Congr. 620-622.

Miller, A. H. 1955. The avifauna of the Sierra del Carmen of Coahuila, Mexico. Condor 57:154-178.

Miller, A. H. 1958. Adaptation of breeding schedule to latitude. Proc. 12th Intern. Ornithol. Congr:513-522.

Miller, A. H. 1963. Desert adaptation in birds. Proc. 13th Intern. Ornithol. Congr.:666-674.

Montgomery, T. H. 1905. Birds of Brewster, Co., Texas. Auk 22:12-15.

Moore, D. R. 1965. Breeding biology and nest usage of the Verdin in southern New Mexico. Unpublished M.S. thesis, Las Cruces, New Mexico State Univ.

Nice, M. M. 1941. The role of territory in bird life. Am. Midl. Nat. 26:441-487.

Nice, M. M. 1957. Nesting success in altricial birds. Auk 74:305-321.

Noy-Meir, I. 1974. Desert ecosystems: higher trophic levels. Ann. Rev. Ecol. Syst. 5:195-214.

Oberholser, H. C. 1974. The bird life of Texas. University of Texas Press, Austin.

Ohmart, R. D. 1973. Observations on the breeding adaptations of the Roadrunner. Condor 75:140-149.

Orians, G. H. 1966. Food of nestling Yellow-headed Blackbirds, Cariboo Parklands, British Columbia. Condor 68:321-337.

Patterson, T. L. and L. Petrinovich. 1978. Territory size in the White-crowned Sparrow (Zonotrichia leucophrys): measurement and stability. Condor 80:97-98.

Payne, R. B. 1977. The ecology of brood parasitism in birds. Ann. Rev. Ecol. Syst. 8:1-28.

Potter, P. E. 1972. Territorial behavior in Savannah Sparrows in southeastern Michigan. Wilson Bull. 84:48-59.

Raitt, R. J. and R. L. Maze. 1968. Densities and species composition of breeding birds of a creosotebush community in southern New Mexico. Condor 70:193-205.

Raitt, R. J. and S. L. Pimm. 1976. Dynamics of bird communities in the Chihuahuan Desert, New Mexico. Condor 78:427-442.

Ricklefs, R. E. 1967. A graphical method of fitting equations to growth curves. Ecology 48:978-983.

Ricklefs, R. E. 1968. Patterns of growth in birds. Ibis 110:419-451.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contribution to Zool. 9:1-48..

Robins, J. D. 1971a. A study of Henslow's Sparrow in Michigan. Wilson Bull. 83:39-48.

Robins, J. D. 1971b. Differential niche utilization in a grassland sparrow. Ecology 52:1065-1070.

Scott, W. E. D. 1887. On the avifauna of Pinal Co., with remarks on some birds of Pima and Gila Counties, Arizona. Auk 4:196-205.

Small, A. 1974. The birds of California. Winchester Press, New York.

Smyth, M. and G. A. Bartholomew. 1966. The water economy of the Black-Throated Sparrow and the Rock Wren. Condor 68:447-458.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freemand and Co., San Francisco, Calif.

Stamp, N. E. 1978. Breeding birds of riparian woodland in south-central Arizona. Condor 80:64-71.

Stefanski, R. A. 1967. Utilization of the breeding territory in the Black-capped Chickadee. Condor 69:259-267.

Stenger, J. 1958. Food habits and available food of Ovenbirds in relation to territory size. Auk 75:335-346.

Tomoff, C. S. 1974. Avian species diversity in desert scrub. Ecology 55:396-403.

Tompa, F. S. 1962. Territorial behavior: the main controlling factor of a local Song Sparrow population. Auk 79:687-697.

Wauer, R. H. 1962. A survey of the birds of Death Valley. Condor 64:220-233.

Weeden, J. S. 1965. Territorial behavior of the Tree Sparrow. Condor 67:193-209.

Welch, D. A. 1975. Savannah Sparrow breeding and territoriality on a Nova Scotia Dune Beach. Auk 92:235-251.

Whitford, W. G. 1972. International Biological Program, Jornada Validation Site. Research Memorandum 2.4:1-138.

Wiens, J. A. 1973. Interterritorial habitat variation in Grasshopper and Savannah Sparrows. Ecology 54:877-884.

Wiens, J. A. 1974. Climatic instability and the ecological saturation of bird communities in North American grasslands. Condor 76:385-400.

Wiens, J. A. 1976. Population responses to patchy environments. Ann. Rev. Ecol. Syst. 7:81-120.