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PHYSIOLOGICAL AND ETHOLOGICAL ADAPTATIONS OF THE RUFOUS-WINGED SPARROW (AIMOPHILA CARPALIS) TO A DESERT ENVIRONMENT.

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PHYSIOLOGICAL AND ETHOLOGICAL ADAPTATIONS
OF THE RUFOUS-WINGED SPARROW (AIMOPHILA CARPALIS)
TO A DESERT ENVIRONMENT

by

Robert Dale Ohmart

A Dissertation Submitted to the Faculty of the

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GRADUATE COLLEGE

I hereby recommend that this dissertation prepared under my direction by Robert D. Ohmart

entitled Physiological and Ethological Adaptations of the Rufous-winged Sparrow (*Aimophila carpalis*) to a Desert Environment.

be accepted as fulfilling the dissertation requirement of the degree of Doctor of Philosophy

Stephen M. Russell
Dissertation Director

26 August 1968
Date

After inspection of the final copy of the dissertation, the following members of the Final Examination Committee concur in its approval and recommend its acceptance:*

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*This approval and acceptance is contingent on the candidate's adequate performance and defense of this dissertation at the final oral examination. The inclusion of this sheet bound into the library copy of the dissertation is evidence of satisfactory performance at the final examination.

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SIGNED: Robert D. Ohmart

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

A 4-year study was conducted to determine the physiological and behavioral means whereby the Rufous-winged Sparrow, an endemic resident of the Sonoran Desert, successfully meets the demands of a hot, dry desert.

Pair bonds and territories are maintained for life, but when reproductive rates were high (2.7 young fledged per pair), several additional birds associated with the territorial pair in winter. Territorial defense was year round in years of lower reproductive success.

A daily summer foraging cycle was present, in which the birds foraged on unshaded ground surfaces at moderate temperatures early and late in the day, moved into shaded ground situations as temperatures rose and foraged in shrubs during the highest daily temperature. During the hottest portion of the day, foraging ceased and the birds sat in the shade inactive. Insect and possible plant materials were consumed during the shrub shade foraging. Foraging habits combined with an efficient kidney allows the species to exist without free water in a hot, xeric environment.

Rufous-winged Sparrows normally nest only after the beginning of summer rains in July; gonadal recrudescence occurs from early March into mid-June. The sparrows may nest

in spring following unusually heavy winter and spring rains. Gonadal enlargement may be completed as rapidly as 3 weeks. Summer rainfall appears to be the stimulus initiating summer nesting, but an abundant food supply may stimulate spring breeding.

Mean fledging success in summer ranged from 1.1 (6 pairs) to 2.7 (10 pairs) young per pair. Greatest success was associated with high insect densities resulting from heavy initial summer rains followed by frequent moderate showers. High insect densities serve as a buffer and reduce predation upon vulnerable Rufous-winged Sparrow nests. Low summer rainfall and low insect densities were associated with heavy nest destruction and low fledging success. Spring nesting occurred only twice and an average of 0.3 (4 pairs) and 1.1 (11 pairs) young per pair fledged.

The data was highly suggestive that clutch size was regulated by food supply. Clutches following the summer rains all contained three eggs. Clutches laid in spring or subsequent clutches after the rains, contained from two to four eggs.

I feel that the present age difference between New World deserts and the more ancient deserts of the Old World is less important for the evolution of highly specialized adaptations to a desert existence than is currently believed.

Magnitude of the desert and selection pressure resulting from aperiodic rainfall appears to have been more important for avian specialization than time.

INTRODUCTION

Animals living in arid or semi-arid hot environments face unique problems in obtaining water to replace daily losses. Birds may meet water requirements through consumption of free water, absorption of preformed water in the diet, and utilization of metabolic water. The ability of birds to produce uric acid (uricotelism) instead of urea aids in two ways: twice as much nitrogen can be voided per molecule of uric acid than in a molecule of urea and uric acid can be excreted in semi-solid form whereas urea must be passed in an aqueous solution. Birds also have a high metabolic rate, which means a greater amount of metabolic water is produced. However, Bartholomew and Cade (1963) state "...it is inviting to postulate that reliance on oxidative metabolism as the only source of water is a rare and perhaps nonexistent condition among small birds." Seed eating birds, especially, would be at a disadvantage in a dry, hot environment and would be expected to be in constant water imbalance. Cade (1964) stated "....if granivorous birds are to occupy desert regions, they must in most cases rely on the availability of free water to restore their large daily deficits."

Much of the research conducted thus far to assess water economy and renal efficiency has been centered primarily around granivorous birds. Available data regarding water deprivation has demonstrated that only a few species can survive on a diet of air dried seeds under normal ambient temperatures. Those reported thus far to possess this ability are the Salt Marsh Savanna Sparrow (Passerculus sandwichensis) (Cade and Bartholomew, 1959), the Scaly-feathered Finch (Sporopipes squamifrons) (Cade, 1965), the Black-throated Sparrow (Amphispiza bilineata) (Smyth and Bartholomew, 1966), the Brewer's Sparrow (Spizella breweri) (Ohmart and Smith, unpublished), the Cut-throat Finch (Amadina fasciata) (Edmonds, 1968) and domesticated stock of two species found in Australia, the Budgerygah (Melopittacus undulatus) (Cade and Dybas, 1962), and the Zebra Finch (Taeniopygia castanotis) (Calder, 1964, and Cade, Tobin, and Gold, 1965). The Cut-throat Finch and Scaly-feathered Finch were tested under semi-natural conditions and data were not presented to indicate if the deprived birds reduced their activity. Data on the Desert Sparrow and Zebra Finch indicates that activity of the unwatered birds equaled that of watered birds. The actual process by which these animals can exist without reducing activity while on a diet of dry seeds is not fully understood.

The varying ability of caged birds to utilize different concentrations of sodium chloride solutions provides an experimental test of renal efficiency. At present, no terrestrial bird is known to possess a functional salt gland as is found in marine birds. Bartholomew and Cade (1963) state, "Most, if not all, land birds must rely on their kidneys for salt excretion. It is to be expected, therefore, that most land birds will be unable to drink sea water or to use water from saline springs or lakes with a salt concentration more than about 1 per cent." Only a few of the land birds studied have demonstrated the ability to survive while consuming saline solutions equaling the concentration of sea water. Some races of the Savanna Sparrow possess this ability (Cade and Bartholomew, 1959). Other species which can utilize molar concentrations equivalent to sea water are the Black-throated Sparrow (Smyth and Bartholomew, 1966), the Zebra Finch (Oksche, et al., 1963), and the Brewer's Sparrow (Ohmart and Smith, unpublished). In general, avian species whose kidneys have been studied thus far do not have the concentrating ability of mammals. This may be because bird kidneys lack the loop of Henle, as pointed out by Bartholomew and Cade (1963). Species possessing the ability to process molar concentrations of sodium chloride equivalent to sea water indicates water conservative capabilities, which is advantageous in a xeric environment.

Studies of desert birds have demonstrated that environmental cues other than photoperiod may stimulate breeding. Lack (1954) proposed that the breeding season evolved in relation to the ultimate factor, food supply, with reproduction occurring when productivity of the habitat is at or near maximum. In arid regions, the habitat productivity is usually highest when adequate water is available. Immelman (1963) reported that sight of falling rain influenced gonadal development and breeding behavior in two species of Australian birds. Serventy and Marshall (1957) also reported breeding correlated with rainfall during their work in Australia, and Lack (1950) discussed birds breeding with response to rain in the Galapagos Islands. Gilliard (1959) proposed that some birds in northern Venezuela use rain as the proximate factor while Marchant (1959) reported similar findings in southwestern Ecuador. Experiments by Marshall and Disney (1957) showed availability of suitable nesting material will stimulate nest construction. These phenomena have been reported in other deserts; only the data of Marshall (1963) on the Abert's Towhee (*Pipilo aberti*) and Brown Towhee (*P. fuscus*) indicate that some North American desert species may have specialized to the degree of using cues other than photoperiod to stimulate nesting activity.

The objective of my research was to determine if specific physiological and/or ethological adjustments to a desert environment have evolved in the Rufous-winged Sparrow (*Aimophila carpalis*). I selected this species because the following criteria suggested that it might possess adaptations for a desert existence.

1) The species is endemic to the Sonoran Desert area.

2) It is small (14-16 grams), and feeds primarily on seeds.

3) It has appeared and disappeared from southern Arizona (see Phillips, Marshall, and Monson, 1964), in a manner suggesting climatic factors may have been responsible.

4) Very little information is known about its life history.

5) Marshall (1963) reported that it breeds only after the summer rains.

With these points in mind, I conducted a 4-year study of the biology of the species.

MATERIALS AND METHODS

A desert grassland area on Wilmot Road, southeast of Tucson, Arizona, was selected as the principal study site. The tract of approximately 35 acres was located 7 miles south and 7 miles east of Tucson at an elevation of about 2,760 feet. A pocket transit and chain were used to establish north-south and east-west grid lines 200 feet apart. Intersecting grid lines were marked with plastic survey tape and wooden stakes.

Data on plant density and composition were obtained by randomly selecting eight grid markers in the study area and reading three 15-meter line intercepts at each point. Directions were determined by placing a watch with a sweep second hand on the grid marker and running the line in the direction the sweep hand was pointing when referred to at undetermined intervals.

Climatological data were from three sources. Summer rainfall data were obtained from a rain gauge in the study area. When torrential rains washed the gauge away, and in winter months when rainfall was less localized, data were obtained from Davis-Monthan Air Force Climatological Station, 3.2 miles north-northwest of the study area. Tucson mean monthly temperature and precipitation data were obtained from the Atmospheric Physics Laboratory at the University of Arizona.

Study of the species began in February, 1965, and was continued until July, 1968. The study area was visited regularly throughout the 4 years, with the majority of the observations being conducted from March through October; visits were made almost daily when the birds were breeding. Direct observations with the aid of 7x35 binoculars yielded general information on breeding activities and foraging behavior. These data, along with observations of the condition of the habitat, were recorded at each visit to the study area. Birds were captured with Japanese mist nets placed in strategic regions in the study area and were marked with plastic color bands and aluminum Fish and Wildlife Service bands. Numbers in the text refer to the last three digits in the Fish and Wildlife Service band. Individuals were recaptured when their reproductive status was in question.

Data on foraging behavior were obtained by following pairs with a stop watch to determine duration of activities on exposed ground surface, shaded ground surface, exposed in shrubs, or shaded in shrubs. Ground surface and shaded ground surface temperatures were monitored hourly to determine if the foraging behavior of the birds was correlated with temperature.

Information documenting gonadal recrudesence was obtained from many pairs collected at intervals from early in the year until the beginning of the breeding season during each of the 4 years. All pairs were collected within 3 miles of the study area and no closer than 1 mile. The specimens were preserved as rapidly as possible after collection (maximum of 1 hour) in AFA consisting of two parts acetic acid, two parts 95% ethanol, one part formalin, and five parts distilled water. After about 3 days in the fixative, the specimens were transferred to 70% ethanol for storage. The gonads were removed at a later time to be weighed and measured.

Clutch size was determined by examining the nests at about 0800 hours daily to mark and record each egg laid. Data on clutch size regulation came only from nests where the eggs were marked daily or where the number observed could be trusted with reasonable accuracy, i.e., four or three in a clutch containing no Brown-headed Cowbird (Molothrus ater) eggs. Reproductive success was determined by counting only young fledged.

Grasshopper densities in the study area were determined by randomly sampling areas approximately 1 yard square. I counted all animals that flushed as I approached, then I systematically worked a stick over the quadrat to flush the more persistent insects. Any observed entering the sample plot were subtracted from the total count. Ten or more of these counts were made and the mean determined. The counts were repeated each time there appeared to have been a change in numbers.

Birds used in salt tolerance tests were netted and held in an outside aviary for a week or more to acclimate them to captivity. They were then transferred to individual cages measuring 22 x 22 x 36 cm, and placed in a windowless chamber where the ambient temperature was maintained at 20 C. A photoperiod from 1200 hours to 2400 hours was maintained with an electrical timer. A finch seed mix and chicken mash was available at all times. Tenebrio larvae were supplied between tests and two were given each bird every 5 days during all tests because of an apparent vitamin deficiency when the birds were maintained on the finch seed and chicken mash combination. During the experiments with the more concentrated solutions, the test birds were given two larvae every 4 days. Graduated cylinders with L-shaped tubes were used to supply salt solutions to the test birds. Only the horizontal portion of the L-tube, which contained the orifice for drinking, was placed in the cage to minimize spillage. All tests were conducted for 21 days. Body weight and fluid consumption were recorded between 1000 and 1200 hours daily to insure the animals would be in a postabsorptive state.

STUDY AREA

The major topographical features of the study area were a slight drop in elevation from east to west and the presence of two large washes. One wash entered near the northeast corner of the area and the other came in along the southern border. The washes converged at the western border (Wilmot Road) of the study area. The northern wash was not as broad as the southern one and had a central channel which ranged in width from 5 to 15 feet. The broad southern wash lacked the channels and had a dense stand of tobosa grass (*Hilaria mutica*) throughout it. The portion of the study area between the two washes was 12-24 inches higher than the wash areas and consequently was better drained (Fig. 1).

The area was considered a bunch-grass/thornbush association (see Table 1), or swale habitat as described by Phillips (1968). Along the northern portion of the study area was a plant community which was composed primarily of creosote (*Larrea tridentata*). The two large washes, and the area where they coalesce, housed dense stands of desert hackberry (*Celtis tala*), mesquite (*Prosopis juliflora*) and burroweed (*Haplopappus tenuisectus*). Other shrubs found in the wash areas, but not recorded in the sampling, were palo verde (*Cercidium* sp.), catclaw (*Acacia greggi*), and saltbush

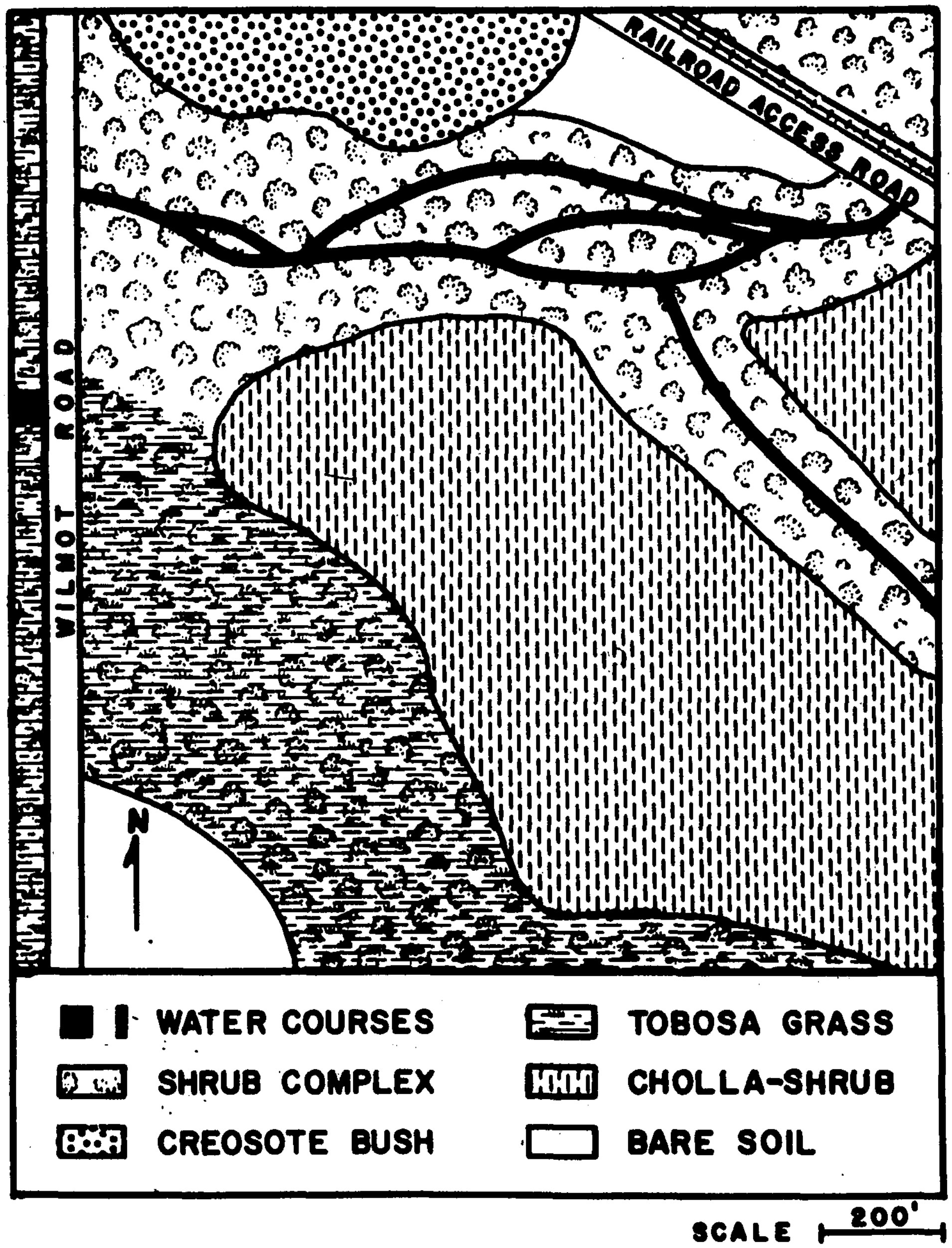

Fig. 1. Study area drawing from an aerial photograph showing general vegetation composition. For a full description, see text.

TABLE 1. COMPOSITION AND DENSITY
OF VEGETATION ON THE STUDY AREA

	Density (%)[a]	Frequency (%)[b]
<u>SHRUBS</u>		
Haplopappus tenuisectus	7	66
Prosopis juliflora	6	37
Celtis tala	5	37
Mimosa biuncifera	0.4	5
Baccharis glutinosa	[c]T	5
Acacia constricta	T	5
Ephedra trifurca	T	5
Gutierrezia lucida	0.4	16
<u>CACTI</u>		
Opuntia sp. (round stemmed)	0.5	16
Opuntia engelmannii	T	9
Echinocactus wislizeni	T	1
<u>PERENNIALS (SMALL)</u>		
Sida sp.	T	5
Hoffmanseggia microphylla	T	5
Psilostrophe cooperi	T	5
Mirabilis sp.	T	12
<u>GRASSES</u>		
Hilaria mutica	10	37
Aristida ternipes	0.5	29
Setaria sp.	0.5	16
Trichachane californica	T	12
Panicum obtusum	T	16

[a]Expresses per cent ground cover.
[b]Expresses per cent of the 24 line intercepts on which the species was recorded.
[c]Trace; less than 0.4%.

(*Atriplex* sp.). The better drained area between the two washes supported similar shrub components, but also had dense stands of round stemmed chollas (*Opuntia* sp.). The shrubs in this area were stunted and, in many, as much as 50% of the above ground portion was dead. The major vegetational difference between the two washes was the presence of the dense tobosa grass and panic grass (*Panicum obtusum*) in the large southern wash. The small amount of grass present in the northern wash consisted of scattered bunches of tobosa and Arizona cottontop (*Trichachane californica*). During the summer rains, an annual grama grass (*Bouteloua* sp.) became common. Burroweed was much more common in the northern wash.

Territories were located along the two large washes and contained numerous shrubs and areas of bare soil. The tobosa grass of the southern territories was replaced by burroweed in the northern ones.

NATURAL HISTORY

The Rufous-winged Sparrows were found to have some habits unique among small North American fringillids. Adults remained on their territories throughout the year, and the 10 marked males in the study area defended their territories year round, except in the winter of 1965 and 1966 when small flocks were formed. The flocks, which I call territorial flocks, usually consisted of the resident male and female plus about four to six immature birds. These flocks were not familial groups as was suspected by Phillips (1968) for I found that the young leave the nest area soon after they obtain their first winter plumage. I noted an occasional song in the winter and in six cases where I identified the singing individual, it was the territorial male. I believe territorial flocks form when the reproductive rates are high, for they were formed in the winter of 1965 when 2.7 young were fledged per pair. In other years, when the reproductive rate was lower, the resident male prevented ingression of the wandering immatures and flocks were not formed. Apparently, once the male establishes the territory, he remains there until the area is destroyed or he dies.

Pair bond appears to be for life, although in one case, I observed a female moving to another male in the study. One pair, male no. 598 and female no. 597, was banded together in 1965 and was still together in July 1968. Other females in the study associated with their mates as long as 3 years before disappearing.

Pairing appears to occur quite early in young birds. In July of 1966, there were two males in the study that had lost their mates in the winter, and another that had lost his female (no. 541) at the end of spring. These three males paired with immature females that were estimated to be between 2 and 3 months of age. Pairing and pair relationship appeared to be normal, but the males were unable to stimulate the females to breed. Nesting did not occur by the three pairs until after the summer rains in 1967.

Nest building and incubation were conducted solely by the female, but the male aided the female in caring for the young. When the female attempted renesting, the male completely took over the care of the young of the first brood shortly after they fledged. The sedentariness and pair bond behavior are very similar to the much larger Brown Towhee (Pipilo fuscus) reported by Marshall and Johnson (1968) and Childs (1968a, b).

The nest of the species is a conspicuous, deeply cupped structure which is usually placed on the periphery of a spinescent shrub such as hackberry or palo verde. The nestling at hatching is dark-skinned and sparsely covered with dark down, but obtains a feather covering by the seventh day of age.

FORAGING BEHAVIOR

Foraging data from the spring and summer months showed a pattern differing from that of the winter. Whether the birds were in territorial flocks or pairs, the winter foraging pattern consisted primarily of ground surface foraging interspersed with shrub foraging. A bird would hop along, peck a few times and continue hopping or fly into a shrub. After foraging through the shrub, the bird exits at ground level or flies from the shrub to the ground to resume ground surface foraging. In the spring and summer months, from sunup (0500 hours) to about 0700 hours, the birds foraged over the ground surface exposed to all radiation until the exposed ground surface temperature approached 32 C (see Fig. 2). From 0700 hours to approximately 1000 hours, the birds foraged on the ground surface in the shade. The exposed shrub value in Fig. 2 was derived primarily from periods in which the males were singing from shrub tops. As the ground shade temperature approached 37 C, the birds ceased ground shade foraging and continued feeding in the lower branches of the shrubs. In many observations of foraging, I recorded a bird perched in a shrub removing seeds from a nearby grass infloresce nse. In one instance, a Rufous-winged Sparrow foraged for 30 minutes on grass heads

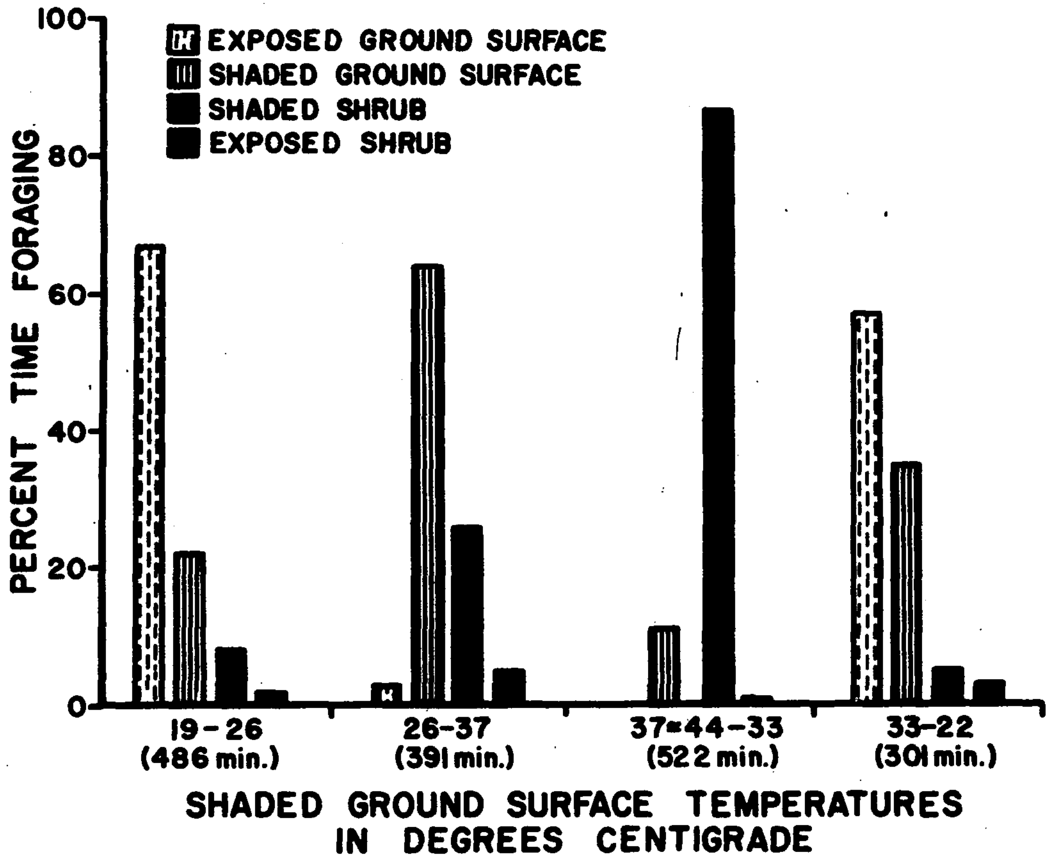

Fig. 2. Histogram of foraging activities with respect to shaded ground temperatures. The notation of 37=44 C signifies that maximum daily temperature may vary from day to day.

protruding from a Cactus Wren (Campylorhynchus brunicapillus) nest constructed in a desert hackberry. The highest ambient temperatures were recorded from about 1000 hours to approximately 1700 hours; during this time the birds foraged in the deep shaded portion of the shrub. Occasionally, the observed pair would move from one shrub to another, but as temperatures reached their maximum, the birds always sought a large, dense heavily leafed desert hackberry. They would normally perch in the shrub between 1.5 and 3.5 feet above the ground with eyes closed, mandibles open, and the wings slightly elevated and held away from the body. In two instances, there was a slight breeze and the birds faced into the wind. This behavior usually lasted for about 45 minutes to 1 hour before the birds began foraging slowly in the deep shaded portion of the shrub.

General observations of other species in the area showed that Verdins (Auriparus flaviceps), Cactus Wrens, Curve-billed Thrashers (Toxostoma curvirostre) and Black-tailed Gnatcatchers (Polioptila melanura) were still foraging in direct sunlight as much as an hour after Rufous-winged Sparrows moved into the shade.

SODIUM CHLORIDE METABOLISM

I conducted laboratory experiments on metabolism of sodium chloride in the Rufous-winged Sparrow to determine renal efficiency. These experiments were not completed because of nutritional problems encountered while trying to maintain live animals in the laboratory, but the available information provides a good indication of the renal efficiency of the species. When the birds were supplied with ad libitum distilled water, their consumption (15 birds) was 38% body weight (14 g), with two SE being ± 2.5. Six birds on a 0.1 M solution of sodium chloride and 12 on a 0.2 M solution showed little deviation from the distilled water values. Eleven birds tested on a 0.3 M solution differed significantly from distilled water values. The birds reduced their water intake to 11% body weight with two SE being ± 1.2. The response on a 0.4 M solution was similar, except the birds reduced their intake to 0.8% body weight per day and two SE for the six birds was ± 0.1.

TESTICULAR RECRUDESCENCE AND REPRODUCTION

Gonadal cycles document the growth and reproductive readiness of the population. Knowledge of the seasonal fluctuations in the size of the gonads are even more important in this species because of its peculiar breeding periods.

1965 Breeding Season

When the field work was initiated in 1965, the birds in the study area were paired. It appears from Fig. 3 that the males' testes began enlarging about the beginning of March in 1965. Size increase was gradual until maximum size was attained in late June.

Breeding in 1965 followed the summer rains, except on 11 June, female no. 101 constructed a nest that was destroyed after two eggs were laid. No other birds are known to have attempted to nest until after the beginning of the summer rains. Five days of intermittent overcast preceded the 2 inches of rain that fell on the afternoon of 8 July. Two females began carrying nesting material on the morning of 9 July. A trace of rain was recorded on the afternoon of 9 July and 0.38 inch the following morning. Four females were observed in early stages of nest construction on the

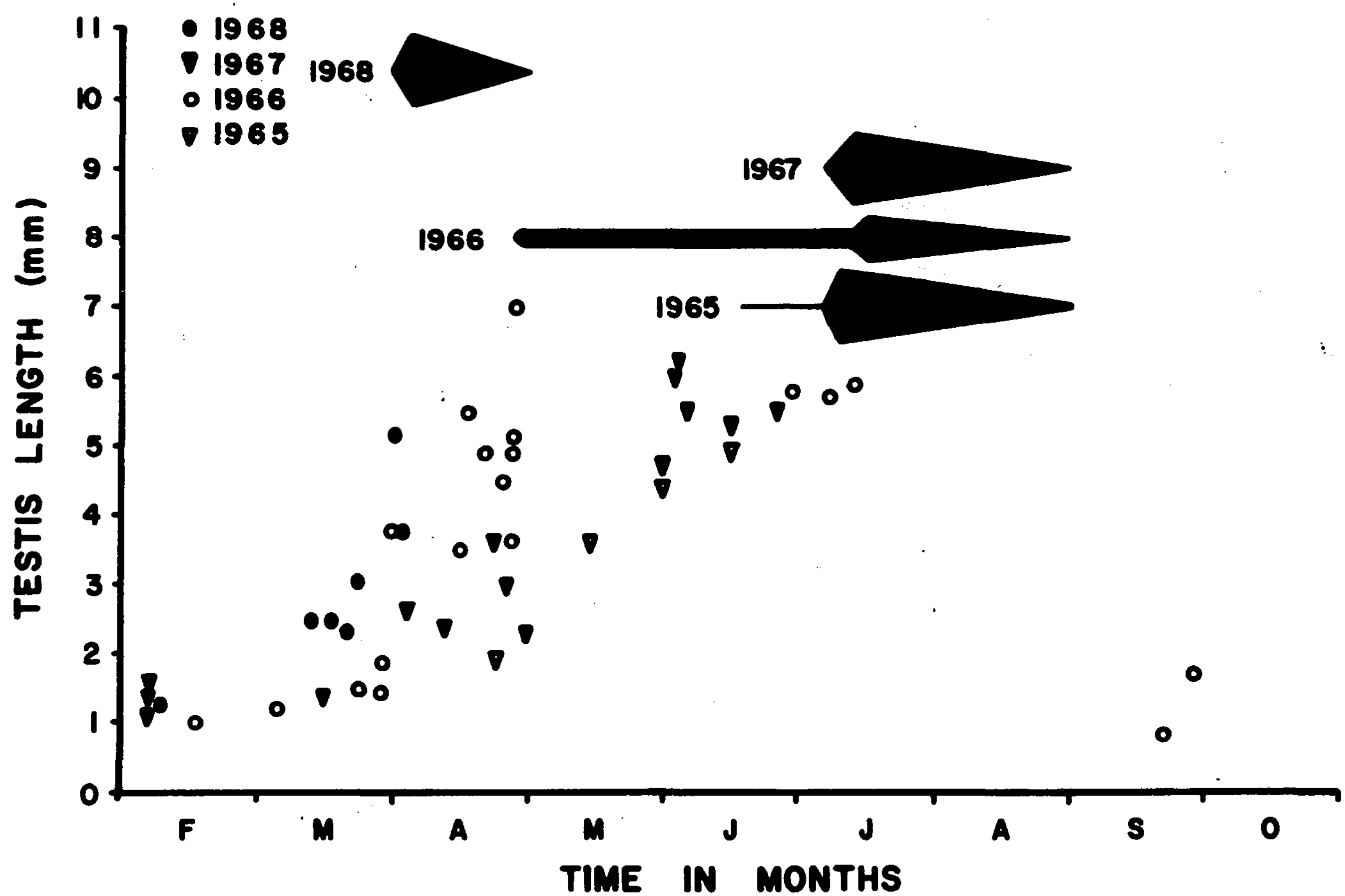

Fig. 3. Gonadal recrudescence during the four year study. Length of shaded bars represent initiation and completion of breeding activities of birds in the study area. Rapidity at which full width of bar is reached indicates the relative percent of birds breeding.

morning of 11 July and one on 12 July. One female (no. 541) delayed nest construction until 17 July, while another (no. 546) began construction 18 July (see Fig. 4). The mate of female no. 541 did not remain consistently with his mate, but also spent much time with female no. 546, which I believed delayed nest construction. Female no. 556 was not included in the study until early August. I presume she constructed an earlier nest. The mean number of days between the construction of the female's first nest and the deposition of her first egg was 5.2 (n = 9, 1 undetermined).

New grasses and forbs became evident in the study area in 1965 on 20 and 21 July. By 27 July, these plants were between 4-6 inches in height. Leaf densities on the desert hackberry were high by 1 August. On 27 July, I recorded numerous grasshopper instars over the study area, and by early August, numbers ranged from 9-13 per square yard.

1966 Breeding Season

The recrudescence pattern in 1966 and 1968 was different from that in 1965 and 1967. Initial size increase began about the same time as in the other years, but in late March and early April, increase in testis size was extremely rapid with maximum size being reached the latter part of April in 1966 and the first part of April in 1968.

Precipitation was heavy in December of 1965, and in January and February of 1966 (Fig. 5). Only traces were

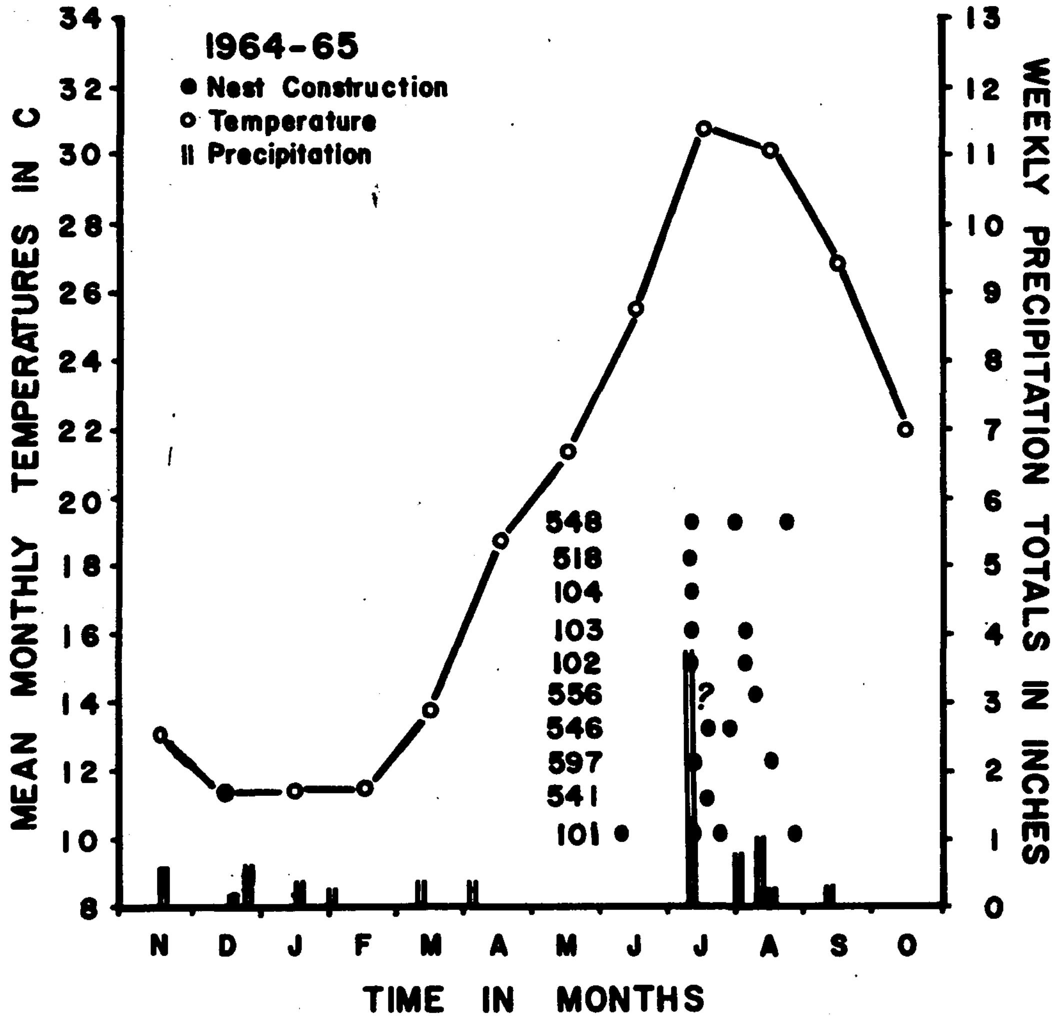

Fig. 4. Temperature, precipitation, and timing of nest construction during the 1965 breeding season. Individual nesting females are identified by numbers in the graph.

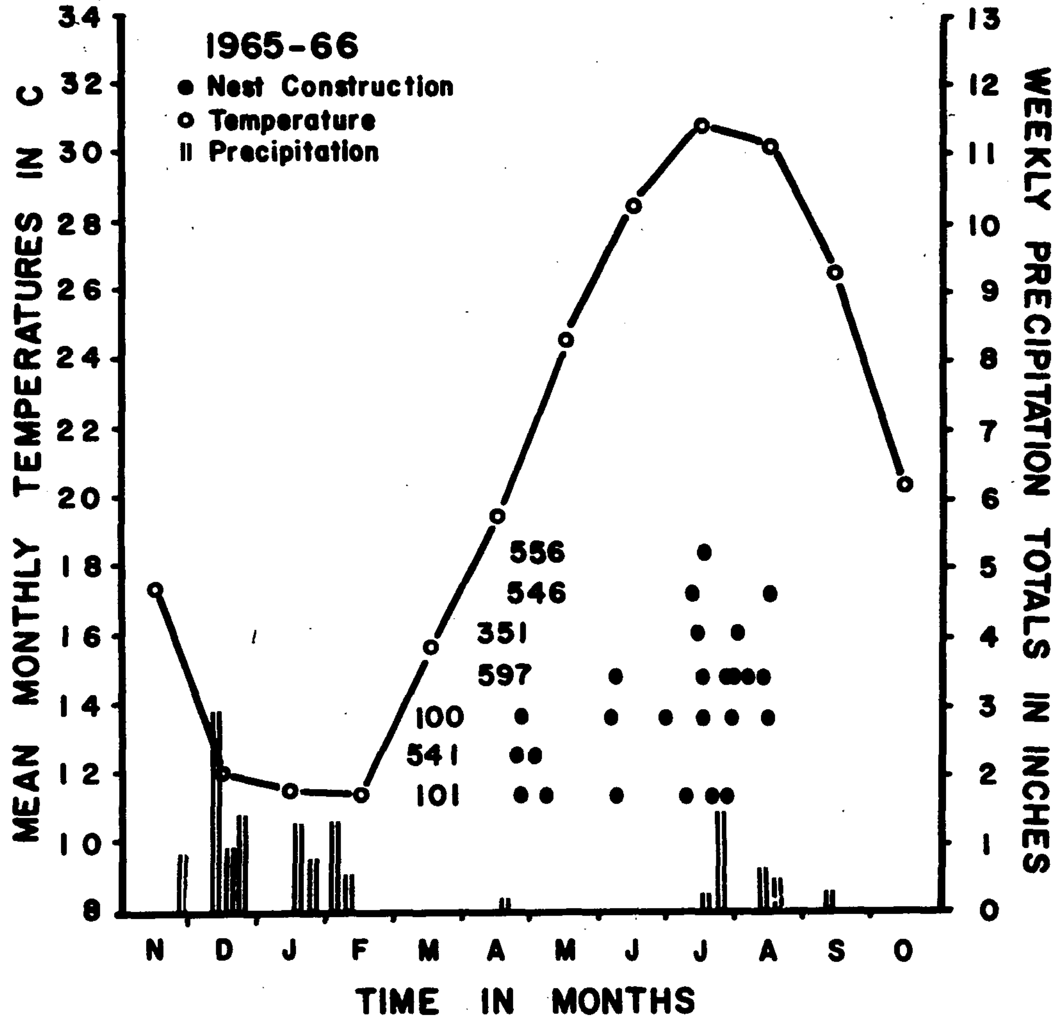

Fig. 5. Temperature, precipitation, and timing of nest construction during the 1966 breeding season. Individual nesting females are identified by numbers in the graph.

recorded in March, and 0.29 inch recorded in April, but the earlier rains had percolated deeply and moisture was available to the shrub roots. The shrub response in the spring of 1966 was much greater than observed in 1965 and 1967, but about equal to that in 1968. New leaves were observed on the mesquites and desert hackberries on 29 March, and were fully leaved by mid-April. From late April until the summer rains in July, the surface soil was extremely dry, but the shrubs in the study area were very green. The desert hackberry produced a light crop of berries in May and early June, and another light crop in August after the summer rains. The vegetation response observed in the summer of 1966 was low compared to 1965. Annual grasses and forbs grew to only 2 or 3 inches in height and were confined to the shaded areas or low regions where soil moisture was highest. The few annuals that did appear were evident in the study area on 5 August.

Three of the seven pairs of Rufous-winged Sparrows in the study area began nest building in late April of 1966. One female, no. 541, fledged one young in her second attempt in early March, and then disappeared from the study area. The other two females, no. 100 and no. 101, repeatedly had their nests destroyed, but attempted to bring off young on into August. One female, no. 597, constructed a nest in June, but it was destroyed as well.

The summer rains in 1966 were late in coming and light in amount. Traces were recorded up to 16 July at which time

0.14 inch was recorded and 0.16 inch on 19 July. The first intense rainfall (0.92 inch) was recorded on 25 July.

There appeared to be a resurgence of breeding activity following traces of rainfall in the second week of July (Fig. 5). The three hens which had not constructed nests previously (nos. 546, 351, and 556) built their first nest on 10, 14 and 18 July, respectively. The mean number of days between construction of the female's first nest and deposition of her first egg was 5.0 (n = 6).

1967 Breeding Season

The testicular recrudescence pattern in 1967 compares closely with the 1965 curve. The initial response appears to have begun in early March reaching maximum length in early June (Fig. 3). Rainfall patterns for the 2 years were identical, i.e., normal winter and spring precipitation with summer rains occuring in July (see Fig. 4 and Fig. 6).

Rain was recorded in late May and mid-June and the summer rains began in early July in 1967 (Fig. 6). The first new vegetation in 1967 was recorded on 13 July. Annual grasses and forbs were noted growing around the base of shrubs where soil moisture and shade were prevalent. The desert hackberries began to show new leaves on 24 July. Grasshopper densities were low until around 31 July, when I recorded first and second instar densities ranging from six to nine per square yard.

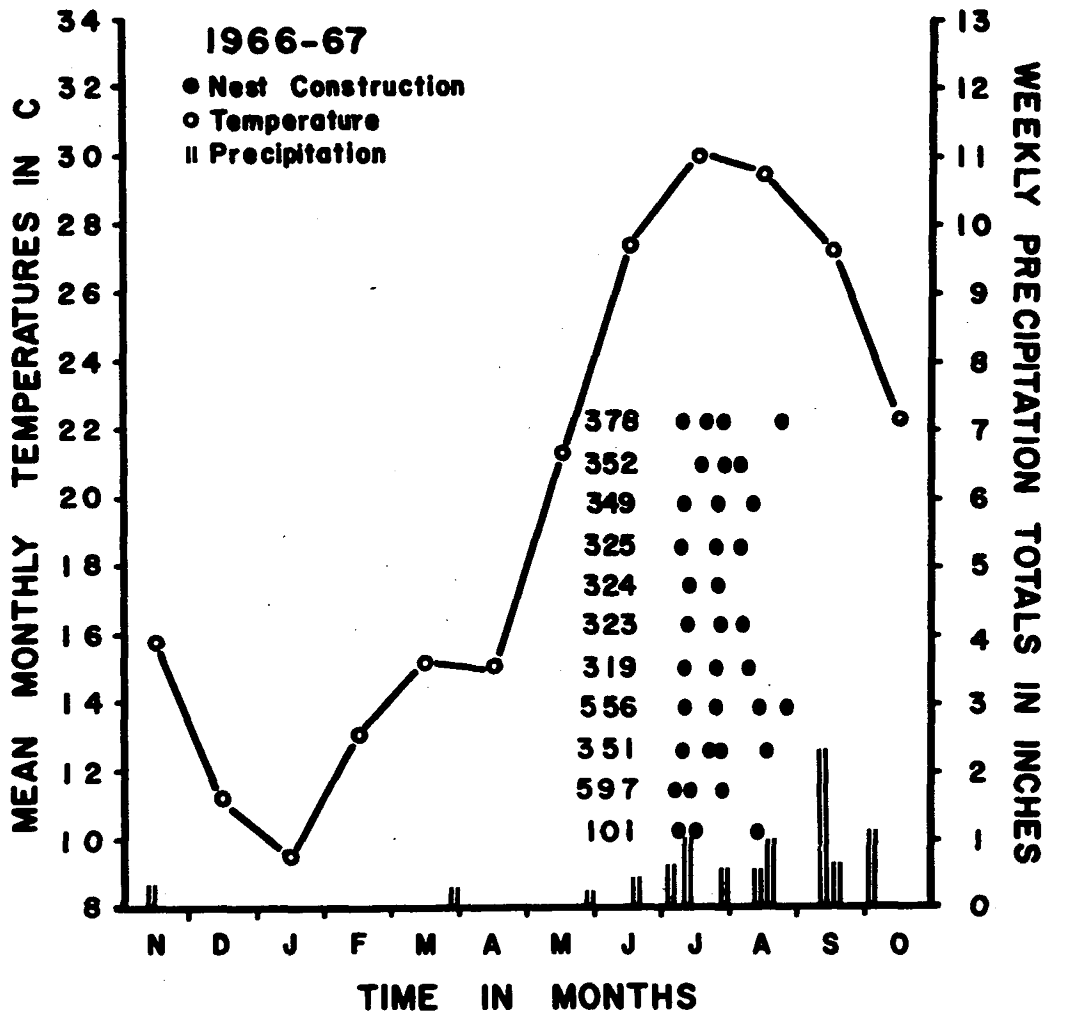

Fig. 6. Temperature, precipitation, and timing of nest construction during the 1967 breeding season. Individual nesting females are identified by numbers in the graph.

Eleven pairs of Rufous-winged Sparrows were studied in 1967. Following a trace of rain on 5 July and 0.54 inch on 6 July, the first nest construction was observed on 7 July. Three other rainy days were recorded: 11 July (0.47 inch), 12 July (0.43 inch), and 26 July (0.39 inch). One female initiated nest building on 8 July, three on 9 July, one on 10 July, three on 11 July, one on 12 July, and one on 17 July. The mean number of days between the initial construction of the female's first nest and the deposition of her first egg was 7.1 (n = 10, 1 undetermined).

1968 Breeding Season

In 1968, the recrudescence pattern was similar to that in 1966. By mid-March, testis length had increased to 2.5 mm, and by the latter part of March, maximum size was attained. Heavy rainfall was recorded during the winters preceding the 1966 and 1968 spring breedings. The primary difference was the absence of rainfall in late February and March of 1966, whereas in February, March, and April of 1968, heavy amounts were received.

Heavy precipitation (3 inches) was recorded in December, 1967, and heavy spring rains fell in February, March, and April of 1968 (Fig. 7). On 11 March 1968, I recorded abundant annuals and some species were blooming. The desert hackberries had tiny new leaves. By 15 March, annual mustards (Cruciferae) and composites (Compositae) 3 to 4

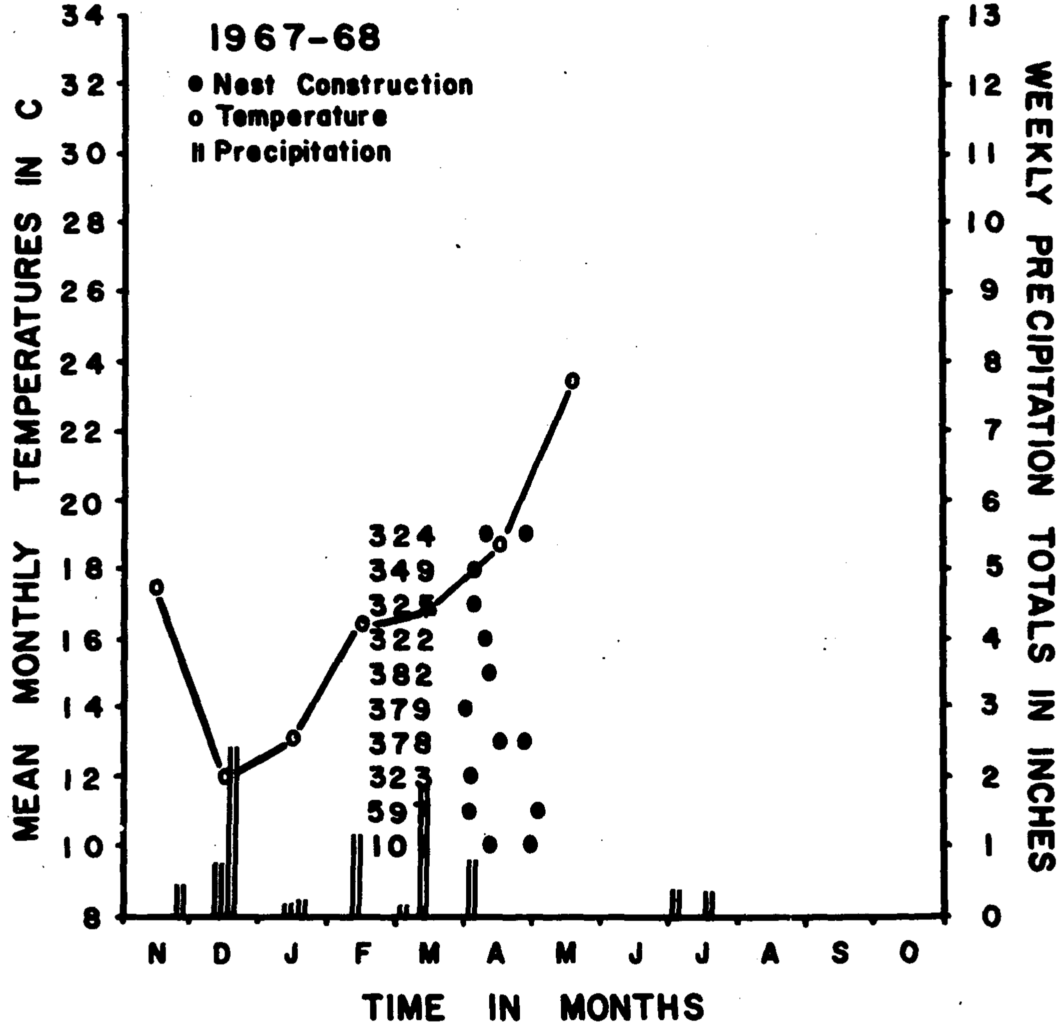

Fig. 7. Temperature, precipitation, and timing of nest construction during the 1968 breeding season. Individual nesting females are identified by numbers in the graph.

inches high covered the areas which were normally bare soil. The tobosa grass had new leaves and was beginning to produce seed heads. The deciduous mesquites, catclaws and whitethorns were putting on new leaves. Optimum conditions appeared present by the latter part of March. Numerous butterflies were recorded from mid-April to mid-May and their larval forms were abundant in the shrubs. Grasshopper densities remained below a mean level of 3 per square yard.

Nesting was initiated in the spring of 1968 in late March and April. One female began nest construction on 29 March, two on 1 April, one on 3 April, two on 5 April, two on 7 April, and one each on 11 and 14 April. All pairs in the study area attempted to nest. Most pairs attempted only one nest, but four renested after the first nests were destroyed. The mean number of days between the initial construction of the female's first nest and deposition of her first egg was 5.1 ($n = 6$, 5 undetermined).

Strong winds combined with high temperatures in late April caused extensive drying and by the end of April, all the annuals were dead. By the middle of May, food abundance was greatly reduced and breeding appeared to be over. No more nests were found until early July following the summer rains.

Normally, when the birds respond to the summer rains in July, the nesting season extends to about mid-September. I have never observed a female constructing a nest in September, but they will continue to care for eggs and young into the month. When conditions are normal, the birds have only about 6 to 8 weeks to fledge young. When the rains are late, as in 1967, the breeding season is reduced to 4 to 5 weeks.

REPRODUCTIVE SUCCESS

Reproductive success varied greatly during the study (see Table 2). Greatest success was observed in 1965 when the initial summer rainfall was heavy and was followed by heavy precipitation, which maintained high productivity of desert vegetation throughout August. Insect densities were high and remained so throughout the breeding season.

Data for 1966 indicate two breeding seasons, an early season with four nesting pairs and the normal season with six nesting pairs. Winter rainfall was exceedingly heavy with very little spring precipitation. Insect densities appeared higher than the previous spring, but only three female sparrows were stimulated to nest. The summer rains were later and much lighter than those recorded in 1965. Sustaining rain fell in August, but the initial rainfall was not adequate to produce the desert productivity which was observed in the previous year.

The precipitation pattern in 1967 was similar to that in 1965, except that the initial rains were inadequate to create the high plant response observed in the desert in 1965. Insect abundance was lower than that of 1965, as was reproductive success (Table 2).

TABLE 2. NATALITY INFORMATION FOR THE RUFOUS-WINGED SPARROW DURING THE FOUR-YEAR STUDY

	1965 Summer	1966 Spring	1966 Summer	1967 Summer	1968 Spring
No. Females Nesting	10	4	6	11	10
Average No. Nests/Female	1.8	2.0	2.6	3.1	1.4
Total No. Eggs Laid	60	13	26	100	39
Percent Eggs Hatched	53	23	34	30	46
Percent Fledged of Eggs Hatched	80	33	77	70	61
Percent Fledged of Eggs Laid	45	8	27	21	28
Average No. Young Fledged/Female	2.7	0.3	1.1	1.6	1.1

The high spring reproduction in 1968 was preceded by heavy winter and spring precipitation. Lepidopteran densities were high from mid-March throughout April. Even though the rain was heavy, grasshopper densities remained low through the birds' spring breeding season. The area began drying out by late April and high temperatures in May increased the desiccating effect and nesting ceased. Reproductive success was as high as the summer breeding season in 1966, and almost equaled the summer breeding season in 1967.

Nest abandonment was noted only twice in the 4-year study. In mid-September of 1965, a female did not return to incubate three eggs; the eggs disappeared in a few days. Another female failed to return to her two newly hatched young and one egg in mid-September of 1967. In both cases, the females were not observed again. It is assumed that both females died.

Parasitism by Brown-headed Cowbirds could affect the reproductive success values for the Rufous-winged Sparrow. However, cowbird success depended upon the success of the sparrow nest, and in the more productive years, more of each species was fledged. The number of Brown-headed Cowbirds fledged was three in 1965, one in 1966, and three in 1967. No cowbird parasitism was observed in the spring breeding seasons.

REGULATION OF CLUTCH SIZE

Data regarding clutch size were collected over the 4-year study. Table 3 lists females that were in the study for two or more consecutive years, and shows their clutch sizes. In 1965, eight complete clutches laid at the onset of the summer rains each contained three eggs. A clutch of four was recorded on 6 August (female no. 105) and another on 8 August (female no. 556). Outside the study area, 1.5 miles south, I found another clutch that contained four fresh eggs on 30 July. Clutch size was known on six nests which were built after 26 July and each contained three eggs.

During the 1966 spring breeding season, the first nests of the early attempts were destroyed except for female no. 597, whose first clutch contained two eggs. The three females that did not nest until after the rains in July all produced clutches of three. Five clutches laid in late July and August (second, third and fourth clutches) contained three eggs each, but one female, no. 351, laid a second clutch of two. In the 1966 breeding season, no clutches of four were found in the study area, but one was found north of Tucson on 26 April.

Nine of the 11 females in 1967 laid a first clutch of three eggs following the July rains. The remaining two hens'

TABLE 3. CLUTCH SIZES OF FEMALES IN THE STUDY TWO YEARS OR MORE

Female Number	1965 Clutch Number 1	2	3	4	1966 Clutch Number 1	2	3	4	5	6	1967 Clutch Number 1	2	3	4	1968 Clutch Number 1	2
	Eggs/Clutch				Eggs/Clutch						Eggs/Clutch				Eggs/Clutch	
101	**D1	D2	3	3	D2	*A	3	3	D1	3	3	D1	3		4	4
541	3				D2	3										
546	3	3			3	3										
597	3	3			2	D1	A	A	D2	3	A	3	4		3	D2
556	?	4			3						3	4				
323											3	D2	4		3	
325											3	D1	4		3	3
349											3	4	3			
378											D1	3	4	D2	D1	3

**D = nest destroyed; accompanying digit indicates clutch size at time of destruction.
*A = nest abandoned before laying occurred.

nests were destroyed before the clutches were complete. Clutches of four appeared in the second clutch of no. 556 and the third of no. 597. One female's second clutch contained only two eggs. A total of seven clutches of four were recorded in the study area in 1967. Two clutches were completed on 31 July, three on 2 August, one on 18 August, and one on 19 August. From 29 July to September, seven clutches of three were recorded.

In the spring breeding of 1968, two clutches of four were recorded in the study area and one outside the area. Female no. 101 laid the two clutches of four, and prior to this, all of her completed clutches contained three eggs. All other complete clutches in the study area contained three eggs.

DISCUSSION

Territories and Pair Bonds

Establishment of lifetime territories and pair bonds may be advantageous for birds in the Sonoran Desert. In winter, it would promote more efficient utilization of suitable habitat by spacing individuals more evenly. It would allow the young to determine vacant territories for occupancy and energy expenditure for establishing territories and competing for mates would be reduced. This behavior would also insure the presence of mated birds should a wet winter or spring occur and breeding be stimulated early.

Lifetime territories and pair bonds were found in the Rufous-winged Sparrow and similar findings have been reported for the Cactus Wren (Anderson and Anderson, 1959) and the Brown Towhee (Marshall and Johnson, 1968). However, this apparently does not hold true for the Black-throated Sparrow (Smyth and Bartholomew, 1966).

Nests and Young

The unusual depth of the nest cup for a species of this size has been commented on by various authors (Bendire, 1882; Wolf, 1966; and Phillips, 1968). Nests are usually placed on the periphery of a shrub. A deep nest cup helps in shading and hiding the nestlings. The dark skin and down of the young birds also aids in making them less conspicuous. I doubt that the darkness of the nestlings is important as a heat absorption mechanism, as the female spends a considerable amount of time covering the young before they are feathered.

Water Economy

The most extreme conditions of temperature and aridity in the Sonoran Desert normally exists from May through mid-July. These months were suspected of being critical in the life of the Rufous-winged Sparrow because of experiments by Ohmart and Dawson (unpublished), in which it was found that individuals cannot produce enough metabolic water to offset pulmo-cutaneous water loss in the zone of thermoneutrality. As the ambient temperature increases above the thermal neutral zone, water loss is even greater and must be restored through the intake of free water or preformed water in the diet if a balance is to be maintained.

The foraging activities in response to ambient temperature are documented in Fig. 2. Seed is the primary food item taken by the Rufous-winged Sparrow, but in both winter and summer, the birds were observed gleaning insects in shrubs. The taking of insects in the winter is probably more important for satisfying the nutritional needs observed in the laboratory, than for water intake. Additionally, in the summer months, the preformed water obtained through the consumption of insects would be important in maintaining water balance. During the hottest portions of the day, the birds were observed perched, and inactive, with wings slightly elevated and mandibles gaped. Possibly, the amount of water required to dissipate the heat gained from foraging movements was greater than the amount of preformed water that would be gained. Thus, a point of diminishing return may be reached and the most efficient behavior was to sit quietly and lose heat through evaporative water losses associated with respiration.

Sodium Chloride Metabolism

Experiments dealing with metabolism of sodium chloride by the Rufous-winged Sparrow demonstrated that the species can process solutions containing as much as 2% salt. Bartholomew and Cade (1963) suggested that probably all land birds must rely on their kidneys for salt excretion, and that most will be unable to drink solutions greater than about 1% salt. The maximum salinity reported for weight maintenance in the House Finch (*Carpodacus mexicanus*) was 1.5% (Bartholomew and Cade, 1958), and 0.75% for the Mourning Dove (*Zenaidura macroura*) (Bartholomew and MacMillen, 1960). The body fluids of birds contain about 1% salt. Those species capable of processing sodium chloride solutions of greater concentrations, must do it through the renal system if they do not have functional salt glands. Thus, an index to renal efficiency is obtained from experiments in sodium chloride metabolism.

I feel that through ethological and physiological adaptations, the Rufous-winged Sparrow has become independent of free water in its desert existence. The birds avoid direct radiation and thus are conservative with respect to heat absorption, which in itself is a water retaining adaptation. Excess heat accumulated while foraging in direct radiation would have to be dissipated through evaporative water loss. Consumption of succulent plant and animal material for a number of hours during the day yields a considerable quantity of preformed water which can be utilized by the efficient renal system. These evolutionary adaptations become extremely important during the summer months when free water is not present and ambient temperatures are 40 C or higher.

Gonadal Recrudescence

The consistent pattern of initial testicular size increase in the 4-year study strongly suggests that photoperiod is involved in initiating the gonadal cycle. Once the cycle had begun, the birds could be stimulated to breed by food supply in the spring and rainfall during the summer months. It is not known if rainfall will stimulate breeding in the spring months. The gonadal recrudescence patterns obtained in the 4-year study shows similar curves for 1965 and 1967, and for 1966 and 1968. The pattern in 1965 and 1967 is probably the normal growth curve in the Sonoran population because the area does not receive rainfall from storms moving in from the Pacific Northwest during winter months as does the Tucson region. The curves for 1966 and 1968 are not totally unexpected for a species which responds so closely to environmental changes.

The gradual size increase of the gonads observed in 1965 and 1967, which I feel are representative of the normal recrudescence pattern in the species, bears out the thoughts of Miller (1960). In referring to the reproductive organs of the avian species which apparently nest during the rainy season in the southern Arizona and New Mexico area, he states,

> "........ whether a physiologic state of readiness is attained much earlier and held until finally triggered into action by the onset of rains. This has been suggested but I think it is doubtful, as the rains are fairly regular in their timing, unlike those of Australian deserts, and to wait long in readiness would seem to be wasteful of energy."

Breeding Stimuli

The breeding response of the Rufous-winged Sparrow to rainfall was most pronounced in the summer of 1965. All females in the study except two had begun nest construction within 4 days following the first rain. The two exceptions were involved in pairing problems, and I feel this was responsible for their delay.

In July of 1967, 6 to 9 days elapsed between successive rains and none was heavy. Ten of the females in the study began building nests within 7 days after the first intense rain (6 July, 0.54 inch). One female, for reasons unknown, did not start building until 17 July.

In 1967, the delay between initiation of nest construction and deposition of the first egg was 7.0 days compared with 5.2 days in 1965. Paucity of rainfall at the beginning of the rains in 1967 was probably responsible for this disparity. Summer rainfall is the releasing stimulus to induce nest construction, but if the intensity is not great enough or the first rain is not followed closely by additional rainfall, a delay occurs between nest construction and deposition of the first egg. Once the first egg is deposited, others are laid on consecutive days. For 1966, the time period was about the same (5.0 days) as in 1965. Possibly, this was because four hens attempted to nest throughout the spring while the other three females must have been near the point of breeding. When the first rains came in July, the birds immediately began nest construction and egg laying.

In 1966, the abnormally heavy winter rains stimulated a luxuriant shrub growth the following spring. This vegetative response in turn caused a higher than normal density of shrub inhabiting insects. I feel this above normal food supply stimulated a rapid development of the reproductive organs, but the stimulus was marginal and only induced breeding in four of the seven pairs. An important factor which occurred in the spring of 1968, but not in 1966, was sufficient spring rainfall to induce annual plant growth. The combined annuals and shrub vegetation in 1968 yielded a greater food supply to the primary consumers than was available in 1966 when shrubs alone were the major producers. The best indication of this disparity in insect density was noted in the large number of lepidopteran larvae and adults in 1968. The increased food supply caused rapid gonadal maturation, and the stimulus (food) was strong enough that all pairs in the study area attempted to breed. The stimulus was sufficient in both years (1966 and 1968) to induce rapid size increase of gonads, but insufficient in 1966 to stimulate all pairs to breed.

It could be argued that rainfall was the proximal breeding stimulus in 1966 and 1968. There was no rain in the spring of 1966 other than 0.25 inch in April; had this amount been an adequate stimulus, then early breeding should have occurred in March and April of 1965 when two rains were recorded, each measuring 0.40 inch. Also, early breeding should have been recorded in 1967 during the months of March, May or June at which time rains also fell ranging from 0.20 to 0.40 inch.

As was mentioned previously, the spring breeding in 1966 and 1968 are probably abnormal for the entire population and the heavy rainfall for southern Arizona was far from normal. The percent probability of obtaining the amounts of rain recorded before the breeding seasons as reported by Kangieser and Green (1965) are:

1966		1968	
Month	%	Month	%
December, 1965	less than 5	December, 1967	less than 5
January, 1966	less than 10	February, 1968	less than 30
February, 1966	less than 10	March, 1968	less than 10
		April, 1968	less than 25

Even though the birds attempted to breed early in 2 of the 4 years, the climatic factors leading to such behavior can be expected much less frequently than the observed results. The statement by Marshall (1963) ".... the Rufous-winged Sparrow breeds only after the summer rains." is more applicable than the 1966 and 1968 data indicate.

Breeding has never occurred before late March in a yearly cycle, indicating a refractory period may be present in the species. In 1968, the habitat appeared to be suitable to stimulate breeding in March, but the birds did not breed and the gonads of both sexes were not fully developed. Also, the young birds appear to be incapable of reproducing during the first year as was indicated by the three immature females paired with adult males, in which nesting did not occur until the following year. Two immature females which were paired with adult males were collected off the study area in July, and both had small ovaries and no enlarged follicles. Irby and Blankenship (1966) found that in Mourning Doves, the birds of the year were capable of reproduction and some nested in the latter part of the 8-month breeding season. This phenomenon has also been reported in xerophylic birds inhabiting the Australian deserts. The evolution of a refractory period in the juveniles of the Rufous-winged Sparrow would probably be selected for because in normal years of reproduction, it would be around October before the young were mature enough to breed.

Reproductive Success

Fledging success was higher when the rainfall pattern in the Tucson area was more like that from Navojoa, Sonora (see Fig. 8), where the species is most abundant. Heavy rainfall is needed to initiate luxuriant vegetational growth, but subsequent rains are needed to maintain this response. When these conditions are met, as they were in 1965, high insect densities occur and for a short period of the year, food supply for insectivorous and carnivorous animals is extremely abundant. It is in this time period that natural selection has favored the breeding of the Rufous-winged Sparrow. Potential nest predators would expend more energy in investigating a peripherally placed nest in a spinescent shrub than in consuming the readily available grasshoppers and lepidopteran larvae. Thus, there has not been a strong selective factor for nest concealment as there possibly was in the other north temperate _Aimophilae_ (_cassinii_, _botterii_,

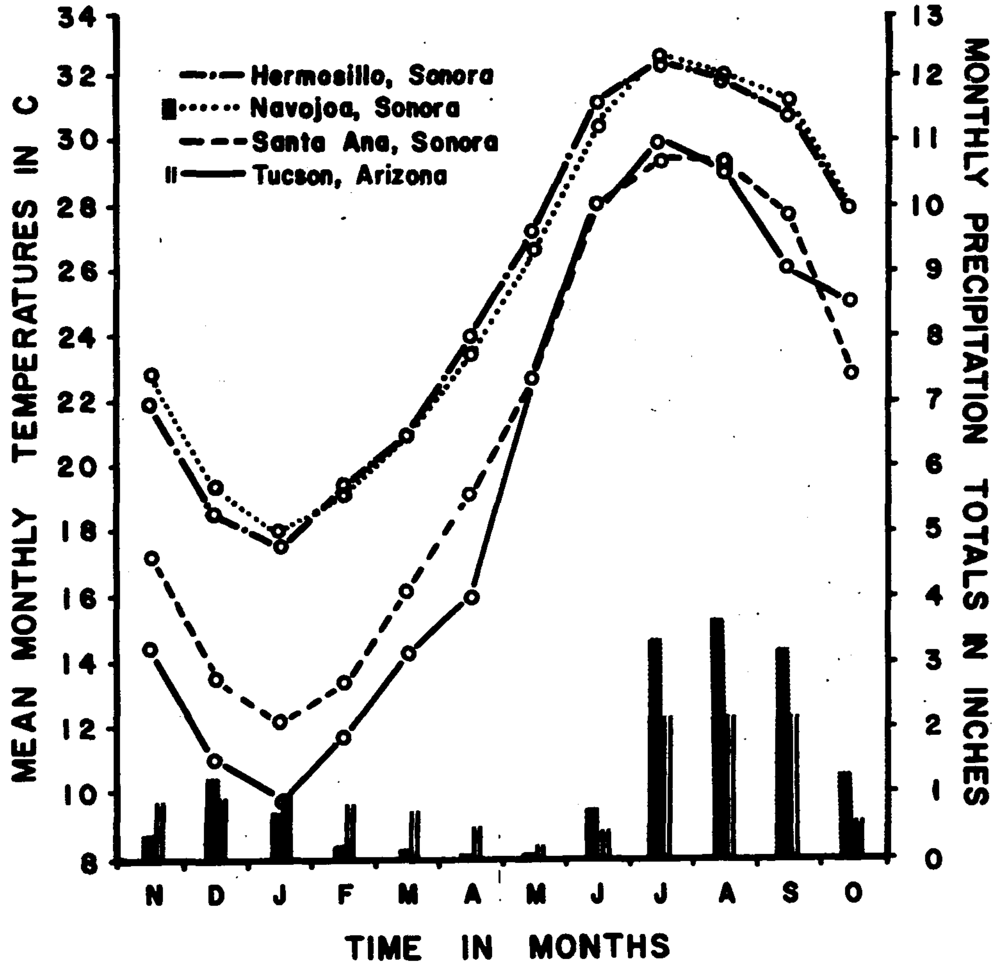

Fig. 8. Temperature and precipitation at the northern limits (Tucson) and center of distribution (Navajoa) of the Rufous-winged Sparrow. (Sonoran values from Hastings, 1964).

ruficeps and *astivalis*). Phillips, et al., (1964) made this comparison with reference to the Rufous-winged Sparrow, ".... and nests, are easily visible in the edges of bushes, not hidden away in dense grass as other *Aimophilae* and their nests." The fledging success in the spring of 1968 was high compared with the 1966 spring or with the summer of 1966 and 1967. Had the food supply been more abundant in the spring of 1968 to help serve as a buffer against nest destruction, the success may have been greater. The lepidopteran component was as dense as in 1965, but grasshopper densities remained low.

A prominent adaptation in the Sonoran Desert is the carnivorous or omnivorous habit. Such species as the Sonora spiny lizard (*Sceloporous clarki*), Coachwhip (*Masticophis flagellum*), Roadrunner (*Geococcyx californianus*), Mockingbird (*Mimus polyglottos*), Curve-billed Thrasher, Loggerhead Shrike (*Lanius ludovicianus*) and others may take the eggs and young of the Rufous-winged Sparrow when other food supplies are scarce. Marchant (1959) working in Ecuador presented evidence which indicated that low rainfall reduced the supply of food for the young and he felt the mortality ".... was due to the young birds dying of starvation". This was not the case with the Rufous-winged Sparrow. An abundant food supply acted as a buffer and helped insure the success of the nest, but when the food supply was low, the eggs and young were readily found and taken by predators, as was indicated by the large number of nests which were built and destroyed in 1966 and 1967.

Another important factor in reducing reproductive success in the Rufous-winged Sparrow in the Tucson area appears to be the duration of the breeding season. Normally, the breeding season lasted from 6 to 8 weeks when suitable heavy rainfall occurred in early July, but could be reduced to 4 weeks in years when the rain is late. In 1967, the habitat response to the summer rains had just begun when breeding terminated in late August. Duration of the breeding season would only be important when the food supply was sufficient to reduce nest destruction.

Temperature appears to be the main factor involved in terminating the northern breeding season. The mean monthly temperatures in Fig. 8 show there is approximately 5 C difference between Navojoa and Tucson in September. The mean temperature in Navojoa in October is approximately 2 C warmer than the September temperature in Tucson. Pitelka (1951) found birds just out of the nest on 1 November in Sonora, and Moore (1946) reported that C.C. Lamb found heavily incubated eggs on 2 October in Sinaloa. The nest which contained the young found by Pitelka (1951) would have been constructed in early October and the one reported by Moore (1946) would have been constructed in mid-September. I have never found a nest under construction in September in the Tucson area.

Interestingly enough, unusually wet springs characterized the 2 years for which Phillips (1968) had the most data on the species. Phillips (1968) stated,

> "It does not seem, however, that mere abundance of plants or insects or a given amount of rain will _per se_ cause the rufous-winged sparrow to nest. Nesting depends on the readiness of the female, because in most if not all years the male seems to be in breeding condition long before actual nesting occurs."

I found the latter statement true, for maximum testis size was reached approximately 6 weeks before the females began nest building, except in 1966 and 1968. I have presented detailed information on rainfall, condition of habitat, and behavior of individuals that demonstrates rainfall and food supply act to stimulate breeding.

The capricious existence of the species in Arizona (see Phillips, et al., 1964) has probably been influenced to a great extent by low precipitation or drought conditions. Phillips (1968) stated ".... the most important enemy of the rufous-winged sparrow is the unscrupulous cattlemen". Range desecration is normally greater during drought years because the livestock are held on the grasslands until the last blade is consumed with the hope that the rains will come. Low reproductive rates in Arizona, combined with habitat impoverishment may well be important in limiting the northern distribution of the Rufous-winged Sparrow.

The data presented on regulation of clutch size suggests that this phenomenon occurs. Clutches laid following the summer rains always contained three eggs, but following clutches may contain two, three, or four eggs depending on food supply. Marchant (1959) reported similar findings for the Vermilion Flycatcher (Pyrocephalus rubinus) and a type of mockingbird (Mimus longicaudatus).

Rainfall as the proximal stimulus to induce summer breeding in the Rufous-winged Sparrow is significant in that this phenomenon has not been found to exist in North American desert birds. Marshall (1963) found a correlation between rainfall and nesting in the Abert's Towhee (Pipilo aberti), but he discussed egg dates throughout the year. It appears the Abert's Towhee, like the Brown Towhee (Marshall, 1963), has a long nesting season with nesting resurgence following the rains. Dawson (1968) presented 92 Arizona egg dates of Abert's Towhee from 28 February to 4 September, of which 46 were from early April to May 31. Because of the bizarre adaptations found in Old World desert birds, Udvardy (1958) has suggested that the differences in age of the Old World deserts allowed for greater desert specialization in these avifaunas. Bartholomew and Cade (1963), after establishing Old World desert antiquity, concur with Udvardy (1958) by stating, "The desert birds of the Old World could, therefore, reasonably be expected to show more conspicuous physiological adaptations to arid conditions than their ecological counterparts in the New World".

I believe that numerous highly specialized North American desert forms have not evolved primarily because of two factors: (1) lack of strong selective forces, and (2) smallness of the North American deserts. A comparison of the Sonoran Desert with the Australian Desert demonstrates the disparities involved. The Australian desert is characterized by aperiodic rainfall and temperatures which allow breeding year round. These conditions have selected for an avifauna that responds, in general, to cues other than photoperiod to insure that the breeding season coincides with optimum habitat conditions. Also, selection would tend to favor the maintenance of gonadal tissue at a high level of development to allow a more rapid response to favorable environmental changes. Immelman (1963) describes the Australian rainfall pattern as "... rain may be lacking for months or even years". A selective factor such as this combined with the year round breeding has resulted in a highly specialized desert avifauna.

Antithetically, the Sonoran Desert is characterized by a highly periodic rainfall with heavy rains occurring in the hot summer months and lighter amounts in the cool winters (Fig. 8). At least two types of breeding patterns have evolved in response to these selective factors: (1) breeding being initiated in the spring and continuing late into the summer months with nesting resurgence following the rains (in some species), and (2) breeding occurring following the summer rains, e.g., the Rufous-winged Sparrow. Photoperiod could be used as a cue to stimulate nesting in the first group, but some other factor, such as rainfall, would be more reliable to insure that nesting and optimum food supply coincide.

Physiography also plays an important part in desert adaptation. There are approximately 2 million square miles of arid and semi-arid land comprising the Australian Desert. This region is divided into plateau and basin with a few scattered mountains in the plateau area (see Keast, 1959, for a more complete description). A liberal estimation of 160,000 square miles for land area of the Sonoran Desert reveals the differences involved in land mass between the two arid regions. Also, the Sonoran Desert is interrupted by numerous mountain ranges which may be as high as 9,000 feet in elevation; along the eastern edge is the Sierra Madre de Occidental range which has elevational points of 9,000 feet. The extremely large land mass constituting the Australian Desert combined with strong selective forces would favor the development of highly specialized forms. The Sonoran Desert is small and few specialized forms exist. Mountain ranges throughout the desert area would act as refugia when conditions did become severe and any selection would then become swamped by reinvasion from these sanctuaries.

It appears that the age differences between the Sonoran and Australian Desert is less important than once believed, and the physiological adjustment demonstrated by the Rufous-winged Sparrow indicates time has been adequate for these specializations to occur in the New World desert avifauna. This is also confirmed from findings by Gilliard (1959) and Marchant (1959) in arid portions of South America.

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