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The Ethoecology of *Anolis nebulosus* (Sauria, Iguanidae)

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ABSTRACT—A population of *Anolis nebulosus* located near Tepic, Nayarit, Mexico was studied in the field and laboratory from June, 1965 to September, 1968. The population showed a female : male sex ratio of 50:49. The males in the spring were larger than the females, averaging 41.4 and 35.8 mm, respectively; however, no difference in the length-weight relationship occurred between the sexes. The Nayarit study area supported 90 lizards totalling 120 gm/1,000 m² during the spring, prior to breeding. Few lizards appeared to live more than a year in nature.

A. nebulosus were limited baskers, seeking shade when their cloacal temperatures reached approximately 29.7 C. There was a partial subdivision of the habitat between the larger males and the remaining members of the population with regard to perch height and microhabitat. Males also had much larger home ranges than females, averaging 1.99 ± 0.23 and 0.62 ± 0.14 m², respectively. There was a trend for the bigger animals to possess larger home ranges. The home ranges were not uniformly distributed on the study area, but were associated with certain features of the habitat. While the home ranges of the large males overlapped those of the smaller males, the large male home ranges were exclusive of those of other large males. Few home ranges of females touched one another, yet the distribution of female home ranges was an almost perfect overlap with the male home ranges.

Males and females shared a common behavioral repertoire, although the frequency of use and social context differed at times. Males and females were territorial and showed pronounced agonistic behavior toward members of their own sex.

The reproductive season was correlated with the rainy season. Mating lasted from late May through August, and the appearance of hatchlings from the latter part of August to the end of October.

* * *

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INTRODUCTION

Natural history studies of anoline species have been largely restricted to our own North American *Anolis carolinensis* (Gordon, 1956; Greenberg and Noble, 1944), and to a few West Indian species (Collette, 1961; Rand, 1962, 1964a, 1967a; Rand and Williams, 1969; Schoener, 1968; Schoener and Gorman, 1968; Webster, 1969). With the exception of *Anolis barkeri* (Kennedy, 1965; Robinson, 1962) and *Anolis limifrons* (Sexton, Heatwole, and Meseth, 1963; Sexton, Heatwole, and Knight, 1964; Sexton, 1966; Sexton and Heatwole, 1968), very little attention has been given the ecology and behavior of mainland anoles.

The present study investigates the ethoecology of *Anolis nebulosus* (Wiegmann), one of 42 species of *Anolis* in Mexico. This small, semi-arboreal lizard is found in western Mexico from Sinaloa to the Isthmus of Tehuantepec. Although it is widely distributed and reasonably common within its range, very little is known about *A. nebulosus*. Besides a biogeographical account of the Michoacan herpetofauna (Duellman, 1965), the literature on *A. nebulosus* is almost exclusively devoted to collection localities and taxonomic descriptions (Wiegmann, 1834; Bocourt, 1873; Cope, 1879; Boulenger, 1885; Thominot, 1887; Gunther, 1885-1902; Gadow, 1905; Taylor, 1936; Smith, 1939; Schmidt and Shannon, 1947; Smith and Taylor, 1950; Davis and Smith, 1953; Davis, 1954; Peters, 1954; Lewis and Johnson, 1955, 1956; Smith and Grant, 1958; Etheridge, 1959; Grant and Smith, 1960; Davis and Dixon, 1961; and Duellman, 1961). Furthermore, these reports and studies have failed to settle even the basic question of the taxonomic status of *A. nebulosus*. As Williams (1959: 188) points out, the anoline genus is such a large, complex group that conventional museum techniques cannot solve its many classification puzzles. It will require ethological and ecological investigations to help order the taxonomy and systematics of this largest of iguanid genera.

The present study is the first to characterize the behavior and ecology of *A. nebulosus*. The resulting data present the opportunity to compare the habits of this distantly related and distributed species of *Anolis* with the more studied species of the southeastern United States and the West Indies.

METHODS AND MATERIALS

The study was conducted over a 3-1/3 year period from June, 1965 to September, 1968. During this time over 300 *A. nebulosus* were observed in the field and laboratory. All studied individuals were of the same population which is located 35 kilometers east of Tepic, Nayarit, Mexico.

Laboratory

During March, 1965, August, 1966, March, 1967, and April, 1968, animals were collected and brought back to the Animal Behavior Laboratory at Norman, Oklahoma. The lizards were studied indoors where they were housed in a large room with controlled fluorescent lighting and heat, and in the laboratory's greenhouse. During one summer, research was conducted on the anoles at the University of Oklahoma Biological Station. The anoles were maintained in 4 X 4 X 3 foot, 6 X 2 X 2 foot, and 50 gallon enclosures. They fared well in captivity with daily attention. Provisioned with fresh water, small insects from net sweepings during the warmer months, and nymphal crickets, meal worm and blowfly larvae in the winter, these diminutive lizards remained in robust health throughout the year. Adults lived as long as 2½ years in captivity, and some hatchlings, fed on vestigial winged fruit flies, were successfully reared to adulthood.

The lizards were toe clipped for individual recognition and a permanent record was kept for each anole. In this record were entered bimonthly weight and length measurements, reproductive condition, pattern markings, fight scars, shedding notes, and other data of interest. Body weights were determined to the nearest 0.01 gm on a Sartorius balance. Snout-vent lengths were taken by gently pressing the lizard on a transparent millimeter rule and measuring from the tip of the snout to the edge of the anterior lip of the cloaca.

For the purpose of observing behavior, one 2 X 2 X 6 foot enclosure and three 50 gallon aquaria were set up with simulated habitat and a small population of 2-3 males and 4-5 females in each. These crowded conditions catalyzed social interaction which resulted in a fairly complete list of the lizards' behavior repertoire. Through repeated appearance of a particular behavior it was possible to correlate preceding social situations with the observed behavior. (Although such observational correlations are not proof of a behavior's function, they do give the social context in which certain behavior appears.)

Field

A concentrated field study was conducted on *A. nebulosus* 35 kilometers east of Tepic, Nayarit from 24 April to 9 May 1968. The purpose was twofold; first, to gain a familiarization with the general ecology of *A. nebulosus* so that behavior patterns could be placed in perspective. Second, a knowledge of the anoles' behavior under natural conditions was desired to compare with lab-observed behavior.

Some preliminary collecting was done to select a study area where the lizard population appeared to have a high density. A 30.5 X 30.5 meter study area was then marked off using a compass and metal tape. The selected study area was situated so that it included two different types of habitats, an oak woodland with heavy leaf litter and a grassy hillside containing scattered oak coppice. Every piece of prominent vegetation was labeled as well as fence posts and rocks. A rough map was drawn showing the labeled landmarks. This permitted quick and accurate determination of perch site locations of observed lizards. At the conclusion of the study, transects were carefully laid out and a large, accurate map was drafted to determine movement distances and area of territories.

The anoles were collected from within and around the study plot. Upon capture, cloacal temperatures were taken with a Schultheis thermometer. The thermometer was also held shaded at the capture site to get an approximate substrate reading. Notations were made whether the lizard had been in the shade or sun prior to capture, its position on the perch, and the locality of the perch.

At a small mobile laboratory, the captured anoles were weighed to the nearest 0.01 gm on a Harvard Trip Balance, their total and snout-vent lengths recorded, and their toes clipped for permanent identification. Quick drying paint was also applied to the lizards' backs for visual identification; the system employed proved very efficient for these small animals. The position of paint spots on the back represented different numbers (Fig. 1). Any number between 1 and 9 was obtainable through the combination of the four back numerals (1, 2, 4, and 7). Yellow paint marks were placed on females and orange marks on males. The tails were painted different colors for the tens column (e.g. white—10's, green—20's, blue—30's). Anoles from off the area were given a distinct toe clip series and all received a blue paint mark on the body. Natural body markings and any structural peculiarities were also noted. The lizards were then returned to the exact site of their capture and released.

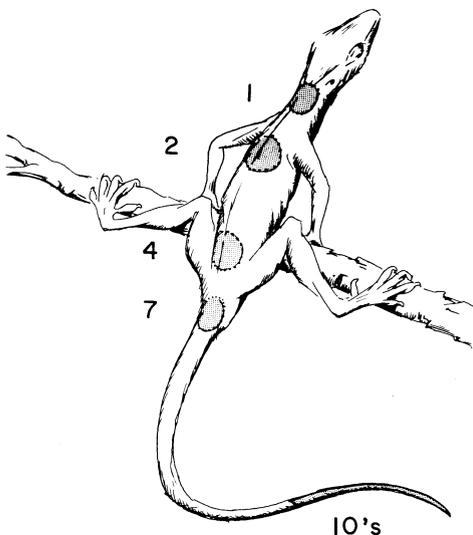


FIGURE 1. Numerical values assigned to dorsal paint spots for individual identification.

Observations began before sunrise and continued through the day until after sunset. One night was spent on the study area to take temperatures and check sleeping sites. Seven power binoculars were used to follow the movements and behavior of the lizards; with this magnification, marked anoles could be identified from across the entire study area. A Beaulieu Super 8 camera (Model 2008S) was

used to make a permanent record of behavioral interactions.

Habitat temperatures were recorded at various times during each day of the study period. Air temperatures were recorded in the shade at breast height. Temperatures were also taken of the leaf litter in both the shade and the direct sunlight; these measurements were made both on the leaf litter and under 8-10 centimeters of leaves. Weston stemmed thermometers provided the deep substrate readings.

A vegetation analysis was conducted on the study plot. Since no keys were of practical value for the Nayarit area, the various vegetation types were assigned a letter for immediate recognition and several specimens were collected of each plant type for later identification.

The following calculations were taken of tree species: basal area, relative basal area, and relative density per species. An importance percentage was computed for each species by adding its relative density and relative basal area together and dividing by two. This calculation was used to determine the dominant species.

Those tree specimens with a girth greater than 10 centimeters at breast height were defined as trees, and saplings were those specimens with less than a 10 centimeter girth, but taller than 2 meters. Tree specimens under 2 meters high were arbitrarily called seedlings. A distinction was made for coppice which were abundant on the study area; these were stumps of trees which had resprouted, but were also under 2 meters high.

DESCRIPTION OF REGION

Physiography

Nayarit is a coastal state midway down the western side of Mexico. From its coastal lowlands the escarpment of the Sierra Madre Mountains rises dramatically to heights of 2,000 - 3,000 m. Long canyons, or barrancas, and elongated valleys lead up to the plateau of the Mesa Central region. The city of Tepic is situated at the end of one of these valleys in the basin of Tepic. In less than 35 kilometers, the landscape elevates from sea level to 1,030 m at Tepic.

The topography of the mountains is very rugged with a succession of northwest-southeast ridges. The roughness is due to severe downcutting of the mountains rather than upheaval. Consequently, they appear as eroded mesas. The southern end of the mountainous Sierra Madre Occidental region meets the northwestern extension of the Mesa Central along a line between Tepic and Guadalajara. The study area is situated along this junction of physiographic regions, approximately 35 kilometers southeast of Tepic. The surface features of Mesa Central were created by extensive volcanic activity during the mid-Tertiary, reaching a climax in the Pleistocene. Sanganguey and Ceboruco are two large volcanoes in Nayarit, and numerous conical hills produced by volcanic vents are common about Tepic and the study area.

Climate

The weather and climate of Nayarit are very much influenced by the mountains and winds. Although the study area is below the Tropic of Cancer, its altitude of over 1300 meters places it in a region of lower temperatures known as *tierra templada*. Here, yearly temperatures average between 15 and 20 C. Diurnal temperatures are mild (24-27 C), but in the afternoons of the dry season (March - May), readings of over 35 C usually occur (Vivo Escoto, 1964: 199). Nights are cool (14-20 C) and can produce frost in December and January. Because the wet season arrives during the summer, the hottest temperatures occur in March, April, and May. No annual temperature and precipitation data are available for the study area. However, this information is provided for Tepic (Table 1), but it only approximates the conditions of the study area as the latter is about 300 m higher than Tepic.

High summer temperatures in northwestern Mexico cause air masses to move in from the Pacific Ocean, producing a monsoon season during June, July, and August in Nayarit. This state also experiences approximately 70 days of severe thunderstorms during the year (Vivo Escoto, 1964: 196), the highest incidence of any region in Mexico, and hurricane tracks are common from August through October. These events produce the summer and fall rainy season which is

TABLE 1. Weather data during 1942 for Tepic, Nayarit, Mexico, located approximately 35 kilometers northwest of study area (after Contreras-Arias, 1942).

Weather Data	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
Temperature (C)													
Average	17.2	17.9	18.6	20.7	21.5	23.7	23.5	23.5	23.5	23.0	20.2	18.0	20.9
Average High	25.9	26.9	28.1	31.0	31.8	29.7	28.9	28.9	28.5	28.8	28.2	25.7	..
Absolute High	32.5	34.6	36.4	37.0	38.9	37.0	35.0	35.2	35.0	36.2	35.0	33.0	38.9
Average Low	8.8	8.2	8.5	9.2	12.3	17.5	18.4	18.3	18.6	16.6	12.1	10.5	..
Absolute Low	2.0	1.9	2.0	2.5	5.2	7.7	13.0	11.0	12.4	8.0	5.1	3.2	1.9
Precipitation													
Millimeters	32	21	1	tr.	2	170	344	288	202	75	9	53	1197
No. of Days	1	1	0	0	0	14	23	22	17	8	2	4	92

common to Mexico. Wallen (1955) presented the approximate average monthly rainfall for the Nayarit region which clearly shows the demarcation between dry and wet seasons. Expressed in mm of precipitation, the monthly data are as follow: Jan.—10, Feb.—7, Mar.—5, April—3, May—8, June—150, July—250, Aug.—210, Sept.—160, Oct.—60, Nov.—20, Dec.—40. The region in which the study area is situated experiences very consistent annual rainfall; the amount of precipitation does not vary more than 20 percent from year to year. The humidity is subject to the greatest seasonal variation of any region in Mexico. Desert-like air (30-50 percent relative humidity) prevails in March and April, as contrasted to humid conditions (60-70 percent relative humidity) during the rainy season.

Vegetation

Of the 12 vegetation types listed for Mexico by Leopold (1950), the study area is in the largest, the pine-oak forest. This zone is made up of many distinct communities from the scrub oak adjacent to the deserts to the pine forest bordering the fir belt of the high mountains. All of the 112 species of oaks given by Standley (1920-1926) are found in the pine-oak zone.

Leopold (1950) divided the major pine-oak forest into four general vegetation types of which his pine-oak woodland describes the region of the study area. The studied population of anoles was within a predominantly oak woodland containing a few scattered pines. However, identification of dominant oak species of this region was not made due to the large number of oaks in this vegetation zone and the general lack of information on the Nayarit flora.

The study area is included in the southern end of the Sierra Madre Occidental Biotic Providence (Goldman and Moore, 1946), just bordering the Nayarit-Guerrero Biotic Providence. Though it is not entirely clear from his general discussion, Goldman's (1951) Arid Upper Tropical Zone appears to apply to the study area; however, it may be better characterized by the Transitional Zone as the study plot probably has some frost in the winter.

DESCRIPTION OF STUDY AREA

The countryside about the study area is very hilly. Some of the nearby canyons possess precipitous sides. The soil is sandy in composition and many large masses of granite and lava boulders dot the hillsides. Oak trees (*Quercus spp.*) of small to moderate size form an open woodland in these mountains. Interspersed among the oaks is an occasional pine, and on the higher slopes are small stands of conifers. On the bases of the trees in many places were seen charred bark, giving evidence of fairly recent brush fires. The leaf litter, strong winds, and the 3-4 month dry season probably make a ground fire a real threat to small terrestrial animals.

The weather conditions at the study area during the 2½ week investigation were typical for the time of year and very constant from day to day. It being the dry season, no rain fell, though there was a light dew in the late evening and early morning. The sun rose a little after 0600 at which time the air was still. Minutes after the sun cleared the surrounding hill tops, its direct rays struck the leaf litter on the hillside causing the leaves to crackle. Soon after this the lizards began appearing. From 0700 to 0730 the warming slopes produced the first breezes of

the day; the breeze continued to increase, becoming very noticeable by noon. At 1500-1600 the conditions were windy with gusts up to 25-35 k.p.h. With the exception of one cloudy day, the sun was always bright. Occasionally there were clouds, but these were high and thin.

Air temperatures rose gradually through the morning reaching a peak at 1200-1400 (29-33 C). After 1530 the air temperature rapidly declined due mainly to the wind. Sunset came shortly after 1730, with the leaves again crackling as the ground surface cooled.

The study area was laid out through the edge of an oak woodland and down a grassy slope (Fig. 2). The gently sloping hillside has a 5° grade, and there was some evidence of erosion under the trees. The open, grassy area comprised approximately 1/3 of the 30.5 × 30.5 m plot, with the remainder holding at least two species of oak trees of various sizes. A heavy leaf litter of fallen oak leaves blanketed the ground about the trees. Where small gullies had formed from past erosion, the leaves were particularly deep, measuring 10-15 cm in depth. In contrast to the thick leaf layer in the woodland section, the grassy area was quite open; soil and rock showed over approximately 15 percent of the surface, and the grass was short and dry. Small, scattered plants of *Acacia*, *Mimosa*, and *Solanum* provided some submarginal perch sites for the resident anoles; the grass was not utilized by the lizards except during infrequent forages.

Between the two habitat types within the study area ran a barbed wire fence. Its posts were taken from locally cut oaks and a few live trees which fortuitously grew in the path of the fence. On either side of the fence were numerous stumps from which the fence posts were taken. These stumps had all resprouted into small, brush-like growth forms known as coppice. The coppices, particularly in the grassy areas in and around the study area, were heavily used by the lizards.

At the initiation of the study almost all of the oaks had a full complement of dead leaves still on their branches. There was a large amount of shade afforded by this old foliage which is very important in the thermoregulation of the anoles. It was soon evident, however, that the habitat was in transition. The wind was causing the old leaves to drop as the buds of the new leaves were developing. During the period when the old leaves had been shed and prior to expansion of the new foliage, the effective shade cast by the trees was drastically decreased. This had an observable effect on the movement and territories of the lizards below. Leaf abscission was not uniformly occurring in all of the trees, as defoliation and new growth were observed at different stages on the various trees of the study area.

The trees on the study area were all oak species (*Quercus spp.*). One of three apparent species on the study area predominated (Table 2). With the exception of two specimens (species A and B), the trees were generally small and scrubby.

TABLE 2. Species analysis of trees located on 30.5 x 30.5 m study area located 35 kilometers southeast of Tepic, Nayarit, Mexico.

Tree Species	Number of Specimens	Average Height (cm ²)	Basal Area (cm ²)	Avg. Basal Area/Tree (cm ²)	Relative Basal Area	Relative Density	Importance Percent
Trees (over 10 cm at breast height)							
<i>Quercus</i>							
A	11	10.2	6,146.7	588.7	96.9%	91.7%	94.3%
B	1	9.2	194.7	194.7	3.1	8.3	5.7
C
Total	12	10.1	6,341.4	555.9	100.0	100.0	100.0
Saplings (under 10 cm at breast height)							
<i>Quercus</i>							
A	41	3.4	1,076.2	26.2	98.5%	97.6%	98.1%
B
C	1	4.9	16.4	16.4	1.5	2.4	1.9
Total	42	3.4	1,092.6	26.0	100.0	100.0	100.0



FIGURE 2. The study area near Tepic, Nayarit, Mexico, during May, 1968.

POPULATION DESCRIPTION

Sex ratio

The sex ratio for 150 female and 147 male *Anolis nebulosus* collected from the Tepic population was 50:49. Since these collections were made in late March and April, most of the individuals were adults or soon would be. No data, then, are available for differences between sex ratios of age classes.

There is some question whether a bias occurred during collecting as males are larger than females and generally occupy more conspicuous perch sites. The 44 female and 41 male anoles (50:46.6) taken on the study area should be a reasonably accurate reflection of the population's sex ratio as the area was completely collected. If a collection bias did exist in favor of males, it was probably small. The population as a whole appeared to have close to a 50:50 sex ratio with slightly more females than males.

Sexual dimorphic pattern

Besides the difference in size and coloration of the dewlap between the sexes of *A. nebulosus*, some of the females also possessed a body pattern and coloration different from the males. A rusty color was occasionally found on the females which was never observed on male specimens. This color occurred in isolated patches on the body, though the site varied. Of 137 female lizards examined, 27 (19.7 percent) possessed the rust coloration; 22 anoles had this color on their heads, 4 on the tail, and 1 on the dorsal region of the back.

A dorsal striped pattern was also present in only the females. This condition is common to other species of *Anolis*, and has previously been reported for *A. nebulosus* (Duellman, 1961). As is true of the dorsal pattern and background coloration of the males, the female patterns showed a good deal of variation between individuals. The stripe varied from an orange through a light tan to a brownish yellow color. The shape of the stripe was generally scalloped along the edge and extended from the occipital region of the head down the dorsum to the distal end of the tail. In individuals which had broken their tails, the stripe was absent on the regenerated portion. The stripes of a few females were bordered in grey longitudinal bands which lack the scalloped lateral edges. Forty (29.2 percent) of the 137 females examined had the dorsal pattern and 5 (3.7 percent) of the sampled females had both a dorsal stripe pattern and some rusty coloration.

Duellman (1961: 63) mentioned that one male *A. nebulosus* from Dos Aguas, Michoacan had a cream-colored lateral stripe. Many of the Tepic males had a continuous, narrow stripe running from the supralabials back along the neck, sides of the abdomen, and past the hind legs. If the background color of the male was brown, the stripe was a yellowish brown; if the animal was grey, the stripe was lighter grey. Prominence of the lateral stripe pattern varied between individuals. This pattern on males from Manzanillo was quite noticeable.

Size and growth

Besides exhibiting sexual dimorphic color patterns, there was also a difference in body size between the sexes. Males were much larger (Fig. 3). The mean snout-vent length of 147 males was 41.4 mm, while 150 females averaged 35.8 mm. These mean values were significantly different. The 95 percent confidence limits for the mean length of the males and females were 40.72 - 41.98 mm, and 35.40 - 36.28 mm, respectively. All 297 anoles of the sample were collected and measured in April.

It is very difficult to detect age classes from the distribution of the snout-vent sizes for several reasons. First, there is evidence which indicates an almost complete turnover in the population each year. Second, the reproductive season spans the summer months, and so the young of the year are produced over an extended period of time causing a wide distribution in length frequencies. The skewed distribution of the length frequencies, particularly for the males, may reflect this long breeding season (Fig. 3).

In the field during April, 1968, body weights and snout-vent lengths were recorded for 78 male and 96 female lizards. The scatter diagram of the length-weight relationship revealed no

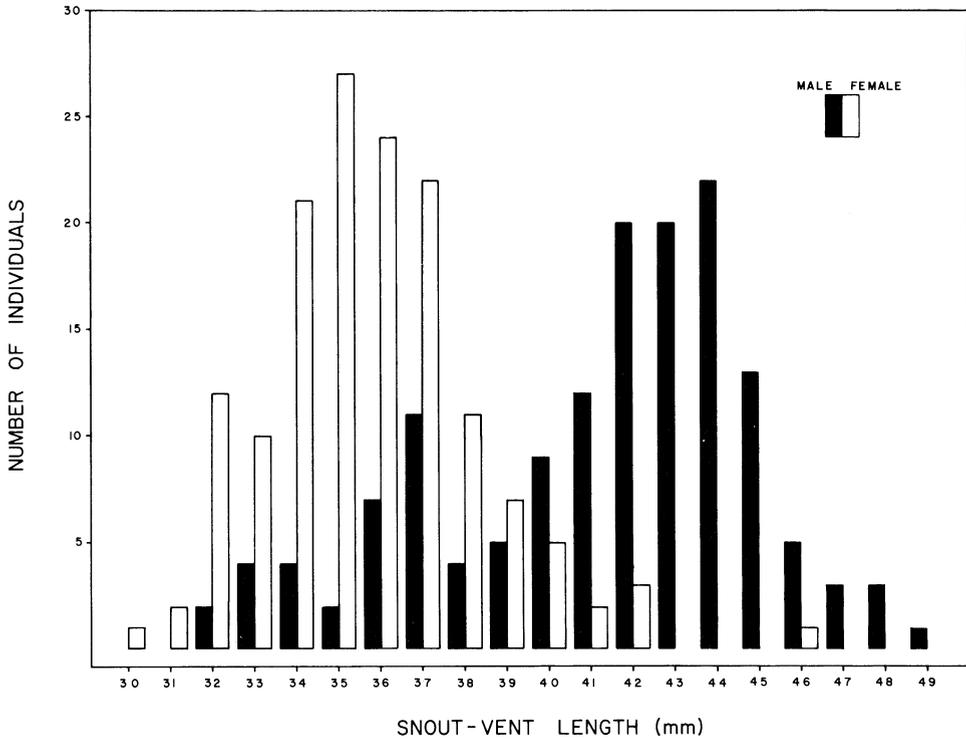


FIGURE 3. Snout-vent length frequencies of 297 *Anolis nebulosus* collected near Tepic, Nayarit, Mexico, during April - May, 1968.

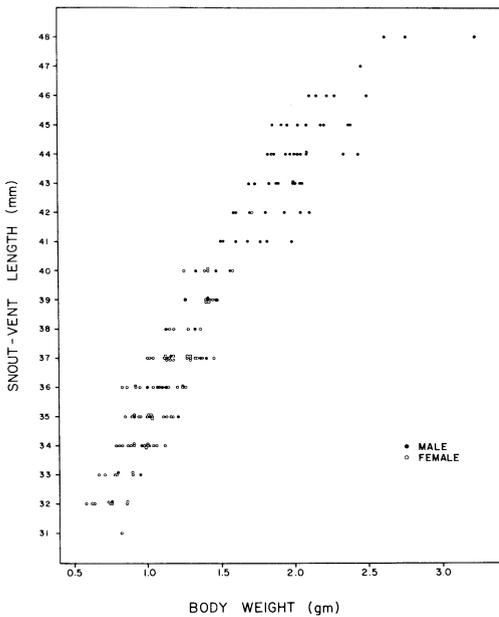


FIGURE 4. Body length - body weight relationship of 174 *Anolis nebulosus* collected near Tepic, Nayarit, Mexico, during April - May, 1968.

weight differences between the sexes at any particular snout-vent length (Fig. 4). This was not true, however, during the breeding season when females were gravid. For example, in the laboratory the mean body weight of 6 gravid females in June, all with a snout-vent length of 39 mm, was 2.0 gm as compared with a 1.4 gm average for the 9 female anoles of the same length in April. The mean weight in June of four lab-held males with a 39 mm snout-vent length was 1.3 gm. Therefore, there is a significant weight increase in gravid females.

Because the field study was short-term, all available growth data were taken from lab-held animals. For this reason only rough estimates can be made for the natural population. The data do provide, however, growth potentials for various age classes.

Growth records were kept on 40 males and 36 females from the period of April through August, 1967. Some of the animals had been collected the year before and were known to be more than a year old, and so constituted a partially known age group. Table

TABLE 3. Growth rates of snout-vent length for each of 40 male and 36 female lab-held *Anolis nebulosus* from Nayarit, Mexico, recorded from April 19, 1967 to August 24, 1967.

Growth Apr.-Aug. (mm)	Initial April S-V Lengths (mm) of Anoles Grouped According to their Growth Increments										Mean April S-V Length (mm)	Mean August S-V Length (mm)	
Males													
1	42*	42*	44	44	47*	49*						44.7	45.7
2	36	37	40	43	44	44	44	45*				41.6	43.6
3	37	42	42	42	43	43	43	45	47	50		43.4	46.4
4	38	40	41	41	42	43	43					41.1	45.1
5	36	40	40	41								39.2	44.2
6	32	33	39	41								36.2	42.2
7	37											37.0	44.0
Females													
1	39	42	42*	44*	44*	45*	45*					43.0	44.0
2	40*											40.0	42.0
3	36	38	38	41*								38.2	41.2
4	35	35	39									36.3	40.3
5	32	33	34	34	34	35	35	36	36	38	38	35.0	40.0
5	35	36	36									35.7	41.7
7	32	33	33	34	34 ⁺	35	37					34.0	41.0

*Known to be over one year of age.

+Known to be under one year of age.

3 lists the April snout-vent lengths for each of the 76 anoles and their increment of body length increase over the 5 month period. Those lizards which grew the most were also the smallest. Conversely, those which grew least were the largest to begin with and in most cases were probably the oldest. For both males and females the general trend was for a slower growth rate as the lizards increased in length.

By the end of August, the mean snout-vent length for each group presented in Table 3, regardless of the initial snout-vent length averages in April, was between 42-46 mm for males and 40-44 mm for females. Within these groups were individuals in their first year of life as well as some completing at least their second year. One female was known to be a hatchling in August, 1966, with a snout-vent length of 19 mm. By April, 1967, she was 34 mm long and by June, 1967, she had reached a snout-vent length of 41 mm and was observed to be gravid.

The largest *A. nebulosus* was a male with a 54 mm snout-vent length. He was collected as an adult (44 mm) in August, 1966, and died of an injury two and one-half years later. The largest anole collected in nature was a male 49 mm long. It is doubtful whether any member of the population lives more than two or at the most three years under natural conditions.

Lengths of tails which did not appear to have been previously broken were recorded for 56 males and 70 females in April, and for 6 hatchlings in August. When expressing each tail length as a percentage of the total body length, there was no difference found between the sexes (61.7 percent average for both males and females), and no significant differences between the various sized lizards collected in April. However, the August hatchlings had a mean percent tail length of 54.5. This was a significant deviation from the percent values of the April sample in which no lizard had a tail less than 59 percent of its total body length. Apparently, the tail grows at a faster rate than the rest of the body during the early part of the lizard's life.

Population density and biomass

A. nebulosus was very abundant throughout the region of the study area. Eighty-five lizards (41 males and 44 females) utilized the study area itself. The males had a mean snout-vent length and body weight of 40.6 ± 0.68 mm and 1.67 ± 0.09 gm, respectively; the females averaged

34.8 ± 0.31 mm and 0.99 ± 0.03 gm. The combined weights of the 85 lizards for the 930 square meters of the study area were 111.9 gm, or 90 lizards at 120 gm per 1000 m². These figures for population density and biomass when extrapolated for an acre are 366 individuals with a total weight of 488 gm. These values are restricted to the pre-breeding months of April and May.

The above estimate may be high. To provide a conservative estimate, only those individuals which were observed repeatedly throughout the study period are included in the following calculations. Fifty-three anoles were sighted with sufficient frequency to allow calculation of their home ranges, thus assuring their permanent residency on the study area. Of these, 25 were males and 28 females; their mean snout-vent lengths and body weights were: males—40.7 ± 0.94 mm, 1.71 ± 0.13 gm; females—35.4 ± 0.37 mm, 1.04 ± 0.05 gm. The conservative estimates of population density and biomass based on these 53 anoles are: 57 anoles at 77 gm per 1000 m², or 231 anoles at 314 gm per acre.

Comparison of density and biomass of *A. nebulosus* with other species of anoles is not extensive due to the lack of information. Heatwole and Sexton (1966) and Sexton (1967) estimated up to 250 resident *Anolis limifrons* per acre in Panama with a maximum of 600 individuals/acre under unusual conditions. Tinkle (1967) estimated 60 gm/acre for the April-May biomass of *Uta stansburiana*. He also provided a summary of the literature dealing with saurian population density. From the few studies available, the population density of *A. nebulosus* is high. An exception is the 500 *Hemidactylus granoti* observed on edifices in a 2400 square foot area (Cagle, 1964); this value extrapolates to approximately 10,000 lizards per acre.

ETHOECOLOGY

Habitat preference

Duellman (1965) in his biogeographic account of the herpetofauna of Michoacan, Mexico, listed *Anolis nebulosus* as principally a lowland species which has invaded the higher altitudes of the plateau. He found the species abundant in the arid tropical scrub forest and tropical semi-deciduous forest, and in moderate abundance in the pine-oak forest of the highlands. The present study was made on the lizards in this latter vegetation division.

The anoles used the majority of their available habitat. Only the grass in open areas and the upper portions of the trees were not frequented by the lizards. However, there was evidence of a semi-partitioning of the habitat between the sexes.

The structural habitat used by the population did not differ to any large extent among the age and sex classes as all lizards were observed on the various types of perch sites. However, the frequency with which a particular type of perch was occupied by members of the age and sex categories was the differentiating factor. The larger males had territories which included trees or fence posts upon which they spent the majority of their diurnal hours. The females and smaller males were not so conspicuous. Many of these latter individuals were in the leaf litter, bushy oak seedlings, and coppice. Only during the afternoon hours when the substrate temperatures of the leaf litter approached their maximum readings and exceeded the anoles' preferred body temperature did the females appear abundant. A similar type of intra-specific difference between habitat distribution of the sexes was recorded for *Anolis lineatopus* on Jamaica (Rand, 1967a, c), *Anolis sagrei* on Cuba (Collette, 1961) and Bimini (Schoener, 1968), and *Anolis conspersus* on Grand Cayman (Schoener, 1967).

The height of the perch site taken by the males was significantly different from the females (Table 4). Male perch sites averaged approximately 0.8 meters above the ground while female perch heights averaged a third of that distance. There was a great deal of variation between individuals of both sexes. The larger males tended to be higher than small males. One male with a snout-vent length of 48 mm was seen about 6 meters up in a large tree on his territory. Once a female was chased 3 meters up a small tree by a courting male. But these are rare instances, and as a group, *A. nebulosus* took perches under 2 meters in height.

A record was kept of the time of day and the general vegetation types chosen by the observed lizards as perch sites. The perch categories are: (1) trees and fence posts, (2) coppice and bushy seedlings, (3) small woody growth as *Acacia* and *Mimosa* plants, and (4) on the ground.

TABLE 4. Comparison of perch heights (cm) between male and female *Anolis nebulosus* near Tepic, Nayarit, Mexico, during April - May, 1968.

Perch Site	Numbers Observed	Mean Perch Height	Standard Deviation	Standard Error	95% Confidence Limits of Mean	
					Lower	Upper
Tree Trunks						
Males	180	79.9	75.4	5.6	68.8	90.1
Females	98	29.3	24.6	2.5	24.4	34.2
Posts						
Males	61	54.3	31.2	4.1	46.2	62.2
Females	21	32.8	28.2	6.2	20.0	45.6
Total						
Males	241	73.4	67.8	4.4	64.8	82.0
Females	119	29.9	25.2	2.3	25.3	34.5

TABLE 5. Daily percent frequency of perch types utilized by male (M) and female (F) *Anolis nebulosus* during April - May, 1968, near Tepic, Nayarit, Mexico.

Perch Types	Time of Day									
	0800 - 0959		1000 - 1159		1200 - 1359		1400 - 1559		0800 - 1559	
	M	F	M	F	M	F	M	F	M	F
Trees and fence posts	51.9%	37.0%	68.8%	46.8%	61.9%	60.9%	51.1%	47.1%	58.2%	46.8%
Coppice and bushy seedlings	31.9	33.0	16.8	27.8	28.9	23.2	30.4	32.1	27.0	29.2
Small woody plants	2.5	7.0	5.6	11.4	4.1	7.2	5.4	3.8	4.3	7.5
Ground	13.7	23.0	18.8	14.0	5.1	8.7	13.1	17.0	10.5	16.4
Total Percent	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Total Observations	160	100	125	79	97	69	92	53	474	301

The number of observations for each perch category was converted to a percentage of the total number of sightings for a particular time interval during the day; these percentages were kept separate for males and females (Table 5). The observations were the outcome of regular censuses of the area throughout the day either by foot or with binoculars. A perch site was not recorded unless an individual had moved since its previous position was noted. For this reason the largest number of recordings were made during the morning hours when the lizards were most active. It should be emphasized now that this summary is only of observed animals and does not include those individuals which were concealed (i.e. under the leaf litter).

Of the 775 perch observations 61 percent were of males; yet females accounted for over 50 percent of the population. This disproportion reflects to some extent the greater utilization of the leaf litter by the females. Another indication of the differential use of the leaf litter was the larger number of sightings of females on the ground. For all 4 periods of the day, the percentage of females on the ground was approximately a third greater than for males (Table 5). In addition, it was noted that during the warmest part of the day (1200-1400 hours) the females appeared in increasing numbers, being seen around the shaded bases of the trees and posts. These sightings are reflected in Table 3. Presumably, the females were emerging from the fallen leaves in response to rising substrate temperatures (Fig. 5).

Smaller males were generally seen in the coppice and shrubby vegetation, while the larger males frequented higher perch sites. To test this subjective evaluation based on observations and collecting experience, the average snout-vent length was calculated for males with home ranges lacking trees and compared with the mean length of males with trees in their ranges. The resulting mean from 6 males with treeless ranges was 39.1 ± 1.97 mm as compared with 43.0 ± 1.23 mm

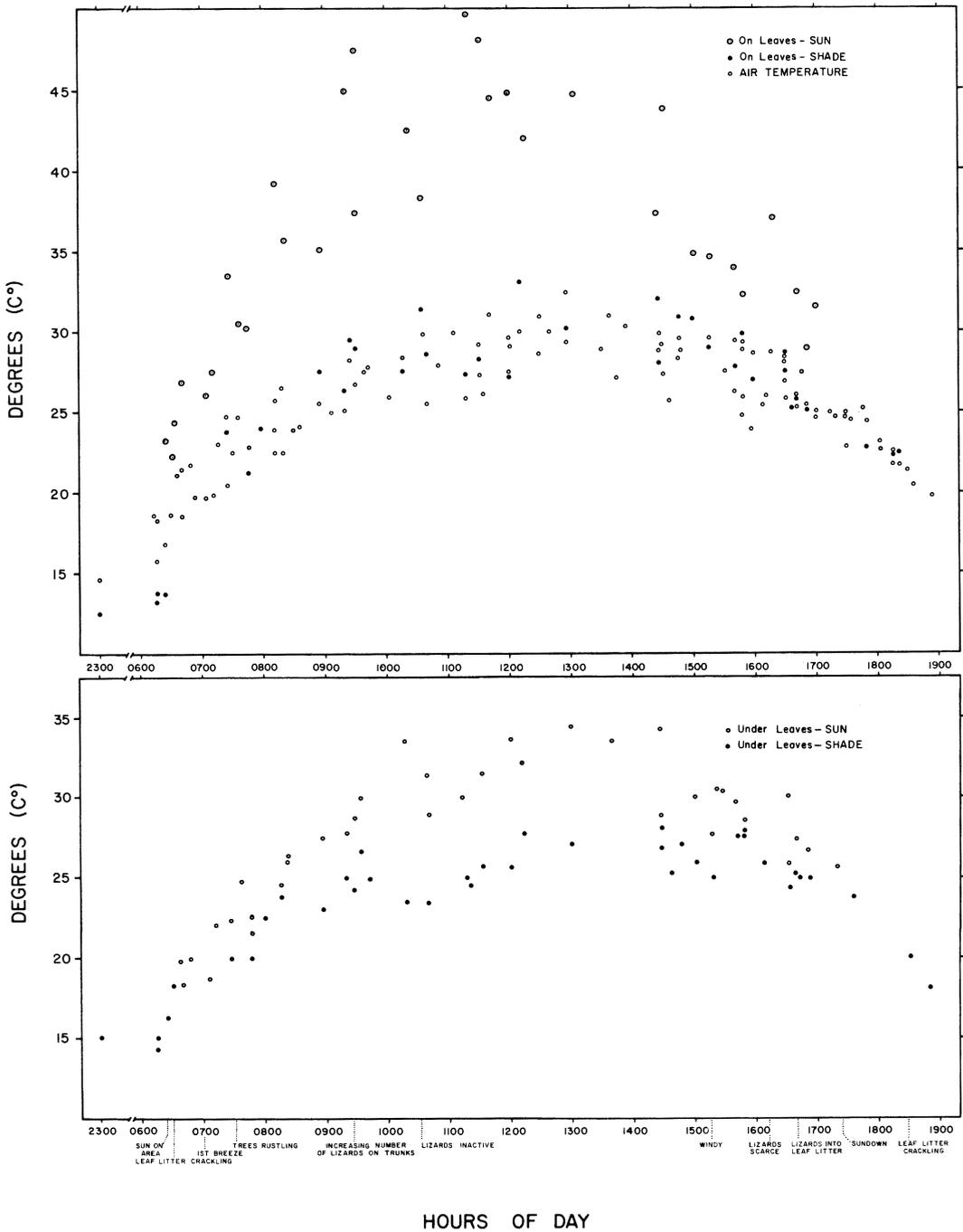


FIGURE 5. Air and leaf litter temperatures for the study area near Tepic, Nayarit, Mexico, during April - May, 1968.

for 16 males with trees. The presence or absence of trees in plotted home ranges, though an impartial way to analyze the sample, actually decreased the real difference between the two groups since a number of small males resided primarily in coppice beneath the trees, but by definition were still assigned to the tree-containing group.

From reports in the literature, most species of *Anolis* sleep above ground on grass stems or on the outer branches and leaves of trees and bushes. Similar sleeping sites are given for those *A. nebulosus* observed in Michoacan (Duellman, 1965; Schmidt and Schannon, 1947). However, the Tepic, Nayarit population was unique in this respect; they all retired under the leaf litter at sunset. Individual lizards were watched until they left their perch sites and crawled into the fallen leaves. The next morning before sunrise, the leaves at these sites were carefully excavated to reveal the same individuals observed the previous day. On one occasion the study area was thoroughly searched at 2300 hours. No anoles were found to be sleeping on any of the living vegetation, and several were uncovered in the leaf litter where they had entered earlier. The one exception was a male which crawled into a dead, curled leaf still attached to an oak coppice.

In summary, the males generally occupied perch sites further from the ground than the females who more frequently utilized the leaf litter during the diurnal hours of greatest activity. The partitioning, however, is more of a temporal division since lizards of both sexes will use all of the habitat types on occasion. The small males tended to occupy the coppice and shrub vegetation, while the larger males had home ranges which contained trees. These latter home ranges are probably more preferred as the trees provided higher perch sites, furnished more enduring shade throughout the day, and better foraging areas in the fallen leaves. Lastly, the anoles on the Nayarit study area slept under the leaf litter. This terrestrial sleeping site is the first to be reported for *A. nebulosus* and is unique to most species of *Anolis* which have been found to utilize arboreal or at least elevated sleeping sites.

Thermal relationships

From the reviews of Bogert (1949), Schmidt-Nielsen and Dawson (1964), Brattstrom (1965), and Fry (1967), it is evident that the thermal relationship of an exotherm with its environment is very important in understanding a species' behavior, ecology, and evolution. Some care must be exercised, however, in collecting and interpreting saurian cloacal temperatures since body temperature alone has little value in describing a species' thermoecology (Heath, 1964; Licht, et al., 1966a, b). To provide an adequate picture of the thermal characteristics of *A. nebulosus*, a summary of hourly readings of cloacal and microenvironmental temperatures was made for the species' diurnal activity period.

In the morning before the sun rose above the mountains, the air temperature was about 14 - 15 C. The cloacal temperature of 9 lizards in their sleeping sites beneath the leaf litter averaged 16.3 C (15.3 - 17.3 C) while the sleeping sites approximated air temperature, averaging 14.8 C (13.8 - 15.9 C); the lizards were slightly warmer than their immediate environment. These temperatures probably hold throughout the night as a sleeping anole at 2300 had cloacal and site temperature readings of 17.1 and 15.9 C, respectively. The surface temperature of the leaves was slightly cooler than the sleeping sites (Fig. 5).

The first rays of sunlight hit part of the study area around 0620. From this time on, substrate temperatures quickly increased (Fig. 5). The top of the leaf litter in the shade followed air temperatures. Temperature readings 8 or more centimeters into the shaded leaf litter were also close to air temperatures, though slower to rise. Even the morning temperatures of the deep leaf litter in the sun were close to corresponding air temperatures. The largest jump in microhabitat temperature occurred on or just under the surface leaf litter which was exposed to direct sunlight. During the night this surface layer was the coldest and in the day registered the highest temperatures (Fig. 5). The rapid change in heat caused the leaves to crackle both in the morning and evening.

It was under the rapidly heating surface layer of leaves that many of the lizards reached their activity temperatures in the morning. Most likely crawling up from the deeper layers, they would lie under a surface leaf, still hidden from view and gain heat. Some lizards just emerging from the leaf litter during the 0600-0659 hour had cloacal temperatures of 24.7, 25.2, 25.8,

and 29.1 C. In this hour (0600-0659) the sun did not warm the study area uniformly due to the variation in overhead shading within the plot. This differential heating is reflected in the cloacal and site temperatures of captured lizards (Fig. 6); some were thermoregulating in the sun while others were still under shaded leaf litter and had not yet become active.

Almost all lizards collected from 0700 to 0759 were in the sun. Their mean cloacal temperature (28.8 C) was significantly higher than the corresponding mean of their site temperatures (26.4 C) demonstrating that the lizards were basking and had not yet reached their preferred temperatures. Three anoles were taken in the shade during 0700-0759. Two were still inactive and the other anole had reached a high body temperature (32.4 C) and had entered the shade. This large temperature range resulted in the wide confidence limits appearing in Fig. 6.

At 0800-0859 hour the majority of the observed lizards were still in direct sunlight (Table 6); those anoles captured had a mean body temperature which was the same as this class group from the previous hour, 28.8 C. The cloacal temperatures of lizards in the shade were generally higher than those in the sun. The anoles in the shade at this time represent animals which had been basking during the previous hour, but had reached their preferred temperatures and retired

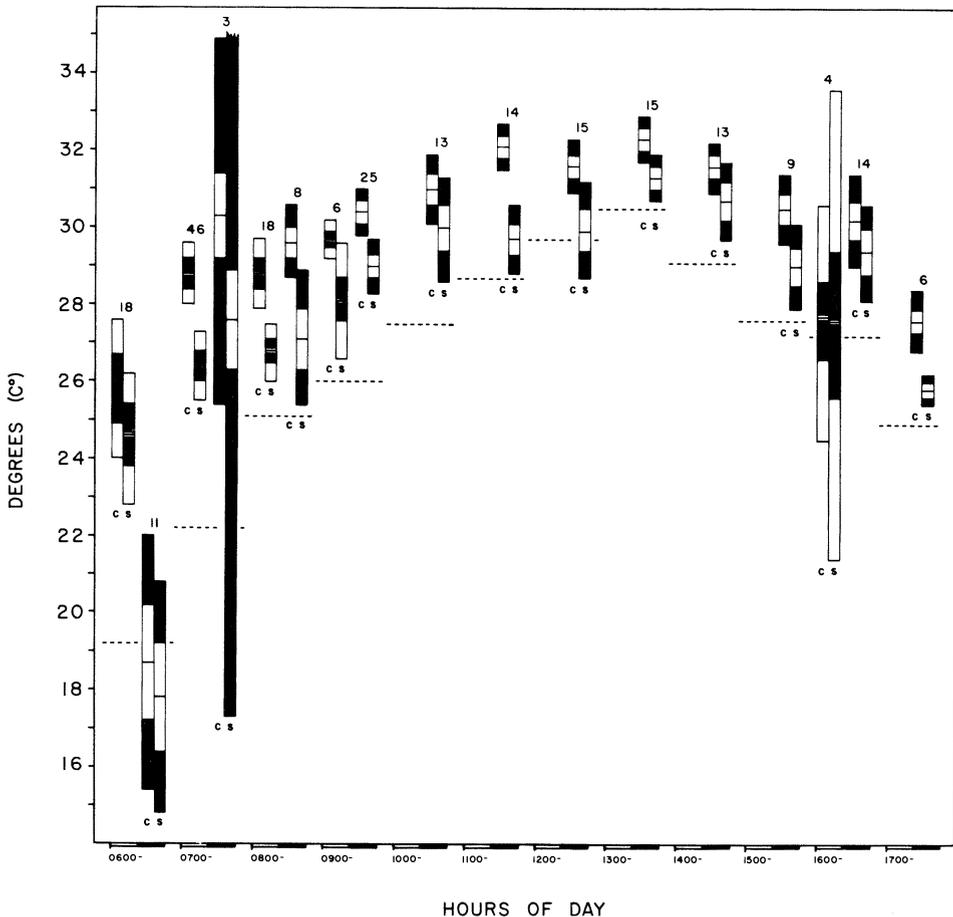


FIGURE 6. Hourly cloacal (C) and site (S) temperatures of *Anolis nebulosus* near Tepic, Nayarit, Mexico, during April - May, 1968. Ends of bars give 95 percent confidence limits of the mean, medial horizontal line of bars is the mean, and ends of inner box within the bars represent the standard error of the mean. Outer boxes of bars which are black represent lizards in the shade and white outer boxes represent lizards collected in the sun. Horizontal dashed lines give mean air temperature for the hour. Numbers over bars provide sample size.

TABLE 6. Hourly distribution of *Anolis nebulosus* on shaded and sun-exposed perch sites near Tepic, Nayarit, Mexico, during April - May, 1968.

Hour	% Lizards in Shade	% Lizards in Sun	No. of Lizards Observed
0600-0659	33.3	66.7	39
0700-0759	7.6	92.4	92
0800-0859	42.4	57.6	73
0900-0959	75.3	24.7	85
1000-1059	93.5	6.5	76
1100-1159	96.2	3.8	52
1200-1259	97.5	2.5	40
1300-1359	100.0	0.0	55
1400-1459	97.2	2.8	35
1500-1559	86.7	13.3	45
1600-1659	75.8	24.2	33

to the shade. The mean for this latter group (29.6 C) is very likely close to the value for the population's thermal preferendum since air and site temperatures were still considerably below observed body temperatures.

The various microhabitat temperatures at 0900-0959 were approaching their maxima. A marked increase in numbers of anoles was observed as they emerged from the leaf litter to apparently seek cooler substrate on elevated perch sites. Though 75 percent of observed animals were now in the shade (Table 6), some were still basking. Of those latter individuals, 6 were measured and had cloacal readings averaging 29.7 C; this mean is almost the same as that of the 0800-0859 group from the shade, and is probably the preferred temperature.

Activity began waning during the 1000-1059 hour. Almost all of the observed lizards were now in the shade (Table 6). No body temperatures were obtained from the few anoles seen in the sun. However, the mean cloacal temperature of the lizards in the shade at this time was 31.0 C, and was probably above that preferred by the anoles.

From 1100-1359 environmental temperatures continued to increase to their highest value (Fig. 5). Deep leaf litter temperatures during the afternoon exceeded the preferred body temperatures of the lizards, thus forcing many of the females in the leaf litter up onto exposed perch sites. Via binocular censuses a greater number of females were observed in the coppice and lower portions of tree trunks during the heat of the afternoon than during the late morning hours (Table 5).

In the afternoon cloacal and site temperatures progressively rose with air temperatures; all three readings reached their maximum during the 1300-1359 hour, averaging 32.3, 31.3, and 30.5 C, respectively. Every lizard observed at this hour was in the shade. Certain posturing was also noted which is probably employed to increase body heat dissipation. Many of the animals had their forelimbs extended so that their bodies were held away from the perch substrate. This posture was most frequently observed in animals on vertical perches. The claws of the hind legs were anchored on the rough textured substrate, and in a head-down orientation the lizard would hang away from the surface of the perch site with little apparent effort.

A wind was noticeable around 1400, and temperatures began to fall. After 1500 the wind became strong and the substrate as well as air temperatures decreased rapidly. During 1600-1659, 24 percent of the observed anoles had moved into the sunlight as mean cloacal, site, and air temperatures became almost equal at about 28 C. Those lizards still in the shade had body temperatures averaging 30.2 C, slightly above the preferred mean. Field records also indicate that the animals were becoming scarce. Observations of individual anoles showed that some were leaving their elevated perch sites during 1600-1659 and moving into the leaf litter and out of the wind. Cloacal temperatures of these individuals were still fairly high (e.g. 26.9, 27.3, 29.1, 29.7, 30.0, 30.1, 30.8, 31.6 C) and well within their activity range. Apparently the cue or cues to retire into the leaf litter may not always involve actual body temperature, but rather a decreasing body temperature, or decreasing illumination, or very possibly increased desiccation from the wind. This last possibility may be an important factor. March - May are the months of

the dry season, and besides a very light dew in the morning, all available water to the lizards was from prey items. Water conservation is undoubtedly a concern. Clausen (1967) found as much as 70 percent of the water loss in *Anolis carolinensis* can occur cutaneously. And in comparing the rate of water loss for the relatively dry-adapted *Anolis auratus* with the forest dwelling *Anolis limifrons*, Sexton and Heatwole (1968) felt *A. auratus* is able to conserve water to a greater extent through behavioral adaptations. Perhaps the extensive use of the leaf litter, particularly for sleeping sites, is a behavioral adaptation of *A. nebulosus* to combat the low humidity and lack of rain by decreasing cutaneous evaporation.

Most of the lizards were out of sight in the leaf litter by 1700, although a few anoles remained on their perches as long as there was sunlight. One male moved from the shaded side of a tree trunk into the sun at 1625. He remained on the sunny side of the perch, and as the air temperature lowered, oriented his body perpendicular to the sun. Seven minutes after the sun went down (1732), the male left the tree and entered the leaf litter. He was then captured and his cloacal temperature was found to be 26.0 C. By 1800, however, all lizards of the study area were in the leaf litter.

When plotting the body temperatures of the basking anoles, approximately 84 percent of the sample was clustered between 27.5 - 31.4 C and 75 percent of the sample fell between 28.0 - 31.4 C. The distribution curve was slightly skewed to the left (lower cloacal temperatures); this reflects those animals which were beginning to warm during the early morning hours. The mean class for 75 percent of the basking lizards was 29.5 - 29.9 C, and the group mean was 29.6 C (95 percent confidence limits of 29.4 and 30.0 C). These values for preferred body temperature agree well with the 29.7 C average estimated previously by inspection of Fig. 6. The maximum and minimum cloacal temperatures recorded for the population were 35.2 and 14.8 C; both were from lizards collected in the shade. The lower temperature was recorded from the anole sleeping under the leaf litter after sundown.

A comparison of male and female temperatures was made on all cloacal temperatures (sun and shade) above 27.4 C recorded between the hours of 0700 and 1559. The male body temperatures averages 29.9 ± 0.27 C (95 percent confidence limits of 29.3 and 30.4 C); corresponding values for female anoles were 28.5 ± 1.12 C (95 percent confidence limits of 26.2 and 30.8 C). Females tended to have slightly lower body temperatures, but the difference was not significant.

Although the lower temperature limit of the activity range for *A. nebulosus* has not been determined, a few examples are available. One male was observed still displaying at 1625; his cloacal temperature was 25.2 C. A female was found sluggishly moving through some grass toward a coppice at 0645 before the sun had reached her sleeping site. Her body temperature was 16.6 C. This is probably close to the lower temperature limit of movement, as Gordon (1956) found *A. carolinensis* to become torpid at approximately 13 C.

If body temperatures are to be of value for comparing lizard species ecologically and phylogenetically as evidence indicates they can be (Licht, et al, 1966; Licht, 1968, Ushakov, 1964), it is imperative that field investigations provide a complete thermal profile for the studied species, and attempt to establish its thermal preferendum. Merely giving average cloacal temperatures over a limited portion of the day is of uncertain value. For example, *A. nebulosus* experienced a wide range of body temperatures during a single day, much of which was only tolerated by the lizards. Figure 6 shows that if cloacal temperatures were only recorded between 1000 and 1500 hours a biased interpretation would result in which the average cloacal temperature of *A. nebulosus* would appear to be over 31 C. Yet it is during these hours that the lizards were unable to hold their preferred body temperatures and were at the mercy of ambient temperatures. These non-preferred temperatures found within the anoles' daily temperature profile are also subject to vary with the season of the year and with habitat.

In summary, cloacal temperatures of *A. nebulosus* are comparable to other anoline species living in filtered sunlight conditions (Brattstrom, 1965; Brooks, 1968; Carpenter, 1965; Fitch, 1968; Heatwole, et al, 1969; Rand, 1967a; Ruibal, 1961), and can be classified as a diurnal, limited basker (Brattstrom, 1965: 412-413), or a facultative non-heliotherm (Ruibal, 1961: 109). Its preferred mean body temperature appeared to be 29.7 C. The lizards were observed to bask in the early morning hours (0600-0959) and then retire to the shade where their cloacal temperatures

continued to rise along with ambient temperatures. *A. nebulosus* were generally inactive during the warmest hours of the day (1100-1459) at which time their body temperatures were over 31.0 C. Almost without exception, cloacal temperatures were higher than corresponding site temperatures.

Home range

Determination of the home range of *A. nebulosus* simply included every location where an individual was sighted or captured, and reflects the amount of space required by a lizard to fulfill its daily needs. These locations for each animal were recorded and plotted on a scale map of the study area (Fig. 7). By connecting the outermost locality sightings, a minimum polygon was produced for each animal (Fig. 8 and 9). Area determinations were then extrapolated by weighing the scaled home ranges cut from graph paper against a known scaled area (10 m²) also cut from the same paper. These weights were made on a Mettler balance accurate to 0.001 gm. To check the weight consistency of the graph paper, three known area samples (scaled equivalent of 10 m²) were cut and weighed; all three pieces were within 0.007 gm of each other (2 percent error).

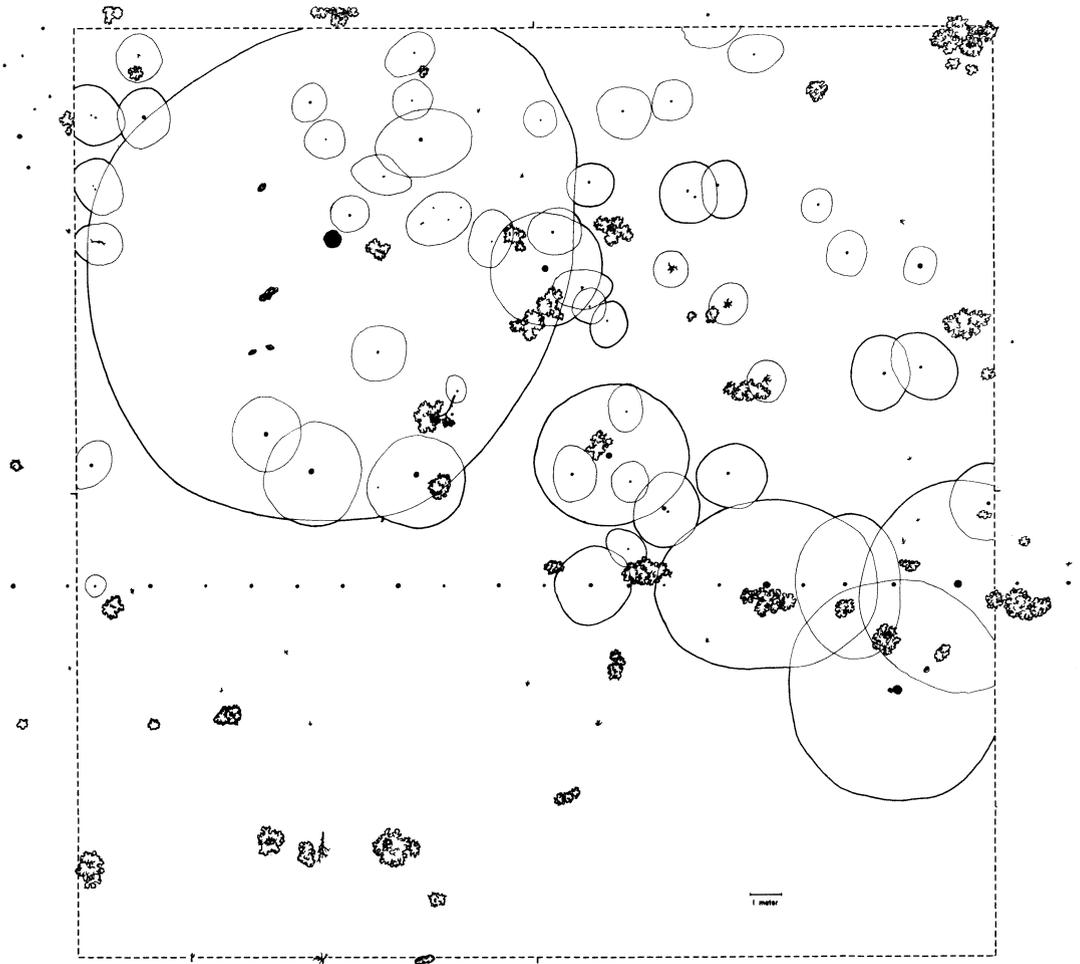


FIGURE 7. Scale map of the 30.5 x 30.5 m study area showing seedlings, coppice, fence posts, and trees with their overhead canopy outlined.

The location of 25 males and 27 females was recorded with enough frequency throughout the investigation to know that they were residents of the study area. Three males and 1 female did not seem to have a definite home range, but they did remain on the study area (Tables 7 and 8).

Males had significantly larger home ranges than females. The 22 male home ranges averaged $1.99 \pm 0.23 \text{ m}^2$ with 95 percent confidence limits of the mean at 1.43 and 2.55 m^2 . The home ranges of the 26 females averaged $0.62 \pm 0.14 \text{ m}^2$ with 95 percent confidence limits of 0.34 and 0.90 m^2 . Male lizards also moved further between observations than females (Tables 7 and 8); the distances were significantly different. The 95 percent confidence limits for the mean distance per move were 2.78 and 3.74 m for the males, and 1.29 and 2.49 m for the females.

Home range sizes for males are probably very accurate since almost all of their movements were easily seen due to their exposed perch sites. However, the females' movements could not be followed while they were in the leaf litter. For this reason their home range estimates may tend to be conservative. The numbers of observations per female are also fewer than for males, but as Tinkle (1967: 94) pointed out for *Uta stansburiana*, there is little correlation between larger estimates for the size of a territory with increased observations; eleven captures yielded a reasonably accurate estimate of a home range.

Within the sexes there also appeared to be some differences in home range size as related to the length of the anole (i.e. the larger the lizard, the larger the home range). To illustrate this, animals having calculated home ranges in Tables 7 and 8 were divided into three groups. Since these data were arranged according to snout-vent lengths, the groups contained individuals

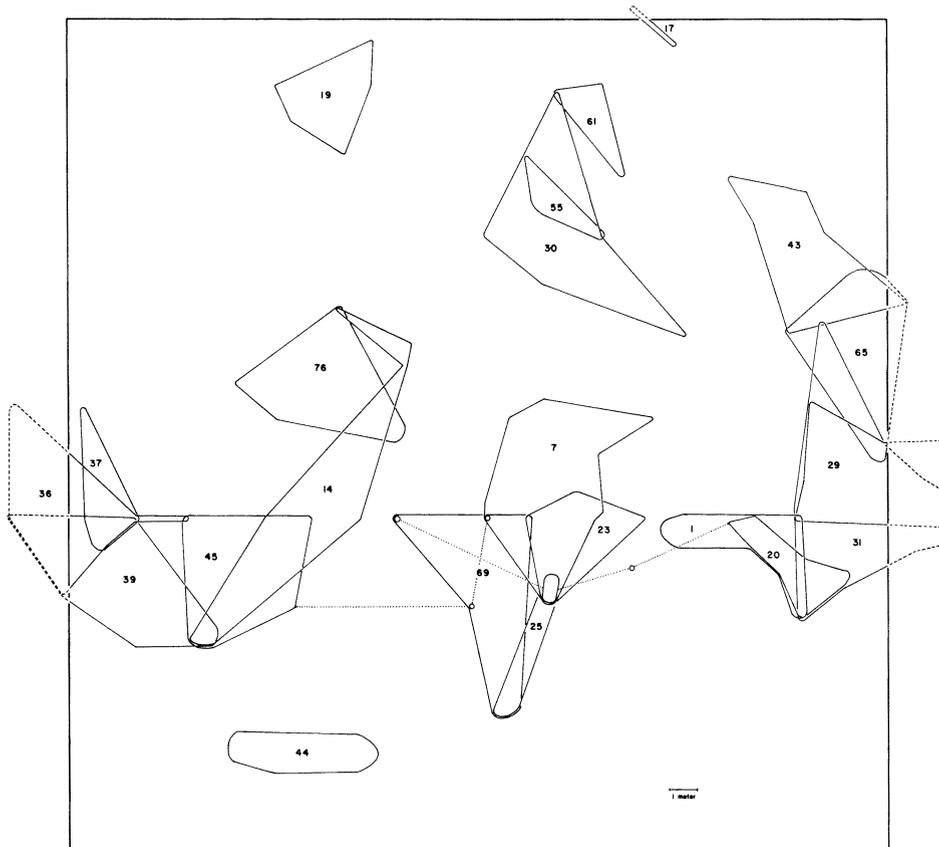


FIGURE 8. Scale map of study area with home range of 22 male *Anolis nebulosus* superimposed.

TABLE 7. Movement and home range size for male *Anolis nebulosus* near Tepic, Nayarit, Mexico, during April - May, 1968.

Individual	S-V Length	Times Moved	Avg. Meters per Move	Number of Observations	Home Range (m ²)
30	48	10	3.70	14	3.02
43	48	19	3.05	40	2.17
1	48	34	1.92	69	1.16
31	46	36	3.84	50	4.52
37	46	7	3.14	18	1.72
29	44	18	4.94	27	4.52
7	44	20	2.65	28	3.19
65	44	12	2.56	23	2.40
44	43	3	0.70	7	0.99
46*	43	9	3.75	16	..
14	42	11	5.12	26	2.98
61	41	5	3.02	11	0.49
70*	41	9	7.59	4	..
45	39	13	3.72	23	2.46
19	39	6	3.69	14	1.10
25	39	11	4.15	23	0.54
17	39	8	2.32	17	0.06
76	38	6	4.30	10	2.19
6*	38	13	3.81	19	..
69	37	8	4.27	11	2.46
20	36	13	4.51	15	0.77
23	35	7	2.20	8	1.32
39	35	12	3.23	29	2.90
36	33	14	2.47	25	2.37
55	32	3	2.17	12	0.39
Average	40.7	12.5	3.26	22.3	1.99

*Not included in group average as home range was not apparent.

the most shade were occupied by the large male lizards. The overhead canopy, however, was in a state of flux. The dead oak leaves which were retained on the branches in large numbers at the start of the investigation were being dropped in quantity as the study progressed. Areas which were once well shaded became exposed to more and more direct sunlight before the new foliage was put forth by the trees. This process caused some of the lizards to shift their home ranges, particularly those without an understory of coppice and shrubby seedlings in their territories. For one male the decrease in overhead shade was believed to be responsible for his disappearance from the study area.

Male No. 19 was consistently seen in the upper left quadrant of the study area where he occupied some small saplings (Fig. 8). This part of the study area contained little understory, and when the dead leaves were being dropped from these small trees and the larger one in the male's vicinity, very little shade occurred, especially in the early afternoon. Recorded cloacal temperatures for male No. 19 during the first week of the study generally followed the daily cycle presented in Figure 6. However, at 1244 on May 2, he had a cloacal temperature of 34.1 C with a site temperature of 33.0 C. The following day at 1610 his body temperature reading was 34.6 C, the site temperature 34.0 C, and the adjacent side of the tree trunk measured 42.8 C. This was the last day male No. 19 was seen. Thermal stress may have caused him to establish a new home range elsewhere.

There was considerable overlapping of male home ranges (Fig. 8). Some of this was due to shifts in home ranges over the time span of the study where one animal took over part of another's habitat. This is especially true of the larger lizards. However, a few males actually co-inhabited the same area. This relationship was always small male with large male. From field and laboratory observations it was found that the large males will tolerate the presence of small males. No. 20 (S-V 36 mm) co-existed with No. 1 (48 mm), No. 55 (32 mm) with No. 30

TABLE 8. Movement and home range size for female *Anolis nebulosus* near Tepic, Nayarit, Mexico, during April - May, 1968.

Individual	S-V Length	Times Moved	Avg. Meters per Move	Number of Observations	Home Range (m ²)
64	39	7	1.89	16	0.05
4	38	17	2.50	24	1.69
52	38	8	3.54	16	1.14
2	37	21	3.36	30	2.11
33	37	16	2.52	23	2.09
8	37	9	2.90	29	1.84
27	37	3	3.02	8	0.85
9	37	6	3.97	17	0.29
3	37	12	1.77	22	0.29
48	37	0	0.00	6	0.03
51	36	3	3.54	6	0.85
13	36	1	4.55	5	0.55
22	36	4	1.53	7	0.12
67	36	0	0.00	3	0.02
62	35	11	3.05	19	1.31
47	35	7	3.66	16	0.94
75	35	0	0.00	3	0.02
11	34	7	2.14	10	1.03
74	34	0	0.00	3	0.11
54	34	5	2.01	11	0.03
18	34	0	0.00	8	0.02
10	34	0	0.00	3	0.01
56	33	4	1.68	20	0.34
53	33	3	1.53	3	0.19
32	33	0	0.00	5	0.02
72*	32	3	9.73	5	.
5	32	0	0.00	11	0.05
Average	35.5	5.5	1.89	12.5	0.62

*Not included in group average as home range was not apparent.

(48 mm), No. 36 (33 mm) and No. 39 (35 mm) with No. 37 (46 mm), and No. 23 (38 mm) with No. 7 (44 mm). Much less overlapping of home ranges occurred between the females (Fig. 9). Only 9.1 percent of the males had isolated home ranges as compared with 61.6 percent for females.

Both males and females will defend the majority of their home ranges, and in general the home range for *A. nebulosus* may be considered its territory. However, on occasion certain lizards were seen to make apparent exploratory movements. When the lizard encountered agonistic responses from adjacent lizards during these wider movements, the anole would retreat.

The distribution of female home ranges is almost a perfect overlap with male home ranges. Female anoles residing within the home ranges of males have been reported for *A. lineatopus* (Rand, 1967a: 35), *A. sagrei* (Evans, 1938a: 123), *A. carolinensis* (Greenberg and Noble, 1944: 413), and *A. distichus* (Rand, 1962: 5), and is probably true of many other anoline species. For *A. nebulosus*, at least, this behavioral feature tends to promote monogamy. The females are very territorial and drive other females from their territories; this decreases the number of potential mates for those males who have a resident female in their territories.

The size of the home ranges of *A. nebulosus* is not only influenced by the size and sex of a lizard and the distribution of perch sites, but also by individual behavioral characteristics. From extensive field observations, it soon became apparent that these anoles were all very much individuals. Even though the lizards carried identifying paint marks, many could easily be recognized solely from their unique behavior (i.e. manner in which they carried themselves). One of the easier subjective clues to individual recognition was the frequency and intensity of aggressiveness. This behavioral aspect helped determine an animal's territory size; however, it is not a direct relationship as will be seen from the following examples.

TABLE 9. Comparison of length of lizard to movement and home range size.
Data taken from Tables 7 and 8.

Sample Size	Avg. S-V (mm)	Avg. Meters per Move	Avg. Home Range (m ²)
Males			
8	46.0	3.23	2.84
7	40.3	3.25	1.23
7	35.1	3.31	1.77
Females			
9	37.4	2.83	1.15
8	35.8	2.04	0.48
9	33.4	0.82	0.20

On the right half of the study area where most of the large males had their territories, an interesting interplay was observed between males No. 1, 29, 31, 43, and 65. Male No. 1 was the largest anole of the study, weighing 3.22 gm, and was probably a two year old animal. Besides his stout morphology, No. 1 was characterized by his slow, deliberate movements. His home range was not particularly large (Table 7, Fig. 8), but its borders were rigidly defended. During a ritualized dispute involving only display exchange, No. 1 turned back male No. 31 who was beginning to enter No. 1's territory. Only a small male (No. 20) was ever seen in the territory. No. 1 was never seen to venture out of his territory.

Like No. 1, male No. 43 possessed a very stable and well defended territory of moderate size (2.17 m²). He also turned back No. 31 during a display exchange when No. 31 attempted to enter No. 43's territory. Neither male No. 1 nor 43 were seen to initiate a territorial dispute.

In contrast to No. 1 and 43 was male No. 29. He too was aggressive, but in a different manner. No. 29 had fast, quick movements and showed little consistency in returning to a particular perch as was true of No. 1 and 43. He made frequent excursions into the home ranges of adjacent lizards where serious territorial encounters resulted. A dramatic film sequence was obtained of a naturally occurring fight between No. 29 and an adjacent male off the area. Twisting and thrashing in the leaf litter, the lizards repeatedly locked jaws until No. 29 was driven off. No. 29 was never seen to challenge No. 1 and 43, but did cause No. 31 and No. 65 to retreat when he entered their home ranges. Consequently, No. 29 had a large home range (4.52 m²).

Male No. 31 occupied a home range bordered on one side by an open grassy area, and on the other three sides by the territories of No. 1, 43, and 29 (Fig. 7 and 8). No. 31 was often seen foraging about in the leaf litter or resting in a coppice, but was not seen to take a high perch as was true of his neighboring males. His home range was one of the largest (4.52 m²), being equal to that of No. 29; yet No. 31 was never seen to defend it. Instead, this male would shift his position to avoid interaction with other large males. Male No. 65 possessed similar behavioral traits, but restricted himself to a few perch sites in a coppice and some saplings; unlike No. 31's home range, there was little overhead shade, which may have limited his movements.

It is interesting to note that both the most aggressive and least aggressive of the observed male lizards had the largest home ranges. There was an obvious difference in the degree of territorial defense between the various males. These differences in individual aggressive levels which are subtly expressed in the field are very noticeable in the laboratory. Lizards confined together in enclosures with no means of avoiding one another quickly express these aggressive differences via formation of dominance hierarchies.

Social behavior

The repertoire of social behavior patterns observed for *A. nebulosus* was surprisingly large. However, deriving the information communicated by these behavior patterns is difficult, particularly when the only practical approach is through casual observation. Behavioral functions deduced by correlating observed behavior patterns with various types of social interaction are for

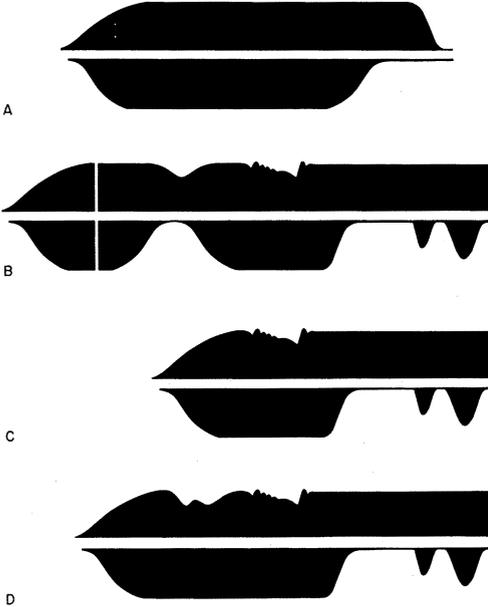


FIGURE 10. Four display patterns commonly observed in male *Anolis nebulosus*. Upper block represents amplitude (vertical axis) and duration (horizontal axis) of head movement and lower block represents dewlap movement. a.—“flagging” display, b.—“flagging” display added to assertion display, c.—assertion display, d.—challenge display.

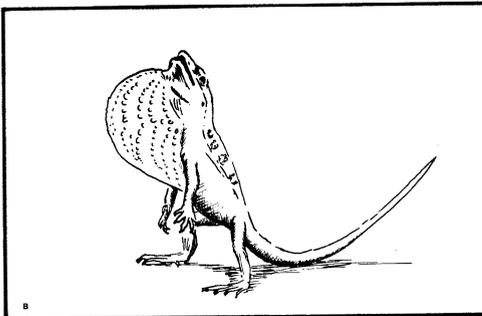
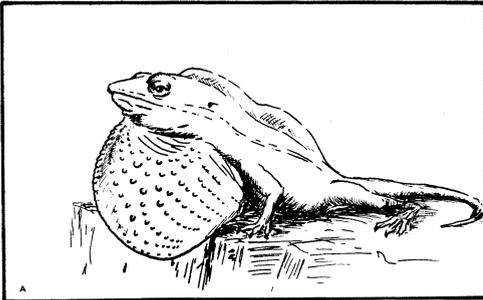


FIGURE 11a. Assertion display of *Anolis nebulosus*. b. Challenge display of *Anolis nebulosus*.

the most part speculative. Interpretation is complicated by some patterns being used in two or more contexts. Furthermore, such modifying factors as a lizard's past experience and its physiological state are for the most part unknown to the observer. Therefore, the following discussion represents a purely descriptive account of the anoles' social behavior.

In many of the behavior patterns the dewlap plays a prominent role. The dewlap, or throat fan, is large in *A. nebulosus* and is produced through the modification of the hyoid apparatus (Von Geldern, 1919). Four display patterns have been observed in both male and female *A. nebulosus* which incorporate the extension of the dewlap (Fig. 10).

Assertion display.—The basic display-action-pattern (DAP) most frequently seen fits the behavioral definition named by Carpenter (1962) as the assertion display (Fig. 10c). This DAP was extremely stable and characteristic for the population (Jenssen, 1969). The lizards initiated the display while on vertical to horizontal perches. The forelimbs were straightened with the head being raised slowly as the dewlap was extended. Once the forelimbs lifted the lizard's chest off the substrate, the head and dewlap were the only parts moved in this low intensity display. Occasionally the nuchal crest or roach was raised which indicated a higher level of excitement of the displaying animal (Fig. 11a). Although the lizards gave the assertion display from all parts of their habitat, the males most often selected elevated perches from which to display. The displaying animals gave a lateral presentation to the lizard of their attention.

Under crowded conditions in the laboratory a single male soon dominated all other lizards in an enclosure, and of the males, he alone performed this assertion display. During hourly observation periods it was common to record over 50 assertion displays by the dominant male. If a newly introduced male performed the assertion DAP, or even extended his dewlap, there was an immediate display or chase by the dominant male. The male lizards also performed the assertion display when individually isolated from all other lizards.

In the field territorial males were seen giving the assertion DAP repeatedly. This display was usually given when the male stopped on a new perch site within his territory. The assertion display was observed far less frequently

than in the laboratory enclosures. Twenty-three displays in an hour's observation period was the maximum recorded for a male in the field.

Both in the field and the laboratory, territorial males performed the assertion display when sighting another male at a distance. This distance was not specific, but usually past the territorial boundary of the displaying male. The assertion DAP was also given to distant females, though it was not as predictable an occurrence. Somewhat contrary to the above social contexts, the males many times gave the assertion display during prolonged courtship when it seemed certain they recognized the other lizard as a female; this would seem inappropriate if the assertion DAP is purely an aggressive signal.

The female used the assertion display when approached by another female or smaller male which was in her territory. In enclosure studies, however, this behavior was largely suppressed by the dominant male. If all males larger than most of the females were removed from the enclosure, a dominant female became evident. She frequently presented the assertion DAP and chased the other females and smaller males. The assertion display was also presented to courting males by the females. This was often seen both in the laboratory and the field.

Hatchlings under a day old executed the assertion display as well. On one occasion the hatching of two lizards was being observed. Both lizards emerged from their eggs about 5 minutes apart. After an hour their movements became coordinated and they began moving about the cage. Soon they encountered each other and one hatchling gave an exact replication of the adult assertion display including extension of the minute dewlap. The other hatchling responded by trying to run in the opposite direction. This behavior occurred 1 hour and 9 minutes after hatching and in the absence of any other lizards.

For the most part, the assertion display of *A. nebulosus* appeared to be an agonistic behavior pattern, and as suggested for other iguanid lizards (Carpenter, 1967: 87), seemed to be a warning for adjacent lizards to keep their distance. During the period when adult males demonstrated territorial behavior (approximately January - September), this individual distance was much greater than during the winter refractory period. Very few assertion displays were seen in the holding enclosures in the winter.

Challenge display.—This is a high intensity display which usually occurs during male-to-male encounters at close range (Carpenter, 1962). Basically, the *A. nebulosus* challenge display is composed of the assertion display with a preceding unit of head bowing (Fig. 10d). The male to male challenge has many subtleties besides the challenge display itself which makes the behavior sequence somewhat unpredictable and much more variable than the assertion DAP. In the field the encounter usually progressed from a long range exchange of assertion displays between a resident and nonresident male and built up to a high intensity interaction at close range. During the first part of this interplay, the roach or nuchal crest was raised, lateral compression of the body occurred, and the body pattern became more contrasted. As the encroaching male continued to approach the territorial male, their displays began to alter with posturing and the assertion display itself being exaggerated. Then the challenge DAP appeared. The male anole lifted his head high, forelegs straight and back arched, as the dewlap was extended to its fullest. The head was raised and lowered several times in a rocking, bowing type motion before the appearance of the head nods which mark the initiation of the assertive portion of the challenge DAP. This head rocking sequence can be so intense that when the male arches his back he pulls himself into a semi-erect posture, being supported by the hind legs and tail with the forelegs draped against his sides (Fig. 11b). When he returns to a four-legged stance, the dewlap may or may not be retracted before the assertion display. The extension of the dewlap during the head rocking sequence may be prefaced by short, jerky, four-legged hops.

The displaying males positioned their bodies parallel to one another during the performance of the display. *A. nebulosus* many times oriented head-to-head and tail-to-tail rather than the head-to tail "face-off" described for other iguanids (Carpenter, 1967: 93). With engorged throat, raised dorsal roach, and compressed sides, the males offered an enlarged presentation of their real size.

If neither antagonist retreated during this ritualized combat, actual aggression ensued. Either one male lunged at the other during the latter's display, or they came face-to-face and

began sparring with open jaws, their heads tilted sideways towards one another. Once the jaws were locked, the animals tugged at each other or twisted violently until the hold was broken. The contest proceeded again until one of the males retreated. The other male usually gave chase for a short distance, and then performed a series of exaggerated assertion displays. If the fight occurred in an enclosure, the defeated male never was seen to contest the dominant male again. In several cases where both males were of approximately the same size and the fights had been long, the defeated males rapidly lost their healthy appearance and many times died soon after the fight. Such a fatal aftermath was not suggested during field observations.

Though the females were also territorial and very aggressive, only two instances were observed of a female-to-female challenge encounter, and these took place in the field. The following is transcribed from field notes.

4/29/68

- 1658 Female No. 8 chased from C-0 (Coppice No. 0) by female No. 3. Female No. 8 traveling through leaf litter toward C-4.
- 1705 Female No. 5 came out of leaves under C-4 and chased female No. 8 west. As No. 8 fled, No. 5 stopped, oriented laterally, and gave three assertion displays toward female No. 8 (which is larger of two) and continued the chase.
- 1708 When approximately 5 m from C-4, female No. 8 stopped and performed a high intensity, male-type assertion display (laterally oriented) toward female No. 5. Both females then faced off head-to-head and gave challenge displays which appeared identical to the male encounters. Female No. 8 then lunged at female No. 5 and after a short scuffle drove female No. 5 back toward C-4.

5/3/68

- 0730 Female No. 4 was observed chasing female No. 3 in leaf litter near C-0 (Coppice No. 0). Both females stopped and laterally presented. Female No. 4 rocked back on hind legs with dewlap out, but DAP was not seen. Female No. 3 also had dewlap extended. Female No. 4 then dashed past female No. 3 around north side of T-6 (Tree No. 6) and into leaf litter. Female No. 4 also left vicinity of C-0). This was probably due to observer's presence.

No challenge displays were seen performed by hatchlings. And with the exception of staged fights where one male was released in another's territory, the challenge display occurred very infrequently in the field.

The challenge display almost always showed itself when a territorial male was approached by another male at close range. Two possible exceptions were noted from this social context. One was stated above when the chased female No. 8 made a stand against female No. 5. Although territorial protection probably initiated the chase, territorial defense did not cause female No. 8 to make her stand. The other exception was first noted when a *Urosaurus ornatus* passed down a tree trunk close to a perched male anole. The anole immediately flashed his dewlap out and rocked as occurred at the beginning of the challenge display; however, the assertion component of the challenge DAP did not follow this behavior. The same behavior was repeated when the two species were placed in an aquarium while on the study area. The large *Urosaurus* may be a predator of *A. nebulosus*, particularly of the smaller individuals, and thus represent a threat.

Direct injury resulted from the male fighting. Not only were scars evident on the males' snouts from wounds inflicted by jaw holds, but broken dewlaps and tails were also found in field collected animals. Several events observed in the laboratory suggested how some of these injuries may have resulted during territorial disputes.

2/23/68

Males AB and CS were performing challenge displays during their face-off when AB lunged at CS grabbing CS by his dewlap. AB then rolled his body from side to side causing the extended dewlap of CS to be twisted. It was noted several days later that the dewlap presentation of CS was unusual. The *processus retrobasalis* of the hyoid apparatus was apparently broken.

2/2/68

Male CB had just defeated another male when male D approached and tried to laterally position itself in front of CB for a display. However, as soon as the dewlap was extended, CB lunged at D. Again

D tried to position himself, but in so doing moved his tail by CB who bit it. D struggled, leaving a 5-6 mm segment of tail in CB's mouth. D left the area while CB gave an assertion display and proceeded to eat the piece of tail.

"Flagging."—This behavior pattern is very simple; the lizard raises its head and extends the dewlap as in the initiation of the assertion DAP. After an indeterminate period of time (1-18 seconds) the dewlap is retracted as the head lowers (Fig. 10a); no head nodding occurs. The pattern is extremely variable in duration, even within the same individual. The social function of this behavior pattern is an enigma as it was observed within a myriad of various social contexts.

Sometimes "flagging" was preliminary to aggressive situations. When a piece of cardboard was removed from between two adjacent aquaria, the flagging pattern was given by the dominant male of one aquarium as he first saw the dominant male of the other aquarium; soon they exchanged assertive and challenge displays. A male flagged at a nearby female when she began to display. A very exaggerated and intense flagging appeared when a *Urosaurus ornatus* passed close to an anole as he was perched on the side of a tree trunk; this is the same behavior pattern occasionally seen during the challenge behavior in which the male performs while on his hind legs and tail. A dominant male flagged when approached by a female. Females commonly flagged when approached by another female or when displayed at during courtship by a male. Females flagged while being mounted by courting males. The held dewlap extension was consistently seen when a male was placed in a strange cage, and in the field as a male emerged from the leaf litter within his home range. The flagging pattern was also used during shedding.

The flagging pattern seemed to be used socially as a low intensity form of the assertion display and mainly appeared (1) at the initiation of an agonistic situation, and (2) at times when entering a portion of the home range which previously had been out of view, or when entering an unfamiliar area. Under the latter conditions a male showing his dewlap would quickly notice other males in the area as this behavior would elicit their assertion displays.

"Flagging" plus assertion display.—This behavior was not observed often. The social contexts in which it was seen were low-keyed events, and it is possible this behavioral pattern is intermediate in function between the flagging and assertion displays of which it is comprised (Fig. 10b). This display was performed by males when approached by receptive females, and by females when courted by males. It was also used by a female during copulation. The execution of the display is identical to its two component displays. The duration of the flagging unit was extremely variable.

Tail wag.—This is a behavior description suggested by Ruibal (1967) and used by Gorman (1968) in their observations of West Indian anoles. For *A. nebulosus* the tail wag is a slow lateral movement of the tail which can be performed in a multitude of ways (i.e. wide, sweeping motion to cat-like twitching of just the tip of the tail).

The tail wag was seen in asocial situations; all age and sex groups of anoles both in the field and laboratory occasionally tail wagged as they stalked a prey item. During social interactions the tail wag was commonly performed in the laboratory by subordinate males. They were seen to flatten themselves against their perches and slowly wag their tails from side to side when approached by the dominant male. Females also gave the tail wag and flattened posture when approached by the dominant male. Sometimes the tail wag was initiated by a female seemingly without being evoked by any previous act on the part of adjacent lizards; the following is an example of this behavior observed in an enclosure.

6/25/65

- 1642 Blue female (B-F) on a twig above white male (W-M). She twitches her tail. W-M moves away and crosses terrarium to bush where yellow female (Y-F) is perched. At his approach, Y-F flags her dewlap and W-M performs 2 assertion displays. From across the enclosure B-F twitches her tail and W-M looks at her.
- 1644 Y-F moves further up in the bush away from W-M.
- 1645 W-M climbs the bush toward Y-F and gives an assertion DAP. B-F shifts position slightly and W-M looks at her.
- 1646 B-F is slowly moving her tail again and W-M looks at her.
- 1647 W-M is now one-half inch from Y-F who begins extending her dewlap. B-F again shifts position with a small tail wiggle.

- 1648 B-F wiggles her tail slowly and W-M notices. She repeats the tail wag. W-M then leaves Y-F's bush and runs to a large rock in the center of the terrarium where he flags twice (4.8 and 2.7 sec. duration).
- 1649 B-F again is wiggling her tail very slowly and also curls and uncurls it.
- 1652 B-F still intermittantly wagging her tail.
- 1654 B-F wiggles tail. Yellow male (subordinate male) leaves his perch and approaches B-F who twitches tail. She has increased the vigor of her tail curling, at times leaving the tail to dangle over the edge of the twig with a quiver in it.
- 1655 The dominant male, W-M flags once (4.5 sec.) and gives an assertion display. B-F continues to undulate her tail. Now W-M leaves the rock and climbs the same twig on which B-F is perched.
- 1656 W-M starts up twig toward B-F, stopping to give a flag-assertion display. B-F increases tail wiggle.

These notes continue for another 55 minutes during which time B-F approached W-M a number of times and displayed much tail wagging. Y-M (the subordinate) then ran up the twig and put his head on B-F's back. W-M left his perch site and ran toward Y-M. The observation period ended with intermittant chasing of Y-M by W-M, the latter giving over 22 assertion displays in a 10 minute span.

The tail wag was observed in many forms and in various social and asocial contexts. During social contacts the tail wag at times appeared to be a submissive gesture, at times a sexual rejection behavior, and at other times a sexual enticement.

Courtship and copulation.—The courtship and copulatory behavior of *A. nebulosus* followed a general pattern similar to that described for *A. carolinensis* (Evans, 1938b; Greenberg and Noble, 1944; Gordon, 1956). The usual behavior pattern associated with courtship which is performed by male *A. nebulosus* consists of a sequence of shallow, rapid head nods. This behavior is typical of courting iguanid males (Carpenter, 1967) and has been called "jiggling" (Evans, 1938b; Ruibal, 1967), "courtship nodding" (Greenberg and Noble, 1944; Carpenter, 1962), and "shuddering" (Ferguson, 1969).

Although the saurian courtship performance has been reported as highly stereotyped (Noble and Bradley, 1933: 94), considerable individual variation was observed for *A. nebulosus* and other iguanid species (Clarke, 1965). The rapid head nods of the courting male were at times preceded by one or more assertion displays. Assertion displays were also given between intervals of head nodding, particularly if the courtship was prolonged. Frequently the females responded by flagging, giving an assertion display, or tail wagging from both normal and flattened postures. Most often the females retreated before the advance of the males; these females were considered non-receptive as copulation was not observed if the females made a determined retreat.

Transcribed from field notes is an example of a male courting an apparently non-receptive female.

5/4/68

- 0807 Male No. 7 seen with roach up, located 0.2 m up T-15 (Tree No. 15); he is giving rapid head nods. Female No. 4 was at base of T-15 and she gave an assertion display towards him, but with no lateral presentation. He rapidly head nodded and she gave two more assertion displays. Then she "squirreled" around tree and climbed quickly past the male. She stopped and presented the assertion DAP. He gave a rapid head nod and she climbed further up the tree.
- 0810 Male went up tree after female. He rapid head nodded and she ran still higher - 1.3 m up. He gave 2 assertion displays. She also displayed. Female was on branch 2.1 m up and male was on trunk 0.3 m below her. She jumped to trunk and ran up still higher (3 m up). He displayed assertion DAP.
- 0818 Male is now 3 m up and she is at top of sapling (3.3 m). He gives assertion display and moves up to her. Female "squirrels" past him. He gives rapid head nods and an assertion display while female runs down tree.
- 0822 Male turns with head down and gives assertion display. They then alternately move down the sapling with the male occasionally giving assertion displays. At 0832 female disappears into the leaf litter.

In the laboratory it was not uncommon for males to show no courtship behavior at all, but to merely rush across the enclosure and attempt to secure a copulatory hold on the female.

Receptive females were passive. The males would advance and move into the copulatory position while the females remained still.

7/10/65

- 1123 W0-Male vibrates (rapid head nodding) at Ybar-Female, comes across and jumps on her back. She gives a very extended flag display and then an assertion display as he remains over her, though not in a copulatory position. He vibrates his head occasionally, but she does not move.
- 1124 Female gives an assertion display and then flags.
- 1125 Neither lizard has moved. W0-Male vibrates his head and Ybar-Female flags. The male sticks his head under her chin and hits the female's dewlap. He takes the coital position, biting her shoulder. She accepts his advances. Copulation lasts 30 minutes.

The copulatory position for *A. nebulosus* is identical to that described for other species of iguanid lizards (Carpenter, 1967), and is the most consistent aspect of the courtship and mating procedure. Usually the male *A. nebulosus* will grip the skin of the female's neck, but may initially obtain a mouth hold anywhere on her back. The mouth hold, however, eventually is made on the skin of the female's neck or shoulder. He then swings the hind leg nearest the female over her rump, brings his cloaca up to hers, and inserts the hemipenis. Data for the total duration of coitus are available for only 6 matings. The times ranged from 29 to 55 minutes with a mean of 37 minutes.

After coitus the hemipenis was retracted and the male was usually seen arching the base of his tail and dragging the cloaca on the substrate in a manner identical to post-eliminative behavior. Often the rump was moved laterally from side to side in a wiping motion.

Breeding structure.—Male *A. nebulosus* are highly territorial as are the females. In the field, it was common to find a female's home range associated with a male's territory. The males defended their territories against other adult males, and the females were observed to maintain their territories free of other females. This association created a semi-monogamous relationship as the territorial males had a limited number of potential mates.

Under crowded laboratory conditions, however, the dominant male was very much a polygamist. Furthermore, the males' courtships were not restricted to their own species. When an enclosure was stocked with female *Anolis sericeus* and *A. nebulosus*, it was found the *A. nebulosus* males freely courted and copulated with *A. sericeus* females.

If the mating habits for male *A. nebulosus* are true for other anoline species, a very unstable mating structure would occur for sympatric congeners should the male be responsible for mate selection. However, there is evidence the females exercise mate selection. The *A. nebulosus* female appears to be attracted to those males performing an assertion display typical of her own species population (Jenssen, 1969). In the field, particularly for sympatric species, it is most probable that the anoline female avoids nonpreferred mates on the basis of the males' species-typical displays. In enclosures, where avoidance was not usually possible, frequent interspecific copulation was observed.

The social and mating structures of *A. nebulosus* can find parallels in unrelated animal groups. Of interest is the breeding structure of blackbird species which is extraordinarily similar to that of *A. nebulosus*. There is also a striking resemblance in the use of social displays between these avian species and *A. nebulosus*. In studies by Nero (1956a, b, 1964), Selander (1965), Selander and Giller (1961), and Wiens (1965), the observed icterid males established exclusive territories and were polygamous. The females selected their mates from the displaying males and then defended their mates' territories against other females.

The territorial male blackbirds give a visual and auditory display called a "song-spread" or "ruff-out" which proclaims the male's territory and serves to attract the females. As is true of the assertion display in *A. nebulosus*, the "song-spread" is directed frequently at other adult males, but is also given to females and by solitary males on territory when no other birds are in sight. The "bill-tilting" display used by male blackbirds during close range male-to-male territorial disputes appears analogous to the anole's challenge display. During these aggressive encounters the "bill-tilting" can include "song-spread" just as the challenge display includes the assertion display.

Breeding cycle

The breeding cycle for *A. nebulosus* was reconstructed from annual laboratory and limited field observations. Beginning in September, territorial behavior and male aggressiveness noticeably decreased. From October through December very little displaying was observed between males. In January the males began to interact more frequently, and by March were demonstrating pronounced territorial behavior. During the field study of *A. nebulosus* in April and May, both males and females had established home ranges and defense of most of these ranges was frequently observed. No copulations were seen even though male courtship behavior was common.

In the laboratory, first copulation was seen on 29 May, with mating continuing through August. The first gravid female was recorded on 12 June. Eggs were found from 9 July through 28 August.

Five eggs laid between 22 and 24 August hatched on 22 and 23 October. During their incubation the eggs were subjected to greenhouse temperatures which may have been a bit warmer than in Nayarit, Mexico at the same time of year. An 8-9 week incubation period is estimated for eggs of *A. nebulosus*. At the time of hatching the eggs averaged 15 X 11 mm in diameter.

During a field trip to Mexico, a large number of hatchlings were collected on 19 August. Using an 8 week incubation period, the latest laying date for the eggs from which these hatchlings emerged is calculated as 23 June. A few of the collected hatchlings no longer had visible yolk stalk scars indicating that some egg deposition in the field probably occurs before 23 June.

The estimated calendar for the breeding population of *A. nebulosus* in Nayarit is as follows: mating begins in late May and continues through August; egg deposition occurs from the last half of June through August; and hatchlings appear from the last half of August to the end of October.

The rainy season in Nayarit coincides with the breeding and reproductive period (June - October); it appears the moisture is important to anoline reproduction. Gordon (1956: 131) reported that female *A. carolinensis* were stimulated to lay their eggs by spraying water into their cages. The same relationship occurred for *A. nebulosus*. During the summer of 1966 the females were kept in a greenhouse and their enclosures were sprinkled daily. Many eggs were deposited in the provided moss or buried under the damp sand of the enclosures. However, during the summers of 1967 and 1968 all animals were kept in the laboratory where the only available moisture was in the water bowls. Even though almost all the females were gravid, very few viable eggs were deposited. A few were laid in the sand around the water bowls and a number of yellow, undeveloped eggs were deposited openly on the substrate.

Escape behavior

No quantitative study was made on the escape behavior of *A. nebulosus* as has been conducted on some anoles (Heatwole, 1968; Rand, 1964b). Instead, the following is an account of incidental observations made in the field.

As described for *Anolis lineatopus* (Rand, 1967a: 18), *A. nebulosus* rests on the upper side of horizontal or slanting perches, and positions itself head down when resting on vertical perches. This head down position is characteristic of *A. nebulosus* when inactive; the whole body can be against the substrate, or during the warmer part of the day the lizards will extend their forelimbs so that their body arches away from the perch at approximately a 45° angle.

A. nebulosus is small and cryptic in coloration, blending with the twigs, tree trunks, and leaf litter on which it is found. The lizard's ability to avoid detection is revealed in the time it took to mark all the anoles on a 30.5 X 30.5 m study plot. The following are the numbers of lizards caught and marked per day by two collectors: 4/24 (partial day) - 19; 4/25 - 24; 4/26 - 18; 4/27 - 7; 4/28 - 2; 4/29 - 6; 4/30 - 3. A few were transients, but the large majority of anoles were found repeatedly on the area.

Upon being approached the lizards' usual response was to flatten against the substrate while the observer was still 3-5 meters away. Some males, however, would maintain their initial posture. A common escape behavior for both males and females was to rotate or "squirrel" slowly around their perch, keeping it between them and the observer.

In general, the males appeared reluctant to leave their perch sites. If on a tree trunk, they would move a short distance up or down the trunk, but would usually stay on the tree. It was not unusual to reach a seemingly unoccupied tree, only to glance at the trunk's far side and find a male perched there. It was also difficult to induce the males to climb very far up a tree. The large majority of males would double back down the trunk before running more than 2.5 meters up the tree. If harassed for long, the males jumped to the leaf litter either running over its surface to another tree or clump of vegetation, or down into the leaves.

Females, which usually perched lower on the trees than the males, used the leaf litter to a greater extent for their escape. When approached, the females "squirreled." If further threatened, they would leap to the leaf litter where it was extremely difficult to find them. The females did not share the males' reluctance to leave the perch site. At times the females, when watched at a distance by a second observer, were seen to shift to the opposite side of the tree trunk or post and immediately jump into the leaf litter while the threatening object was still 4-5 meters away.

Females occasionally exhibited a slightly different escape behavior when in the low copice and seedling oaks which frequently grew close together. In this habitat the female anoles were seen to jump from the stems, enter the leaf litter where they travelled swiftly undetected to an adjacent group of seedlings, and there climbed another stem.

The apparent difference in escape behavior between the sexes may be a reflection of their perch site preferences. Males are more arboreal than females. Perch site preference seems associated with escape behavior of other anoline species. Collette (1961: 145) reported the difficulty of forcing the trunk dwelling *A. porcatus* down a tree while the more terrestrial *A. sagrei* will seldom climb to avoid capture. A similar correlation exists for *A. cybotes* (perch sites under 3 m above the ground), *A. distichus* (perch sites 3-5 m above the ground), and *A. chlorocyanus* (which is the most arboreal of the three). Rand (1962) found *A. cybotes* leaps to the ground to avoid capture, *A. distichus* attempts to escape by evasive behavior on the tree trunks, and *A. chlorocyanus* retreats into the top of the trees.

Shedding behavior

Some of the endocrine and histological changes occurring during anoline ecdysis have been described (Adams and Craig, 1951; Lillywhite and Maderson, 1968; Maderson and Licht, 1967; Ratzersdorfer, Gordon, and Charipper, 1949). Yet the gross aspects of shedding and the associated behavior have been neglected. The following account provides the frequency of shedding, some overt characteristics of the shedding process, and behavior patterns which facilitate shedding in *A. nebulosus*.

In the field, the occurrence of shedding for the 84 anoles on the study area in Nayarit, Mexico was closely followed. The duration of the study, however, was shorter than the lizards' interslough period as no lizard was found to shed twice. Nevertheless, it was possible to estimate the interslough period by the following method. From field notes it was known how many days each lizard was under observation (from the time it received its identifying paint marks, until the conclusion of the study). A grand total of observation days was compiled by adding together the total number of observation days for each of the lizards on the study area; this was then divided by the number of times these lizards had shed. From a grand total of 832 days, 24 occurrences of molting were recorded, yielding an estimated sloughing frequency of 35.1 days during the period of late April through early May.

The interslough period of lab-held *A. nebulosus* was considerably shorter than for the field anoles. During July and August, 1968, the average molting frequency of 25 anoles was once every 26.3 ± 1.1 days. This is comparable to the mean shedding frequency (20.6 days) reported for lab-held *A. carolinensis* (Maderson and Licht, 1967).

The variation in the interslough period between field and lab-held *A. nebulosus* may be a reflection of differences in experienced temperature fluctuations. Maderson and Licht (1967: 165) stated that *A. carolinensis* kept on a fluctuating temperature cycle (20 - 32 C) molted less frequently than those maintained at a constant 32 C. From a field study, *Uta stansburiana* was found to shed more often in the summer than during the spring or fall (Tinkle, 1967). The *A. nebulosus* studied in the field during the spring were subjected to a temperature range of at

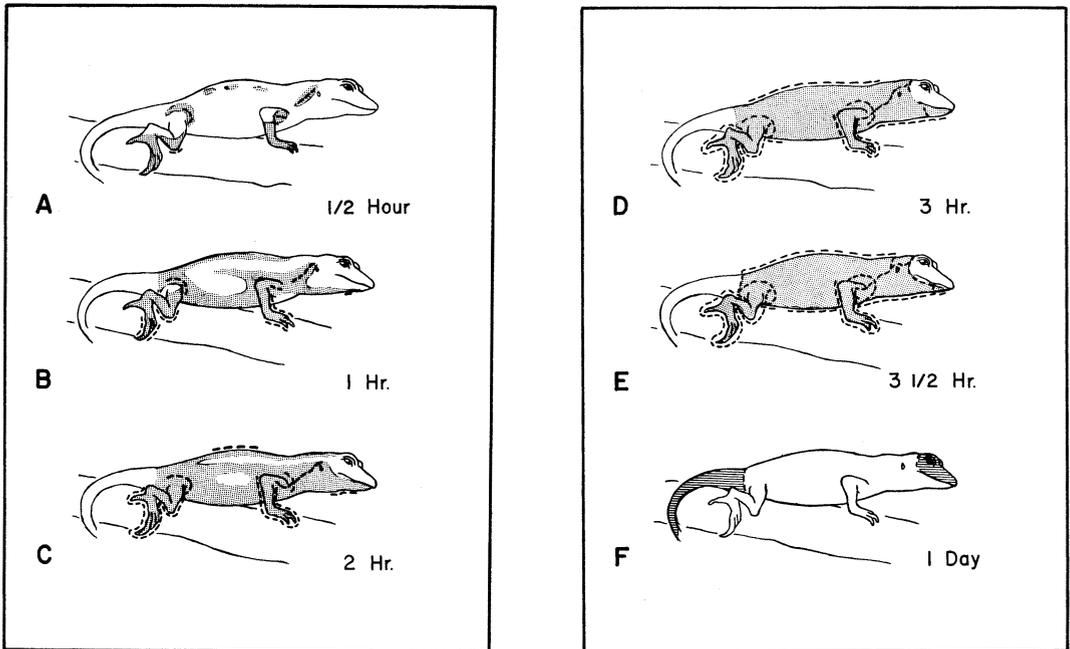


FIGURE 12. Shedding sequence of *Anolis nebulosus*; dashed lines denote skin splitting, and stippled areas show loosened skin.

least 15 - 35 C, while the lab-held anoles observed in the summer experienced a temperature fluctuation between 25 - 35 C. The wider range of temperatures during the spring may be responsible for the lower frequency of ecdysis in the field observed anoles.

The overt manifestations of shedding in *A. nebulosus* consisted of a sequential appearance of fissure lines in the old epidermis. The locations of these epidermal fractures and their order of appearance were consistent and predictable (Fig. 12).

The first indication of ecdysis was a fading of skin color on the extremities of the limbs, on the body just anterior to the hind limb, on the lateral anterior edge of the upper forelimb, and on the side of the neck posterior to the ear opening. The lightened areas were caused by the splitting of the *oberhautchen* layer between the outer and inner epidermis (Maderson, 1968; Maderson and Licht, 1967). Soon the skin began to split in these areas. As the breaks lengthened, other regions of the skin loosened and more fissure lines occurred.

At the conclusion of the molt, the epidermis was split in the following locations: (1) across the head posterior to the supraorbital semi-circular scales, dropping ventrally to the posterior edge of the lower jaw, there turning and running parallel to the mouth; (2) from the posterior edge of the orbit, down the neck dorsal to the ear opening, along the lateral anterior margin of the forelimbs, around each of the phalanges dorsal to their lamaellar scales, up the lateral posterior side of the forearm, and usually ending at the elbow; (3) dorsally down the midline from the posterior margin of the interparietal scale, to the end of the body, and laterally around the base of the tail at the vent; (4) along the ventral midline of the body from the anterior gular scales, down the ventral margin of the dewlap, usually appearing on the belly, and ending just anterior to the anal scales; (5) along the entire anterior lateral edge of the hind limb, around the phalanges, dorsal to their lamaellar scales, up the posterior lateral edge of the lower leg, and usually terminating at the backside of the knee; and (6) in two semicircles on the body, one each around the proximal portion of the fore and hind limbs, and both joining the mid-ventral fissure line.

The actual time to complete the shedding process was variable, depending upon a number of factors including the effectiveness of behavioral aids. Sloughing, however, was usually

accomplished within four hours. The epidermis on the tail and a small area on the head were shed several days after the body molt. The epidermis loosened in large sheets, being continuous between the fissure lines.

A number of behavioral patterns were used by the anoles to aid the molting process. At the onset of shedding the lizards wiped their chins back and forth against the substrate. Soon the skin was seen to split under the chins (Fig. 12b). The lizards, particularly the males, then began to expand their dewlaps and hold them extended in a "flag" position or slowly pulse the throat fan. This behavior seemed to quicken the development of the mid-ventral fissure line (Fig. 12c).

Within 2-3 hours after the initiation of the molt, the outer epidermis on the back was loose and the mid-dorsal fissure line well developed. The lizards performed a "serpentine" movement of the body apparently to facilitate the shedding in this area. During this behavior the dewlap was extended and the head arched back while the body and head were undulated in exaggerated lateral movements. The epidermis broke free along the neck in two large flaps of skin, one on either side of the mid-dorsal fissure line. The snake-like movements were continued until the skin was freed from the animal's sides.

Simultaneously with the dorsal epidermal molt was the loosening of the skin on the limbs. Because the skin split along the lateral margin of the limbs and phalanges, the outer epidermis was shed like the upper and lower halves of a glove. As the skin loosened the anoles bent their heads around toward their bodies, sometimes extending a limb to their mouths, and tore off portions of the sloughing epidermis. As other saurians (Bustard and Maderson, 1965), *A. nebulosus* ingested the shed epidermis. At times the lizards rolled partially on their sides as they bent back to grasp less accessible pieces of freed skin such as the flaps of dorsal epidermis. Again the animals ate all the epidermis they were able to tear off. It was not unusual to find the lizards' identifying paint markings in their fecal droppings.

Some portions of the shedding skin such as that on the upper neck and head could not be reached with the mouth; this epidermis was pulled off by scratching with the hind foot. The pieces broken off by this method were also eaten.

The last behavioral aid to molting was noted only in passing and its significance was not associated with shedding at the time. It was recorded, however, that sometimes the eyes of recently shed anoles protruded abnormally from their orbits. It is very likely this was the head swelling described by Smith (1946: 6) by which lizards are able to free the more tenacious epidermal covering of the head region (Fig. 12f).

Eliminative behavior

Defecation was usually observed following a meal. *Anolis nebulosus* performed this behavior in a manner common to the members of the family Iguanidae. The hind legs were spread and partially extended and the rump slightly raised. The proximal portion of the tail was arched as the feces was eliminated.

Although not consistently observed, a post-eliminative behavior was performed which consisted of raising the tail, partially squatting the hind quarters, and dragging or wiping the cloacal region on the substrate.

Animal associates

Lizards on the study area other than *A. nebulosus* were *Urosaurus ornatus* and *Cnemidophorus sackii*. At least five *Urosaurus* lived in the crowns of the oak trees on the area. Occasionally they would come down to cross to another tree or to forage for brief moments in the leaf litter. One interaction was seen between *A. nebulosus* and *U. ornatus*. A male *A. nebulosus* reacted violently to the presence of *U. ornatus* by giving exaggerated dewlap extensions while rocking onto its hind legs and tail. This response was repeated by placing male *A. nebulosus* in an enclosure which contained a *U. ornatus*. By virtue of habitat preference, these two species occasionally overlap in their activity range. The *U. ornatus* is almost twice as large as *A. nebulosus* and may possibly be a predator.

One *Cnemidophorus sackii* was collected on the study area. This species forages exclusively

on the ground and is considerably larger than *A. nebulosus*. It is likely that it also could prey upon the small anoles, particularly the subadults and females which frequent the leaf litter.

Other lizards collected within a 6 kilometer radius of the study area were: *Sceloporus asper*, *S. clarki boulengeri*, *S. horridus albiventrus*, *S. melanorhinus calligaster*, *S. nelsoni*, *S. utiformis* and *Eumeces sp.* (escaped before positive identification could be made).

A number of birds were identified on the study area. They were turkey vulture, black vulture, common nighthawk, acorn woodpecker, magpie jay, common raven, bridled titmouse, cedar waxwing, solitary vireo, hepatic tanager, chipping sparrow, and lark sparrow. Several other species were seen, but species verification was not obtained.

Birds are known to be potential predators of anoles (Beal, 1912; Gordon, 1956; Wetmore, 1916). On the study area the common raven seemed a very likely predator of *A. nebulosus*. Several ravens were noted to have flight paths which they regularly flew throughout the day. On occasion they would land in the woodland and forage. One afternoon (1450) a raven landed approximately 30 meters from the observer and began probing the leaf litter with its beak. The bird repeatedly hopped up into the air with a flap of its wings. It poked about in the leaves with its beak, and then flapped its wings and hopped again. After 3-4 minutes of this behavior, the raven took off. Lizards in the leaf litter would undoubtedly be stimulated to run by the raven's actions, thus revealing their presence to the bird.

Daily activity log

The following daily logs from field observations contain the various ethoecological factors which were previously discussed separately. The daily activities of males No. 31 and No. 1 furnish an idea of general behavior held in common by the lizard population, and also point out the differences in kinds and frequency of behavior which made each individual unique.

5/3/68 Male No. 31

- 0715 Seen in leaf litter between C-27 (Coppice No. 27) and T-1 (Tree No. 1). He went to C-28 where he flagged when he stopped by a small protruding root. Fed twice on small lepidoptera in the leaf litter. Moved towards C-28, stopped and flagged.
- 0738 Climbed onto a twig of C-28 and moved up to some sunlight filtering down through the overhead tree canopy.
- 0805 Perch is now out of sun. No. 31 leaves perch and climbs the stump of C-28 (0.5 m up) which is exposed to some filtered sunlight.
- 0835 Sunlight is beginning to hit this area which is heavily shaded by T-5 (air temp. 25.5 C).
- 0845 No. 31 moves to top of stump and gives two assertion displays - no other lizards seen in area.
- 0912 Jumped down to leaf litter and moved 0.5 m north of C-28 and ate a small insect. He then flagged, returned to twig of C-28 and flagged weakly.
- 0930 Shifted position on perch site, now facing downward on slanting twig.
- 0940 Leaped 0.5 m off perch, lunged another 0.2 m and grabbed a large caterpillar in the leaf litter. Larva is one-fourth the size of the male, but he ingested it. After defecating and wiping rump on leaf, he returned to the stump of C-28 and flagged three times.
- 0946 Moved from stump to old perch site on twig of C-28.
- 1010 Full sunlight has now reached No. 31's perch.
- 1035 Changed from horizontal to vertical branch of coppice which is shaded by a leaf.
- 1205 No. 31 has not moved since last entry.
- 1307 Jumped to base of stump and then climbed up to twig perch.
- 1445 As sun moved and shone on No. 31, he slightly adjusted perch site to remain in shade. He is now on north side of the stump. Air temperature cooling - 29.5 C.
- 1540 On same perch as one hour ago - just flagged.
- 1605 Bending tail to one side and trying to pull paint marking off tail with mouth.
- 1655 Same perch site, has not moved.
- 1700 Female No. 62 moving through leaf litter near C-28. As she approached, male No. 31 gave rapid head nods and then performed an assertion display. Female disappeared back into leaf litter.
- 1727 Jumped to adjacent twig and ate something. Then he gave an assertion display. He climbed to top of twig and displayed twice more.
- 1731 Climbed down C-28 and entered leaf litter. Moved through the leaf litter to the fence post 1 m south of C-28.
- 1736 Appeared at base of fence post, flagged at the bottom, moved a few centimeters, flagged, moved up some more, and flagged again.

- 1740 Turned, left post and crawled into the leaf litter under base of C-11 (0.6 m south of fence post) for the night.
- 5/3/68 Male No. 1
- 0744 Seen giving two assertion displays on leaf litter next to C-1 (Coppice No. 1). Then moved to stump of C-1 and asserted and then ate something. Female No. 22 is on C-1. No. 1 moved up stump of C-1 and gave an assertion display. He then moved towards the female and displayed (assertion). Female moved up her stem away from male.
- 0747 Male moved to shady perch in C-1. Female jumped to leaf litter and then up another stem of C-1 further from No. 1. He in turn gave an assertion display in her direction.
- 0754 Male's perch now in sun. He shifted to shady perch - head up at a 45° angle.
- 0759 He moved to top of twig and displayed (assertion).
- 0805 Moved to stump and slowly climbed up, stopping to display (assertion) three times - now in sun. Female moves down twig away from No. 1.
- 0807 Male moved to shady perch (Air temp. 25.7 C).
- 0817 Male performed 4 series of rapid head nods and then gave an assertion display but not at female No. 22 who is on adjacent stem.
- 0818 Male then moved up stem and flagged. Female No. 8 now seen in adjacent coppice (C-2).
- 0856 Male and female relatively inactive. Breeze is picking up.
- 0903 Male moved to a sunny perch on C-1 and displayed (assertion).
- 0905 Turned and moved up the stem to shade. He gave 2 assertion displays enroute.
- 0907 Jumped to leaf litter and twice ate something. Moved to a fallen branch and fed again. He then flagged.
- 0916 Walked back toward C-1. He defecated and dragged his rump. Moved past C-1 and paused at the base of T-5 (large tree in No. 1's territory); then he flagged, moved up tree, flagged, climbed higher (0.7 m) and flagged again. At 1 m up T-5 he gave a full assertion display and then turned head down in shade and displayed (assertion) once more. From here he has a good view of entire territory.
- 0940 Gave an assertion toward male No. 31 who was in leaf litter catching an insect close to No. 1's territory.
- 0941 No. 1 moved up a few centimeters and displayed (assertion).
- 0944 No. 1 has shifted his perch site on the side of T-5 three times and each time he gave an assertion display towards No. 31. No. 31 now flags. Male No. 1 has his roach up and gives three assertion displays. No. 31 moves away. No. 1 gives two more assertion displays and turns with head down and body on substrate.
- 1025 No change.
- 1030 No. 1 pulls his head up and displays (assertion) and then flags - object of his attention not seen. Male then runs down tree and stops at base. He then eats something.
- 1100 Crosses leaf litter to a large rock 0.1 m away and displays.
- 1126 He gives rapid head nods. Female No. 22 seen still in C-1 - possible recipient of his nods.
- 1135 Climbs a branch next to rock and gives two assertion displays.
- 1148 Now crosses back to T-5 and begins climbing. Each time he stops he gives an assertion display - ten in all and he is 4 m up - highest seen for *A. nebulosus*. He still is in a head up position.
- 1245 Is now 5 m up T-5, but now head down and in shade.
- 1327 No change - now in partial sunlight.
- 1400 Sun is lowering and light is striking upper trunk of T-5. Male No. 1 now moving back down.
- 1405 Air is cooling and breeze is picking up some.
- 1407 Male moves to C-1. Pauses to catch a dipteran, but misses - gives an assertion display.
- 1424 Ate something at base of C-1.
- 1430 Female No. 22 still on C-1; she has not moved all day.
- 1436 Female now jumps into leaf litter and male watches.
- 1446 Male moves into weak sunlight.
- 1503 Moves around stump of C-1 into shade.
- 1510 *Urosaurus ornatus* just ran down T-5 and up T-1; wonder if there was any interaction when No. 1 was so far up.
- 1518 Male drops into leaf litter after an insect and then displays. Stays in leaf litter; latter registers 31.9 C in shade.
- 1532 Climbs out of leaf litter onto base of stump at C-1 (in shade and out of wind).
- 1600 No change; air temp. 28.9 C.
- 1629 No change; air temp. 28.6 C.
- 1655 No change; air temp. 26.0 C.
- 1720 Dropped back to leaf litter and ate something. Male is now in sun on leaf litter. He gave two assertion displays and moved into leaf litter at base of C-1 for the night.

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