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ETHOECOLOGY AND DISPLAY ANALYSIS OF *Anolis nebulosus* (SAURIA, IGUANIDAE)

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

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BY

THOMAS A. JENSSEN

Norman, Oklahoma

1969

ETHOECOLOGY AND DISPLAY ANALYSIS OF *Anolis nebulosus*

(SAURIA, IGUANIDAE)

APPROVED BY

[signatures]

DISSERTATION COMMITTEE

Vis-a-vis

Green lizard, his pygmy head inclined toward earth
Embraced a twig of bougainvillea vine.
Eyes lit with gleams of chameleonic mirth
Met eyes, as there on the ground I lay supine
Casting my glances skyward, blocked by this
Minuscule beast that eyed my outstretched hand.
Locked vision held, and I would be remiss
To lack a wonder what the lizard scanned
To mock at. I felt in him the mystery
Of ancient, curious life. What he in me?

MARY E. GROSS

ACKNOWLEDGMENTS

With the possibility of sounding sentimental, I must say that it is Dr. Charles Carpenter's knowledge and enthusiasm for natural history which has been my touchstone; without his advice and concern my doctoral research would have been an onerous task. He never failed to find time to talk with me and during our association managed to tolerate my eccentricities.

My committee members, Drs. Gerald Braver, Elroy Rice, Frank Sonleitner, and the late Arthur Bragg, have all contributed to this dissertation as well as to my professional training. However, to Dr. Frank Sonleitner I owe a special debt. Were it not for his time and competence with statistics, I would still be sitting before a desk calculator suffering from digititis.

Dr. Teague Self generously allowed me to accompany him to Mexico during a collecting trip for his parasitology studies. It will not be forgotten how he went out of his way to help beat the Tamaulipas brush for the elusive anole.

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For their valuable assistance I am very thankful to Dr. George Goodman and Jim Massey who struggled to identify the little-known plants collected in Mexico, and to Dr. William Duellman for his verification of my specimens of Anolis nebulosus.

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And then there is my sharpest critic, unselfish helper, and ardent companion; my wife, Risa, is not only a fine typist, she also holds my greatest esteem.

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ETHOECOLOGY AND DISPLAY ANALYSIS OF *Anolis nebulosus* (SAURIA, IGUANIDAE)

CHAPTER I

INTRODUCTION

Anolis nebulosus (Wiegmann) is one of 42 species of *Anolis* in Mexico. It is a small, semi-arboreal lizard found in western Mexico from Sinaloa to the Isthmus of Tehuantepec (Fig. 1). Although it is widely distributed and reasonably common within its range, very little is known about *A. nebulosus*. With the exception of 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; Schmidt and Shannon, 1947; and Davis and Smith, 1953). 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 order the taxonomy and systematics of this largest of iguanid genera.

The present study is the first to characterize the behavior and ecology

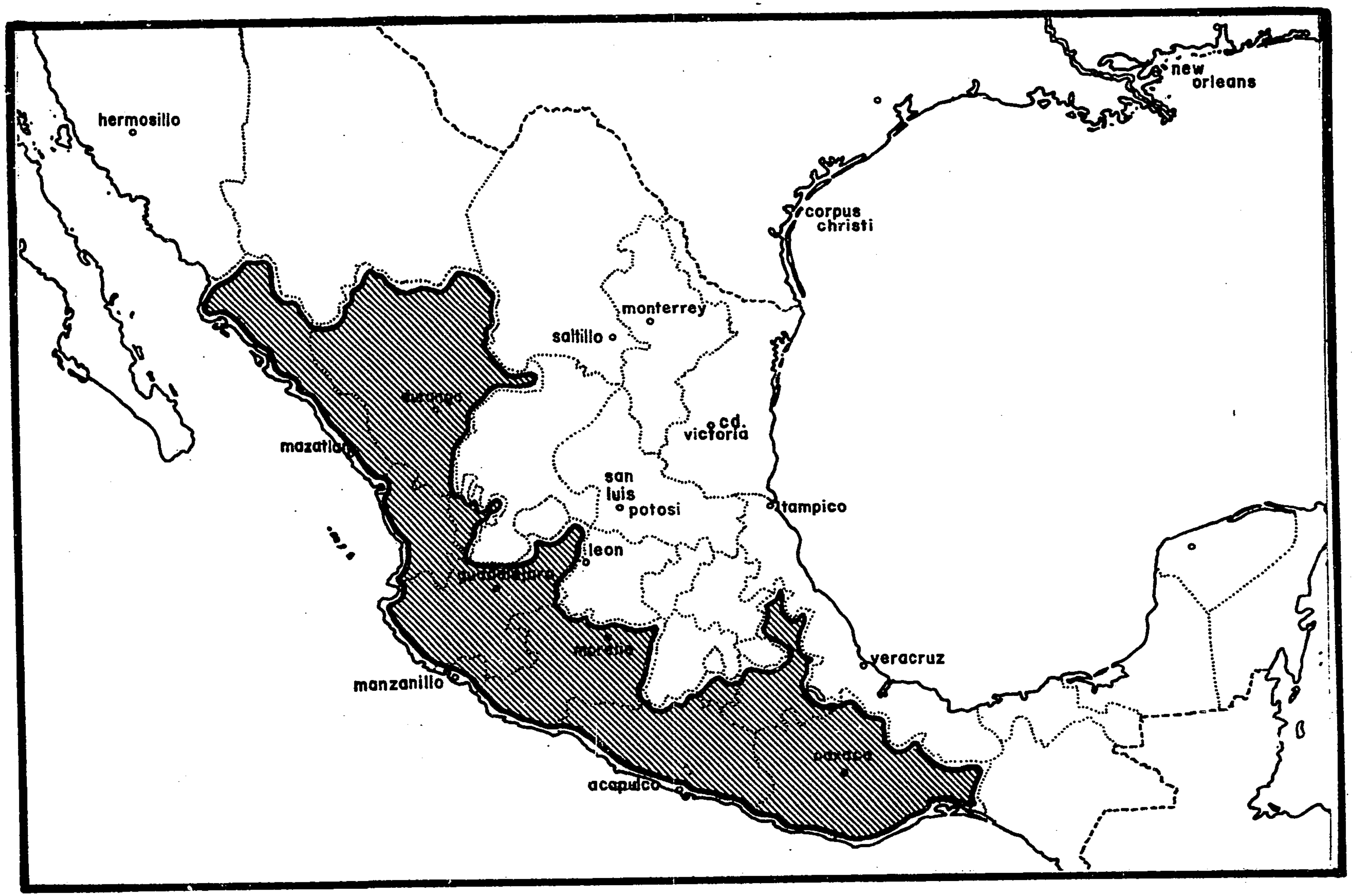

Fig. 1. Geographic distribution of Anolis nebulosus.

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of *A. nebulosus*. Included in this investigation is an estimate of the variability of the species' display-action-pattern (DAP). As others have found (Carpenter, 1962b, 1963, 1965; Clarke, 1965; and Gorman, 1968), the behavioral display can be valuable as a taxonomic criterion; however, until this time very few statistical studies have been made of the variation of a species' display (Ferguson, 1969a; Griffith, 1966). Experimental data were also gathered as to the social significance of the display of *A. nebulosus*.

CHAPTER II

TAXONOMY AND PHYLOGENY

1834 Dactyloa nebulosa Weigmann, Herpetologia Mexicana, p. 47.

1873 Anolis nebulosus Bocourt, Mission Scientifique au Mexique et dan l'Amerique Centrale, Etudes sur les reptiles, livr. 2: 68-69.

1887 Anolis boulengerianus Thominot, Bull Soc. Philom., ser. 7, vol. 11 (Mus. Hist. Natur. Paris, three cotypes, Isthmus of Tehuantepec, F. Sumichrast, collector).

TYPE Zool. Mus. Berlin, two cotypes; F. Deppe, collector.

TYPE LOCALITY Restricted to Mazatlan, Sinaloa, Mexico (Smith and Taylor, 1950a: 343).

The characteristics which separate Anolis nebulosus from all other anoline species of Mexico are not yet definite. Boulenger (1885: 76-77) gives the identifying morphological features of the early collected specimens as follows:

> Head about once and two thirds as long as broad, longer than the tibia; forehead concave, frontal ridges distinct, short, divergent; upper head-scales smooth; scales of the supraorbital semicircles large, in contact medially, produced forwards as frontal series; three or four large, smooth, transverse supraocular scales forming a single longitudinal series, separated from the supraorbitals by a row of granules; occipital much larger than the ear-opening, separated from the supraorbitals by one or two series of scales; canthus rostralis angular, canthal scales three or four, loreal rows four or five; six or seven labials to below the centre of the eye; ear-opening small,

oval. Gular appendage large, extending posteriorly beyond the thorax, small in the female; gular scales keeled. Body not or but slightly compressed; no dorso-nuchal fold. Dorsal scales oval, subrhomboidal, subimbricate, keeled, a little smaller than the ventrals, passing gradually into the laterals, which are minutely granular; ventrals rhomboidal, imbricate, strongly keeled. The adpressed hind limb reaches the posterior border of the orbit, or nearly that point; digital expansions moderate; thirteen to sixteen lamellae under phalanges II. and III. of the fourth toe. Tail cylindrical, not twice as long as head and body, covered with equal strongly keeled scales. Male with enlarged postanal scales. Brownish above, with dark brown spots, sometimes arranged in a double longitudinal series on the back, or forming angular cross bars with the angle pointing backwards; a more or less distinct dark streak from the eye to the nape; sometimes black lines radiating from the eye; limbs with dark cross bands; lower surfaces whitish; gular appendage grey or brown.

Taylor (1936: 518) reported on three specimens taken from Presido, Sinaloa, which is near the type locality. He describes characteristics for the species as:

body slightly compressed; forehead concave; supraorbitals are in contact and continue forward as two divergent frontal series, but not forming a frontal keel; normally 3 supraoculars separated from the supraorbitals by a row of granular scales; 4 rows of loreals; 4 canthals; slight nuchal crest; occipital large, very much larger than ear opening; 6-7 labials to below middle of eye; gulars slightly keeled; ventrals keeled, slightly smaller than dorsals which pass gradually into the granular lateral scales; enlarged postanals; 14 scales under the 2nd and 3rd phalanges of 4th toe; gular appendage large, reaching beyond thorax - grey or pinkish tinge; marking indistinct except lines radiating from about eye.

However, Smith and Taylor (1950b: 66) state their dissatisfaction with the species description. They found that A. nebulosus and Anolis nebuloides are frequently confused, and that both of these species are inadequately characterized. Duellman concurs with Smith and Taylor. From his collections of lizards from Michoacan, Duellman (1961) also found the determination between A. nebulosus and A. nebuloides uncertain.

The features which Bocourt (1873: 75) used to separate A. nebuloides from A. nebulosus were (1) head scales keeled, not smooth; (2) snout narrower; (3) ear opening larger; (4) supraorbital semicircles separated by a row of small scales and not in contact; and (5) dorsal scales larger and subequal in size to the belly scales. These same characteristics were also cited by Boulenger (1885: 77). Yet Duellman (1961: 62) reports that there is sufficient variation in these characters to prevent a consistent differentiation between these two species. Peters (1954: 11) and Stuart (1955: 4) also recognized the nebulosus-nebuloides complex as an outstanding taxonomic puzzle.

Furthermore, Etheridge (1959) found from an extensive osteological investigation of the genus that Anolis schmidti, A. nebuloides, and A. nebulosus were extremely difficult to distinguish. These three similarly appearing forms showed extreme variability in their parasternal formula and presacral vertebrae. Because of the variation in the key osteological characteristics, Etheridge not only was unable to positively separate them, he was also uncertain of their relationship to the other species of his beta grouping.

The coloration of the dewlap is frequently provided in species descriptions since it is a fairly constant feature within a species (Taylor, 1956: 64). The dewlaps of the A. nebulosus collected near Tepic, Nayarit, and used in this present study exhibited sexual dimorphism. The throat fans of the females were small and uniformly pink in color. The males possessed very large dewlaps of a deep orange color which were adorned with a number of white scales arranged singly in rows. The extreme anterior margin of the male dewlap tended to be of slightly lighter coloration. Three males collected near Manzanillo, Colima, had dewlaps of identical coloration except there was a broad white band on the anterior margin. Smith and Grant (1958) found this latter condition in A. nebulosus collected between Nayarit and

Colima in the state of Jalisco.

The above descriptions conflict with those of Lewis and Johnson (1955). Their collection was also made in Nayarit; however, *A. nebulosus* were reported as having red dewlaps. Lewis and Johnson (1956) also found red dewlaps on this species taken from Sinaloa. In both notes they failed to mention the sex of the lizards. It is possible their collections contained only females or that the lizards were actually *A. nebuloides* which has a pink dewlap. Even more confusing are the papers by Davis (1954) and Davis and Dixon (1961) which describe the dewlaps of *A. nebulosus* from Guerrero as being yellow with a bluish or purplish spot in the anterior corner.

The taxonomic status of Mexican anoles other than *A. nebulosus* has been questioned. Etheridge (1959: 99) cites Mexico as containing 42 species of *Anolis* while Smith and Taylor (1950b: 56) list 32 species. However, Stuart (1955) feels the list can be further shortened. He suggests that several are synonyms (*beckeri* = *pentaprion*; *heliactin* = *sericeus*; *metallicus* = *tropidonotus*), *damulus* and *impetigosus* were described without a type locality, and other forms occur only south of the Isthmus of Tehuantepec (*biporcatus*, *capito*, *cosumelae*, *mayensis*, *pentaprion*, *rodriquezi*, *uniformis*, *ustus*). Of the remaining species, Stuart groups most into what he calls the *nebulosus*-*nebuloides* complex, and states that some may actually be duplicates (*dunni*, *gadovi*, *liogaster*, *megapholidotus*, *taylori*, and *schmidti*). Etheridge (1959) has attempted to order the systematics of *Anolis* on the basis of osteological characteristics. For the time being, phylogenetic considerations of *Anolis* must rely primarily on Etheridge's investigation as classical morphological studies for this group have resulted in many disagreements. Recently, however, corroborating biochemical and karyotypic studies (Gorman and Dessauer, 1966; Gorman and Atkins, 1968; Maldonado and Oritz, 1966) on some West Indian anoles have lent support to Etheridge's phylogenetic scheme of Anolis.

Using the caudal vertebrae, Etheridge divided the genus into two sections, alpha and beta. The alpha species have no or nearly no transverse processes on autotomic caudal vertebrae. The beta species possess a pair of long, bifurcate forward-directed processes on all of the autotomic caudal vertebrae. In general, the alpha species demonstrate a more primitive skeletal morphology than the beta section. The alpha species show a greater diversity than the betas and are distributed mainly in the Antilles (48 spp.) with only 20 species on the mainland. The beta section contains mostly mainland forms with only 9 of its 109 species in the Antilles (Fig. 2).

The original dichotomy in caudal structure of the primitive anoles most likely occurred during the late Paleocene after the formation of the Panamanian portal (Savage, 1966: 741-742). The primordial alpha and beta stocks were probably isolated from each other until the re-establishment of the Isthmus Link in the late Cenozoic. Etheridge postulates the alpha group evolved in northern South America and spread up into southern Central America and through the Antilles. The more primitive alphas are found in Hispaniola with the most advanced alpha species in Cuba. The beta stock (Fig. 3), which was isolated in Central America, moved south into the Amazon Basin and northward into Mexico.

Etheridge (1959) divides the beta species into the following series: grahami (Jamaica and Cayman Islands, introduced into Bermuda), sagrei (Swan Island, Cayman Island, Cuba, Bahama Islands west of Crooked Island Passage,

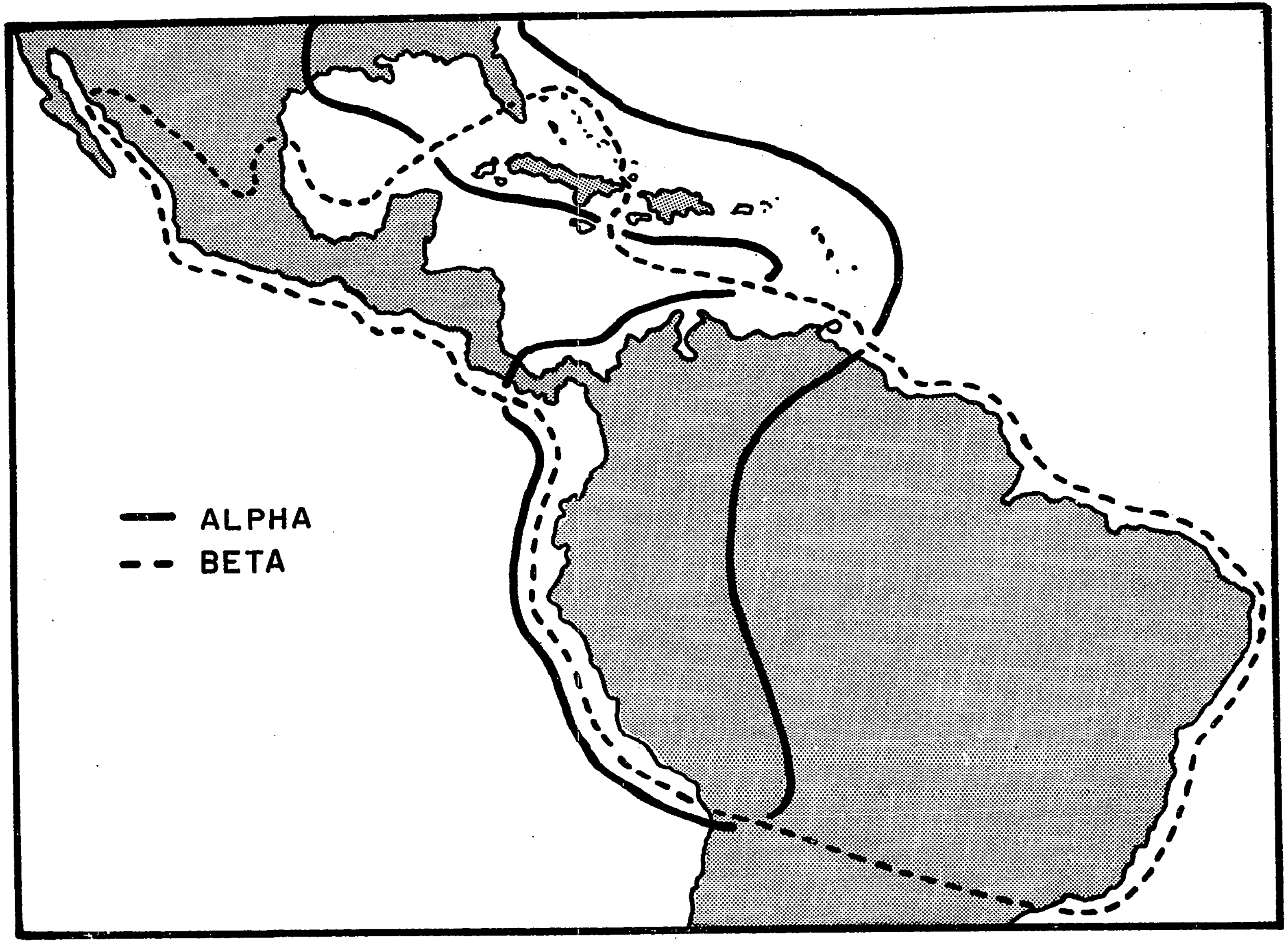


Fig. 2. Geographic distribution of the Alpha and Beta species of Anolis (after Etheridge, 1959).

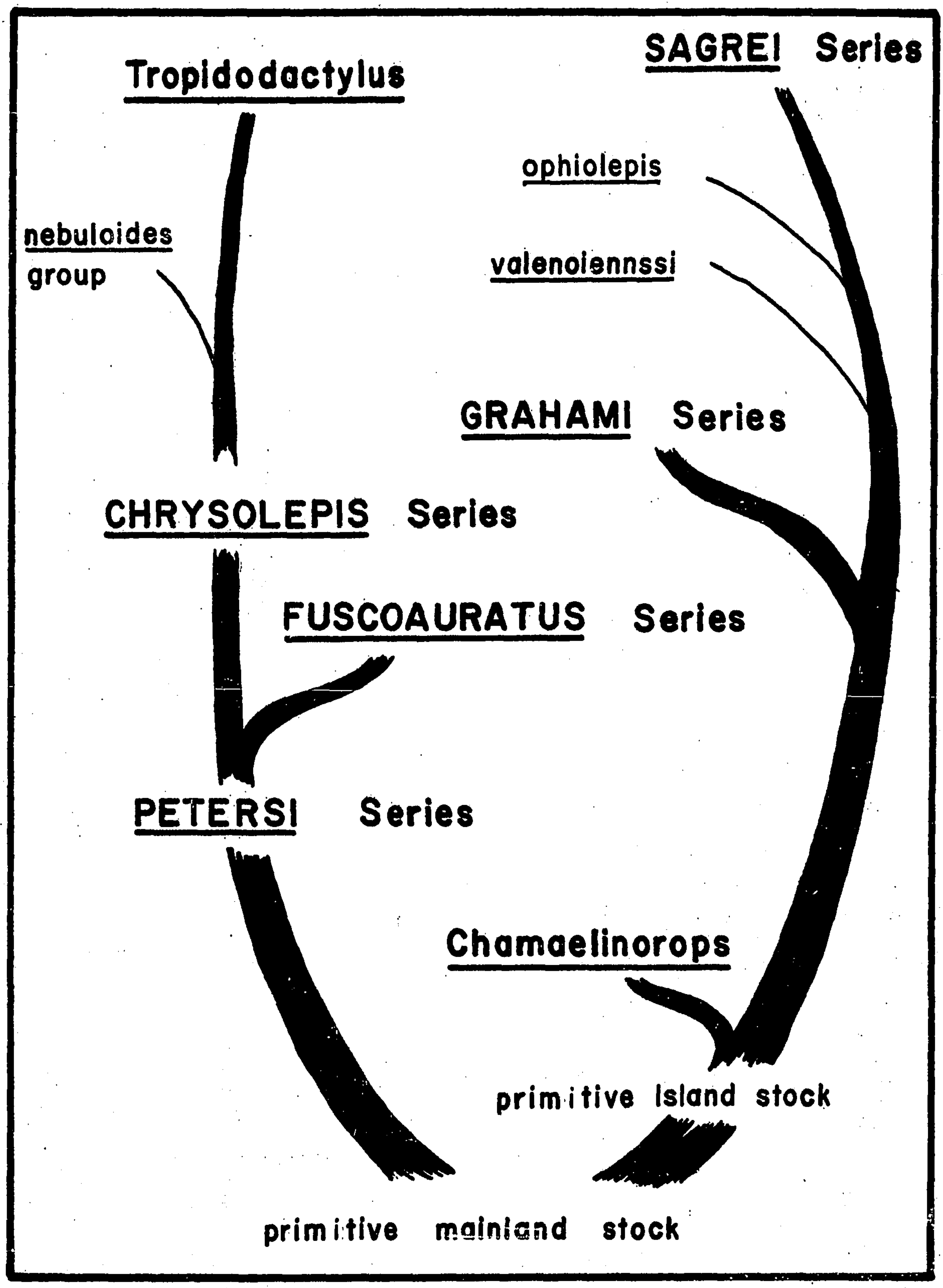


Fig. 3. Proposed relationships of the Beta section of Anolis and related genera (after Etheridge, 1959).

southern Florida and Florida Keys, and introduced into Jamaica and Caribbean coast of Mexico and central Mexico), petersi (eastern Mexico from Tamaulipas south to the Isthmus of Tehuantepec, south through Central America into northern Colombia), fuscoauratus (Honduras and Costa Rica south through Central America to northern and western South America), and chrysolepis (Tamaulipas and Sonora south along both coasts to the Isthmus of Tehuantepec, through Central America into northern and western Colombia, northern Venezuela, and British Guiana; Dutch Leeward Islands and Trinidad; and the Cocos Islands). With the exception of a few introduced forms, species of the primitive petersi series and the chrysolepis series make up the Mexican anoles. The petersi series are along the eastern side of Mexico and the chrysolepis species are found in Tamaulipas and in western Mexico.

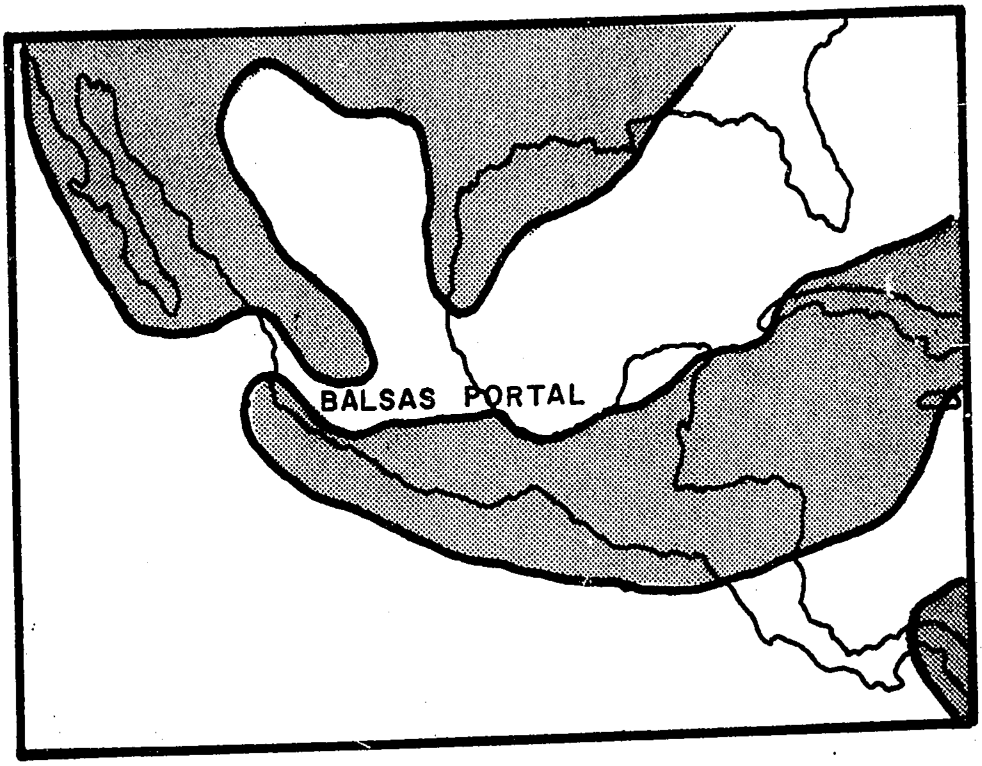
The beta section also contains a "residue" of several species which do not lend themselves to the above series. Included in these species of uncertain position is A. nebulosus which Etheridge places with A. nebuloides and A. schmidti and designates as the nebuloides group. Etheridge feels the nebuloides group of western Mexico is the most specialized of the beta species and was probably derived from the chrysolepis series. The open water portal through the Isthmus of Tehuantepec in the early Pliocene could have effectively isolated the Mexican anoles from those in Central America. Etheridge suggests this barrier and the Balsas portal north of the extant Sierra Madre del Sur during the upper Cretaceous would have permitted the differentiation of the nebuloides group from the more southerly distributed chrysolepis species (Fig. 4).

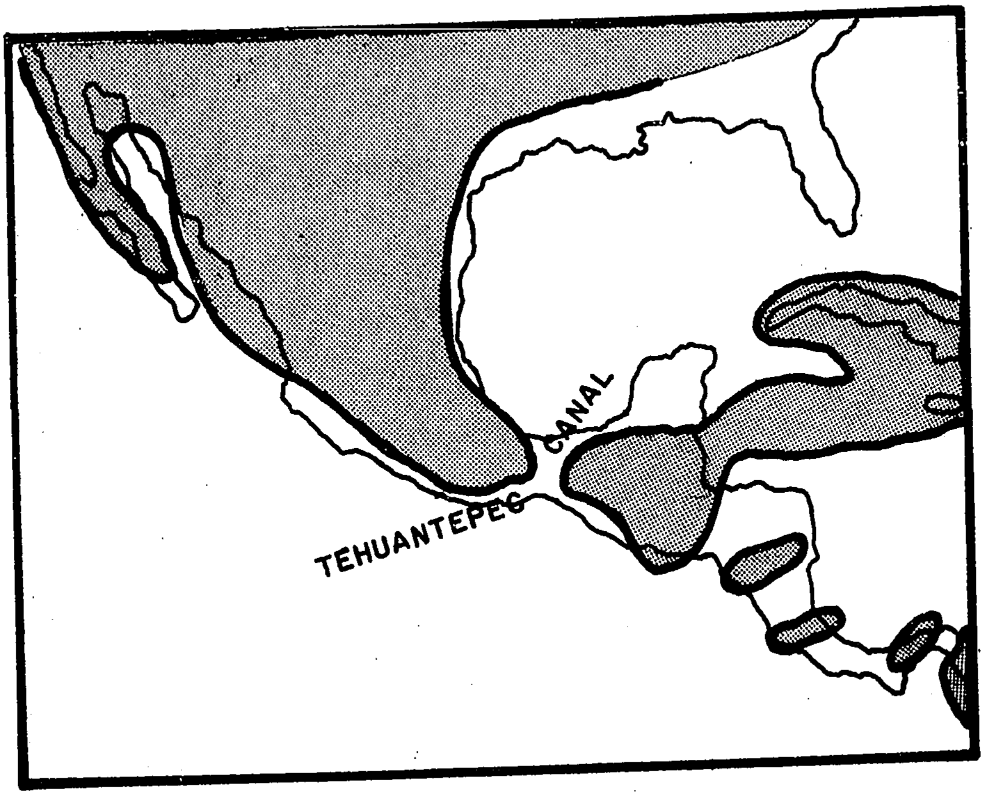
From the preceding discussion it is obvious that a good deal of work remains to be done to adequately characterize A. nebulosus as well as many other species within the genus.

Fig. 4a. Mid-Cretaceous paleogeography of Middle America and adjacent areas. (after Maldonado-Koerdell, 1964)

Fig. 4b. Mid-Tertiary paleogeography of Middle America and adjacent areas. (after Maldonado-Koerdell, 1964)

Stippled areas indicate land


BALSAS PORTAL


TEHUANTEPEC
CANAL

CHAPTER III

ETHOECOLOGY

Introduction

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

Besides ecological notes on *Anolis barkeri* (Kennedy, 1965; Robinson, 1962), almost all information on the ecology and behavior of Mexican anoles is found as incidental references within distribution and taxonomy papers. The present study is the first investigation of the natural history of *Anolis nebulosus*, a species distributed exclusively along the western side of Mexico. The resulting data also present an opportunity to compare the habits of a 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 present study was conducted over a $3\frac{1}{4}$ 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 $2\frac{1}{2}$ years in captivity, and 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 millimeter rule and measuring from the tip of the snout to the edge of the anterior lip of the cloaca; a transparent rule facilitated these measurements.

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 April 24 to May 9, 1968. The purpose was two-fold; first, to gain a familiarization with the general ecology of *A. nebulosus* so that behavior patterns could be placed into 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, oak woodland with heavy leaf litter and 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 areas 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. 5). Any number between 1 and 9 is 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 (i.e. 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. Body markings and any structural peculiarities were also noted, and the lizards were then returned to the exact site of their capture and released.

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

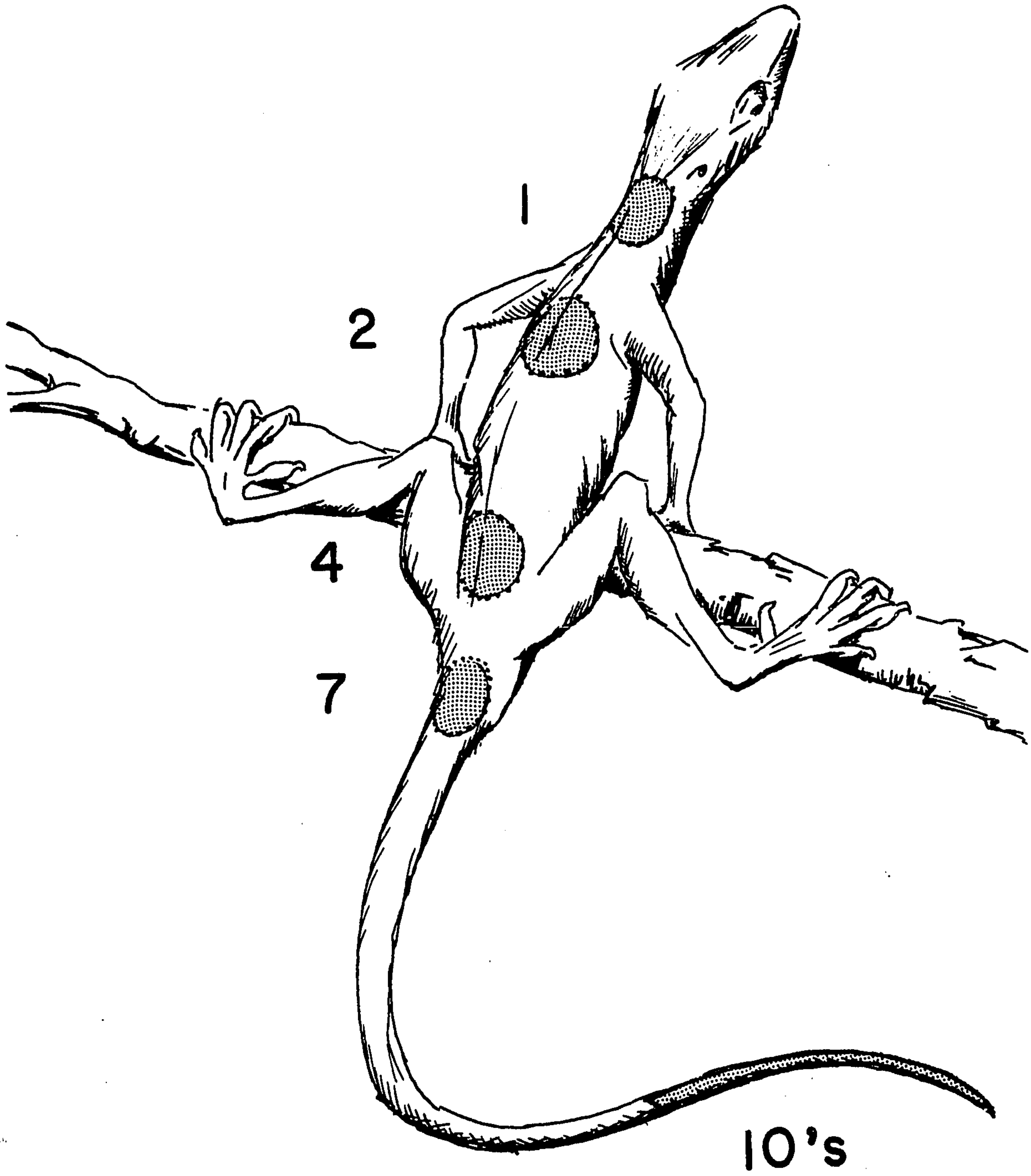


Fig. 5. Numerical values assigned to dorsal paint spots for individual identification.

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 interaction.

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 both in 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 recogntion 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 those 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 an area of lower temperatures known as <u>tierra templada</u>. 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 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% from year to year. The humidity is subject to the greatest seasonal variation of any region in Mexico. Desert-like air (30-50% relative humidity) prevails in March and April, as contrasted to humid conditions (60-70% relative humidity) during the rainy season.

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

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 forests 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 investigation 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 a surrounding hill top, 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. 6). The gently sloping hillside had a 5° grade, and there was some evidence of erosion under the trees. The open, grassy area comprised approximately ⅓ of the 30.5 x 30.5 m plot, with the remainder holding at least two species of oak trees of various sizes. A heavy leaf

Fig. 6. The study area near Tepic, Nayarit, Mexico, during May, 1968.

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 except for occasional foraging.

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, bush-like growth forms known as coppice. The coppice, 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. However, it was soon evident 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 absission 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.

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 occurs during collecting, for 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 appears 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 possess 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%) 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.

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 (m)	Basal Area (cm^2)	Avg. Basal Area/Tree (cm^2)	Relative Basal Area	Relative Density	Importance Percent
Trees (over 10 cm at breast height)							
Quercus							
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)							
Quercus							
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

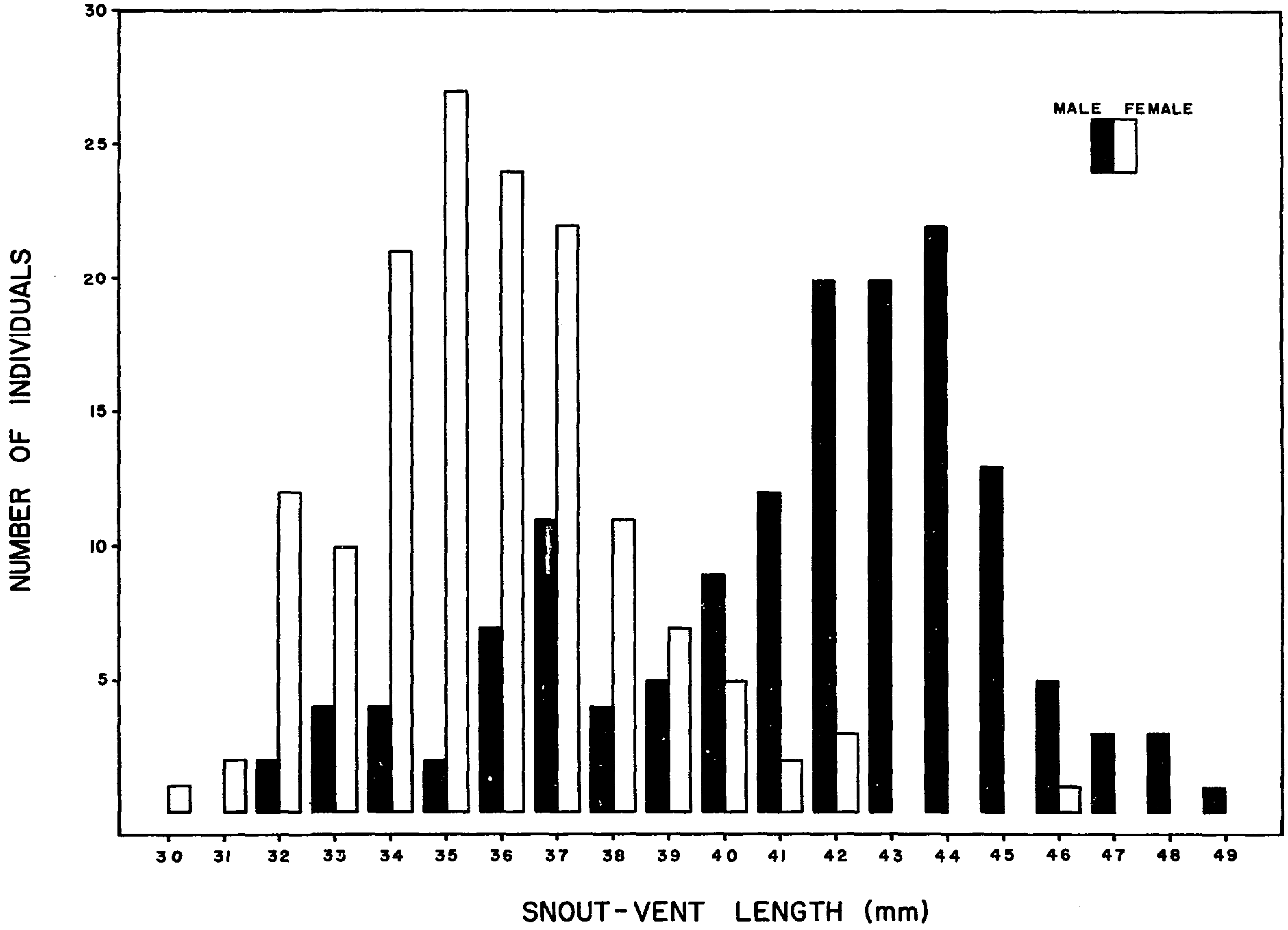
A dorsal striped pattern is also present in only the females. This condition is common to other species of Anolis, and has previously been reported for A. nebulosus (Duellman, 1961). As is true of the dorsal pattern and background coloration of the males, the female patterns showed a good deal of variation 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 lacked the scalloped lateral edges. Forty (29.2%) of the 137 females examined had the dorsal pattern and 5 (3.7%) 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. 7). 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%

Fig. 7. Snout-vent frequencies of 297 Anolis nebulosus collected near Tepic, Nayarit, Mexico, during April - May, 1968.


NUMBER OF INDIVIDUALS
30
25
20
15
10
5
MALE FEMALE
30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49
SNOUT-VENT LENGTH (mm)

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.

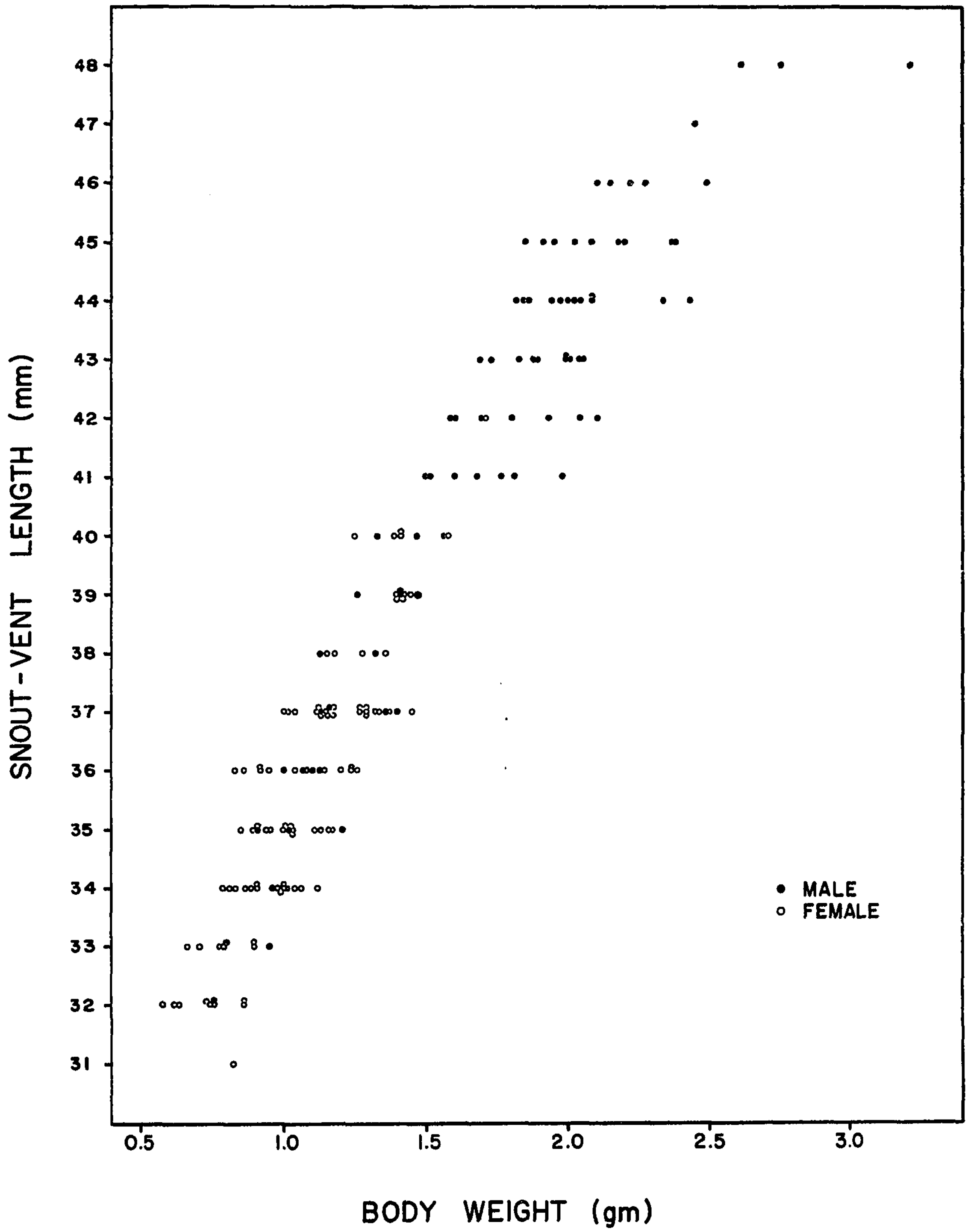
It is very difficult to detect age classes from the distribution of the snout-vent sizes for several reasons. First, there is evidence which indicates an almost complete turnover in the population each year. Second, the reproductive season appears to span the summer months, and so the young of the year 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 show the effects of this long breeding season (Fig. 7).

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 weight differences between the sexes at any particular s-v length (Fig. 8). 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 s-v length of 39 mm, was 2.0 gm as compared with a 1.4 gm average for the 9 anoles of the same length in April. The mean weight in June of four lab-held males with a 39 mm s-v 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. However, the data do provide growth potentials for various age classes.

Growth records were kept on 40 males and 36 females from the period of

Fig. 8. Body length - body weight relationship of 174 *Anolis nebulosus* collected near Tepic, Nayarit, Mexico, during April - May, 1968.


SNOUT-VENT LENGTH (mm)
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
0.5
1.0
1.5
2.0
2.5
3.0
BODY WEIGHT (gm)
MALE
FEMALE

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 3 lists the April s-v 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 s-v length for each group presented in Table 3, regardless of the initial s-v 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 s-v 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 s-v 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 48 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% 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

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
6	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.

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% 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 $\pm$0.68 mm and 1.67 $\pm$0.09 gm, respectively; the females averaged 34.8 $\pm$0.31 mm and 0.99 $\pm$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 m^2. 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 of the study area. Of these, 25 were males and 28 females; their mean snout-vent lengths and body weights were: males - 40.7 $\pm$0.94 mm, 1.71 $\pm$0.13 gm; females - 35.4 $\pm$0.37 mm, 1.04 $\pm$0.05 gm. The conservative estimates of population density and biomass based on these 53 anoles and their body weights are: 57 anoles at 77 gm per 1000 m^2, 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) provide some estimates for density of Anolis limifrons in Panama; up to 250 residents/acre are reported with a maximum of 600 individuals per 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 study area is a part of 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 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), 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 s-v 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. 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).

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.

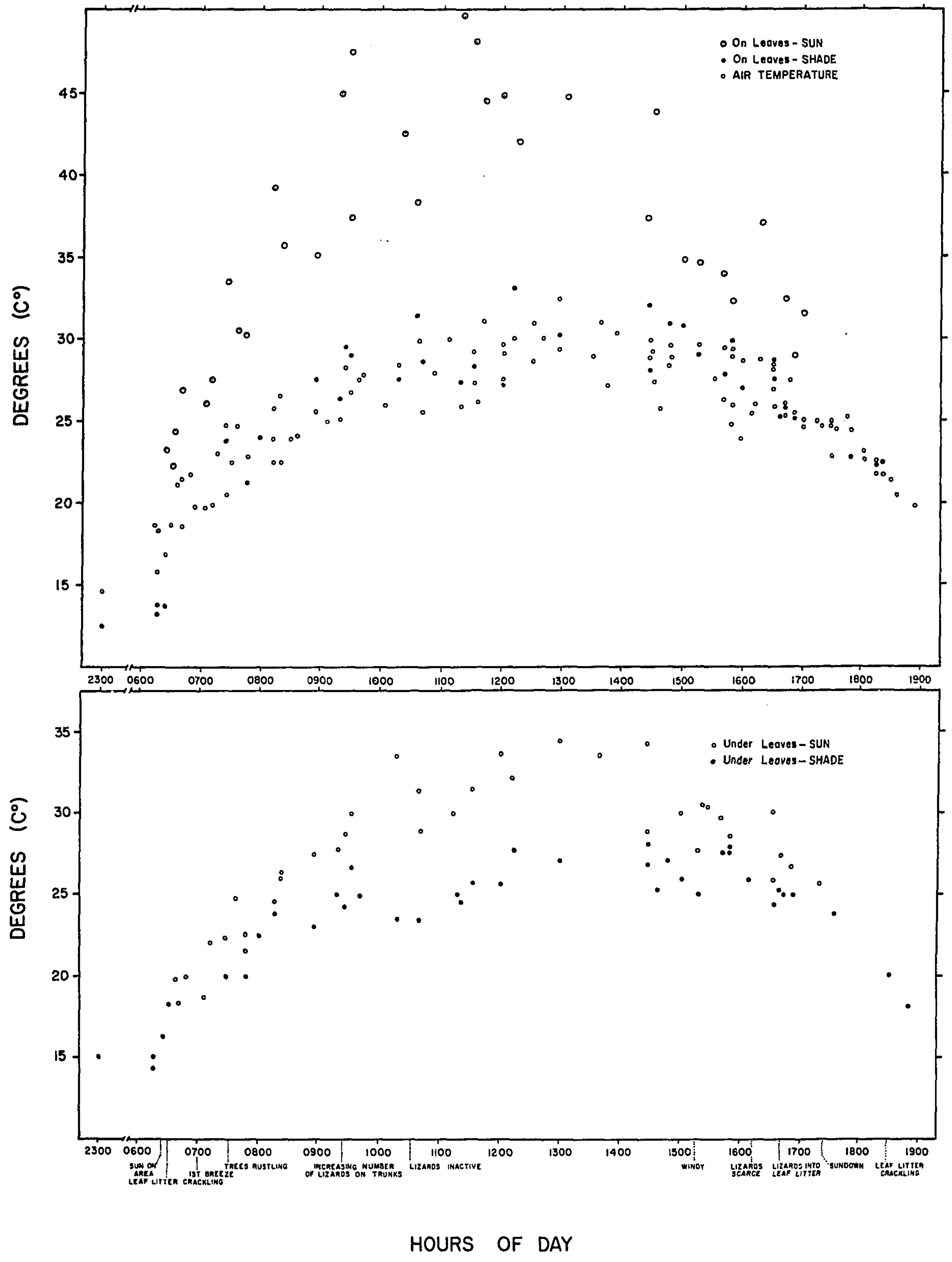
Perch Types	Time of Day									
	0800 - 0959		1000 - 1159		1200 - 1359		1400 - 1559		0800 - 1559	
	M	F	M	F	M	F	M	F	M	F
Trees and fence posts	51.9%	37.0%	68.8%	46.8%	61.9%	60.9%	51.1%	47.1%	58.2%	46.8%
Coppice and bushy seedlings	31.9	33.0	16.8	27.8	28.9	23.2	30.4	32.1	27.0	29.2
Small woody plants	2.5	7.0	5.6	11.4	4.1	7.2	5.4	3.8	4.3	7.6
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 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% were of males; yet females accounted for over 50% 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 four 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. 9).

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 for 16 males with trees. The presence or absence of trees in plotted home ranges seems an impartial way to analyze the sample.

Fig. 9. Air and leaf litter temperatures for the study area near Tepic, Nayarit, Mexico, during April - May, 1968.


On Leaves - SUN
On Leaves - SHADE
AIR TEMPERATURE
DEGREES (C°)
45
40
35
30
25
20
15
2300 0600 0700 0800 0900 1000 1100 1200 1300 1400 1500 1600 1700 1800 1900
Under Leaves - SUN
Under Leaves - SHADE
DEGREES (C°)
35
30
25
20
15
2300 0600 0700 0800 0900 1000 1100 1200 1300 1400 1500 1600 1700 1800 1900
SUN ON AREA
LEAF LITTER CRACKLING
1ST BREEZE
TREES RUSTLING
INCREASING NUMBER OF LIZARDS ON TRUNKS
LIZARDS INACTIVE
WINDY
LIZARDS SCARCE
LIZARDS INTO LEAF LITTER
SUNDOWN
LEAF LITTER CRACKLING
HOURS OF DAY

However, the difference between the two groups was decreased by a number of small males primarily residing in coppice beneath the trees, but which were still assigned to the tree-containing group by definition.

From reports in the literature, most species of <u>Anolis</u> sleep above ground on grass stems or the outer branches and leaves of trees and bushes. Similar sleeping sites are given for those <u>A. nebulosus</u> observed in Michoacan (Duellman, 1965; Schmidt and Shannon, 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. However, some care must be exercized 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.

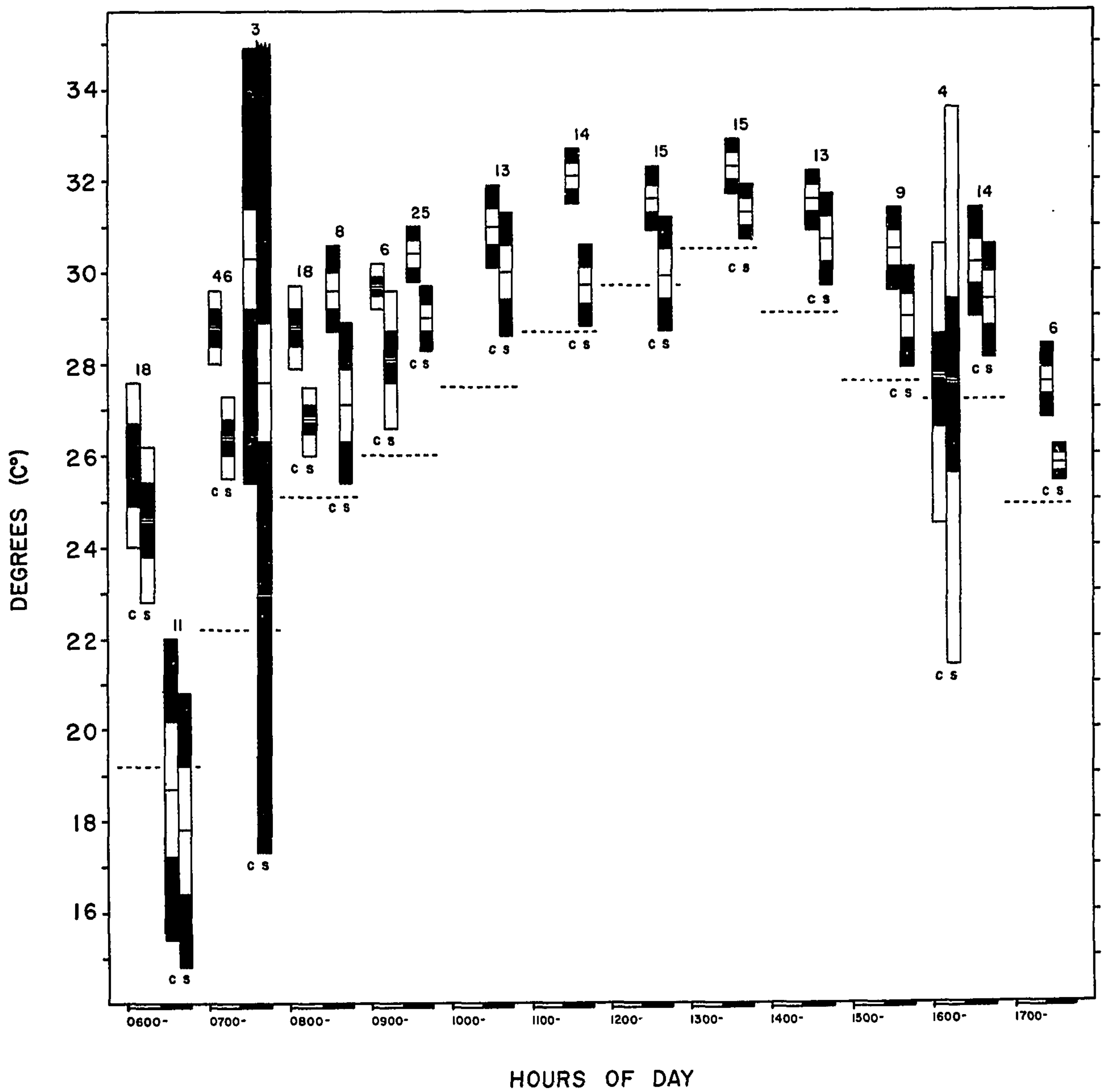
In the morning before the sun rose above the mountains, the air temperature was about 14 - 15 C. The cloacal temperature of 9 lizards in their sleeping sites beneath the leaf litter averaged 16.3 C (15.3 - 17.3 C), while the sleeping sites approximated air temperature, averaging 14.8 C (13.8 - 15.9 C); 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. 9).

The first rays of sunlight hit part of the study area around 0620. From this time on, substrate temperatures quickly increased (Fig. 9). The top of the leaf litter in the shade followed air temperatures. Temperature readings eight or more centimeters into the shaded leaf litter were also close to air temperatures, though slower to rise. Even 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. 9). 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. 10); 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 large confidence limits appearing in Fig. 10.

Fig. 10. Hourly cloacal (C) and site (S) temperatures of *Anolis nebulosus* near Tepic, Nayarit, Mexico, during April - May, 1968. Ends of bars give 95% 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.


DEGREES (C°)
34
32
30
28
26
24
22
20
18
16
18
11
46
3
18
8
6
25
13
14
15
15
13
9
4
14
6
C S
0600-
0700-
0800-
0900-
1000-
1100-
1200-
1300-
1400-
1500-
1600-
1700-
HOURS OF DAY

At 0800-0859 hour the majority (58%) of the observed lizards were still basking; 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 probably represent animals which had been basking during the previous hour, but which reached their preferred temperatures and had retired 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% of observed animals were now in the shade, some were still basking. Of those latter individuals, 6 were measured and found to have 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 (93%) were now in the shade. No body temperatures were obtained from the few anoles seen in the sun. However, the mean cloacal temperatures of the lizards in the shade at this time was 31.0 C, and was probably above that preferred by the anoles. This thermal threshold is more obvious if a heat gradient is available for comparison of lizard heat with potential perch site temperatures. During the afternoons, readings were taken of several lizards, their actual perch sites, and the nearest alternative perch exposed to different temperature conditions (Table 6). With one exception, all lizards with body temperatures over 29.7 C were in the cooler location of their immediate microhabitat (shaded vs. sunlit side of tree limb).

From 1100-1359 environmental temperatures continued to increase to their highest value (Fig. 9). 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 the 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% of the observed anoles had moved into the sunlight as mean cloacal, site, and air temperatures became

Table 6. Cloacal temperatures (C.T.) of *Anolis nebulosus* with temperatures of their respective perch sites (S.T.) and closest alternative perch sites (A.S.T.), recorded during April - May, 1968, near Tepic, Nayarit, Mexico.

C.T. (C)	S.T. (C)	A.S.T. (C)	Time of Day
29.9	28.0	33.8	1210
30.5	28.8	34.6	1215
32.4	28.8	32.9	1218
30.8	29.5	32.9	1220
31.7	30.8	39.5	1220
32.5	31.2	33.3	1230
32.4	30.5	34.2	1235
29.4	29.0	35.5	1240
31.8	30.4	35.9	1240
30.2	32.0	38.1	1330
32.7	31.5	34.0	1335
32.4	33.0	36.4	1342
33.4	30.7	33.7	1350
31.4	31.4	34.7	1405
31.7	32.0	35.7	1440
32.8	30.8	34.6	1444
30.0	29.0	31.2	1600
30.3	29.5	32.5	1605
32.2	32.4	39.8	1610
28.3	27.7	31.0	1626
29.5	33.0	29.1	1635

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 at this hour and moving into the leaf litter and out of the wind. Cloacal temperatures of these individuals were still fairly high (i.e. 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 possibly even increased dessication 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 water taken in by the lizards would have to come from prey items. Water conservation is undoubtedly a concern. Claussen (1967) found as much as 70% 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% of the sample was clustered between 27.5 - 31.4 C and 75% 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% of the basking lizards was 29.5 - 29.9 C; the group mean was 29.6 C (95% 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. 10. 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 an 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 averaged 29.9 $\pm$0.27 C (95% confidence limits of 29.3 and 30.4 C); corresponding values for female anoles were 28.5 $\pm$1.12 C (95% 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 slowly moving up from the leaf litter into 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.

According to the classification given by Brattstrom (1965: 412-413), A. nebulosus is characterized as a diurnal, limited basker. Or it can be called a facultative non-heliothermic species (mean body temperature less than 31 C) as established by the criteria of Ruibal (1961: 109). As there is evidence that the thermal preferendum is a relatively reliable criterion for comparing lizards (Licht, 1968), Table 7 provides a general idea of how the temperature preference of A. nebulosus compares with other members of its genus.

In summary, A. nebulosus has a preferred temperature comparable to other anoline species living in filtered sunlight conditions, and can be classified as a diurnal, limited basker. Its preferred mean body temperature appears to be 29.7 C. The lizards are observed to bask in the early morning hours (0600-0959) and then retire to the shade where their cloacal temperatures continue to rise along with ambient temperatures. A. nebulosus was 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 includes 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

Table 7. Comparative temperature data (C) for some species of <u>Anolis</u>.

Species	Locality	Cloacal Temperature Mean	Cloacal Temperature Range	Critical Thermal Maximum	Air Temperature	Authority
<u>A. carolinensis</u>	Louisiana	33.0	29.2 - 35.9	41.8	. .	Licht (1968) and Brattstrom (1965)
<u>allogus</u>	Cuba	29.2 $\pm$0.06	26.2 - 33.5	. .	26.0 - 32.4	Ruibal (1961)
<u>lucius</u>	Cuba	29.3 $\pm$0.10	24.8 - 32.4	. .	26.0 - 32.4	Ruibal (1961)
<u>homolechis</u>	Cuba	31.8 $\pm$0.14	26.2 - 35.0	. .	28.2 - 33.4	Ruibal (1961)
<u>sagrei</u>	Cuba	33.1 $\pm$0.22	27.4 - 36.1	. .	27.4 - 35.0	Ruibal (1961)
<u>allisoni</u>	Cuba	33.0 $\pm$0.21	28.2 - 36.6	. .	27.4 - 35.0	Ruibal (1961)
<u>lineatopus</u>	Jamaica	. .	28.0 - 31.0 (preferred)	. .	. .	Rand (1967a)
<u>occulatus</u>	Dominica, West Indies	28.2 $\pm$1.8	23.2 - 33.0	35.5	27.6 $\pm$1.8	Brooks (1968)
<u>aenus</u>	Grenada, West Indies	31.6 - 32.0*	. .	. .	. .	Schoener and Gorman (1968)
<u>richardi</u>	Grenada, West Indies	29.6 - 30.0*	. .	. .	. .	Schoener and Gorman (1968)
<u>pentaprion</u>	Barro Colorado, Panama	28.0	. .	36.0	. .	Brattstrom (1965)
<u>townsendi</u>	Cocos Island	30.9	28.7 - 32.6	. .	. .	Carpenter (1965)
<u>scypheus</u>	N.E. Ecuador	27.5 $\pm$0.88	24.0 - 32.8	. .	. .	Fitch (1968)

*Mean class group estimated from cloacal temperature distributions.

for each animal were recorded and plotted on a scale map of the study area (Fig. 11). By connecting the outermost locality sightings, a minimum polygon was produced for each animal (Fig. 12 and 13). Area determinations were then extrapolated by weighing the scaled home ranges cut from graph paper against a known scaled area (10 m^2) 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 to 10 m^2) were cut and weighed; all three pieces were within 0.007 gm of each other.

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 (Table 8 and 9).

Males had significantly larger home ranges than females. The 22 male home ranges averaged 1.99 $\pm$0.23 m^2 with 95% 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 m^2 with 95% confidence limits of 0.34 and 0.90 m^2. Male lizards also moved further between observations than females (Table 8 and 9); the distances were significantly different. The 95% confidence limits for the mean distance per move were 2.78 and 3.74 meters for the males, and 1.29 and 2.49 meters for the females.

The 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

Fig. 11. Scale map of the 30.5 x 30.5 m study area showing seedlings, coppice, fence posts, and trees with their overhead canopy outlined.

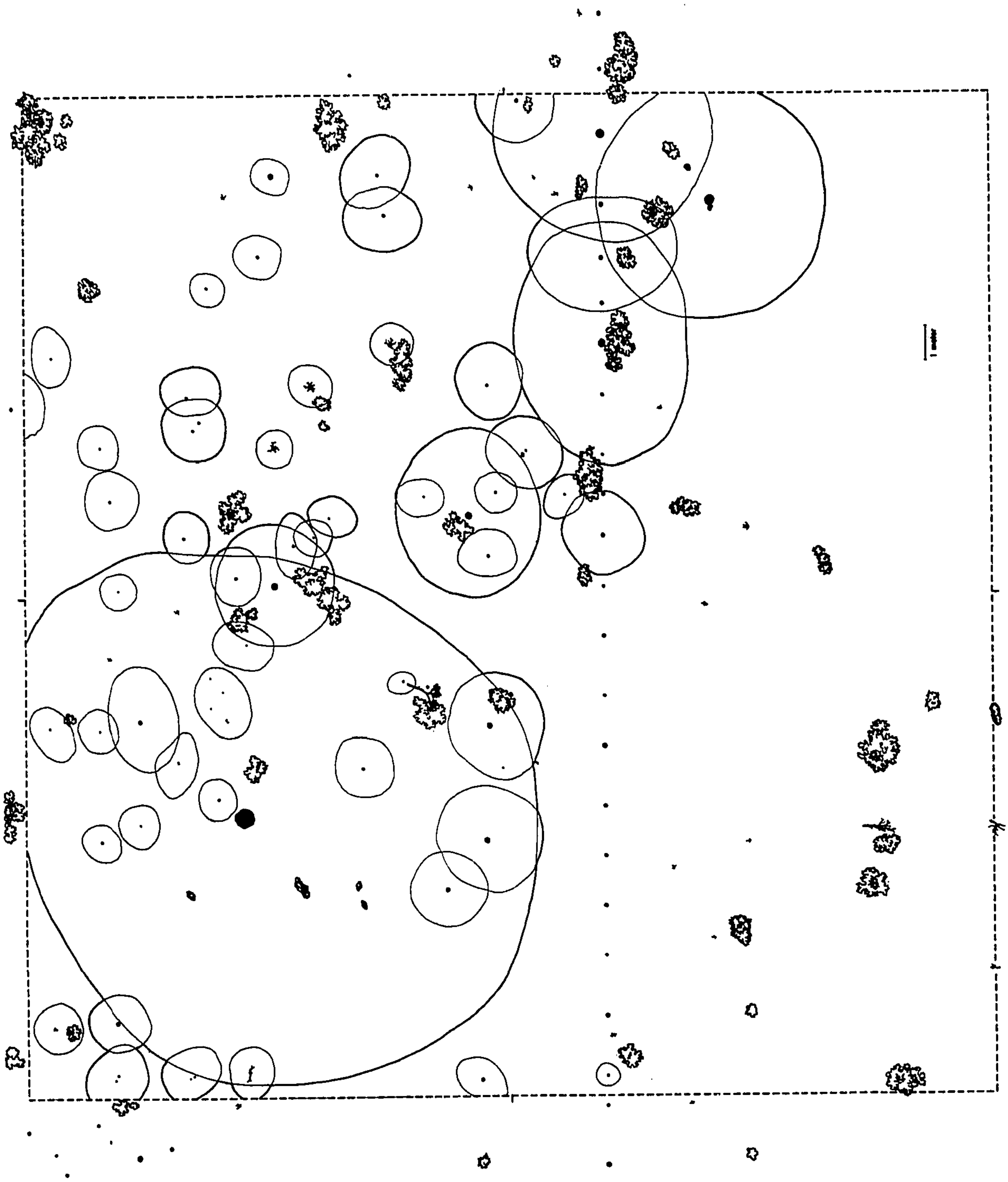


Fig. 12. Scale map of study area with home range of 22 male *Anolis nebulosus* superimposed.

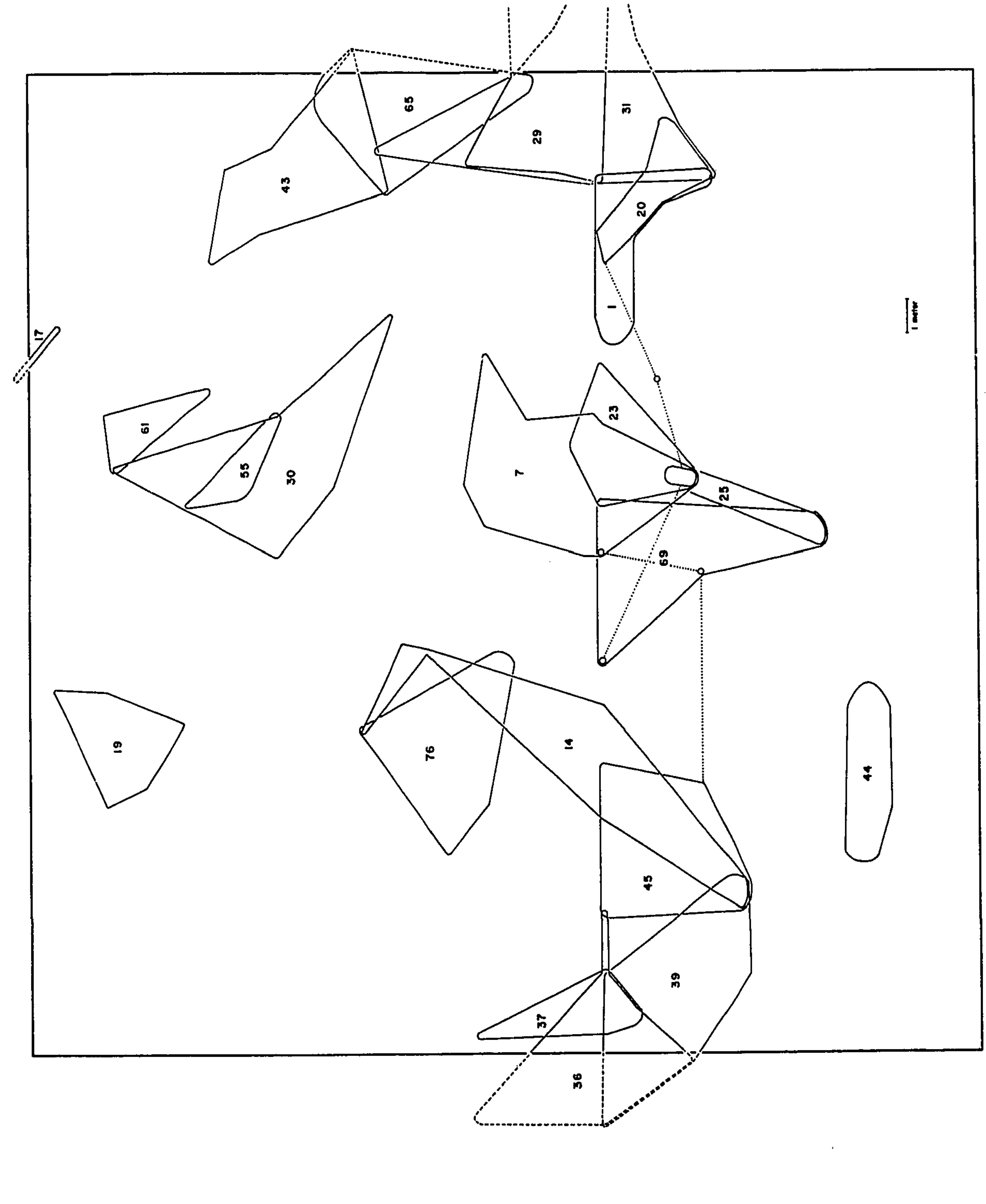

65
29
31
43
20
1
1 meter
17
61
55
30
7
23
25
69
19
76
14
44
45
39
37
36

Fig. 13. Scale map of study area with home range of 26 female <u>Anolis nebulosus</u> superimposed.

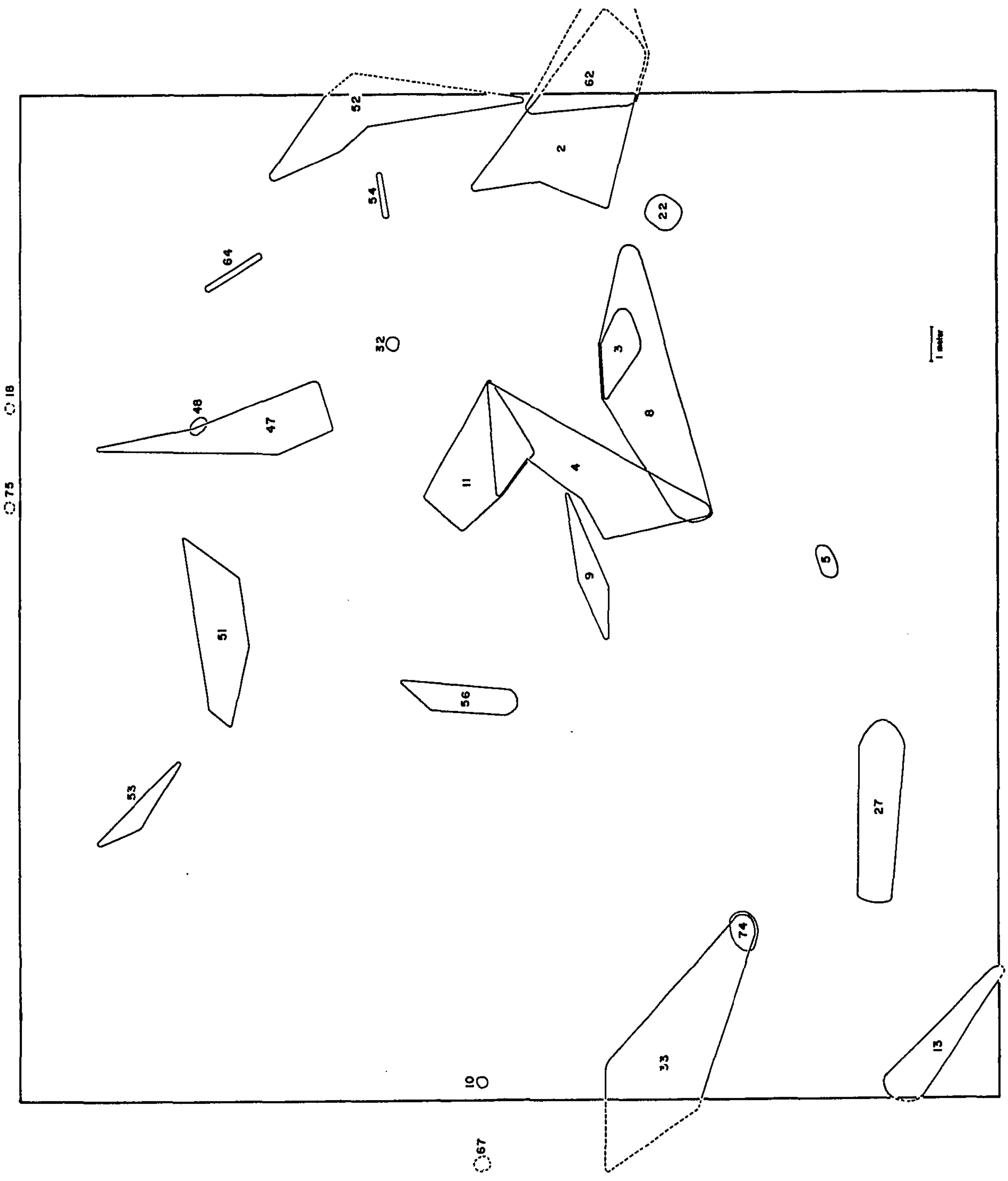

52
62
2
54
22
64
32
3
1 meter
18
48
47
8
4
11
75
9
5
51
56
53
27
74
13
33
10
67

Table 8. 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.

Table 9. 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.

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 observation; 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 8 and 9 were divided into three groups. Since these data were arranged according to snout-vent lengths, the groups contained individuals of progressively decreasing size (Table 10). The longest anoles of each sex tended to have the largest home ranges for their respective sex class; this trend was also true of A. lineatopus (Rand, 1967b). Evident only for female A. nebulosus was an apparent correlation between larger home range areas and greater distances moved between captures (Table 10).

The territories did not uniformly cover the study area, but were associated with certain features of the habitat. The males made extensive use of the fence posts which ran across the lower third of the study area (Fig. 11). Two areas of the observation plot did not hold any resident lizards: that part of the grassy region in the lower third of the study area where no coppice grew, and the upper left quadrant of the plot where the ground was also free of much shrubby vegetation.

For the males, at least, elevated perch sites as well as adequate shade throughout most of the day seemed to be two immediate needs. By comparing the snout-vent length of the individual males listed in Table 8 with their home ranges in Fig. 12, it is noted that most of the larger males are found along the treed length of the fence row, and in the upper right quarter of the study area. Presumably, those areas were of greatest attractiveness and the larger animals (i.e. No. 30, 43, 1, 31, 29, 7, 65) successfully competed for them. Males No. 37 and 44 were the other large anoles of the study plot not found in the above areas. Male 37 was the only large male occupying the treeless section of the fence row and male 44 was found inhabiting a series of coppice in the grassy area.

Table 10. Comparison of length of lizard to movement and home range size. Data taken from Tables 8 and 9.

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

From the discussion of the lizards' thermo-regulation it is known that shade is a most important requirement at this time of the year. It appeared that those areas in the study area with 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. 12). 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 10. 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. 12). 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 (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. 13). Only 9.1% of the males had isolated home ranges as compared with 61.6% 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 by adjacent lizards during these wider movements, the anole would retreat.

The distribution of female home ranges is almost a perfect overlap with the 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. In 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 helps determine an animal's territory size; however, it is not a direct relationship as will be seen in the following examples.

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 area, 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 8, Fig. 12), 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 m^2). 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 very dramatic film sequence was obtained of a naturally occuring 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 m^2).

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. 11 and 12). No. 31 was often seen foraging about in the leaf litter or resting in a coppice, but did not appear to take a high perch as was true of his neighboring males. His home range was one of the largest (4.52 m^2), 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. 21's home range, there was little overhead shade, which may have limited his movements.

It is interesting to note that 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 agressive 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 interactions are for 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, and gives a basis for future experimental studies needed to provide greater evidence of the behaviors' functions.

In many of the behavior patterns the dewlap plays a prominent role. The dewlap, or throat fan, is very large in A. nebulosus and is produced from 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. 14).

Assertion display. -- The basic display-action-pattern most frequently seen fits the behavioral definition named by Carpenter (1962a) as the assertion display (Fig. 14c). This DAP was extremely stable and characteristic for the population (Chapter IV). 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. 15a). Although the lizards gave the assertion display from all parts of their habitat, the males most

Fig. 14. 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.

A

B

C

D

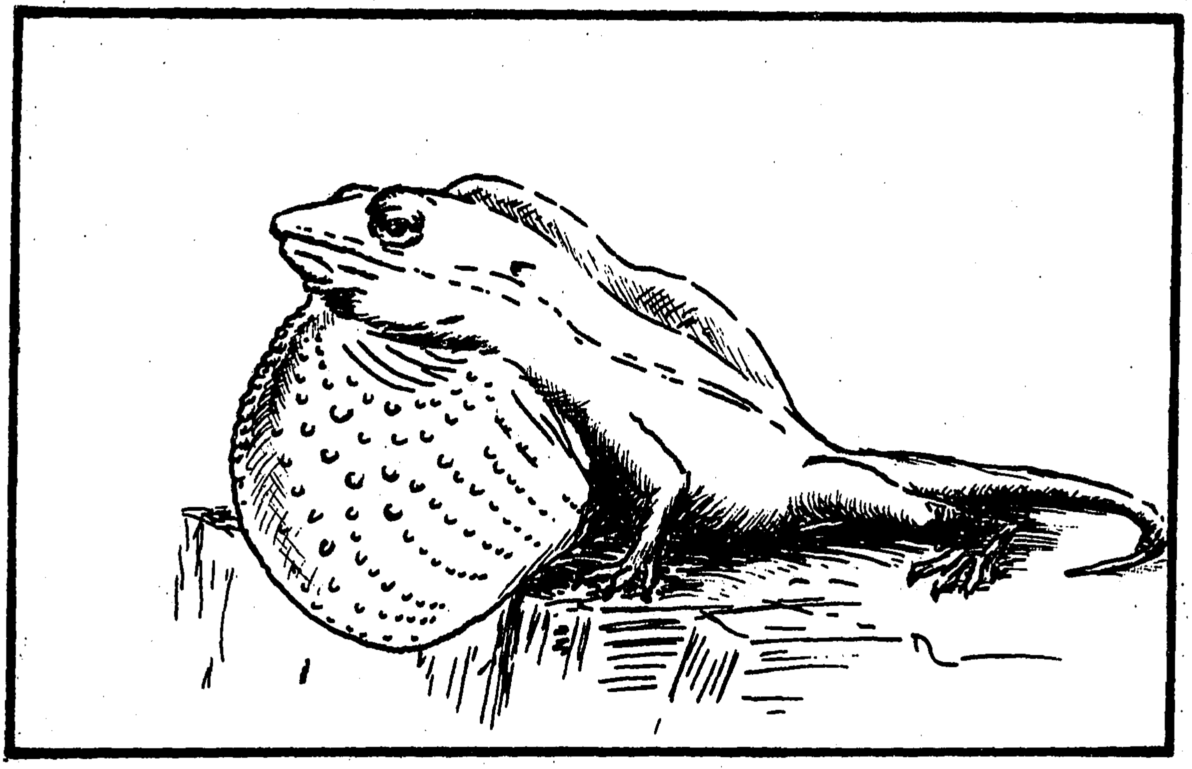


Fig. 15a. Assertion display of *Anolis nebulosus*.

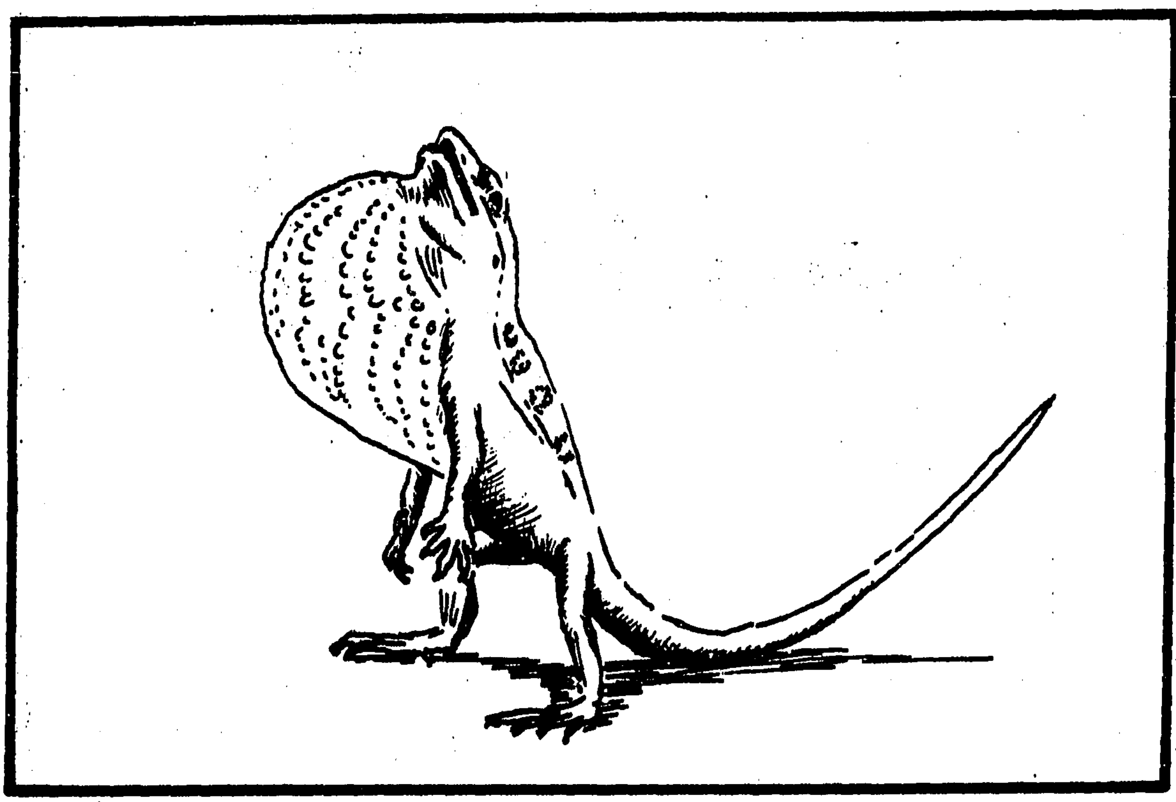


Fig. 15b. Challenge display of *Anolis nebulosus*.

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. However, the assertion display was observed far less frequently than in the laboratory enclosures. Twenty-three displays in a hour's observation period was the maximum recorded for a male in the field. An example of display frequency by a male and his associated movements appears in Figure 16; no other lizards were visible to the observer in the immediate vicinity.

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 extended 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 DAP is purely an aggressive signal.

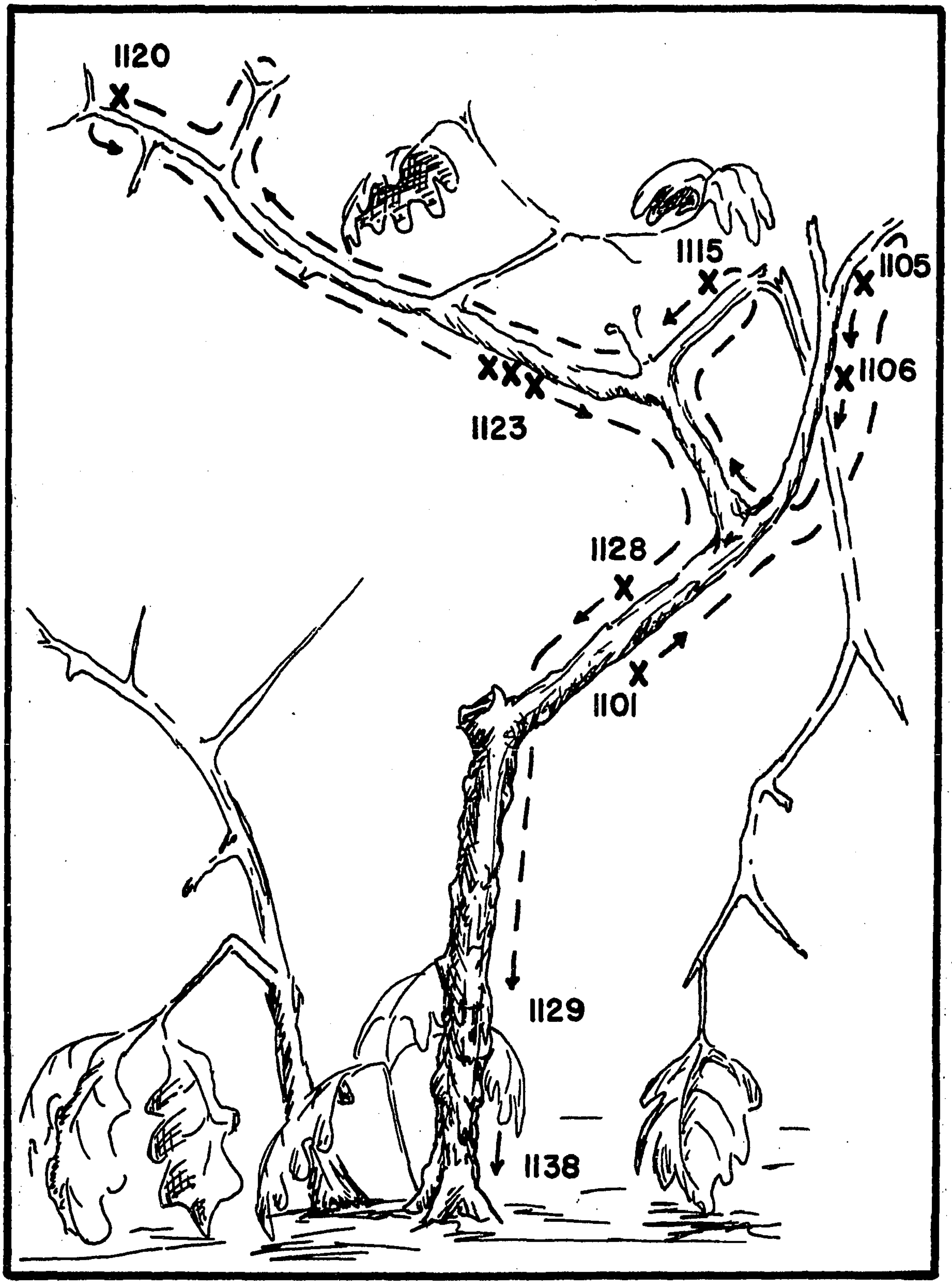


Fig. 16. Movements of male No. 19 in his territory showing locations and times of his displays.

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. 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, 1967b: 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, 1962a). Basically, the challenge display is composed of the assertion display with a preceding unit of head bowing (Fig. 14a). 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 a non-resident 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. 15b). 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, 1967b: 93). With engorged throat, raised dorsal roach, and compressed sides, the males offered an enlarged presentation of their real size (Fig. 17).

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 are 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 towards 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 towards 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.

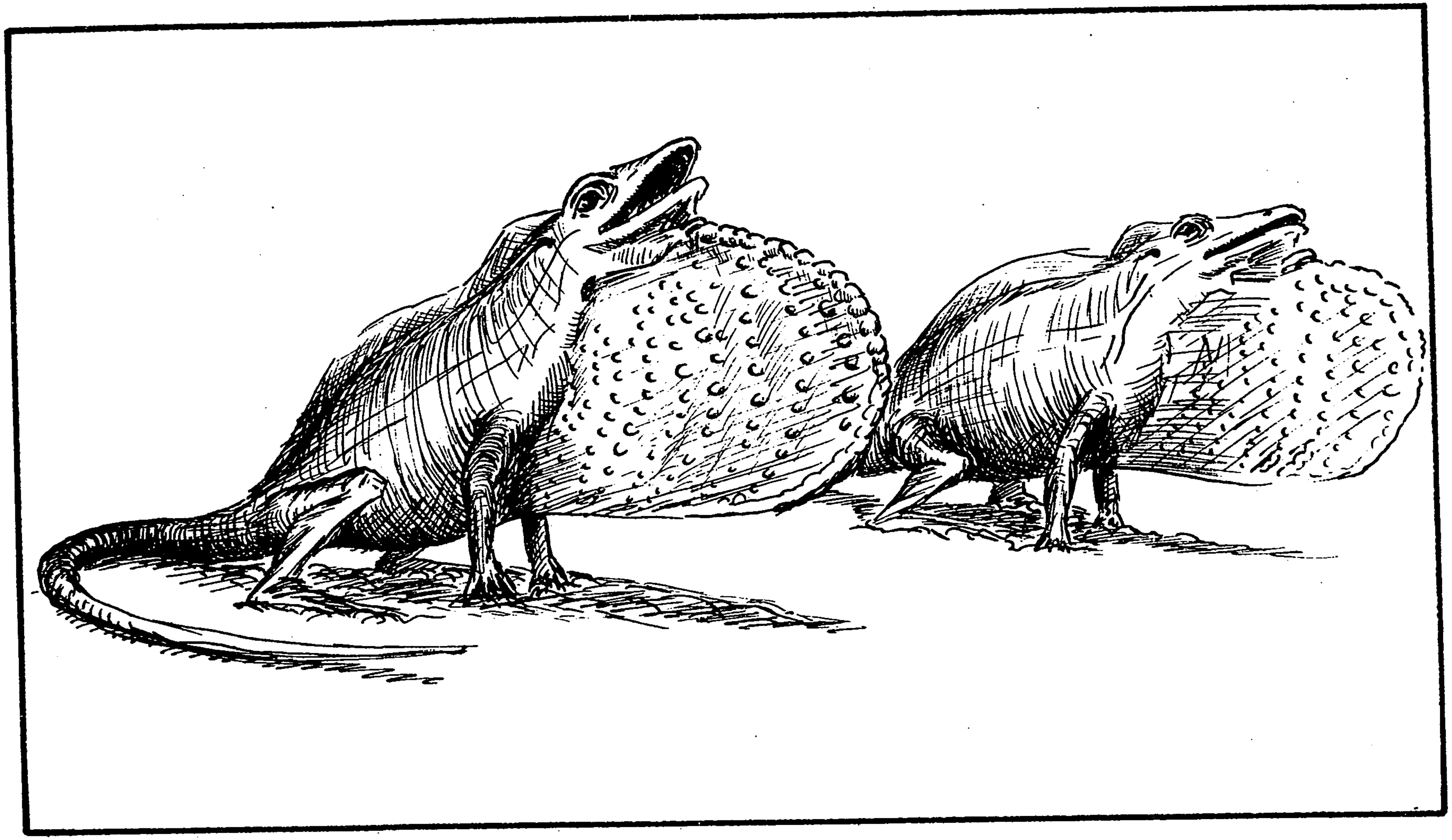


Fig. 17. "Face-off" orientation of challenging male Anolis nebulosus.

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 C0). 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 one male approached a territorial 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 occurs 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 suggest 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. 14a); 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 it 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. 14b). 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 (Fig. 18) 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.

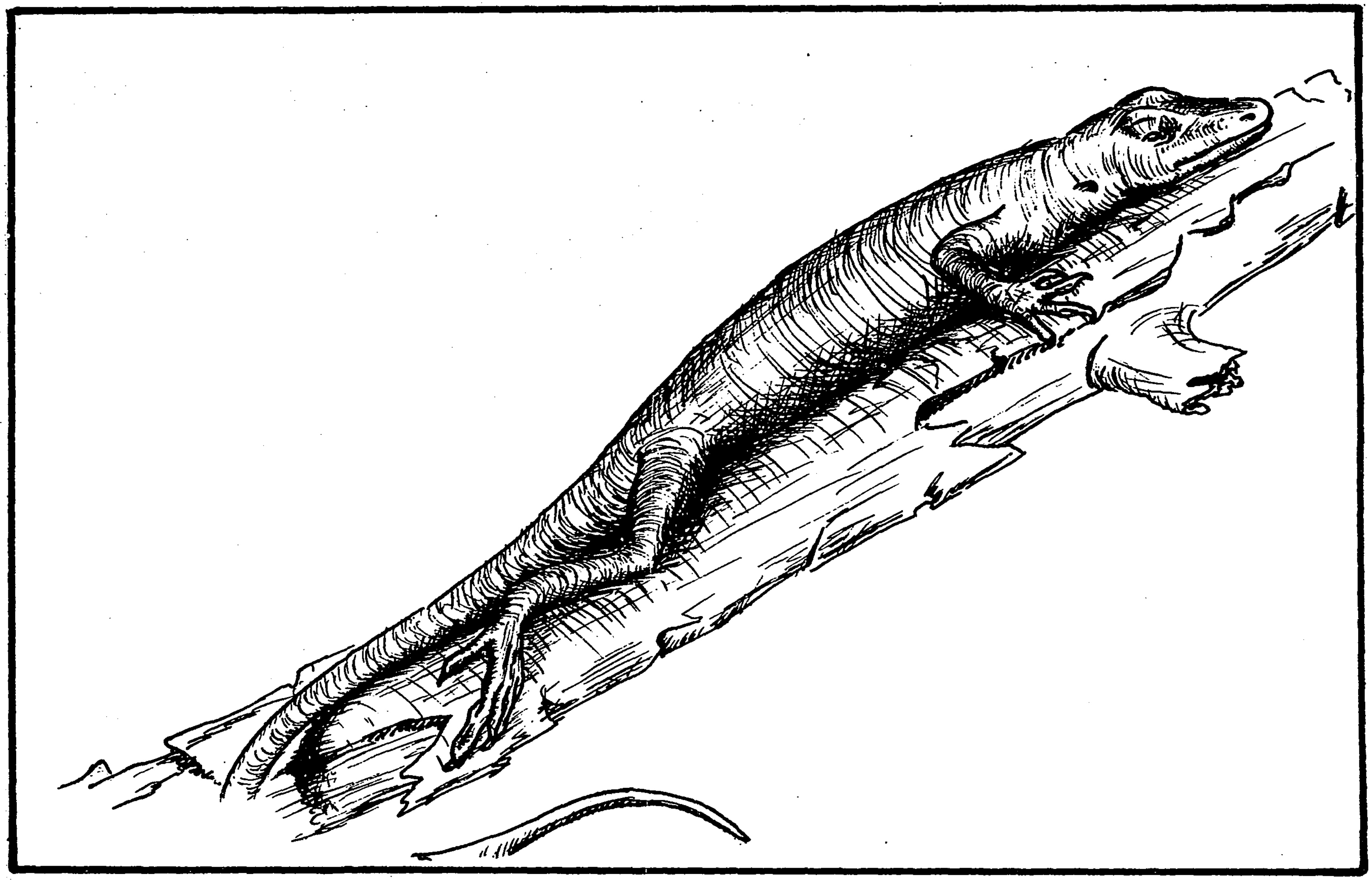


Fig. 18. Flattened posture of <u>Anolis nebulosus</u>.

1656 W-M starts up twig towards B-F, stopping to give a flag-assertion display. B-F increases tail wiggle.

These notes continue for another 55 minutes during which 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, 1967b) and has been called "jiggling" (Evans, 1938b; Ruibal, 1967), "courtship nodding" (Greenberg and Noble, 1944; Carpenter, 1962a), and "shuddering" (Ferguson, 1969a).

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 WO-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. WO-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 (Fig. 19a) is identical to that described for other species of iguanid lizards (Carpenter, 1967b), 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 (Fig. 19b). 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.

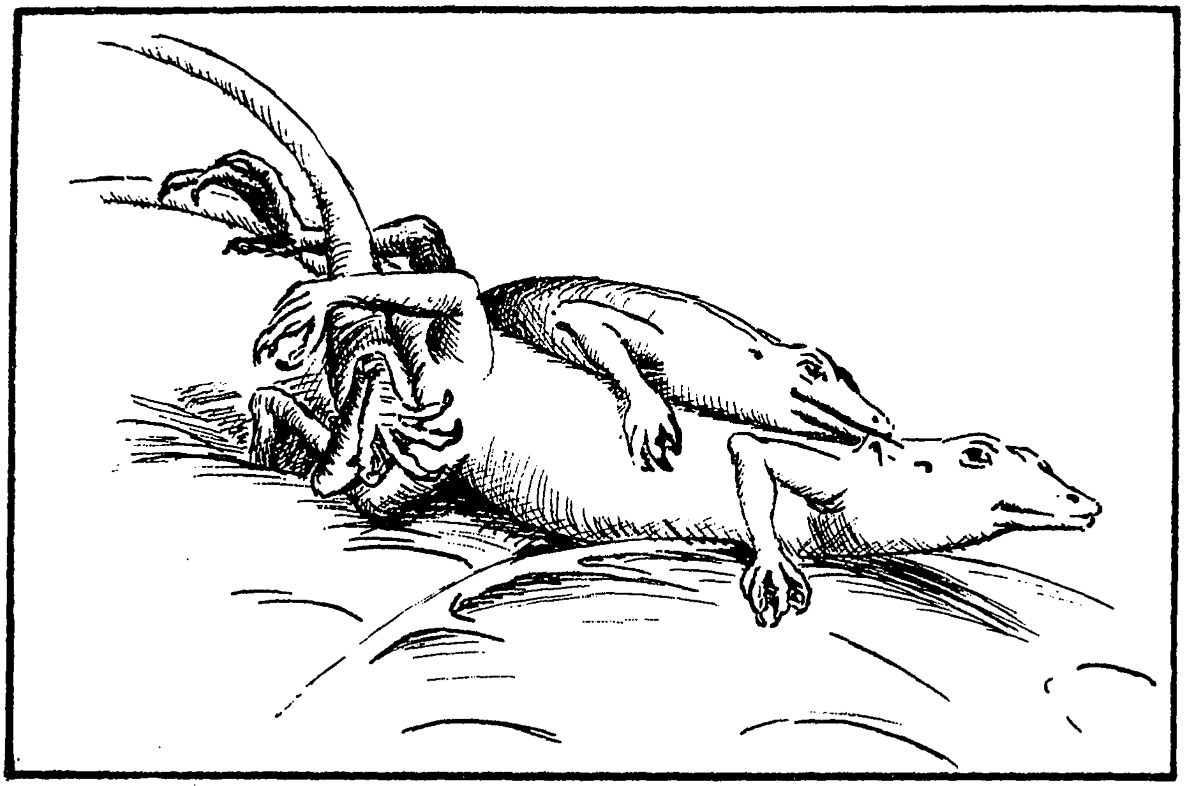


Fig. 19a. Copulatory position of Anolis nebulosus.

Fig. 19b. Eliminative posture of Anolis nebulosus.

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 (Chapter V). 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 May 29, with mating continuing through August. The first gravid female was recorded on June 12. Eggs were found from July 9 through August 28.

Five eggs laid between August 22 and 24 hatched on October 22 and 23. 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 August 19. Using an 8 week incubation period, the latest laying date for the eggs from which these hatchlings emerged is calculated as June 23. A few of the collected hatchlings no longer had visible yolk stalk scars indicating that some egg deposition in the field probably occurs before June 23.

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 breeding and reproductive season (June - October) correlates well with the rainy season in Nayarit (Table 1).

Rain appears to be 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 at times found 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^{o} 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: 5/24 (partial day) - 19; 5/25 - 24; 5/26 - 18; 5/27 - 7; 5/28 - 2; 5/29 - 6; 5/30 - 3. A few were transients, but the large majority of anoles were found to be residents of the area.

Upon being approached the lizards' usual response was to flatten against the substrate when the observer was 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 coppice 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.

Eliminative behavior

Defecation was usually observed following a meal. Anolis nebulosus perform this behavior in a manner common to the members of the family Iguanidae. The hind legs are spread and partially extended and the rump is slightly raised. The proximal portion of the tail is arched as the feces is eliminated (Fig. 19b).

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.

Cows were observed to browse on the study area. If they did not step on some lizards, they undoubtedly caused a few coppice to become unsuitable habitat for the anoles by eating the leaves.

Daily activity log

The following daily logs 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 behavior which made each individual unique. No. 31 was a relatively passive and non-aggressive animal, while No. 1 rigidly enforced his territorial boundaries. The kinds and numbers of displays presented during the day by these two males are quite different.

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 lepidopterans 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 moves 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 passed 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 towards 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.

1254 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.

CHAPTER IV

DISPLAY ANALYSIS

Introduction

In lizard behavior the term "display" refers to behavioral movements resembling pushups or head bobs which are characteristic of iguanid lizards. Brief descriptions of these displays for anoline lizards have been in the literature for some time. Monks (1881) recorded the head nodding and dewlap pulsing of _Anolis carolinensis_ and referred to it as ceremonious courtship. Large aggregations of anoles were observed by Barbour (1926) spreading their dewlaps in the bright sunlight. Noble and Bradley (1933) provided some aspects of the _A. carolinensis_ display as it relates to courtship and fighting. The sequence of the display of _Anolis sagrei_ was outlined by Evans (1938a). Evans (1935, 1936, 1938b) and Greenberg and Noble (1944) also offered more detailed descriptions of the display of _A. carolinensis_. However, Carpenter (1961a, b), Carpenter and Grubitz (1961), and Hunsaker (1962) were the first to graph these display-action-patterns (DAP) by using the y-axis of a graph to show amplitude of head movements and the x-axis for duration of the display. Their work suggests that these displays are species-specific. The DAP graph technique and its proposed taxonomic application have been used on a number of iguanid genera (Carpenter, 1962a, b, 1963, 1966, 1967a; Clarke, 1965; Ferguson, 1969a; Griffith, 1966; Lynn, 1965) as well as Anolis (Carpenter, 1965; Garcea and Gorman, 1968; Gorman, 1968; Kastle, 1963; Ruibal, 1967).

From published data, there is growing evidence that the iguanid displays are stereotypic and seemingly unique for populations, if not for entire species. However, no study has been initiated which explicitly investigated the possible genetic basis of the saurian display. Nor has there been any published data which quantifies the stability of the lizard's display under varying conditions. Even more fundamental, and an area which has been largely neglected, is the need to establish the amount of variation present within the display of a species.

In the present study a statistical analysis was conducted on the assertion display of Anolis nebulosus to determine the amount of variation found within individuals, between individuals, between members of different populations, between lab-held animals and those in the field, and due to maturation. These data are basic to any consideration of a lizard's display being species-specific.

Methods and Materials

A statistical analysis of the display variation in Anolis nebulosus was computed from 599 displays of 59 males. These males were from two populations. One collection site was 35 kilometers east of Tepic, Nayarit, Mexico, and the other was located just outside of Manzanillo, Colima, Mexico. The collection localities are approximately 250 air kilometers apart. The lizards' displays were filmed both in the laboratory and the field.

Males brought back to the laboratory were kept indoors in a room with controlled heat and lighting. During the summer months, however, the temperature frequently was higher than the thermostatic setting as the lab had no air conditioning. The animals were housed in two 4 x 4 x 3 foot enclosures. To prevent territorial fighting from killing many of the males and to retard the establishment of social hierarchies which could possibly affect future behavioral performances, the male lizards were kept in the dark except for a few hours during their daily feeding period.

For maximum accuracy, all displays were filmed and then analyzed on a frame-by-frame basis. A Beaulieu (Model 2008S) Super 8 camera was used for all filming. Two quartz iodine flood lights (Colortran Quartz-King Dual 650) provided more than adequate lighting at minimum heat levels during laboratory filming. Frame-by-frame analysis was accomplished on a specially modified Bell and Howell Super 8 projector (Model 482A).

The filming speed for most of the sample was 18 f.p.s. During some aspects of analysis it was increased to 50 f.p.s. The accuracy of the film speed settings indicated on the side of the camera was checked by taking movies of a stop watch at the two film advance settings. The number of exposed frames of these films was then counted against the actual elapsed time as shown by the filmed stop watch. The indicated speed and the actual frames per second are as follows: 18 f.p.s. (17-18) and 50 f.p.s. (47-49).

A 6 x 2 x 2 foot observation chamber was used for filming. It was outfitted with a number of perches and stocked with several female *A. nebulosus*. Only one male was ever present in the cage at a time. Therefore, no male-to-male challenge displays were used in this study. All movies were taken during late spring and summer months when males exhibited strong territorial behavior.

Typically, a newly introduced male soon began to display. As the habitat was continuous within the cage, the male established several selected sites about the cage which he alternately visited. Each time the male stopped at a particular perch it was almost routine for him to display. In the field the same type of behavior was observed. Even when no other lizards were visible, the male often displayed when reaching a new perch within his territory. This kind of display is called the assertion display (Carpenter, 1962a: 137), and was found to be very consistent for A. nebulosus. The challenge display, which is characteristic of male-to-male encounters, is much more variable since it reflects different levels of intensity; it was therefore not used for this analysis.

The displays analyzed in this study were from four sources. Forty-three males taken from the study area near Tepic, Nayarit had their displays filmed in the laboratory. Of these, 13 individuals were refilmed one year later to observe the effects of maturation upon the display. Another 13 lizards at the Nayarit study area had their displays filmed in the field to compare with the displays of lab-held animals. And a sample of 3 males collected from Manzanillo, Colima had their displays filmed in the laboratory to check for any interpopulational differences.

For the purpose of analysis, the display was divided into 9 artificial units. These units were chosen because of clearly recognizable characteristics of the display-action-pattern (DAP) which precisely separated each unit from the others. Each unit from the assertion DAP of each male was examined separately with a statistical format programmed for the IBM 360/40 computer. The program converted the number of filmed frames for every unit to actual seconds and then calculated the mean, standard error, upper and lower confidence limits (0.95 level), and maximum-mininum values (Appendix Tables 14, 17, 20, 23). The same statistics were computed when each unit was expressed as a percentage of the total display after angular transformation (Appendix Tables 16, 19, 22, 25). An analysis of variance was also run to compare the display variation within individuals with the variation in displays between lizards of a sample (Appendix Tables 15, 18, 21, 24).

There was one aspect of the experimental procedure which might have been improved. The temperature during the filming session was not controlled. It is most probable that the speed of display in the exothermic anoles is in some way related to their body temperature. However, on many occasions the same lizards were filmed on different days and with varying duration of floodlight exposure so that each animal was exposed to a large range of temperature conditions. Still, as will be seen, the display variability for each lizard was surprisingly small. If temperature is a variable in the sequence of the assertion DAP, its effects were negligible in this study.

Results

This study of display variation investigated a number of interrelating factors. However, for clarity, the data obtained from the assertion DAP of lizards collected near Tepic, Nayarit and studied in the laboratory will be discussed first and used as a standard. The other factors such as interpopulation differences and effects of maturation upon the display will be compared back to this standard.

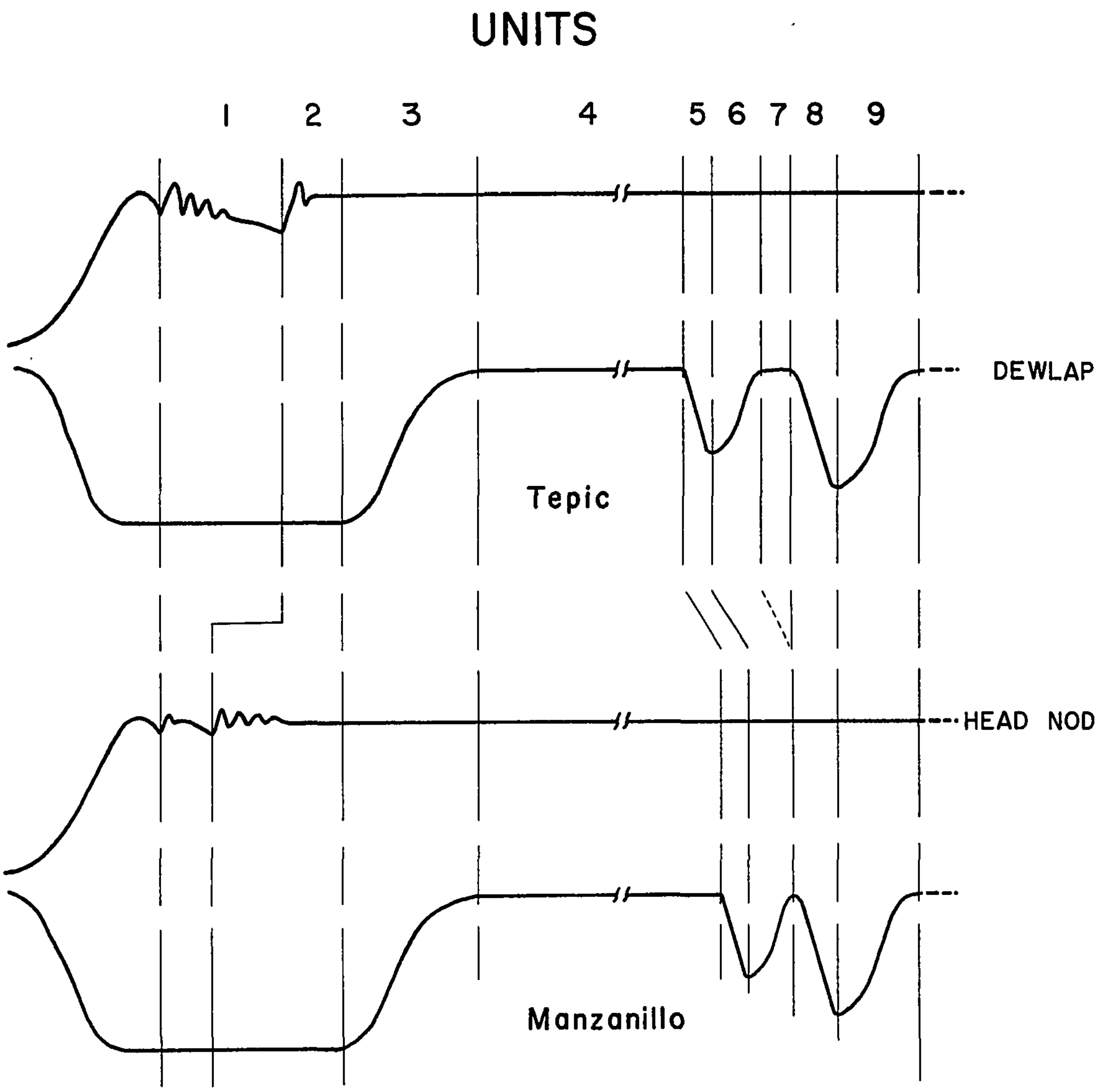
To compare displays, it was necessary to establish artificial subdivisions of the display pattern which would reflect subtle differences upon analysis. Figure 20 diagrammatically illustrates the behavior criteria delineating the 9 units as well as showing an interpopulation difference in the display of _A. nebulosus_. The length of the DAP graph represents passage of time (cadence), while the height of the two lines of each figure provide relative amplitude of the head movement and extension of the throat fan.

Units of generalized display

The initial raising of the head and concomitant dewlap extension was eliminated from the analysis as this act was temporally variable and greatly dependent upon level of excitement and position of the head preceding the display. The first unvarying landmark of the generalized display for the Tepic population was a sharp head nod which is more accurately described as a head jerk; this initiated Unit 1. After the upward head jerk there occurred a series of head bounces which progressively dampened down. A second head jerk followed which marked the end of Unit 1 and began Unit 2. More head bouncing may or may not follow the second head jerk; if the bounces did occur there were far fewer in number than those following the first head jerk. This concluded all head nodding in the generalized display of the Tepic population.

Unit 2 starts with the second head jerk and ends with the initiation of the dewlap retraction. Unit 3 represents the time required for retraction of the dewlap. Unit 4 is a waiting period before the next dewlap extension. Units 5 and 6 are the extension and retraction of the first dewlap pulse. Unit 7 is the waiting period before the extension (Unit 8) and retraction (Unit 9) of the second dewlap pulse. The display analysis ended at this point even though the display was not usually completed until the head was

Fig. 20. Diagrammatic assertion displays for two populations of *Anolis nebulosus* showing arbitrary unit divisions used for display analysis. Vertical axis reflects amplitude of head movement and dewlap extension, and horizontal axis reflects display duration.


UNITS
1
2
3
4
5
6
7
8
9
DEWLAP
Tepic
HEAD NOD
Manzanillo

lowered; however, as with the raising of the head, there was considerable variation.

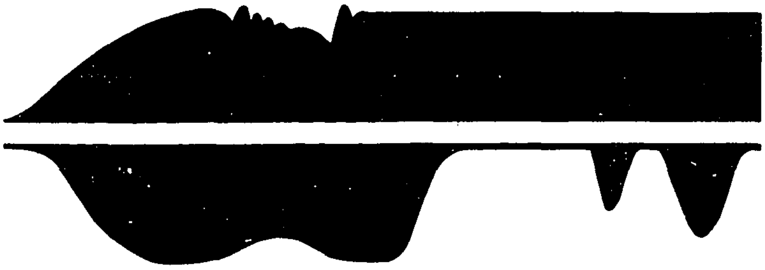
Population-typical and anomalous displays

The generalized display-action-pattern for the Tepic population was performed with amazing consistency. Out of 56 males in the analysis and observations on well over 150 other Tepic anoles, only five lizards had displays which varied from the generalized pattern (Fig. 21b-d), and then these "abnormal" displays were given infrequently. One male would partially retract and then extend his dewlap during Unit 1. Another male was observed to skip the first of the two dewlap pulses. The duration of the sequence (total display) of this latter anomalous pattern did not vary from that of the lizard's usual display; instead Unit 4 was lengthened by the amount of time usually occupied by Units 5 and 6 (first dewlap pulse). The last abnormal pattern was found in three males. They inserted a weak dewlap pulse between the two normally occurring pulses. Again, it was found that the total time of the display did not change from that of the animal's normal display. The third dewlap pulse was substituted for Unit 7.

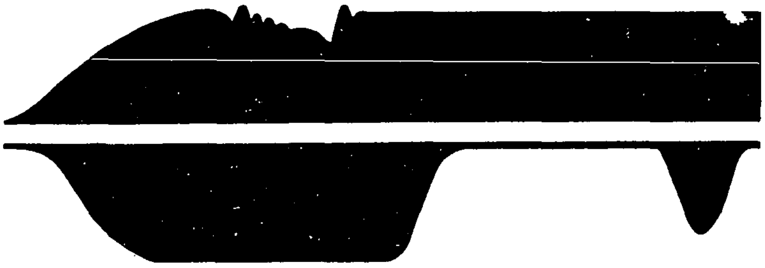
Not only was the generalized assertion DAP shared by all observed members of the Tepic population, but the elapsed times of the display units from any one lizard were practically unvarying (Tables 14, 20). A lizard performed its assertion display almost identically time after time. Thus, the confidence limits for duration of the total display were very narrow for each individual (Fig. 22); this was likewise true for each of the 9 units. Most lizards, however, were significantly different from one another in the amount of time it took to complete a particular unit or the entire display sequence. The analysis of variance for the Tepic population

Fig. 21. Four assertion display-action-patterns (DAP) observed in Anolis nebulosus. Upper black represents amplitude (vertical axis) and duration (horizontal axis) of head movement and lower black represents dewlap movements. a. -- normal assertion DAP; b, c, and d. -- unusual variation of normal assertion DAP.

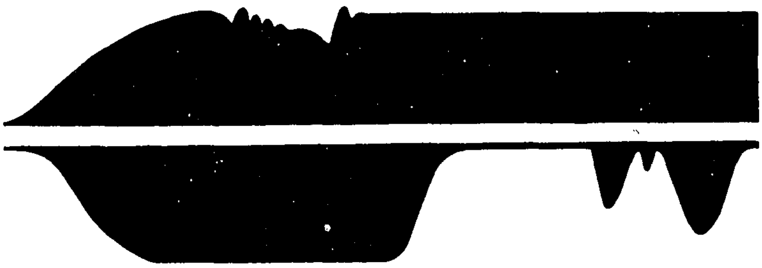
A



B

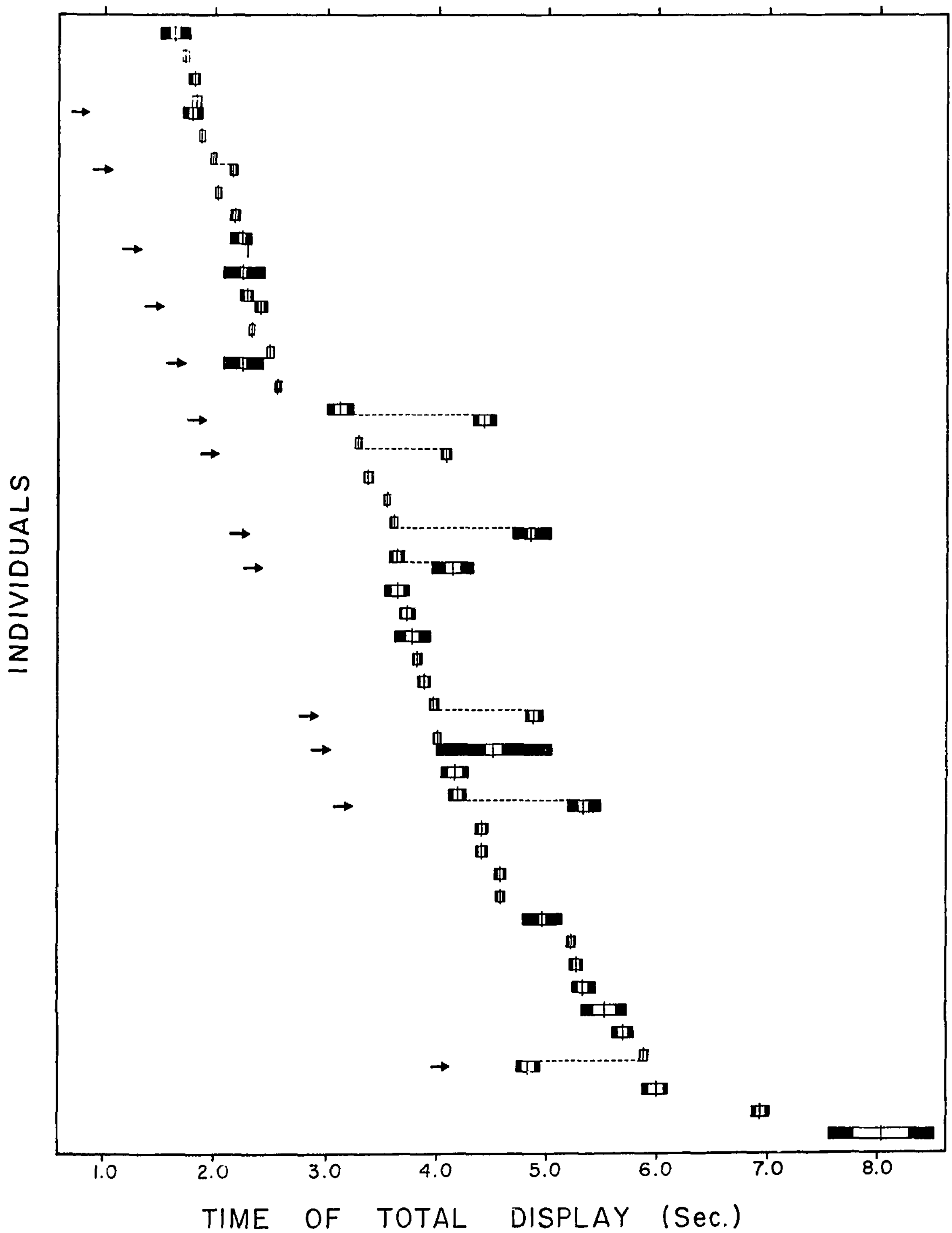


C



D

Fig. 22. Duration (expressed as seconds) of the total assertion display of 43 Anolis nebulosus from Nayarit, Mexico, filmed during the summer, 1967; arrows indicate those individuals whose displays were again filmed during the summer, 1968. Ends of outer black bars give 95% confidence limits of the mean, medial vertical line of bars is the mean, ends of the inner white bars represent the standard error of the mean.


INDIVIDUALS
1.0
2.0
3.0
4.0
5.0
6.0
7.0
8.0
TIME OF TOTAL DISPLAY (Sec.)

demonstrated that of the total variation in elapsed time of the display approximately 98% was attributed to comparisons between lizards, while only about 2% of the variation occurred when comparing displays of the same individual (Tables 15, 21).

Effects of maturation

Thirteen males had their displays refilmed one year later to see if maturation had any effect upon the displays' temporal relationships. In the year interval between filming sessions, the males increased in size and weight and were in good health. It was found that 10 of the 13 anoles (77%) had longer displays than previously recorded. Of these 10 lizards, 8 possessed significantly longer displays (Fig. 22 and Table 17). There appeared to be a slight trend for the display sequence to lengthen as the lizard aged.

By comparing the confidence limits calculated for the display units of the initial filming with those from the display units of the following year (Tables 14, 17), it can be determined which units significantly changed in time over the year's period. For the majority of the displays the alteration in time was reflected proportionally in all units. However, in the remaining cases only a few units were primarily responsible for the temporal shifts in the total display. Unit 1 deviated significantly in 46% of the refilmed displays and Units 3 and 4 in 48% of the compared displays. These three units were also the longest, with Units 1, 3, and 4 composing approximately 31, 9, and 30 percent, respectively, of the generalized display. Their long duration alone increased the chances for variation.

The trend for displays to lengthen as a lizard matures suggested that the larger lizards possessed relatively longer displays since reptiles experience indeterminate growth. To test this idea, the 43 lab-filmed anoles from Tepic were arranged from fastest to slowest displaying individuals. This sample was divided into one group of 10 members and three groups of 11 lizards each. The snout-vent length and weight were recorded for each lizard at the approximate time its displays were filmed. The resulting group averages are as follows: group I (fastest displays) - 46.5 mm, 2.57 gm; group II - 44.8 mm, 2.38 gm; group III - 44.9 mm, 2.29 gm; group IV (slowest displays) - 44.6 mm, 2.30 gm. There was little difference between the group averages; if anything, the first group with the fastest displays had the largest size and weight means.

The tendency for lengthening displays in older lizards appeared to be evident only on an individual level. As previously discussed, an individual A. nebulosus performed its display with almost no variation in its duration. Thus, it requires very little change in a display's cadence to effect a significant difference from the other displays of a particular lizard. Such was the case for most of the 13 anoles who had their assertion DAPs refilmed 12 months later. These slight, but statistically significant, differences on an individual level were masked when viewing the population as a whole because of the large inter-lizard variation existing for display times.

Effect of cadence on the display

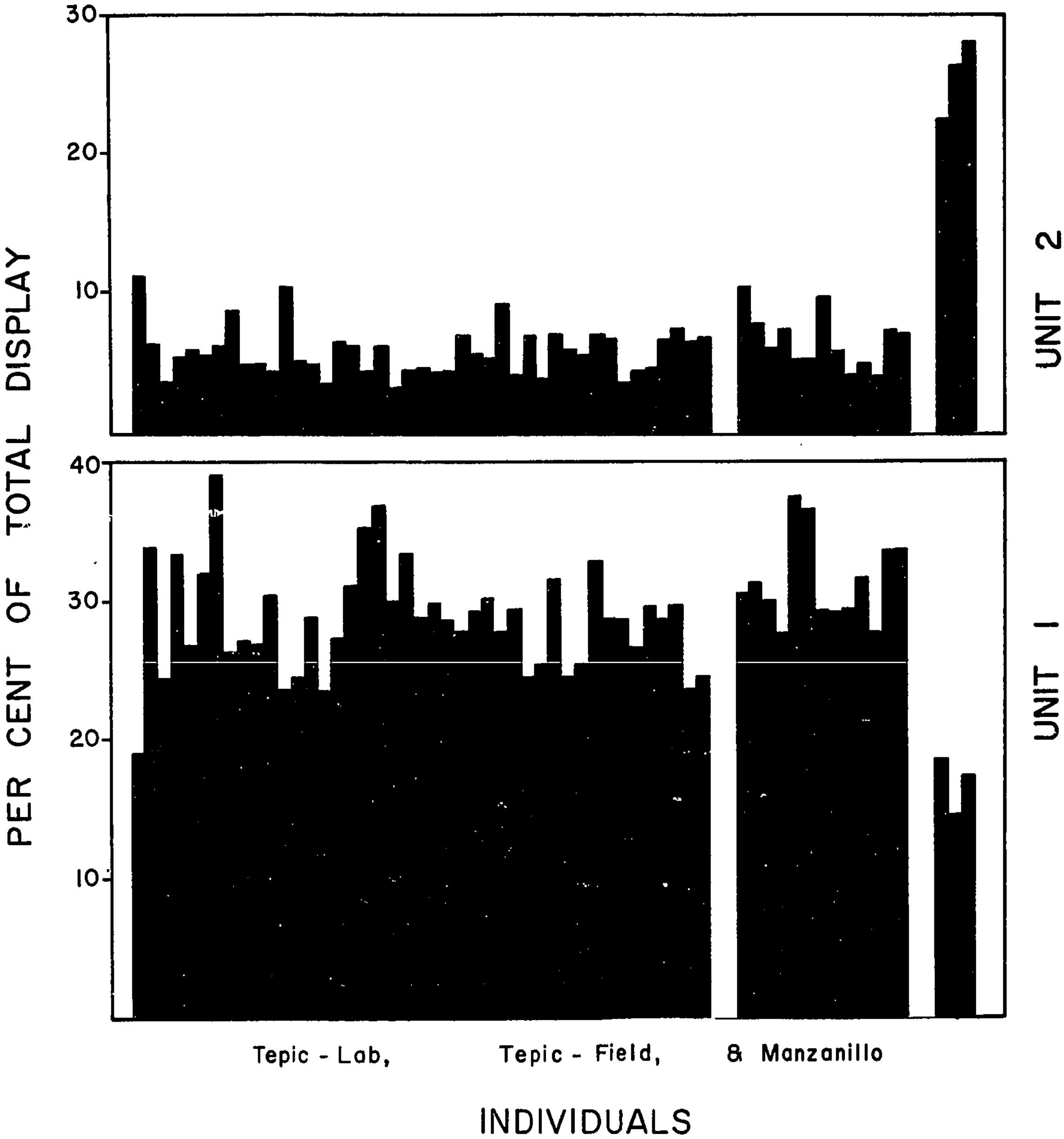
As a group, A. nebulosus presented a wide spread in display times; some lizards completed their pattern in less than 2 seconds, while others required almost 8 seconds to finish (Fig. 22). The question arose whether each unit maintains its same relative proportion in a short display as in a long display. To derive an answer, all displays were made directly comparable by expressing the time interval of each unit as a percentage of its display's total duration. Mean percentages for the 9 units were calculated for each of the 56 lizards in the analysis and presented in Figures 23, 24, and 25; these data are arranged in three groups for purposes of analysis. Within each group the unit percentages are ordered with those from the fastest displaying lizard on the left to the unit percentages from the slowest displaying anole on the right.

Units 1 and 2 of Tepic displays revealed no consistent alterations in their percent importance with progressive changes in the display's total times (Fig. 23). Unit 3, the time interval required to retract the dewlap, usually decreased in its percent importance as the display lengthened. To some extent this was due to the fact that the lizards retract their throat fans at about the same rate. Therefore, this unit's percent would decrease as the total time of the display increased.

The fourth unit, a waiting period before the dewlap pulses, was primarily responsible for increasing the duration of the Tepic display (Fig. 24). There was a strong trend for a disproportionate increase of this waiting period in those lizards with long displays. The percent importance of Units 5 and 6 (the first dewlap pulse) reduced progressively as the display became longer. Although this tendency was not as marked as in Unit 3, it still reflected the constant rate of dewlap extension and retraction regardless of display duration.

A strong correlation existed between Unit 7 and the total time of the display. Those lizards possessing fast displays usually lacked Unit 7; however, as the display increased in length, this waiting period between the dewlap pulses appeared and correspondingly lengthened in duration (Fig. 25). The percentages for the dewlap extension and retraction of the last pulse (Units 8 and 9), showed a weak tendency, if any, to decrease as the display increased in time.

Fig. 23. Units of the *Anolis nebulosus* assertion display (expressed as percent of total display) presented for 43 lizards collected in Nayarit, Mexico, and filmed in the lab (Tepic-Lab); 13 lizards collected in Nayarit, Mexico, and filmed in the field (Tepic-Field); and 3 lizards collected in Colima, Mexico (Manzanillo). Within each block the mean values are given for the fastest displaying anole on the left to the slowest displaying anole on the right.



30
20
10
40
30
20
10
PER CENT OF TOTAL DISPLAY
UNIT 2
UNIT 1
Tepic - Lab,
Tepic - Field,
& Manzanillo
INDIVIDUALS

Fig. 24. Units of the _Anolis nebulosus_ assertion display (expressed as percent of total display) presented for 43 lizards collected in Nayarit, Mexico, and filmed in the lab (Tepic-Lab); 13 lizards collected in Nayarit, Mexico, and filmed in the field (Tepic-Field); and 3 lizards collected in Colima, Mexico (Manzanillo). Within each block the mean values are given for the fastest displaying anole on the left to the slowest displaying anole on the right.

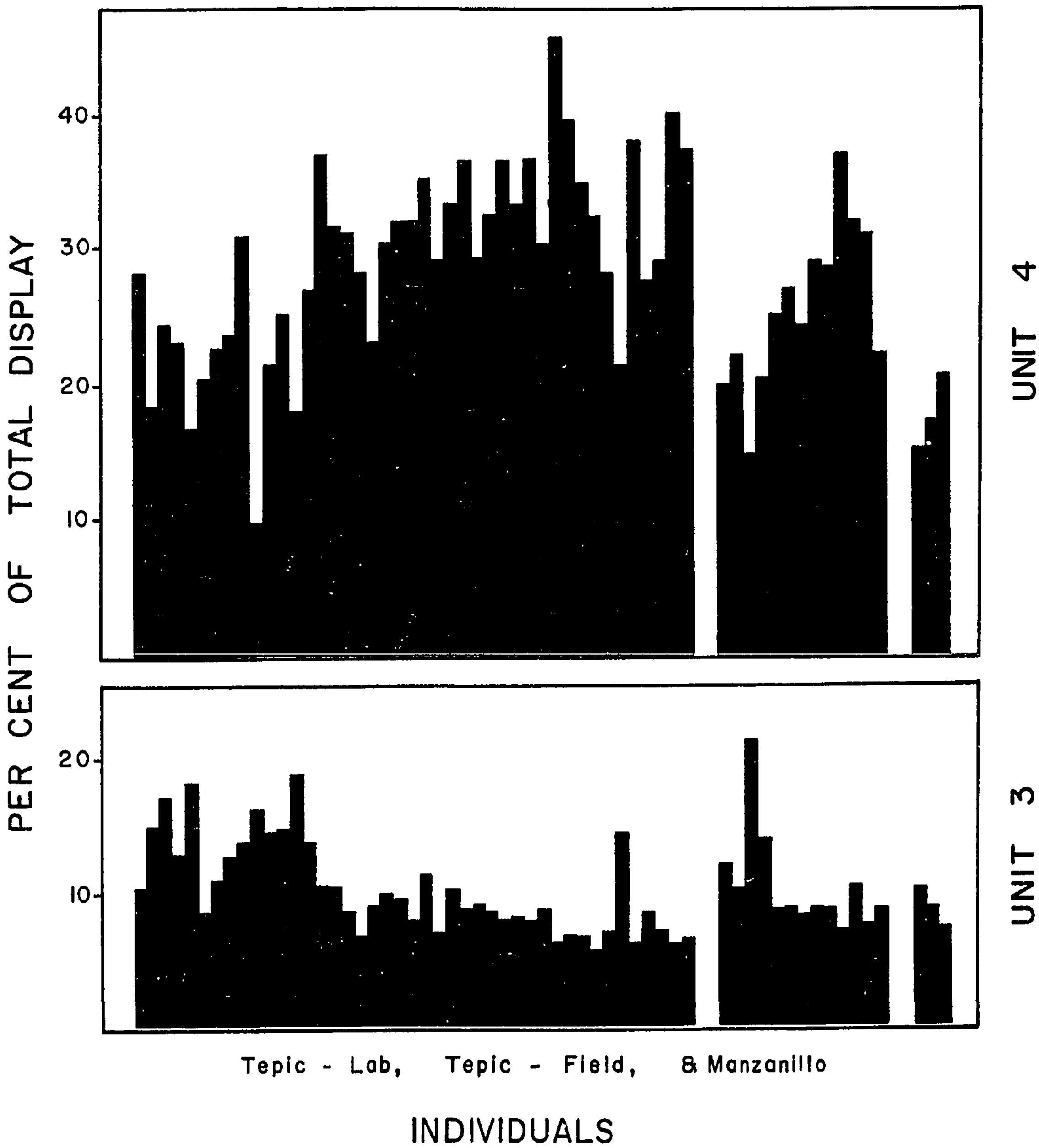
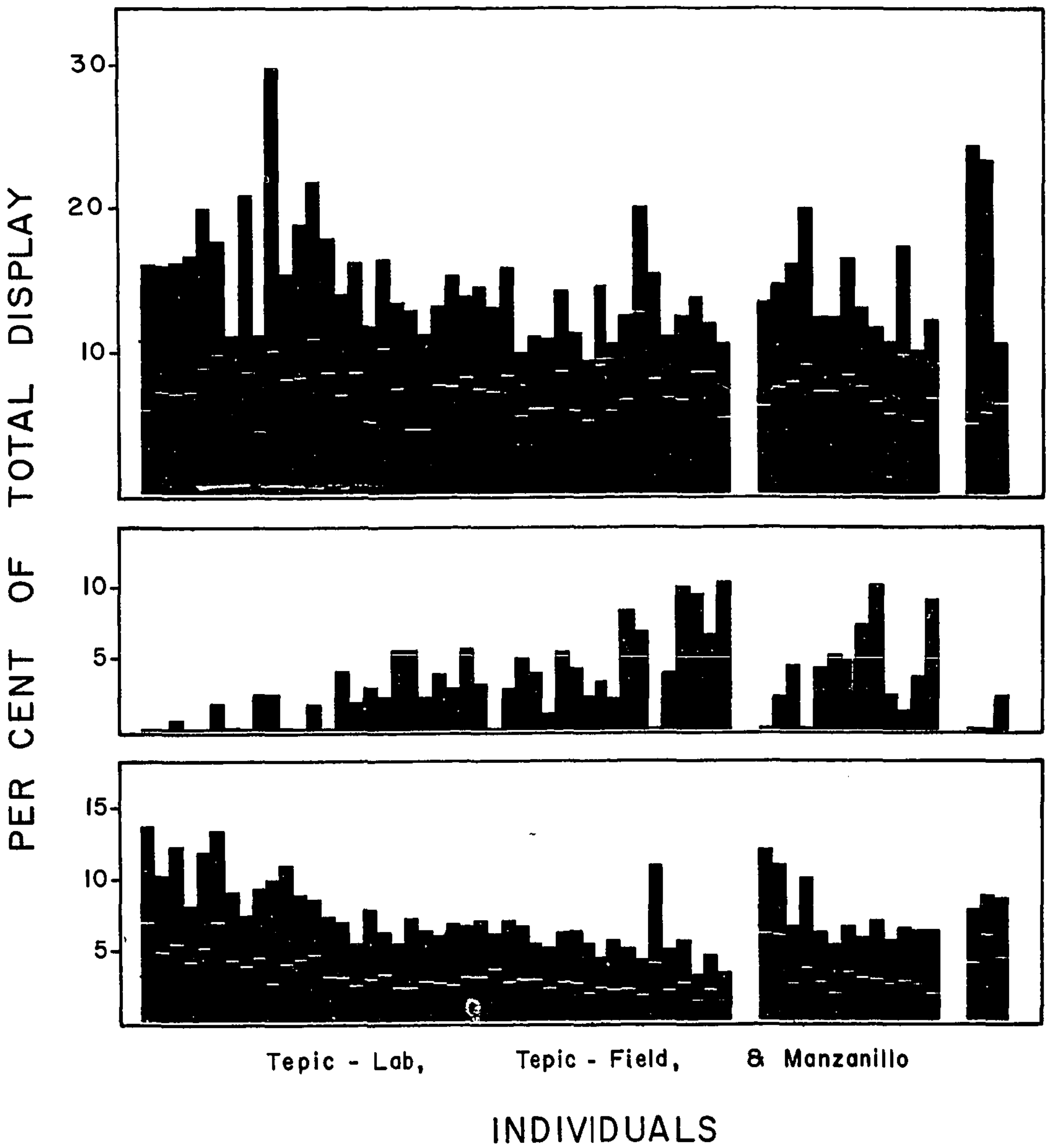

PER CENT OF TOTAL DISPLAY
40
30
20
10
20
10
UNIT 4
UNIT 3
Tepic - Lab, Tepic - Field, & Manzanillo
INDIVIDUALS

Fig. 25. Units of the <u>Anolis nebulosus</u> assertion display (expressed as percent of total display) presented for 43 lizards collected in Nayarit, Mexico, and filmed in the lab (Tepic-Lab); 13 lizards collected in Nayarit, Mexico, and filmed in the field (Tepic-Field); and 3 lizards collected in Colima, Mexico (Manzanillo). Within each block the mean values are given for the fastest displaying anole on the left to the slowest displaying anole on the right.


PER CENT OF TOTAL DISPLAY
30
20
10
UNITS 8 & 9
10
5
UNIT 7
15
10
5
UNITS 5 & 6
Tepic - Lab, Tepic - Field, & Manzanillo
INDIVIDUALS

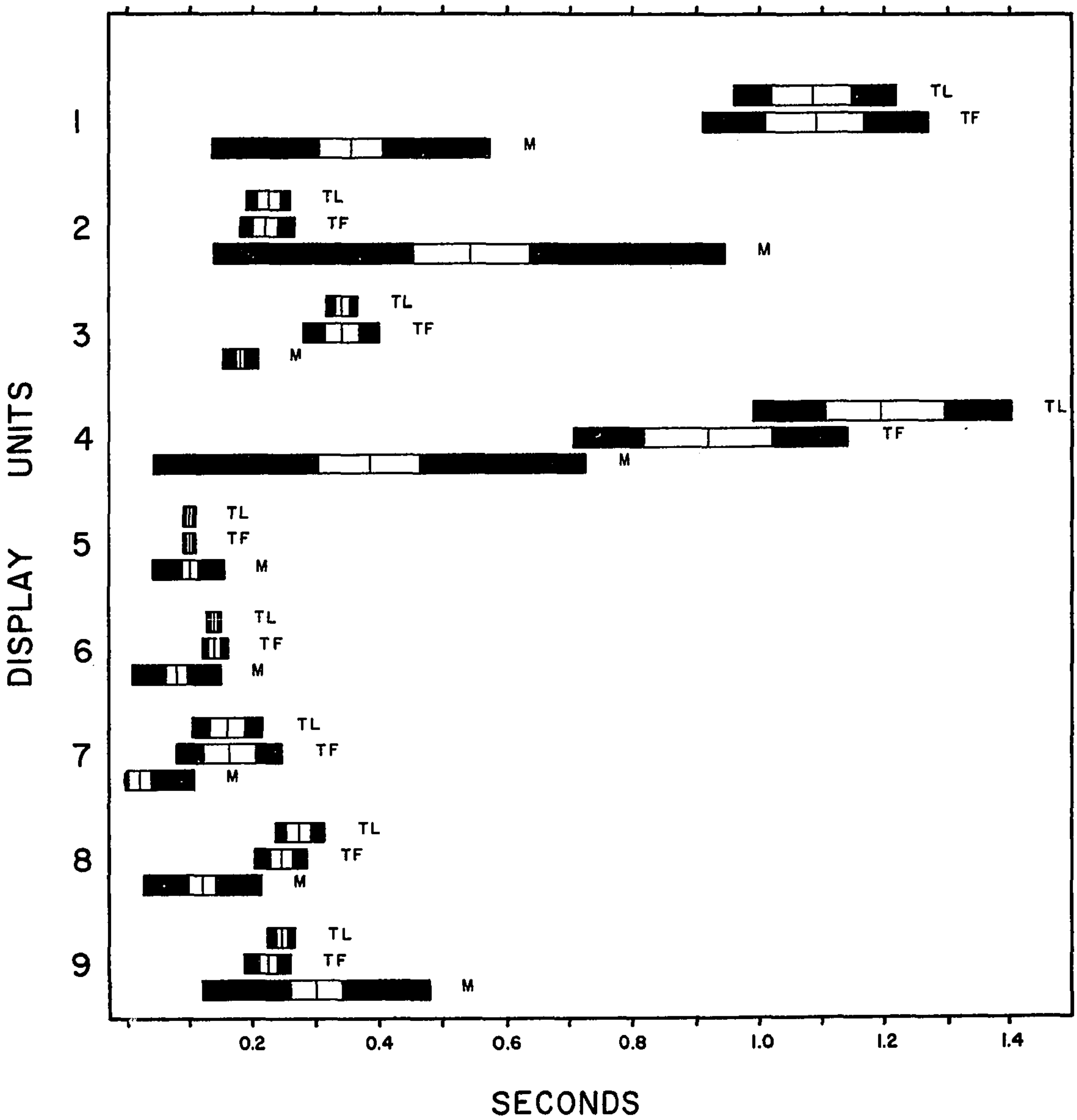
Four generalizations appear from this analysis. First, the initial two units proportionally increase as the total display gains in duration and thereby maintain their percent importance. Second, those units containing dewlap movement (3, 5, 6, 8, and 9) tend to have reduced percent importance as the display lengthens. This is partially attributed to a relatively constant rate of extension and retraction of the throat fan irrespective of display duration. Third, Unit 7 is non-existent in the displays of most lizards which perform quickly. The percent importance of this waiting period between the dewlap pulses only appears and increases as the display concomitantly lengthens. Last, as a display increases in duration, the majority of the added time is taken up by Unit 4.

Effect of environment upon the display

Lizards from the same population were filmed in both the laboratory and the field to ascertain if any behavioral abberation occurs to the display of confined animals. Fifty-six displays were recorded in the field from 13 male anoles. These display records were compared with 458 lab-filmed displays taken of 43 additional lizards.

Statistical comparisons of the field-filmed group with the lab-filmed group revealed very little difference (Fig. 26). Only Unit 4 varied to any extent and the difference was not significant. The raw times for the field displays, as well as their individual units, were distributed within the range of times recorded for lab displays; Unit 3 was the only exception (Tables 14, 20). No significant differences were evident when the units were expressed as a percentage of the total displays and compared on an individual basis. The unit percentages for field animals likewise fell within the range of corresponding lab derived values with the exception of

Fig. 26. Duration of the units of the <u>Anolis nebulosus</u> assertion display from 43 lizards collected in Nayarit, Mexico and filmed in the lab (TL), 13 lizards from Nayarit filmed in the field (TF), and 3 lizards from Colima, Mexico (M). Ends of outer black bars give 95% confidence limits of the mean, medial vertical line of bars is the mean, ends of the inner white bars represent the standard error of the mean.


DISPLAY UNITS
1
2
3
4
5
6
7
8
9
TL
TF
M
0.2
0.4
0.6
0.8
1.0
1.2
1.4
SECONDS

individual No. 4 from the field whose third unit was again the largest of the lab-field samples (Tables 16, 22). Few differences were seen when the averages for the units of each sample were converted to percentages and compared (Table 11). The similarities of the units from field-recorded displays to the lab-filmed displays are obvious (Fig. 23, 24, 25).

Table 11. Mean unit values (expressed as percent of the total display) for sample of Anolis nebulosus -- 43 lizards from Nayarit, Mexico, filmed in lab (Tepic Lab), 13 lizards from Nayarit, filmed in field (Tepic Field), 56 lizards pooled from Tepic Lab and Tepic Field (Tepic Lab-Field), 3 lizards from Colima, Mexico (Manzanillo), and 10 lizards with fastest displays from Tepic-Lab-Field group (Tepic Fast).

Unit Number	Tepic Lab	Tepic Field	Tepic Lab-Field	Manzanillo	Tepic Fast
1	30.7%	31.6%	31.0%	12.8%	29.8%
2	5.5	6.4	5.7	27.6	7.3
3	8.8	9.8	9.0	9.2	12.7
4	31.2	26.7	30.2	19.4	22.2
5	2.6	2.9	2.7	5.9	5.2
6	3.6	4.0	3.7	4.0	5.8
7	4.1	4.7	4.2	1.0	0.6
8	7.1	7.3	7.1	5.9	7.4
9	6.4	6.6	6.4	15.2	9.0

From observations and analysis of filmed displays, there were no observed differences in the display patterns of lab-held animals as compared to those under natural conditions in the field.

Comparison of inter-population displays

There was a major difference between the displays of *A. nebulosus* collected near Tepic, Nayarit and those from Manzanillo, Colima. Units 1 and 2 were in reversed order when comparing the two populations. The first unit of the Tepic display was longer than Unit 2. This situation was inverted in the Manzanillo display (Fig. 20, 23, 24, 25, 26, and Table 11). Unlike the lizards from Tepic, Manzanillo A. nebulosus produced more head bouncing after the second head nod than after the first; no exceptions to this were observed.

There were also minor variations between the displays of the two populations. However, since the Manzanillo population is represented by only three lizards, some caution must be employed when generalizing for this population on more subtle display characteristics.

The three Manzanillo males had quick displays averaging 2.08 seconds duration as compared with a 3.76 second mean for the Tepic anoles. However, a few individuals from Tepic had displays as fast as the Manzanillo ones (Tables 14, 23). Most of the differences between the two populations appear related to the speed of the display, for as the duration of the various displays decreased, the units became crowded together with some unit percentages decreasing disproportionally (Tables 16, 25). The effect of display speed upon the percent importance of the units for the two populations was estimated by comparing 10 of the fastest displaying anoles from Tepic (mean display duration of 1.90 sec.) with the Manzanillo lizards (Table 11). The quickness of the display appeared responsible for the population differences of Units 4, 5, 6, 7, and possibly 8 and 9. As mentioned previously for the Tepic DAP, as display increased in duration, the unit percentages tended to increase for Units 4 and 7 and decrease for those units involved in the dewlap pulses (3, 5, 6, 8, and 9). These trends seemed to explain most of the Tepic -

Manzanillo display differences.

The important distinction between the displays of lizards from the two populations is the transposition of Units 1 and 2. This constitutes an alteration in the sequence of the motor patterns and, therefore, produces a pattern unique from the Tepic display. Since all observed anoles from Tepic performed an identical display-action-pattern, it is highly probable the three males from Manzanillo accurately reflect a generalized DAP typical of their population.

Salient to this comparison of inter-population behavior is the discovery that every Manzanillo male possessed a broad white band on the anterior margin of his dewlap; this pattern was not present in the Tepic specimens. A careful morphological examination may disclose further differences between these populations. Here, then, is an example of divergent behavioral and morphological characteristics between two very closely related populations. This situation is an excellent case in point for the usefulness of the saurian display as an additional criterion for taxonomic determinations.

Hobart Smith (personal communication) believes _A. nebulosus_ is actually a complex rather than a single species. The data presented here would support Smith's contention. It is most probable that display analysis can play an important role in delineating subspecific and possibly specific taxonomic differences when future attention is given to _A. nebulosus_.

Individual variation

Besides temporal variations, other aspects of the Tepic display varied among individuals. The head nodding was a good example of different variations of the same behavioral theme. This behavior sequence is covered by

Unit 1, the interval between the two head jerks, and part of Unit 2, the portion of the display from the second head jerk to the start of the first dewlap retraction. Comparisons between lizards showed a wide range in the number of head bounces following the head jerks, though all Tepic lizards produced more head bouncing after the first head jerk than after the second (Fig. 27). Those displays whose first two units were of long duration contained the greatest number of head bounces. Averages for 43 lizards showed 4.1 bounces after the first head jerk and 1.4 bounces after the second.

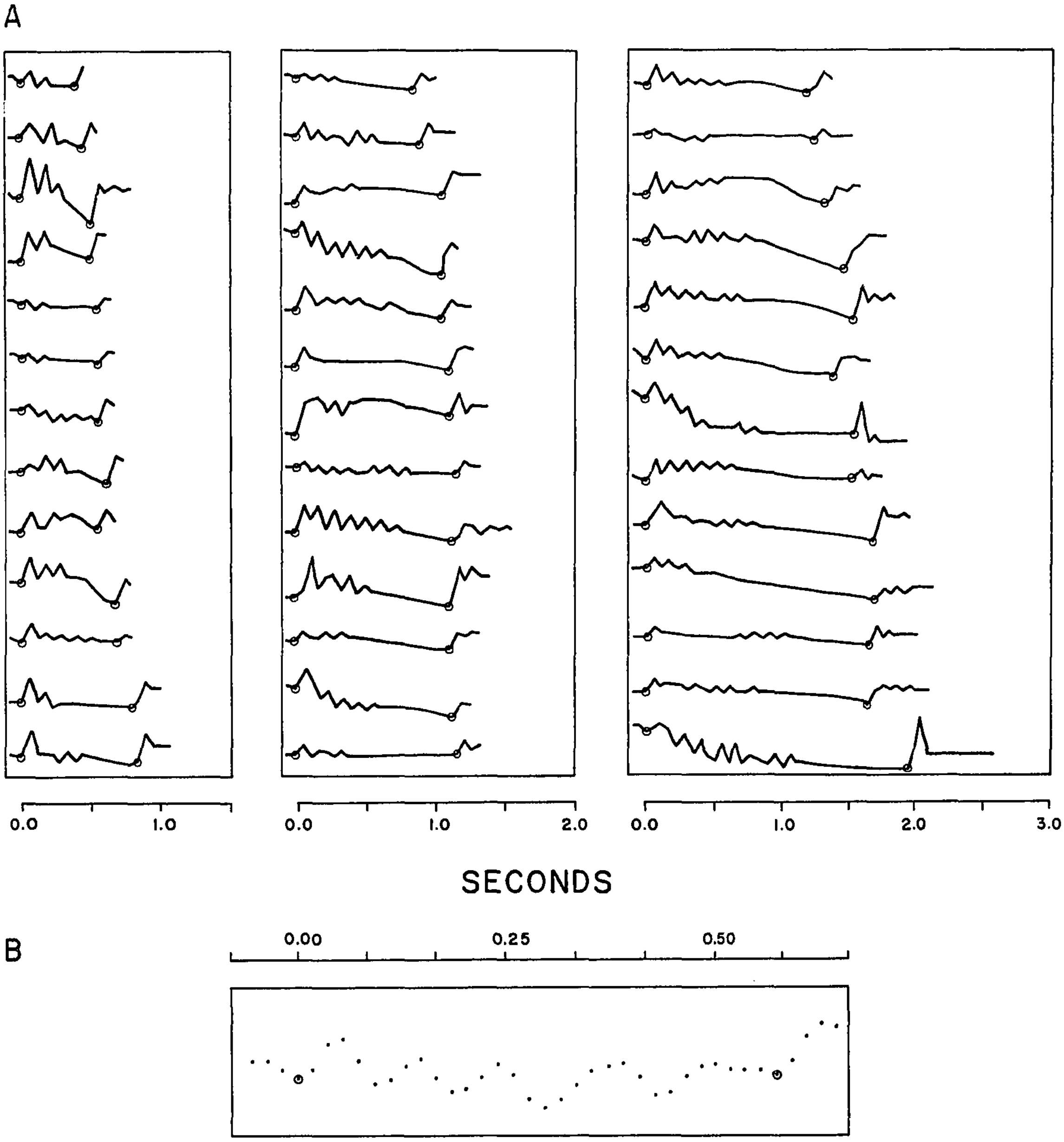
There was also a large variation in the deflection of the head during head nodding; this behavior ranged from shallow to very exaggerated nods. From film analysis it appeared that each lizard possessed an amplitude characteristic for itself. However, precise quantification of head amplitude from the films was impractical since camera angle, distance from camera to object, and size of lizards were never exactly the same.

The tracings made from the display films of each lizard's head nods (Fig. 27) were taken from sequences shot at 18 f.p.s. This filming speed caused the head bounces to graph as spikes. When filming at 50 f.p.s., however, the head bounces of even the fastest displaying lizard were shown to be rounded waves (Fig. 27b).

The amplitude of the two dewlap pulses was also a source of individual variation. From a sample of 43 lizards, 72.1% performed displays with the second pulse of greater amplitude than the first. A few lizards (16.3%) gave pulses of approximately equal extension. Least common (11.6%) were lizards with displays having the first pulse of greatest amplitude.

The initial dewlap extension during the head nods was always of greatest amplitude. This amplitude was arbitrarily considered as 100% for purposes

Fig. 27. DAP graphs for Unit 1 and part of Unit 2 of the *Anolis nebulosus* assertion display from lizards collected near Tepic, Nayarit, Mexico. a. -- traced from displays filmed at 18 f.p.s. b. -- traced from display filmed at 50 f.p.s.


A
0.0
1.0
0.0
1.0
2.0
0.0
1.0
2.0
3.0
SECONDS
B
0.00
0.25
0.50

of comparing the magnitude of the subsequent dewlap pulses. Using a millimeter rule, measurements of dewlap extension were taken off the display films during frame-by-frame analysis. The difference between the tangential distances from the edge of the relaxed dewlap and the edge of the extended dewlap to a body marking on the throat provided these measurements. The value obtained from the initial dewlap extension was divided into each of the dewlap pulse measurements and expressed as a percentage. It was found the first dewlap pulse averaged 67% (S.D. ±10.4%) of the initial throat fan expansion and the mean percentage of the second dewlap pulse was 81% (S.D. ±8.0%).

Male and female displays

The female *A. nebulosus* has a diminutive throat fan in comparison with the male. Her dewlap is also a different color, being of pinkish hue. From many observations it was found the females used their dewlaps frequently and in the same manner and during similar social encounters as the males (Chapter III). Upon inspection of the filmed assertion displays from 7 females of the Tepic population, no differences were found from the generalized DAP determined for the males. It appears that the display is population-typical for both males and females of the Tepic area.

Discussion

The objective of this display analysis was to determine how specific the assertion display pattern is for a population of lizards. It was found that there was a considerable difference in the length of the display by the various lizards. Each individual, though, performed its own display with amazing consistency. But more important, the population shared without exception a common display pattern. The various motor acts which compose this behavior pattern were present in the displays of all members of the population and were ordered in a rigid sequence. A very few lizards occasionally gave an altered version of the generalized pattern, but they were also observed displaying normally. Though this study did not investigate the possible existence of a genetic basis for the display, it did establish that the Tepic population of A. nebulosus possessed a stereotyped display (Fig. 28). Such a stable characteristic should be of taxonomic value.

The assertion display is a low intensity display given frequently by the territorial male as he moves about from perch to perch. It was by far the most common stereotyped behavior observed in the field, while high intensity agonistic encounters and their concomitant challenge displays were infrequently observed. There is also some evidence that the female of the species uses the assertion display of the male as a means of mate selection (Chapter V). This suggests the assertion display may be genetically determined and can act as an isolating mechanism for sympatric species. Hence, this display would tend to be consistent and unique for at least a population.

In contrast, the challenge display (associated with male - male encounters at close range) is much more complex than the assertion display and seems to be a composite of several different act systems. During strong agonistic encounters, the males occasionally reared back on hind legs and tail and rocked back and forth with dewlap extended; this never occurred in the assertion display. Challenging males also performed a high intensity assertion display, frequently preceded by several head bows. The male - male interactions produced a number of behavior patterns which appeared in various combinations. Though these combats were ritualized for the most part, there was nevertheless sufficient improvisation to create a confusing amount of variability.

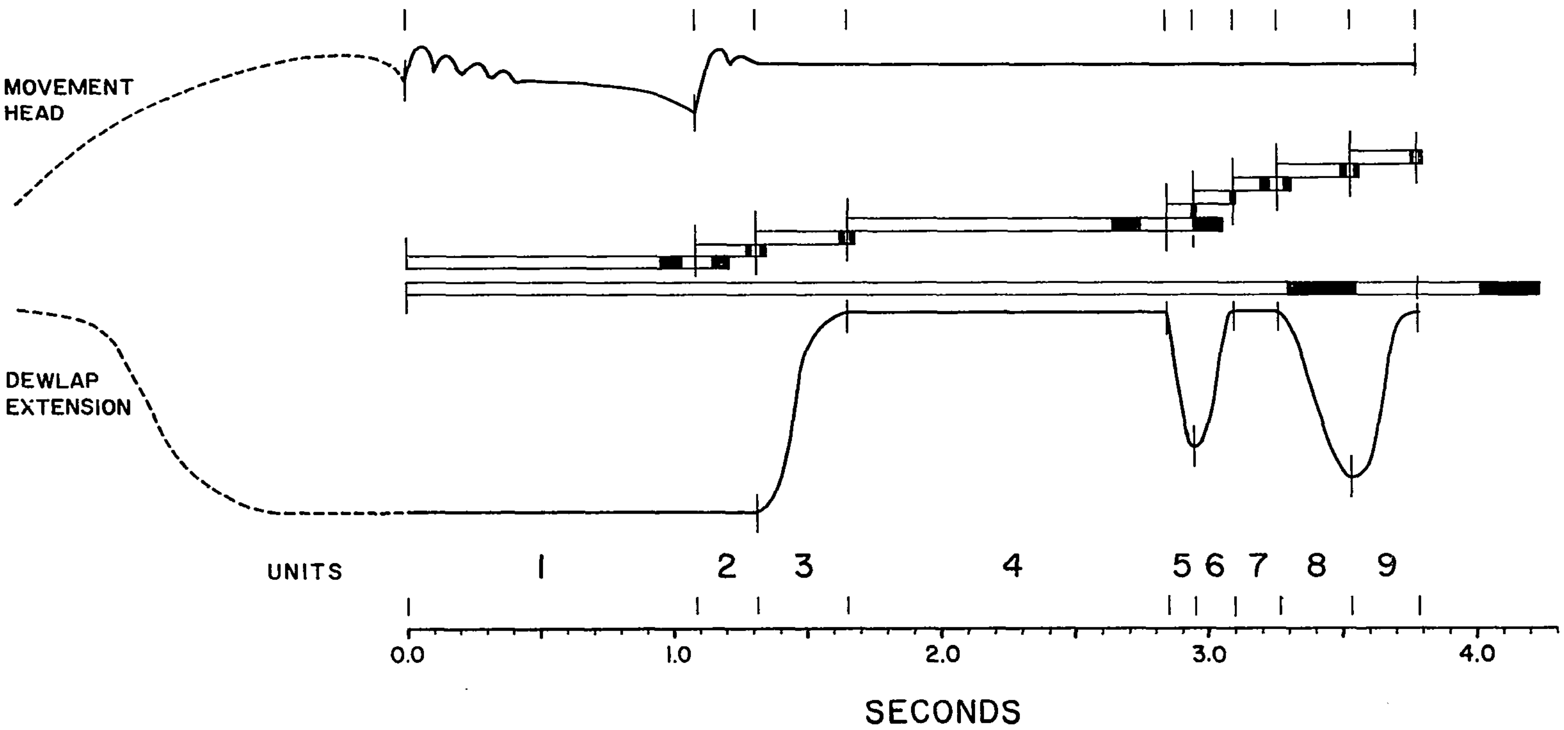


Fig. 28. DAP graph of the Anolis nebulosus assertion display derived from statistical analysis of 458 displays from 43 lizards collected 35 kilometers east of Tepic, Nayarit, Mexico. Bars indicate duration of each display unit, outer ends of black bars give 95% confidence limits of the unit mean, medial vertical line between black bars is the mean, ends of the inner white bars represent the standard deviation of the mean.

Garcea and Gorman (1968), Gorman (1968), and Ruibal (1967) made comparative behavior investigations of anoles in the West Indies. It was their intention to evaluate the applicability of the displays to anoline systematics. Ruibal restricted his behavioral comparisons to the intital reaction of territorial males to a tethered lizard. From his data presentation of the 12 studied species, there seemed to be a great amount of variation in the incipient response which he labeled the "threat display". Consequently, Ruibal (1967: 136) concluded "the analysis of the initial response in these anoles demonstrates that the behavioral patterns are of limited value in determining relationships within the West Indian species of Anolis." By using only the most intense response, which in the present study of A. nebulosus was found to yield considerable variability, Ruibal undoubtedly prejudiced his study and did not do justice to the potential of display analysis.

Gorman (1968) also studied the male challenge displays. Unlike Ruibal, he used the entire challenge behavior and found sufficient trends in the roquet group of Anolis to recommend the use of behavior in anoline systematics. However, his data, like Ruibal's showed large variability for a species. Surprisingly, Gorman relied heavily on the measured time of the various types of movement components within the challenge sequence to derive his comparative data. As seen in the analysis of A. nebulosus, the raw times were the most variable aspect of the assertion display.

From the descriptions given by Gorman (1968: 9) of the roquet group, it appears that the agonistic behavior of his studied species share many behavior patterns in common. Their challenge behavior has a sequential ordering as follows: (1) extend dewlap, (2) rise high on all four limbs, (3) raise tail, then lower it, (4) lower the body, (5) give rapid head bob,

(6) retract dewlap. This pattern is also similar to the A. nebulosus challenge behavior with a few modification. In the latter species the males (1) extend dewlap, (2) rise high on the hind legs and tail, (3) curl tail up and rock bodies backwards and forwards, (4) fall back onto all fours, (5) give an exaggerated assertion display, (6) lower head and retract dewlap. In the sequences for A. nebulosus and the 8 members of the roquet group, these six steps were not always present in every encounter. But no matter which behavioral components were present during a particular challenge, they were observed to retain the order outlined above. However, this behavioral arrangement still presents considerable variation between the behavior patterns of any two challenge encounters of the same species and even of the same individuals. The challenge display, then, does not seem to readily lend itself to species differentiation.

The similarities in the challenge displays found within the roquet group suggest that this behavior may be useful in comparing higher taxa within the genus such as species groups rather than distinguishing separate species. For example, there was a basic difference in the challenge sequence which set off A. nebulosus from the species of the roquet group; A. nebulosus rear up on the hind legs and tail while the roquet species go up on all four legs.

Similarities in aggressive behaviors of related species are not surprising. From studies of avian behavior where much more work has been done, it is known that many passerine families use the same head-up posturing as a fight signal (Marler and Hamilton, 1966: 375). Miller (1968: 62) does not believe it is merely fortuitous that sympatric species share many behavior patterns. The retention of behavior patterns which are common to competing species permits interspecific communication and is an effective mechanism in the process of competitive interference. It seems the challenge display of anoline species may be analogous to these agonistic signals in birds.

The assertion display, on the other hand, may possibly have evolved as an isolating mechanism, functioning primarily between members of the same species. Taxonomically, this display seems well adapted to distinguish between individual species and subspecies, but may have little phylogenetic bearing beyond comparisons of near relatives. Sibley (1957: 187) pointed out that those characters which are seemingly selected for strong specific distinctiveness, particularly in sexual dimorphic animals, are actually species characteristics. As such, these features lose their systematic value above the specific or generic level.

In widely distributed species of lizards, population differences in the species display may also be quite large. This appears to be the situation in Uta stansburiana (Ferguson, 1969a), and may very likely apply to A. nebulosus. Ferguson found the push-up display (DAP) of Uta was less variable within populations that between populations. These differences were large enough for him to consider the displays useful for subspecific diagnosis. Ferguson's study showed that geographic variation in the display can be of sufficient magnitude to preclude the use of "species-specific" as applied to a single, representative display pattern for a species.

CHAPTER V

DISPLAY FUNCTION IN MATE SELECTION

Introduction

Lizards of the family Iguanidae possess stereotypic behavior which many times incorporates sexual dimorphic color patterns and structures. In Anolis the large size and spectacular coloration of the dewlap is characteristic of the males; Etheridge (1959: 74) listed a few exceptions. The dewlap functions as an integral part of the anoline display which undoubtedly is used as a means of communication. However, the type of information conveyed by these visual displays and their social significance have long been subjects of speculation.

Investigation of the function of lizard displays in mate selection have been restricted for the most part to purely observational data. In his The Origin of Species, Darwin reasoned that the development of sexual dimorphism in males was caused by females choosing to mate with those males having the most prominent ornamentation. Following this hypothesis, Mertens (1926) suggested that the large and brilliantly colored dewlaps of male anoles serve to attract females to their own species. This idea had a large following. However, from their observations of lizard courtship and mating, Noble and Bradley (1933: 86) stated that the bright colors of the male anoline dewlaps evolved as a frightening device, and do not stimulate the female to mate.

Evans (1938a, b) disagreed with the latter interpretation, believing the male display of Anolis sagrei and Anolis carolinensis is very important in sexually stimulating the female.

Actual attempts to experimentally test the effect of the male's display-action-pattern (DAP) upon the female have been few. Only the investigations of Greenberg and Noble (1944), Harris (1964), and Hunsaker (1962) have contributed to this area of study. Much more objective data must be gathered before a realistic appraisal can be made of the role, if any, of the male's display in mate selection.

In the present study a film loop technique was implemented which has advantages over methods used by previous investigators. Female Anolis nebulosus were presented two color films duplicated from the same sequence of a displaying male. One of the film duplicates, however, was altered so that it no longer portrayed the DAP characteristic of A. nebulosus. The choices made by the female anoles to the projected displays provided insight into the display's social significance as will be discussed in this section. The film loop technique described here for the first time has wide application for the behaviorist as a tool for future experimental studies.

Methods and Materials

Before initiating a study to evaluate the function of a behavioral pattern, it is obvious the investigator must know the dynamics of that pattern. From a thorough analysis of the display characteristics of a population of A. nebulosus, a reliable estimate was available for the variability in this population's display. Such an estimate is mandatory if the basic display is to be altered for experimental purposes; otherwise there is no point of reference for comparing the changed display with the normal condition.

Five male and 31 female <u>A. nebulosus</u> used in the following experiments were collected from the same population 35 kilometers east of Tepic, Nayarit, Mexico, during the spring of 1967 and 1968. The sexes were held separately in 4 x 4 x 3 foot enclosures. During most of the year the males had to be kept in the dark or else a large number would have been lost due to territorial fighting.

<u>Experimental apparatus</u>

A frame was designed to hold a 16 mm cinema projector and three flanged idler wheels which were to support the film loop (Fig. 29). Two of these film loop frames were constructed of three-eighths inch plywood. They were placed at both ends of a 6 x 2 x 2 foot enclosure. Fitted around an angle iron frame, a glass panel composed the front wall, sliding screen wire doors formed the top, and the remaining sides of the observation chamber were made of masonite (Fig. 29). Rear projection screens were fitted to the ends of the chamber where the film loop frames were positioned. Sand on the floor, a centrally placed release box and water dish, and oak leaves with a few branches at both ends by the projection screens comprised the internal appointments of the observation cage. A 4 x 4 x 5 foot blind was also constructed. To ensure absolute concealment of the observer, the blind was light proofed except for several short three-eighths inch wide observation slots. A flashlight furnished the needed light for note taking. Within the blind were switches to control the running of the projectors.

Two Bell and Howell 16 mm Analyst projectors (Model 173) were used with the film loops. This model projector allowed considerable flexibility.

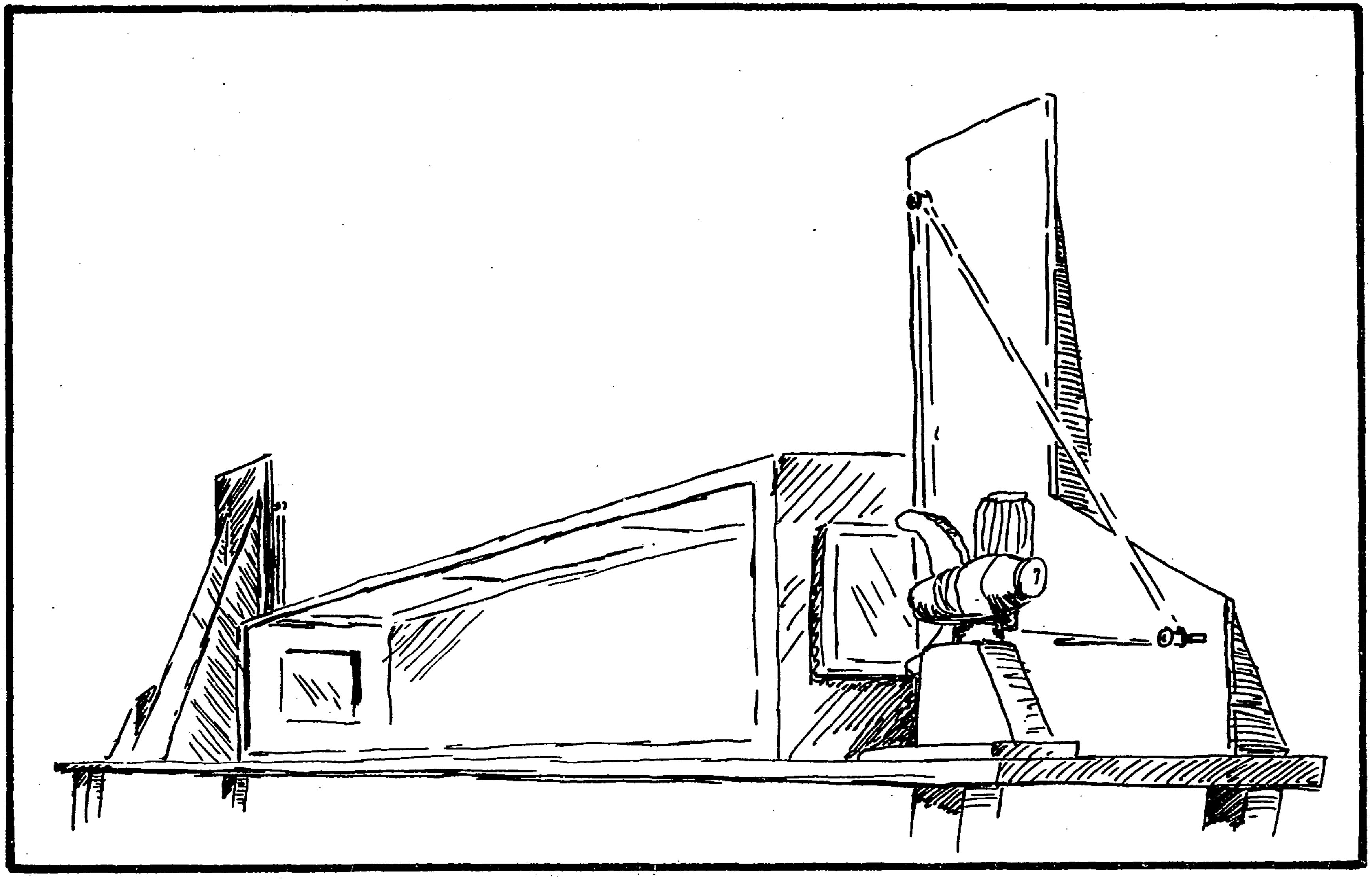


Fig. 29. Film loop apparatus.

The projection speed can be varied from approximately 6 to over 24 frames per second by means of a calibrated rheostat. Still, forward, and reverse projection are possible. An iris in one of the projector's lenses permitted the illumination of the projected displays to be matched so that no bias resulted from one image being brighter than the other. The size of the projected images were also matched by adjusting the distance of the projector from the screen.

The film sequence which was used as the standard stimulus in all film loop experiments was taken with Kodachrome II indoor film at 24 frames per second. This sequence was of a large male performing an assertive display from a simple perch. During the filming the lighting was set so that only the subject was illuminated and the background remained unexposed. Thus, when the resulting film was projected upon a dark screen, a "framing" effect was eliminated and only the lizard and his perch were seen. A few branches were placed under the projected image, producing an exceedingly realistic effect. In addition, the screen itself was set into the enclosure's wall an inch to enhance the three-dimensional illusion.

A number of duplicates were made from the original filmed display. From most of these copies, alterations of the original display were produced. These altered displays were created by adding and/or removing certain parts of the display. The resulting film strips were again duplicated to eliminate the splices. Each film loop was constructed by splicing together the ends of a filmed sequence and threading it onto the film loop apparatus.

Methods evaluation

Some theoretical considerations should be given to the feasibility of using motion pictures in behavior studies. The illusion of motion obtained from a rapid progression of separate pictures results from the visual system fusing these photos into a continuum. The particular point at which the eye no longer sees individual pictures or flashes is known as the critical fusion frequency (CFF). This is a characteristic phenomenon of the visual system which has been known for some time (Landis, 1953).

Although much data concerning the flicker fusion phenomenon have been gathered (Henkes and van der Twill, 1964), there are very few reports of its manifestation in lizards. Crozier and Wolf (1939, 1941) determined the CFF for the gecko Sphaerodactylus inagual, (rod retina) and for the horned toad, Phrynosoma cornutum, (core retina); their critical fusion frequencies were 27 and 56 hertz, respectively. Conceivably, the CFF for Anolis is near the 56 hertz threshold found for the horned toad since members of both genera have many retinal features in common (Walls, 1942).

The number of hertz produced by the projection apparatus is of the utmost importance. The Bell and Howell projector used in the present investigation has a partial disc which rotates in front of the film gate aperture. The partial disc is geared so that each frame shown by the projector is interrupted or flashed three times. Thus, a film running at 24 frames per second, as was the case in these experiments, is flashed onto the screen at 72 hertz. This frequency is greater than the CFF for Phrynosoma cornutum and presumably greater than the CFF of A. nebulosus. It is highly probable the experimental animals of the present study were perceiving a moving image.

Another important consideration of anoline vision deals with color. Not only do their retinas contain large numbers of cones (Walls, 1942), but Tansley (1957: 97) reported that A. carolinensis can discriminate hues. Therefore, color film was used in attempting to create a realistic stimulus.

However, a major problem encountered in utilizing a cinematic stimulus is the lack of a three dimensional image. This is particularly relevant to anoles. Underwood (1951) found the eyes of Anolis lineatopus, grahami, and opalinus possess two foveae, a feature shared only with some birds. The largest fovea is located centrally in the retina and is the area of fine vision during monocular operation; this is the primary mode of sight. The more shallow temporal foveae are used for binocular vision. A similar situation is described for Anolis carolinensis (Polyak, 1957). Therefore, it is very likely A. nebulosus can also perceive depth. To what extent this limitation of the experimental technique decreased its effectiveness cannot be evaluated; however, behavioral observations did show the animals responded to the image as if it were real.

To evaluate the effectiveness of the film loop technique, five preliminary tests were made using male A. nebulosus. The territorial male makes a good subject as a very predictable agonistic behavior pattern is evoked in him by the presence of a displaying male. The appearance of the aggressive behavior indicates the male believes he has an adversary; this behavioral indicator was established as the criterion for the film loop's success.

In the preliminary tests a male was placed in the observation chamber where after a short time he selected a particular habitat at one end of the chamber. After a 24 hour period, the normal display was projected onto the screen across the enclosure from the resident male. Almost immediately he responded in a manner characteristic of aggressive encounters. The nuchal crest rose, his body became laterally compressed, the gular area was inflated slightly, and the light and dark areas of his body pattern became more contrasted. The male oriented himself laterally to the displaying image across the cage and either flagged or gave the complete assertion display (Fig. 15a). All five males involved in these tests crossed the cage, displaying on the way, and reached the illusionary lizard. Two males actually leaped at the "challenging male" on the screen.

The filmed sequence of a displaying lizard appeared to be an effective substitute for the actual animal. The advantages of the film loop, many of which are yet to be exploited, are the control of: (1) the sequential order of the units within the behavior pattern by means of splicing techniques, (2) the image size, (3) the speed of the behavior, (4) the initiation and repetition of the behavior, and (5) the general color of the image via use of black and white film and colored filters. In addition, one has an exact replication of the animal and its behavior which is more accurate and much easier to produce than building an animated model of the species.

Experimental procedure

Twenty female lizards were used in each of the experiments with the exception of the last (a number of lizards escaped from the holding cage prior to the fourth experiment and only 18 females were available). Before the run, each female was held in the release box for 15 minutes. The door to the box was then slid open. Upon emergence the film loops were shown and the experimental animal was allowed 45 minutes to reach the habitat at either one end of the enclosure or the other; such a move constituted a choice, otherwise the trial was scored as no choice.

During the duration of each trial, two film loops were employed. Every run was made with the normal display as well as with an altered film loop. The projectors were not run simultaneously, but were alternated. Two display sequences were shown first from one projector and then two displays from the other. This continuous alternation between projectors proceeded irrespective of the experimental animal's behavior.

From some preliminary tests, it was found that the addition of a clump of moss just in front of the release box was of great benefit. Without the moss, females emerging from the box onto the sand substrate spent little or no time examining their surroundings, but rather bolted for the oak leaves distributed at the ends of the enclosure. With the moss present, the female lizards spent several minutes in this semi-protective cover at the center of the cage. This behavior allowed them time to observe both displays.

Two experimental designs were established for the four experiments. The first experimental design (Fig. 30) was used with Expt. No. 1, while Expt. No. 2, 3, and 4 followed the second design (Fig. 31).

Experiment No. 1 -- Each of 20 females was given three consecutive trials with a 15 minute rest period between runs. Two normal displays were presented, except one was shown in reverse sequence (Fig. 32c). After each trial the projectors' polarities were switched so that the backward display never appeared on the same screen twice in succession.

Experiments No. 2, 3, and 4 -- In these experiments each female ran only one trial per experiment. During each experiment the altered display was projected onto one screen for the first half of the trials and then switched to the opposite screen for the remaining females. The film loops used in these experiments were as follows: Expt. No. 2 -- normal display (Fig. 32a) and display containing no head nods and six dewlap pulses (Fig. 32d), Expt. No. 3 -- both loops were of normal display, and Expt. No. 4 -- normal display and display with only one dewlap pulse eliminated (Fig. 32b).

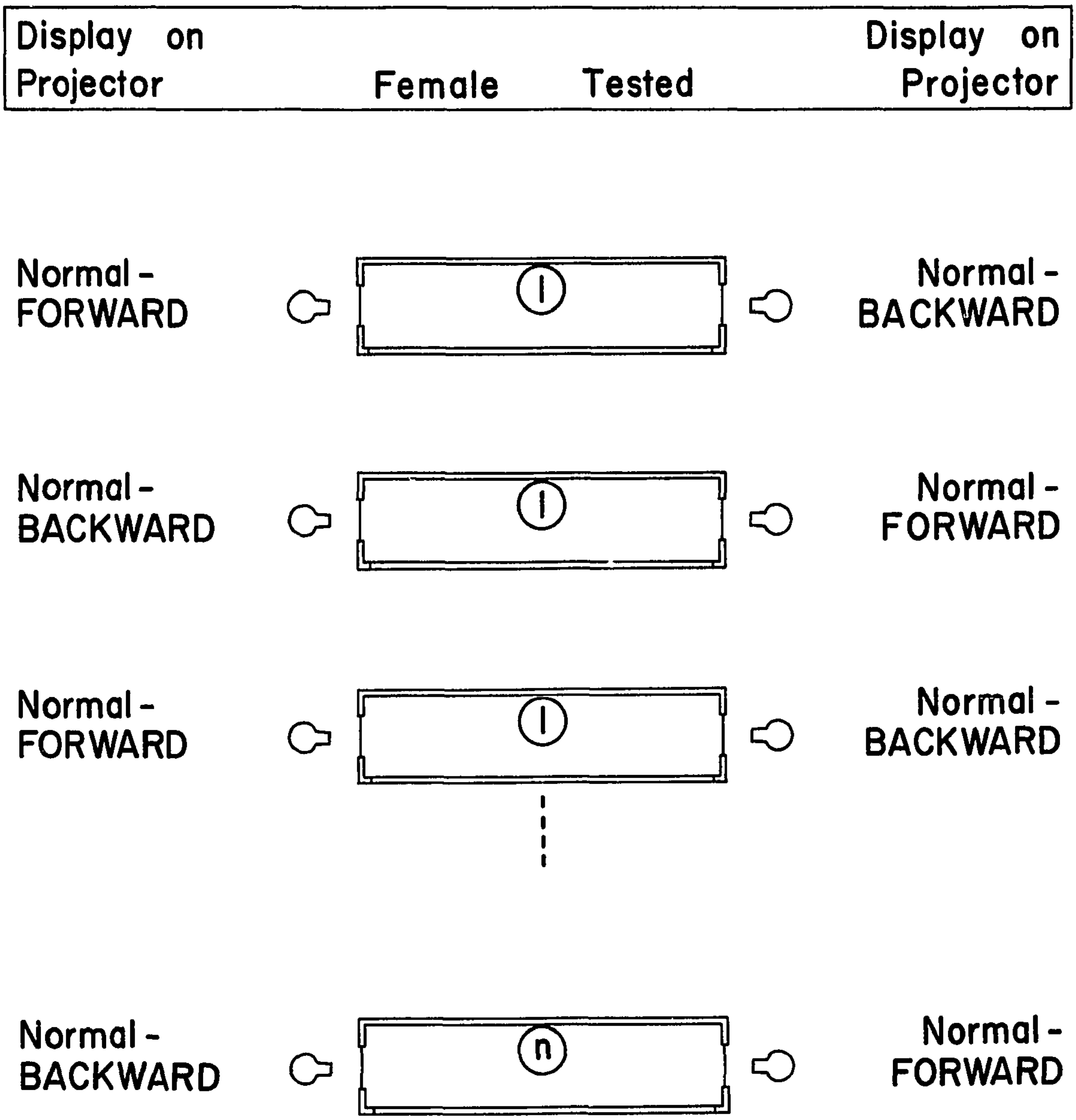


Fig. 30. Experimental design for first experiment; see text for explanation.

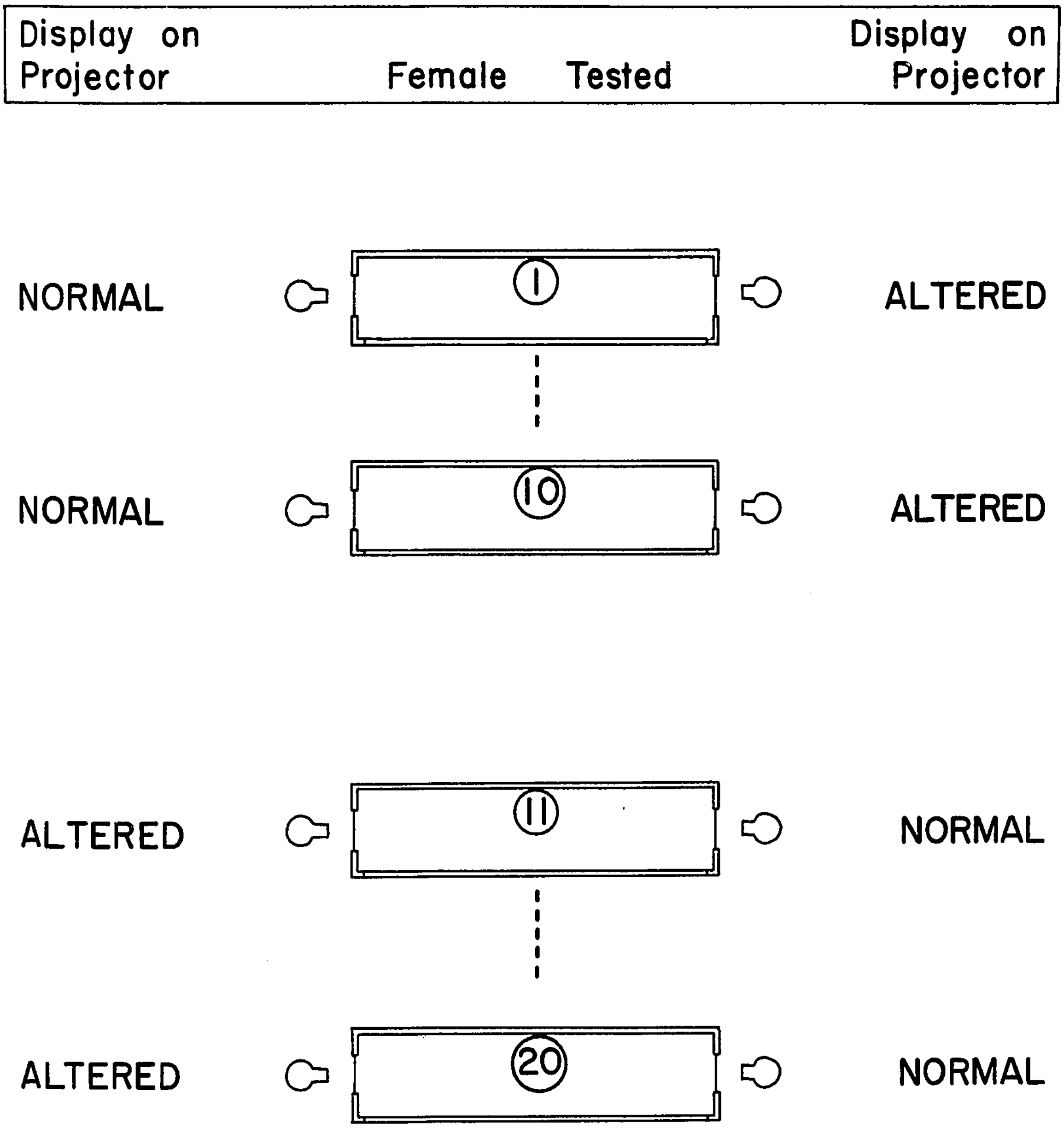
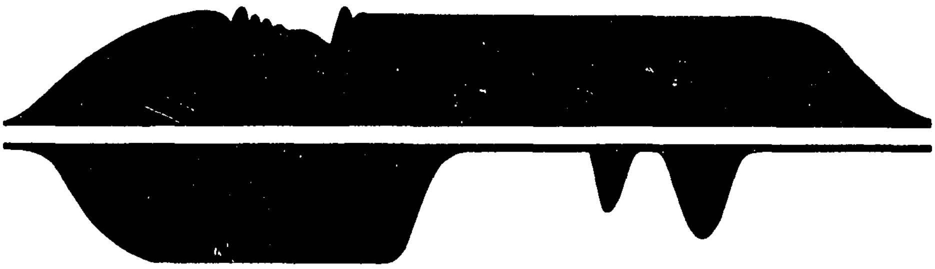


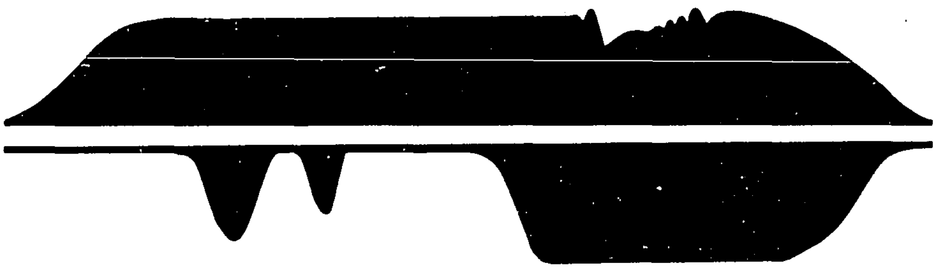
Fig. 31. Experimental design for second, third, and fourth experiments; see text for explanation.

Fig. 32. Display patterns used in film loops during mate selection experiments with female Anolis nebulosus. Upper block represents amplitude (vertical axis) and duration (horizontal axis) of head movement and lower block represents dewlap movement. a. -- normal display; b, c, d. -- altered displays.

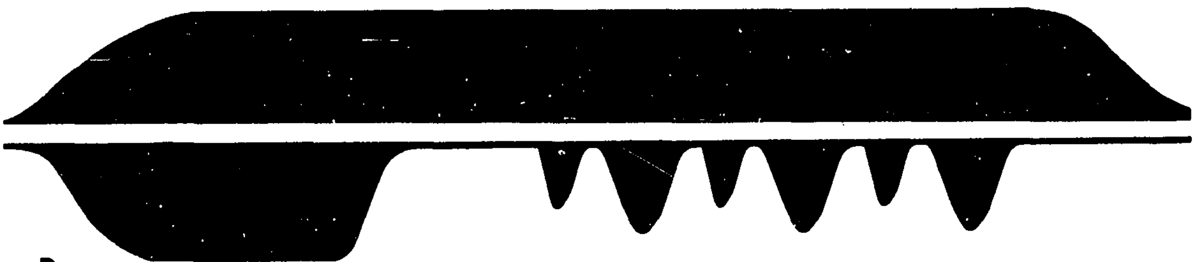


A

B



C



D

Results

Female A. nebulosus were shown two filmed sequences of displaying males of their own species. With the exception of Expt. No. 3, one of the two projected displays was an alteration of the normal behavior pattern. The females were allowed to choose between the displaying images. The results of these experiments and their statistical significance are summarized in Table 12.

In Expt. No. 1 the altered display was a normal film loop run backwards. On the initial trial 14 females chose the habitat of the normally displaying male while only 5 females entered the habitat of the image giving the reversed display. This 2.8:1 ratio (females toward normal display : females toward altered display) was statistically significant at the 5% level as analyzed both by the Chi Square method and from the expected frequencies of a binomial distribution.

When the reversed display was switched to the opposite end of the enclosure for the second trial, a much more even split was observed (1.6:1). The ratio increased to 2:1 in the third trial when the reversed film loop was shifted back to its initial end of the enclosure. A 2.1:1 choice ratio resulting from the combination of all trials was statistically significant indicating there was less than a 5% probability that this distribution should occur by chance alone.

The departure from the overall trend seen in the choice ratio of trial 2 cannot be unequivocally accounted for. There is some evidence, however, which indicates that the deviation resulted from a secondary motivation of the female lizards. From both field and laboratory observations,

Table 12. Statistical evaluation of choices of female *Anolis nebulosus* in response to normal and altered film loop displays.

Experiment	Female Responses			Chi Square Values	Chi Square Probabilities	Probabilities of Binomial Distribution
No. 1	Normal Display	No Choice	Altered Display			
Trial 1	14	1	5	4.26*	$P_{0.05} = 3.84$ $P_{0.01} = 6.64$	0.03*
Trial 2	11	2	7	0.89	$P_{0.50} = 0.46$ $P_{0.30} = 1.07$	0.24
Trial 3	12	2	6	2.00	$P_{0.20} = 1.64$ $P_{0.10} = 2.71$	0.12
All Trials	37	5	18	6.56*	$P_{0.05} = 3.84$ $P_{0.01} = 6.64$	
No. 2	Normal Display	No Choice	Altered Display			
	14	2	4	5.56*	$P_{0.05} = 3.84$ $P_{0.01} = 6.64$	0.02*
No. 3	Left Side	No Choice	Right Side			
	8	1	11	0.49	$P_{0.50} = 0.46$ $P_{0.30} = 1.07$	0.32
No. 4	Normal Display	No Choice	Altered Display			
	12	0	6	2.00	$P_{0.20} = 1.64$ $P_{0.10} = 2.71$	0.12

*Significant

it is known that A. nebulosus females are very territorial and remain within relatively small areas (Chapter III). During some tests in which the film loops were not used, it was found that females exhibit a type of "territoriality" and "homing" within the observation cage. When released repeatedly within a short time span, the individual females would return in the majority of cases to the end of the enclosure of their initial choice. If left undisturbed, they would also remain in the chosen habitat of the chamber for at least three days (the longest period tested). Relevant to this discussion are the observations of Greenberg and Noble (1944: 431). They found that once a female A. carolinensis was residing in a male's territory, she was usually not induced to desert by an adjacent rival's display, even when the resident male's dewlap was held retracted by collodion. The experimental design of Expt. No. 1 permitted this territorial tendency to show itself, and thus introduced a second variable. To eliminate this variable, a female was used for only one observation in each of the remaining experiments.

As in Expt. No. 1, the altered film loop of Expt. No. 2 bore little resemblance to the normal display. All of the head nods were removed and four dewlap pulses were added to the display sequence. The resulting choice ratio (3.5:1) was heavily weighted in favor of the normal display and was statistically significant (Table 12).

Expt. No. 3 employed two identical normal display loops. This experiment was set up as a control to see if there was any intrinsic feature of the enclosure which in itself would attract the lizards. Eight females entered the left habitat and 11 chose the right side, which is close to a 1:1 split. As a further check, a tally was kept for all four experiments on the number of times the left and right habitats were entered. The left habitat was chosen 50 times and the right 60 times. The Chi Square value for these data was 0.91 ($P_{0.50} = 0.46$, $P_{0.30} = 1.07$); there was no significant deviation from a random distribution. Since the altered displays appeared with equal frequency at both ends of the enclosure they were not a factor in this analysis. The females as a group demonstrated no apparent preference for one end of the enclosure over the other.

In the last experiment, the altered film loop was of particular significance as it simulated an actual behavioral anomaly which occurred in approximately 5% of the sampled population. One of the two dewlap pulses was eliminated from the generalized display pattern. Although the results were not statistically significant, the resulting choice ratio of 2:1 possibly reflects some discrimination on the part of the females.

There are two criticisms of the present investigation which should be considered for future behavioral studies of this type. More consistent data would have been gathered if the tested sample had shared a common physiological state. The female lizards used in this study were not all in the same stage of estrous during the experiments, and a few were gravid; these latter individuals accounted for most of the lizards in the "no choice" category. They exhibited apparent rejection behavior during exposure to the filmed male displays and were most unpredictable in their habitat choices. It is also suggested that an experimental animal enter the test facilities completely naive and after the trial never be used again. This would eliminate any chance for cage conditioning.

Discussion

In general, the females gave a graded response to the film loops. When expressed in terms of choice ratios, there was an increasing proportion of animals attracted to the normal display as the altered display contained a greater number of changes from the generalized pattern (Table 13).

Table 13. Ratio of female Anolis nebulosus entering the habitat with a normal displaying film loop to the habitat with an altered display film loop during mate selection experiments.

Expt. No.	Control Display	Experimental Display	Choice Ratio Control : Exper.
3	Normal	Normal display	1.4 : 1
4	Normal	One dewlap pulse eliminated	2.0 : 1
1*	Normal	Normal display reversed	2.8 : 1
2	Normal	Head nods eliminated, 6 dewlap pulses	3.5 : 1

*Trial 1

Several experimental studies have been made on species recognition and courtship behavior in iguanid lizards (Ferguson, 1966, 1969a, b; Pyburn, 1955). However, very few investigators worked directly with the lizard display and its significance. Harris (1964) constructed a rough model of an Agama agama made out of two jointed wood blocks. By pulling a string, Harris could make the simulated lizard nod. He found that when his model was painted in the same pattern and colors as a territorial male, it would elicit strong aggressive reactions from nearby dominant male rainbow lizards. Gorman (1968), on the other hand, constructed a wooden model of Anolis trinitatis with appropriate body and dewlap coloration; unlike the positive responses obtained by Harris from the agamid rainbow lizards, Gorman drew no reactions from the anoles with his dummy lizard. Thus, his intended experimentations with dewlap coloration as social releasers did not materialize.

Greenberg and Noble (1944) were concerned with the effect the color of the male's dewlap had upon the attraction of females. Working with Anolis carolinensis under semi-natural conditions, they allowed two males to establish territories on either side of a greenhouse. Branches served as bridges connecting both territories with a centrally situated release box. The release box had a glass top enabling the female to observe the displaying males. One of the males either had his pink dewlap colored green, or the extension of the dewlap was prevented by a coat of collodion. After 3-5 minutes the box was opened and the female's choice recorded.

From 56 trials Greenberg and Noble concluded that the color of the dewlap is not innately attractive to females. However, they believed that the color serves to bring attention to the displaying male, and it is the display itself which causes receptive females to gravitate toward the male.

Greenberg and Noble (1944: 430-431) pointed out some difficulties with their procedure. There were differences in the type and intensity of the males' behavior as well as their proximity and visibility to the female. A lack of control over the males resulted in an inability to completely standardize the experiments.

Hunsaker (1962) also manipulated the male's display to gain insight into its function. His study dealt with the Sceloporus torquatus group which lacks the large dewlap found in the anoles; sceloporine lizards primarily perform pushups during their display. Hunsaker attempted to show how the display-action-patterns act as an interspecific isolating mechanism. He presented the DAP graphs of seven species of Sceloporus, labeling them as species-specific. Some of these patterns were incorporated into a bobbing apparatus which consisted of a model lizard activated by a thread tied to a rod riding over the notches of a rotating wheel. A motor rotated the notched wheel at about 100 RPM. The display data of *S. mucronatus* and *S. torquatus* were programmed onto separate wheels via the notches and used in the following experiments.

A 2 x 1 foot enclosure was partially divided into three sections with a bobbing machine at both ends. Females were placed into the enclosure and random observations made to note in which chamber a female was located. One bobbing machine was programmed with a display simulating that of the species of the female in the cage. The other bobbing machine contained a "random" notched wheel, or one which simulated the display of another species which was represented in the cage by a second female. Five different experiments were run with a total of seven lizards.

Hunsaker observed the females most frequently in the chambers occupied by the model lizard which was simulating the females' species-specific bob. When the bobbing machines were shut off, he found the females distributed themselves randomly among the chambers. From these observations Hunsaker concluded that the species-specific display of the males serves as a species recognition signal and permits the females to establish territories close to males of their own kind.

The experimental methods used by Hunsaker contained several weaknesses. His conclusions were based on the performance of only seven lizards. Each experiment consisted of many observations on not more than two lizards. Cage preferences on the part of the females could have accounted for Hunsaker's results, as he made repeated observations on a female without exchanging the bobbing machines between ends of the enclosure during each of his experiments.

Another criticism is directed at the bobbing machines themselves. The motor used for the bobbing apparatus turned the notched display wheel at about 100 RPM, causing the wheel to revolve completely once every 0.6 seconds. Hunsaker placed the display-action-patterns of S. mucronatus and S. torquatus on the wheels and yet he shows both of these displays to be of greater duration than 0.6 seconds. Under such conditions, it is improbable the experimental lizards could discern where one display finished and the other began. At best, species recognition from the model lizard would be difficult. There is also some question as to the accuracy of the "species-specific" displays employed in these experiments. Charles Carpenter (personal communication) has observed via closed circuit television much more elaborate behavioral patterns for members of the torquatus group which he believes are the actual species-typical displays.

The two papers cited above as well as the present study furnish evidence that the male display of some lizards can attract the females of their respective species. Presumably, the display could serve as an ethological isolating mechanism in areas of cohabitation with closely related species. However, it should be stressed that these reports are only preliminary investigations, and that much more work needs to be done before any positive statement can be made. In his discussion of the role of visual communication in reproductive isolation, Marler (1961: 96-97) mentioned how small the body of direct evidence is for a field where great advances are likely to be derived through an experimental approach. Perhaps the relative lack of good experimental data can be attributed to the difficulty in assessing the real functions of ethological factors. Too frequently, unproven but often repeated hypotheses and indirect observational data have been substituted for needed research.

CHAPTER VI

SUMMARY

The present study is the first investigation of the ecology and behavior of *Anolis nebulosus*, a species distributed exclusively along the western side of Mexico. From June, 1965 to September, 1968, over 300 *A. nebulosus* were studied in the laboratory and the field; these individuals were from two populations located near Tepic, Nayarit and Manzanillo, Colima, Mexico. The research included a description of the species' ecology and behavior, a statistical analysis of the assertion display-action-pattern (DAP), and experiments indicating a possible social function of the assertive DAP. The following are the results of this investigation.

1. Not only is the taxonomy of the genus *Anolis* unsettled, but the literature contains many conflicting descriptions of *A. nebulosus*. It is likely *A. nebulosus* represents a complex rather than a single species.

2. *A. nebulosus* was studied in a deciduous oak woodland which due to its altitude has a distinct temperate climate with a dry (spring) and rainy (summer) season.

3. During the spring the sample from the Nayarit population had a female : male sex ratio of 50:49.

4. The species exhibits sexual dimorphism. Males have larger dewlaps colored orange and white, while the female dewlaps are pink. Of the

collected females, 19.7% possessed a rusty body coloration and 29.2% had a dorsal striped pattern which was not found on males.

5. Body size also differed between the sexes with snout-vent lengths averaging 41.4 mm for the males and 35.8 mm for females during the spring.

6. No obvious difference in length-weight relation occurs between the sexes. The only exceptions were gravid females which were the heaviest for their lengths.

7. From growth data collected in the laboratory it was found that smaller lizards grew faster than larger ones. In April lizards showed a wide range of s-v lengths. By August almost all lizards were of adult proportions. Within the sample were animals known to have completed their second year and others were less than a year old.

8. Few A. nebulosus live more than a year in nature.

9. The Nayarit study area supported 90 lizards totalling 120 gm per 1000 m^2 during the spring. Compared with other species of lizards, the biomass of A. nebulosus was fairly high.

10. The elevated perch sites of male lizards tended to be higher (79.9 cm) than those of females (29.3 cm).

11. Males, particularly the larger ones, tended to choose tree trunks as their perch sites most often, while females and subadult males utilized bushy vegetation types and the leaf litter to a greater extent. This results in a partial subdivision of the habitat between the adult sexes and may decrease intraspecific competition.

12. Contrary to reports for other anoles and for A. nebulosus in other parts of its range, the Tepic population during the spring slept in the leaf litter and not on elevated perches. This may have been in response to the

low humidity and windy conditions of the dry season.

13. Cloacal temperatures from 75% of basking anoles were grouped between 28.0 - 31.4 C, with a mean of 29.6 C. The average body temperature when the lizards were moving into the shade was 29.7 C, and probably represents the average preferred body temperature of A. nebulosus.

14. Although females tended to have a lower daily mean body temperature (28.5 C) than the males (29.9 C), the difference was not significant.

15. The lizards basked in the early morning (0600-0959) and then retired to the shade for the remainder of the day. The anoles were least active during the warmest part of the day (1100-1459) at which time their cloacal temperatures were over 31.0 C.

16. A. nebulosus can be classified as a diurnal, limited basker.

17. Males had significantly larger home ranges than females, averaging 1.99 ± 0.23 m^2 and 0.62 ± 0.14 m^2, respectively.

18. Between observations, the average distances moved by males (3.26 ± 0.70 m) was significantly longer than for females (1.89 ± 0.88 m).

19. There was a trend for the larger individuals to have the larger home ranges for their respective sex class.

20. Home ranges were not uniformly distributed on the study area, but were associated with certain features of the habitat (i.e. adequate shade and perch sites).

21. Home ranges of smaller males overlapped those of larger males, but 62% of the female home ranges did not touch those of other females.

22. Distribution of female home ranges was an almost perfect overlap with the male home ranges.

23. Differences were noted in aggressive levels of individuals;

this was reflected in the intensity of territorial defense.

24. The most frequently observed display-action-pattern (DAP) was the assertion display. In field observations the challenge DAP was seldom seen, whereas in crowded enclosures, the challenge DAP and fighting occurred much more frequently.

25. Males and females shared a common behavior repertoire, although frequency of use and social context differed many times.

26. Courtship and copulatory behavior of A. nebulosus followed the general pattern described for Anolis carolinensis and most other iguanid species.

27. Due to females being agonistic toward other females and usually sharing a male's territory, a semi-monogamous relationship existed even though males were observed to be polygamists when placed in crowded enclosures.

28. A. nebulosus appears to have social displays which are comparable to those of some bird species with the same type of breeding structure.

29. It is estimated that the Nayarit population of A. nebulosus begin to mate late in May and continue through August. Egg deposition occured from the last half of June through August. Hatchlings appeared from the last half of August to the end of October.

30. The mating and reproductive season directly corresponds with the rainy season. It is likely rain stimulates the females to lay as well as facilitating hatching.

31. A. nebulosus possesses cryptic coloration which it used to avoid detection.

32. Escape behavior consisted of the lizards flattening themselves against the substrate and shifting their position to keep their perch between

them and the threatening object.

33. Females made greater use of the leaf litter as a route of escape than the males.

34. Eliminative posturing was the same as that observed in most other iguanid species.

35. Of the animal associates, Urosaurus ornatus was the closest ecological equivalent to A. nebulosus in the study area. There was evidence of behavioral interaction between them. Birds, especially thr raven, may act as predators on the anoles.

36. From daily logs it was evident the lizards shared common types of activities; however, these activities were carried out in a manner unique to each lizard.

37. There was a population-typical assertion display shared by all 56 male A. nebulosus examined.

38. Each lizard performed his assertion DAP and each of its component units with remarkable consistency.

39. The duration of the units and the combined sequence, however, showed large inter-lizard variation.

40. Two series of filmed displays were taken from 13 individuals one year apart. The displays of 10 of these lizards had lengthened over the year, 8 of which were significantly longer than those previously filmed. However, there was no apparent trend on a population level for larger lizards having longer displays.

41. Duration of assertion display sequence for the population ranged from under 2 to over 8 seconds. It was found as the time of display increased, Units 4 and 7 increased disproportionally. The units containing dewlap

movement (3, 5, 6, 8, and 9) tended to decrease to a lesser proportion as the display sequence lengthened.

42. No difference could be found between displays filmed from lab-held animals and those performing in the field.

43. A. nebulosus from Colima, Mexico possessed an assertion DAP which differed from the Tepic population. Units 1 and 2 were transposed.

44. A. nebulosus collected in Colima also possessed different dewlap coloration from those in Nayarit; they may well be a different subspecies.

45. Within the ordering of the unit sequence of the population-typical assertion DAP, individual differences were common. Lizards differed with regard to their head amplitude, number of "head bounces," amplitude of dewlap pulse extension, duration of display sequence, and duration of each unit.

46. No differences were found between the male and female assertion DAP.

47. Display analysis appears to be a good taxonomic tool for sub-species and species differentiation.

48. The challenge DAP showed much intraspecies variation and therefore seems inferior to the assertion DAP for taxonomic differentiation at the species level. However, some elements of the challenge behavior sequence of A. nebulosus differ while others are shared with the challenge displays reported for other anoles. Perhaps the entire challenge behavior can be taxonomically useful for differentiating taxa higher than species.

49. Females were presented with two film loops of displaying males. One portrayed the assertion display typical of their population and the other was altered. The more the one film loop display was altered, the larger were the numbers of females which approached the "normally" displaying film loop.

50. It is possible the male's assertion DAP is used by the female for species recognition and mate selection.

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APPENDIX

Table 14. Duration (expressed in seconds) of each unit within the assertion display of Anolis nebulosus from Nayarit, Mexico, computed from displays filmed in the laboratory, summer, 1967.

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
Unit One								
1	16	0.615	0.006	0.604	0.625	0.556	0.667	0.111
2	2	0.611	0.000	0.000	0.000	0.611	0.611	0.000
3	11	1.455	0.001	1.428	1.481	1.389	1.500	0.111
4	9	1.333	0.009	1.316	1.351	1.278	1.389	0.111
5	14	1.702	0.007	1.689	1.715	1.667	1.722	0.055
6	11	1.217	0.016	1.189	1.246	1.167	1.333	0.166
7	9	1.136	0.010	1.118	1.154	1.111	1.167	0.056
8	21	1.487	0.011	1.467	1.507	1.389	1.556	0.167
9	4	0.444	0.000	0.000	0.000	0.444	0.444	0.000
10	11	1.697	0.017	1.666	1.728	1.611	1.778	0.167
11	15	1.174	0.011	1.155	1.193	1.111	1.222	0.111
12	15	1.252	0.007	1.239	1.265	1.222	1.278	0.056
13	10	1.656	0.014	1.630	1.681	1.611	1.722	0.111
14	15	1.133	0.011	1.115	1.152	1.056	1.167	0.111
15	14	0.555	0.008	0.541	0.570	0.500	0.611	0.111
16	15	1.104	0.009	1.088	1.119	1.056	1.167	0.111
17	5	1.244	0.014	1.215	1.273	1.222	1.278	0.056
18	8	1.972	0.018	1.937	2.007	1.889	2.056	0.167
19	9	0.636	0.010	0.618	0.654	0.611	0.667	0.056
20	6	0.611	0.000	0.000	0.000	0.611	0.611	0.000
21	15	0.796	0.012	0.776	0.817	0.722	0.833	0.111
22	22	1.528	0.013	1.505	1.550	1.333	1.611	0.278
23	6	0.741	0.019	0.703	0.778	0.722	0.833	0.111
24	8	1.729	0.016	1.698	1.760	1.667	1.778	0.111
25	11	1.096	0.011	1.076	1.116	1.056	1.167	0.111
26	8	1.479	0.018	1.445	1.513	1.389	1.556	0.167
27	10	0.589	0.009	0.572	0.606	0.556	0.611	0.056
28	9	1.086	0.013	1.061	1.111	1.056	1.167	0.111
29	7	1.056	0.012	1.032	1.079	1.000	1.111	0.111
30	6	1.546	0.023	1.501	1.591	1.500	1.611	0.111

Table 14. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit One (Continued)				
31	22	1.081	0.014	1.056	1.106	0.944	1.167	0.223
32	14	1.798	0.031	1.742	1.853	1.611	2.000	0.389
33	15	1.159	0.007	1.146	1.172	1.111	1.222	0.111
34	4	0.611	0.000	0.000	0.000	0.611	0.611	0.000
35	2	1.278	0.000	0.000	0.000	1.278	1.278	0.000
36	8	0.722	0.000	0.000	0.000	0.722	0.722	0.000
37	12	0.741	0.008	0.727	0.755	0.722	0.778	0.056
38	15	1.219	0.016	1.191	1.246	1.111	1.333	0.222
39	3	1.130	0.019	1.076	1.184	1.111	1.167	0.056
40	3	0.315	0.037	0.207	0.423	0.278	0.389	0.111
41	17	0.503	0.009	0.487	0.519	0.444	0.556	0.112
42	11	0.904	0.008	0.890	0.918	0.889	0.944	0.055
43	10	0.578	0.009	0.561	0.594	0.556	0.611	0.055
				Unit Two				
1	16	0.132	0.007	0.119	0.144	0.111	0.167	0.056
2	2	0.111	0.000	0.000	0.000	0.111	0.111	0.000
3	11	0.328	0.005	0.319	0.337	0.278	0.333	0.055
4	9	0.228	0.006	0.217	0.240	0.222	0.278	0.056
5	14	0.393	0.004	0.386	0.400	0.389	0.444	0.055
6	11	0.217	0.005	0.208	0.226	0.167	0.222	0.055
7	9	0.278	0.000	0.000	0.000	0.278	0.278	0.000
8	21	0.310	0.009	0.294	0.325	0.222	0.389	0.167
9	4	0.069	0.014	0.037	0.102	0.056	0.111	0.056
10	11	0.328	0.012	0.307	0.350	0.222	0.389	0.167
11	15	0.226	0.004	0.219	0.232	0.222	0.278	0.056
12	15	0.159	0.007	0.146	0.172	0.111	0.222	0.111
13	10	0.456	0.011	0.435	0.476	0.389	0.500	0.111
14	15	0.170	0.004	0.164	0.177	0.167	0.222	0.055
15	14	0.246	0.013	0.224	0.268	0.167	0.333	0.166

Table 14. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
Unit Two (Continued)								
16	15	0.170	0.004	0.164	0.177	0.167	0.222	0.055
17	5	0.178	0.011	0.154	0.201	0.167	0.222	0.055
18	8	0.556	0.018	0.521	0.590	0.500	0.611	0.111
19	9	0.111	0.000	0.000	0.000	0.111	0.111	0.000
20	6	0.102	0.009	0.083	0.121	0.056	0.111	0.055
21	15	0.130	0.007	0.117	0.142	0.111	0.167	0.056
22	22	0.359	0.006	0.348	0.369	0.333	0.389	0.056
23	6	0.111	0.000	0.000	0.000	0.111	0.111	0.000
24	8	0.375	0.009	0.358	0.392	0.333	0.389	0.056
25	11	0.121	0.007	0.109	0.133	0.111	0.167	0.056
26	8	0.333	0.000	0.000	0.000	0.333	0.333	0.000
27	10	0.111	0.000	0.000	0.000	0.111	0.111	0.000
28	9	0.272	0.006	0.260	0.283	0.222	0.278	0.056
29	7	0.214	0.015	0.186	0.242	0.167	0.278	0.111
30	6	0.194	0.012	0.169	0.219	0.167	0.222	0.055
31	22	0.174	0.006	0.165	0.184	0.111	0.222	0.111
32	14	0.448	0.007	0.436	0.461	0.389	0.500	0.111
33	15	0.385	0.007	0.374	0.397	0.333	0.444	0.111
34	4	0.111	0.000	0.000	0.000	0.111	0.111	0.000
35	2	0.278	0.000	0.000	0.000	0.278	0.278	0.000
36	8	0.104	0.007	0.091	0.117	0.056	0.111	0.055
37	12	0.125	0.007	0.112	0.138	0.111	0.167	0.056
38	15	0.167	0.000	0.000	0.000	0.167	0.167	0.000
39	3	0.167	0.000	0.000	0.000	0.167	0.167	0.000
40	3	0.185	0.019	0.131	0.239	0.167	0.222	0.055
41	17	0.111	0.000	0.000	0.000	0.111	0.111	0.000
42	11	0.217	0.005	0.208	0.226	0.167	0.222	0.055
43	10	0.194	0.012	0.172	0.217	0.167	0.278	0.111

Table 14. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	Upper	Minimum Value	Maximum Value	Range
				Unit Three				
1	16	0.465	0.014	0.440	0.490	0.389	0.556	0.167
2	2	0.361	0.028	0.186	0.537	0.333	0.389	0.056
3	11	0.404	0.008	0.390	0.418	0.389	0.444	0.055
4	9	0.321	0.018	0.288	0.354	0.278	0.444	0.167
5	14	0.504	0.016	0.476	0.532	0.389	0.556	0.167
6	11	0.364	0.009	0.348	0.379	0.333	0.389	0.056
7	9	0.284	0.006	0.272	0.295	0.278	0.333	0.055
8	21	0.357	0.006	0.347	0.368	0.333	0.389	0.056
9	4	0.306	0.016	0.268	0.343	0.278	0.333	0.055
10	11	0.354	0.008	0.338	0.369	0.333	0.389	0.056
11	15	0.344	0.006	0.334	0.355	0.333	0.389	0.056
12	15	0.237	0.007	0.225	0.249	0.222	0.278	0.056
13	10	0.422	0.012	0.400	0.445	0.389	0.500	0.111
14	15	0.344	0.006	0.334	0.355	0.333	0.389	0.056
15	14	0.341	0.008	0.327	0.355	0.278	0.389	0.111
16	15	0.267	0.010	0.250	0.384	0.222	0.333	0.111
17	5	0.378	0.027	0.320	0.436	0.278	0.444	0.166
18	8	0.521	0.010	0.502	0.540	0.500	0.556	0.056
19	9	0.167	0.000	0.000	0.000	0.167	0.167	0.000
20	6	0.231	0.009	0.213	0.250	0.222	0.278	0.056
21	15	0.219	0.004	0.212	0.225	0.167	0.222	0.055
22	22	0.298	0.006	0.288	0.308	0.278	0.333	0.055
23	6	0.324	0.009	0.305	0.343	0.278	0.333	0.055
24	8	0.347	0.009	0.330	0.364	0.333	0.389	0.056
25	11	0.359	0.012	0.337	0.379	0.278	0.389	0.111
26	8	0.535	0.015	0.507	0.563	0.500	0.611	0.111
27	10	0.256	0.009	0.239	0.272	0.222	0.278	0.056
28	9	0.395	0.017	0.363	0.427	0.278	0.444	0.166
29	7	0.286	0.008	0.270	0.301	0.278	0.333	0.055
30	6	0.370	0.012	0.347	0.394	0.333	0.389	0.056

Table 14. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit Three (Continued)				
31	22	0.290	0.008	0.276	0.304	0.222	0.333	0.111
32	14	0.421	0.010	0.404	0.438	0.333	0.444	0.111
33	15	0.352	0.009	0.336	0.367	0.278	0.389	0.111
34	4	0.306	0.016	0.268	0.343	0.278	0.333	0.055
35	2	0.333	0.000	0.000	0.000	0.333	0.333	0.000
36	8	0.327	0.007	0.313	0.340	0.278	0.333	0.055
37	12	0.347	0.007	0.334	0.360	0.333	0.389	0.056
38	15	0.341	0.007	0.328	0.354	0.278	0.389	0.111
39	3	0.426	0.019	0.372	0.480	0.389	0.444	0.055
40	3	0.167	0.000	0.000	0.000	0.167	0.167	0.000
41	17	0.337	0.009	0.321	0.352	0.278	0.389	0.111
42	11	0.338	0.009	0.322	0.355	0.278	0.389	0.111
43	10	0.272	0.006	0.262	0.282	0.222	0.278	0.056
				Unit Four				
1	16	0.451	0.011	0.432	0.471	0.389	0.556	0.167
2	2	0.222	0.000	0.000	0.000	0.222	0.222	0.000
3	11	1.399	0.015	1.372	1.426	1.333	1.500	0.167
4	9	0.840	0.022	0.799	0.880	0.722	0.944	0.222
5	14	1.643	0.016	1.614	1.672	1.500	1.722	0.222
6	11	1.182	0.015	1.154	1.209	1.111	1.278	0.167
7	9	2.105	0.011	2.084	2.126	2.056	2.167	0.111
8	21	1.479	0.022	1.441	1.517	1.389	1.178	0.389
9	4	0.444	0.000	0.000	0.000	0.444	0.444	0.000
10	11	2.182	0.020	2.147	2.218	2.056	2.278	0.222
11	15	1.459	0.010	1.441	1.477	1.389	1.500	0.111
12	15	1.004	0.009	0.989	1.019	0.944	1.055	0.111
13	10	2.800	0.019	2.765	2.835	2.722	2.944	0.222
14	15	1.630	0.022	1.591	1.669	1.556	1.778	0.222
15	14	0.591	0.011	0.572	0.611	0.556	0.667	0.111

Table 14. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
Unit Four (Continued)								
16	15	1.281	0.015	1.255	1.308	1.222	1.444	0.222
17	5	1.544	0.021	1.500	1.589	1.500	1.611	0.111
18	8	3.042	0.187	2.688	3.395	2.500	4.111	1.611
19	9	0.407	0.009	0.390	0.425	0.389	0.444	0.055
20	6	0.426	0.012	0.402	0.450	0.389	0.444	0.055
21	15	0.463	0.007	0.451	0.475	0.444	0.500	0.056
22	22	1.725	0.022	1.686	1.763	1.500	2.056	0.556
23	6	1.157	0.036	1.084	1.231	1.111	1.333	0.222
24	8	1.840	0.019	1.803	1.877	1.778	1.944	0.166
25	11	1.116	0.014	1.091	1.141	1.000	1.167	0.167
26	8	1.986	0.044	1.902	2.070	1.778	2.167	0.389
27	10	0.322	0.011	0.302	0.343	0.278	0.389	0.111
28	9	1.179	0.018	1.146	1.212	1.111	1.278	0.167
29	7	1.056	0.012	1.032	1.079	1.000	1.111	0.111
30	6	1.519	0.037	1.444	1.593	1.389	1.611	0.222
31	22	1.318	0.018	1.287	1.350	1.167	1.500	0.333
32	14	1.758	0.037	1.692	1.824	1.667	2.111	0.444
33	15	1.381	0.064	1.268	1.495	0.500	1.500	1.000
34	4	0.694	0.016	0.647	0.732	0.667	0.722	0.055
35	2	1.972	0.028	1.797	2.148	1.944	2.000	0.056
36	8	0.493	0.016	0.472	0.524	0.444	0.555	0.111
37	13	0.694	0.011	0.675	0.714	0.667	0.778	0.111
38	15	1.170	0.035	1.109	1.232	1.056	1.389	0.333
39	3	1.111	0.032	1.017	1.205	1.056	1.167	0.111
40	3	0.463	0.019	0.409	0.517	0.444	0.500	0.056
41	17	0.317	0.012	0.295	0.339	0.222	0.389	0.167
42	11	1.045	0.015	1.019	1.072	1.000	1.111	0.111
43	10	0.517	0.008	0.501	0.532	0.500	0.556	0.056

Table 14. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	Upper	Minimum Value	Maximum Value	Range
				Unit Five				
1	16	0.111	0.000	0.000	0.000	0.111	0.111	0.000
2	2	0.056	0.000	0.000	0.000	0.056	0.056	0.000
3	11	0.116	0.005	0.107	0.125	0.111	0.167	0.056
4	9	0.080	0.010	0.062	0.098	0.056	0.111	0.055
5	14	0.147	0.007	0.134	0.160	0.111	0.167	0.056
6	11	0.101	0.007	0.089	0.113	0.056	0.111	0.055
7	9	0.086	0.010	0.068	0.105	0.056	0.111	0.055
8	21	0.103	0.009	0.088	0.118	0.000	0.167	0.167
9	4	0.097	0.014	0.065	0.130	0.056	0.111	0.055
10	11	0.116	0.005	0.107	0.125	0.111	0.167	0.056
11	15	0.141	0.007	0.128	0.154	0.111	0.167	0.056
12	15	0.111	0.000	0.000	0.000	0.111	0.111	0.000
13	10	0.150	0.008	0.134	0.166	0.111	0.167	0.056
14	15	0.111	0.000	0.000	0.000	0.111	0.111	0.000
15	14	0.099	0.006	0.088	0.110	0.056	0.111	0.055
16	15	0.111	0.000	0.000	0.000	0.111	0.111	0.000
17	5	0.111	0.000	0.000	0.000	0.111	0.111	0.000
18	8	0.104	0.007	0.091	0.117	0.056	0.111	0.055
19	9	0.136	0.009	0.118	0.154	0.111	0.167	0.056
20	6	0.074	0.012	0.050	0.098	0.056	0.111	0.055
21	15	0.085	0.007	0.072	0.098	0.056	0.111	0.055
22	22	0.114	0.004	0.106	0.121	0.056	0.167	0.111
23	6	0.093	0.012	0.069	0.116	0.056	0.111	0.055
24	8	0.104	0.007	0.091	0.117	0.056	0.111	0.055
25	11	0.081	0.009	0.065	0.097	0.056	0.111	0.055
26	8	0.111	0.000	0.000	0.000	0.111	0.111	0.000
27	10	0.083	0.009	0.066	0.100	0.056	0.111	0.055
28	9	0.111	0.000	0.000	0.000	0.111	0.111	0.000
29	7	0.095	0.010	0.075	0.115	0.056	0.111	0.055
30	6	0.093	0.012	0.069	0.116	0.056	0.111	0.055

Table 14. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit Five (Continued)				
31	22	0.093	0.006	0.084	0.103	0.056	0.111	0.055
32	14	0.079	0.008	0.066	0.093	0.056	0.111	0.055
33	15	0.111	0.000	0.000	0.000	0.111	0.111	0.055
34	4	0.097	0.014	0.065	0.130	0.056	0.111	0.055
35	2	0.111	0.000	0.000	0.000	0.111	0.111	0.000
36	8	0.090	0.010	0.071	0.110	0.056	0.111	0.055
37	12	0.079	0.008	0.064	0.094	0.056	0.111	0.055
38	15	0.096	0.007	0.085	0.108	0.056	0.111	0.055
39	3	0.093	0.019	0.039	0.147	0.056	0.111	0.055
40	3	0.111	0.000	0.000	0.000	0.111	0.111	0.000
41	17	0.095	0.006	0.084	0.106	0.056	0.111	0.055
42	11	0.081	0.009	0.065	0.097	0.056	0.111	0.055
43	10	0.083	0.009	0.066	0.100	0.056	0.111	0.055
				Unit Six				
1	16	0.101	0.006	0.091	0.111	0.056	0.111	0.055
2	2	0.167	0.000	0.000	0.000	0.167	0.167	0.000
3	11	0.177	0.010	0.158	0.195	0.111	0.222	0.111
4	9	0.117	0.006	0.106	0.129	0.111	0.167	0.056
5	14	0.187	0.009	0.170	0.203	0.167	0.278	0.111
6	11	0.182	0.008	0.168	0.196	0.167	0.222	0.055
7	9	0.167	0.000	0.000	0.000	0.167	0.167	0.000
8	21	0.148	0.012	0.128	0.168	0.000	0.222	0.222
9	4	0.125	0.014	0.092	0.158	0.111	0.167	0.056
10	11	0.172	0.005	0.163	0.181	0.167	0.222	0.055
11	15	0.104	0.005	0.095	0.113	0.056	0.111	0.055
12	15	0.111	0.000	0.000	0.000	0.111	0.111	0.000
13	10	0.172	0.013	0.148	0.196	0.111	0.222	0.111
14	15	0.163	0.004	0.156	0.169	0.111	0.167	0.056
15	14	0.107	0.004	0.100	0.114	0.056	0.111	0.055

Table 14. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
Unit Six (Continued)								
16	15	0.148	0.007	0.136	0.160	0.111	0.167	0.056
17	5	0.111	0.000	0.000	0.000	0.111	0.111	0.000
18	8	0.167	0.000	0.000	0.000	0.167	0.167	0.000
19	9	0.130	0.009	0.112	0.147	0.111	0.167	0.056
20	6	0.074	0.012	0.050	0.098	0.056	0.111	0.055
21	15	0.100	0.006	0.090	0.110	0.056	0.111	0.055
22	22	0.159	0.006	0.150	0.169	0.111	0.222	0.111
23	6	0.130	0.012	0.106	0.153	0.111	0.167	0.056
24	8	0.174	0.013	0.150	0.197	0.111	0.222	0.111
25	11	0.182	0.008	0.168	0.196	0.167	0.222	0.055
26	8	0.222	0.010	0.202	0.242	0.167	0.278	0.111
27	10	0.111	0.000	0.000	0.000	0.111	0.111	0.000
28	9	0.160	0.006	0.149	0.172	0.111	0.167	0.056
29	7	0.167	0.000	0.000	0.000	0.167	0.167	0.000
30	6	0.194	0.019	0.156	0.233	0.167	0.278	0.111
31	22	0.131	0.006	0.121	0.141	0.111	0.167	0.056
32	14	0.111	0.000	0.000	0.000	0.111	0.111	0.000
33	15	0.163	0.004	0.156	0.169	0.111	0.167	0.056
34	4	0.111	0.000	0.000	0.000	0.111	0.111	0.000
35	2	0.111	0.000	0.000	0.000	0.111	0.111	0.000
36	8	0.160	0.007	0.147	0.173	0.111	0.167	0.056
37	12	0.111	0.000	0.000	0.000	0.111	0.111	0.000
38	15	0.137	0.007	0.124	0.150	0.111	0.167	0.056
39	3	0.167	0.000	0.000	0.000	0.167	0.167	0.000
40	3	0.111	0.000	0.000	0.000	0.111	0.111	0.000
41	17	0.127	0.006	0.116	0.139	0.111	0.167	0.056
42	11	0.101	0.007	0.089	0.113	0.056	0.111	0.055
43	10	0.083	0.009	0.066	0.100	0.056	0.111	0.055

Table 14. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit Seven				
1	16	0.059	0.016	0.032	0.086	0.000	0.278	0.278
2	2	0.056	0.000	0.000	0.000	0.056	0.056	0.000
3	11	0.197	0.009	0.181	0.213	0.167	0.222	0.055
4	9	0.204	0.009	0.186	0.221	0.167	0.222	0.055
5	14	0.587	0.008	0.574	0.601	0.556	0.611	0.055
6	11	0.116	0.009	0.100	0.133	0.056	0.167	0.111
7	9	0.111	0.000	0.000	0.000	0.111	0.111	0.000
8	21	0.056	0.005	0.046	0.065	0.000	0.111	0.111
9	4	0.278	0.016	0.010	0.066	0.000	0.056	0.056
10	11	0.227	0.009	0.211	0.244	0.167	0.278	0.111
11	15	0.011	0.006	0.001	0.022	0.000	0.056	0.056
12	15	0.085	0.007	0.072	0.098	0.056	0.111	0.055
13	10	0.467	0.015	0.440	0.494	0.389	0.556	0.167
14	15	0.244	0.007	0.232	0.257	0.222	0.278	0.056
15	14	0.000	0.000	0.000	0.000	0.000	0.000	0.000
16	15	0.219	0.004	0.212	0.225	0.167	0.222	0.055
17	5	0.167	0.000	0.000	0.000	0.167	0.167	0.000
18	8	0.833	0.046	0.747	0.920	0.722	1.056	0.334
19	9	0.049	0.011	0.029	0.070	0.000	0.111	0.111
20	6	0.000	0.000	0.000	0.000	0.000	0.000	0.000
21	15	0.148	0.007	0.003	0.026	0.000	0.056	0.056
22	22	0.447	0.014	0.423	0.471	0.333	0.611	0.278
23	6	0.130	0.012	0.106	0.153	0.111	0.167	0.056
24	8	0.118	0.007	0.105	0.131	0.111	0.167	0.056
25	11	0.207	0.020	0.171	0.243	0.167	0.389	0.222
26	8	0.167	0.028	0.114	0.219	0.000	0.278	0.278
27	10	0.000	0.000	0.000	0.000	0.000	0.000	0.000
28	9	0.123	0.008	0.108	0.139	0.111	0.167	0.056
29	7	0.103	0.008	0.088	0.119	0.056	0.111	0.055
30	6	0.370	0.019	0.333	0.408	0.333	0.444	0.111

Table 14. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit Seven (Continued)				
31	22	0.149	0.007	0.137	0.161	0.556	0.167	0.111
32	14	0.567	0.009	0.552	0.583	0.500	0.611	0.111
33	15	0.207	0.009	0.192	0.222	0.167	0.278	0.111
34	4	0.056	0.000	0.000	0.000	0.056	0.056	0.000
35	2	0.167	0.000	0.000	0.000	0.167	0.167	0.000
36	8	0.014	0.009	0.003	0.031	0.000	0.056	0.056
37	12	0.005	0.005	0.004	0.013	0.000	0.056	0.056
38	15	0.089	0.014	0.064	0.114	0.056	0.222	0.167
39	3	0.111	0.000	0.000	0.000	0.111	0.111	0.000
40	3	0.000	0.000	0.000	0.000	0.000	0.000	0.000
41	17	0.003	0.003	0.002	0.009	0.000	0.056	0.056
42	11	0.066	0.007	0.053	0.078	0.056	0.111	0.055
43	10	0.000	0.000	0.000	0.000	0.000	0.000	0.000
				Unit Eight				
1	16	0.267	0.008	0.254	0.281	0.222	0.333	0.111
2	2	0.222	0.000	0.000	0.000	0.222	0.222	0.000
3	11	0.263	0.008	0.248	0.277	0.222	0.278	0.056
4	9	0.259	0.009	0.242	0.276	0.222	0.278	0.056
5	14	0.381	0.005	0.371	0.391	0.333	0.389	0.056
6	11	0.323	0.007	0.311	0.336	0.378	0.333	0.055
7	9	0.228	0.006	0.217	0.240	0.222	0.278	0.056
8	21	0.259	0.007	0.247	0.271	0.167	0.278	0.111
9	4	0.125	0.014	0.092	0.158	0.111	0.167	0.056
10	11	0.379	0.010	0.360	0.397	0.333	0.444	0.111
11	15	0.278	0.000	0.000	0.000	0.278	0.278	0.000
12	15	0.356	0.007	0.343	0.368	0.333	0.389	0.056
13	10	0.578	0.009	0.561	0.594	0.556	0.611	0.055
14	15	0.374	0.009	0.359	0.389	0.333	0.444	0.111
15	14	0.187	0.007	0.173	0.200	0.167	0.222	0.055

Table 14. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
Unit Eight (Continued)								
16	15	0.307	0.007	0.294	0.320	0.278	0.333	0.055
17	5	0.244	0.014	0.215	0.273	0.222	0.278	0.056
18	8	0.417	0.010	0.397	0.436	0.389	0.444	0.055
19	9	0.191	0.010	0.173	0.210	0.167	0.222	0.055
20	6	0.130	0.012	0.106	0.153	0.111	0.167	0.056
21	15	0.111	0.000	0.000	0.000	0.111	0.111	0.000
22	22	0.341	0.006	0.331	0.350	0.278	0.389	0.111
23	6	0.213	0.009	0.194	0.232	0.167	0.222	0.055
24	8	0.299	0.010	0.279	0.218	0.278	0.333	0.055
25	11	0.237	0.015	0.210	0.265	0.111	0.278	0.167
26	8	0.375	0.058	0.265	0.485	0.000	0.500	0.500
27	10	0.122	0.007	0.109	0.136	0.111	0.167	0.056
28	9	0.278	0.000	0.000	0.000	0.278	0.278	0.000
29	7	0.167	0.000	0.000	0.000	0.167	0.167	0.000
30	6	0.676	0.017	0.642	0.710	0.611	0.722	0.111
31	22	0.278	0.005	0.269	0.287	0.222	0.333	0.111
32	14	0.496	0.014	0.472	0.520	0.389	0.556	0.167
33	15	0.219	0.007	0.207	0.230	0.167	0.278	0.111
34	4	0.097	0.014	0.065	0.130	0.056	0.111	0.055
35	2	0.444	0.000	0.000	0.000	0.444	0.444	0.000
36	8	0.181	0.009	0.163	0.198	0.167	0.222	0.055
37	12	0.213	0.006	0.202	0.224	0.167	0.222	0.055
38	15	0.233	0.008	0.219	0.247	0.167	0.278	0.111
39	3	0.278	0.000	0.000	0.000	0.278	0.278	0.000
40	3	0.111	0.000	0.000	0.000	0.111	0.111	0.000
41	17	0.163	0.003	0.158	0.169	0.111	0.167	0.056
42	11	0.273	0.005	0.264	0.282	0.222	0.278	0.056
43	10	0.183	0.008	0.168	0.199	0.167	0.222	0.055

Table 14. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
Unit Nine								
1	16	0.292	0.021	0.254	0.329	0.000	0.333	0.333
2	2	0.444	0.000	0.000	0.000	0.444	0.444	0.000
3	11	0.253	0.009	0.237	0.268	0.222	0.278	0.056
4	9	0.222	0.000	0.000	0.000	0.222	0.222	0.000
5	14	0.345	0.009	0.330	0.360	0.278	0.389	0.111
6	11	0.308	0.014	0.283	0.333	0.222	0.333	0.111
7	9	0.198	0.010	0.179	0.216	0.167	0.222	0.055
8	21	0.222	0.005	0.213	0.232	0.167	0.278	0.111
9	4	0.167	0.000	0.000	0.000	0.167	0.167	0.000
10	11	0.242	0.008	0.227	0.258	0.222	0.278	0.056
11	15	0.237	0.010	0.219	0.255	0.167	0.278	0.111
12	15	0.222	0.000	0.000	0.000	0.222	0.222	0.000
13	10	0.244	0.012	0.222	0.267	0.222	0.333	0.111
14	15	0.252	0.007	0.239	0.265	0.222	0.278	0.056
15	14	0.206	0.007	0.194	0.219	0.167	0.222	0.055
16	15	0.219	0.004	0.212	0.225	0.167	0.222	0.055
17	5	0.222	0.000	0.000	0.000	0.222	0.222	0.000
18	8	0.424	0.015	0.396	0.451	0.389	0.500	0.111
19	9	0.154	0.008	0.139	0.170	0.111	0.167	0.056
20	6	0.176	0.009	0.157	0.194	0.167	0.222	0.055
21	15	0.111	0.000	0.000	0.000	0.111	0.111	0.000
22	22	0.316	0.006	0.306	0.325	0.278	0.333	0.055
23	6	0.222	0.000	0.000	0.000	0.222	0.222	0.000
24	8	0.250	0.010	0.230	0.270	0.222	0.278	0.056
25	11	0.237	0.015	0.210	0.265	0.111	0.278	0.167
26	8	0.333	0.049	0.240	0.427	0.000	0.444	0.444
27	10	0.139	0.009	0.122	0.156	0.111	0.167	0.056
28	9	0.278	0.000	0.000	0.000	0.278	0.278	0.000
29	7	0.230	0.008	0.215	0.246	0.222	0.278	0.056
30	6	0.389	0.000	0.000	0.000	0.389	0.389	0.000

Table 14. (Continued)

Indi-vidual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit Nine (Continued)				
31	22	0.212	0.009	0.196	0.228	0.167	0.278	0.111
32	14	0.317	0.007	0.305	0.330	0.278	0.333	0.055
33	15	0.189	0.007	0.176	0.202	0.167	0.222	0.055
34	4	0.153	0.014	0.120	0.185	0.111	0.167	0.056
35	2	0.278	0.000	0.000	0.000	0.278	0.278	0.000
36	8	0.194	0.028	0.142	0.247	0.000	0.222	0.222
37	12	0.245	0.011	0.226	0.265	0.222	0.333	0.111
38	15	0.185	0.015	0.159	0.212	0.000	0.222	0.222
39	3	0.296	0.019	0.242	0.350	0.278	0.333	0.055
40	3	0.167	0.000	0.000	0.000	0.167	0.167	0.000
41	17	0.209	0.006	0.199	0.219	0.167	0.222	0.055
42	11	0.258	0.008	0.242	0.273	0.222	0.278	0.056
43	10	0.272	0.006	0.262	0.282	0.222	0.278	0.056
				Total Display (All Units)				
1	16	2.493	0.017	2.462	2.524	2.333	2.611	0.278
2	2	2.250	0.028	2.075	2.425	2.222	2.278	0.056
3	11	4.591	0.023	4.550	4.632	4.500	4.778	0.278
4	9	3.605	0.020	3.569	3.641	3.556	3.722	0.167
5	14	5.889	0.024	5.846	5.931	5.778	6.056	0.278
6	11	4.010	0.164	3.980	4.040	3.944	4.111	0.167
7	9	4.593	0.021	4.554	4.631	4.500	4.667	0.167
8	21	4.421	0.034	4.362	4.480	4.167	4.667	0.500
9	4	1.806	0.016	1.768	1.843	1.778	1.833	0.055
10	11	5.697	0.054	5.599	5.795	5.333	6.056	0.722
11	15	3.974	0.024	3.932	4.017	3.778	4.111	0.333
12	15	3.537	0.013	3.514	3.560	3.444	3.611	0.167
13	10	6.944	0.044	6.864	7.025	6.722	7.222	0.500
14	15	4.222	0.032	4.367	4.478	4.222	4.667	0.445
15	14	2.333	0.012	2.313	2.354	2.222	2.389	0.167

Table 14. (Continued)

Indi-vidual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	Upper	Minimum Value	Maximum Value	Range
Total Display (All Units Continued)								
16	15	3.826	0.019	3.792	3.860	3.722	4.000	0.278
17	5	4.200	0.038	4.120	4.280	4.111	4.333	0.222
18	8	8.035	0.253	7.555	8.514	7.278	9.333	2.055
19	9	1.981	0.016	1.952	2.011	1.889	2.056	0.167
20	6	1.824	0.017	1.790	1.858	1.778	1.889	0.111
21	15	2.030	0.016	2.001	2.058	1.944	2.111	0.167
22	22	5.285	0.034	5.226	5.344	4.944	5.611	0.667
23	6	3.120	0.056	3.007	3.234	3.000	3.389	0.389
24	8	5.236	0.023	5.193	5.279	5.167	5.389	0.222
25	11	3.636	0.035	3.572	3.701	3.444	3.833	0.389
26	8	5.542	0.104	5.344	5.739	4.944	5.833	0.889
27	10	1.733	0.014	1.708	1.759	1.667	1.778	0.111
28	9	3.883	0.028	3.830	3.936	3.778	4.056	0.278
29	7	3.373	0.023	3.328	3.418	3.333	3.500	0.167
30	6	5.352	0.051	5.249	5.455	5.222	5.500	0.278
31	22	3.727	0.042	3.655	3.800	3.444	4.167	0.723
32	14	5.996	0.067	5.877	6.114	5.667	6.667	1.000
33	15	4.167	0.073	4.038	4.295	3.167	4.389	1.222
34	4	2.236	0.035	2.154	2.318	2.167	2.333	0.166
35	2	4.972	0.028	4.797	5.148	4.944	5.000	0.056
36	8	2.285	0.029	2.230	2.339	2.111	2.389	0.278
37	12	2.560	0.014	2.534	2.586	2.500	2.667	0.167
38	15	3.637	0.065	3.523	3.751	3.389	4.056	0.667
39	3	3.778	0.056	3.616	3.940	3.667	3.833	0.166
40	3	1.630	0.049	1.487	1.773	1.556	1.722	0.166
41	17	1.866	0.010	1.849	1.883	1.778	1.944	0.166
42	11	3.283	0.014	3.258	3.308	3.222	3.389	0.167
43	10	2.183	0.019	2.149	2.217	2.056	2.278	0.222

Table 15. The distribution of variation (expressed by an analysis of variance) found in the displays of the sampled population of *Anolis nebulosus* from Nayarit, Mexico, appearing in Table 14.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Value	Percent of Variation
		Unit One			
Among Individuals	73.195	42	1.743	800.604	98.76
Within Individuals	0.903	415	0.002		1.24
Total Variation	74.099	457			
		Unit Two			
Among Individuals	5.697	42	0.136	206.785	95.37
Within Individuals	0.272	415	0.001		4.63
Total Variation	5.970	457			
		Unit Three			
Among Individuals	2.648	42	0.063	56.033	84.62
Within Individuals	0.467	415	0.001		15.38
Total Variation	3.115	457			
		Unit Four			
Among Individuals	174.368	42	4.152	360.207	97.29
Within Individuals	4.783	415	0.012		2.71
Total Variation	179.151	457			
		Unit Five			
Among Individuals	0.156	42	0.004	6.387	35.01
Within Individuals	0.241	415	0.001		64.99
Total Variation	0.397	457			

Table 15. (Continued)

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Value	Percent of Variation
		Unit Six			
Among Individuals	0.464	42	0.011	16.900	61.39
Within Individuals	0.271	415	0.001		38.61
Total Variation	0.735	457			
		Unit Seven			
Among Individuals	15.419	42	0.367	248.622	96.12
Within Individuals	0.613	415	0.001		3.88
Total Variation	16.032	457			
		Unit Eight			
Among Individuals	5.401	42	0.129	108.003	91.45
Within Individuals	0.494	415	0.001		8.55
Total Variation	5.895	457			
		Unit Nine			
Among Individuals	1.760	42	0.042	27.233	72.40
Within Individuals	0.639	415	0.002		27.60
Total Variation	2.399	457			
		Total Display			
Among Individuals	926.454	42	22.058	839.756	98.82
Within Individuals	10.901	415	0.026		1.18
Total Variation	937.355	457			

Table 16. Proportion (expressed as percent) of each unit to the total duration of the assertion display of Anolis nebulosus from Nayarit, Mexico, computed from displays filmed in the laboratory, summer, 1967.

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit One				
1	16	24.66	0.0011	24.17	25.15	22.22	26.66	4.44
2	2	27.16	0.0014	25.07	29.31	26.83	27.50	0.67
3	11	31.68	0.0008	31.20	32.16	30.12	32.93	2.81
4	9	36.99	0.0006	36.55	37.43	35.82	37.88	2.06
5	14	28.91	0.0002	28.69	29.13	28.30	29.81	1.51
6	11	30.35	0.0025	29.53	31.19	28.38	33.80	5.42
7	9	24.73	0.0003	24.44	25.02	24.10	25.61	1.51
8	21	33.64	0.0002	33.38	33.89	32.10	35.07	2.97
9	4	24.62	0.0006	24.11	25.14	24.24	25.00	0.76
10	11	29.79	0.0005	29.42	30.16	28.43	30.39	1.96
11	15	29.54	0.0003	29.25	29.83	28.57	30.55	1.98
12	15	35.39	0.0003	35.09	35.70	34.38	36.51	2.13
13	10	23.84	0.0001	23.64	24.04	23.20	24.41	1.21
14	15	25.63	0.0008	25.21	26.06	23.81	26.92	3.11
15	14	23.80	0.0013	23.25	24.34	21.43	25.58	4.15
16	15	28.85	0.0004	28.52	29.17	27.94	30.43	2.49
17	5	29.63	0.0004	29.26	30.00	29.33	30.26	0.93
18	8	24.67	0.0063	23.39	25.97	20.83	26.71	5.88
19	9	32.08	0.0017	31.37	32.79	30.55	33.33	2.78
20	6	33.52	0.0011	32.89	34.15	32.35	34.37	2.02
21	15	39.21	0.0012	38.60	39.81	37.14	40.54	3.40
22	22	28.90	0.0004	28.59	29.22	26.73	29.90	3.17
23	6	23.73	0.0006	23.29	24.16	23.21	24.59	1.38
24	8	33.02	0.0012	32.40	33.65	31.91	34.04	2.13
25	11	30.15	0.0013	29.56	30.75	28.79	32.26	3.47
26	8	26.75	0.0057	25.50	28.02	25.49	31.46	5.97
27	10	33.97	0.0023	33.14	34.80	31.25	35.48	4.23
28	9	27.97	0.0003	27.68	28.27	27.54	28.77	1.23
29	7	31.29	0.0007	30.83	31.75	30.00	31.75	1.75
30	6	28.89	0.0004	28.51	29.26	28.42	29.59	1.17

Table 16. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit One (Continued)				
31	22	28.99	0.0007	28.59	29.39	26.66	30.30	3.64
32	14	29.97	0.0016	29.32	30.61	27.78	32.11	4.33
33	15	27.93	0.0032	27.04	28.82	26.32	35.09	8.77
34	4	27.35	0.0022	26.36	28.34	26.19	28.21	2.01
35	2	25.70	0.0003	24.80	26.61	25.55	25.84	0.29
36	8	31.64	0.0020	30.87	32.42	30.23	34.21	3.98
37	12	28.93	0.0013	28.35	29.52	27.08	30.43	3.35
38	15	33.56	0.0014	32.92	34.19	31.51	36.07	4.56
39	3	29.91	0.0026	28.56	31.27	28.99	30.43	1.45
40	3	19.17	0.0446	14.57	24.25	17.24	22.58	5.34
41	17	26.94	0.0019	26.26	27.62	24.24	29.41	5.17
42	11	27.53	0.0004	27.22	27.85	27.12	28.81	1.69
43	10	26.46	0.0015	25.83	27.08	25.00	28.21	3.21
				Unit Two				
1	16	5.24	0.0036	4.78	5.72	4.35	6.82	2.47
2	2	4.94	0.0002	4.56	5.33	4.88	5.00	0.12
3	11	7.15	0.0005	6.94	7.36	6.10	7.41	1.31
4	9	6.33	0.0008	6.07	6.59	6.06	7.46	1.40
5	14	6.67	0.0002	6.55	6.79	6.42	7.48	1.06
6	11	5.41	0.0008	5.18	5.64	4.22	5.63	1.41
7	9	6.05	0.0000+	6.00	6.10	5.95	6.17	0.22
8	21	6.97	0.0011	6.68	7.26	5.19	8.75	3.56
9	4	3.75	0.0324	2.31	5.52	3.03	6.06	3.03
10	11	5.74	0.0017	5.40	6.09	4.17	6.73	2.56
11	15	5.68	0.0005	5.51	5.86	5.40	7.04	1.64
12	15	4.47	0.0026	4.11	4.84	3.13	6.25	3.12
13	10	6.55	0.0013	6.24	6.88	5.51	7.32	1.81
14	15	3.85	0.0005	3.71	3.99	3.57	5.00	1.43
15	14	10.46	0.0077	9.53	11.43	6.98	13.95	6.97

Table 16. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
Unit Two (Continued)								
16	15	4.45	0.0005	4.29	4.61	4.17	5.80	1.63
17	5	4.22	0.0043	3.67	4.80	3.85	5.33	1.48
18	8	6.92	0.0018	6.52	7.34	5.81	7.59	1.78
19	9	5.61	0.0001	5.52	5.70	5.40	5.88	0.48
20	6	5.52	0.0156	4.43	6.72	3.03	6.25	3.22
21	15	6.33	0.0044	5.77	6.91	5.26	8.57	3.31
22	22	6.78	0.0005	6.59	6.97	5.94	7.45	1.51
23	6	3.57	0.0003	3.44	3.69	3.28	3.70	0.42
24	8	7.16	0.0012	6.83	7.49	6.38	7.52	1.14
25	11	3.31	0.0019	3.03	3.60	2.94	4.48	1.54
26	8	6.03	0.0006	5.80	6.25	5.71	6.74	1.03
27	10	6.41	0.0001	6.32	6.51	6.25	6.67	0.42
28	9	6.99	0.0016	6.62	7.38	5.48	7.35	1.87
29	7	6.31	0.0066	5.56	7.10	5.00	7.94	2.94
30	6	3.61	0.0036	3.18	4.08	3.06	4.25	1.19
31	22	4.66	0.0013	4.40	4.92	3.17	6.35	3.18
32	14	7.48	0.0003	7.31	7.64	6.73	8.26	1.53
33	15	9.27	0.0019	8.84	9.72	7.89	12.28	4.39
34	4	4.97	0.0003	4.79	5.15	4.76	5.13	0.37
35	2	5.59	0.0000+	5.39	5.79	5.56	5.62	0.06
36	8	4.52	0.0069	3.89	5.20	2.44	5.26	2.82
37	12	4.85	0.0044	4.35	5.38	4.17	6.67	2.50
38	15	4.60	0.0003	4.46	4.74	4.11	4.92	0.81
39	3	4.41	0.0003	4.22	4.61	4.35	4.55	0.20
40	3	11.34	0.0368	8.04	15.13	9.68	13.79	4.11
41	17	5.96	0.0000+	5.90	6.01	5.71	6.25	0.54
42	11	6.61	0.0011	6.31	6.91	5.09	6.90	1.81
43	10	8.84	0.0097	7.85	9.89	7.32	12.82	5.50

Table 16. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	Upper	Minimum Value	Maximum Value	Range
				Unit Three				
1	16	18.62	0.0050	17.66	19.59	15.22	22.22	7.00
2	2	16.02	0.0200	10.05	23.07	15.00	17.07	2.07
3	11	8.79	0.0008	8.51	9.08	8.43	9.75	1.32
4	9	8.87	0.0080	7.94	9.83	7.46	12.50	5.04
5	14	8.53	0.0022	8.07	9.00	6.60	9.61	3.01
6	11	9.05	0.0011	8.71	9.40	8.33	9.72	1.39
7	9	6.18	0.0007	5.94	6.42	5.95	7.23	1.28
8	21	8.07	0.0007	7.83	8.32	7.14	9.21	2.07
9	4	16.90	0.0145	14.83	19.07	15.15	18.75	3.60
10	11	6.20	0.0009	5.95	6.46	5.66	6.93	1.27
11	15	8.66	0.0005	8.43	8.89	8.22	9.72	1.50
12	15	6.68	0.0012	6.38	6.99	6.25	7.94	1.69
13	10	6.07	0.0010	5.79	6.35	5.60	7.14	1.54
14	15	7.79	0.0008	7.53	8.05	7.14	8.97	1.83
15	14	14.61	0.0024	14.00	15.23	11.63	16.67	5.04
16	15	6.94	0.0024	6.51	7.38	5.80	8.82	3.02
17	5	8.94	0.0114	7.69	10.28	6.76	10.26	3.50
18	8	6.52	0.0032	6.00	7.05	5.36	7.53	2.28
19	9	8.41	0.0002	8.29	8.54	8.11	8.82	0.72
20	6	12.67	0.0054	11.70	13.68	11.76	15.15	3.39
21	15	10.76	0.0009	10.44	11.08	8.57	11.43	2.86
22	22	5.63	0.0008	5.41	5.86	5.05	6.74	1.69
23	6	10.38	0.0021	9.82	10.96	9.26	10.91	1.65
24	8	6.62	0.0009	6.34	6.92	6.38	7.44	1.06
25	11	9.84	0.0028	9.28	10.42	7.69	11.29	3.60
26	8	9.66	0.0036	9.00	10.35	8.74	11.24	2.50
27	10	14.72	0.0060	13.73	15.73	12.50	16.67	4.17
28	9	10.14	0.0055	9.32	10.98	7.14	11.59	4.45
29	7	8.47	0.0020	7.98	8.96	7.94	10.00	2.06
30	6	6.92	0.0029	6.38	7.48	6.06	7.45	1.39

Table 16. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	Upper	Minimum Value	Maximum Value	Range
				Unit Three (Continued)				
31	22	7.77	0.0015	7.41	8.13	5.88	9.52	3.64
32	14	7.02	0.0016	6.66	7.38	5.56	7.84	2.29
33	15	8.46	0.0021	8.01	8.91	6.58	10.53	3.95
34	4	13.64	0.0106	12.02	15.35	12.50	15.38	2.88
35	2	6.70	0.0001	6.47	6.94	6.67	6.74	0.07
36	8	14.29	0.0027	13.61	14.98	12.20	15.79	3.59
37	12	13.55	0.0016	13.06	14.05	12.50	15.22	2.72
38	15	9.36	0.0005	9.14	9.59	8.07	9.84	1.77
39	3	11.27	0.0089	9.59	13.07	10.14	12.12	1.98
40	3	10.24	0.0025	9.37	11.15	9.68	10.71	1.04
41	17	18.00	0.0039	17.18	18.85	14.29	20.59	6.30
42	11	10.29	0.0021	9.79	10.81	8.47	11.86	3.39
43	10	12.46	0.0018	11.96	12.98	10.26	13.51	3.25
				Unit Four				
1	16	18.08	0.0032	17.33	18.84	14.89	21.74	6.85
2	2	9.88	0.0004	9.12	10.66	9.76	10.00	0.24
3	11	30.47	0.0008	29.99	30.95	29.27	32.10	2.83
4	9	23.26	0.0040	22.27	24.26	20.31	25.37	5.06
5	14	27.89	0.0009	27.41	28.38	25.96	29.25	3.29
6	11	29.46	0.0015	28.83	30.10	27.78	31.08	3.30
7	9	45.84	0.0007	45.34	46.33	44.58	46.91	2.34
8	21	33.48	0.0039	32.46	34.50	30.95	41.56	10.61
9	4	24.62	0.0006	24.11	25.14	24.24	25.00	0.76
10	11	38.30	0.0003	38.00	38.60	37.26	39.22	1.96
11	15	36.73	0.0010	36.21	37.26	34.72	38.57	3.85
12	15	28.37	0.0007	27.97	28.78	26.98	30.16	3.17
13	10	40.32	0.0004	39.95	40.70	39.20	41.32	2.12
14	15	36.83	0.0011	36.27	37.39	35.00	39.02	4.02
15	14	25.32	0.0027	24.53	26.13	23.26	28.57	5.31

Table 16. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
Unit Four (Continued)								
16	15	33.48	0.0010	32.96	34.01	31.88	36.11	4.23
17	5	36.78	0.0048	35.36	38.22	35.53	39.19	3.66
18	8	37.61	0.0121	35.60	39.64	34.35	44.05	9.70
19	9	20.55	0.0030	19.73	21.38	19.44	22.86	3.41
20	6	23.35	0.0071	21.93	24.80	20.59	25.00	4.41
21	15	22.82	0.0023	22.11	23.53	21.05	25.71	4.66
22	22	32.61	0.0007	32.17	33.04	30.00	36.63	6.63
23	6	37.05	0.0029	36.00	38.10	35.71	39.34	3.63
24	8	35.14	0.0009	34.61	35.68	34.04	36.17	2.13
25	11	30.69	0.0009	30.20	31.19	29.03	32.31	3.28
26	8	35.92	0.0148	33.73	38.14	33.33	43.82	10.49
27	10	18.56	0.0069	17.39	19.75	15.63	21.88	6.25
28	9	30.36	0.0016	29.67	31.05	28.99	32.86	3.87
29	7	31.30	0.0020	30.49	32.12	30.00	33.33	3.33
30	6	28.35	0.0027	27.40	29.31	26.60	29.59	2.99
31	22	35.37	0.0013	34.77	35.96	31.82	39.68	7.86
32	14	29.29	0.0019	28.59	29.99	27.52	32.41	4.89
33	15	32.73	0.0214	30.33	35.17	15.79	35.53	19.74
34	4	31.05	0.0032	29.83	32.29	30.00	32.50	2.50
35	2	39.66	0.0012	37.54	41.80	39.33	40.00	0.67
36	8	21.57	0.0080	20.19	22.98	19.05	24.39	5.34
37	12	27.11	0.0017	26.46	27.77	25.53	29.17	3.64
38	15	32.09	0.0025	31.28	32.91	29.69	35.21	5.52
39	3	29.40	0.0032	27.90	30.92	28.79	30.44	1.65
40	3	28.39	0.0022	27.16	29.65	27.59	29.03	1.44
41	17	16.90	0.0080	15.75	18.09	11.76	21.21	9.45
42	11	31.84	0.0021	31.07	32.61	30.51	33.90	3.39
43	10	23.65	0.0012	23.12	24.19	22.50	25.00	2.50

Table 16. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
Unit Five								
1	16	4.46	0.0001	4.40	4.52	4.26	4.76	0.50
2	2	2.47	0.0001	2.28	2.67	2.44	2.50	0.06
3	11	2.52	0.0010	2.34	2.71	2.33	3.62	1.29
4	9	2.16	0.0080	1.70	2.67	1.54	3.13	1.59
5	14	2.47	0.0016	2.25	2.70	1.87	2.88	1.02
6	11	2.49	0.0037	2.16	2.84	1.35	2.82	1.47
7	9	1.83	0.0064	1.45	2.25	1.19	2.44	1.25
8	21	2.08	0.0120	1.58	2.66	0.00	3.61	3.61
9	4	5.29	0.0328	3.54	7.35	3.13	6.25	3.13
10	11	2.03	0.0006	1.91	2.16	1.89	2.75	0.86
11	15	3.51	0.0027	3.18	3.85	2.74	4.41	1.67
12	15	3.14	0.0000+	3.12	3.16	3.08	3.23	0.15
13	10	2.14	0.0019	1.92	2.38	1.54	2.44	0.90
14	15	2.51	0.0000+	2.48	2.55	2.38	2.63	0.25
15	14	4.18	0.0054	3.68	4.72	2.33	4.88	2.55
16	15	2.90	0.0000+	2.88	2.93	2.78	2.99	0.21
17	5	2.64	0.0001	2.60	2.70	2.56	2.70	0.14
18	8	1.30	0.0030	1.07	1.54	0.60	1.53	0.93
19	9	6.78	0.0081	5.96	7.65	5.56	8.33	2.78
20	6	3.95	0.0239	2.83	5.25	3.03	6.25	3.22
21	15	4.08	0.0081	3.47	4.73	2.70	5.71	3.01
22	22	2.13	0.0007	2.00	2.27	1.12	3.06	1.94
23	6	2.91	0.0159	2.12	3.83	1.64	3.70	2.06
24	8	1.97	0.0028	1.70	2.26	1.08	2.13	1.05
25	11	2.15	0.0056	1.77	2.56	1.54	3.03	1.49
26	8	2.01	0.0002	1.93	2.08	1.91	2.25	0.34
27	10	4.67	0.0155	3.76	5.69	3.13	6.67	3.54
28	9	2.86	0.0000+	2.82	2.90	2.74	2.94	0.20
29	7	2.77	0.0098	2.17	3.43	1.64	3.33	1.69
30	6	1.69	0.0081	1.26	2.19	1.02	2.13	1.11

Table 16. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit Five (Continued)				
31	22	2.46	0.0028	2.18	2.75	1.37	3.23	1.86
32	14	1.28	0.0027	1.08	1.50	0.92	1.94	1.02
33	15	2.68	0.0003	2.58	2.78	2.53	3.51	0.98
34	4	4.26	0.0249	2.89	5.89	2.56	5.00	2.44
35	2	2.23	0.0000+	2.16	2.31	2.22	2.25	0.03
36	8	3.85	0.0138	3.04	4.76	2.33	4.88	2.55
37	12	2.99	0.0084	2.45	3.57	2.08	4.44	2.36
38	15	2.60	0.0038	2.27	2.96	1.41	3.28	1.87
39	3	2.39	0.0253	1.18	4.01	1.52	2.90	1.38
40	3	6.83	0.0016	6.25	7.43	6.45	7.14	0.69
41	17	4.98	0.0071	4.36	5.64	2.86	6.25	3.39
42	11	2.39	0.0071	1.95	2.88	1.69	3.39	1.69
43	10	3.72	0.0129	2.97	4.54	2.50	5.41	2.91
				Unit Six				
1	16	3.98	0.0036	3.58	4.40	2.22	4.54	2.32
2	2	7.41	0.0003	6.84	8.00	7.32	7.50	0.18
3	11	3.82	0.0035	3.42	4.24	2.41	4.88	2.47
4	9	3.24	0.0016	2.98	3.51	3.03	4.48	1.45
5	14	3.14	0.0017	2.89	3.40	2.75	4.59	1.83
6	11	4.51	0.0020	4.19	4.85	4.11	5.63	1.52
7	9	3.63	0.0000+	3.60	3.66	3.57	3.70	0.13
8	21	3.01	0.0169	2.29	3.83	0.00	4.76	4.76
9	4	6.88	0.0234	5.17	8.81	6.06	9.38	3.32
10	11	3.01	0.0006	2.86	3.17	2.75	3.88	1.13
11	15	2.58	0.0018	2.35	2.82	1.45	2.86	1.41
12	15	3.14	0.0000+	3.12	3.16	3.08	3.23	0.15
13	10	2.45	0.0041	2.10	2.83	1.54	3.25	1.71
14	15	3.68	0.0007	3.51	3.86	2.47	3.95	1.48
15	14	4.57	0.0023	4.22	4.93	2.33	5.00	2.67

Table 16. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
Unit Six (Continued)								
16	15	3.84	0.0025	3.51	4.19	2.78	4.48	1.70
17	5	2.65	0.0001	2.60	2.70	2.56	2.70	0.14
18	8	2.08	0.0005	1.97	2.21	1.79	2.29	0.50
19	9	6.49	0.0085	5.66	7.36	5.41	8.57	3.16
20	6	3.95	0.0238	2.83	5.25	2.94	6.06	3.12
21	15	4.86	0.0059	4.30	5.46	2.63	5.71	3.08
22	22	2.99	0.0011	2.80	3.20	1.98	4.49	2.51
23	6	4.11	0.0068	3.48	4.80	3.57	5.45	1.88
24	8	3.29	0.0051	2.82	3.79	2.06	4.30	2.24
25	11	4.99	0.0029	4.57	5.42	4.35	6.25	1.90
26	8	4.00	0.0021	3.66	4.35	3.16	4.90	1.74
27	10	6.41	0.0001	6.32	6.51	6.25	6.67	0.42
28	9	4.12	0.0019	3.80	4.45	2.86	4.41	1.55
29	7	4.94	0.0001	4.88	5.01	4.76	5.00	0.24
30	6	3.60	0.0092	2.92	4.36	3.03	5.26	2.23
31	22	3.48	0.0012	3.27	3.71	2.94	4.69	1.75
32	14	1.86	0.0001	1.82	1.89	1.67	1.96	0.29
33	15	3.92	0.0012	3.68	4.17	2.53	5.26	2.73
34	4	4.97	0.0003	4.79	5.15	4.76	5.13	0.37
35	2	2.23	0.0000+	2.16	2.31	2.22	2.25	0.03
36	8	6.98	0.0049	6.32	7.66	4.76	7.89	3.13
37	12	4.34	0.0000+	4.30	4.38	4.17	4.44	0.28
38	15	3.74	0.0031	3.38	4.12	2.74	4.84	2.10
39	3	4.41	0.0003	4.22	4.61	4.35	4.55	0.20
40	3	6.83	0.0016	6.25	7.43	6.45	7.14	0.69
41	17	6.77	0.0041	6.22	7.34	5.88	9.09	3.21
42	11	3.04	0.0045	2.63	3.47	1.67	3.45	1.78
43	10	3.71	0.0124	2.98	4.52	2.44	5.13	2.69

Table 16. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
Unit Seven								
1	16	1.78	0.0421	0.96	2.86	0.00	11.36	11.36
2	2	2.47	0.0001	2.28	2.67	2.44	2.50	0.06
3	11	4.27	0.0023	3.92	4.63	3.49	4.94	1.45
4	9	5.63	0.0035	5.13	6.15	4.48	6.25	1.77
5	14	9.97	0.0005	9.73	10.21	9.18	10.58	1.40
6	11	2.85	0.0049	2.45	3.29	1.37	4.23	2.86
7	9	2.42	0.0000+	2.40	2.44	2.38	2.47	0.09
8	21	1.12	0.0067	0.84	1.43	0.00	2.47	2.47
9	4	0.78	0.2589	0.10	4.26	0.00	3.13	3.13
10	11	3.97	0.0015	3.70	4.25	2.91	4.90	1.99
11	15	0.06	0.0163	0.00+	0.21	0.00	1.45	1.45
12	15	2.34	0.0048	1.99	2.73	1.56	3.22	1.66
13	10	6.70	0.0014	6.37	7.05	5.64	7.69	2.05
14	15	5.51	0.0011	5.24	5.79	4.88	6.41	1.53
15	14	0.00	0.0000	0.00	0.00	0.00	0.00	0.00
16	15	5.71	0.0005	5.53	5.89	4.41	5.97	1.56
17	5	3.97	0.0001	3.89	4.04	3.84	4.05	0.21
18	8	10.32	0.0019	9.81	10.83	9.49	11.31	1.82
19	9	1.93	0.0764	0.77	3.60	0.00	5.88	5.88
20	6	0.00	0.0000	0.00	0.00	0.00	0.00	0.00
21	15	0.20	0.0384	0.01	0.62	0.00	2.78	2.78
22	22	8.41	0.0018	8.01	3.32	6.74	1.13	4.59
23	6	4.12	0.0094	3.38	4.93	3.28	5.45	2.17
24	8	2.24	0.0014	2.03	2.46	2.13	3.09	0.97
25	11	5.61	0.0131	4.69	6.60	4.41	11.29	6.88
26	8	2.57	0.0573	1.33	4.20	0.00	4.90	4.90
27	10	0.00	0.0000	0.00	0.00	0.00	0.00	0.00
28	9	3.15	0.0028	2.82	3.51	2.82	4.29	1.47
29	7	3.02	0.0057	2.54	3.55	1.67	3.33	1.66
30	6	6.90	0.0040	6.27	7.56	6.12	8.16	2.04

Table 16. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
Unit Seven (Continued)								
31	22	3.94	0.0023	3.62	4.27	1.59	4.76	3.17
32	14	9.47	0.0007	9.20	9.74	8.33	10.18	1.85
33	15	4.96	0.0018	4.64	5.29	3.95	6.33	2.38
34	4	2.49	0.0002	2.40	2.58	2.38	2.56	0.18
35	2	3.35	0.0000+	3.23	3.47	3.33	3.37	0.04
36	8	0.15	0.0635	0.01	0.74	0.00	2.38	2.38
37	12	0.02	0.0155	0.01	0.12	0.00	2.22	2.22
38	15	2.26	0.0114	1.74	2.86	1.54	6.56	5.02
39	3	2.94	0.0002	2.82	3.07	2.90	3.03	0.13
40	3	0.00	0.0000	0.00	0.00	0.00	0.00	0.00
41	17	0.01	0.0103	0.01	0.08	0.00	2.94	2.94
42	11	1.96	0.0043	1.64	2.30	1.64	3.39	1.75
43	10	0.00	0.0000	0.00	0.00	0.00	0.00	0.00
Unit Eight								
1	16	10.70	0.0023	10.18	11.22	8.70	13.64	4.94
2	2	9.88	0.0004	9.12	10.66	9.76	10.00	0.24
3	11	5.71	0.0014	5.40	6.03	4.82	6.17	1.35
4	9	7.18	0.0027	6.69	7.68	5.97	7.81	1.84
5	14	6.47	0.0004	6.30	6.63	5.66	6.73	1.07
6	11	8.05	0.0010	7.74	8.37	6.85	8.45	1.60
7	9	4.97	0.0010	4.72	5.22	4.76	6.10	1.34
8	21	5.84	0.0011	5.58	6.12	3.95	6.49	2.54
9	4	6.86	0.0189	5.32	8.59	6.06	9.09	3.03
10	11	6.64	0.0011	6.34	6.94	5.88	7.55	1.67
11	15	6.99	0.0001	6.92	7.07	6.76	7.35	0.59
12	15	10.04	0.0013	9.67	10.42	9.23	11.29	2.06
13	10	8.32	0.0006	8.08	8.56	7.69	8.87	1.18
14	15	8.44	0.0007	8.18	8.71	7.59	9.52	1.93
15	14	7.96	0.0032	7.43	8.51	6.98	9.76	2.78

Table 16. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	Upper	Minimum Value	Maximum Value	Range
				Unit Eight (Continued)				
16	15	8.02	0.0013	7.68	8.37	6.94	8.82	1.88
17	5	5.80	0.0035	5.22	6.41	5.33	6.58	1.25
18	8	5.20	0.0007	4.97	5.43	4.76	5.88	1.12
19	9	9.61	0.0062	8.76	10.49	8.33	11.43	3.10
20	6	7.04	0.0127	5.92	8.24	6.06	9.09	3.03
21	15	5.48	0.0001	5.40	5.56	5.26	5.71	0.45
22	22	6.45	0.0006	6.24	6.66	5.15	7.86	2.71
23	6	6.81	0.0038	6.20	7.45	5.46	7.41	1.95
24	8	5.69	0.0018	5.32	6.07	5.15	6.38	1.23
25	11	6.44	0.0078	5.68	7.25	3.23	7.81	4.58
26	8	5.84	0.1280	3.07	9.42	0.00	9.09	9.09
27	10	7.01	0.0066	6.27	7.79	6.25	9.68	3.43
28	9	7.16	0.0001	7.06	7.25	6.85	7.35	0.50
29	7	4.94	0.0001	4.88	5.01	4.76	5.00	0.24
30	6	12.62	0.0021	12.01	13.24	11.70	13.68	1.98
31	22	7.45	0.0006	7.23	7.67	6.35	8.82	2.47
32	14	8.25	0.0012	7.92	8.59	6.73	9.35	2.62
33	15	5.25	0.0020	4.91	5.60	3.95	7.02	3.07
34	4	4.26	0.0249	2.89	5.89	2.56	5.00	2.44
35	2	8.94	0.0001	8.63	9.26	8.89	8.99	0.09
36	8	7.89	0.0070	7.06	8.76	6.98	10.53	3.55
37	12	8.30	0.0018	7.88	8.72	6.67	8.89	2.22
38	15	6.42	0.0029	5.96	6.89	4.92	8.06	3.14
39	3	7.36	0.0004	7.04	7.68	7.25	7.58	0.33
40	3	6.83	0.0016	6.25	7.43	6.45	7.14	0.69
41	17	8.75	0.0013	8.40	9.10	5.88	9.37	3.49
42	11	8.30	0.0010	7.99	8.62	6.67	8.62	1.95
43	10	8.36	0.0040	7.73	9.01	7.50	10.26	2.76

Table 16. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
Unit Nine								
1	16	10.98	0.0532	8.58	13.63	0.00	13.95	13.95
2	2	19.76	0.0009	18.24	21.32	19.51	20.00	0.49
3	11	5.48	0.0016	5.16	5.82	4.82	6.10	1.28
4	9	6.17	0.0000+	6.10	6.23	5.97	6.25	0.28
5	14	5.85	0.0009	5.61	6.10	4.76	6.67	1.91
6	11	7.64	0.0042	7.03	8.27	5.63	8.45	2.82
7	9	4.28	0.0024	3.91	4.66	3.66	4.88	1.22
8	21	5.01	0.0006	4.83	5.19	3.90	6.02	2.12
9	4	9.23	0.0002	9.04	9.43	9.09	9.38	0.28
10	11	4.24	0.0012	4.00	4.50	3.77	4.95	1.18
11	15	5.92	0.0023	5.52	6.33	4.35	6.94	2.59
12	15	6.28	0.0000+	6.24	6.32	6.15	6.45	0.30
13	10	3.50	0.0017	3.23	3.78	3.17	4.61	1.44
14	15	5.68	0.0013	5.39	5.97	4.82	6.41	1.59
15	14	8.81	0.0030	8.27	9.37	6.98	10.00	3.02
16	15	5.71	0.0005	5.53	5.89	4.41	5.97	1.56
17	5	5.29	0.0001	5.19	5.39	5.13	5.41	0.28
18	8	5.27	0.0006	5.07	5.48	4.76	5.81	1.05
19	9	7.73	0.0054	7.02	8.48	5.71	8.57	2.86
20	6	9.61	0.0050	8.79	10.46	9.09	11.76	2.67
21	15	5.48	0.0001	5.40	5.56	5.26	5.71	0.45
22	22	5.97	0.0006	5.76	6.18	4.95	6.74	1.79
23	6	7.13	0.0006	6.88	7.38	6.56	7.41	0.85
24	8	4.76	0.0021	4.39	5.14	4.26	5.38	1.12
25	11	6.44	0.0074	5.69	7.22	3.23	7.81	4.58
26	8	5.20	0.1091	2.78	8.32	0.00	7.77	7.77
27	10	7.93	0.0080	7.06	8.84	6.45	9.68	3.23
28	9	7.16	0.0001	7.06	7.25	6.85	7.35	0.50
29	7	6.81	0.0020	6.38	7.26	6.35	8.20	1.85
30	6	7.27	0.0002	7.13	7.41	7.07	7.45	0.38

Table 16. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	Upper	Minimum Value	Maximum Value	Range
Unit Nine (Continued)								
31	22	5.64	0.0025	5.25	6.04	4.41	7.94	3.53
32	14	5.29	0.0009	5.06	5.53	4.46	5.88	1.42
33	15	4.52	0.0017	4.22	4.83	3.90	5.26	1.36
34	4	6.79	0.0166	5.34	8.39	5.00	7.69	2.69
35	2	5.59	0.000+	5.39	5.79	5.56	5.62	0.06
36	8	7.43	0.1555	4.00	11.81	0.00	9.76	9.76
37	12	9.54	0.0039	8.89	10.20	8.51	12.50	3.99
38	15	4.72	0.0258	3.59	5.99	0.00	6.45	6.45
39	3	7.83	0.0065	6.61	9.14	7.25	8.70	1.45
40	3	10.24	0.0025	9.37	11.15	9.68	10.71	1.03
41	17	11.17	0.0025	10.63	11.73	8.82	12.50	3.68
42	11	7.83	0.0024	7.36	8.31	6.67	8.62	1.95
43	10	12.45	0.0009	12.09	12.82	10.81	12.82	2.01

Table 17. Duration (expressed in seconds) of each unit within the assertion display of 13 Anolis nebulosus from Nayarit, Mexico, which had their displays recorded one year earlier; times computed from displays filmed in the laboratory, summer, 1968.

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit One				
1	2	0.611	0.000	0.000	0.000	0.611	0.611	0.000
4	2	1.389	0.000	0.000	0.000	1.389	1.389	0.000
5	17	1.389	0.008	1.374	1.403	1.333	1.444	0.111
6	2	1.361	0.028	1.186	1.537	1.333	1.389	0.056
11	10	1.428	0.014	1.401	1.454	1.333	1.500	0.167
17	3	1.519	0.019	1.464	1.573	1.500	1.556	0.056
19	6	0.694	0.012	0.669	0.719	0.667	0.722	0.056
20	5	0.611	0.018	0.574	0.649	0.556	0.667	0.111
23	5	1.022	0.022	0.975	1.070	1.000	1.111	0.111
25	3	1.630	0.074	1.413	1.846	1.556	1.778	0.222
34	1	0.611	0.000	0.000	0.000	0.611	0.611	0.000
36	6	0.759	0.023	0.712	0.806	0.667	0.833	0.166
42	5	1.089	0.014	1.060	1.118	1.056	1.111	0.055
				Unit Two				
1	2	0.111	0.000	0.000	0.000	0.111	0.111	0.000
4	2	0.361	0.028	0.186	0.537	0.333	0.389	0.056
5	17	0.536	0.008	0.522	0.550	0.500	0.611	0.111
6	2	0.306	0.028	0.130	0.481	0.278	0.333	0.055
11	10	0.378	0.011	0.357	0.398	0.333	0.444	0.111
17	3	0.278	0.000	0.000	0.000	0.278	0.278	0.000
19	6	0.148	0.012	0.125	0.172	0.111	0.167	0.056
20	5	0.122	0.011	0.099	0.146	0.111	0.167	0.056
23	5	0.189	0.014	0.160	0.218	0.167	0.222	0.055
25	3	0.222	0.032	0.129	0.316	0.167	0.278	0.111
34	1	0.111	0.000	0.000	0.000	0.111	0.111	0.000
36	6	0.111	0.014	0.082	0.140	0.056	0.167	0.111
42	5	0.322	0.032	0.253	0.391	0.278	0.444	0.166

Table 17. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	Upper	Minimum Value	Maximum Value	Range
				Unit Three				
1	2	0.278	0.000	0.000	0.000	0.278	0.278	0.000
4	2	0.444	0.000	0.000	0.000	0.444	0.444	0.000
5	17	0.366	0.013	0.344	0.388	0.333	0.500	0.167
6	2	0.361	0.028	0.186	0.537	0.333	0.389	0.056
11	10	0.339	0.006	0.329	0.349	0.333	0.389	0.056
17	3	0.556	0.000	0.000	0.000	0.556	0.556	0.000
19	6	0.250	0.012	0.225	0.275	0.222	0.278	0.056
20	5	0.244	0.014	0.215	0.273	0.222	0.278	0.056
23	5	0.478	0.014	0.449	0.507	0.444	0.500	0.056
25	3	0.296	0.019	0.242	0.350	0.278	0.333	0.055
34	1	0.222	0.000	0.000	0.000	0.222	0.222	0.000
36	6	0.287	0.022	0.242	0.332	0.222	0.333	0.111
42	5	0.467	0.022	0.419	0.514	0.389	0.500	0.111
				Unit Four				
1	2	0.528	0.028	0.352	0.703	0.500	0.556	0.056
4	2	1.694	0.028	1.519	1.870	1.667	1.722	0.055
5	17	1.350	0.136	1.113	1.587	0.500	1.833	1.333
6	2	1.583	1.944	0.356	2.811	1.389	1.778	0.389
11	10	1.844	0.041	1.769	1.920	1.667	2.111	0.444
17	3	2.000	0.032	1.906	2.094	1.944	2.055	0.111
19	6	0.352	0.012	0.328	0.375	0.333	0.389	0.056
20	5	0.356	0.022	0.308	0.403	0.278	0.389	0.111
23	5	1.589	0.028	1.528	1.649	1.500	1.667	0.167
25	3	1.056	0.000	0.000	0.000	1.056	1.056	0.000
34	1	0.778	0.000	0.000	0.000	0.778	0.778	0.000
36	6	0.556	0.020	0.515	0.596	0.500	0.611	0.111
42	5	1.333	0.018	1.296	1.371	1.278	1.389	0.111

Table 17. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit Five				
1	2	0.111	0.000	0.000	0.000	0.111	0.111	0.000
4	2	0.111	0.000	0.000	0.000	0.111	0.111	0.000
5	17	0.127	0.008	0.114	0.141	0.111	0.222	0.111
6	2	0.111	0.000	0.000	0.000	0.111	0.111	0.000
11	10	0.106	0.006	0.095	0.116	0.056	0.111	0.055
17	3	0.111	0.000	0.000	0.000	0.111	0.111	0.000
19	6	0.130	0.012	0.106	0.153	0.111	0.167	0.056
20	5	0.089	0.014	0.060	0.118	0.056	0.111	0.055
23	5	0.111	0.000	0.000	0.000	0.111	0.111	0.000
25	3	0.074	0.019	0.020	0.128	0.056	0.111	0.055
34	1	0.111	0.000	0.000	0.000	0.111	0.111	0.000
36	6	0.083	0.012	0.058	0.108	0.056	0.111	0.055
42	5	0.067	0.011	0.043	0.090	0.056	0.111	0.055
				Unit Six				
1	2	0.111	0.000	0.000	0.000	0.111	0.111	0.000
4	2	0.167	0.000	0.000	0.000	0.167	0.167	0.000
5	17	0.199	0.013	0.177	0.221	0.111	0.333	0.222
6	2	0.139	0.028	0.000	0.314	0.111	0.167	0.056
11	10	0.150	0.008	0.134	0.166	0.111	0.167	0.056
17	3	0.167	0.000	0.000	0.000	0.167	0.167	0.000
19	6	0.148	0.012	0.125	0.172	0.111	0.167	0.056
20	5	0.100	0.011	0.076	0.124	0.056	0.111	0.055
23	5	0.167	0.000	0.000	0.000	0.167	0.167	0.000
25	3	0.130	0.019	0.076	0.184	0.111	0.167	0.056
34	1	0.167	0.000	0.000	0.000	0.167	0.167	0.000
36	6	0.148	0.012	0.125	0.172	0.111	0.167	0.056
42	5	0.111	0.000	0.000	0.000	0.111	0.111	0.000

Table 17. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit Seven				
1	2	0.000	0.000	0.000	0.000	0.000	0.000	0.000
4	2	0.222	0.056	0.000	0.573	0.167	0.278	0.111
5	17	0.451	0.090	0.294	0.608	0.222	1.500	1.278
6	2	0.139	0.083	0.000	0.665	0.056	0.222	0.166
11	10	0.044	0.007	0.031	0.058	0.000	0.056	0.056
17	3	0.167	0.000	0.000	0.000	0.167	0.167	0.000
19	6	0.000	0.000	0.000	0.000	0.000	0.000	0.000
20	5	0.011	0.011	0.000	0.035	0.000	0.056	0.056
23	5	0.167	0.018	0.129	0.204	0.111	0.222	0.111
25	3	0.315	0.067	0.120	0.510	0.222	0.444	0.222
34	1	0.000	0.000	0.000	0.000	0.000	0.000	0.000
36	6	0.056	0.000	0.000	0.000	0.056	0.056	0.000
42	5	0.111	0.000	0.000	0.000	0.111	0.111	0.000
				Unit Eight				
1	2	0.250	0.028	0.075	0.425	0.222	0.278	0.056
4	2	0.222	0.000	0.000	0.000	0.222	0.222	0.000
5	17	0.242	0.042	0.168	0.316	0.111	0.889	0.778
6	2	0.278	0.000	0.000	0.000	0.278	0.278	0.000
11	10	0.361	0.009	0.344	0.378	0.333	0.389	0.056
17	3	0.278	0.000	0.000	0.000	0.278	0.278	0.000
19	6	0.222	0.000	0.000	0.000	0.222	0.222	0.000
20	5	0.100	0.011	0.076	0.124	0.056	0.111	0.055
23	5	0.411	0.022	0.364	0.458	0.333	0.444	0.111
25	3	0.241	0.037	0.133	0.349	0.167	0.278	0.111
34	1	0.111	0.000	0.000	0.000	0.111	0.111	0.000
36	6	0.176	0.009	0.157	0.195	0.167	0.222	0.055
42	5	0.311	0.014	0.282	0.340	0.278	0.333	0.055

Table 17. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit Nine				
1	2	0.250	0.028	0.075	0.425	0.222	0.278	0.056
4	2	0.250	0.028	0.075	0.425	0.222	0.278	0.056
5	17	0.186	0.008	0.172	0.201	0.111	0.222	0.111
6	2	0.250	0.028	0.075	0.425	0.222	0.278	0.056
11	10	0.244	0.009	0.228	0.261	0.222	0.278	0.056
17	3	0.278	0.000	0.000	0.000	0.278	0.278	0.000
19	6	0.222	0.000	0.000	0.000	0.222	0.222	0.000
20	5	0.156	0.011	0.132	0.179	0.111	0.167	0.056
23	5	0.300	0.014	0.271	0.329	0.278	0.333	0.055
25	3	0.185	0.019	0.131	0.239	0.167	0.222	0.055
34	1	0.167	0.000	0.000	0.000	0.167	0.167	0.000
36	6	0.231	0.017	0.197	0.266	0.167	0.278	0.111
42	5	0.267	0.011	0.243	0.290	0.222	0.278	0.056
				Total Display				
1	2	2.250	0.028	2.075	2.425	2.222	2.278	0.056
4	2	4.861	0.028	4.686	5.037	4.833	4.889	0.056
5	17	4.846	0.061	4.740	4.953	4.278	5.167	0.889
6	2	4.528	0.083	4.002	5.054	4.444	4.611	1.667
11	10	4.894	0.038	4.824	4.965	4.667	5.056	0.389
17	3	5.352	0.049	5.209	5.495	5.278	5.444	0.166
19	6	2.167	0.014	2.138	2.196	2.111	2.222	0.111
20	5	1.789	0.041	1.702	1.876	1.722	1.944	0.222
23	5	4.433	0.048	4.331	4.535	4.333	4.611	0.278
25	3	4.148	0.067	3.953	4.343	4.056	4.278	0.222
34	1	2.278	0.000	0.000	0.000	2.278	2.278	0.000
36	6	2.407	0.031	2.345	2.470	2.278	2.500	0.222
42	5	4.078	0.022	4.030	4.125	4.000	4.111	0.111

Tabl 18. The distribution of variation (expressed by an analysis of variance) found in the displays of the sampled population of *Anolis nebulosus* from Nayarit, Mexico, appearing in Table 17.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Value	Percent of Variation
		Unit One			
Among Individuals	7.627	12	0.636	299.210	98.35
Within Individuals	0.115	54	0.002		1.65
Total Variation	7.742	66			
		Unit Two			
Among Individuals	1.709	12	0.142	101.219	95.25
Within Individuals	0.076	54	0.001		4.75
Total Variation	1.785	66			
		Unit Three			
Among Individuals	0.474	12	0.039	24.575	82.50
Within Individuals	0.087	54	0.002		17.50
Total Variation	0.561	66			
		Unit Four			
Among Individuals	19.598	12	1.633	16.667	75.81
Within Individuals	5.291	54	0.098		24.19
Total Variation	24.889	66			
		Unit Five			
Among Individuals	0.027	12	0.002	3.281	31.33
Within Individuals	0.037	54	0.001		68.67
Total Variation	0.064	66			

Table 18. (Continued)

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Value	Percent of Variation
		Unit Six			
Among Individuals	0.067	12	0.006	4.667	42.31
Within Individuals	0.064	54	0.001		57.69
Total Variation	0.131	66			
		Unit Seven			
Among Individuals	2.046	12	0.170	4.090	38.19
Within Individuals	2.251	54	0.042		61.81
Total Variation	4.297	66			
		Unit Eight			
Among Individuals	0.442	12	0.037	3.800	35.90
Within Individuals	0.523	54	0.010		64.10
Total Variation	0.965	66			
		Unit Nine			
Among Individuals	0.111	12	0.009	10.033	64.37
Within Individuals	0.050	54	0.001		35.63
Total Variation	0.161	66			
		Total Display			
Among Individuals	97.457	12	8.121	331.275	98.51
Within Individuals	1.324	54	0.025		1.49
Total Variation	98.781	66			

Table 19. Proportion (expressed as percent) of each unit to the total duration of the assertion display of 13 *Anolis nebulosus* from Nayarit, Mexico, which had their displays recorded one year earlier; percentages computed from displays filmed in the laboratory, summer, 1968.

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit One				
1	2	27.16	0.0014	25.07	29.31	26.83	27.50	0.67
4	2	28.57	0.0003	27.55	29.61	28.41	28.74	0.33
5	17	28.72	0.0022	27.98	29.47	26.67	32.47	5.80
6	2	30.06	0.0000+	29.68	30.44	30.00	30.12	0.12
11	10	29.17	0.0007	28.72	29.63	27.47	30.23	2.76
17	3	28.37	0.0002	27.99	28.76	28.13	28.57	0.44
19	6	32.04	0.0027	31.07	33.02	30.77	33.33	2.56
20	5	34.17	0.0068	32.51	35.84	31.25	35.48	4.23
23	5	23.05	0.0011	22.46	23.64	22.50	24.10	1.60
25	3	39.24	0.0141	35.88	42.66	37.84	41.56	3.72
34	1	26.83	0.0000	0.00	0.00	26.83	26.83	0.00
36	6	31.50	0.0056	30.11	32.92	29.27	33.33	4.06
42	5	26.71	0.0025	25.77	27.65	25.68	27.78	2.10
				Unit Two				
1	2	4.94	0.0002	4.56	5.33	4.88	5.00	0.12
4	2	7.42	0.0102	4.43	11.09	6.90	7.95	1.05
5	17	11.08	0.0018	10.62	11.55	9.89	13.58	3.69
6	2	6.73	0.0095	3.98	10.14	6.25	7.23	0.98
11	10	7.71	0.0021	7.27	8.16	6.74	9.20	2.44
17	3	5.19	0.0001	5.05	5.33	5.10	5.26	0.16
19	6	6.79	0.0124	5.70	7.96	5.13	7.89	2.76
20	5	6.77	0.0073	5.89	7.71	6.25	8.57	2.32
23	5	4.24	0.0048	3.66	4.85	3.75	5.06	1.31
25	3	5.30	0.0256	3.40	7.58	4.05	6.49	2.44
34	1	4.88	0.0000	0.00	0.00	4.88	4.88	0.00
36	6	4.54	0.0258	3.29	5.98	2.22	7.32	5.10
42	5	7.83	0.0187	6.34	9.47	6.76	10.81	4.05

Table 19. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit Three				
1	2	12.35	0.0005	11.40	13.33	12.20	12.50	0.30
4	2	9.14	0.0001	8.82	9.48	9.09	9.20	0.11
5	17	7.54	0.0026	7.07	8.01	6.45	10.11	3.66
6	2	7.97	0.0197	3.85	13.41	7.23	8.75	1.52
11	10	6.92	0.0006	6.70	7.15	6.59	7.95	1.36
17	3	10.38	0.0002	10.11	10.66	10.20	10.53	0.33
19	6	11.51	0.0082	10.37	12.70	10.00	12.82	2.82
20	5	13.68	0.0207	11.64	15.85	11.43	16.13	4.70
23	5	10.77	0.0026	10.11	11.45	10.00	11.54	1.54
25	3	7.14	0.0088	5.79	8.61	6.49	8.11	1.62
34	1	9.76	0.0000	0.00	0.00	9.76	9.76	0.00
36	6	11.83	0.0180	10.14	13.63	9.30	13.64	4.34
42	5	11.42	0.0076	10.27	12.63	9.46	12.33	2.87
				Unit Four				
1	2	23.44	0.0124	17.75	29.65	22.50	24.39	1.89
4	2	34.86	0.0065	30.08	39.80	34.09	35.63	1.54
5	17	26.62	0.1036	21.81	31.72	9.68	36.26	26.59
6	2	34.86	0.1471	14.41	58.79	31.25	38.55	7.30
11	10	37.64	0.0037	36.57	38.73	35.63	41.76	6.13
17	3	37.37	0.0008	36.57	38.16	36.84	37.76	0.92
19	6	16.22	0.0042	15.27	17.19	15.38	17.95	2.57
20	5	19.80	0.0182	17.56	22.14	16.13	21.88	5.75
23	5	35.84	0.0039	34.58	37.11	34.18	37.50	3.32
25	3	25.46	0.0022	24.28	26.65	24.68	26.03	1.35
34	1	34.15	0.0000	0.00	0.00	34.15	34.15	0.00
36	6	23.05	0.0089	21.48	24.67	20.45	25.58	5.13
42	5	32.70	0.0018	31.85	33.54	31.51	33.78	2.27

Table 19. (Continued)

Indi-vidual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	Upper	Minimum Value	Maximum Value	Range
				Unit Five				
1	2	4.94	0.0002	4.56	5.33	4.88	5.00	0.12
4	2	2.29	0.0000+	2.20	2.37	2.27	2.30	0.03
5	17	2.62	0.0033	2.30	2.95	2.15	4.94	2.79
6	2	2.45	0.0002	2.18	2.75	2.41	2.50	0.09
11	10	2.14	0.0022	1.90	2.40	1.10	2.38	1.28
17	3	2.08	0.0000+	2.02	2.13	2.04	2.11	0.07
19	6	5.93	0.0123	4.92	7.03	5.00	7.69	2.69
20	5	4.84	0.0310	3.36	6.58	3.13	6.45	3.32
23	5	2.51	0.0001	2.45	2.56	2.41	2.56	0.15
25	3	1.74	0.0289	0.68	3.27	1.30	2.74	1.44
34	1	4.88	0.0000	0.00	0.00	4.88	4.88	0.00
36	6	3.38	0.0225	2.37	4.56	2.22	4.88	2.66
42	5	1.60	0.0098	1.11	2.17	1.35	2.74	1.39
				Unit Six				
1	2	4.94	0.0002	4.56	5.33	4.88	5.00	0.12
4	2	3.43	0.0000+	3.31	3.55	3.41	3.45	0.04
5	17	4.06	0.0044	3.62	4.53	2.60	7.41	4.81
6	2	3.04	0.0381	0.27	8.65	2.41	3.75	1.34
11	10	3.04	0.0029	2.72	3.39	2.20	3.57	1.37
17	3	3.11	0.0001	3.03	3.20	3.06	3.16	0.10
19	6	6.79	0.0124	5.70	7.96	5.13	7.89	2.76
20	5	5.50	0.0204	4.20	6.98	3.23	6.45	3.22
23	5	3.76	0.0001	3.68	3.85	3.62	3.85	0.23
25	3	3.10	0.0168	1.92	4.54	2.60	4.05	1.45
34	1	7.32	0.0000	0.00	0.00	7.32	7.32	0.00
36	6	6.11	0.0117	5.11	7.19	4.55	7.32	2.77
42	5	2.73	0.0000+	2.69	2.76	2.70	2.78	0.08

Table 19. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit Seven				
1	2	0.00	0.0000	0.00	0.00	0.00	0.00	0.00
4	2	4.50	0.0726	0.19	14.03	3.45	5.68	2.23
5	17	8.44	0.0781	5.93	11.35	4.44	29.03	24.59
6	2	2.79	0.3333	3.83	25.77	1.20	5.00	3.80
11	10	0.73	0.0203	0.35	1.24	0.00	1.19	1.19
17	3	3.11	0.0001	3.03	3.20	3.06	3.16	0.10
19	6	0.00	0.0000	0.00	0.00	0.00	0.00	0.00
20	5	0.13	0.1304	0.17	1.27	0.00	3.23	3.23
23	5	3.71	0.0097	2.96	4.55	2.53	4.82	2.29
25	3	7.44	0.0899	3.52	12.67	5.48	10.81	5.33
34	1	0.00	0.0000	0.00	0.00	0.00	0.00	0.00
36	6	2.31	0.0001	2.25	2.37	2.22	2.44	0.22
42	5	2.73	0.0000+	2.69	2.76	2.70	2.78	0.08
				Unit Eight				
1	2	11.07	0.0306	5.14	18.89	10.00	12.20	2.20
4	2	4.57	0.0000+	4.41	4.74	4.55	4.60	0.05
5	17	4.69	0.0291	3.51	6.03	2.47	20.78	18.31
6	2	6.14	0.0006	5.44	6.87	6.02	6.25	0.23
11	10	7.37	0.0013	7.03	7.72	6.59	8.05	1.46
17	3	5.19	0.0001	5.05	5.33	5.10	5.26	0.16
19	6	10.26	0.0001	10.12	10.40	10.00	10.53	0.53
20	5	5.50	0.0204	4.20	6.98	3.23	6.45	3.22
23	5	9.26	0.0099	8.07	10.52	7.23	10.13	2.90
25	3	5.73	0.0384	3.36	8.68	4.05	6.85	2.80
34	1	4.88	0.0000	0.00	0.00	4.88	4.88	0.00
36	6	7.29	0.0056	6.53	8.10	6.67	9.30	2.63
42	5	7.61	0.0032	6.99	8.26	6.85	8.11	1.26

Table 19. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit Nine				
1	2	11.09	0.0477	4.01	21.12	9.76	12.50	2.74
4	2	5.13	0.0185	2.02	9.57	4.55	5.75	1.20
5	17	3.81	0.0016	3.55	4.09	2.60	4.65	2.05
6	2	5.51	0.0246	1.89	10.87	4.82	6.25	1.43
11	10	4.98	0.0020	4.63	5.34	4.40	5.95	1.55
17	3	5.19	0.0001	5.05	5.33	5.10	5.26	0.16
19	6	10.26	0.0001	10.12	10.40	10.00	10.53	0.53
20	5	8.65	0.0119	7.39	10.00	6.45	9.68	3.23
23	5	6.75	0.0029	6.19	7.34	6.25	7.59	1.34
25	3	4.45	0.0142	3.13	5.99	3.90	5.48	1.58
34	1	7.32	0.0000	0.00	0.00	7.32	7.32	0.00
36	6	9.54	0.0109	8.34	10.81	7.32	11.36	4.04
42	5	6.53	0.0036	5.91	7.17	5.40	6.94	1.54

Table 20. Duration (expressed in seconds) of each unit within the assertion display of Anolis nebulosus from Nayarit, Mexico, computed from displays filmed in the field, spring, 1968.

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit One				
1	13	1.624	0.013	1.601	1.647	1.556	1.722	0.166
2	4	1.167	0.000	0.000	0.000	1.167	1.167	0.000
3	11	1.293	0.020	1.257	1.329	1.167	1.389	0.222
4	4	0.819	0.069	0.656	0.983	0.611	0.889	0.278
5	4	0.569	0.027	0.507	0.632	0.500	0.611	0.111
6	4	0.722	0.023	0.669	0.776	0.667	0.778	0.111
7	2	1.194	0.028	1.019	1.370	1.167	1.222	0.055
8	1	1.500	0.000	0.000	0.000	1.500	1.500	0.000
9	1	1.111	0.000	0.000	0.000	1.111	1.111	0.000
10	5	1.133	0.022	1.086	1.181	1.111	1.222	0.111
11	5	0.867	0.022	0.819	0.914	0.833	0.944	0.111
12	1	1.000	0.000	0.000	0.000	1.000	1.000	0.000
13	1	1.167	0.000	0.000	0.000	1.167	1.167	0.000
				Unit Two				
1	13	0.346	0.014	0.321	0.372	0.278	0.444	0.166
2	4	0.167	0.000	0.000	0.000	0.167	0.167	0.000
3	11	0.202	0.008	0.187	0.217	0.167	0.222	0.055
4	4	0.167	0.023	0.113	0.220	0.111	0.222	0.111
5	4	0.194	0.016	0.157	0.232	0.167	0.222	0.055
6	4	0.181	0.014	0.148	0.213	0.167	0.222	0.055
7	2	0.167	0.000	0.000	0.000	0.167	0.167	0.000
8	1	0.333	0.000	0.000	0.000	0.333	0.333	0.000
9	1	0.222	0.000	0.000	0.000	0.222	0.222	0.000
10	5	0.167	0.000	0.000	0.000	0.167	0.167	0.000
11	5	0.233	0.011	0.210	0.257	0.222	0.278	0.056
12	1	0.333	0.000	0.000	0.000	0.333	0.333	0.000
13	1	0.167	0.000	0.000	0.000	0.167	0.167	0.000

Table 20. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit Three				
1	13	0.419	0.008	0.405	0.433	0.389	0.444	0.055
2	4	0.333	0.000	0.000	0.000	0.333	0.333	0.000
3	11	0.288	0.007	0.276	0.300	0.278	0.333	0.055
4	4	0.569	0.014	0.537	0.602	0.556	0.611	0.055
5	4	0.222	0.000	0.000	0.000	0.222	0.222	0.000
6	4	0.236	0.014	0.203	0.269	0.222	0.278	0.056
7	2	0.278	0.000	0.000	0.000	0.278	0.278	0.000
8	1	0.333	0.000	0.000	0.000	0.333	0.333	0.000
9	1	0.333	0.000	0.000	0.000	0.333	0.333	0.000
10	5	0.422	0.014	0.393	0.451	0.389	0.444	0.055
11	5	0.433	0.021	0.389	0.478	0.389	0.500	0.111
12	1	0.278	0.000	0.000	0.000	0.278	0.278	0.000
13	1	0.278	0.000	0.000	0.000	0.278	0.278	0.000
				Unit Four				
1	13	1.073	0.024	1.030	1.115	0.944	1.222	0.278
2	4	1.139	0.016	1.101	1.177	1.111	1.167	0.056
3	11	1.510	0.020	1.475	1.546	1.389	1.611	0.222
4	4	0.403	0.014	0.370	0.435	0.389	0.444	0.055
5	4	0.375	0.027	0.312	0.438	0.333	0.444	0.111
6	4	0.514	0.014	0.481	0.547	0.500	0.556	0.056
7	2	0.806	0.028	0.630	0.981	0.778	0.833	0.055
8	1	1.389	0.000	0.000	0.000	1.389	1.389	0.000
9	1	1.111	0.000	0.000	0.000	1.111	1.111	0.000
10	5	1.311	0.038	1.231	1.391	1.222	1.444	0.222
11	5	0.644	0.014	0.615	0.673	0.611	0.667	0.056
12	1	0.833	0.000	0.000	0.000	0.833	0.833	0.000
13	1	0.833	0.000	0.000	0.000	0.833	0.833	0.000

Table 20. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
Unit Five								
1	13	0.120	0.006	0.109	0.130	0.111	0.167	0.056
2	4	0.111	0.000	0.000	0.000	0.111	0.111	0.000
3	11	0.101	0.007	0.089	0.113	0.056	0.111	0.055
4	4	0.069	0.014	0.037	0.102	0.056	0.111	0.055
5	4	0.111	0.000	0.000	0.000	0.111	0.111	0.000
6	4	0.111	0.000	0.000	0.000	0.111	0.111	0.000
7	2	0.083	0.028	0.000	0.259	0.056	0.111	0.055
8	1	0.111	0.000	0.000	0.000	0.111	0.111	0.000
9	1	0.111	0.000	0.000	0.000	0.111	0.111	0.000
10	5	0.111	0.000	0.000	0.000	0.111	0.111	0.000
11	5	0.111	0.000	0.000	0.000	0.111	0.111	0.000
12	1	0.111	0.000	0.000	0.000	0.111	0.111	0.000
13	1	0.056	0.000	0.000	0.000	0.056	0.056	0.000
Unit Six								
1	13	0.184	0.007	0.171	0.197	0.167	0.222	0.056
2	4	0.167	0.000	0.000	0.000	0.167	0.167	0.000
3	11	0.126	0.008	0.112	0.140	0.111	0.167	0.056
4	4	0.111	0.000	0.000	0.000	0.111	0.111	0.000
5	4	0.111	0.000	0.000	0.000	0.111	0.111	0.000
6	4	0.139	0.016	0.101	0.177	0.111	0.167	0.056
7	2	0.111	0.000	0.000	0.000	0.111	0.111	0.000
8	1	0.167	0.000	0.000	0.000	0.167	0.167	0.000
9	1	0.111	0.000	0.000	0.000	0.111	0.111	0.000
10	5	0.156	0.011	0.132	0.179	0.111	0.167	0.056
11	5	0.200	0.014	0.171	0.229	0.167	0.222	0.055
12	1	0.111	0.000	0.000	0.000	0.111	0.111	0.000
13	1	0.111	0.000	0.000	0.000	0.111	0.111	0.000

Table 20. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	Upper	Minimum Value	Maximum Value	Range
				Unit Seven				
1	13	0.436	0.014	0.411	0.461	0.333	0.500	0.167
2	4	0.403	0.014	0.370	0.435	0.389	0.444	0.055
3	11	0.101	0.007	0.089	0.113	0.056	0.111	0.055
4	4	0.125	0.014	0.092	0.158	0.111	0.167	0.056
5	4	0.014	0.014	0.000	0.047	0.000	0.056	0.056
6	4	0.056	0.000	0.000	0.000	0.056	0.056	0.000
7	2	0.139	0.028	0.000	0.314	0.111	0.167	0.056
8	1	0.167	0.000	0.000	0.000	0.167	0.167	0.000
9	1	0.278	0.000	0.000	0.000	0.278	0.278	0.000
10	5	0.056	0.000	0.000	0.000	0.056	0.056	0.000
11	5	0.000	0.000	0.000	0.000	0.000	0.000	0.000
12	1	0.167	0.000	0.000	0.000	0.167	0.167	0.000
13	1	0.167	0.000	0.000	0.000	0.167	0.167	0.000
				Unit Eight				
1	13	0.316	0.007	0.303	0.329	0.278	0.333	0.055
2	4	0.250	0.016	0.212	0.288	0.222	0.278	0.056
3	11	0.222	0.000	0.000	0.000	0.222	0.222	0.000
4	4	0.208	0.014	0.176	0.241	0.167	0.222	0.055
5	4	0.111	0.000	0.000	0.000	0.111	0.111	0.000
6	4	0.167	0.000	0.000	0.000	0.167	0.167	0.000
7	2	0.222	0.000	0.000	0.000	0.222	0.222	0.000
8	1	0.222	0.000	0.000	0.000	0.222	0.222	0.000
9	1	0.278	0.000	0.000	0.000	0.278	0.278	0.000
10	5	0.389	0.000	0.000	0.000	0.389	0.389	0.000
11	5	0.278	0.000	0.000	0.000	0.278	0.278	0.000
12	1	0.278	0.000	0.000	0.000	0.278	0.278	0.000
13	1	0.222	0.000	0.000	0.000	0.222	0.222	0.000

Table 20. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit Nine				
1	13	0.265	0.007	0.253	0.277	0.222	0.278	0.056
2	4	0.208	0.014	0.176	0.241	0.167	0.222	0.055
3	11	0.202	0.008	0.187	0.217	0.167	0.222	0.055
4	4	0.222	0.000	0.000	0.000	0.222	0.222	0.000
5	4	0.139	0.016	0.101	0.177	0.111	0.167	0.056
6	4	0.167	0.000	0.000	0.000	0.167	0.167	0.000
7	2	0.167	0.000	0.000	0.000	0.167	0.167	0.000
8	1	0.222	0.000	0.000	0.000	0.222	0.222	0.000
9	1	0.222	0.000	0.000	0.000	0.222	0.222	0.000
10	5	0.311	0.014	0.282	0.340	0.278	0.333	0.055
11	5	0.344	0.021	0.300	0.389	0.278	0.389	0.111
12	1	0.278	0.000	0.000	0.000	0.278	0.278	0.000
13	1	0.167	0.000	0.000	0.000	0.167	0.167	0.000
				Total Display				
1	13	4.782	0.046	4.699	4.865	4.444	5.111	0.667
2	4	3.944	0.023	3.891	3.998	3.889	4.000	0.111
3	11	4.045	0.018	4.013	4.078	3.944	4.111	0.167
4	4	2.694	0.070	2.530	2.859	2.500	2.833	0.333
5	4	1.847	0.042	1.749	1.945	1.778	1.944	0.166
6	4	2.292	0.042	2.194	2.390	2.222	2.389	0.167
7	2	3.167	0.056	2.816	3.517	3.111	3.222	0.111
8	1	4.444	0.000	0.000	0.000	4.444	4.444	0.000
9	1	3.778	0.000	0.000	0.000	3.778	3.778	0.000
10	5	4.056	0.043	3.964	4.147	4.000	4.222	0.222
11	5	3.111	0.056	2.993	3.230	2.944	3.278	0.334
12	1	3.389	0.000	0.000	0.000	3.389	3.389	0.000
13	1	3.167	0.000	0.000	0.000	3.167	3.167	0.000

Table 21. The distribution of variation (expressed by an analysis of variance) found in the displays of the sampled population of Anolis nebulosus from Nayarit, Mexico, appearing in Table 20.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Value	Percent of Variation
		Unit One			
Among Individuals	6.190	12	0.516	135.886	99.26
Within Individuals	0.163	43	0.004		0.74
Total Variation	6.353	55			
		Unit Two			
Among Individuals	0.284	12	0.024	18.974	94.73
Within Individuals	0.054	43	0.001		5.27
Total Variation	0.338	55			
		Unit Three			
Among Individuals	0.492	12	0.041	55.151	98.19
Within Individuals	0.032	43	0.001		1.81
Total Variation	0.524	55			
		Unit Four			
Among Individuals	8.353	12	0.696	165.612	99.40
Within Individuals	0.181	43	0.004		0.60
Total Variation	8.534	55			
		Unit Five			
Among Individuals	0.012	12	0.001	3.111	67.85
Within Individuals	0.014	43	0.000+		32.15
Total Variation	0.026	55			

Table 21. (Continued)

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Value	Percent of Variation
		Unit Six			
Among Individuals	0.055	12	0.005	8.062	87.60
Within Individuals	0.025	43	0.001		12.40
Total Variation	0.080	55			
		Unit Seven			
Among Individuals	1.553	12	0.129	128.036	99.22
Within Individuals	0.043	43	0.001		0.78
Total Variation	1.596	55			
		Unit Eight			
Among Individuals	0.281	12	0.023	72.181	98.61
Witnin Individuals	0.014	43	0.000+		1.39
Total Variation	0.295	55			
		Unit Nine			
Among Individuals	0.188	12	0.016	20.556	95.14
Within Individuals	0.033	43	0.001		4.86
Total Variation	0.221	55			
		Total Display			
Among Individuals	46.354	12	3.863	284.658	99.65
Within Individuals	0.584	43	0.014		0.35
Total Variation	46.938	55			

Table 22. Proportion (expressed as percent) of each unit to the total duration of the assertion display of Anolis nebulosus from Nayarit, Mexico, computed from displays filmed in the field, spring, 1968.

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
Unit One								
1	13	33.97	0.0003	33.66	34.27	32.58	35.00	2.42
2	4	29.58	0.0003	29.18	29.98	29.17	30.00	0.83
3	11	31.95	0.0025	31.11	32.80	29.58	33.80	4.23
4	4	30.22	0.0478	25.61	35.04	24.44	32.65	8.21
5	4	30.84	0.0318	27.04	34.78	26.47	34.38	7.90
6	4	31.50	0.0045	30.04	32.98	30.00	32.56	2.56
7	2	37.72	0.0005	36.36	39.08	37.50	37.93	0.43
8	1	33.75	0.0000	0.00	0.00	33.75	33.75	0.00
9	1	29.41	0.0000	0.00	0.00	29.41	29.41	0.00
10	5	27.93	0.0009	27.38	28.50	27.40	28.95	1.55
11	5	27.85	0.0038	26.69	29.03	26.79	29.82	3.03
12	1	29.51	0.0000	0.00	0.00	29.51	29.51	0.00
13	1	36.84	0.0000	0.00	0.00	36.84	36.84	0.00
Unit Two								
1	13	7.21	0.0031	6.70	7.73	5.62	9.30	3.68
2	4	4.23	0.0000+	4.17	4.28	4.17	4.29	0.12
3	11	4.97	0.0023	4.60	5.36	4.11	5.63	1.52
4	4	6.10	0.0287	4.34	8.15	4.08	7.84	3.76
5	4	10.49	0.0197	8.55	12.59	8.82	12.50	3.68
6	4	7.86	0.0161	6.33	9.54	6.98	10.00	3.02
7	2	5.26	0.0004	4.70	5.86	5.17	5.36	0.19
8	1	7.50	0.0000	0.00	0.00	7.50	7.50	0.00
9	1	5.88	0.0000	0.00	0.00	5.88	5.88	0.00
10	5	4.11	0.0001	4.02	4.20	3.95	4.17	0.22
11	5	7.49	0.0040	6.79	8.22	6.78	8.77	1.99
12	1	9.84	0.0000	0.00	0.00	9.84	9.84	0.00
13	1	5.26	0.0000	0.00	0.00	5.26	5.26	0.00

Table 22. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit Three				
1	13	8.75	0.0008	8.46	9.05	7.87	9.52	1.65
2	4	8.45	0.0001	8.34	8.57	8.33	8.57	0.24
3	11	7.11	0.0010	6.82	7.41	6.76	8.22	1.46
4	4	21.19	0.0173	18.72	23.77	19.61	24.44	4.83
5	4	12.04	0.0017	11.42	12.69	11.43	12.50	1.07
6	4	10.28	0.0082	9.02	11.61	9.30	11.90	2.60
7	2	8.77	0.0007	7.83	9.77	8.62	8.93	0.31
8	1	7.50	0.0000	0.00	0.00	7.50	7.50	0.00
9	1	8.82	0.0000	0.00	0.00	8.82	8.82	0.00
10	5	10.41	0.0044	9.56	11.28	9.21	11.11	1.90
11	5	13.90	0.0058	12.79	15.04	12.28	15.25	2.97
12	1	8.20	0.0000	0.00	0.00	8.20	8.20	0.00
13	1	8.77	0.0000	0.00	0.00	8.77	8.77	0.00
				Unit Four				
1	13	22.40	0.0020	21.73	23.08	19.77	24.72	4.95
2	4	28.87	0.0012	28.14	29.61	28.17	29.58	1.41
3	11	37.32	0.0024	36.47	38.18	35.14	39.73	4.59
4	4	14.96	0.0069	13.60	16.38	13.73	16.33	2.60
5	4	20.22	0.0192	17.67	22.90	18.75	23.53	4.78
6	4	22.42	0.0020	21.54	23.31	21.43	23.26	1.83
7	2	25.43	0.0024	22.76	28.20	25.00	25.86	0.86
8	1	31.25	0.0000	0.00	0.00	31.25	31.25	0.00
9	1	29.41	0.0000	0.00	0.00	29.41	29.41	0.00
10	5	32.30	0.0049	30.92	33.70	30.56	34.21	3.65
11	5	20.71	0.0010	20.18	21.25	20.00	21.43	1.43
12	1	24.59	0.0000	0.00	0.00	24.59	24.59	0.00
13	1	26.32	0.0000	0.00	0.00	26.32	26.32	0.00

Table 22. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit Five				
1	13	2.49	0.0011	2.31	2.67	2.17	3.37	1.20
2	4	2.82	0.0000+	2.78	2.86	2.78	2.86	0.08
3	11	2.46	0.0036	2.14	2.81	1.37	2.82	1.45
4	4	2.50	0.0184	1.60	3.60	2.04	3.92	1.88
5	4	6.02	0.0008	5.71	6.34	5.71	6.25	0.54
6	4	4.85	0.0004	4.65	5.06	4.65	5.00	0.35
7	2	2.55	0.0695	0.00+	10.31	1.79	3.45	1.66
8	1	2.50	0.0000	0.00	0.00	2.50	2.50	0.00
9	1	2.94	0.0000	0.00	0.00	2.94	2.94	0.00
10	5	2.74	0.0001	2.68	2.80	2.63	2.78	0.15
11	5	3.57	0.0003	3.44	3.71	3.39	3.77	0.38
12	1	3.28	0.0000	0.00	0.00	3.28	3.28	0.00
13	1	1.75	0.0000	0.00	0.00	1.75	1.75	0.00
				Unit Six				
1	13	3.83	0.0017	3.55	4.12	3.37	5.00	1.63
2	4	4.23	0.0000+	4.17	4.28	4.17	4.29	0.12
3	11	3.10	0.0029	2.77	3.44	2.70	4.23	1.52
4	4	4.13	0.0008	3.88	4.39	3.92	4.44	0.52
5	4	6.02	0.0008	5.71	6.34	5.71	6.25	0.54
6	4	5.99	0.0158	4.66	7.47	5.00	7.14	2.14
7	2	3.51	0.0003	3.13	3.91	3.45	3.57	0.12
8	1	3.75	0.0000	0.00	0.00	3.75	3.75	0.00
9	1	2.94	0.0000	0.00	0.00	2.94	2.94	0.00
10	5	3.82	0.0072	3.16	4.54	2.63	4.17	1.54
11	5	6.41	0.0097	5.42	7.48	5.26	7.55	2.29
12	1	3.28	0.0000	0.00	0.00	3.28	3.28	0.00
13	1	3.51	0.0000	0.00	0.00	3.51	3.51	0.00

Table 22. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit Seven				
1	13	9.09	0.0021	8.63	9.56	7.50	10.59	3.09
2	4	10.20	0.0024	9.51	10.92	9.86	11.11	1.25
3	11	2.45	0.0035	2.14	2.80	1.37	2.82	1.45
4	4	4.63	0.0219	3.28	6.20	3.92	6.67	2.75
5	4	0.19	0.1855	0.34	2.07	0.00	2.94	2.94
6	4	2.43	0.0002	2.32	2.53	2.33	2.50	0.17
7	2	4.35	0.0547	0.39	12.27	3.45	5.36	1.91
8	1	3.75	0.0000	0.00	0.00	3.75	3.75	0.00
9	1	7.35	0.0000	0.00	0.00	7.35	7.35	0.00
10	5	1.37	0.0000+	1.34	1.40	1.32	1.39	0.07
11	5	0.00	0.0000	0.00	0.00	0.00	0.00	0.00
12	1	4.92	0.0000	0.00	0.00	4.92	4.92	0.00
13	1	5.26	0.0000	0.00	0.00	5.26	5.26	0.00
				Unit Eight				
1	13	6.61	0.0010	6.33	6.88	5.68	7.23	1.55
2	4	6.32	0.0070	5.39	7.31	5.56	7.04	1.48
3	11	5.49	0.0000+	5.45	5.54	5.41	5.63	0.22
4	4	7.70	0.0046	6.87	8.57	6.67	8.16	1.49
5	4	6.02	0.0008	5.71	6.34	5.71	6.25	0.54
6	4	7.28	0.0006	6.97	7.59	6.98	7.50	0.52
7	2	7.02	0.0006	6.26	7.82	6.90	7.14	0.24
8	1	5.00	0.0000	0.00	0.00	5.00	5.00	0.00
9	1	7.35	0.0000	0.00	0.00	7.35	7.35	0.00
10	5	9.59	0.0003	9.38	9.81	9.21	9.72	0.51
11	5	8.94	0.0008	8.60	9.28	8.47	9.43	0.96
12	1	8.20	0.0000	0.00	0.00	8.20	8.20	0.00
13	1	7.02	0.0000	0.00	0.00	7.02	7.02	0.00

Table 22. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
Unit Nine								
1	13	5.53	0.0009	5.29	5.78	4.71	6.25	1.54
2	4	5.26	0.0067	4.44	6.16	4.23	5.71	1.48
3	11	4.97	0.0023	4.60	5.36	4.05	5.63	1.58
4	4	8.26	0.0016	7.75	8.78	7.84	8.89	1.05
5	4	7.43	0.0182	5.85	9.18	6.25	8.82	2.57
6	4	7.28	0.0006	6.97	7.59	6.98	7.50	0.52
7	2	5.26	0.0004	4.70	5.86	5.17	5.36	0.19
8	1	5.00	0.0000	0.00	0.00	5.00	5.00	0.00
9	1	5.88	0.0000	0.00	0.00	5.88	5.88	0.00
10	5	7.66	0.0033	7.02	8.32	6.94	8.33	1.39
11	5	11.02	0.0073	9.91	12.19	9.43	12.50	3.07
12	1	8.20	0.0000	0.00	0.00	8.20	8.20	0.00
13	1	5.26	0.0000	0.00	0.00	5.26	5.26	0.00

Table 23. Duration (expressed in seconds) of each unit within the assertion display of Anolis nebulosus from Colima, Mexico, computed from displays filmed in the laboratory, summer, 1968.

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
Unit One								
1	10	0.450	0.015	0.422	0.478	0.389	0.500	0.111
2	1	0.278	0.000	0.000	0.000	0.278	0.278	0.000
3	7	0.333	0.017	0.300	0.367	0.278	0.389	0.111
Unit Two								
1	10	0.722	0.008	0.707	0.737	0.667	0.778	0.111
2	1	0.500	0.000	0.000	0.000	0.500	0.500	0.000
3	7	0.405	0.034	0.339	0.470	0.333	0.555	0.222
Unit Three								
1	10	0.189	0.009	0.172	0.206	0.167	0.222	0.055
2	1	0.167	0.000	0.000	0.000	0.167	0.167	0.000
3	7	0.183	0.010	0.163	0.202	0.167	0.222	0.055
Unit Four								
1	10	0.539	0.008	0.523	0.554	0.500	0.556	0.056
2	1	0.333	0.000	0.000	0.000	0.333	0.333	0.000
3	7	0.278	0.024	0.231	0.325	0.222	0.389	0.167
Unit Five								
1	10	0.111	0.000	0.000	0.000	0.111	0.111	0.000
2	1	0.111	0.000	0.000	0.000	0.111	0.111	0.000
3	7	0.071	0.010	0.052	0.091	0.056	0.111	0.055

Table 23. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
Unit Six								
1	10	0.111	0.000	0.000	0.000	0.111	0.111	0.000
2	1	0.056	0.000	0.000	0.000	0.056	0.056	0.000
3	7	0.071	0.010	0.052	0.091	0.056	0.111	0.055
Unit Seven								
1	10	0.061	0.006	0.051	0.071	0.056	0.111	0.055
2	1	0.000	0.000	0.000	0.000	0.000	0.000	0.000
3	7	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Unit Eight								
1	10	0.161	0.006	0.151	0.171	0.111	0.167	0.056
2	1	0.111	0.000	0.000	0.000	0.111	0.111	0.000
3	7	0.087	0.011	0.065	0.109	0.056	0.111	0.055
Unit Nine								
1	10	0.217	0.010	0.198	0.235	0.167	0.278	0.111
2	1	0.333	0.000	0.000	0.000	0.333	0.333	0.000
3	7	0.349	0.029	0.293	0.406	0.222	0.444	0.222
Total Display								
1	10	2.561	0.027	2.512	2.610	2.444	2.722	0.278
2	1	1.889	0.000	0.000	0.000	1.889	1.889	0.000
3	7	1.778	0.017	1.744	1.811	1.722	1.833	0.111

Table 24. The distribution of variation (expressed by an analysis of variance) found in the displays of the sampled population of *Anolis nebulosus* from Colima, Mexico, appearing in Table 23.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Value	Percent of Variation
		Unit One			
Among Individuals	0.071	2	035	15.742	67.80
Within Individuals	0.034	15	0.002		32.20
Total Variation	0.105	17			
		Unit Two			
Among Individuals	0.423	2	0.211	58.962	89.22
Within Individuals	0.054	15	0.004		10.78
Total Variation	0.477	17			
		Unit Three			
Among Individuals	0.001	2	0.000+	0.336	0.00+
Within Individuals	0.012	15	0.001		100.00
Total Variation	0.013	17			
		Unit Four			
Among Individuals	0.290	2	0.145	69.728	90.76
Within Individuals	0.031	15	0.002		9.24
Total Variation	0.321	17			
		Unit Five			
Among Individuals	0.007	2	0.003	11.458	59.90
Within Individuals	0.004	15	0.000+		40.10
Total Variation	0.011	17			

Table 24. (Continued)

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Value	Percent of Variation
		Unit Six			
Among Individuals	0.008	2	0.004	13.500	64.10
Within Individuals	0.004	15	0.000+		35.90
Total Variation	0.012	17			
		Unit Seven			
Among Individuals	0.017	2	0.008	44.815	86.22
Within Individuals	0.003	15	0.000+		13.78
Total Variation	0.020	17			
		Unit Eight			
Among Individuals	0.023	2	0.011	21.189	74.25
Within Individuals	0.008	15	0.001		25.75
Total Variation	0.031	17			
		Unit Nine			
Among Individuals	0.076	2	0.038	12.885	62.93
Within Individuals	0.044	15	0.003		37.07
Total Variation	0.120	17			
		Total Display			
Among Individuals	2.642	2	1.321	257.845	97.35
Within Individuals	0.077	15	0.005		2.65
Total Variation	2.719	17			

Table 25. Proportion (expressed as percent) of each unit to the total duration of the assertion display of Anolis nebulosus from Colima, Mexico, computed from displays filmed in the laboratory, summer, 1968.

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
				Unit One				
1	10	17.52	0.0038	16.67	18.38	15.56	19.15	3.59
2	1	14.71	0.0000	0.00	0.00	14.71	14.71	0.00
3	7	18.71	0.0172	16.76	20.74	15.15	21.88	6.73
				Unit Two				
1	10	28.21	0.0016	27.55	28.88	26.53	29.79	3.26
2	1	26.47	0.0000	0.00	0.00	26.47	26.47	0.00
3	7	22.60	0.0450	19.25	26.13	18.75	31.25	12.50
				Unit Three				
1	10	7.35	0.0046	6.71	8.01	6.38	9.09	2.71
2	1	8.82	0.0000	0.00	0.00	8.82	8.82	0.00
3	7	10.24	0.0102	9.08	11.46	9.09	12.90	3.81
				Unit Four				
1	10	21.05	0.0022	20.35	21.76	18.37	22.22	3.85
2	1	17.65	0.0000	0.00	0.00	17.65	17.65	0.00
3	7	15.46	0.0286	13.16	17.91	12.50	21.21	8.71
				Unit Five				
1	10	4.34	0.0001	4.26	4.42	4.08	4.55	0.47
2	1	5.88	0.0000	0.00	0.00	5.88	5.88	0.00
3	7	3.91	0.0193	2.94	5.03	3.03	6.45	3.42

Table 25. (Continued)

Individual	Number of Displays	Mean	Standard Error	95% Confidence Limits Lower	95% Confidence Limits Upper	Minimum Value	Maximum Value	Range
Unit Six								
1	10	4.34	0.0001	4.26	4.42	4.08	4.55	0.47
2	1	2.94	0.0000	0.00	0.00	2.94	2.94	0.00
3	7	3.91	0.0193	2.94	5.03	3.03	6.45	3.42
Unit Seven								
1	10	2.35	0.0031	2.05	2.67	2.13	4.08	1.95
2	1	0.00	0.0000	0.00	0.00	0.00	0.00	0.00
3	7	0.00	0.0000	0.00	0.00	0.00	0.00	0.00
Unit Eight								
1	10	6.27	0.0019	5.88	6.67	4.55	6.67	2.12
2	1	5.88	0.0000	0.00	0.00	5.88	5.88	0.00
3	7	4.80	0.0242	3.59	6.17	3.03	6.45	3.42
Unit Nine								
1	10	8.42	0.0044	7.76	9.11	6.38	10.20	3.82
2	1	17.65	0.0000	0.00	0.00	17.65	17.65	0.00
3	7	19.48	0.0452	16.32	22.86	12.50	24.24	11.74