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Ecology and Social Organization In the Iguanid Lizard *Anolis lineatopus*

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Introduction

This paper reports the findings of a 10-month (August 1961 to June 1962) field study of the ecology and behavior, particularly the social behavior, of *Anolis lineatopus,* in edificarian situations, in the vicinity of Kingston, Jamaica.

The geographical variation of this common Jamaican lizard has been discussed by Underwood and Williams (1959) and by Grant (1940) but, beyond brief notes in these papers and in Barbour (1910), its natural history has never been described.

There have been a number of detailed studies on free-living lizards, but most of them have dealt with temperate zone species in temperate environments. Few investigators have had the opportunity to conduct intensive and extensive studies on lizards in the tropics. The few exceptions include Evans (1951), Harris (1964), and Hirth (1963 a and b). No extended field study with an emphasis similar to this one has been published on any tropical *Anolis* though the shorter papers of Evans (1938a) and Oliver (1948) report relevant

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information for *A. sagrei*. Evans (1961) gives a quite complete bibliography of lizard natural history.

Throughout this study I have attempted to verify critical points with counts, censuses, or other objective measurements, and I have used these extensively here. They have the disadvantage of excluding all information which is not being measured and so present a limited picture and one which is sometimes difficult to comprehend by someone who is not familiar with anoline behavior. To offset this and provide a frame of reference, I have included frequent abstracts from my field notes [direct quotes and paraphrasing both are in smaller type—ed.] and have appended two short sections to provide a picture of the general behavior of this species, one reporting the behavior of an individual which was under observation for an entire day, and the other giving a composite and hypothetical account of the usual course of the life of an *A. lineatopus*.

I want to thank first Dr. Ernest E. Williams and my wife Patricia, the two people who contributed most to this study. Dr. Williams, principal investigator of the National Science Foundation grant under which the field work was done, helped organize the project, advised me during our time in the field, and criticized the manuscript at various stages of completion. My wife helped with the field work, did most of the editing and typing of the manuscript, and provided both moral and logistic support.

A number of other people contributed importantly to the work. My father, Dr. A. L. Rand, supplied very valuable criticism of both the ideas and form of the work. Prof. Garth Underwood discussed the problem with me and gave me the benefit of his years of experience with the Jamaican anoles. Dr. P. E. Vanzolini advised on the analysis of the data and criticized the manuscript. Discussion with Dr. W. J. Smith provided additional insight into certain aspects of the behavioral concepts. Drs. M. Moynihan, E. Willis, J. Eisenberg, and W. Milstead read and criticized the manuscript.

I am indebted to Prof. D. Steven, who allowed me to use the facilities of the Zoology Department of the University of the West Indies, and to the rest of the staff there, particularly Prof. Ivan Goodbody and Mr. William Page for their assistance. I wish to thank them and the visitors at the University, such as Mr. Malcolm Edmunds and Dr. Arthur Hughes, for listening to lengthy discourses on anoles and for criticizing them most helpfully.

I am also indebted to Mr. William Page and Mrs. L. Jones for their help in determining the insects found in lizard stomachs.

Finally, I must acknowledge the financial support for this project from National Science Foundation grant number 16066.

Material and Methods

Anolis lineatopus shows considerable geographic variation within Jamaica. Those from the vicinity of Kingston are medium-sized *Anolis*, the adult males about 50 to 70 mm in snout-vent length and reaching about 8 to 9½ grams in weight. The adult females are smaller, about 37 to 47 mm in snout-vent length and about 1¼ to 3 grams in weight. Both sexes are brown to gray brown in color. The adult males are marked with irregular black bars. The females are more variable and may be almost unicolor, or they may have a diamond- or rhomb-shaped pattern on the back or a light middorsal stripe. There is only limited color change, from light to dark. The feet have the usual *Anolis* form with moderately wide toe pads and an intermediate number of lamellae (29–34 under second and third phalanges on fourth toe). The dewlap or throat fan, large and light yellow with an orange central spot, is well developed only in the male. These are called *A. lineatopus lineatopus* by Underwood and Williams (1959).

Anolis are strictly diurnal and depend almost entirely on vision in their social behavior and in locating food. They may respond to sounds but seem to pay no attention to odors.

Jamaica, at 18° north latitude, lies well within the tropics and there is relatively little variation in temperature in the two wet and two dry seasons. The *Anolis* are active year round and neither fighting, courting, nor copulation seems seasonal. There does seem to be some seasonal variation in the production of young: more in the wet season. Whether this is due to variation in egg laying or in egg survival, I do not know.

In the dry lowlands on the south coast of Jamaica, *A. l. lineatopus* is widespread and abundant but much more abundant in some places than others. This is particularly striking when one is trying to collect samples at predetermined intervals along a transect. In some cases the differences in abundance are correlated with ecological differences, but in others I could see no difference in habitat.

The areas where this study was made were all much disturbed by man. Those on which I concentrated were highly artificial gardens, the campus of the University of the West Indies, and roadside hedges and fence rows. Relatively little time was spent in natural habitats and no detailed studies were made therein. Little undisturbed habitat is left in Jamaica and what remains is mangrove swamp, scrub on dogtooth limestone and mountain forest, and all difficult of access. Since the edificarian areas were easier to work in, closer at hand and, most important, usually supported denser populations of lizards, I concentrated on these areas.

Though I made repeated trips to the other parts of the island, the intensive observations reported here were made in two suburbs of Kingston, Barbican and Mona.

In studying social behavior, I concentrated on *A. lineatopus* living in small areas, marking them individually, mapping their positions, and describing their behavior. They were marked by clipping the terminal phalanx from one front and one hind toe, according to a code (removing one additional toe allowed higher numbers). The clipped toes did not regenerate but were not visible from any distance. A number was painted on the back of each lizard with white paint (a quick-drying amylacetate base airplane paint). This was visible at a distance but each *A. lineatopus* had to be recaptured and repainted after each shedding. Though inconvenient, this gave us an opportunity to remeasure these lizards at intervals. The clipping of the terminal phalanx removed the claw but not the pad and did not seem to affect the lizard's climbing or running ability. The white painted numbers interfered slightly with shedding and certainly made the lizard more conspicuous to me and presumably to other predators. The interference with shedding however, was temporary and the increased conspicuousness unavoidable.

The lizards were measured from the tip of the snout to the anterior margin of the vent by holding them along a ruler. The measurements were recorded to the nearest millimeter, and repeated measurements on the same individual during a short period frequently varied by one millimeter but seldom by more. Throughout the paper the anole sizes given are snout-vent lengths in millimeters.

Each lizard was marked in the field as soon as it was caught and released in less than five minutes in the area where it had been captured. Two methods were used in catching the lizards. Some were noosed during the day with a running noose of nylon filament on the end of a slender stick. Others were caught by hand at night while they were sleeping. The latter technique is very effective and is the one Cagle (1948) describes as being used by professional anole collectors in Louisiana.

The marking process disturbed the lizards, and, after being released, a lizard usually remained quiet for an hour or so before resuming its normal activities.

Though the lizards learned to avoid the noose, they soon came to ignore me completely, particularly if I were stitting quietly, even in plain view and only a few feet away. Those in the areas where I spent hours watching them became very tame and would approach me without hesitation to catch an insect. One female even took an insect from my fingers.

Once the lizards had been marked and the study area mapped, observations were usually made daily. Many lizards were not recorded every day, but some were and most were seen repeatedly. In addition to this census, I made general observations, sitting quietly watching one relatively small area and noting the interactions between lizards. Finally, there were continuous observations on individual lizards when we attempted to keep track of everything that an individual did. These were mostly on the order of an hour or half an hour, but in one case we watched a lizard from before sunrise to after sunset.

I supplemented observations on aggressive behavior with experiments with stake-outs. This technique, developed by Evans (1938a) and used by Ruibal (1961) in Cuba and by me in Puerto Rico, consists of tying a lizard to the end of a stick, then placing it in the vicinity of another and recording the reaction of the resident.

Throughout my time in Jamaica, even when I was not engaged directly in studying anoles, I was aware of them and watched what they were doing. Many of my conclusions originated as general impressions based on these casual observations.

Individual Ecological Requirements

The social behavior of *A. lineatopus* can be considered as one of the adaptations of the species to its environment. The form of its social behavior is as strongly influenced by its environment as is its morphology.

In order to understand the social behavior of *A. lineatopus*, it is necessary to consider the ecological demands of each individual and how these are satisfied.

Successful reproduction is a requirement of the population but it is not necessary for the continued life of the individual. Social behavior is so involved with reproductive behavior that discussion of reproductive requirements is postponed until social behavior is being described.

The demands of the individual are of two sorts: fundamental requirements and habitat requirements. The fundamental requirements are those that an animal must satisfy to live. For *A. lineatopus* these include food, water, suitable temperatures, and protection from predators.

The habitat requirements are those structures in the environment that an animal uses to satisfy its fundamental needs. They are usually not necessary for the life of an animal, for a caged individual lives without them, but they are frequently those things that must be present if a wild individual is to settle in an area. For *A. lineatopus* they include an observation and basking perch, cover near the ground, and a sleeping site.

Fundamental Requirements

Food.—As is true of almost all lizards of its size, *A. lineatopus* feed primarily on insects and other small arthropods, occasionally on very small vertebrates and snails.

Anolis lineatopus waits for its prey on a perch a few inches to several feet above the ground rather than foraging for it. This hunting technique is common in visually oriented insectivorous lizards and contrasts with the active searching technique that is typically used by olfactorily oriented lizards such as skinks and teiids as well as some visually oriented iguanids.

Some prey *A. lineatopus* can catch without having to move, but usually it must move and frequently to the ground or nearby foliage. Large individuals move farthest to catch something, sometimes going four or five feet. The approach is a quick run, often broken by one or more pauses, and usually a pause just as the prey is reached. During a pause *A. lineatopus* cocks its head and looks at the prey with one eye and then shifts back to binocular vision. The binocular vision presumably uses the temporal fovea and allows better judgement of distance and direction, the monocular vision probably uses the central fovea, which may give better definition (Underwood, 1951). Sometimes *A. lineatopus* leaps several inches to seize an insect. A small insect is frequently eaten where caught but a larger one is usually carried back to a perch.

The food items in the stomachs of 45 *A. lineatopus* are shown in table 1. The anoles were collected over a period of a week in an area 10 x 50 yards in Mona. They were killed shortly after capture,

Table 1.—*Food items in the stomachs of 45* Anolis lineatopus

	Number of prey individuals
Arachnida	33
Diplopoda	3
Orthoptera (including roaches)	16
Dermaptera	3
Hemiptera (largely Homoptera)	68
Lepidoptera (both larvae and adults)	21
Coleoptera (only adults)	16
Hymenoptera (largely ants)	95
Miscellaneous	8

measured, and their stomachs removed and placed in alcohol. Subsequently the contents were removed and examined. Some food items were found intact but many were represented by a scattering of more resistant parts. A count of the minimum number of prey individuals present was recorded.

A count of prey items is perhaps the best count to indicate food preferences since each capture is weighted equally. It has the disadvantage of ignoring the significant fact that one large insect may supply more food than several small ones. Table 2, which shows the prey by size, makes some correction for this.

Table 2.—*Relation between prey size and lizard size* (first figure in each entry is number of prey individuals; figure in parentheses is number of stomachs)

Lizard size (snout-vent)	Prey size					Total food	Total stomachs
	<0.5 cm		0.5–1.0 cm	1.0–2.0 cm	>2.0 cm		
	Ants	Others					
26–30 mm	12(5)	44(8)	4(2)			60	8
31–40	28(8)	28(10)	4(4)	1(1)	1(1)	62	11+1 empty
41–50	30(9)	25(10)	9(8)	11(8)	2(2)	77	13
51–71	19(6)	3(2)	3(3)	8(6)	3(3)	36	11

Casual observations add dragon flies, Diptera, termites, small snails, and small frogs to the list of prey found in stomachs.

The variety of major types of invertebrates present in appreciable numbers demonstrates that *A. lineatopus* is not a specialist in any particular taxon. The only lizards known to specialize in this manner are those, like *Moloch*, that feed on ants, though some, like the *Cnemidophorous* in parts of Texas, which eat largely termites (Milstead, 1957), may be facultative specialists.

In addition to animals, a few bits of vegetation, a small stone, and a piece of shed lizard skin, probably its own, were found in stomachs. The vegetable material and the stone may have been taken by the lizard along with an insect but the following two incidents suggest other ways in which nonliving material may be taken.

Once, I observed a small male run two feet to a dead insect being carried jerkily by ants. After a minute or so of watching, he picked up the insect, shook off the ants, and ate it.

On another occasion, about one foot from a young adult male, I observed the green base of a hibiscus flower (a cylinder 2½ cm long and 1 cm wide) fall to the ground. The male jumped down to the ground, grabbed and then released the flower except for a small piece that he chewed for some minutes.

Anolis lineatopus feeds on a wide range of sizes of prey, the larger individuals eating more large prey than do the smaller ones.

The sizes of prey found in the stomachs of 45 lizards examined are recorded in table 2 in the following categories: <5 mm; 5–10 mm; 10–20 mm; and >20 mm. Entire insects were measured directly. Fragments were compared with entire insects, either from stomachs or in collections at the University of the West Indies. A few items whose size could not be estimated were omitted.

The increase in number of large prey with increase in lizard size probably reflects a greater ability of large lizards to handle large prey, since food is swallowed whole.

The decrease in the number of small prey and the increase in relative numbers of ants (which is marked only in the largest lizards) must reflect changes in the attitude of a lizard towards potential prey. Ants, unlike most of the insects *A. lineatopus* catches, forage up and down the branches, tree trunks, and fence posts where the larger lizards regularly perch. To catch these ants, a lizard need move only a short distance, if at all. Apparently larger lizards differ from the smaller in taking small insects only when they can do so with minimum effort.

The decrease in number of prey per stomach with increased lizard size is probably largely a reflection of the increase in size of the prey items; however, the smaller lizards are growing more rapidly than the larger ones and so may require more food. In the smallest size class, both sexes are growing rapidly and, when the females' growth slows down, they begin to produce eggs, an activity that must require considerable food. Dessauer (1955) calculated for *A. carolinensis* that "In the course of its 5-month laying season, the individual *Anolis* female must lay down the equivalent of her own total body protein for egg production" (p. 12). The largest lizards are adult males that are growing very slowly though expending considerable energy in display. Harris (1964) found, however, that an *Agama agama* took about the same weight of food per gram of lizard regardless of lizard size.

There are differences in micro-habitat associated with anole size (see p. 17) that may affect what is easily available for food to different sized *A. lineatopus*.

Whatever the reasons for it, *A. lineatopus* of different sizes living in one relatively small and quite uniform area differed in what they had eaten. The smallest took large numbers of small prey, which were predominantly not ants, and the largest took fewer prey, many of which were large, plus an appreciable number of small prey, which were mostly ants. The change from one type of food to the other seems to occur gradually.

Harris (1964) showed conclusively that in *Agama agama* the different size classes of lizards were taking largely different sized prey. Since adult males are larger than adult females and share the same home ranges, this difference must reduce the possibility of intersex competition for food.

Kennedy (1956) demonstrated differences between juvenile and adult *Sceloporus olivaceous* in size of prey and suggested that this produces "a minimum degree of intraspecific food competition between juvenile and adult *S. olivaceous* which is highly advantageous in the rapid development of juvenile lizards . . ." (p. 345). Blair (1960), however, in writing of the same species in the same area concluded that the juveniles never approach the limit of their food supply.

A difference in food size between adults and juveniles has been reported for lizards as varied as *Eumeces fasciatus*, Fitch (1954), and *Basiliscus vittatus*, Hirth (1963a).

A habitat difference between juvenile and adults like that seen in *A. lineatopus* seems common in iguanids. It occurs in at least *Basiliscus vittatus*, Hirth (1963a), *Iguana iguana*, Hirth (1963b), *Uta stansburiana*, Tinkle et al (1962), *Sceloporus olivaceous*, Blair (1960). This habitat difference must certainly reduce the possibility of one sort of intraspecific competition for food. It also reduces the possibility of the adults eating the young.

Certain falcons are sexually dimorphic in size and the larger females catch larger prey (Cade, 1960). Storer (1952) has discussed the possibility that this reduces intersex competition for food. Rand (1952) has reviewed a number of additional types of sexual dimorphisms in birds that may also reduce intersex competition for food. In birds as in lizards it is difficult to prove the applicability of these ideas to any particular case however plausible they are in general.

To evaluate food as a limiting factor in the ecology of these anoles would require a knowledge of both the food requirements of the animals and the availability of food to them. Blair (1960), for *Sceloporus olivaceous* adult females, and Milstead (1957a), for four species of *Cnemidophorus*, concluded that food was at least potentially limiting. Their arguments are convincing, but their proof is not rigorous. For *A. lineatopus* I suspect that food is potentially limiting but the data are adequate only to demonstrate that in the study areas food is neither superabundant nor in very short supply.

My impression is that insects of suitable size are common in Jamaica but this idea must be treated cautiously for not all of the insects present are available to *A. lineatopus* as food. Some insects are too active or too wary to be frequently caught. Others are nocturnal and still others too hard or protected by a nasty taste or smell.

Of the 45 stomachs examined, only 1 was empty of food, suggesting that most *A. lineatopus* catch enough food to keep their digestive systems working most of the time; however, this can be said only of the period when they were collected—early in the dry season, a period when insects appeared abundant.

A captive *A. lineatopus* will live at least several days to a week without food, so presumably in the wild an individual could survive short periods of famine. I rarely saw *A. lineatopus* catch something to eat, and I have the impression that most days it catches only a few insects and some days perhaps none at all.

In contrast to this slow rate of feeding is the response of *A. lineatopus* to food offered them. In my study area, these lizards became very tame and freely took insects tossed to them from a few feet away, running several feet to do so. In a typical session of 45 minutes one afternoon, I tossed insects of moderate size into an area of about four square yards. During this time, 17 insects were captured by eight different lizards, two of them catching 3 insects and one catching 4. This suggests that the slow rate of feeding usually seen is not because *A. lineatopus* are satiated but because suitable insects are not available.

We saw in the field no thin or emaciated individuals among these lizards.

The wide variety of prey taken by *A. lineatopus* means that available food is distributed throughout the habitat and is not densely concentrated in certain areas. Several lines of circumstantial evidence indicate that probably few, if any, established resident *A. lineatopus* starve to death but at the same time that a superabundance of food is not available to them.

WATER.—Probably all the water *A. lineatopus* requires, beyond that present in its food, it gets by licking drops of dew or rain from leaves and twigs with the tip of its tongue. The only report I know of lizards having difficulty securing water is Evans (1951), who reports *Ctenosaura pectinata* making long excursions to drink.

Rain is a frequent occurrence around Kingston. Even in the dry season when no rain falls, dew forms almost every night and remains in the shade until mid- or sometimes late morning. Water is thus available to *A. lineatopus* almost every day.

Anolis lineatopus were only occasionally seen to drink in the field but in cages they were seen to drink frequently.

As I sat watching some marked *A. lineatopus* one afternoon, a light rain began to fall. Only one, an adult male, reacted. He climbed a branch to an orchid and licked several times at one of the wet leaves.

An *A. lineatopus*, which would eagerly take tossed insects, completely ignored the drops of water that formed when I watered the study area. Apparently even during this period in the dry season, when there was not enough rain to keep the grass green, *A. lineatopus* were not short of water.

TEMPERATURE.—*Anolis lineatopus* in the Kingston area has a preferred body temperature (or eccritic temperature) range of 28°–31° C. Sixty-one of 85 lizard temperatures taken under a variety of environmental temperatures fall within this 4° range. Like many other lizards which have been studied (Bogert, 1959; Fitch, 1956b; Inger, 1959; Ruibal, 1961), this species maintains its temperature within this range by behavioral thermoregulation when environmental conditions permit.

I have continued to use the familiar term "preferred body temperature" despite the demonstration of Licht, Dawson, and Shoemaker (1965) that observed field temperatures in some species differ from those chosen in gradient experiments and their suggestion that the term "preferred temperature" be restricted to experimental studies.

The *A. lineatopus* temperatures used here were taken over a wide range of air temperatures but always when the sun was shining. On each occasion a thermal gradient was available to *A. lineatopus* as it was to the lizards in Licht's and his coworkers' experimental setups. On most occasions, the environmental temperatures available, considering substrate as well as air temperatures, extended both above and below the observed *A. lineatopus* range. It seems likely that the observed body temperatures approximate those that would be found in an experimental gradient. Certainly my observations should be more similar to those of an experimental gradient than to the results obtained by measuring all lizards regardless of weather.

The cloacal temperatures of *A. lineatopus* were taken with a Schultheis quick reading 0°–50° C thermometer within a few seconds of noosing.

The body temperature of an *A. lineatopus* is almost always close to and above the air temperature in its vicinity (fig. 1). Body temperatures are higher at high air temperatures than at low air temperatures, but the difference between air and body temperature is greatest at low air temperatures as the following figures (in centigrade) show:

air temperature	*mean body temperature*	*difference*
24	27.5	3.5
27	29.4	2.4
30	31.0	1.0

The *A. lineatopus* temperatures show a slightly greater range (24°–32° C) than do the air temperatures (24°–30° C) but a much more central tendency (variance of air temperatures=6.34; variance of lizard temperatures=3.92).

The distribution of *A. lineatopus* temperatures is skewed so that there are fewer records (7) above the preferred body temperature range (28°–31° C) than below it (14) and the total range extends only 1° above, but 4° below, the preferred range.

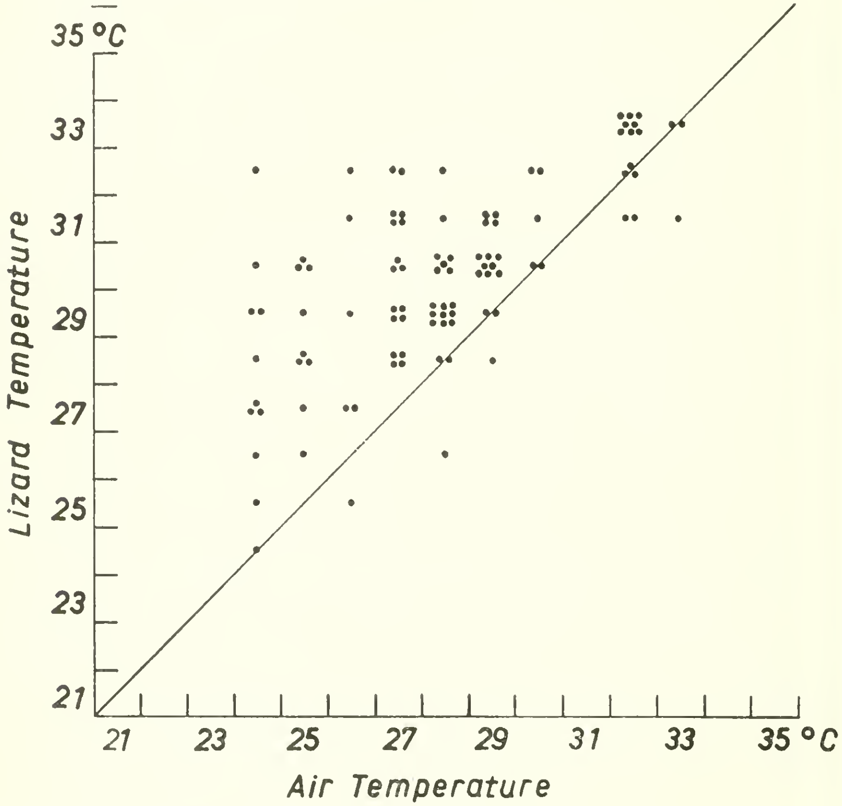


FIGURE 1.—*Anolis lineatopus* cloacal temperatures plotted against air temperature in immediate vicinity at time of capture (temperatures have been recorded to nearest 0.2 degree and have been rounded to nearest degree for plotting).

Heath (1964) in his report on the temperatures of beer cans has shown that body temperatures above the ambient air temperatures do not necessarily demonstrate thermoregulation. But the already described relationships of body and air temperature combined with the behavior patterns reported below are convincing evidence that *A. lineatopus* thermoregulates.

Color change in *A. lineatopus* may play a role in thermoregulation. Casual observation indicates that in the early morning, when *A. lineatopus* are sunning themselves, they are darker than they are during the heat of the day. Since this involves a gradual change in shade rather than an abrupt change in hue, it is difficult to measure in the field and I collected no quantitative data on the point.

The lizard's behavior in moving into and out of the sun was more conspicuous and more easily recorded than the color changes and probably more important in thermoregulation.

The following extract from my field notes shows the sort of behavior frequently seen:

> 30 January—Barbican brush heap, 900 hrs. By this time the *lineatopus* are mostly sitting in the shade. I have the impression that they are avoiding hot perches more than the sun itself. A large male is on a branch which is shaded but he himself is largely in the sun.
>
> One adult female, on the other hand, is sitting in a small patch of shade on a branch in the brush heap. Most of her time is spent in these patches of shade, where she usually sits on top of the branch. When she does leave the shade for a sunny branch, she usually runs along the top, but when she stops she moves in to the shade on the side. Sometimes when she runs along a sunny branch she will stop and run very quickly back to the shade patch as if she had suddenly become too hot.

Table 3 shows the results of seven censuses of adult male *A. lineatopus* along a stone aqueduct that runs north and south. These lizards moved into the sun when they were cool and avoided the sun and hot substrates when they were warm. They seemed more careful

TABLE 3.—*Distribution of adult males on a stone aqueduct under different weather conditions* (aqueduct runs north and south and all data was collected in the morning; temperature readings are given in centigrade)

Weather conditions	Air temperature	East side (in sun)		West side (in shade)	
		Substrate temperature	Number of lizards	Substrate temperature	Number of lizards
Sunny	28.4	30.6	10	28.4	4
cool	28.0	30.8	2	27.0	0
	26.0	31.8	7	25.4	2
			—		—
			19		6
hot	29.6	41.0	1	29.0	13
	29.8	36+	1	30.0	13
			—		—
			2		26
Cloudy	26.0	28.0	4	27.0	6
	25.6	25.6	4	25.4	7
			—		—
			8		13

about avoiding very hot conditions than in seeking warm ones when it was cool.

Anolis lineatopus may remain active at body temperatures appreciably below its preferred body temperature range. Most lizards studied (Bogert, 1959; Fitch, 1956; Milstead, 1957) become inactive at low temperatures but *A. lineatopus* do not do so, and I have seen them on cloudy days and around lights at night feeding, fighting, and copulating at environmental temperatures below 25° C when their body temperatures must have been circa ambient.

In contrast to these observations of activity at low temperatures are those made during the very early morning. *Anolis lineatopus* left their exposed sleeping sites shortly after dawn but well before sunrise and moved into spots where they were concealed. They moved up onto their usual perches only after sunrise, when they began to bask.

Studies on other lizards have shown that the preferred body temperature is usually not far from the upper lethal temperature and this is probably true in *A. lineatopus.* On analogy with other lizards one would expect a thermal death point somewhere in the vicinity of 40° C. Obviously *A. lineatopus* cannot occur in places where its temperature would be forced above the thermal death point; it should be noted that on the sunny aqueduct mentioned above (table 3) one of the stones of the aqueduct had a temperature of 41° C.

The effects of temperatures below the preferred body temperature are almost completely unknown not only in this species but also in most lizards. At very low temperatures, *A. lineatopus* becomes sluggish and torpid, as the following illustrates. One male cooled in a refrigerator was sluggish when cooled to a body temperature of 13° C though still active at 19° C.

Presumably deleterious effects of moderately low temperature are associated with the slowing of temperature-dependent physiological processes such as heart rate, oxygen consumption, rate of enzymatic action (Bartholomew and Tucker, 1963, 1964; Bartholomew, Tucker, and Lee, 1965; Licht, 1961).

Hardy (1962) has reported that in *Cnemidophorus sexlineatus,* at lower temperatures, defecation is delayed and individuals are less efficient at detecting prey, particularly motionless prey, and take several times longer to dig tunnels. No similar changes were seen in *A. lineatopus,* but it was noted that *A. lineatopus* are shyer at lower temperatures and it was suggested that this might be a behavioral compensation for the slowing of muscle or nerve reaction at lower temperatures (Rand, 1964b).

Preferred body temperature range may be an important ecologically limiting factor, for this subspecies is absent from dark forest where sunlight is not available and also from higher elevations where temperatures are lower.

In the lowland edificarian and disturbed areas where these studies were made, there are probably few places from which these anoles are excluded because of generally low temperatures. They do not occur where there is no protection from overheating in the sun.

Predators.—Every animal in Jamaica that preys on small land vertebrates or large insects probably eats *A. lineatopus* at least occasionally, but in the areas studied the predation pressure does not seem to be heavy.

From my observation, the most important predators are domestic cats. One well-fed mother cat that was living with us brought her kittens at least one and sometimes several anoles every day, many of them adult *A. lineatopus*. However, this made no obvious diminution in the population of anoles living around the house.

I also saw dogs catch and kill *A. lineatopus*, and some of them probably do this regularly. Chickens also eat these lizards. I found an *Anolis* in the stomach of one of the few snakes I examined, a *Dromicus callilaemus*. Even though this species of snake is moderately common (one could almost always find one in a couple of hours of searching), it is a ground-living species and probably not an important predator on any *Anolis*. Other snakes are rare in the study area.

Birds are probably important predators on small *Anolis;* Wetmore (1916) reports that in Puerto Rico he found *Anolis* in the stomachs of most of the insectivorous birds, even as small as the tody, and this situation probably applies to Jamaica also. The most common of the larger insectivorous birds around Kingston—mockingbirds, anis, and kingbirds—probably take young and female but few adult male *A. lineatopus*.

The birds that might be expected to feed on adult males, the larger cuckoos, herons, hawks, and owls, are relatively rare in the study areas and probably are thus of relatively little importance.

The common toad, *Bufo marinus* (I counted 25 on the lawn one evening), certainly could eat small to moderate-sized *A. lineatopus*, but, since the toads are nocturnal, they probably catch few.

Anoles themselves eat lizards. *Anolis grahami* at least occasionally eat young *A. lineatopus* and the larger *A. valencienni* and *A. garmani* probably regularly eat at least adult females and young males of *A. lineatopus*. Both these larger species are relatively common (an hour or two search in the correct habitat would reveal at least one of each), but both are primarily lizards of tree crowns and consequently do not feed in the places where *A. lineatopus* are most common.

I only once saw an *A. lineatopus*, a 60 mm male, catch and eat one of its own species, about 20 mm long, but I have several times seen an adult male chase and attempt to catch a young *A. lineatopus* and I have also taken a small *A. lineatopus* (just above hatchling size) from the stomach of an adult male. Cannibalism is probably relatively rare, partly because the young lizards are too active to catch easily and partly because they avoid the principal perches of the adult males. The difference in perch between young and adult males may be in part a direct result of chasing by the adult males.

Predation probably is not an important factor in controlling population density of adults resident in favorable habitats. Predation is probably heavier on juveniles, on dispersing individuals, and on those living in unfavorable habitats.

ESCAPE BEHAVIOR.—Most of my information regarding the reaction of anoles to potential predators relates to their reaction to people. It is possible but unlikely that they react differently to smaller predators.

I noted that the first reaction of *A. lineatopus* to an approaching danger is usually to remain still, sometimes flattening against the perch. If the danger approaches closely, the *A. lineatopus* runs around the perch to the other side and either up out of reach or down into the vegetation at the base. Where possible, adult males usually run upward, small *A. lineatopus* more frequently dodge around on the trunk or even leave the tree to hide in the cover on the ground.

Adult males, when they became familiar with me, did not flee at my close approach but displayed as they would at another male.

A captured lizard usually tries to bite and, if successful, holds on. An adult male, when seized, frequently shows most of his agonistic displays (see p. 38 et seq.), raising dorsal and nuchal crests, lashing his tail, opening his mouth, protruding his tongue, and sometimes holding his dewlap open but never flashing it as does a male displaying to another male.

A captured lizard frequently defecates; the feces produced are usually a pasty material, though they may be very watery or sometimes a normal, dry, compact feces. This material is not pleasant to smell nor presumably to taste but it does not smell very unpleasant.

ELIMINATION OF WASTES.—As many arboreal animals do, *A. lineatopus* defecate on whatever perch they happen to be and the feces usually fall to the ground. As might be expected in a species where olfaction is of little importance, the feces do not seem used in marking as Hardy (1962) has suggested they are in *Cnemidophorus sexlineatus*. The fecal pellets are roughly cylindrical, about 1 cm long, dark in color, and dry and compact to touch. There is a small white cap on the end extruded first; presumably the dark material is fecal material from the intestine and the white cap is nitrogenous wastes from the kidneys.

Habitat Requirements

The three main habitat requirements, perch, cover, and sleeping site, must be satisfied in some way or other within the home range of each *A. lineatopus.* These features of the habitat are essential to the operation of the normal behavior patterns that enable *A. lineatopus* to satisfy its fundamental requirements and also important to those associated with social behavior and reproduction. It is probably these habitat requirements that are used as cues in habitat selection by *A. lineatopus.*

Harris (1964), writing on *Agama agama* in Nigeria, states: "Three important structural components the environment must provide are: (a) suitable display posts, (b) a roosting place and (c) conveniently situated refuges from predators" (p. 132). These categories are almost identical to those used herein for *A. lineatopus* though the structures in the habitat that satisfy these demands are quite different.

PERCHES.—An *A. lineatopus* spends its days waiting on one or another of its perches. From its perch the lizard sees most of the prey which it catches, most of the other lizards which it courts or chases, and most of the predators from which it flees, and it is from its perch that most of its display is given. The perch also provides a sunning site and usually shade as well.

A wide variety of objects are used as perches, among them trees, fence posts, rocks, walls of houses, bushes, and hedgerows. The large majority of *A. lineatopus* seen were within six feet of the ground, and relatively few were seen on slender twigs and branches. In general, adult males perch farther from the ground and on larger diameter perches than do smaller individuals, which are usually seen in bushes, hedges, and brush piles very close to the ground and which seem to avoid the large trees and fence posts, etc., that the adults prefer. Collette (1961) describes similar intraspecific differences in perch preference in *A. sagrei* and *A. porcatus.* Intraspecific differences between juvenile and adult habitats seem widespread in iguanids (see p. 9) (For a more detailed discussion of perches, see Rand, in press). The sorts of perches that are occupied most commonly are herein called preferred perches, and those that were occupied less frequently are referred to as less or subpreferable.

The same individual may be seen on the same perch day after day; most, if not all, lizards use only one or a few perches as the center for their activity. Blair (1960) noted similar behavior in *Sceloporus olivaceus*, particularly in the females. *Anolis lineatopus* may spend most of its time on only a small part of one perch, as O'Brien et al (1965) describe for *Sceloporus undulatus.* I have called the perch or perches where an individual spent most of its time its "usual" perch or perches.

Anolis lineatopus usually rests on the side of a vertical perch or on the upper surface of a slanting or horizontal one, most frequently with the head pointed toward the ground, a habit associated, I suspect, with the large amount of food taken on the ground, as I suggested for *A. cybotes*, a species with similar habits, in Hispaniola (Rand, 1962). Though *A. lineatopus* may spend long periods on the same perch, it seldom spends more than 15 minutes without shifting position or without displaying. Even between shifts the lizard is usually alert, and in one 4-minute period when I watched an adult male on his perch, he moved his head 12 times and the eye that I could see also 12 times (the eyes move independently of each other). During this 4-minute period, the longest time without any movement was 45 seconds and usually only 10 or 15 seconds elapsed.

The sort of perch an anole uses varies from species to species so that sympatric species occupy different microhabitats (Collette, 1961; Oliver, 1948; Ruibal, 1961; and Rand, 1962, 1964a). This probably acts to reduce interspecific competition (Rand, 1964a) just as the different foraging zones do for sympatric wood warblers (MacArthur, 1958).

Cover.—Cover near the ground is a more important habitat requirement for female and juvenile *A. lineatopus* than for adult males. Very few *A. lineatopus* maintain home ranges that include no cover at all. Cover takes several forms: dense vegetation, grass, herbaceous plants or ferns that grow around the perch; a pile of dead sticks; a layer of large dead leaves; or occasionally a pile of rocks. These provide protection against temperature extremes (p. 14) and predators (p. 16).

Sleeping sites.—*Anolis lineatopus* sleep during the night in exposed situations above the ground, generally at elevations of 1 to 10 feet, usually at the ends of branches, the larger usually climbing higher than the smaller individuals. They sleep on leaves, small twigs, and sometimes on grass blades that frequently are slender enough to bend double under the weight of the anole. Many arboreal and semiarboreal iguanids have similar sleeping habits, among them *Iguana iguana*, Hirth (1963b), *Basiliscus vittatus*, Hirth (1963a), at least some *Sceloporus olivaceus*, Blair (1960), and *Urosaurus ornatus*, Cowles and Bogert (1936).

Sleeping *A. lineatopus* are usually visible from outside the bush or tree and consequently are exposed to any flying predator hunting by sight at night; however, they are concealed from any predator that approaches from inside the tree and is forced to climb the branches to reach them. The small diameter of the sleeping perches presumably would protect them from any large climbing predator, and even a small predator would probably be unable to reach a lizard without shaking the perch enough to awaken it.

Though easily awakened at night by a light or by movement of the perch, the lizards are slow to leave their perches and usually do so only when they are shaken quite violently.

The sleeping sites differ sharply in character from the preferred diurnal perches; the sleeping sites are places this species seldom visits during the day except when catching an insect or when engaged in a dispute with another anole.

Some individuals seem to use the same leaf or twig as a sleeping site night after night. Most, however, are not so regular, though they tend to sleep in the same bush, tree, or bunch of grass. There is definitely not the same attachment to a particular sleeping site that there is to the daylight perch.

Anolis lineatopus left their sleeping places soon after it became light and usually did not settle down to sleep until it was too dark for them to be seen even from a few feet away. Blair (1960) reports a similarly long period of activity for *Sceloporus olivaceus* during the summer as does Hirth (1963a) for *Basiliscus vittatus.* Perhaps this is characteristic of lizards sleeping, as these do, in exposed sites in a warm climate.

On one occasion, January 27 in Barbican, I watched a male *A. lineatopus* go to sleep. I first noticed him at 6:13 P.M. when he ran up the stem of the croton and stopped just below the terminal bunch of leaves. The sun had set but the landscape was still bright. A minute and a half later he climbed up among the leaves and out along one of them and stopped in a typical alert position, head raised and neck bent. Two and a half minutes later he flattened out against the leaf, still facing its tip. Six minutes later he turned around facing the stem of the leaf and flattened against the leaf. The sky was still light but the landscape dark. By 6:30 the first stars were out and it was almost full dark. With the flashlight I could see that the lizard's eyes were still open but he was in his normal sleeping position.

Both Mertens (1939) and Rand (1962) noted in Hispaniola that certain species of *Anolis* sleep with their hind legs flexed while others sleep with these legs stretched out along the body. *Anolis lineatopus* may sleep in either position and quite frequently a sleeping *A. lineatopus* was found with one leg flexed and the other extended backward.

Home Range and Activity Range

An *A. lineatopus* seldom travels far and most of the area it visits is visible to it from its usual perch.

I use the term "activity range" for the area visited regularly during the day including the usual perches but excluding the sleeping site when it is outside of this area. "Home range," as used here, includes both activity range and sleeping site. The activity range is described in terms of its horizontal extent and, since *A. lineatopus* are largely arboreal, reference to its vertical extent is also included. I have followed the suggestions of Milstead (1961) and, in calculating activity range size, have omitted the occasional visits that certain *A. lineatopus* made to perches well outside of the area where they were usually seen, but I have plotted these visits on the maps included in this paper.

Anolis lineatopus may sleep in the same area where it spends the day, perhaps climbing up and out onto one of the branches of its principal perch. It may leave the area where it spends the day, however, if there is no suitable sleeping site, and travel several yards to find one. *Anolis lineatopus* that have mutually exclusive activity ranges may all use the same sleeping sites.

Of 15 adult females living in Barbican [fig. 6] for which I have adequate day and some night records, 7 were recorded sleeping only within their activity ranges, 6 both in and outside of their activity ranges, and 2 only outside. The sleeping places usually were less than 5 feet away from where the female spent the day, but for one female they were 10 and 12 feet away. Of the 10 adult males [fig. 4], 5 were recorded sleeping only inside their activity range, 3 both in and out, and 2 only outside their activity range. Two males regularly traveled 10 feet to sleep but for other males the records outside of the activity ranges were mostly 3 to 5 feet away.

The concept of an activity range with a definite size is useful since it gives a datum for comparison with other animals. It is, at best, a crude approximation of the space actually utilized by the lizard. First, it takes only slight account of the vertical range of the animal and, for an animal that spends most of its waking hours above the ground, this is important. Second, the individuals do not visit all parts of their activity ranges equally nor do they always range out in a regular manner from a single center. Finally, an activity range has definite boundaries only where it adjoins the activity range of another *A. lineatopus* of about the same size (see p. 46 et seq.).

Both the size and the shape of an activity range varies with the size and sex of the individual and with the number and distribution of perches available.

For adult males the usual activity range varies between 3 and 10 square yards, seldom probably is less than 3 and sometimes probably as much as 20 square yards. It usually extends vertically from 1 to 3 yards, again sometimes less but probably never less than 1 foot and seldom more than 5 or 6 yards.

The shape is influenced strongly by the distribution of the perches used. Where a single perch is used and the surrounding area is uniform, the activity range is roughly circular with the perch in the center. The activity range of the adult male (no. 4) mapped in figure 2 approaches this. He lived on an isolated tree and in the 40 times he was observed over a period of 21 days, he was on the trunk of the tree below 20 feet (only 6 times going higher than 8 feet or to the ferns at the base, which extended only 3 feet out from the tree).

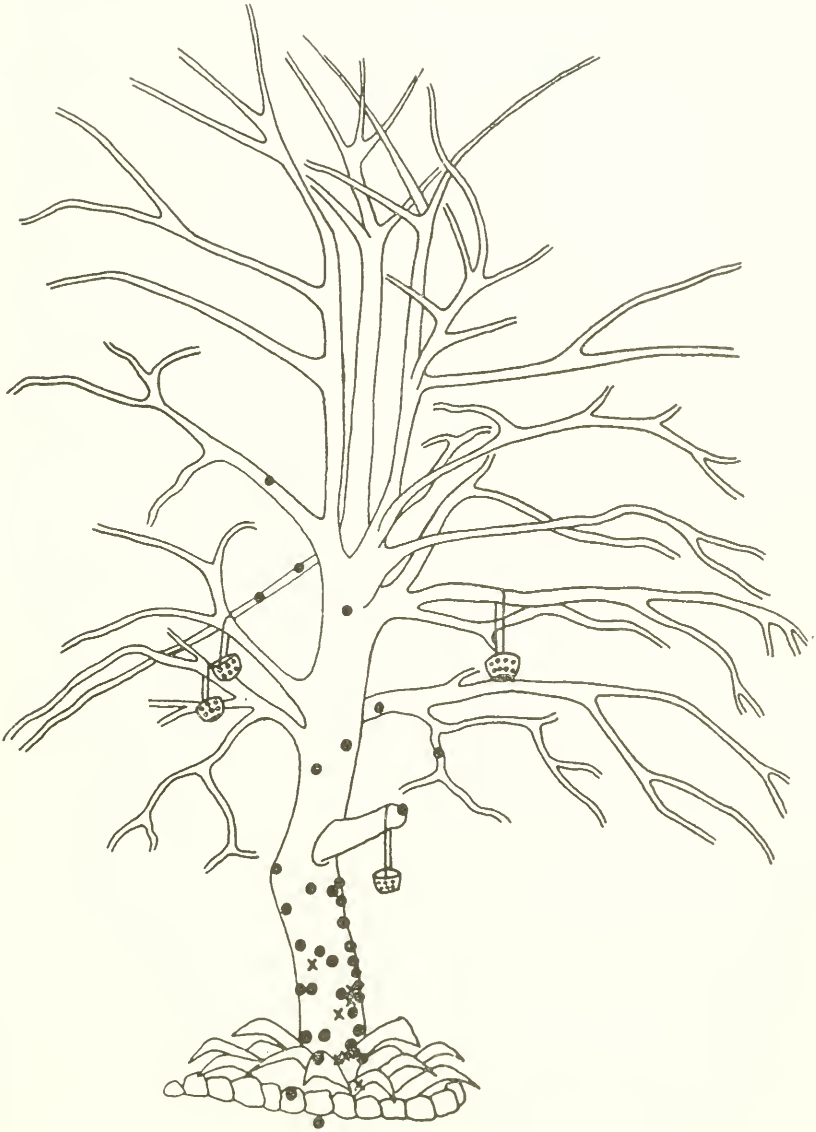


Figure 2.—Record of observations of adult male *Anolis lineatopus* (63 mm) on isolated Indian almond tree, August 22 to September 15 (dots=observations on near side of tree, x's=records on opposite side; preponderance of records on near side primarily reflects usual position of observer).

His activity range was 3 square yards on the ground and extended upward about 3 yards.

In areas with more perches available, the activity ranges are larger in horizontal dimensions. In the Barbican brush heap shown in figure 3, the three resident males had areas of approximately 13, 8, and 6 square yards; the first of the males using a small tree regularly climbed to 6–8 feet, while the other climbed only to about 3 feet. The activity ranges of these males were ovals except that the largest had an elongate projection along the fence.

The other males at Barbican [fig. 4] had activity ranges that fall within the 3–10 yard size range. The relationship of perches to activity range shape is conspicuous in figure 4. The activity range of no. 2 was located on the front porch of my house. He used the L-shaped railing as a perch; the observation records of him outline the railing just as the concentration of observations along the fence indicates the position of the fence posts.

On an abandoned stone aqueduct, the males were found living mostly under the arches and usually restricting their activity to a single arch. Those 16 males on which we have adequate data had activity ranges varying from 4 to 16 square yards in area and mostly between 4 and 8 square yards. They extended vertically between 2 and 10 feet. The activity ranges were mostly quadrangular in plane view, reflecting the shape of the area under an arch.

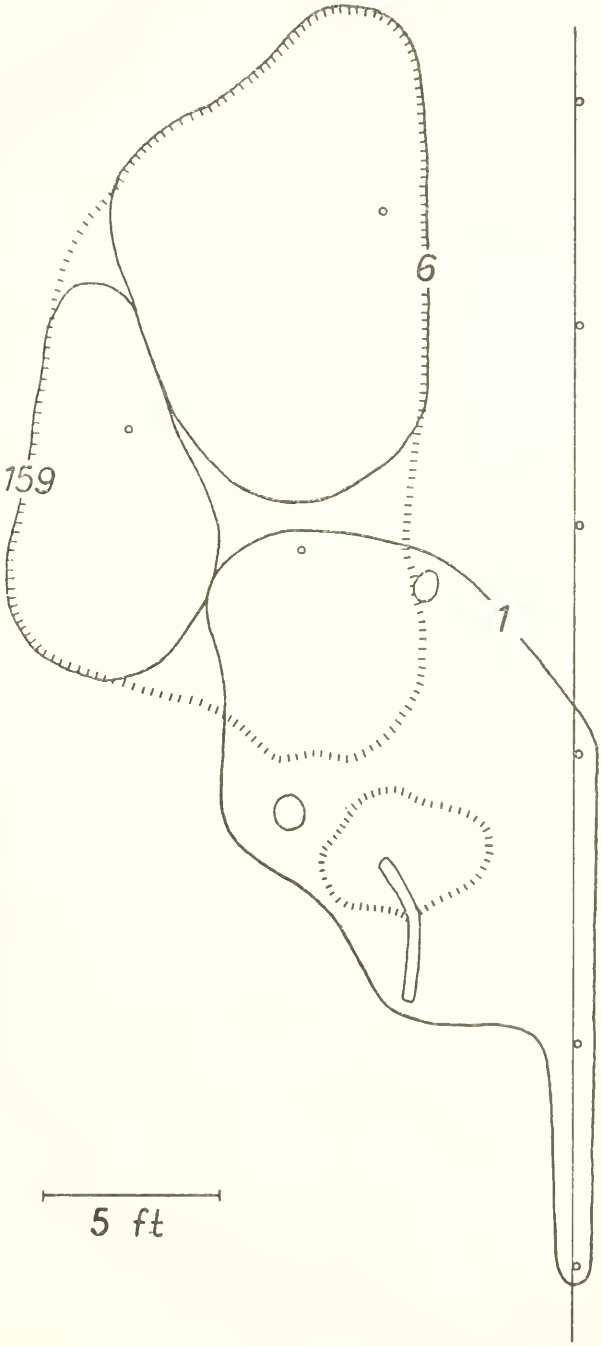
The size of the activity ranges of the adult females is usually considerably smaller than that of those of the adult males, and again structure of the habitat affects size and shape. In general, the female activity ranges averaged about 1 to 2 square yards, sometimes being as much as 3 or 4 square yards and probably sometimes only 2 or 3 square feet. In vertical extent the females usually ranged from 1 to 5 feet and probably sometimes more.

In the isolated tree shown in figure 2 there were 9 resident females. Of these, 8 concentrated their activities below 3 feet, in the ferns at the base and the rock border around it, occasionally climbing the tree to the height of 6 or 8 feet. One female concentrated her activity on the trunk and the side branches between 5 and 9 feet above the ground and only rarely came down into the ferns. For each of these females, the activity range was about 1 square yard in horizontal extent.

In the Barbican brush heap [fig. 5], which was more complex in perch distribution, 3 adult females (nos. 59, 145, and 162) had activity ranges of 1, 1, and 2 square yards and ranged vertically between ½ and 4 feet. The other females in Barbican [fig. 6] have activity ranges that are usually between 1 and 3 square yards in area.

The activity ranges of lizards below adult size are somewhat smaller than those of the adults of the same sex and increase as the lizards grow.

FIGURE 3.—Activity ranges of three adult males (no. 1=59 mm; no. 6=63 mm; no. 159=58 mm) in Barbican brush heap, January 23 to February 23 (heavy continuous lines= approximate activity range boundaries, fine lines=physical features, remaining lines= boundaries of brush heaps).


6
159
1
5 ft

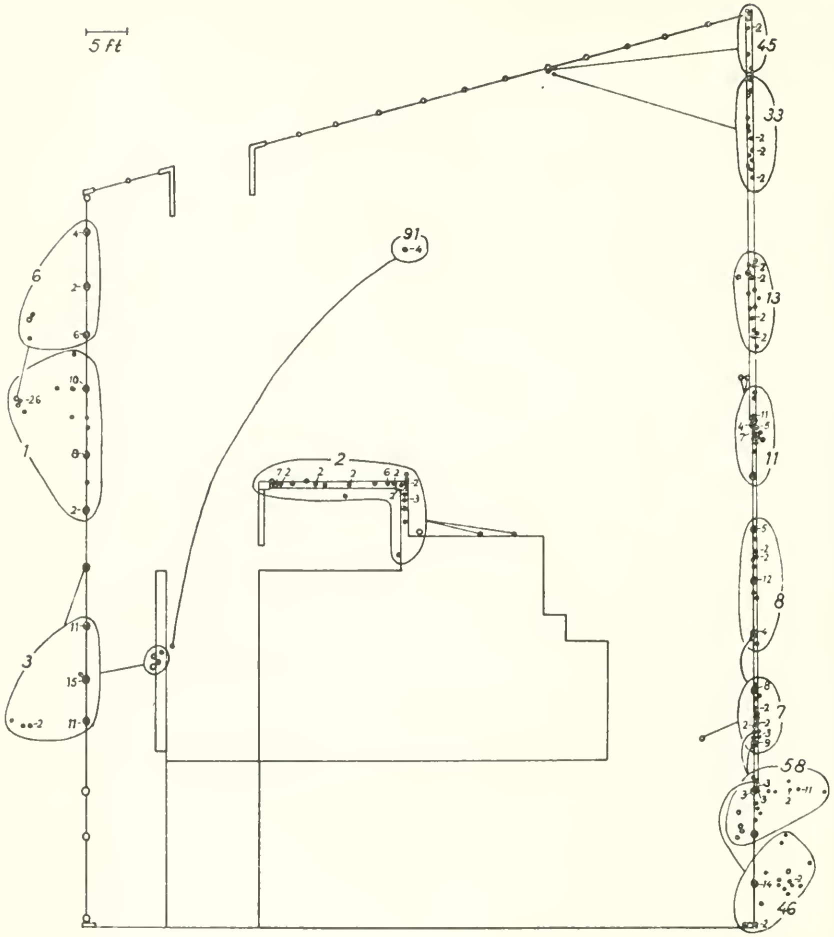


FIGURE 4.—Distribution of adult males larger than 50 mm seen four or more times at Barbican in fenced yard around author's house September 30 to November 7 (dot=day record of each position where lizard was sighted, circle=night record; small number adjacent to dot=more than one record in same position; lines around records for each lizard enclose their activity ranges but indicate boundaries only roughly; observations a long distance from activity range are joined by line that shows only which lizard was involved and not path it took to reach place observed). Three of the males were present for only part of this period. All but no. 91 were marked by October 1. He appeared October 19 on a small, previously unoccupied, tree and was seen there until October 24, when he was found dead in the carport (probably killed by our dog and perhaps carried there by him). No. 2 was found dead on November 1. No. 33 disappeared about October 30 and at about this time no. 45 moved along the wall to occupy no 33's area. These records of no. 45 following no. 33's disappearance have been omitted. (No. 1=59 mm; no. 2=56 mm; no. 3=59 mm; no. 6=62 mm; no. 7=62 mm; no. 8=67 mm; no. 11=61 mm; no. 13=65 mm; no. 33=64 mm; no. 45=67 mm; no. 46=63 mm; no. 58=67 mm; no. 91=55 mm.)

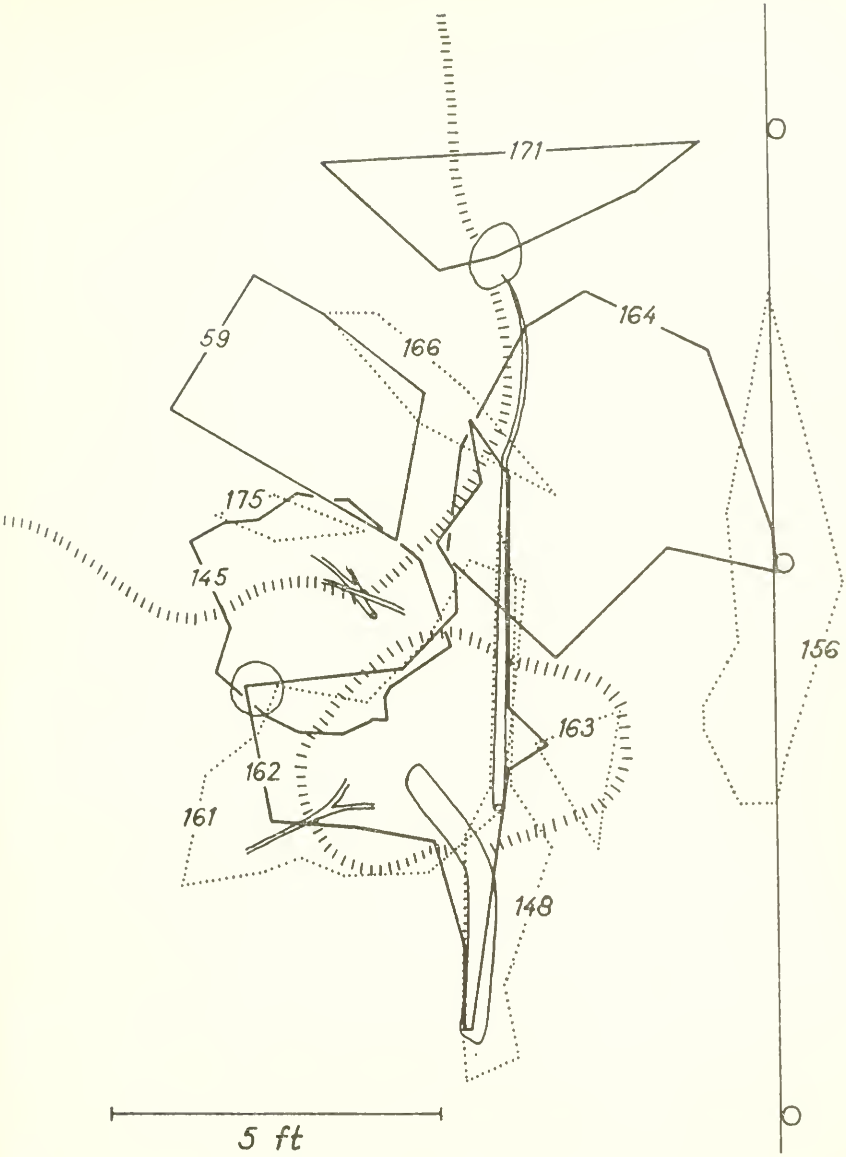


FIGURE 5.—Activity ranges of females and juveniles in part of Barbican brush heap (see fig. 4 for activity ranges of adult males; activity range boundaries were constructed by linking marginal records for each lizard; heavy solid lines=larger individuals, dotted lines=smaller lizards, thin solid lines=structural elements, remaining lines=boundaries of brush heaps; period covered=January 23 to February 23, except for nos. 162, 148, and 163, for which boundaries represent activity ranges before shifts discussed in test (pp. 49 and 52) occurred; in the following list, dates of measurement are given because certain lizards show appreciable growth: no. 59 female=41 mm, January 23; no. 145 female=43 mm, January 9; no. 148 female=26 mm, January 9, to 28 mm, February 1; no. 156 female=25 mm, January 10, to 28 mm, February 7; no. 161 female=29 mm, January 10; no. 162 female=ca. 39 mm; no. 163 female=26 mm, January 24, to 28 mm, February 9; no. 164 female=33 mm, January 26, to 34 mm, February 9; no. 166 male=22 mm, January 30; no. 171 male=31 mm, February 9, to 35 mm, March 11; no. 175 female=24 mm, February 9).

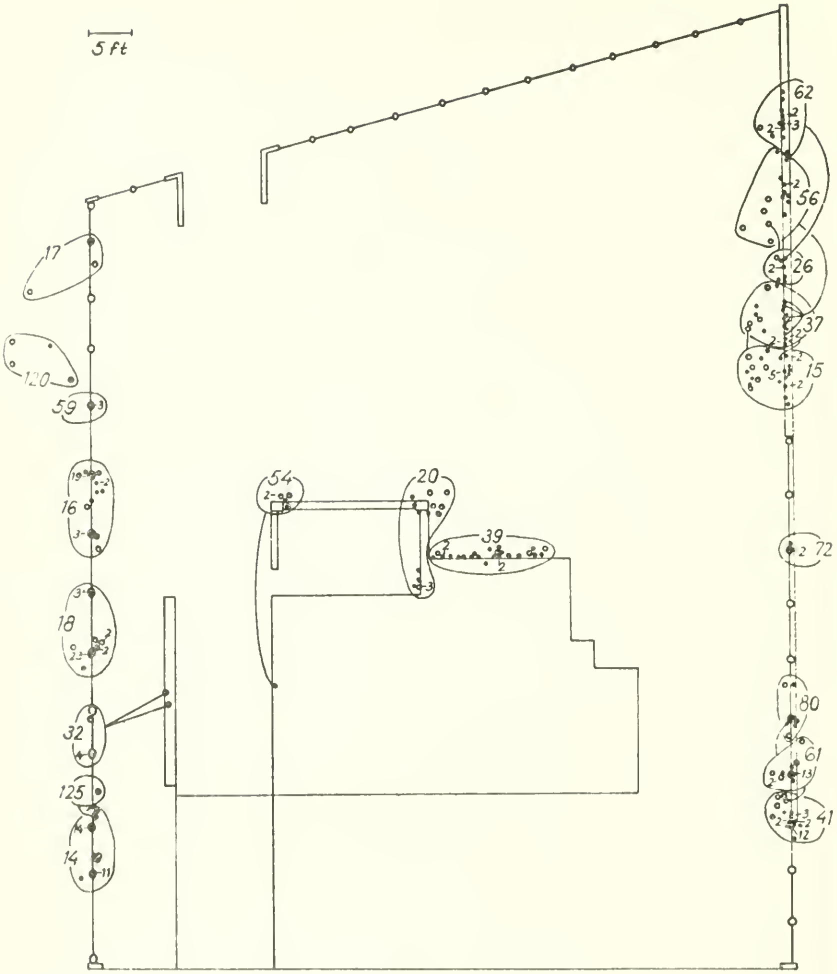


Figure 6.—Distribution of adult females in Barbican September 30 to November 7 (same area and lineal elements as figure 5; all lizards seen more than twice have been mapped; no. 14=44 mm; no. 15=44–45 mm; no. 16=41–42 mm; no. 17=42 mm; no. 18=42–43 mm; no. 20=42–43 mm; no. 26=43 mm; no. 32=42 mm; no. 37=43 mm; no. 39=39–40 mm; no. 41=44–45 mm; no. 54=42 mm; no. 56=43 mm; no. 59=39–40 mm; no. 61=42 mm; no. 62=44 mm; no. 72=43 mm; no. 80=45 mm; no. 120=42 mm; no. 125=41 mm).

The best data on young females come from the Barbican brush heap (fig. 5), where the activity ranges of 6 small females were plotted. These varied in area between 1 and 16 square feet and their shape was strongly influenced by the distribution of the larger branches in the brush heap. The larger activity ranges were mostly held by the large individuals.

The best data on young males come from a study of the Mona hibiscus hedge (fig. 9, table 4) where the activity ranges of 7 were studied. These ranged from about 4 to 18 square feet, being about 4 to 10 for the smaller individuals and about 10 to 18 for the larger.

Since even adult male *A. lineatopus* activity ranges seldom reach 150 square feet, they are well below average size for land vertebrates. No birds or mammals are known with home ranges nearly as small as this; however, at least one frog has a home range of about the same size—*Scaphiopus holbrooki* with an average home range of 108.4 square feet (Pearson, 1955).

Temperate North American iguanids have small home ranges but even the species with the smallest, *Uta stansburiana*, with an average adult male home range of 2600 square feet (Tinkle, et al., 1962), has a range considerably larger than *A. lineatopus*. In contrast, two tropical lizards have home ranges that lie between that of *Uta stansburiana* and *Anolis lineatopus*—*Basiliscus vittatus*, Hirth (1963a), and *Agama agama*, Harris (1964). It may be generally true that tropical lizards have smaller home ranges than do their relatives in temperate regions.

Typically *A. lineatopus* visits all of its principal perches every day, frequently more than once. The frequency of forays that it makes from the principal perches is inversely related to the length of the

TABLE 4.—*Activity range use in Mona hibiscus hedge* (areas in square feet; see p. 28 for discussion)

Lizard number	S–V length (millimeters)	Total area April 10–June 8	Number of records	"5-minute census" results			Comparison of polygon areas	
				Area of polygon enclosing—			Ratio of—	
				100% of records	75% of records	50% of records	50% of records to 100% of records	50% of records to total area
3 ♀	33	6.6	63	5.1	2.4	1.1	.22	.17
4 ♂	ca. 37	9.8	64	4.7	2.4	0.8	.17	.08
5 ♂	43	17.7	64	2.7	0.2	0.1	.04	.006
7 ♀	36	6.5	60	6.5	4.3	2.3	.35	.35
8 ♂	31	4.0	64	3.2	0.6	0.2	.06	.05
10 ♂	43	15.7	54	8.5	2.9	0.3	.04	.02
11 ♂	45	11.5	64	7.4	2.8	0.6	.08	.05
12 ♂	52	49.0	51	36.0	10.8	4.6	.13	.09
13 ♂	61	shifted	63	15.9	2.5	2.5	.16	
15 ♂	ca. 41	4.0	63	3.1	0.7	0.2	.06	.05
25 ♂	36	6.8	55	6.2	2.0	0.3	.05	.04

forays. To measure the utilization of activity range, I recorded at 5-minute intervals the position of each *A. lineatopus* present in a small area of hibiscus hedge during 10 periods of about ½ hour each April 18–23. These records for each individual were compiled and 3 convex polygons drawn, one connecting the outermost points, the next, the smallest including 75 percent of the observations, and a third, the smallest including 50 percent of the records. All the records (April–June) were added and a polygon enclosing them was drawn. The 100 and 75 percent polygons are shown in figure 9. The area of each polygon was calculated. The results (table 4) show that each anole spent half his time in a very small area compared with that which it visited. Fifty percent of the records fall in areas ranging from 4 to 35 percent of the respective areas enclosing all of the census records. In 9 of the 11 cases it is less than 20 percent and in 6 it is less than 10 percent.

The addition of other records for April, May, and June made a great increase in area in only 1 case. In the other 9 cases it less than doubled the area.

The principal perches of *A. lineatopus* and the area immediately around them form what might be called the core area of the activity range, following the usage of Kaufmann (1962). As he found in the raccoon-like coatimundis, the core area is not only the part most heavily used but also the part of the home range with the least overlap with those of others (see p. 46).

The activity range of an adult *A. lineatopus* seems relatively permanent and certainly shows no seasonal variation. Subadults and particularly young males are much more mobile.

In the abandoned aqueduct, that I observed, 5 adult males marked on October 19, were found the following June 1 and all were in the same places where they had been marked. In the yard at Barbican, of the 16 adult males seen more than once in September and October, 7 were still present in the middle of March. Of these, 3 had shown slight shifts to adjacent areas and 4 had shown none. Of those 9 which had not been seen in March, 2 were dead, but it is possible that the other 7 had shifted their areas outside of the study plot.

Of the 24 adult females seen more than once during September and October, 13 were seen in March. Of these, 3 had moved in the interim, all to adjacent areas. Again it is quite possible that some of the females not seen in March had moved rather than had died.

Smaller shifts, which did not involve abandoning the original area, were more common. Perhaps the commonest were brief excursions lasting less than a day and peripheral to the usual area. These were recorded in both adult males (up to 20 feet, 7–10 feet being more common), and females (up to 13 feet, 4–5 feet being more common). Also, not infrequently observed were shifts involving the abandonment of part of the area and certain perches and extending the area to new perches in some other direction. Finally, at least 2 of the females made temporary shifts during the period of September to November 7, abandoning the original area for an adjacent one for a few days and then returning.

A number of the adults marked in September through October but not seen in March probably were marked during temporary shifts and occasional excursions into the study area.

I have no data for longer than 6 months but several members of the faculty of the University of the West Indies have told me of *A. lineatopus* that have lived in the faculty's houses and used the same pieces of furniture for perches over several years. These stories, based on unmarked animals, are inconclusive but not improbable.

The reasons for the shifts observed in the adults include changes in the structure of the environment through the cutting and growth of vegetation and interactions with other adults.

It is possible that changes in available food supply affect the area utilized, a concentration of insects attracting a lizard to a new area and a scarcity forcing a lizard to abandon an area, but I have no evidence on this point.

Both young males and young females may hold activity ranges several days or weeks and perhaps longer, but their activity ranges tend to be less stable and less permanent than those of established adults.

Twenty-five young males in Barbican [fig. 7] were marked from September through November 7. Only 17 of these were seen more than once and 9 of these were seen again in March. All 9 had made changes in their areas. Unlike the adults, only 3 of these changes were to adjacent areas, the other 6 were to distant spots, over distances of 45, 48, 35, 35, 45, and 85 feet, respectively.

Even during the period of intensive observation (September through November 7), disjunct shifts were common. Of the 17 young males seen twice or more in this period, 8 showed changes. Six of these were disjunct with distances of 54, 65, 25, 52, 70, 35 feet, respectively. That these shifts average no farther over the short September-November period than over the long September-March period is indicative only, I think, of the small size of the study area.

The young females in this area show similar instability but less strikingly so than do the young males. Twenty-nine young females were marked. Of these, 14 were seen more than once and, of these, 5 were present in March. Of these 5, 2 show changes, neither disjunct. Of the 12 females seen more than once during September through November 7, only 2 show changes and both of these are disjunct, one of 54 and the other of 55 feet, respectively. The young females are very small and thus frequently missed, and, as the mapping technique was too crude to show very small shifts, these records understate the amount of change. Even so, these young females seem to be more stable than the young males, at least in terms of long distance shifts.

Though the activity ranges of young *A. lineatopus* are more liable to change than those of the adults, the lizards do not usually wander randomly. The brush heap area included the areas of 6 small females and 1 small male. Between January 23 and February 23 4 of these 6 females shifted their activity ranges but in each case only to an adjacent area.

In one of these 4 shifts, the lizard was chased from her original activity range by another *A. lineatopus*. In the other 3 cases, the causes of the shifts are unknown but may relate to the changing requirements of the lizards with age and growth.

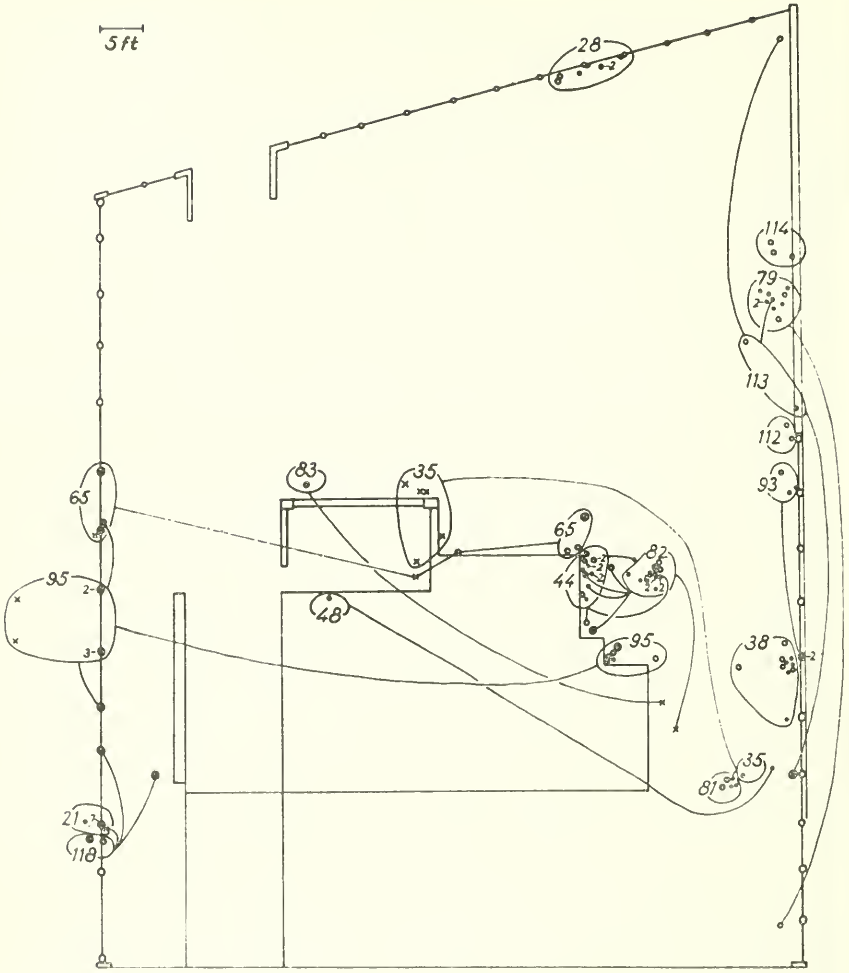


Figure 7.—Distribution of young males at Barbican (same symbols as fig. 5 for period of September 30 to November 7; x's=sightings of lizards several months later, March 8 to 14; all individuals seen more than once during first period and all seen in both periods are mapped; unlike most adults in figs. 5 and 7, these young males showed important growth and first and last measurements are given for them where available; no. 21=47 mm, September 26; no. 28=31 mm, September 26, to 37 mm, October 31; no. 35=44 mm, September 27, to 59 mm, March 10; no. 38=32 mm, September 27, to 38 mm, October 24; no. 44=31 mm, September 29, to 38 mm, October 29; no. 48=44 mm, September 30; no. 65=42 mm, October 5, to 62 mm, March 13; no. 79=29 mm, October 9, to 30 mm, November 2; no. 81=44 mm, October 9, to 65 mm, March 13; no. 82=19 mm, October 9, to 47 mm, March 10; no. 83=18 mm, October 16, to 40 mm, March 11; no. 93=23 mm, October 19, to 57 mm, March 12; no. 95=37 mm, October 19, to 59 mm, March 10; no. 112=22 mm, October 24; no. 113=45 mm, October 42, to 60 mm, March 14; no. 114=37 mm, October 24; no. 118=28 mm, October 29, to 43 mm, March 9).

In the Mona hibiscus hedge studied from April 10 through June 1 there were 10 small males. Of these, 4 changed their activity ranges and the other 6 remained roughly the same.

The data for Barbican indicates that the adults of both sexes have permanent activity ranges and such shifts as they do make are usually to adjacent areas. There is some data from the study area in Mona that contradicts this, though it is a contradiction in detail rather than in substance. When I moved to Mona in mid-April, there were only a few large males that were living on the larger trees, particularly trees with vegetation near the base, a bed of ferns, or a bush. Only a few of these males were marked—those resident in the vicinity of the hibiscus hedge that were being studied in detail—but casual observations were made on the others. It became obvious in the period of mid- to late May that there were many more adult males present and that they were living on trees which had previously been unoccupied. Many of them were smaller than the males which had been present in mid-April. Some of these in one area were marked and their movements watched for about two weeks (fig. 8). These data supported my impressions that there were a number of unestablished adult males moving about in the area. The data show also that there were certain males that did not change their activity ranges during the observation period. The latter males are mostly larger than the former. My interpretation of the data is that the smaller males had recently matured whereas the larger males were older. The older males had been occupying the preferred perches and were successful in keeping the smaller individuals from establishing there, forcing them to spend their time on less favorable perches. That the young males were living in subpreferable areas, coupled with the possibility that they have less site attachment, accounts, I think, for their movements. This is essentially the explanation offered for the situation observed in Barbican. There is a striking difference, however, in the size of the individuals involved in the two situations. In Barbican the males that made activity range shifts were mostly subadults the size of females; in Mona they were fully adult. I think there is a temporal factor herein that explains at least part of the difference. The study in Barbican was terminated in March and that in Mona was not started until May. I think that, if I had remained in Barbican until May, I would have seen an increase in the number of small adult males as the marked juvenile males matured and that these either would have occupied the activity ranges that were not occupied by adult males or would have wandered through the area. Alternatively, had I started my study in Mona in October, I believe I would then have seen a great many movements by young, subadult males.

This study was not designed to investigate either seasonal changes suggested above or dispersal in these lizards; data, therefore, are fragmentary. Clearly both topics are important and need further investigation.

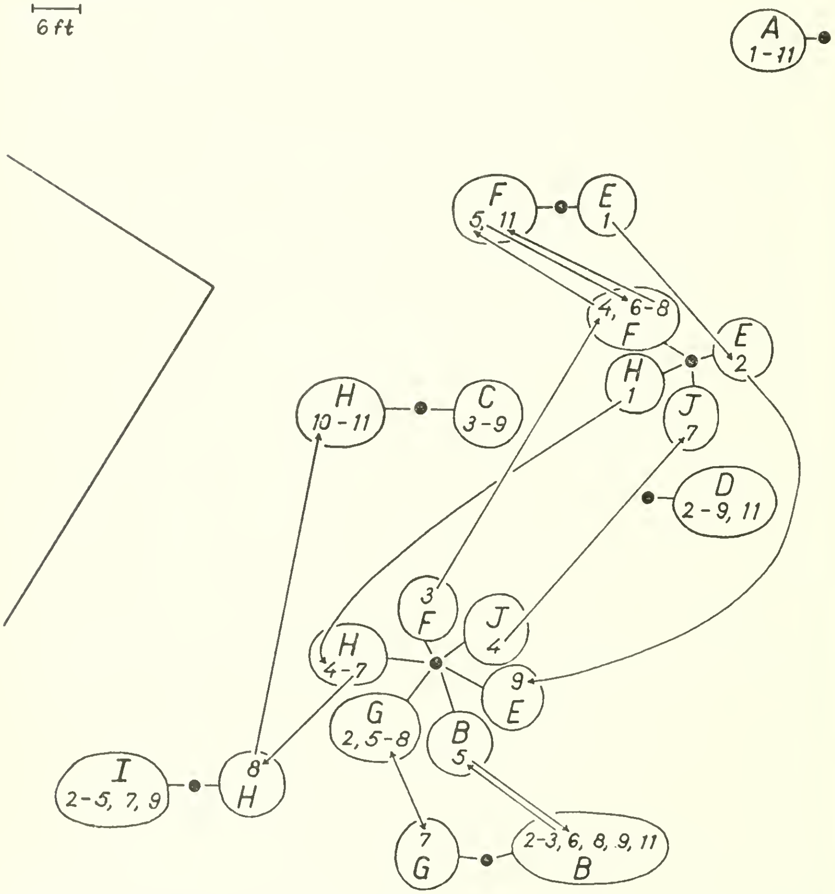


Figure 8.—Distribution of adult males in an area in Mona, May 24 to June 8 (dots=positions of trees on which lizards were seen; lizards: A=68 mm; B=63 mm; C=62 mm; D=60 mm; E=60 mm; F=59 mm; G=57 mm; H=57 mm; I=56 mm; J=51 mm; dates seen: 1=May 24; 2=May 25; 3=May 26; 4=May 28; 5=May 29; 6=May 31; 7=June 1; 8=June 3; 9=June 4; 10=June 5; 11=June 8).

Homing.—Though *A. lineatopus* shows a great deal of site attachment, the only information I have on homing is negative. This is very slight but in the absence of other data is worth recording.

An adult male was moved 200 yards and, after being caged for several days, was released on a small tree unoccupied by any other adult male. He established an activity range there and during the two months under observation showed no sign of attempting to return home.

SPATIAL RELATIONSHIPS BETWEEN ACTIVITY RANGES.—The size, shape, and location of an *A. lineatopus* activity range is influenced not only by the distribution of the habitat requirements but also by the distribution of other *A. lineatopus.*

Even casual observations show that *A. lineatopus* are not distributed randomly with respect to one another. This is particularly obvious along fence rows, where, on almost every fence post, there is one large male but very rarely two. A similar though less conspicuous relationship occurs in the distribution of the adult females.

The simplest situation of this sort that I studied was observed in a series of poui trees planted along a road through the faculty housing of the University of the West Indies at Mona.

The trees had been planted in a strip of grass at about 12 yard intervals, about 4 yards from a hibiscus hedge on one side and about 2 yards from the paved road on the other. They ranged in size from 4 to 12 inches (most of them 8 or 9 inches) in diameter and about 20 to 30 feet high. The spacing of the trees was such that no lizard included two in his activity range. All of the females and most of the males probably had no other principal perches than the trees and the vegetation at their base.

During one afternoon (May 20), I examined the trees along both sides of a kilometer of this road, looking carefully at each tree and examining the vegetation growing at the base. I caught every *A. lineatopus* that I could and sexed, measured, and then released it. A total of 55 trees were examined and 72 *A. lineatopus* seen. Sixty-one were caught, sexed, and measured, plus five more I was able to sex confidently and estimate the size sufficiently to use the data.

The four *A. lineatopus* that I could not size or sex accurately have been omitted from the following discussion as have the other *A. lineatopus* on the same trees with them. This reduced the data analyzed to 51 trees with 62 *A. lineatopus.*

Of males, 32 were sexually mature (i.e. greater than 50 mm snout-vent length), 7 were probably not sexually mature (i.e., less than 50 mm snout-vent length). Twenty-two of the 23 females were probably sexually mature (i.e., greater than 36 mm snout-vent length).

Of the 51 trees, 18 had no adult *A. lineatopus* on them at all, 13 had one, 19 had two, and 1 had three.

The observed distribution departs from random distribution in two ways: there are fewer trees with two adults of the same sex and more with two adults of opposite sex.

Using binomial distribution, the expected number of trees with 0, 1, and 2 lizards were calculated independently for each sex on the assumption that the presence of a lizard on a tree did not affect the probability of another lizard being found on the same tree. These distributions were then compared with the observed distributions (table 5) and the probability that the differences were due to chance were calculated, using an X^2 test. These results show that there are significantly more trees with only a single male (at the .01 level) than would be expected if they were distributed randomly, and fewer trees with two and with no males.

The observed distribution of the females differed from the expected in the same direction (table 5) but not enough to be statistically significant (at the .05 level), perhaps because of the smaller sample size.

Table 6 shows the relationship between adult males and adult females. Trees with no adults and trees with an adult of each sex occur more frequently than would be expected if the distribution of the sexes was independent, while trees with a single male or a single female occur less frequently.

TABLE 5.—*Results of a count of the number of* A. lineatopus *on a line of trees comparing the number of adults per tree with the expected distribution if the adults are distributed independently of one another* (the expected distribution is calculated from the binomial theorem; the sexes are treated separately; the distribution of the adult males differs from the expected at the .01 level, that of the females does not)

	Number of trees		
	With none	With one	With two or more
Males			
observed	21	28	2
expected	27.07	17.32	6.61
Females			
observed	30	20	1
expected	32.99	14.51	3.50

TABLE 6.—*Distribution of males and females with respect to the opposite sex and the null hypothesis (in parentheses) that their distributions are not related*

Females	Males			
	0	1	2	Total
0	18 (12.35)	10 (16.47)	2 (1.18)	30
1	3 (8.24)	17 (10.98)	0 (0.78)	20
2	0 (0.41)	1 (0.55)	0 (0.04)	1
Total	21	28	2	51

This line of poui trees was somewhat unusual in the small number of subadults found, 7 males from 36 to 49 mm and 1 female of 29 mm. The single small female was found on a tree with an adult female and the smallest of the young males. The largest of the young males was found on a tree with an adult male of 62 mm and an adult female of 44 mm. The remaining 5 young males, 40–46 mm, were all on trees that had no other lizards on them.

The distribution of *A. lineatopus* at Barbican during September through November shows a picture similar to that described above but more complex.

The distribution of the adult males is shown in figure 4. They occupy areas that are nearly mutually exclusive though sometimes a male was seen in the activity range of another. The activity ranges of the males in part of this area are mapped in greater detail in figure 3. Again there is little overlap even though in the area where the males meet in the brush heap there are no physical barriers. In fact, all 3 of these males regularly slept in the same tree.

The distribution of adult females in the yard at Barbican (fig. 6) shows a similar mutually exclusive distribution though with more overlap than shown by the adult males. Of the 20 females mapped, all but 3 of them were within the observed activity ranges of adult males.

The distribution of the young males (fig. 7) again shows an almost mutually exclusive distribution, though small ones may overlap with larger ones. The larger subadult males generally show an exclusion also with females. Unlike the females, 7 of the young males lived in areas where there was no adult male.

In contrast to the line of poui trees, the Barbican yard had more females than males and, whereas in the former area there were several males without females, in Barbican there were several females without males.

Figure 2 shows only a single large male living on an isolated tree, but there are 8 adult females and 3 young males also living there. One female lived on the tree trunk and some of the lower branches and seldom visited the ferns on the ground. Seven of the 8 females lived in the ferns at the base of the tree, dividing the area among them so that there was little overlap, though in two cases 2 females occupied the same space at different times. Many of these females also visited the lower tree trunk, where little spatial separation was evident, but none of them used this as a usual perch.

Of the 3 smaller males, 1 had an activity range in the ferns that was largely separated from that of females living in the same area. He also climbed up among the lower branches of the tree. The other 2 small males had activity ranges on the branches of the tree largely distinct from that of the first small male, from all the females, and generally from the large male. These 2 overlapped in space considerably but there is quite a difference in size between them, the larger almost approaching adult size

In addition to the four areas described above, two more were studied that contained a number of young *A. lineatopus* of various sizes. In both of these the spatial relations were more complex than when only adults are considered.

The first of these, Hibiscus hedge, had resident in it: 8 subadult males of various sizes, 1 adult female, and 2 subadult females. It was also visited by 3 adult males. The activity ranges of these 11 lizards (omitting the adult males) is given in figure 9. The first impression of this figure is one of utter confusion. Closer examination, however, reveals several patterns. Though the outlines of many of the activity ranges overlap, there is little overlap between the areas in which the lizards spent 75 percent of their time. Between lizards of approximately the same size, little overlap occurs even at the outer limits of the activity ranges. This exclusion of lizards of the same size operates regardless of sex.

The lizards can be separated into three size classes: the largest with 1 male 49 mm long, which ranged over almost the entire area; the medium-sized lizards, 3 males ca. 44, 42, 42 mm long, which were mutually exclusive; and the smaller lizards, 7 in number, 3 females of 35, 32, 30 mm, and 5 males of 40 to 30 mm, which were also mutually exclusive.

The section of the Barbican brush heap shown in figure 5 had 1 adult male, 4 adult females, and 7 smaller lizards (5 females and 2 males) present. Again their distribution (omitting the adult male) looks confusing until they are sorted by size into two groups: a larger one containing 4 females of 43 to 34 mm and 1 male of 31 mm; and a smaller sized group of 6 females of 30 to 22 mm. Again, though there is considerable overlap between lizards of different sizes, there is little overlap within the size classes. Again, for this size range of lizards, sex is irrelevant. It should be noted that the size groupings used herein

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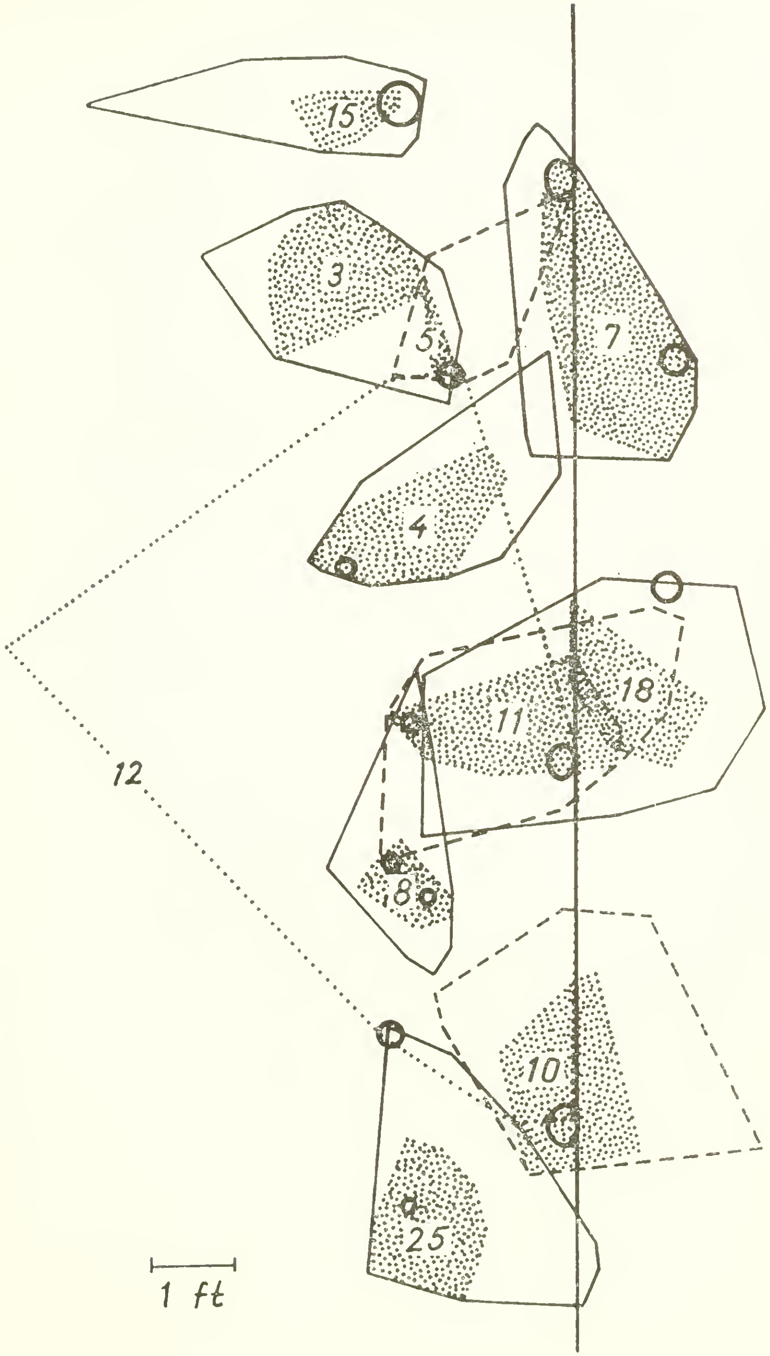
FIGURE 9.—Distribution of females, juveniles, and young adult males in Mona hibiscus hedge; this area also was visited by several larger adult males (circles=fence posts and certain important bushes; several types of lines distinguishing different size classes of lizards based on censuses conducted April 18–23=activity ranges; stippled areas=places where lizard spent 75% of its time (see pp. 28 for explanation); stippled area for no. 12 overlaps those of nos. 8, 10, and 11 and has been omitted for clarity; no. 3 female=32 mm, April 10; no. 4 male=36 mm, April 10; no. 5 male=42 mm, April 10; no. 7 female=35 mm, April 10; no. 8 female=30 mm, April 10; no. 10 male=42 mm, April 10; no. 11 male=44 mm, April 10; no. 12 male=49 mm, April 10; no. 15 male=40 mm, April 11; no. 18 male=36 mm, April 11; no. 25 male=36 mm, April 17).


15
3
5
7
4
18
11
12
8
10
25
1 ft

bear little resemblance to those used in the first case and, in fact, any division seems to be arbitrary.

A basic rule in distribution of *A. lineatopus* seems to be that no two lizards of the same size can have widely overlapping activity ranges. This general rule seems to apply at all sizes, from the smallest studied, 22–24 mm, to the largest adult males, ca. 70 mm, and to apply regardless of sex. *Anolis lineatopus* of different sizes, however, may have widely overlapping activity ranges. Usually the activity ranges of adult males overlap those of adult females, which frequently in turn overlap those of small juveniles. The activity ranges of the small males frequently are like those of similar sized females, but also, and much more frequently than females, they are in areas that are uninhabited by other lizards, either male or female, and some of which, because of the structure or situation, seemed subpreferable. The distribution of adult *A. lineatopus* relative to one another resembles one of the common patterns seen in vertebrates, that of territoriality. The distribution of the juveniles with respect to one another, particularly to the adults, is more novel.

Social Behavior

The regular arrangement of activity ranges with respect to one another is largely the result of direct interaction between individual *A. lineatopus*. These interactions fall into two categories, agonistic behavior and courtship. These interactions, and the display associated with them, are common and make up most of the social behavior of the species. As is general in lizards, parental care, flocking, play, allogrooming, and alarm signalling are absent. Perhaps important in certain circumstances but hardly true social behavior is predation by adult male *A. lineatopus* on juveniles of the species (see p. 15).

An adult male *A. lineatopus* probably spends more time in display than in any other activity except sleeping and watching. One male that I watched for about 11 hours gave 181 displays (averaging about one every 3½ minutes). During this time he was involved in two conflicts with other adult males, copulated twice, and courted unsuccessfully several additional times. In the 8 hours from 8:00 A.M. until 4:00 P.M. there were only 5 periods longer than 10 minutes when no display was seen, the longest being about 30 minutes.

Before describing agonistic behavior and courtship and discussing their effects on the spatial organization of the population, it is necessary to digress briefly into a description of the various displays observed in *A. lineatopus*.

DISPLAY.—No analysis is given here because the displays of West Indian *Anolis*, including *A. lineatopus*, are under study by Dr. R.

Ruibal (in press). "Display" is used here in its usual nontechnical sense.

The displays of *A. lineatopus* can be described under the following categories: back jumping , step bobbing, bobbing, dewlapping, orientation, posture, jaw fencing.

Back jump: The lizard suddenly and violently extends all four legs so that it pushes itself away from the perch and backward along it. A series of one to three of these may be given in sequence. I have seen it only infrequently and always in long disputes between adult males, most often shortly before they meet to lock jaws or between bouts of jaw locking.

Step bobbing: In this display the head and anterior part of the body is raised stiffly in a series of short steps and then lowered in a similar manner, producing a slow, jerky bob that is usually repeated several times in sequence. Step bobbing is somewhat more common than the back jump. It is given by juvenile and adult males (and perhaps females) usually in disputes wherein both lizards are displaying, occurring early as well as late in a dispute. It occurs more rarely in dispute situations wherein the opponent is not displaying and only very occasionally in situations wherein no opponent is visible. It can be combined with dewlapping.

Bobbing: The head or head and shoulders are moved up and down rapidly several times. This is the most common *A. lineatopus* display. It is given in courtship by both sexes and in dispute situations by males and females, both juveniles and adults. The displays included herein are variable in form and, though I did not do so, it may be possible with careful study to separate a male courtship bob from this category, as Greenberg and Noble (1944) did for *Anolis carolinensis* and Kastle (1963) did for *Norops auratus*. A great deal of bobbing by all *A. lineatopus* is not obviously either dispute or courtship. Similar bobbing occurs commonly in iguanids and agamids. Interpretations of its significance are varied. Greenberg and Noble (1944) called it a subordination gesture in *Anolis carolinensis;* Noble and Bradley (1933) called it an aid to vision, increasing depth perception. Carpenter (1962), in *Sceloporus undulatus* and other iguanids, calls it assertion display, and Harris (1964) suggests that in *Agama agama* it functions to keep the group members aware of one another's position. Evans (1936a) suggested that in *Anolis carolinensis* it served as a cue given by a female to a male to indicate her sexual receptivity.

I have recorded the behavior associated with 57 instances of bobbing by marked females and subadults during two sessions of two hours each (tables 7, 8). The most striking correlation is with movement. *Anolis lineatopus* usually bobbed after it had shifted its

TABLE 7.—*Relationship between head bobbing and shifts in position in females and young males*

Apparent reason for shift	Before shift	During shift	After shift	No shift	Total
To feed		7	15		22
To flee or avoid another lizard	1		3*		4
To chase or approach another lizard	3	2	10		15
Unknown	1		7	7	15
Total	5	9	35	7	56

*Plus one instance of step bobbing.

TABLE 8.—*Occurrence of head bobbing in dispute situations among females and young males*

	Neither bobs	Only winner bobs	Only loser bobs	Both bob	Total
Approach-avoid	8		1		9
Chase-flee	3	10			13
Mutual display	1			2	3
Total	12	10	1	2	25

position and did so whether it had moved to chase away another *A. lineatopus*, flee from one, or catch something to eat. Juveniles and young males bobbed as frequently as did females and in a similar manner. In dispute situations the winning or dominant lizard usually bobbed, the loser or subordinate seldom did so.

In *A. lineatopus* bobbing is not a subordinate gesture nor a signal of female sexual receptivity. It is probably not an aid to depth perception. Bobbing probably serves to advertise (or assert) the presence of the displaying *A. lineatopus* to others in the vicinity. It would thus serve much the same function in *Anolis lineatopus* that it does in *Sceloporus undulatus* and *Agama agama*. Presumably it is also analagous to the singing of territorial birds and the sign posting of many mammals.

Dewlapping: The dewlap is flashed—extended to its maximum, as a gular fan, exposing the yellow and orange skin between the more dully colored scales—several times in sequence and then relaxed. In Evans' (1953a) terminology there are 5–12 flashes per volley. The dewlapping display is given by adult males (very occasionally by subadult males, see page 54). This display is commonly seen and is given in courtship and agonistic situations. Like bobbing, it seems also to serve as an advertisement display.

Orientation: Though orientation by itself is not a display, certain stereotyped changes in orientation are important components of almost all displays. In courtship a male orients toward the female, who is usually oriented away from him. He may turn his head to one side so that his dewlap is more visible to her. In a dispute, *A. lineatopus* frequently does not face its opponent directly but turns so that it presents a side view. The amount of turning varies from turning the head slightly to one side, through a position in which the lizard is at right angles to its opponent, to one in which the lizard is facing almost directly away from its opponent. In disputes in which both lizards are displaying, they frequently approach one another obliquely rather than directly.

In watching a prolonged fight between two males, it is possible to predict, on the basis of the angle of each, which one will attack next. Lizards that are parallel to one another will usually display rather than attack. The closer a lizard is to facing his opponent, the more likely he will approach the other; the farther away he is facing from his opponent, the more likely he will retreat.

Posture: Associated with lateral orientation are postural displays that increase the apparent size of the lizard when seen in side view. In lizards of all sizes the sides are pulled in or flattened so that the back is arched and the belly extended with the result that the body appears deeper. The throat is gorged: the base of the hyoid is pulled down so that the throat appears swollen. Frequently the mouth is opened slightly and the tongue, which is short and broad, is raised and pushed forward so that the tip appears as a small ball between the ends of the jaws.

Finally, and in the males only and most conspicuously in adults, the tissue along the center of the neck and back can be raised into nuchal and dorsal crests. The total effect of these changes is to make the lizard, when seen from the side, appear almost twice as bulky as it normally is. The postural displays are all associated with disputes and do not occur in courtship.

Jaw fencing: Though fighting is not properly considered display, combat between *A. lineatopus* adult males is usually so ritualized that is should be considered here. Each male approaches the other slowly until the two are an inch or so apart, head to head. They lunge repeatedly at each other's snout for a moment or so, as if fencing for a hold. They then lock jaws, one biting the other's snout and the latter biting the former's lower jaw. The two lizards then strain against one another, each apparently attempting to dislodge the other from the perch. When one succeeds, the other may fall to the ground or dangle in midair for a moment. Alternately, one lizard may attempt to escape, opening his mouth and scratching with a front foot at the other's snout. This wrestling with locked jaws may last for several minutes and may be repeated two or three times. Usually one of these encounters is decisive and the loser retreats immediately after the bout. I have never seen a defeated lizard so injured or exhausted that it was unable to run away.

Damage sometimes results from these bouts and blood is drawn, though the wounds are restricted to the snout. Some males are found with a swelling on one of the mandibles, probably wounds from this sort of combat that have become infected. (Schmidt, 1928, suggested the same thing for *A. cristatellus* in Puerto Rico.) The infected wounds apparently are painful. One noosed male with an infected jaw repeatedly bit and released my finger rather than biting and holding as a male normally does.

The preceding descriptions of display provide a foundation for discussing the role that social behavior plays in the spatial organization of *A. lineatopus*. Two sorts of social behavior seem important: courtship and agonistic behavior.

Courtship.—This behavior brings together male and female when they are ready to copulate. Evidence suggests that it also influences males and females to establish and maintain overlapping activity ranges and in effect to form pair bonds.

This pattern, a male with a home range shared by one or several females that are his mates, is common among vertebrates. It is perhaps most common among birds and mammals in which the male and female share in care of the young. It seems widespread in lizards, particularly iguanids (*Anolis sagrei*, Evans, 1938a, Oliver, 1948; *Sceloporus olivaceous*, Blair, 1960; *Uta stansburiana*, Tinkle, et al, 1962; *Basiliscus vittatus*, Hirth, 1963a; and *Agama agama*, Harris, 1964). The role of courtship in establishing this pattern is far from clear. Blair (1960) feels that the males of *Sceloporus olivaceous* seek out the females. In *Agama agama*, Harris (1964) has evidence that it is the females that make the choice, joining a male that has established a home range. Hunsaker (1962) showed experimentally that in the *Sceloporus torquatus* group it was the male bobbing display that was attractive to females, and Hunsaker suggested that this influenced them to settle near the male. Perhaps dewlap displays of the adult male *A. lineatopus* are similarly attractive to females.

Though the male *A. lineatopus* spends a considerable amount of time chasing and bobbing and dewlapping to females, I observed copulations infrequently. Chases, though frequent, are seldom persistent, and I never saw a male catch a female that was trying to avoid him.

In the consummated courtships seen, there was relatively little display and the whole process seemed very casual. All of the copulations I observed between marked lizards occurred within the home ranges of the lizards involved. For example, at Barbican (figs. 4, 6), an adult male (no. 1) was seen in copulation with three females (nos. 16, 59, 145), all of whose home ranges widely overlapped his. None of these females was seen to copulate with any other male though this may happen. Among the lizards on an isolated tree (fig. 3), one female was seen to copulate with the adult male and also, on another occasion, with a smaller (ca. 47 mm) but obviously adult male. The activity range of the large male overlapped that of the female while the activity range of the small male overlapped that of the female to some extent.

The following description from my field notes illustrate these consummated courtships:

> 29 October—Barbican. No. 3, adult male, was sitting on a fence post and No. 18, an adult female, on the adjacent fence post about 7 feet away. They had been sitting in these spots for at least ½ hour ignoring each other. The male displayed occasionally: bobbing first, then continuing to bob he began to flash his dewlap, stopped bobbing, and continued flashing dewlap, then stopped; a few bobs were given without any dewlapping. The female moved several times but I saw no display on her part. Then, with no obvious preamble No. 3 climbed along the barbed wire from his post to hers. He stopped on the wire for a moment then proceeded to her post, approached her from behind and straddled her with both fore and hind legs and seized a tiny bit of the loose skin on the back of her neck and they walked together a few inches down the post. They stopped and he twisted the base of his tail under hers and apparently inserted his left hemipenis. Shortly he released his hold on her neck. They remained still except for two short series of bobs by the female. After perhaps 2–3 minutes they separated, both dragged their vents on the post and then the male returned along the wire to his original post.

Once the male had left his original post he did not display and his earlier displays seemed the usual advertisement displays. I had been watching the male but was aware of the female for about a half hour before the male approached her and I noticed no display behavior on her part. The only unusual thing she did was not avoid no. 3's approach. About an hour later these two were in copulation again.

Before any of this happened, I had placed another female, tied to a string, on the male's fence post and, though she was in full view of him, he seemed to ignore her completely.

The other 10 courtships that I saw followed this pattern almost exactly, differing only in that the male occasionally stopped in his approach to the female and dewlapped. In each of these I was impressed by the small amount of display on the part of the male and its almost total absence on the part of the female. The only movements by the female that could be considered display were noted in two of the courtships; in these, just before the male seized her neck, the female moved her head from side to side.

There may be an inviting or receptive display on the part of the female but I was unable to recognize it. Certainly the females do not bob to indicate their receptivity as Evans has recorded for female *A. carolinensis*.

Copulations were observed from August 24 to May 30. They seem to occur throughout the year.

The above description of a copulation mentions that the male copulated with a female that was resident in his area even though there was an adult female closer to him and tethered so that she could not escape. On another occasion, a different male approached about 10 feet, apparently in response to my placing a female stake-out in his home range. When he reached the vicinity of the stake-out and had inspected her, he mated with a free female that was nearby and with which I had seen him before. I tried tethering females within the home ranges of males on several other occasions and in no case did a male attempt to mate with them.

These observations suggest the possibility that the males recognize the females that live within their home ranges as individuals. The observations can also be explained by saying that a female tied up is not a suitable mate or that the tethered females were not receptive while the free-living ones were and that the male could detect this.

There are two other data relevant here. One is that adult male and adult female home ranges overlap intersexually more frequently than one would expect on chance (p. 33). Apparently adults of one sex or the other, and perhaps both, prefer to live in a home range which overlaps that of an adult of the other sex.

The final piece of evidence is the very simple and almost casual way in which copulation occurs and the small amount of display that immediately precedes it. A great deal of display is given by the males in the presence of the females to which the females do not react overtly. If it has any effect on them at all, it must be a cumulative effect over a period of time. This is possible since all of the copulations that I observed involving marked lizards took place within the normal home ranges of the lizards involved. The cumulative effect of the display may result in keeping the female aware of the male's presence, in bringing her into sexual receptivity (as in many birds), or in reducing her fear of or aggression toward him. The studies of Hunsacker (1962), showing that there are two displays in *Sceloporus*, one which attracts the females to stay near the male and another which is precopulatory, suggest that the cumulative effect of display postulated for *A. lineatopus* may occur widely in iguanids.

Since the lizards live together more or less permanently and the females usually mate with a single male (the male with the one or more females that have home ranges within his), there exists what might be considered a pair bond. The evidence that the male *A. lineatopus* may recognize the females as individuals suggests that this pair bond is comparable to that in birds and mammals. A pair bond of some sort has been reported in the largely monogamous *Uta stansburiana*, Tinkle, et al (1962), in certain populations of *Sceloporus merriami*, Milstead (1961), and *Crotophytus collaris*, Fitch (1956a), and in *Cnemidophorus tigris*, Milstead (1961). Kastle (1963) suggests that his captive *Norops auratus* recognized one another as individuals.

The large amount of unconsummated courtship and the very small amount of immediate precopulatory display then could be interpreted together as display that serves to help maintain the pair bond. This is a function of "territorial" display that is quite well established in bird literature.

This discussion of the possible pair bond in *A. lineatopus* is speculation but it suggests a very interesting line of investigation.

The adult males, in addition to courting females, also courted young males that were of female size. I was unable to distinguish between the approach of a male and his display to these young males and that exhibited toward adult females. This contrasts with the situation in *A. carolinensis*, wherein Greenberg and Noble (1944) reported that they could distinguish the approach of an adult male to a female from his approach to any other male.

In no case did I see a homosexual mating though I saw one male start precopulatory behavior with an adult male stake-out. Homosexual matings are reported for caged *A. carolinensis* by Noble and Bradley (1933). These matings probably were due to the crowded conditions under which the lizards were being kept.

The only difference I could detect between females and young males in their response to courtship is that the males always ran and the females ran except when they were receptive. (There is some difference in their shape, particularly when a female is carrying a large egg.)

On one occasion I saw an adult male interrupt a copulation as follows:

> 18 May—Mona. This evening just about suppertime my attention was attracted by rustling in the leaves. When I looked I saw a male holding a female by the neck; as is typical of the terminal stages of courtship, they were walking along slowly. Just then another adult male ran over and jumped up in a bush nearby and bobbed, then he jumped towards the pair and all three disappeared around a flower pot. By the time I maneuvered to where I could see them

again, the pair had separated. Clearly one male had been attracted by the courtship of another and had successfully interrupted it.

This was seen only once, probably because males by their aggressive behavior keep other males out of the area where mating takes place.

Agonistic behavior.—The information on the role of agonistic behavior in the spatial organization of *A. lineatopus* populations is more abundant and more direct than is that on the role of courtship.

Two factors are most important in agonistic behavior: relative size and location. First, *A. lineatopus* is most aggressive toward others of similar size while much less so toward those that are either much larger or much smaller. Second, *A. lineatopus* is most aggressive within its activity range and particularly on its usual perches. As a result, *A. lineatopus* of similar size have activity ranges with little overlap. Greater overlap in activity range is possible between individuals with greater differences in size. *Anolis lineatopus* (particularly females and subadults) behave aggressively toward anoles of other species just as they do toward their own species.

Though the basic pattern is quite simple, the relationships among *A. lineatopus* in the areas studied were complex. Because of the wide range of sizes present, each individual behaved somewhat differently to each of its neighbors.

Collias (1944) has said that individual aggression may be expressed as either of two types: dominance hierarchies and territoriality. This dichotomy has been widely used in studies on lizards (C. C. Carpenter, 1962; Greenberg and Noble, 1944; Evans, 1951, etc.). The behavior of *A. lineatopus* can not be assigned to either of these categories because it has important aspects of each of them. By either a simple definition of territory as "a defended area" (Noble, 1939) or a more complex operational definition—"an area or space in which a particular individual dominates certain categories of intruders who dominate it elsewhere. An individual dominates another when it drives it away, excludes it or supplants it at will" (Rand, in press)—every *A. lineatopus* holds a territory, defending it against neighbors of the same size. At the same time, each is a member of a straight line dominance hierarchy that consists of all those anoles of different sizes whose home ranges overlap its own home range.

Territorial behavior in some form or other is a common behavior pattern in iguanids and has been reported from almost every species that has been studied in detail. Adult males are always involved, and sometimes adult females as well. In a few cases, principally Blair (1960), Fitch (1956a), and Oliver (1948), it has been reported in juveniles.

The establishment of dominance hierarchies is a common phenomenon in caged iguanids: *A. carolinensis*, Evans (1936), *Crotophytus collaris*, Greenberg (1945), *Urosaurus ornatus*, Carpenter and Grubits (1960). Dominance hierarchies in the field also have been reported in *Ctenosaura pectinata*, Evans (1951) and *Sceloporus grammicus*, Evans (1946).

The brief report on the social behavior of *A. sagrei* given by Oliver (1948) suggests that that species is very similar to *A. lineatopus* in its social behavior.

Anolis lineatopus differs from the usual territorial pattern in vertebrates chiefly in the involvement of a variety of sizes of juveniles that hold territories and defend them against one another and, in the case of large subadult males, against adult females. The laboratory studies of Greenberg (1947) show that juvenile green sunfish may hold territories and suggest that in the wild they may behave as do *A. lineatopus*. The basic pattern in *A. lineatopus* and some of the possible complexities can be described effectively by presenting abstracts from my field notes.

In the following series of examples I have begun with interactions between individuals of similar size living in adjacent activity ranges. In these first two cases, the disputes were brief. They occurred on the mutual range boundary or at the point when one *A. lineatopus* entered the activity range of the other and ended when the former left. Either lizard invaded, always as a by-product of some other activity, but the resident always was both the aggressor and the winner.

(1) Hibiscus hedge, Mona [fig. 9]—Seven disputes between No. 4, a 36 mm male and No. 7, a 35 mm female, with activity ranges which overlapped very slightly.

13 April. No. 4 chased a smaller lizard (No. 6) out of his own area and well into that of No. 7. No. 7 charged at No. 4 and he retreated back toward his usual perch.

18 April. Both lizards met at the boundary between the two areas and displayed repeatedly at one another. First No. 7 retreated into her area and No. 4 remained where he had been displaying. After several minutes No. 7 came back toward No. 4 and displayed. No. 4 returned the display and then retreated to his usual perch. No. 7 did not chase him.

20 April. Twice a larger lizard (No. 5) chased No. 4 who fled into the activity range of No. 7. The first time, No. 7 charged at No. 4 and the second time charged, then stopped and displayed. Each time No. 4 fled back to his own activity range. The second time, he stopped when he was well within it to display back at No. 7. In neither case did No. 7 carry her chase beyond her usual activity range.

27 April. The two lizards were seen displaying to each other on the boundary area but a bit nearer one of No. 7's perches than to No. 4's usual perch. No. 4 retreated.

1 May. The two lizards were again seen displaying to each other in the same general area as on 27 April but a bit nearer No. 4's usual perch than last time. This time both retreated with No. 4 moving away first and then No. 7.

(2) Hibiscus hedge, Mona [fig. 9]—A similar set of disputes between No. 4 and No. 18; both 36 mm males. On 14 April both No. 18 and No. 4 at different times were seen chasing the same smaller lizard, No. 6. Once No. 4 chased No. 6 into No. 18's activity range and followed him. No. 18 charged at No. 4, who ran back into his activity range. Twice No. 18, in chasing No. 6, ran into No. 4's area. Each time No. 4 displayed at No. 18 who displayed back and then retreated.

In the preceding two examples the encounters were brief and no changes in activity range boundaries resulted. These were the most common type of disputes seen between similar sized individuals and seemed to serve to maintain the status quo. Occasionally disputes were observed that produced changes in activity ranges. These were longer and often renewed on successive days. Two examples are given below; the first resulted in only a minor boundary change.

(3) Barbican brush heap [fig. 3]—No. 1, 59 mm male; 6, 62 mm male with adjacent activity ranges with one small area of overlap, a stake that was a preferable perch on the North edge of No. 1's activity range and the South edge of No. 6's.

Two encounters illustrate the original situation, when neither male was using the stake frequently.

15 January, 0905 hours. No. 1 sitting on stake well up in view, bobbing occasionally. 0910 hrs. No. 6 appears in the center of the brush heap and runs a foot or two towards No. 1, stops and bobs. No. 1 runs down from stake into brush heap, No. 6 moves back a bit, but No. 1 continues towards tree.

1005 Hrs. No. 6 comes over in brush heap to level of stake, apparently to chase No. 152 (a smaller non-resident adult male). No. 1 comes down from tree through brush to about one foot south of No. 6, tail twitching, dewlaps. No. 6 dewlaps, then retreats a couple of inches. No. 1 jumps towards stake, now on a small twig west of stake. No. 6 retreats toward center of brush heap, bobbing.

[The next day the situation changed:] 1540 hrs. No. 1 runs over into brush heap, bobbing and tail twitching. He goes beyond the stake a short distance [he was probably chasing a non-resident male which I did not see]. No. 6 leaves his perch in the north end of the brush heap and runs toward No. 1, and bobs. No. 1 retreats toward stake and No. 6 moves a bit nearer and bobs again.

1546 hrs. No. 1 jumps to stake, crest up.
1548 " No. 6 dewlaps, his crests are not yet up.
1549 " No. 1 bobs.
1549 ½ " No. 1 dewlaps.
1551 ½ " No. 6 bobs, then jumps east, moving at right angles to No. 1.
1553 " No. 6's crests are up a little.
1555 " No. 6 bobs.
155 " No. 1 dewlaps; No. 6 dewlaps and back jumps, crests now full up.
1608 hrs. No. 6 bobs.
1609 " No. 6 turns and moves west about 6 inches, directly north of stake, side-on to No. 1.
1610 hrs. No. 6 moves about 2 feet farther west; dewlaps.

1611 hrs. No. 6 down into brush heap out of sight.

1613 " No. 6 moves directly toward brush heap, stops one foot away; it begins to rain.

1618 hrs. No. 1 dewlaps. No. 6 is now 3 feet NNW of stake.

1620 " No. 6 runs by stake, but angling toward No. 1, to 2 feet northeast of stake; No. 6 dewlaps, crests full up; No. 1 dewlaps.

1625 hrs. Both display.

1631 " No. 6 moves diagonally a short distance towards No. 1.

1632 " No. 1 dewlaps; No. 6 bobs.

1634 " No. 1 dewlaps.

1637½" No. 1 twitches tail, jumps down into brush heap away from No. 6; No. 6 moves a bit closer; No. 1 jumps back to stake obliquely approaching No. 6; both display dewlapping.

1639 hrs. No. 6 moves a bit closer, mouth open, tongue out; they are now about 1 foot apart, No. 1 on stake, No. 6 on a branch in brush heap.

1645 hrs. No. 1 dewlaps.

1647 " No. 6 displays.

1648 " No. 1 jumps at No. 6, they lock jaws and struggle violently; No. 6 is knocked off his perch and runs 1 foot away.

1649 hrs. No. 6 dewlaps.

1650 " No. 6 bobs; No. 1 twitches tail.

1651 " No. 1 moves back to stake; bobs.

1653 " No. 6 moves about 6 inches further away.

1656 " No. 6 moves back to the north part of the brush heap, then down into brush heap, bobbing.

No. 1, apparently as a result of this encounter, established his claim to the stake and thereafter visited it frequently without being challenged by No. 6, which I did not again see on the stake.

17 January—0900 hrs. No. 1 is on stake, No. 6 on his perch in north part of brush heap. Neither has crest up nor is displaying more than usual.

Anolis lineatopus may expand its activity range slightly at the expense of another as did the adult male in the case above, or it may drive the original lizard out completely as did the juvenile female in the following example.

(4) 27 January—Barbican brush heap [fig. 5], 900–1020 Hrs. No. 148, small female, invaded the activity range of No. 163, small female, and drove her out of it. These lizards have occupied adjacent activity ranges for at least a week. Until today I had seen no conflict between them.

Two small females, Nos. 163 and 161, have divided the small brush heap between them, No. 161 on the west side and No. 163 on the east side. No. 148 has spent its time both north and south of this brush heap, passing without hindrance through it along a central branch which lies between the activity ranges of Nos. 163 and 161.

This morning No. 148 entered the activity range of No. 163 and bobbed at her. No. 163 bobbed back. No. 148 jumped in No. 163's direction and No. 163 retreated east and eventually out of her activity range.

Between 900 and 1000 hrs. while I watched, No. 163 tried twice to re-enter her old activity range and each time No. 148 drove her out. They never came to grips or even displaying at close range. A dash by No. 148 in No. 163's direction sent No. 163 fleeing.

No. 161 ignored all this going on within 2–3 feet of her. When No. 163 retreated from her activity range she approached the fence where another small female lives (No. 156). This female ignored No. 163 today.

1400–1430 hrs. No. 163 made another attempt to enter her old activity range and retreated once more before No. 148's approach.

29 January, 815–830 hrs. No. 163 was back in her activity range this morning but No. 148 soon chased her out again. No. 163 fled toward the fence again but this morning No. 156, who had ignored her on 27 January, chased her back towards the brush heap. No. 148 chased her back toward the fence. No. 156 again chased her away. This time No. 163 moved to a small plant on bare ground midway between the fence and the brush heap and spent the rest of the morning there. No. 148 moved north out of No. 163's old activity range and spent the morning on the branches on the southeast edge of the big brush heap.

Encounters between similar sized individuals sometimes involved a resident and another *A. lineatopus* that was a stranger to the area. Presumably most of these strangers are the subadult and young adult males (p. 31). Probably most *A. lineatopus* that change their home range are attacked when they cross or attempt to settle in an area that is already part of the home range of an *A. lineatopus* of similar size.

In some of the encounters between residents and strangers, the stranger fled quickly, as in the following two incidents.

(5) 2 February—Barbican brush heap [fig. 4]. A stub-tailed adult male appeared within the activity range of No. 159 (adult male). No. 159 approached him to within about 6 inches, both had crests up and both bobbed and dewlapped.

The intruder ran by No. 159, leaving 159's activity range and into that of No. 6 (adult male). No. 159 followed, actually invading the edge of No. 6's activity range, to display at the intruder, who ran a bit farther then climbed down inside the brush heap and disappeared.

After a few moments, No. 159 retreated into his own activity range.

No. 6 had ignored this whole business from his perch on the other side of his territory.

(6) 19 February—Barbican brush heap, 0832 hrs. An unmarked bobtailed adult male appears in the small brush heap. No. 1 is on rock and probably cannot see intruder.

The bobtail hops into shade of log.

0835 hrs. Bobtail hops onto log.
0841½ " Bobtail moves to tree out of sight of No. 1.
0846 " Bobtail moves into full view of No. 1 at 2 feet up on tree.
0849½ " No. 1 begins bobbing, giving several series of step bobs.

0850½ hrs. No. 1 runs toward tree; when No. 1 is still 4 feet away, bobtail jumps to ground on the other side. No. 1 stops in brush heap, step bobs and dewlaps.

0851 hrs. No. 1 jumps 6 inches further towards tree, bobtail runs 2 feet further away.

0851½ hrs. No. 1 moves onto tree. Bobtail leaves area completely, going south.

The intruding lizard, however, is not always defeated.

(7) 6 September—Mona. No. 26 (49 mm male) came to ground [from the

tree where he usually was seen] and ran towards another tree nearby. No. 17 (44 mm female) who was on the ground in his path jumped to the tree [where she usually was seen]. No. 26 changed direction and chased No. 17 around and up the tree. No. 17 fled and No. 26 came back down the tree to sit on No. 17's favorite perch.

Some of the fiercest fighting that I saw occurred between a resident and an intruder that did not retreat when attacked.

(S) 29–30 August—Mona. A large male *lineatopus*, No. 31, was marked on 26 August on a large tree. He measured 67 mm. in snout-vent length. He was next seen on 29 August on a tree about 15 yards away fighting with an unmarked, probably resident, male. The fight included some jaw locking and No. 31 apparently won.

The following day No. 31 and probably the same unmarked male were fighting on the same tree. "This is serious fighting: no display, just biting." First seen on the tree trunk, they soon locked jaws and fell to the ground where they remained for a couple of minutes fencing and biting at each other, not only at jaws but at necks also. Both climbed back onto the tree trunk and the fighting continued, the lizards standing head to head and lunging sideways. They locked jaws and fell again, the unmarked male catching a small plant with his hind legs and letting No. 31 swing past to crash against the trunk with an audible thud, then hang suspended from his jaws. They hung so for better than a minute and then separated. The unmarked lizard ran up the tree and No. 31 up the one next to it. They worked their way up the trees in installments, each male on his move getting higher than the opponent on the adjacent tree. At each stop they displayed, dewlapping and bobbing, until finally they worked their way up into the crown and out of sight.

On September 1 and 2 No. 31 was seen back on the tree where he was first marked.

These accounts of disputes or aggressive encounters between similar sized individuals have illustrated the forms these encounters usually take and the conditions under which they usually occur. It should be stressed further that some sort of dispute occurs on almost every occasion when two similar sized *A. lineatopus* meet. They may not fight when both individuals are outside of their activity ranges or both are frightened. It is sometimes possible for a lizard to remain within the activity range of another of the same size for some time but only if the intruder remains out of sight of the resident. This is possible only in areas where the habitat is structurally complex with many hiding places. Even under these conditions I believe the situation is only temporary.

At the other extreme from these aggressive encounters between similar sized *A. lineatopus* are the relationships between individuals of very different sizes. These may have widely overlapping activity ranges and show very little, if any, aggressive behavior toward one another.

This is particularly true if one individual is an adult male and the other a female. In this case, the male chases the female in courtship.

The female usually ignores the male except for moving to get out of his way and avoiding his courtship unless she is ready to mate.

There may be little aggression even if both lizards are not adult, provided they are quite different in size.

(9) Hibiscus hedge—Mona [fig. 9] No. 11, 44 mm male and No. 8, 30 mm female, held widely overlapping activity ranges and were both seen frequently in sight of each other over a two month period. During this time only three incidents were recorded which could be considered interactions and in each of these No. 8 moved out of the way of No. 11 who happened to approach the perch on which she was sitting. A similar relationship existed between No. 162 (a 40 mm female) and No. 161 (a 29 mm female) in the Barbican brush heap.

Between the above-described extremes of tolerance and intolerance are a number of cases in which a smaller lizard is tolerated by a larger one in parts of the latter's activity range, usually those areas the larger individual visited less frequently, but the latter attacked in other areas particularly on its usual perches.

(10) Barbican brush heap [fig. 6]. Nos. 145 and 162, 43 mm and 39 mm females, demonstrate this. No. 145 held an activity range centered on a small tree. No. 162 was a 39 mm female who spent most of her time in the small section of the brush heap east of the tree, though a number of times I saw her visit the tree itself.

24 January—No. 162 jumps from east brush heap to tree where No. 145 was sitting. No. 145 immediately chased No. 162, who ran up tree. No. 145 did not follow. Twenty minutes later No. 162 runs back down tree and jumps to east brush heap too quickly for No. 145 to do anything.

25 January. No. 162 climbs tree; No. 145, who is in brush heap north of tree, ignores her. No. 162 climbs to 10 feet (unusually high for a female) and stays there for about 40 minutes. During this time No. 145 had moved from north of the tree into the brush heap east of the tree. When No. 162 came back down to the brush heap where No. 145 was, they bobbed at each other for about 15 minutes before No. 162 retreated down into the brush heap.

29 January. No. 145 comes down tree and into east brush heap. No. 162 is in this brush heap about one foot from No. 145 but may not see her. No reaction, and about ½ hour later No. 145 returns to tree and then to north brush heap.

31 January. No. 162 is hopping from east brush heap over towards tree. No. 145, who was in brush heap north of tree, comes over across ground to between No. 162 and tree and bobs. No. 162 runs back to brush heap.

Later No. 145 moves to east brush heap where No. 162 is; they ignore each other.

1 February. No. 162 moves from east brush heap to tree, No. 145 comes from north brush heap to chase her and No. 162 runs up to 9 feet in the tree.

5 February. Both Nos. 162 and 145 are seen in east brush heap. No. 162 bobs at No. 145 but No. 145 runs back to tree but not in response to No. 162.

12 February. No. 145 chases No. 162 from tree. No. 162 runs across east brush heap to rock beyond it. Until today No. 162 has spent most of her time in the section of brush heap just east of the tree with very infrequent excursions north and further east. Today No. 162 moved northeast and was involved in a long and rather violent fight with a lizard well north of where she usually ranges.

13 February. Both Nos. 162 and 145 are seen in east brush heap. They are about one foot apart, lateral to one another, with throats gorged and sides flattened. Both bob. No. 162 moves back and forth at right angles to No. 145 and bobs several times. No. 145 moves to the perch she uses most when she visits east brush heap. No. 162 moves south away from No. 145, and then back past her and out of this section of the brush heap entirely.

Today again No. 162 spends quite a bit of time after this dispute with No. 145 northeast of the section of the brush heap where it occurred and is seen chasing a smaller resident lizard on a fence post which No. 162 has previously seldom visited.

15 February. No. 145 comes from the brush heap north of tree and chases No. 162 out of the brush heap east of tree. No. 162 flees northeast. This is the first time I have seen No. 145 come to this section of the brush heap expressly to chase No. 162.

20 February. No. 145 comes from north of tree to the east brush heap to display to No. 162. No. 162 flattens sides and gorges throat but runs and then down into brush heap.

23 February. Last day of observations. No. 162 seen in small brush heap, No. 145 in brush heap north of tree.

At the first of the study period, No. 145 chased No. 162 from the tree and they largely ignored one another in the brush heap east of the tree, though sometimes bobbing at one another. About February 12–13 they began to display more vigorously to one another in the east brush heap and no. 145 was seen to come to the brush heap to chase or display to No. 162. At about this time No. 162, which had concentrated her activities in the small section of brush heap, began to spend more time north and east of it, chasing and fighting with the other lizards she encountered. Until observations were discontinued, however, she still visited the east brush heap section. This coincidence suggests that the increased number and intensity of disputes with No. 145 in the east brush heap was a factor in No. 162's moving into new areas that No. 145 did not visit.

I have described a variety of interactions that can occur between different individual lizards and under a variety of conditions. I would like to present some of these accounts here and describe the relationships of a single lizard to the others around him.

(11) No. 5 was a subadult male in the Mona hibiscus hedge [fig. 9], 42 mm long when first measured on 10 April and 46 mm long when last measured 8 May. Between these two dates he was seen on 24 different days and interactions recorded with eight other lizards. He used as a principal perch a hibiscus bush and frequently visited a nearby fence post and the ground around both. During the observation period no changes in his activity range were noted.

The activity range of No. 5 overlapped that of three smaller lizards and his relationship with each of these was slightly different.

(11a) No. 3, a 32 mm female, lived entirely within the area visited by No. 5. She spent most of her time on the dead leaves on the ground but frequently visited the hibiscus bush, which was No. 5's principal perch, throughout the period of observation. She usually made these visits when No. 5 was elsewhere and when he returned she sometimes fled back to the ground but more usually No. 5 chased her away, not pursuing her on the ground but merely chasing her out of the hibiscus. Several times No. 5 came to the hibiscus from somewhere else, the fence post, the ground, in order to chase No. 3 away; on other occasions when he returned for other reasons to find No. 3 there he would chase her.

No. 5 usually seemed to ignore No. 3 when she was on the ground, though once when she ran towards the hibiscus bush he chased her away before she reached it. I never saw him leave his perch to chase her except on this occasion. However, if he happened to encounter No. 3 while he was on the ground for some other reason, most frequently to catch an insect, he would frequently chase her for a short distance. Sometimes she would move out of his way under such situations without his paying any attention, and I never saw her display to him under any circumstances. The repeated chases from the hibiscus, and I recorded 15 of them, did not seem to deter No. 3 from returning to it.

(11b) No. 5's activity range also overlapped that of No. 4, a 36 mm male, who lived primarily on the ground among the dead leaves and used a dead stick as a principal perch. Like No. 3, No. 4 visited No. 5's hibiscus but did so much less frequently. No. 5 chased No. 4 on these occasions and, more frequently than with No. 3, chased No. 4 before he actually reached the bush. Both these differences between No. 3 and No. 4 may have been because No. 4 had farther to travel to reach the hibiscus than did No. 3, but it may also have been because No. 4 was larger and No. 5 more aggressive towards him. No. 5 also occasionally came from the hibiscus over to No. 4's perch and once, at least, seemed to do so in order to chase No. 4, who fled and then hid in the leaves. More frequently, when No. 5 came in this direction to catch an insect he would stop on No. 4's perch before returning to his hibiscus. Sometimes he would encounter and chase No. 4 in the process, sometimes No. 4 would move out of the way without being chased, and once No. 4 displayed at No. 5 when No. 5 neared him in the vicinity of No. 4's perch. On this last occasion No. 5 ignored No. 4 completely. Before the end of the study period, No. 4 disappeared from the study area. Whether he died or moved away I don't know and, if he moved, have no idea of the influence of No. 5's chases.

(11c) No. 7 was a 35 mm female who used as principal perches a corn plant and a fence post nearby. No. 5 also visited the fence post not infrequently but was never seen on the corn plant, so that the overlap between these two was not complete. Relatively few encounters between these two were seen and none on the fence post which they both used. No. 7 did not visit No. 5's hibiscus but we saw three chases, one of them quite persistent, which seemed to start when No. 7 approached the hibiscus. In only one of these could I see why. In this case, No. 7 was chasing a smaller lizard and the chasing carried her into No. 5's vicinity near the hibiscus. In the final chase observed No. 5 was chasing a smaller lizard and his chase brought him close to No. 7. He stopped chasing the smaller lizard and chased No. 7 for a bit.

(11d) The smallest lizard whom I saw No. 5 interact with was No. 6, a 29 mm male [not shown in fig. 9 because it appeared at a later date]. During the period when these two interactions occurred, No. 6 was living on the ground near the hibiscus and being chased frequently by No. 3 and particularly by Nos. 4 and 7. Once No. 6 approached No. 5's hibiscus and No. 5 ran towards him and dewlapped; No. 6 fled immediately. The second time, No. 5 chased No. 6 when No. 4 had chased No. 6 towards No. 5. The first of these encounters is curious because it was one of the two times when I saw No. 5 dewlap, the other was in response to a small stake-out I introduced into his area. No. 5 was not sexually mature and consequently was not dewlapping either in disputes or in advertisement display at this time and he is the smallest male I ever saw dewlap.

(11e) On either side of No. 5 lived two lizards approaching him in size: No. 15, a 40 mm male who lived in an oleander bush on one side, and No. 11, a 44 mm male, who lived in the next hibiscus on the other side. These three lizards seldom entered the activity ranges of each other and never were seen to visit each other's principal perches. Perhaps for these reasons few disputes were seen between them, none with No. 11 and only two with No. 15. In one of these, No. 15 had invaded the dead leaves near No. 3 to catch an insect, as he sometimes did, and No. 3 had displayed to him. No. 15 displayed back and No. 3 in turn displayed. At about this point No. 5 left his hibiscus and ran towards the fight. No. 15 fled back to his oleander but No. 3 remained still, No. 5 returned to his hibiscus. On the other occasion, both No. 15 and No. 5 had left their perches and run out onto the bare dirt beyond the dead leaves in order to catch an insect. This brought them close together and they displayed at one another briefly before each retreated to his own area.

(11f) In addition to these smaller and slightly larger lizards, No. 5 also came into contact with three males larger than himself. One of these, No. 14, a 48 mm male, had an activity range which did not overlap that of No. 5 but was near it. On one occasion No. 14, for some unknown reason, left his home range and visited No. 5's hibiscus, arriving when No. 5 was absent and sat there quietly. When No. 5 appeared and climbed the hibiscus, he made several series of bobs at No. 14 who ignored them. No. 5 did not attack No. 14 but after this few minutes of display ignored the motionless No. 14.

(11g) The next large lizard with which No. 5 had contact was No. 24, a 57 mm male. This male was seen off and on throughout the study period but as far as I could tell never established a permanent activity range during this time. I only saw one encounter between the two. I had tossed a grasshopper towards No. 5, who came to the ground for it. He made several attempts, chasing it across the ground and biting at it. No. 24 came towards the grasshopper, scaring No. 5 who seized it and ran back to his perch leaving No. 24 sitting on the ground.

(11h) The final lizard with which I saw No. 5 interact was No. 26, a 58 mm male, who included No. 5's hibiscus in his activity range and for part of the study period visited it quite frequently. Once No. 5 fled at No. 26's approach when they were both on the ground. Twice No. 5 left his hibiscus when No. 26 climbed it. Three times No. 26 chased No. 5 when No. 26 was sitting in No. 5's hibiscus and No. 5 climbed up into it, approaching him. In each of these cases No. 5 fled immediately. In the final interaction, No. 26 was sitting in No. 5's hibiscus and No. 5 was on the ground. No. 5 ran out to seize a large insect and started to carry it back to his hibiscus. On almost reaching it he apparently saw No. 26, for he changed course and ran part way to the fence post. Before reaching it he stopped, turned and, with the grasshopper in his mouth, step-bobbed at No. 26.

The largest male in the area, No. 13, a 60 mm adult, was not seen to pay any attention to No. 5 or No. 5 to him but No. 13 seldom visited the hibiscus.

The aggressive behavior that has been described has involved so far two *A. lineatopus;* such encounters were the commonest seen. Aggressive encounters, however, were seen between *A. lineatopus* and other species of *Anolis.*

There are a total of seven species of this genus in Jamaica, five of them occurring around Kingston. These lizards all have somewhat different structural or climatic niches (Rand, mss.) but they all overlap to a greater or lesser extent. The commonest species after *A. lineatopus* in the study areas is *A. grahami,* a green species that lives generally higher in the trees than does *A. lineatopus.*

The adult males of the two species are about the same size but rather different in shape and in color. They are quite tolerant interspecifically and frequently both species will live on the same tree. Part of the small amount of interaction is due to a difference in preferred perches but sometimes two adult males sit quietly a foot or two apart ignoring each other. Interactions are seen, usually no more prolonged or intense than the following.

(12) 5 February—Barbican brush heap. No. 1 was on south stake. A male *grahami* ran up stake, No. 1 jumped off and bobbed and dewlapped, his crests raised. The male *grahami* dewlapped and then after a moment jumped off in another direction and eventually climbed a tree.

Interactions between females and subadults of the two species were much more frequent and pursued more vigorously than between the adult males.

(13) The best example of this sort of interaction involved a female *grahami*, No. 165, and several female *lineatopus*. The *grahami* lived on the small tree in the Barbican brush heap and the female *lineatopus* frequently visited it. One of them, No. 145 (*ca.* 43 mm long) used the tree as one of her principal perches, as well as using the brush heap around it. The *grahami* repeatedly chased No. 145 off of the tree over the month of observation but seldom followed her into the brush heap and never came to the brush heap to chase her. The other two *lineatopus* females, Nos. 162 (39 mm long) and 161 (*ca.* 29 mm long) visited the tree less frequently. As has been described, the larger *lineatopus* female (No. 145) chased the smaller ones from the tree, and the *grahami* did this also, once following the smallest female, No. 161, into the brush heap and chasing her about for several minutes.

The behavior of the *grahami* to the *lineatopus* was, as far as I could see, identical to her behavior toward other *grahami* except that she did not start to chase the *lineatopus* unless they were on the tree, but once left her tree to chase a female *grahami* that was approaching it and still 4 feet away.

The interaction between the two species is reciprocal, as the following notes show.

(14) 23 January—Barbican brush heap. No. 145 chased a small *grahami*, 35 ± mm SV, making three charges at it. No. 162 at south end of log displayed to a small *grahami* which ran.

(15) 10 April—hibiscus hedge, Mona. A small female-sized *grahami* came down to the ground to drink from the rain water which had accumulated in a cup-shaped dead leaf. A *lineatopus* of about the same size which was sitting on a stick a few inches away first bobbed and then jumped at the *grahami* who fled.

Not only do *A. grahami* and *A. lineatopus* fight but the male of the latter occasionally courted the female of the former and presumably the male *A. grahami* courts the female *A. lineatopus*.

(16) 12 April—hibiscus hedge. No. 13 (60 mm male) chased a female sized *grahami* from the hibiscus next to his usual fence post to the next fence post, clearly courting it. He has also courted No. 11 (a 44 mm male *lineatopus*) twice this morning.

Though most observations were on reactions between *A. lineatopus* and *A. grahami*, I also saw reactions with *A. opalinus* and with *A. garmani*.

(17) 17 May—south of Lloyds. In the course of making movies of display I placed a male *opalinus* on a fence near another male *opalinus* and, incidentally, near a male *lineatopus* almost twice the size of the *opalinus*. Though these two lizards did not pay any attention to each other, they both reacted to the stake-out. The *opalinus* reacted first to approach and dewlap. The *lineatopus* then ran towards the two and the *opalinus*, apparently frightened by this, ran away. The *lineatopus* stopped a few inches away and dewlapped. After a few moments the *opalinus* ran back to the stake-out and both dewlapped and bit at it.

(18) 12 October—reservoir, Mona. A female *lineatopus* displayed (bobbing) to and chased a male *opalinus* slightly smaller than she was. He fled without ado. Also saw a female *garmani* and a large male *lineatopus* side by side within three inches apart and in sight of each other without any indication of conflict.

(19) 30 May—College Common. This afternoon I saw a male *lineatopus* display to a male *garmani* considerably larger than himself. Both lizards were on a two-inch branch of a poui tree about 12 feet above the ground, the adult male *lineatopus* near the trunk and the adult male *garmani* well out among the smaller branches. As I watched, the *garmani* began to move quite slowly along the branch toward the *lineatopus*. When it reached a point about 2 feet away, the *lineatopus* turned its head so that it was orienting its dewlap towards the *garmani* and began to give dewlap flashes. This display was very like, if not identical to, the initial display to another male *lineatopus*. The *garmani* stopped and then immediately jumped from the branch to another, moving at right angles to the *lineatopus*. It jumped again in the same direction and stopped when about three feet from the *lineatopus*, then bobbed.

The result of these interspecific interactions is to reduce overlap in the activity ranges of lizards of the same size regardless of species, but least so in the cases of adult males. This suggests that the significance of the aggressive behavior may be different in females and subadult males than in the adult males. This point is discussed later.

Not only do *A. lineatopus* display to and chase anoles of other species but also they sometimes display to objects that are not lizards at all. Adult males, when they became familiar with me, would sometimes respond to my approach by bobbing and dewlapping as they would to the approach of another male. This display was never carried beyond the initial reaction though, as mentioned under "Escape Behavior" (p. 16), a male held in my hand would flatten his sides and erect his crests, both of which are part of the aggressive display pattern.

The smaller *A. lineatopus* also display sometimes to objects that are not anoles, as the following note shows.

21 April—hibiscus hedge, Mona. *A. lineatopus* (40± mm female) was sitting on a two foot high bamboo stake about six inches from the top. A yellow-faced grassquit lit on the end of the stake. The lizard gorged its throat and flattened its sides. The bird flew away. The lizard's reaction was that typically given on the approach of a somewhat larger lizard.

AGONISTIC BEHAVIOR: DISCUSSION.—Neither of the well-established concepts, dominance hierarchy and territory, will describe the situation in *A. lineatopus* adequately by itself, nor is there a point intermediate between them that will describe it if one considers dominance hierarchy and territoriality to be end points of a continuum as Davis (1959) suggests. It would be possible to do as Greenberg and Noble (1944) did in their paper on *A. carolinensis* and describe certain aspects of *A. lineatopus* behavior in terms of territory and others in terms of hierarchy; even this approach is not completely satisfactory. It seems to me less important to try to fit observed data into labeled pigeon-holes than to describe that data usefully.

An approach to the description of the situation in *A. lineatopus* is suggested in a paper by Allee (1950), wherein he distinguished between two types of hierarchies ("peck right" and "peck dominance") on the degree of predictability of the outcome of disputes. Extending this approach, one can consider agonistic behavior in terms of the kinds of information necessary to predict dispute outcomes. This seems to me to provide the basis of a more general system of description and analysis than does a dichotomy between territory and hierarchy.

Both territory and hierarchy can be described in these terms: territory as a system in which the outcome can be predicted on the basis of the place where the encounter occurs, and hierarchy as a system in which the outcome can be predicted on the basis of the results of previous encounters.

To my knowledge, this approach has never been developed in quite the way I am doing here, though every useful generalization about the social behavior of a species can be paraphrased as a prediction about what an individual will do under the specified conditions. Ethologists (e.g., Neil, 1964, in his study of *Telapia*) have used the predictive approach, but they have been interested largely in predicting the next action of an animal during a dispute rather than in predicting the eventual outcome. The cues the ethologists use seem largely to be evidence that indicate the internal state of the animal, which in turn determines what it will do. The cues discussed below seem to be involved in actually determining or affecting the internal states of the lizards.

From the discussion in the preceding section, two factors suggest themselves as bases for predictions in *A. lineatopus:* relative size of anole and place of encounter.

Among vertebrates generally these two characteristics, size and familiarity with the site, are undoubtedly among the most important. Probably the only factors likely to rival these are sex, breeding condition, and, in some cases, age. Brown (1963) found that, in Steller's jays, where the encounter took place was the most important factor in determining (or predicting) which of the two birds would dominate.

But this could be modified somewhat by sex, state of reproductive cycle, and state of molt.

In figure 10 the size of the winning *A. lineatopus* is plotted against the size of the losing individual in each of 182 disputes. The figure shows that, in a large majority of these, 155, the larger lizard won; thus, the outcome of 85 percent of these disputes could have been predicted correctly on the basis of the size of the lizards alone, and, where the size difference between the lizards was more than 8 mm, all outcomes could have been predicted. Those cases wherein the difference was less than 8 mm are unpredictable on this basis; this range of differences form what conveniently can be called a zone of uncertainty. (These and the following percentages of accuracy of prediction are merely suggestive. A calculation of confidence limits is mathematically possible but, as the sample was not random, is not statistically valid.)

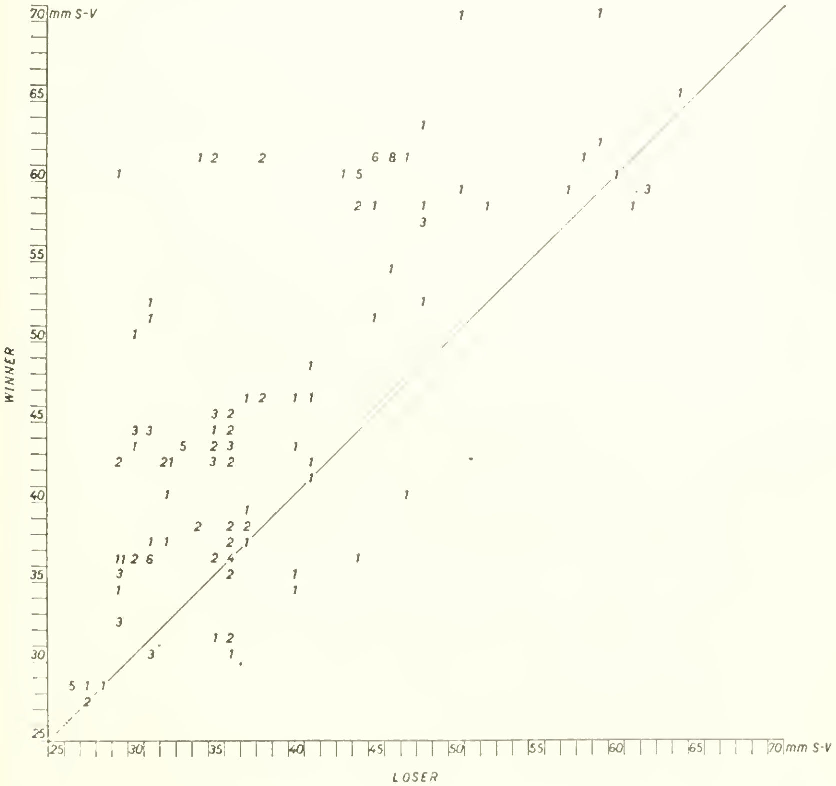


Figure 10.—Relationship between size and outcome of aggressive disputes between *Anolis lineatopus* (figures = number of disputes observed).

Using only the place where a dispute occurs as a basis for predicting the outcome is not as satisfactory as using relative size alone. In part, this is because the prediction is most accurate where only one lizard is resident and an appreciable number of disputes has occurred between lizards that are either both resident or neither resident and, in part, because place influenced disputes only where the difference in size was small.

Location, however, can be combined with size as basis for prediction. Because of the nonrandom nature of the sample, an increase in the percentage predictability is probably a less adequate measure of success in predicting than is a decrease in the zone of uncertainty (in mm of size difference).

Table 9 shows the effect of both size of anole and place of dispute on the outcome. It also shows that, where both were resident (table 9A), the larger always won. Where neither was resident (table 9B), the outcome is doubtful when the difference between the lizards is less than 4 mm, which reduces the zone of uncertainty to about half for these cases.

Table 9C deals with disputes in which one lizard was resident, the other not. In these, the resident lizard always won if it was larger than the nonresident, equal to it in size, or only 1 mm smaller. The zone of uncertainty now includes those disputes involving a resident 2 to 8 mm smaller than its nonresident opponent.

Considering both relative lizard sizes and location of dispute, a basis for prediction can be phrased as follows: If the difference between the lizards is greater than 8 mm, the larger will win (81 of 81 disputes); if the difference is 8 mm or less and if neither or both are resident, the larger will still win (26 of 30 disputes); if the difference is less than 8 mm and only one is resident, the resident individual will win (62 of 71 disputes). Using this set of rules, 169 of the 182 disputes (93 percent) could have been predicted successfully.

Obviously factors other than relative size and place of occurrence are influencing the outcome of disputes in the zones of uncertainty. These probably include the past experience of both individuals (including previous disputes between them) and the psychological and physiological condition of the individuals at the time of the dispute. Still, a system, such as the present, that gives a successful prediction level approaching 95 percent is a good description of the factors influencing outcome.

The nature of a dispute, i.e., the form it takes, is also strongly influenced by relative size and place. The closer in size two *A. lineatopus* are, the more likely that a real fight with physical contact will occur and the closer an *A. lineatopus* is to its usual perch, the more vigorous will be its displays. The most prolonged fights oc-

TABLE 9.—*Effect of both relative anole size and place of occurrence on the outcome of disputes* (numbers of disputes are plotted against difference in size of anoles; only those with a size difference of 8 mm or less are given)

Difference in size: Winner-Loser	A	B	Difference in size: Resident-resident	C	
	Both resident	Neither resident		One resident	
				Resident wins	Nonresident wins
8	6		8	1	
7	6		7	12	
6	3	1	6	6	
5	1	2	5	6	
4			4	2	
3		2	3	4	
2			2	4	
1		5	1	4	
0			0	10	
−1		2	−1	3	
−2			−2		5
−3		2	−3	2	
−4			−4	1	1
−5			−5	3	1
−6			−6	2	1
−7			−7	1	
−8			−8	1	1

curred when an *A. lineatopus* attempted to establish an activity range within the established activity range of a slightly smaller *A. lineatopus*. The least severe conflicts occurred when a small *A. lineatopus* moved to avoid a much larger individual that was ignoring it.

This aspect of disputes is considerably more complex than outcomes, and one important source of complexity is that the adult males have a more elaborate set of aggressive displays than do the rest of the population. No system of predicting the nature of disputes can ignore this factor. The response of an *A. lineatopus* to the initial display of its opponent also affects the nature of the dispute that follows.

The conditions under which disputes occur again show a strong influence of relative size and place. The examples in the preceding section have stressed this point. Again there are complicating factors, e.g., an *A. lineatopus* is much more likely to behave aggressively toward a moving and particularly a displaying individual than toward one that is sitting quietly.

Despite these complications, the same factors that are important in predicting outcomes of disputes have important effects on the moment when a dispute will occur and on the form it will take.

Thus far, predictability of dispute outcomes has been discussed only as a useful way of describing aggressive encounters in *A. lineatopus* and of using relative size of anole and place of occurrence as useful information for predicting. Certain aspects of the behavior of these lizards suggest that the latter two topics have a more fundamental biological meaning.

I have used predictability to mean that an outside observer could foretell the outcome of a dispute. In a large majority of the aggressive encounters I have observed, the lizards behaved as if they themselves were doing the same thing, i.e., predicting the outcome of the dispute. Most disputes were very brief and consisted of one anole retreating as soon as it was threatened or attacked by another or retreating at the approach of another even though the latter showed no aggressive behavior. Disputes wherein both lizards displayed, i.e., behaved aggressively, seldom resulted in physical combat, and usually one lizard retreated without actually testing the strength of its opponent. Even in the fiercest physical combats that I observed, prolonged fights between adult males, fighting was restricted almost entirely to the ritualized jaw wrestling. I have never seen a fight that ended with one anole dead or even physically exhausted.

I am, of course, not suggesting that these lizards are consciously weighing their chances of winning an encounter. The data, however, shows that they are behaving as if they had done so. Phrased differently: A dispute may not be decided by the dispute itself but by the reactions of the individuals involved to circumstances surrounding the dispute, and these reactions may be determined before the dispute starts. Because the lizards themselves behave as if they were predicting the outcome, "predictability of dispute outcome" is more than a convenient way of describing agonistic behavior; it seems to be an important biological or psychological aspect of agonistic behavior.

Having suggested that *A. lineatopus* frequently behave as if they are predicting outcomes, it is possible to ask if they are using the same information that I have found useful. Phrased differently: Are the place where two lizards meet and their relative size important stimuli in determining their behavior in the dispute situations? I think the answer is a qualified yes. Careful experiments would be necessary to demonstrate that this is true, but the field observations certainly suggest it.

That a lizard is more likely to attack an opponent, less likely to flee, and will travel farther to attack when the opponent is in the resident's home range (and particularly when it is on the resident's usual perches) strongly suggests that place of encounter has an important effect on the aggressive behavior of the animal.

The same sort of information suggests that relative size is also important, but here an additional line of evidence is available. In the aggressive displays of these lizards, there are many elements that act to increase the apparent size of the lizard (see p. 41). These elements are developed most highly in adult males but some of the elements, like lateral orientation and flattening, occur in all sizes and in both sexes.

That selection has favored the incorporation of so many devices for increasing the apparent size of *A. lineatopus* into its aggressive displays suggests that it is to the advantage of a lizard not only to be bigger but also to appear bigger. This can only be important if the reaction of an anole to an opponent is based in part on an estimate of its size. (In other words, this sort of display can be important only if apparent size is used by the lizard to "predict" the outcome of the dispute.) Barlow (1963) has shown experimentally that certain fish discriminate between fish of their own size and of those 10 percent larger or smaller. Anoles can probably do at least as well.

In this discussion I have attempted to show that the outcomes of a high percentage of disputes in *A. lineatopus* are predictable on the basis of the relative size of the lizard and on the place of occurrence and that these two factors also influence the nature of a dispute and the conditions under which it occurs. Further, I have attempted to show that the lizards themselves behave as if they were predicting outcomes and were using the same two factors in doing so.

Adaptive Significance of Spatial Distribution

By "adaptive significance" of the spatial distribution of individual *A. lineatopus* in small areas I mean the possible selective advantages that this distribution can have for individual *A. lineatopus* and for the population as a whole. This is equivalent to "function of territory." C. R. Carpenter (1958) and Hinde (1956) have provided extensive lists of the functions of territory in various species of vertebrates. Some of these functions are clearly not applicable because they are related to parental care. The other functions, as Tinbergen (1957) has pointed out, must be divided into those that arise from the fact that individuals have definite activity ranges and those that arise from the distribution of these activity ranges in relation to one another.

One adaptive advantage of an activity range is that the individual can learn thoroughly the structure of the area. *Anolis lineatopus* frequently uses indirect pathways: an anole on a branch may run back up the branch and down the trunk to reach the ground, following a pathway that initially may take it away from its objective. The speed with which these pathways are selected suggests the lizard previously has learned the best routes. *Anolis lineatopus* males living on trees almost invariably run up when frightened; those living on fence posts run down. In each case the anole selects without hesitation the escape route that takes him most surely out of danger.

Residence in an area makes it possible for an *A. lineatopus* to become familiar with the fauna also, to learn good places to watch for insects, and to learn which of the larger animals in the area are potentially dangerous. How important the former element is I do not know, but the changes in reaction to me as a potential predator were striking. Most lizards in the study areas were quite easy to noose the first time I marked them. The next time they were much more difficult. One male became so shy that I could not catch him at all. Most males would allow approach within a few feet but, after several attempts to catch this individual, he would run when I was 30 or 40 feet away.

The effect of familiarity with an area has been reported in a number of other lizards. Fitch (1956) reports a young *Crotaphytus* that usually hid under a particular rock. When he removed the rock, the lizard ran to the same spot where the rock had been and seemed confused at the absence of the rock.

Residence in an area also provides an *A. lineatopus* with the opportunity to learn to recognize other lizards as individuals. Evidence that they do this has been discussed. This familiarity with other individuals over long periods provides the opportunity for pair formation and may reduce the severity if not the frequency of agonistic encounters.

Beyond the advantages arising from the existence of activity ranges, there are a number of advantages that arise from the distribution of these activity ranges with respect to one another (Tinbergen, 1957).

The first of the two patterns in distribution of activity ranges, the overlapping between adult males and adult females, has an obvious advantage in mating. It helps to insure that there is a mate available for a receptive female and it enables the male to find mates without leaving the area with which he is familiar. It may also facilitate mating by allowing the individuals to become familiar with each other and so produce some sort of pair bond.

Interpretation of the adaptive significance of the second pattern, the minimal overlap between the activity ranges of *A. lineatopus* of the same size and the gradual increase in overlap as the difference in size between individuals becomes greater, is more difficult.

There are, I think, three major effects of this pattern. Two are closely interrelated and affect the whole population: the distribution of the population with respect to available food and the control of population density in favorable situations. The third, the distribution of the adult males with respect to potential mates, affects the adult males most directly.

Considering first the lizard's relation to food supply, we have already seen that *A. lineatopus* feeds largely within its home range and largely on insects it sees from its principal perches. I have also shown that there is a tendency for different sized *A. lineatopus* to eat different sized food. The spacing out in an area of individuals of the same size means that there are fewer times when two *A. lineatopus* attempt to catch the same insect and consequently compete directly for food. Also, since the lizards' activity ranges are nonoverlapping, the lizards cover the maximum area possible and a particular insect is most likely to land in the feeding area of one of them. The overlapping of feeding areas of *A. lineatopus* of different sizes means that a greater size range of the insects within an area are potential food to the *A. lineatopus* living there. Thus, both the spacing out of individuals of the same size and the overlap of those of different sizes increases the probability that a given insect will be eaten by an *A. lineatopus* wherever the insect lands.

From this discussion it appears quite possible that one of the important ecological results of the social organization of *A. lineatopus* is in the decreasing of intraspecific competition for food and the increasing of the efficiency with which the available food supply is exploited.

It has been suggested that territorial behavior (which is frequently so defined as to include the social system described herein) has an important function in regulating density in favored areas. In *A. lineatopus* there is a lower limit set by the structure of the environment below which activity ranges cannot be compressed, i.e., the number of available perches. Particularly with adult males, but even with smaller individuals, most perches are indivisible; they are occupied by only one *A. lineatopus* of a particular size. In areas where the only perches are scattered trees or fence posts, the social behavior interacts with the structure of the environment to limit population density. If there were more trees or fence posts, there could be more *A. lineatopus*. But, if *A. lineatopus* peacefully shared perches, there could be more of these lizards in the same number of trees.

In more complex structural habitats, the situation is not so clear. The general constancy of home range size in several rather different places suggests that there is a size limit below which home ranges cannot be compressed. This in turn suggests that even in complex environments, social organization may act as a means of limiting population density. There is another element in the structure of the environment other than available perches that may affect density and this is visibility. In very dense vegetation it might be possible for two *A. lineatopus* to have overlapping home ranges and seldom meet. I do not think this is of great importance, for most home ranges have perches from which much of the area can be seen and it is on these that the lizards spend most of their time. But the presence of a large male in a brush heap for several days, even though he was repeatedly chased by the resident males, suggests that overlapping home ranges are at least temporarily possible. The importance of visibility was emphasized for *A. sagrei* on Bimini by Oliver (1948), who reported that the territories became larger and that less overlap was tolerated when a hurricane increased visibility by defoliating the habitat.

Agonistic behavior of the sort shown by *A. lineatopus* can regulate density only by forcing individuals to move away, since fights to the death are rare, if in fact they ever occur. Subadult, young adult males, and young females do move considerable distances and may settle, at least for short periods, in previously unoccupied areas (p. 29 et seq.). Further, a number of these young males were found to be living in areas that for one reason or another seemed to be subpreferable for the species. It seems likely that they had been forced to move by aggressive behavior on the part of other lizards and forced to settle in unoccupied places because the preferable ones were already occupied.

The evidence suggests that the social organization in *A. lineatopus* tends to set an upper limit to the population density in a particular structural environment and to force the excess lizards, particularly young males and, to a lesser extent, young females, to disperse.

How far these *A. lineatopus* travel during dispersal we have no idea; consequently, it is impossible to judge the importance of social organization in promoting panmixis in the population or in extending the distribution of the species. Certainly that there is dispersal at all reduces the amount of close inbreeding. That the dispersal may take lizards into previously uninhabited areas indicates that it plays some part in extending the distribution of the population.

It has also been suggested that the spacing out of individuals in an area may act to reduce both predation and disease. Both of these are possible but seem unlikely in *A. lineatopus*. In spacing out individuals it is possible that fewer are found by predators, but *A. lineatopus* are most conspicuous when they are displaying and fighting. The increased conspicuousness to a predator must at least partially offset any advantages gained by over-dispersion.

We know almost nothing about disease in lizards but it is possible that the spatial isolation that the social behavior produces may act to reduce the spread of infectious diseases. Two facts, however, argue against its importance. First, only individuals of about the same size are overdispersed and diseases that are restricted to particular sizes within the species must be uncommon. Second, although lizards may be spatially isolated during the day, they frequently sleep in the same places, so that, even if the spread of disease is reduced during the day, it would not be reduced at night.

The final area in this discussion of adaptive significance involves adult males. I have stressed that, while all sizes and both sexes are aggressive, the adult males are more aggressive than any other individuals. The males travel greater distances to attack intruders than do other *A. lineatopus;* they are more persistent in their attacks and they fight more frequently and more fiercely. They have structural modifications, nuchal and dorsal crests, used exclusively in agonistic behavior, that are lacking in females and young.

This sort of difference in behavior is known in other iguanid lizards. In some, the males have larger home ranges from which they exclude other males even though, unlike the *Anolis*, the males are smaller than the females (Blair, 1960). In other species, only the males are aggressive at all (Blair, 1960). In *A. carolinensis*, males defend their home ranges most aggressively during the well-marked breeding season (Greenberg and Noble, 1944).

Finally, in *A. lineatopus* adult males are less tolerant of individuals of their own species and size than are the females and juveniles, but they are more tolerant of males of other species.

I think the general occurrence of aggressive behavior and the spacing out it produces in all sizes of *A. lineatopus* can be explained by the ecological advantages that have been discussed in the foregoing discussion, but the greater aggressiveness of the adult males requires additional explanation. I think the explanation lies in a function of territory discussed at length by Tinbergen (1957), which demonstrates the selective advantage that is conferred on an adult male if he can insure himself exclusive mating rights to certain females by keeping other males away from them. If he can do this for a single female, he insures that he will father at least some offspring, and the more females he can keep isolated, the more offspring he will have and the greater his contribution to the gene pool of the next generation. This being true, there must be a strong selection pressure for any mechanism that will insure a male exclusive mating rights to one or more females. The aggressive behavior of adult male *A. lineatopus* that keeps other males out of the area in which females are permanently living is just such a mechanism. I think that the selective advantage to the individual male of having exclusive mating rights accounts for the greater aggressiveness in the adult males of this species, while the other ecological advantages to the population as a whole of spacing individuals of the same size accounts for the existence of aggressiveness in all of the individuals of the species.

The Life of a Lizard

In this section I want to describe what probably happens to a lizard throughout its life history in general terms of its social relations and its spatial distribution in a densely populated area. There are many gaps in my information that I must bridge with hypotheses. Some of the imagery may be wrong but it is the best I can do to demonstrate as vividly as possible some of the gaps in our knowledge.

A lizard hatches from an egg buried under a log, the edge of a rock, or in leaf litter and soon settles into a home range; how far it wanders before doing so we do not know. The initial activity range differs from those of the adults. The former is smaller, and the hatchling avoids large perches and is not attracted by the presence of an individual of the other sex. The avoidance of large diameter perches is adaptive since these are frequently occupied by adult males that eat hatchlings when the adults can catch them.

These hatchlings are aggressive and soon space themselves out so that their home ranges do not overlap, though the home range of a young lizard may be overlapped by those of several larger lizards. As the young lizard grows, it enlarges its home range. At the same time, there seems to be a shift in perch preference with the result that the growing lizard begins to visit the usual perches of the larger individuals.

Initially, the young lizard is generally ignored by the larger neighbors and avoids them. But as it grows larger and begins to visit their perches, they begin to chase it, both when it visits one of their perches and when they encounter it elsewhere. At first the young lizard tolerates this behavior and flees the larger individual without changing its activity range. Such a situation may last for several weeks and perhaps several months. During this period the same lizard also is chasing from its own activity range others smaller than itself, and it may expand its activity range at the expense of another by chasing it away. The young lizard also may be forced to move by another slightly larger lizard's moving into its area; I believe this action produces some of the long distance shifts recorded for juveniles.

Even if another juvenile does not displace it, this lizard's continued growth soon brings it into more serious conflict with the adults whose activity ranges overlap its own—first, with adult females since they are smaller than adult males. The decreasing difference in size between the adult female resident and the more rapidly growing juvenile seems to produce serious conflicts for two reasons. First, the female becomes less tolerant and begins to chase the young lizard, not only from her preferred perch but in other parts of the home range. Second, the young lizard begins to become aggressive towards the adult and to display back and attempt to chase her. This is probably a gradual change but eventually the young lizard must either defeat the adult and chase her away or—much more likely since the young one is as yet smaller than the adult—be defeated and move. This change seems to occur as the young females are approaching sexual maturity but while the young males are still immature. As either sex approaches adult female size, they begin to attract the attention of the adult male, no longer as food but now as potential mates, and he begins courtship chasing. For the maturing females this probably has no effect on their home range, but for the young males this may be a factor in forcing them to move.

When an *A. lineatopus* of this size moves, it may travel considerable distances, at least 50 to 80 feet and probably more. During this time it must continually come into conflict with other *A. lineatopus* of about its size, and probably it is chased repeatedly from the suitable activity ranges that it visits. These *A. lineatopus* sometimes settle in places that are unoccupied because they are subpreferable, and we find young males living in unusual activity ranges, up in trees, on very small isolated perches, etc.

Because there is a continual mortality among the adults, however, desirable activity ranges are always becoming vacant. If a young male *A. lineatopus* is fortunate enough for this to happen to the female whose home range overlaps his own, then he may not be forced to move at all. But probably and more frequently, he must travel and perhaps visit a number of suitable sites before he finds one from which he either can oust the resident or which he can occupy unchallenged. Probably another frequent occurrence is for a lizard to move into an area that lies on the boundaries of two residents and establish himself in an activity range that includes part of two other activity ranges. Such a course involves defeating both residents but only in parts of their activity range that they do not use frequently and, consequently, do not defend as vigorously as they would their preferred perches.

For an adult female, this is probably her last move. If her new activity range overlaps that of an adult male and contains the requisites in food, temperature, and cover, she probably will remain there the rest of her life, mating with the male, perhaps leaving the area to lay her eggs if no suitable laying site is immediately available, perhaps shifting the boundaries or moving either temporarily or permanently to an adjacent area, but making no further major moves. She will defend the area against intruders of her own size, at first tolerating young lizards and then, as they grow—whether they are her own offspring or not—gradually driving them out.

The problems of a male the size of an adult female are not solved even when he finds a suitable activity range. As he continues to grow, his activity range requirements change; he now prefers a larger perch. He has grown big enough so that no female can chase him from his established area, but he is also growing big enough to challenge the adult male whose activity range may overlap his. Again two things seem involved in the increasing conflict. The large male's interest in him changes from courtship chases to more vigorous aggressive attacks, and he himself becomes more aggressive toward the big male. Though the big male may die or the younger may defeat him and so remain and enlarge his area, it is more likely that the young male will be driven out. The younger male is now adult though small. With the activity range requirements of an adult male, he finds that usually the best, most preferable home ranges are already occupied by larger adult males that will not tolerate him on any of their perches. Again he may have to travel considerable distances, establishing himself temporarily in undesirable sites, perhaps staying within the activity range of a large adult but avoiding him by staying hidden, probably moving several times before he finally finds a suitable place where he can establish; and he, like the female, settles here more or less permanently, making minor boundary changes or occasional shifts to adjacent areas or forays to nearby perches. But he is now an established resident who will court all the female-sized lizards, mate with receptive females, eat the hatchlings, including his own children, if he can catch them, and drive out any intruding adult male.

Daily Routine

In previous sections I have discussed by topic various aspects of the ecology and behavior of *A. lineatopus*. To bring these aspects together and present a picture of the daily routine, this section describes the behavior of a single adult male that I and another observer, working in shifts, kept under surveillance for one full day. We watched him from before sunrise until after sunset and lost sight of him only for two 10-minute periods, though he was out of sight for a few seconds a number of times. During the day, we saw him catch and eat food twice, copulate twice, drive another male from his home range, and dispute with a nearby male over the common boundary of their home ranges.

This male, no. 1, was a marked individual (60 mm S–V) that we had kept under observation for several months. He had a home range (fig. 3) which included a small tree about 20 feet tall that branched at the ground into six trunks, each about three inches in diameter. It also included part of an adjacent brush heap and a small log and three nearby fence posts.

We started observations at 6:05 a.m., when it was just light enough to make notes. The nocturnal frogs were still calling but the cocks had started to crow and mockingbirds were singing. It was still cool (19° C at 6:15). I could see no anoles yet, though I knew from previous nights that many were asleep in the small tree, stretched out along the twigs or leaves near the ends of branches.

At 6:17 a.m. I located the first *A. lineatopus*, an adult male, still in his sleeping position on top of a leaf at the end of a branch but already awake with his eyes open. It was light now and, three minutes later, he left his sleeping site for the inner branches of the tree. During the next 20 minutes, there was considerable movement in the tree as anoles moved about and departed for the adjacent brush heap. The individual we had decided to observe, no. 1, appeared at 6:22 a.m., moving down one of the tree trunks and then across to the brush heap. After about 10 minutes he moved down into the brush heap so that he was almost completely concealed by the tangle of branches above him. He ignored the other anoles moving about him, including a large male that came down the tree and jumped into the brush heap.

By 7:00 a.m. both tree and brush heap were quiet again and none of the *A. lineatopus* were sitting up on the perches where we usually saw them during the day. They had all left their exposed sleeping sites for more concealed spots, where they were waiting quietly.

The sun rose and at 7:16 a.m. its rays struck the brush heap, but no. 1 was still in the shade. He waited only a minute and a half before moving out into the sun and, three minutes later, climbed up onto the surface of the brush heap to sit in partial sunlight for a few moments before moving toward the tree and into full sunlight. About the same time other *A. lineatopus* also began to move, and the area that had appeared empty moments before was now full of anoles basking in the sun. Two large males began displaying to each other across the boundary of their home ranges in the brush heap. Though they continued this for about 20 minutes and were less than five feet from no. 1, they were outside of his home range and he ignored them.

By 8:00 a.m. it had warmed up considerably (24° C at 8:10 a.m.) and no. 1 was moving about frequently and displaying, both dewlapping and bobbing. Though I saw him bob once shortly after he first appeared (6:23 a.m.), he did not display again for over an hour and did not begin displaying frequently until he had been sitting in the sun for some minutes.

About 8:30 a.m. no. 1 dashed for the tree, ran up and, with pauses for display, ran out toward the end of one of the higher branches. He dashed around among the foliage for a confusing few moments and then another male jumped from the tree into the brush heap and disappeared. No. 1 did not follow but moved to one of the larger branches and displayed. The other male had probably slept in the tree and had been late in leaving it. No. 1 finally had seen him and chased him out. During the chase, no. 1 seemed to be trying to get above the other male and to drive him down from the tree.

Now fully active, no. 1 spent most of the rest of the day in the tree (a total for the whole day of 7 hours and 55 minutes) though he visited the brush heap three more times (a total of 3 hours and 30 minutes) and made one sortie to a small log near the base of the tree, spending 11 minutes on it and the ground nearby. One small branch of the tree seemed particularly attractive and he visited it eight times, spending 3 hours and 48 minutes there. This branch was about five feet above the ground and from it he could overlook his entire home range; he had used this same perch day after day. He spent another hour and 57 minutes on other parts of the trunk from which this small branch grew, 1 hour and 47 minutes on a second trunk, 10 and 7 minutes respectively on two more trunks, and 16 minutes in the crown foliage. Two trunks he did not visit at all.

The next few hours were routine. No. 1 sat on one perch for a while and then shifted to another to sit there, moving then either to a new perch or back to the first. Though he did nothing I could interpret as searching, he seemed always to be watching his surroundings alertly. Even when on the same perch he made frequent small shifts in position, up, down, or around the perch, and with even more frequent head and eye movements.

One of the things for which no. 1 apparently was watching was food. During the day we saw him catch only two items. In both cases he ran down the trunk of the tree from his perch and picked up something small from the bark and swallowed it. He may have made more captures during the few periods when he was out of sight but, if so, they must have been few and small because large prey is conspicuously chewed before being swallowed.

Most shifts in position were followed by some sort of display, either bobbing or dewlap flashing. During the day there were only eight periods of 10 or more minutes without display, the longest being about 20 minutes.

Most displays did not seem to be directed at anything in particular and probably served to advertise his presence to any potential intruder or prospective mate, though the bobbing also may have a function in improving his depth perception.

Though most of the observed display did not seem to be directed at any particular lizard, several times we saw him unsuccessfully court a female, chasing her and displaying to her.

No. 1's activity reached its highest peak in the earlier part of the morning, perhaps because he was moving frequently to take advantage of patches of sunlight and shadow to thermoregulate. During the heat of the day all the *A. lineatopus* were less active than they had been in the morning, and they spent longer periods sitting in the same places in the shade avoiding both the direct sun and the perches that had been warmed by the sun. Later in the afternoon, they all again became more active but perhaps not as active as they had been in the morning.

It was midafternoon before no. 1's routine of waiting and watching was markedly interrupted. At 3:48 p.m. he mated with a female that also used the tree as one of her perches. He moved around the tree trunk and came upon her as she rested head downward. He moved up along side of her and attempted to seize the skin on the back of her neck with the tips of his jaws; she moved her head from side to side as if avoiding this but did not run. Shortly after he secured the grip and twisted his tail under hers to bring their cloacas into contact. They copulated for about three minutes and then separated. As usual the successful courtship was casual and with little display.

No. 1 returned to his usual routine until 5:00 p.m., when he moved to the brush heap to display vigorously to another large male that had moved to a stake on the boundary between their home ranges. The resulting dispute lasted about 20 minutes; both lizards dewlapped, oriented laterally, and bobbed at each other. Eventually both retreated, leaving the stake unoccupied. Several days later, no. 1 was able to expand his home range to include this stake but only after a prolonged dispute with the other male. (Details of this dispute are given on p. 48.)

Soon after this dispute the sun set at 5:44 p.m. and shortly afterward no. 1 climbed up the tree into the higher branches. He moved out onto the smaller branches and appeared to be selecting a sleeping site.

Suddenly he came back to one of the main trunks and bobbed at a small unmarked adult female and ran toward her. She jumped to a branch, he followed and seized her by the skin on the neck and walked with her a few steps. They then copulated for two and a half minutes and separated.

No. 1 displayed and then moments later climbed out among the small branches and foliage. At 6:11 p.m. he was stretched out on a very small branch about 10 feet above the ground, apparently ready to go to sleep. It was already quite dark and by 6:13 it was too dark to see him or to make notes.

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