LITERATURE CITED

BRATTSTROM, B. H. 1955. The coral snake "mimic" problem and protective coloration. Evolution 9: 217–219.

BROWER, J. V. Z. 1960. Experimental studies of mimicry. IV. Amer. Nat. 94:271–282.

CHAUDHURI, D. K., S. R. MAITRA AND B. N. GHOSH. 1971. Pharmacology and toxicology of the venoms of Asiatic snakes, p. 3–18. *In*: Venomous animals and their venoms. Vol. II. W. Brucherel and E. E. Buckley (eds.). Academic Press, New York.

DEORAS, P. J. 1971. The story of some Indian poisonous snakes, p. 19–34. *Ibid.*

DERANIYAGALA, P. E. P. 1955. A colored atlas of some vertebrates from Ceylon. Vol. 3, serpentoid Reptilia. Colombo, Govt. Press.

DUNN, E. R. 1954. The coral snake "mimic" problem in Panama. Evolution 8:97–102.

GANS, C. 1961. Mimicry in procryptically colored snakes of the genus *Dasypeltis*. Evolution 15:72–91.

———, AND M. LATIFI. 1973. Another case of presumptive mimicry in snakes. Copeia 1973:801–802.

GUNTHER, A. 1869. Report on two collections of Indian reptiles. Proc. Zool. Soc. :500–507.

HECHT, M. K., AND D. MARIEN. 1966. The coral snake mimic problem: a reinterpretation. J. Morph. 98:335–365.

MINTON, S. A., JR. 1966. A contribution to the herpetology of West Pakistan. Bull. Amer. Mus. Nat. Hist. 134:27–184.

SMITH, M. A. 1943. The fauna of British India. Vol. III, Serpentes. London, Taylor & Francis.

WALL, F. 1908a. Two new snakes from Assam. J. Bombay Nat. Hist. Soc. 18:272–274.

———. 1908b. A popular treatise on the common Indian snakes, part VII. J. Bombay Nat. Hist. Soc. 18:543–554.

———. 1921. Ophidia Taprobanica or the snakes of Ceylon. Colombo, Govt. Printer.

WICKLER, W. 1968. Mimicry in plants and animals. New York, McGraw-Hill.

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Territorial Behavior and Population Regulation in the Lizards, *Anolis acutus* and *A. cristatellus*

RICHARD PHILIBOSIAN

Two allopatric and ecologically similar species of lizards, *Anolis cristatellus* and *A. acutus*, exist at two different population densities. *A. cristatellus* has a lower density and larger territory size than has *A. acutus*. Field tests were performed involving the relocation of animals to new sites, removal of animals from an area, replacement of removed animals, addition of territory surface area to a habitat, and removal of territory surface area. Experimentally increasing the density of *A. cristatellus* did not result in a decrease of territory size. Death rates of lizards caged at various densities were highest for *A. cristatellus* at densities usual for *A. acutus*. It is concluded that *A. cristatellus* requires a larger minimum territory than does *A. acutus*. The territory requirement usually limits the *A. cristatellus* population density on a tree, and is less often in effect to limit the per tree density of *A. acutus*. It is suggested that the territory requirement of *A. cristatellus* limits the density of the breeding population.

THE first descriptions of territoriality in animals have been followed by several hundred additional studies. The emphasis has been on birds primarily through observation of behavior in natural populations (Reviews: Lack and Lack, 1933; Hinde, 1956; Brown, 1969a).

Often considered is the possibility that territorial behavior may regulate the population density of a species. Wynne-Edwards (1962) has suggested that this, along with other forms of social behavior, is of fundamental importance in regulating population density, long before the limit of food supply is reached. However, Lack (1966) concludes that for birds, territoriality and other related forms of social behavior serve mainly to disperse the members of the population and are rarely involved as ultimately limiting agents. In a comprehensive analysis of bird studies, Brown (1969a) concluded that most studies do not prove a density limitation by territoriality, partly because too often there is a reliance on observation alone without experimentation. After that publication experimental evidence for territorial regulation of density has been obtained for certain species. Clarke (1970) concluded that the territorial breeding requirement of the fish *Hypsypops rubicunda* limited the numbers in one study area, and that food supply was probably limiting in another. Watson and Jenkins (1968) performed experiments on red grouse involving removal of all members of the population from certain areas, removal of selected individuals, and replacement of some of the removed birds. This work demonstrated that the breeding density was limited by territory requirements. Krebs (1971) found that the breeding density of great tits was limited by territory in an optimum habitat, but that the total breeding population was not so limited.

What may be the only published studies on the territorial regulation of numbers for reptiles are by Bustard (1968, 1969, 1970). He concluded that the density of the gecko *Gehyra variegata* is regulated by territorial requirements and suggested that territorial limitation also acts on populations of the lizards *Heteronotia binoei, Egernia striolata* and *Diplodactylus williamsi*.

During preliminary work on *Anolis cristatellus* and *A. acutus* it was found that although the species are ecologically similar, the density of *A. acutus* appeared to be many times greater than that seen for *A. cristatellus.* Since these two lizards are strongly territorial, it was felt that a study of the relationship between density and territorial behavior might provide some explanation for the large difference between densities. It was hypothesized that *A. cristatellus* maintains a larger territory size compared to *A. acutus*, and that this limits the population density below that of *A. acutus*.

Evidence for territorial regulation of the density of adult male and female *A. cristatellus* on individual trees will be presented. It will be suggested that territory also limits the total number of lizards and restricts the breeding density. It will be shown that *A. cristatellus* maintains a larger minimum size territory than *A. acutus* and so exists at a lower density on a tree. It will be suggested that *A. acutus* reaches densities, localized in time and area, at which territory size becomes limiting.

Species

A. cristatellus is a diurnal, arboreal lizard found throughout the Puerto Rico Bank (Puerto Rico east to Anegada), in the Eastern Caribbean. All studies on this lizard were made on the island of St. John in the United States Virgin Islands. Adult males reach a snout-vent length of 70 mm, females, 49 mm. Males <50 mm in size can be confused with females, as pattern dimorphism diminishes with decreasing size; consequently, one can only make positive identification of males >50 mm, unless the animal is captured for closer examination. Since females are smaller and more disruptively patterned than adult males, a lower percentage of them is seen (Ruibal and Philibosian, 1974a).

Adults usually occupy vertical territories such as trees and walls. Since a lizard defends all of the area in which it is found, except perhaps its sleeping and egg laying sites, territory almost equals home range. Generally an animal spends the entire daylight period moving from one frequented perch site to another, often spending several minutes at a single site. A typical perch position is with the body vertical and head pointing toward the ground at various angles. Main activities within the territory include feeding, copulation and defense usually against members of the same species, sex and similar size. Adults tend to stay in one territory until death, while younger animals are more mobile (Table 1). Juveniles <35 mm are usually spatially separated from adults, perching on small rocks and low vegetation. Subadults are often tolerated within adult territories. Territories of males and females may overlap. The lizard is essentially carnivorous, eating almost any animal small enough to be swallowed. Predators observed include several species of birds, Indian mongoose (*Herpestes auropunctatus*) and the domestic cat.

With the exception of geographic range and male size, all of the above applies to *A. acutus* as well. Males reach a size of 66 mm. *A. acutus*

TABLE 1. MOVEMENTS OF 200 DIFFERENT LIZARDS BASED ON TWO CAPTURES OF EACH INDIVIDUAL. Ratio of the number of individuals captured twice on same tree/number of individuals recaptured on different tree.

Species, sex and size when first captured	Months between captures		
	1–10	11–20	>20
A. acutus males >59 mm	15/0	7/1	2/0
A. acutus males 30–59 mm	7/1	1/2	1/1
A. acutus females >39 mm	31/4	8/2	9/3
A. acutus females 30–39 mm	0/2	2/1	0/1
A. cristatellus males >59 mm	19/2	3/1	0/0
A. cristatellus males 30–59 mm	16/21	0/2	0/0
A. cristatellus females >39 mm	29/1	4/0	0/0
A. cristatellus females 30–39 mm	0/1	0/0	0/0

is endemic to St. Croix, also a U.S. Virgin Island but with no history of land connection to the Puerto Rico Bank (Whetten, 1966). *A. acutus* occurs in all terrestrial habitats except grassland, and is the only *Anolis* on St. Croix.

A. cristatellus occurs in the same types of habitats as *A. acutus*, but is sympatric with *A. pulchellus* and *A. stratulus* on St. John. *A. pulchellus* rarely contacts *A. cristatellus*, as it is almost exclusively on small diameter perches in areas of grass and brush. *A. stratulus* is syntopic with *A. cristatellus* and often overlaps territories with it. If *A. stratulus* is present on a tree, there is usually one of each sex, both primarily in the crown and on the upper levels of the trunk. If a single *A. cristatellus* male is present, with or without *A. stratulus*, he moves on and defends the entire tree, although he usually perches within 1.5 m of the ground. If *A. stratulus* moves close to *A. cristatellus*, it is usually chased a short distance but not pursued.

Field Study Sites and Tree Analysis

Both species were studied in coastal forest and landscaped sites near human habitations. The areas for St. Croix have been described (Ruibal and Philibosian, 1974a). Studies on St. John were made in and near the research station at Lameshur. Sites included the borders of dirt roads, trees in cleared areas around the station, and trees within the forest. Mean annual rainfall and temperature in the St. John study area were 1,200 mm and 26.1 C (Bowden, 1970); in the St. Croix field site annual means were 1,200 mm (11-year personal record by John Yntema) and 27.6 C (Bowden, 1968). The climate is similar for both areas since they are coastal and St. John is only 70 km north of St. Croix.

Because both species are arboreal, the number of individuals in an area can be affected by the number of trees present. For this reason it was not considered valid to compare lizard densities over large areas of the study sites, since the yards or coastal forests were not identical in distribution of trees or tree types. The most meaningful comparison can be made by noting the numbers of lizards on two reasonably equal surface areas which are also qualitatively similar. This introduces two problems: 1) determining the surface area of a tree, and 2) making a qualitative description of a tree which can be validly compared with the descriptions of other trees.

The most precise method of determining surface area is to measure the lengths and circumferences of all parts of a tree. A modification of this method was used which included measuring all woody surfaces of a tree which had a circumference of 13 cm or more. This measure excluded all leafy surfaces and the smallest twigs and branches. This "estimated surface area" was measured as a sum of surfaces of average cylinders representing the trunk and limbs of a tree. Details for this method are in Philibosian (1972).

The problem of making a qualitative description of a tree is more difficult to resolve, but it is at least as important as the surface area computation. For example, a tree with one bifurcation at 3 m into two main branches may have a surface area equal to one which spreads into four branches at 1.5 m. The tree configuration affects the number of lizards in the visual field of the resident at particular perches, and consequently, may influence the area the resident occupies. Also the length of territory contiguous with others and the number of contiguous territories may affect the area defended.

In consideration of this qualitative and quantitative evaluation of a tree, a large amount of time was spent in selecting trees on each island which were similar enough to be used in comparisons between species. For any test series on both species, wherever it was necessary and possible, trees were selected on the basis of similarity of height, species, branching characteristics and surface area. The estimated surface area was measured on four trees. This served as a basis for making reasonable approximations of surface areas of trees qualitatively similar. For certain tests it was sufficient to measure the surface area of part of a tree.

The four species of trees which were most commonly used will be referred to by common name as follows: tamarind (*Tamarindus indica*), saman (*Samanea saman*), flamboyant (*Delonix regia*) and genip (*Melicoccus bijugatus*).

Methods

The specific methods for each type of test will be presented separately. Techniques of marking and observation are described in Ruibal and Philibosian (1974a, b).

Territories were delimited by noting the locations of the lizard and its interactions with others of the same sex. The territory was defined as the area in which all of the daytime positions of the lizard were located, except those positions which were in areas where the lizard lost any aggressive interaction with another. These aggressive interactions (termed encounters) between members of the same sex were

TABLE 2. COMPARISON OF POPULATIONS ON PAIRS OF TREES WITH SIMILAR SIZE AND BRANCHING CONFIGURATION. *A. cristatellus* numbers represent total population on a tree; *A. acutus* numbers represent minimum possible total. Estimated surface area given for genips A and A′.

Tree	*A. cristatellus* Males	*A. cristatellus* Females
Genip A (26.8 m^2)	1	3
Genip B	1	2
Tamarind A	1	2
Tamarind B	1	2
Saman A	1	4
Mean/tree	1	2.6

Tree	*A. acutus* Males	*A. acutus* Females + males <50 mm
Genip A′ (24 m^2)	12	11
Genip B′	7	2
Tamarind A′	9	7
Tamarind B′	15	10
Saman A′	8	6
Mean/tree	10.2	7.2

defined as 1) any of the stereotyped displays common in anoles such as dewlap extension, raising of the nuchal and dorsal crests, head bobs and push-ups which appeared to be directed at a specific lizard, and 2) any moving of one lizard toward another, with or without physical contact. The loser of an encounter was that lizard which ran away from the other or was thrown off the tree. When neither lizard was clearly the loser, or if both appeared to run from each other, the encounter was termed a tie. An area in which ties occurred between two lizards was interpreted as the boundary between territories. For *A. cristatellus* males, encounters were not usually necessary in delimiting territories, since in almost all cases only one lizard occupied one tree. Encounters proved useful for *A. acutus* males and for females of both species, since these often had contiguous territories on the same tree. Aggression indices were computed from encounters according to Ruibal and Philibosian (1974b).

Often an observation period of one day was sufficient to record enough positions and encounters involving the residents on a tree to make reasonably accurate territory descriptions. For most of the studies observations continued for an additional 1–2 days, but these did not substantially change the territory limits drawn from the observations of the first day. Following this 1–3 day period in which territories were mapped, the particular experiment was initiated.

TABLE 3. TERRITORIES (IN M^2) PER LIZARD ON LARGE TREES. Four territories were measured for each category.

	A. cristatellus males	*A. acutus* males	*A. cristatellus* females	*A. acutus* females
	26.8	1.8	2.3	.7
	21.6	1.6	1.4	.5
	15.6	.9	1.3	.3
	12.0	.6	1.1	.3
Mean	19.0	1.2	1.5	.5

DENSITY AND TERRITORY

All of the data in this and the next two sections were obtained by direct visual observation of the natural populations. No experiments were involved. For reasons already given the densities of the two species are most meaningfully compared on a per tree basis. Selection of pairs of trees based on the preceding analysis yielded the comparisons listed in Table 2. The mean male *A. acutus* density was 10 times that of *A. cristatellus* males; mean density of *A. acutus* females was 3 times that for *A. cristatellus* females. This difference in density is likely far greater than the factors of 10 and 3. The numbers of *A. cristatellus* represent the total population on a tree. This was determined by marking presumably all individuals and observing the tree for at least five days, during which time no unmarked lizards appeared. The numbers of *A. acutus* are not based on so precise a measure. Not all lizards on a tree could be marked and the figures given represent the sum of the highest count made of the unmarked lizards plus the total known marked on the tree (whether seen or not during that highest count). Several counts were made on each tree until a peak figure appeared. For each peak count that was made, no more than 50% of the marked lizards were seen. Consequently, based on the Lincoln Index measure for this species as analyzed by Ruibal and Philibosian (1974a), these peak counts probably represent about 50% of the true population density, making the difference with *A. cristatellus* even more pronounced.

Table 3 lists the sizes of four territories for each sex of both species. Boundaries were delimited as described and the estimated surface

TABLE 4. SUMMARY OF NEAREST NEIGHBOR SAMPLING.

Neighbor pair	Mean distance (m) between pair members		% of pairs with both members on same tree	
	A. cristatellus	*A. acutus*	*A. cristatellus*	*A. acutus*
Male–male (100 pairs)	6.8	1.5	2	89
Female–female (100 pairs)	2.1	.7	10	83
Male–female (50 pairs)	1.4	.5	52	87

area was then determined. The magnitude of difference parallels that for the density measure. Except for a specific case discussed in a separate section, no hierarchy systems were seen.

DISTRIBUTION

Nearest neighbor sampling is usually employed to determine randomness of distribution of a population (if density is known) or density of the population (if it is known to be randomly distributed) (Southwood, 1966). For this study it was used simply as an interspecific comparison of distances between individuals, because the density of the populations in the areas tested was not known and both species seemed to be distributed non-randomly. Nearest neighbor data for *A. acutus* have been previously presented (Ruibal and Philibosian, 1974a). Identical measures were made on *A. cristatellus* and the data for both species are summarized in Table 4. Pairs of *A. cristatellus* males or pairs of females tended to be on different trees and farther apart than pairs of *A. acutus* which usually consisted of neighbors on the same tree. The means of male pairs and female pairs were significantly different between species at $P < .001$. Members of male-female pairs were often on the same tree and the difference between means of both species may not be significant ($P = .05$).

A second measure of distribution was made by counting all lizards that could be seen on trees taller than 5 m. One hundred trees were sampled for both species of lizards, with observations lasting about 2 min per tree (Figs. 1 and 2). Besides the problem created by combining females and juvenile males, the measure is weakened by the inability to see all the lizards on a tree in such a short period. From the 43 trees on which no *A. cristatellus* males were seen, 10 were randomly selected and watched for 20 min each. After that longer observation period, one male each was seen on eight of those 10 trees.

Because of these biases, no definite conclusions can be made from the results of the Chi-square test on the index of dispersion. There is an indication that 1) *A. cristatellus* males had a uniform distribution, 2) *A. cristatellus* females were random at $P = .999$, but uniform at $P = .99$ and 3) both sexes of *A. acutus* had a clumped distribution. A uniform distribution would be expected for a population that was limited by territory size.

AGGRESSION

Aggression indices were computed from observations on seven trees for *A. cristatellus* and 11 for *A. acutus*. Each tree was observed for 1–4 hours. Mean indices were as follows: *A. cristatellus* males 0.7, females, 0.4; *A. acutus* males 0.3, females, 0.5. The range is broad and there is no significant difference between any two of the four categories. Most of the male *A. cristatellus* encounters were between a floater and a resident. For the other categories the majority of encounters were between adjacent residents.

FIELD EXPERIMENTS

Relocation of lizards.—The most direct test to determine the relationship between territory size and population density is to increase the density of animals in an area and observe the social and spatial changes that follow. The simplest form of this test is to release different numbers of lizards on a tree and observe the territories established. This method does not work for either species because most or all of the released animals leave the release site whether or not it is already occupied by a resident. Desertion of the site is not due to the general disturbance accompanying release, since if the original resident is also handled and released along with the relocated lizards, he remains on his original territory. Some lizards were also held in terraria and fed for 3–4 days prior to their relocation; no difference was noted as all departed from the release site. The abandonment of the release site, which is almost universal among adults of either sex in both

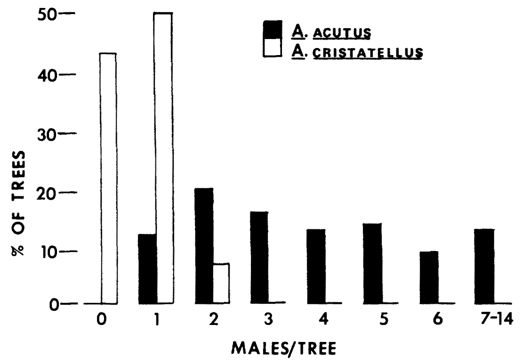

Fig. 1. The number of males per tree in a sample of 100 trees on each island. Mean/tree *A. acutus* = 4.2; *A. cristatellus* = 0.6.

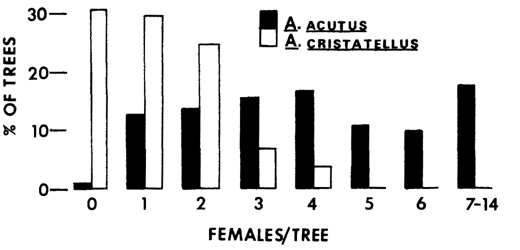

Fig. 2. The number of females (including males <50 mm) per tree in the same sample for Figure 1. Mean/tree *A. acutus* = 4.3; *A. cristatellus* = 1.3.

species, is interpreted as a homing effort. Homing capabilities are present in both species, and have been measured for *A. acutus* (Ruibal and Philibosian, 1974a).

Slow removal.—The density of *A. cristatellus* males per tree may be low compared to that of *A. acutus* because the number of males available for recruitment is fewer than the number of *A. acutus* available. In this case one could say that there is a single male *A. cristatellus* on a tree because only he is available to occupy it, and should another male be available, he could be accommodated on the tree and two territories would then be established. This addition could continue until a possible limit to the territory size is reached.

The alternative suggestion in the case of *A. cristatellus*, is that there is a single male on a tree because that tree is maintained as a single territory, even under pressure from colonization by other males with no territory or with nearby, less preferable territories. In the situation where no recruits are available, removal of the resident should not result in an occupation of the territory by a new adult for some time. In the second situation, with colonizing pressure on the tree, removal of the male should result in a fairly rapid reoccupation of the tree.

To test this for *A. cristatellus* a genip and a saman were selected. Three adult males and four adult females were on the saman (the apparently atypical density of males will be discussed). All males were marked on day 1 and territories were marked on days 2 and 3. One territory comprised almost the entire tree and will be called the central territory, initially occupied by male A. The other two territories occupied by males B and C, were designated "peripheral" as each included only the terminal 2 m of a single branch and was not defended. Since A was found in all parts of the tree with circumference greater than about 13 cm, the estimated surface area of the entire tree, 21.6 m^2, equaled the territory. Males B and C were on perches less than 5 cm in diameter. From observations on days 2 and 3, activity of males B and C can be contrasted with that of male A. Males B and C moved only short distances around the terminal ends of the branches and were never seen to feed, copulate or display. Male A moved extensively and was seen on several occasions to feed, copulate and give assertion displays as defined by Carpenter (1967).

Males A, B, C and E were removed during the next 3 days, and each was caged separately and fed insects. Male A was removed on day 4, and within 1 hour B occupied the central territory; C remained in his same peripheral area. Male D entered the tree from one 4 m away (with branches contacting the saman) and chased B back to its peripheral territory, but did not remain on the saman. After D left the saman, B returned to the central territory. Male E entered the tree (from an unknown previous location) and occupied the central territory after chasing B back to his original area. On day 5 males B and C were on the peripheral areas, D was seen both on the nearby tree and occasionally on the saman at the boundary of the central territory, and E occupied the central territory. Male E was removed and B and C engaged in encounters within the central territory, which was eventually occupied by C; B returned to his original space. Male C was removed and B then repeatedly entered the central territory, but each time was repulsed by D. On day 6 B occupied the central territory and D did not enter the tree. At this time B was seen in copulation. It was the only time that either "peripheral" male was seen copulating (territories of all four females were within the central territory), but the resident had been removed. Male B was removed and for the remainder of the day no males were on the tree. On day 7 male F entered the tree (from unknown previous location) and occupied the central territory. Male G (not seen prior to day 7) entered from a slender sapling 6 m from the saman and was chased off by F.

Following each removal except B, the aggression increased as a result of the attempts of different males to occupy the central territory (Fig. 3). The final removal (B) did not result in any aggression, since no male was present to occupy any part of the tree until the next day. At that time aggression again increased with encounters between F and G.

Within 3 days of the first removal, six males including two from the saman had attempted to occupy the central territory. In each case only one male eventually occupied the territory, while others either left the tree or returned to their original locations on the tree (B and C). Within those days there was pressure by at least seven males (including the first one removed) to occupy the central territory. If territory size did not limit the density on the tree, one would expect that all or most of the seven males could occupy the tree, presumably sectioning the central territory into several smaller ones.

The relocation tests showed that lizards could not be directly transferred to another tree to artificially raise the density, since they immediately attempted to return home. However, an immediate homing response did not occur when lizards which were caged during a slow removal test were finally returned to the test tree. This is probably a result of two conditions. First, each lizard was the occupant of the territory for some time before he was removed. Second, if any colonizer was a floater (a lizard which had no territory but moved through the area) it had no territory prior to the test toward which it could home.

A high density male population was created on the saman when all four previously removed males were released on day 8. These, plus F already present on the central territory, plus the re-entrance of D and a newly entering male, H, created a condition where seven males competed for the central territory at the same time. Since all were engaged in aggressive encounters occurring in the central territory, and none attempted to immediately leave the tree, it is assumed that a division of the central territory would have occurred if density regulated ter-

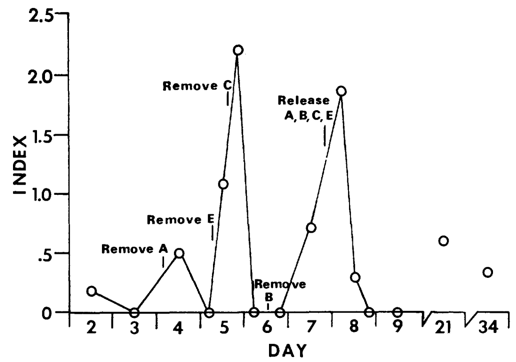

Fig. 3. Aggression index for *A. cristatellus* males during removal test on saman.

ritory size. In the first hour after all were returned to the tree, aggression was high, but diminished during subsequent observations as each male who lost encounters retreated from the central territory (Fig. 3). By the end of the day, F occupied the central territory, B and C were in their original peripheral areas, and A, D, E and H had left the tree. This condition continued through day 9, the last day of regular observations.

On day 21 male B, the only male on the tree, occupied and successfully defended the central territory, while F and an unmarked male both attempted to move onto the tree several times. On day 34 the only resident male was B, although F, then occupying a nearby bush, attempted unsuccessfully to move onto the tree. These later observations indicate that there was probably continual pressure on the tree, yet this did not result in an increase of density on it.

The absence of C in the follow-up observations supports what was a guess at the start of the test. That is, because B and C were not found in typical territories and displayed none of the typically assertive behavior of a territory holder, they were considered floaters. If this was true, it would be one explanation for the subsequent absence of C, with B remaining because he displaced F.

Not all of the colonizers could be considered unqualified floaters. For example, D had a territory on an adjacent tree. Male F was not recorded prior to day 7, but did remain on various bushes in the area through day 34. The attempts of these lizards to move to the central territory indicated that although they may already have had a territory, another was preferred. Since a continuum probably exists, no precise distinction will be made between a floater and a lizard temporarily defending or existing in a low-preference site.

The site of the second removal experiment was a genip 1 km from the previous study tree. Each lizard was removed from the tree as soon as possible following a cumulative total of 24 hours of occupation. This contrasts with the method used on the saman where some lizards were removed after a few hours of occupation in the central territory. It was assumed that an animal removed after 24 hours would have a greater tendency to reestablish a territory when returned to the tree, than one removed after a much shorter period of occupation. The 24-hour minimum was thus established to enhance the possibility that when all removed lizards were returned to the tree, they would attempt to establish territories in a manner even more intense than that displayed by lizards on the saman. Each male removed was retained as in the previous test.

One male and two females comprised the *A. cristatellus* resident on the genip. The territory of the male equaled the estimated surface area of the tree, 26.8 m^2. He was removed and occupation by other males began within 3 hours.

The results and conclusions are similar to those of the previous study on the saman. During 7 days, eight males including the original resident were involved in occupying the genip. In that time there was almost constant pressure by more than one male to occupy the tree, but within several hours after each removal, only one male remained. Five males were removed during the test. A high density was created in the same manner as on the saman by releasing the four previously caged males (one had died) onto the tree occupied by one male. A sixth male also moved onto the tree, many encounters occurred, and at the end of the day only one male was present.

Two experiments identical in methods to those for the male removal on the saman were performed using only female *A. cristatellus.* The first tree selected was occupied by three females and one male. One female was removed and during the next 5 days six females attempted to occupy that territory. As with the males, only one was successful in doing so after much aggression. During the removal period the three resident females were caged. These were released onto the tree while one new occupant was present. By the end of the day each of the released females was on its original territory and no other females remained on the tree. The second test with females was made on a tree occupied by one male and two females. One female was removed and during the next 4 days four females attempted to occupy that territory. No more than one female occupied the territory at one time and three, including the two original residents were removed during the test. While a new occupant was in both territories, the three caged females were released. After one day of intense aggression among those four plus another female who moved onto the tree, only the original two residents remained.

The similar results of these two tests indicate that, like the males, there was considerable pressure on female territory sites. When females were removed, others occupied the vacated territories. When the removed were replaced, most attempted to occupy the space on the tree, but no increase in density occurred. Although female territories, in contrast to a male, did not all together occupy all of a tree, apparently all of the space suitable for females was occupied.

Two experiments were made on *A. acutus* in which all lizards were removed from a tree. In the first test three males and one female were removed from a genip 7 m high. This was the lowest density that could be found in the study area at the time. Presumably more territories could exist on the tree, but colonizing lizards were not arriving there. If this was true, a total removal of all lizards would not result in a rapid recolonization of the tree. No lizards of either sex were seen on the tree for 5 days following removal and observation was terminated. The tree was observed 15 months later and had a resident population of seven males and three females. This supports the original presumption that the density of three males and one female was below the maximum that could exist on the tree.

The second removal of all lizards was from a saman 6 m high. Even though this tree had more surface area than the genip, the large number of lizards removed, 46 males and 33 females (26 males >57 mm and 29 females >40 mm), indicated a higher density. Another difference is that the saman was further from other trees than was the genip, and this probably made colonization more difficult. Nevertheless colonization did rapidly occur, suggesting that this tree was sustaining a maximum density. Counts were made of all lizards seen on the tree for several days. At least four males and seven females had entered the tree by the fifth day after total removal. After 15 months the population had reached 41 males and 20 females, which was still short of what is suggested as the maximum density tolerated.

Rapid removal.—In the slow removal tests on *A. cristatellus*, males were allowed to establish territories on the trees before their removal; thus there was no indication of the maximum number of males that would have moved onto a tree during the removal phase. By removing male *A. cristatellus* as soon after they enter a tree as possible, one can determine the potential maximum occupation pressure for any given period of time. This was tested on a tree 12 m high. It was not always possible to remove a lizard immediately after it was sighted, and consequently some lizards occupied the tree longer than others. Removals were made for 121 hours, during which time the tree was checked at least once every 3 hours of the day. Ten adult males were removed from the tree, the first eight by the 51st hour. Five males were removed in one 3-hour period.

A high density test was made by replacing the 10 removed males onto the tree. The main difference between this test and those on the saman and genip is that many lizards were on the tree less than 1 hour before removal. A previously uncaptured male moved onto the tree, making a total of 11 on the tree at the time of release. Aggression by some, but not all of the lizards was observed. Continuous observations were made for 6 hours, during which time seven males left the tree. Observations of the tree and surrounding area were made for three more days. The fourth male to be removed was the only one on the test tree and five males which had left the tree were located within 5 m of it. They had moved to territories which they had probably occupied prior to the test, but were apparently less preferable than the test tree. Since the other five males were not seen after the release day, some probably had no territory to return to.

A second test with males was performed on a relatively isolated tree which was 8 m tall. It was presumed that because the tree was situated in a parking area and was separated by bare ground from the next nearest tree 7 m away, colonization would be difficult. The sole male *A. cristatellus* resident was removed. For the following 4 days, one male per day moved onto the tree and each was removed within 2 hours of the first sighting. All of the males were from 47–55 mm. Although one or two lizards in this size range are occasionally tolerated within the territory of a large adult, the removed resident apparently had not tolerated such males. These males were approaching adult size but were probably restricted to juvenile type territory (bushes, saplings, etc.) because trees in the area were occupied by adults. Thus they either were in less preferable territories and probably about to become complete floaters or were already floaters. No replacement test was made.

A test was made for female *A. cristatellus* on a tamarind 6.5 m tall. Two resident females occupied the tree and were removed in the first 10 min. Within the following 5 hours, nine females were removed from the tree. No new females appeared in the next 19 hours. All of the colonizers came from the ground or low shrubbery within 3 m of the tamarind, and all but two were <39 mm but >34 mm; two were adults. The subadult females were floaters or held territories in less preferable areas since they deserted the ground and low shrubbery habitat for the tree. They were probably in the same category as the young males who were colonizing the isolated tree. That is, they were approaching adult size, but were still restricted to juvenile type territory because the trees in the area were occupied by adult females, presumably at maximum density.

The 11 removed females were released onto the tree for a high density test. At the end of 2 hours of aggression the original residents occupied the tree and all other females were on the ground or shrubbery. During the next 2 days, six of the nine females disappeared from the area, indicating that they were probably not of resident status and were attempting to move out of juvenile type territory. They were also probably more vulnerable to predation in their positions near the ground (see Conclusions).

Addition of territory surface.—Territory requirements can be said to be limiting the population density only if the surface available for territories is in short supply. In which case one could also say that space is limiting, but it is doing so because territory requirements have caused the available space to be occupied. If surface is limiting, then providing more (such as a tree limb) should increase the number of individuals in a tree.

Tree limbs of the sizes used in the following experiments may not have been adequate territory sites (see discussion of qualitative and quantitative evaluation of territory), but did at least present new vertical surfaces. By placing tree limbs in the field, and observing the subsequent events that involved the new sites, information on two questions was obtained. First a measure was made of the speed with which the limb was colonized and the numbers of animals involved. This indicated to what extent territory sites were limiting. If sites in an area were absolutely limiting, one would predict rapid colonization, possibly in less than 1 hour. If sites were relatively limiting, one would predict that colonization times would vary considerably, occasionally taking up to several days. No colonization even after several days would indicate no shortage of sites in the area or that the limb was unsuitable for occupation.

The second question has been raised previously: what is the number of lizards attempting to occupy a space compared to the number that eventually establish territories in that space? The hypothesis predicts that regardless of the number of lizards attempting colonization, no more than one adult male *A. cristatellus* will eventually establish a territory, since the limbs used were all smaller than any known adult male territory. However, since 1–3 females were occasionally found with territories on a tree that was comparable in size to the added limbs, one could predict that three would be the approximate limit for females on the limb.

It was not possible to use the same limb for all tests on both islands, but an attempt was made to use limbs that were as similar as possible. All were 5–6 m long, circumference at base, 20–25 cm, and circumference at midpoint of length, 10–12 cm. In each case a limb was placed so that its base was 2–3 m from the base of a tree, with the upper 1–2 m of the limb contacting branches of the tree. Territories of lizards in each area were mapped for 2 days prior to the limb placement. Unless otherwise stated, all males discussed were >59 mm, and females, >40 mm.

Two tests were made on *A. cristatellus*. In site 1 the limb was placed in contact with a tree which was bordered on two sides by buildings. After 3 hours a female moved to the added limb from a territory on the building. Although she remained on the limb for the entire day, she was on her original territory by day 2 and remained there until day 5, when regular observations terminated. The next female (not previously sighted) to occupy the limb arrived on day 4, but left by day 5. No females were seen on the limb for the rest of the study including the follow-up 2 months later.

Eight hours after placement the first male, A (54 mm), arrived on the limb from a territory on the building. On day 2 he was chased off by male B who occupied the tree which was supporting the added limb. It appeared that B was enlarging his territory to include the new limb which contacted his original territory. During day 2 male A made a second move onto the limb and was again chased off. On day 3 male C moved from a building to the limb and was chased off by B. Male D (56 mm), also from a building, and A moved to the limb and were chased off by B. Four males moved onto the limb during day 4 and were each chased off by B: E (not previously sighted), F (44 mm, not previously sighted), D, and G (52 mm, from a building). On day 5 both F and H (not previously sighted) were chased from the limb by B.

The area was left undisturbed and a follow-up study was made 2 months after introduction of the limb. Male B was not found, although the entire site was searched. Male D, who was then 66 mm, occupied the original territory of B plus the added limb. For this site, at a specific time, there was evidence for a lack of suitable territory sites available for males. The same was not true for females since only two temporarily occupied the limb.

At site 2 a limb was placed next to a saman tree 7 m in height. Several other trees were nearby. On day 1 the male from the saman occupied the limb. For the 5-day duration of the study this male occupied both limb and tree; no other males were sighted attempting to occupy either structure. On day 1 a single female occupied the limb, and by day 4 two more females were also present. None of these females had been previously sighted, and apparently all three established a territory on the limb. One perched in the lowest 1 m, the second was found between 1 and 3 m, and the third was in the branches of the tree and last 2 m of the limb. This is evidence for a shortage of female territory sites, but it is not so strong as that for males in the previous experiment, since fewer animals were involved and no aggression or eviction was observed. There was no evidence for a shortage of male territories.

Four tests were made on *A. acutus*. Two tests were at sites where the density of lizards was typically high, and two tests were at sites of unusually low density. The typical sites were trees with more than 10 adults of each sex resident; the unusual sites were trees with fewer than five adults of each sex. Each low density tree was matched with one of high density as closely as possible with regard to size and branching habit. All four studies were done within 30 days and no change was measured in the total population density during that time. The limb (5 m long, 24 cm base circumference) was about equal in size to the smallest *A. acutus* male territory seen, but several females could often be found on trees of that size.

Site 1 was a flamboyant tree with high density; the test lasted 4 days. On day 2 four subadult males (50–55 mm) were on the limb, and for the rest of the study, from 1–4 of these males were sighted there. No aggression among them was seen. Two females occupied the limb on day 3 and during the rest of the study two to five were sighted on the limb at any time. On day 3 two adult males engaged in aggressive encounters in the upper 2 m of the limb, one left and the other remained there through day 5. It is not possible to state where all of these lizards came from, but it is likely that most or all were on the tree or nearby shrubbery. For example there were at least nine males (50–55 mm) on the tree who had no territory. They remained within adults' territories and were occasionally tolerated, but at other times chased by the adults. This test indicated that the density in the area was above the amount of available territories for both sexes. Presumably, as those young males grew they would have had to displace the older males off the tree, obtain a territory left vacant by a death, or leave the tree.

Site 2 was a low density flamboyant tree with three adult males, four adult females and no juveniles. Since the other tree of equivalent size and branching had a much higher density, it would be expected that the population at site 2 could also have reached that density. A further prediction would be that given site 2 at below maximum density, there should be no evidence for a shortage of territory sites. The test lasted 5 days. On day 1 a female moved from the tree to the limb, and was seen on both for the rest of the study. On day 2 a male moved from tree to limb and was also seen on both through day 5. Each animal retained part, but not all of its previous territory, which resulted in some minor shifts by some of the other residents on the tree. There was no evidence for a shortage of territory sites for either sex.

A genip tree with high density was site 3. There were over 10 adults of each sex plus at least seven young males (50–55 mm). During day 1 a young male and two adults were seen on the limb. Each of the two adults had a territory on the tree. On day 2 the young male was still on the limb, in the lower 2 m, and occupied that section for the remaining 3 days of the study. The same two adult males were occasionally sighted on the limb above 2 m through day 5. They remained on their original territories most of the time, and it appeared that they were each incorporating part of the limb. One female with territory on the tree was seen once on the limb. This was evidence for a shortage of territory space for males.

Site 4 was a genip tree with four adult males and two adult females. The limb was left in place for 9 days, during which time no males and one female (from the tree) were seen on it. The female was sighted on the limb infrequently, and it could not be determined if the limb had become part of her territory. There was no evidence of a shortage of territory space for either sex.

Whether a tree had a high or low density of *A. acutus*, most or all of the tree was defended by males. Outside of the study area some trees were found with single males; these defended most or all of the tree in the same manner as the usually single *A. cristatellus* male. The territories of *A. acutus* males in low density situations could be divided into smaller units, since the numbers defending territories on a tree often fluctuated as reported for various studies in this paper.

Removal of territory surface.—The reverse process of the preceding tests is the decreasing of territory surface by removal of branches or trees. Two studies were made in areas where cutting for landscape purposes had occurred. Advance notice of the cutting could not be obtained to allow for a prior study of territories.

One would predict that if territory surface were diminished among an *A. cristatellus* population, some members of the population would be forced out of the area. If lizards whose territories were removed shifted onto the remaining structures without a concurrent displacement of residents from those structures, one could conclude that the population density could be increased and territory was not limiting.

On St. John an area with 7 m radius around an 8 m tree was cleared of all woody vegetation. This left the tree surrounded by herbaceous vegetation less than 0.2 m high. The lizards on the remaining tree had been marked 5 days prior to the clearing (which was completed in 1 day), but none in the cleared area had been marked. Seven lizards were on the tree prior to the clearing (Fig. 4). On the day after clearing 15 were present. Most likely the additional

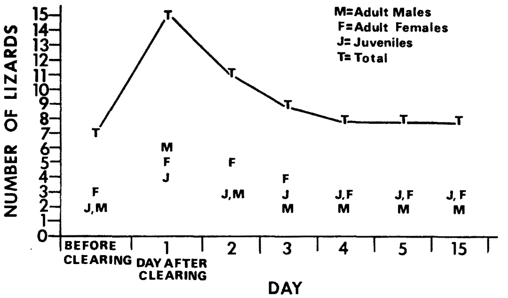

Fig. 4. *A. cristatellus* on a saman before and after removal of surrounding vegetation.

animals had come from territories destroyed by the clearing. Lizards were counted daily for 5 days following the clearing. By the fourth day the only adults on the tree were the original residents. Three juveniles, including the two present before clearing, remained on the tree. Fifteen days after clearing the population was unchanged from day 5, except that one of the males was absent. Occupying his territory was one of the males which had appeared following the clearing. If lizards were displaced onto the tree by territory removal, this test demonstrated that a maximum number of lizards was already present on the tree, since an increase in density resulted in an unstable situation which lasted fewer than 5 days.

A tree from which all branches had been removed near or at the point of bifurcation from the trunk was found on St. Croix. No lizards had been marked in the area, but it was determined that the tree had been pruned 3 weeks prior to the time it was located for study, and a photograph of the tree before pruning was available. Thus a rough measure could be made of surface area removed, about 23 m², but no information on the population before pruning or for the following 3 weeks was obtained. The total surface area available after pruning consisted of little more than a trunk 4 m high. This equaled 7.5 m², an area less than the smallest *A. cristatellus* male territory measured. Nine males and 10 females were counted on this surface. Of course it cannot be determined if this population equaled all or nearly all of those present before pruning, but it does represent a tolerance for a population density not tolerated by *A. cristatellus*. It is possible that these lizards were still at an unstable point and would eventually reach a diminished density. This did occur for adult males, as 3 months later, four adult males and 13 females were counted on the tree. This was still extremely close packing of individuals even compared to other trees with dense *A. acutus* populations. It is likely that some effects of pruning were still present. Had the same territory requirements been imposed on this population that have been suggested for *A. cristatellus*, a maximum of one male and three females should have been occupying the tree.

Although no replications could be performed, the results of these two tests support the hypothesis. The two *A. cristatellus* males and three females remained on the tree following a brief increase in density. The tree was about 20 m², and each male occupied about 10 m². The females occupied 1.5 m², 1.8 m² and 2.1 m², respectively. Following the pruning of the St. Croix tree, the average male and female territories were 0.83 m² and 0.75 m², respectively; this was computed by dividing 7.5 m² by the total of each sex present. After 15 weeks these averages were, males, 1.9 m² and females, 0.5 m².

High density A. cristatellus.—A single tamarind with a high density of *A. cristatellus* was found. Twelve males >59 mm, 11 males 51–59 mm, and at least 13 females and juveniles were seen on the tree. This density was clearly unique for *A. cristatellus* since the tree with the next highest density found on St. John had only four adult males and five females. A possible cause for this anomaly is the configuration of the tree. This tamarind was far from being the largest tree surveyed in terms of height, canopy or total surface area. Its dimensions were 10 m high, 13 m canopy diameter and trunk diameter of 1.3 m at 1 m from the ground. Surface area below 7 m was 59 m². The unique feature was that at 1–1.2 m, the single trunk ramified into 13 vertical branches ranging in diameter from 15–30 cm just above the bifurcation. This demonstrates the need for a qualitative analysis of a tree; its level of branching is just 1 m short of creating 13 trees, and this may be significant in the arrangement of territories.

The territorial structure was studied for 3 days. Only males >50 mm were marked and followed. The two largest males occupied the largest territories. One covered the five southern branches below 4 m and won all of his encounters. The other male ranged over the six central and northern branches, and was not seen in any encounters. Several of the lizards <60 mm were apparently tolerated in parts of his territory. Excluding these two largest males, the remaining 21 males seen on the tree were in one of the following categories: 1) occupied a single limb; often only above 3 m, 2) moved among various plants in the area; not seen to occupy a delimited space on the tamarind, or 3) seen in almost all parts of the tamarind; lost all encounters. Each male is listed by size (mm) in the category in which it was placed: Category 1: 66, 65, 64, 62, 62, 59, 59, 59, 58, 57, 53, 52; Category 2: 64, 63, >60, >60, 60, 56, 55; Category 3: 52, 51.

Many *A. cristatellus* in category 1 were within the territory of a dominant male, and in view of that male, but were only occasionally chased out. This was interpreted as a partial tolerance for males within another's territory. In this case the area each lizard occupied does not fit the strict definition of territory, since it was not always defended against members of the same sex and general size. For convenience, the term is still used here. This social structure is unique among *A. cristatellus* in that this tolerance was not seen in any other study.

The social structure on the tamarind is also unique when compared to the social structure of *A. acutus* in comparably high densities. In such densities, no *A. acutus* male was seen occupying a territory as large as half the surface area of a tree below 3–4 m. Each adult male *A. acutus* tolerated no others of similar size within his territory. Thus when *A. cristatellus* reached a density as high as that typical for *A. acutus*, it did so under a social structure that was different from *A. acutus*.

It is possible that a dense population existed on the tamarind because of the difficulty involved in defending the complex of branches as a single territory. If either of the two lizards with the two large territories had attempted aggression with all males within their respective territories, they might have utilized almost all of the daylight hours fighting. As the high density was approached because of the difficulty of territorial defense, lizards might have adapted to the density (by not maintaining an exclusive territory) as they aged in the area.

Laboratory Studies

Tests in cages were made to compare the effect of different densities on the survival and territory size of both species.

Materials and methods.—Three cages were used for this study. To avoid the chance of bias from using the same cage for all tests on the same species, all three cages were used for each type of test for each species. No particular effects were observed which could be ascribed to a specific cage. Each cage was 244 cm square, consisting of window screen on a wood frame. A symmetrical arrangement of eight 1 l jars inverted over plastic trays automatically supplied deionized water, and eight plastic petri dishes filled with *Tenebrio* larvae and bran provided food for 2 weeks per filling.

All three cages were in the same room of a greenhouse. Partitions prevented lizards in one cage from seeing the observer or lizards in another cage. Artificial light was supplied by ultraviolet and infrared lamps, but since the building was made of glass, total illumination and radiant heat varied with the time of year. Air temperatures in the cages ranged from 22–33. The relative humidity was kept above 65%. Fresh air supply entered the room after passing over filters of activated charcoal.

All animals used in these tests were captured near the study areas and were transferred by air to Riverside, California. Upon arrival each was given a unique toe clip and placed in a 20 l glass terrarium. Deionized water and *Tenebrio* larvae were provided *ad libitum*. Cardboard screens separated each terrarium so that each lizard was visually isolated from any other. All terraria were housed in a windowless room with several ultraviolet, infrared, and fluorescent lamps on a 12-hour on/off cycle.

Males selected for testing were >58 mm, had no observable infirmities, and showed no decrease in body weight >5% of total weight for at least 2 weeks prior to use. No animal was used in more than one test. Lizards were weighed to the nearest 0.1 g at the start and the termination of certain tests. Each was given a paint mark on the first day of a test. It was often necessary to enter a cage once or twice during a test to repaint the color code. Whenever possible, remarking was done when the cage had to be entered to replace the food. This was done at 2 weeks from the start; water lasted without replacement.

Three experiments ran simultaneously. On days during which observations occurred, lizards in each cage were watched for 2–4 hours in intervals of at least ½ hour. The position of each lizard was marked at 5-min intervals and all encounters were recorded.

For the first few days of any experiment lizards usually moved a great deal. Positions and encounters recorded after the fifth day of the test were used in delimiting territories. Since lizards were infrequently found on the roof of the cage, and since no encounters were seen there, the roof was not considered potential

TABLE 5. TERRITORY SIZES OF MALES IN 12 TESTS WITH 8 MALES/CAGE. Total number of males in each territory size category.

Test	Territory size in % of cage area								
	≤14	20	30	40	50	60	70	80	90
A. acutus									
1	7	1							
2	7	1							
3	7	1							
4	5	2	1						
5	6	2							
6	7	1							
A. cristatellus									
7	6	1			1				
8	6	2							
9	8								
10	6			1	1				
11	7								1
12	7				1				

TABLE 6. DEATH RATES IN CAGES FOR 36 DIFFERENT GROUPS OF ADULT MALES.

Males per cage	Total dead per cage	
	A. acutus	*A. cristatellus*
8	0	3
8	1	2
8	0	3
8	1	3
8	0	3
8	1	1
8	1	3
4	1	0
4	0	1
4	0	1
4	2	1
4	0	2
4	0	0
2 (5 tests/species)	all 0	all 0
	Mean deaths per cage	
8	.6	2.6
4	.5	.8
2	0.0	0.0

territory space. This left 4 walls and the floor each 244 cm square, for a total of 29.8 m^2; this will be referred to as the cage area. A territory was defined as the minimum polygon which included all the positions recorded for 5 days (days 6–10) except those in areas where encounters were lost. Boundaries were also defined along lines where the outcome of any encounter was termed a tie. Records for only 5 days in the early part of each experiment were used to avoid the complication of territory shifting which occurred as deaths took place (no deaths occurred prior to day 11 for any test). All territories which were ≤14% (≤4.2 m^2) of the cage area were placed in the same category. All other sizes were rounded to the nearest 10% of the cage area.

Results and discussion.—Seven tests were made on each species in which eight males were placed in a cage and observed for 33 days. There was no significant difference between species in weight change or aggression index. Table 5 lists the territory sizes for six of the seven tests on each species (territorial data were not recorded for two tests). All *A. acutus* except one occupied territories <30% of the cage (<8.9 m^2). In four of the six tests on *A. cristatellus* one male of each test occupied at least 50% of the cage (14.9 m^2). In one test all males occupied ≤14%, but three died. Following those deaths, one male occupied 40% (11.9 m^2). In the other test results were similar to those for any *A. acutus* experiment.

The death rates from each test are recorded in Table 6. The significantly higher mean deaths per cage for *A. cristatellus* ($P = .01$) may be due to lack of accommodation to the density and/or to an inherently higher death rate than *A. acutus* in the laboratory environment. Death rates for adult males in the terraria were nearly identical. Naturally the terraria do not constitute suitable controls, so 33-day tests were made in the cages with two and four males per cage. Mean deaths per cage dropped 1.8 for *A. cristatellus* and 0.1 for *A. acutus* in six tests each with four males per cage (Table 6). The results for five tests each with two males per cage were the same for both species with no deaths occurring (Table 6).

After adjusting for the three different densities, the mean number of deaths per cage for each series were compared using Student's t-test. At four males per cage the likelihood of a significant difference between the means was still high, $P = .02$, but the means were identical at two males per cage. The comparison between *A. cristatellus* at eight per cage and two per cage yielded $P \ll .001$; the same comparison for *A. acutus* gave $.05 > P > .02$. This significant change in death rate for *A. cristatellus* is most likely a result of the change in density. There may be some effect of density on the *A. acutus* groups, but it was not so pronounced. These tests indicate that when *A. cristatellus* males are subjected to a density equivalent to that typical for *A. acutus*, the death rate is higher than for *A. acutus* and higher than the rate for *A. cristatellus* caged at the density typically seen on St. John.

Conclusions

To conclude that there is a density-dependent limitation of the breeding population of *A. cristatellus*, involving territorial requirements and territory resources, one must show that there are both males and females prevented from holding territories and that these animals rarely or never breed. To demonstrate that there exists some minimum territory size tolerated, one must show that a crowding of individuals does not result in a decrease in territory size. However, evidence of a minimum territory size does not prove that a population is limited by territorial behavior.

The laboratory tests have shown that under atypically high density *A. cristatellus* males had an increased death rate and in four of six cases a single male occupied at least half of the cage. Efforts to increase density in the field by addition of males and females and by the removal of territory surface did not result in decreasing territory sizes. From these results it is concluded that *A. cristatellus* requires a large minimum territory size compared to *A. acutus*.

It is more difficult to determine if the territory size acts to control the size of a breeding population. In the removal tests for *A. cristatellus* it was shown that there was often considerable colonization pressure by both sexes. Similarly, addition of territory space often resulted in rapid colonization. Information on the prior territorial status of colonizing lizards was not always known. Some individuals were known to colonize by leaving the area they defended or the area they occupied but were not defending. This suggests that the new area made available was preferred over the area the colonizer previously occupied. These presumably low-preference areas were saplings, the ground, terminal portions of branches, and buildings. In a few cases a resident adjacent to the vacated (or added) territory expanded the area he defended by moving into the new territory without ceasing defense of the original territory. If these were the only types of colonizer observed, there would be no argument in support of the hypothesis. As Brown (1969b) showed in a model, breeding in low-preference habitat does not prove that the breeding population is limited by territory space. A third group of colonizers were lizards who had no territory, the floaters. These were lizards who were not found in the area studied prior to any experiment and were not found following the test (unless occupying the tested territory). Some individuals were also deemed to have no territory because they did not successfully defend any area, but were seen to move onto various trees from which they were subsequently chased by a resident. In some cases they were seen before the manipulation phase of an experiment began. Results from these tests show that the density per tree is almost always at the maximum possible, and that this density is determined by the minimum territory size defended.

The floaters provide the key to determining whether or not there is a limitation to the breeding population. If their mortality is equal to that of lizards holding territory, then territory does not limit the numbers of lizards present in the population. Further, if their breeding success is equal to the success of those with territories, the territory is not limiting the size of the breeding population. Unfortunately, the floaters could not be sufficiently followed to determine their mortality and breeding success.

It can only be suggested that the lizard lacking a territory is likely to have a significantly lower breeding success than one with a territory. Several observations indicate that this is so. Lizards on a territory were seen to react to a predator such as a bird, cat or mongoose by using the same set of escape routes; if a hole or crevice was present in the territory, it was almost always used for cover. A lizard without a territory cannot be so familiar with specific escape routes. Such an animal is most often on the ground, where there is a minimal amount of cover compared to the branches and crevices in any tree; hence it is most vulnerable to predators. No cat or mongoose was seen to climb above 1 m from the ground in pursuit of a lizard.

Males and females holding overlapping territories were frequently seen copulating. In order for a male floater to copulate, he would have to 1) reach a female who is within a male's territory and complete the act before discovery by the resident male, given that the female would allow copulation (this is what male B managed to do after the resident was removed from the saman in the first test described), 2) complete the act with a female whose territory is not within a male's (such females were rarely seen) or 3) find a female floater (this would probably be a rare event compared to the frequency of copulation between two adults with overlapping territories, since floaters are not abundant, and a pair would have to be, by chance, in the same place at the same time). A female floater would have similar problems, except that she would have a better chance of entering a male's territory not overlapped by a female, than the chance the male floater has for alternative "2."

Most populations of *A. acutus* were clearly existing at far higher densities than *A. cristatellus*. Tests on *A. acutus* showed that these densities were made possible by a tolerance of a much smaller territory. This was most dramatically demonstrated in the comparison of removal of territory surface for both species. Both sexes of *A. acutus* displayed a high tolerance for proximity on a tree with so little branching complexity (after pruning) that each territory was contiguous with many others; each lizard often had several others of its sex within its probable field of vision. Even with this high tolerance for packing, there were indications from some tests on removal of animals and addition of territories that a minimum territory size did exist. Yet because the densities of *A. acutus* on some trees were seen to vary considerably with time, one could not conclude that the population was usually territory limited. It is concluded that *A. acutus* populations probably reach densities where territory becomes limiting, but that these situations are narrowly localized in time and place. Ruibal and Philibosian (1974a) suggested that egg and juvenile mortality may limit the population.

One can only speculate as to why *A. acutus* tolerates a smaller territory than *A. cristatellus*. It is possible that *A. cristatellus* must have a larger territory because it shares it with congeners. Several species occur with *A. cristatellus* on Puerto Rico and some of them, besides *A. pulchellus* and *A. stratulus*, may have been present on St. John during the time it was connected to Puerto Rico. Although there is significant niche partitioning by Puerto Rican *Anolis*, there is still some overlap among certain species (Rand, 1964). Thus if the density of all Puerto Rican *Anolis* on a tree were about equal to the density of all *A. acutus* on a tree, one might have the reason for the difference in territory size. In the section on species the syntopy of *A. cristatellus* and *A. stratulus* was described. However, the density of both species on a tree still does not approach *A. acutus*, since there are rarely more than four *A. stratulus* per tree. The presence of *A. stratulus* then, does not seem to explain the difference.

If the defense of a larger territory size has evolved because of the presence of congeners with *A. cristatellus*, it could only have evolved at a time when more than the two species occurred on the same tree. Situations such as that exist on Puerto Rico but territories have not been studied. It is also possible that in the past even more species of *Anolis* were present with *A. cristatellus*. The three species on St. John may be what is left of a previously richer anoline fauna from Puerto Rico; recent extinction of *Anolis* species on Puerto Rico may also have occurred.

The above discussion assumed that the minimum territory size tolerated was an inherited trait. This study has not tested that assumption. Probably the next field test to perform is to alter more than the surface area available for territories and the number of lizards in an area. An experimental alteration of the food supply seems to be the next logical choice to provide some answers.

One should not infer from this paper that most *Anolis* populations are regulated by territoriality. Both of these species occur in densities which are high compared to many other *Anolis*. In densities of this nature it seems that territory can become a limiting factor. But for many species which exist at much lower densities, territory could not possibly be limiting the population unless extremely large territories were maintained, and such have not been found. Some anoline species may be found to be non-territorial, and with this added possibility, any generalization for the genus is unwarranted.

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Literature Cited

BOWDEN, M. J. 1968. Water balance of a dry island. Geogr. Pub. at Dartmouth no. 6.

———. 1970. Climate, water balance and climatic change in the north-west Virgin Islands. Caribbean Res. Inst., St. Thomas, Virgin Islands.

BROWN, J. L. 1969a. Territorial behavior and population regulation in birds. Wilson Bull. 81:293–329.

———. 1969b. The buffer effect and productivity in tit populations. Amer. Nat. 103:347–354.

BUSTARD, H. R. 1968. The ecology of the Australian gecko, *Gehyra variegata*, in northern New South Wales. J. Zool., London 154:113–138.

———. 1969. The population ecology of the gekkonid lizard (*Gehyra variegata* (Dumeril and Bibron)) in exploited forests in northern New South Wales. J. of Anim. Ecol. 38:35–51.

———. 1970. The role of behavior in the natural regulation of numbers in the gekkonid lizard *Gehyra variegata*. Ecology 51:724–728.

CARPENTER, C. C. 1967. Aggression and social structure in iguanid lizards, p. 87–105. *In*: Lizard ecology: a symposium. W. W. Milstead (ed.). Univ. of Missouri Press, Columbia.

CLARKE, T. A. 1970. Territorial behavior and population dynamics of a pomacentrid fish, the garibaldi, *Hypsypops rubicunda*. Ecol. Monogr. 40:189–212.

HINDE, R. A. 1956. The biological significance of the territories of birds. Ibis 98:340–369.

KREBS, J. R. 1971. Territory and breeding density in the Great Tit, *Parus major* L. Ecology 52:2–22.

LACK, D. L. 1966. Population studies of birds. Clarendon Press, Oxford.

———, AND L. LACK. 1933. Territory reviewed. Brit. Birds 27:179–199.

PHILIBOSIAN, R. 1972. Territorial behavior and population regulation in anoline lizards. Unpubl. Ph.D. thesis, Univ. of California, Riverside.

RAND, A. S. 1964. Ecological distribution in anoline lizards of Puerto Rico. Ecology 45:745–752.

RUIBAL, R., AND R. PHILIBOSIAN. 1974a. The population ecology of the lizard *Anolis acutus*. Ecology 55:525–537.

———, AND ———. 1974b. Aggression in the lizard *Anolis acutus*. Copeia 1974:349–357.

SOUTHWOOD, T. R. E. 1966. Ecological methods. Methuen and Co., Ltd., London.

WATSON, A., AND D. JENKINS. 1968. Experiments on population control by territorial behavior in the Red Grouse. J. of Anim. Ecol. 37:595–614.

WHETTEN, J. T. 1966. Geology of St. Croix, U.S. Virgin Islands. Geol. Soc. Am. Memoir 98:177–239.

WYNNE-EDWARDS, V. C. 1962. Animal dispersion in relation to social behavior. Hafner Pub. Co., New York.

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