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The Social Behavior of *Anolis valencienni*

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ABSTRACT. *Anolis valencienni* is highly cryptic and displays many features atypical of other *Anolis*. Adult females are completely nonterritorial and nonaggressive, frequently passing within centimeters of each other. Adult females overlap with each other extensively in their daily movements. Sometimes as many as 40 females may occupy a common feeding space. Males are aggressive to each other but show broad overlap in the space occupied. It is not uncommon for five adult males or more to share much of the same space. Consistent with their lack of territories, adult females wander slightly greater distances than do adult males, even though they are smaller. Males appear to suffer differential mortality, and the adult sex ratio is biased toward females. Both sexes feed by searching slowly over the substrate of trees and bushes for insects, many of which are cryptic and at rest. Because many adults of both sexes encounter each other daily, there are unusual opportunities for female choice. Females copulate often during the summer, sometimes, and probably often, more than once a day. Over a period of six weeks a female may copulate with five or more males. Experiments were conducted to test the criteria females use in choosing males, but these were not successful. Field data show that both adult males and adult females copulate more often as they increase in size, but for males this relationship appears to be weaker than in the more size-dimorphic *Anolis garmani*. It is proposed that the many unusual features of *A. valencienni* result from the primary feeding adaptation of searching for stationary, cryptic prey.

INTRODUCTION

In appearance, *Anolis valencienni* is the most cryptic of Jamaica's seven species of anoline lizards. It is also the

slowest moving, crawling deliberately and very slowly over the trees it inhabits. Both in size and in secondary sexual structures such as the dewlap, it is likewise unique in that females are never aggressive toward each other and tolerate the presence of other females at distances of centimeters. More than a year of field work on this species suggest to us that the above attributes of *valencienni* are all interrelated and ultimately explained by *valencienni*'s unique feeding specialization: individuals search actively for and feed upon cryptic insects, many of which may be diurnally immobile. We describe here the results of this field work.

METHODS

Anolis valencienni was studied in two different localities and at several different times in each locality.

Study site 1 (Maryfield) was located in a suburban area of Kingston and consisted of the three acre grounds of the Maryfield Guest House. These, in turn, consisted of scattered large trees (usually over 10 m high) typical of Jamaica, mostly mangos (*Mangifera indica*) but also *Persea americana*, *Guaiacum officinale*, *Delonix regia*, *Terminalia catappa*, *Haematoxylum campechianum*, *Swietenia mahagoni*, *Gliricida sepium*, and *Brya ebenus*. During 12 days in September 1968, feeding behavior was studied by following (through binoculars) unmarked lizards. From June 15 to September 14, 1969, the social behavior of these

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lizards was studied for a total of eleven weeks by capturing, sexing, measuring, marking, releasing and later following 265 lizards in the study area. Brief visits to this study area (to recapture marked individuals) were made in January 1970, and again in April 1970. All observations of study area were made by Trivers and no assistants were employed. *A. valencienni* were abundant in this study site, but because the site consisted of many large trees, the lizards were difficult to resight (and recapture) and most of our data on social behavior come from the second study site.

Study site 2 (Southfield) was located in rural St. Elizabeth and was chosen because *valencienni* were abundant and because the study site consisted of many bushes and short trees (most were under 6 m in height). Typical tree species, in addition to mangos, were *Pimenta officinalis*, *Cocos nucifera*, *Manilkara zapotilla*, *Blighia sapida*, *Chrysophyllum cainito*, and *Persea americana*. Social behavior was studied for two weeks in June 1971, by Trivers with the help of field assistants, and for seven weeks in July and August 1973, by Hicks with help of field assistants. All resightings of individuals, including copulations and aggressive encounters, were confirmed by Trivers or Hicks even if first made by one of the assistants. The second site was visited by Trivers for eleven days in December 1973 to January 1974 in order to recapture marked *valencienni*. In addition, Trivers studied *Anolis garmani* for a year in Southfield, where *valencienni* were abundant, and he made numerous casual observations during this year. Finally, five months of field work in the spring of 1976 and in July 1977, concentrated on measuring female choice.

Social behavior was studied as in *A. garmani* (Trivers, 1976); that is, an effort was made to capture, sex, measure, and mark all adults in the study area. Individuals were given a permanent mark by clipping two or three toes in a pattern unique for each lizard. Likewise, a num-

ber was painted on each lizard's back, permitting identification in the field without recapture. As molting takes place about every three weeks in *valencienni*, individuals were often recaptured and repainted. Such recapture work permitted some systematic data on growth rates, and these are analyzed below as a function of size, sex, and rate of dispersal. When an effort was made to gather copulation data (see below), the study area was systematically searched for copulating lizards. If these were marked, numbers were recorded. If one or both were unmarked, the unmarked individuals were captured. It was not possible to estimate precisely to what extent the sample was a biased sample of those copulations actually occurring, but some biases were apparent. These, and other methodological problems are discussed, where relevant, below. Resightings were recorded while searching for unmarked lizards and for copulating pairs. The data from resightings are analyzed below. In addition, observations of aggressive, sexual, and neutral encounters were made in the process of the work described.

RELATIVE CRYPTICITY

Anolis valencienni is unusually cryptic (Lynn and Grant, 1940; Underwood and Williams, 1959; Rand, 1967a; T. W. Schoener and A. Schoener personal communication), and experienced Jamaicans routinely assert that *valencienni* is the most cryptic anole on the island. Several lines of evidence support this opinion. In what follows, we emphasize the comparison between *valencienni* on the one hand and *A. lineatopus* and *A. grahami* on the other; because the latter two species are similar in size to *valencienni*, they often occupy similar perches, and they both occur in our two study areas.

Sightings. 1) On a typical day in either of the study sites, individual *lineatopus* and *grahami* were sighted first, although we were searching for *valencienni*. 2) Marked *grahami* and *lineatopus* are

much more frequently resighted than marked *valencienni*. (This is partly due to the greater crypticity of *valencienni* and partly due to its less predictable choice of perches.) 3) In both study sites, *valencienni* initially appeared to be rare, but marking revealed *valencienni* to be more common than *grahami* in both study sites, more common than *lineatopus* in the second study site, and only slightly less common than *lineatopus* in the first study site. 4) Rand's (1967a) census study of Jamaican anoles found *valencienni* to be less common than any other species except *garmani*. This is expected since lizards were not marked and each study area was traversed only once per day. Underwood and Williams (1959) likewise point out that *valencienni* is much more common than the number of collected specimens would suggest "for it is very clever at concealing itself." 5) It is a common experience to be attracted to a tree because one spots one or more *lineatopus* or *grahami* and after watching these for several minutes to notice an overlooked *valencienni*, often because it finally moves.

Morphology. 1) *A. valencienni* is usually grey in color (sometimes brown) with irregular dark markings which tend to obliterate body outline. This contrasts with the solid blue (or dark brown) color of *grahami* and the regular, reticulated pattern of *lineatopus*. 2) In contrast to *grahami* and *lineatopus*, the splotched, irregular pattern of *valencienni* covers the entire body, including the belly, the face and lower jaw. 3) All other Jamaican anoles have a bright, yellow eye-ring. This eye-ring is obliterated when the lizards are frightened in social encounters and their entire bodies darken. *A. valencienni* lacks the eye-ring entirely.

Behavior. Individual *valencienni* move very close to the surface they are climbing on. When they do move, they move very slowly, so that they appear to glide quietly and nearly invisibly from place to place.

SEXUAL DIMORPHISM

Both in size and in secondary sexual characteristics, *valencienni* is, along with *A. reconditus* (Hicks, 1973), the least dimorphic Jamaican anole.

Data on adult size dimorphism from different visits to the two study areas give consistent results. Since the data from the summer of 1973 (Southfield study site) are the most complete, they are presented here. The snout-vent length of the largest five males averages 85.2 mm while that for the largest five females averages 73.8 mm. The smallest adult male seen copulating was 54 mm in size (= snout-vent length), while the smallest female seen copulating was 50 mm in size. Using these sizes as size of sexual maturity, the average adult male size ($N = 93$) is 72.8 mm, while the average adult female size ($N = 98$) is 64.8 mm. At all sizes for which data are available, males grow faster than females of similar size (Fig. 1). Like other anoles, male *valencienni* have larger jaws than females of similar snout-vent length.

It is of particular interest to know whether the size dimorphism in *valencienni* results entirely from differential growth rate or whether males hatch out at a larger size than females. A sample of 55 *valencienni* hatched from eggs (and then preserved) is available at the Museum of Comparative Zoology. These were measured and then sexed. Forty-nine of these could be sexed unambiguously (by the enlarged post-anal scales of the males), but six individuals had post-anal scales intermediate in size. Although these are probably males, they have been treated separately. No sex difference in size at hatching is apparent. Mean size of known males ($N = 22$) is 23.8 mm, while the mean size of known females ($N = 27$) is 23.7 mm. If the six uncertain individuals are indeed males then the mean size of males ($N = 28$) is 24.0.

There are no pronounced secondary sexual structures in *valencienni* except the dewlap, which is very large and

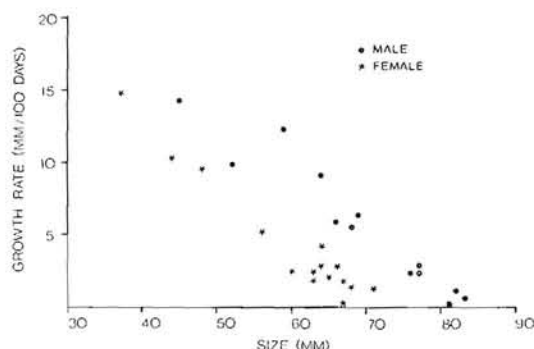


Figure 1. Growth Rate (mm/100 days) is plotted as a function of initial size (snout-vent length in mm) for males and females between summer 1973 and winter 1973-74 in Southfield. On average each individual of both sexes was recaptured six months after initial capture.

bright purple in the male and smaller and less brightly colored in the female, often showing many white scales.

ADULT SEX RATIO

In all visits to both study areas more adult females were captured than adult males. We divide the data by study area, however, because at Maryfield females were easier to capture (Table 1) while males were easier at Southfield (Table 2). In order to make inferences about differential mortality by sex, we present not only the number of adult males captured (≥ 55 mm), but also the number of males ≥ 50 mm captured, since the latter category certainly contains individuals younger than the youngest adult females (see below).

During the summer of 1969 at Maryfield 198 adult females (≥ 50 mm) were captured compared to 69 adult males (≥ 50 or 55 mm). These data are certainly biased, because males were much less often sighted and were less often captured when sighted (since they stayed higher in the trees). As evidence of this bias, for example, the first 29 individuals captured in the study area were females.

TABLE 1. NUMBERS OF MALES AND FEMALES CAPTURED AT MARYFIELD.

	females (≥ 50 mm)	males (≥ 55 mm or ≥ 50 mm)
Summer 1969	199	62
Winter 1969-1970	26*	9†

*Of these 26 females, 20 had been marked in the summer of 1969.

†Of these 9 males, 3 had been marked in the summer of 1969.

Likewise, of the 121 adult females captured on or before August 6, 48% (58) were, at one time or another, recaptured, but of the 41 adult males marked on or before August 6, only 31.7% (13) were ever recaptured. Thirty-seven females marked on three large connected trees on or before August 6 (see "Female Movements") were resighted a total of 19 times after August 6 for an average of 0.51 resighting per female, while 12 males marked on or before August 6 were resighted thereafter a total of only once, for an average of 0.08 resighting per male.

Recapture data permit a crude estimate of the real adult sex ratio at Maryfield. During seven days in December 1969 to January 1970 and during three days in April 1970, a total of 35 adults were captured of whom 23 had been marked in the summer of 1969. Of the 26 females captured 88.5% (23) were marked the preceding summer, while of the nine adult males captured only 33% (3) had been marked. It is unlikely that many lizards migrated in and out of the study area, which was very large and bounded on three sides by roads. A very crude estimate of the real adult sex ratio at Maryfield (assuming no differential migration) is 186 males and 259 females.

At Southfield males appeared to be slightly easier to spot than females and, once sighted, very few individuals of either sex eluded capture. The 92 adult males captured were resighted a total of 158 times for an average of 1.72 resighting

ing per male while the 97 adult females were resighted a total of 151 times for an average of 1.56 resighting per female. Yet each visit to Southfield showed more adult females than adult males (Table 2). None of the differences are significant; nor, when combined, are the totals significantly different.

Recapture data appear to confirm that more females than males remained uncaptured during the summer of 1973. Of the 31 females captured during the winter of 1973 to 1974, 67% (21) had been marked during the preceding summer, while of the 24 males captured 75% (18) had been marked in the preceding summer. These data may partly reflect greater female mobility, as data from the summer of 1973 show a slightly greater distance between successive sightings of females than of males (see below). Assuming no difference in mobility, a crude estimate of the real adult sex ratio in the summer of 1973 is 92 males and 123 females. The male : female sex ratio for animals of all sizes at Southfield (1973) was 110 : 121.

Males grow faster than females at all sizes for which we have data. If, as in *A. grahami* (Trivers, 1976) and *A. lineatopus* (Rand, unpublished data), the sex difference in growth rates extends to small individuals (as appears likely) then a female 50 mm in length is in fact, older than a male of the same size. Likewise, a newly adult female is almost certainly older than a newly adult male. Thus, the

sex ratio for adults of the same age is expected to be more strongly biased toward females than our data on all adults (and on all individuals ≥ 50 mm) show. If the sex ratio of hatchlings is 50/50 (as expected, since there is no size difference between the sexes at hatching), then our data suggest differential male mortality. What data we have suggest that the sex ratio at hatching may, indeed, be 50/50 but the data are few and our ability to recognize males, imperfect. Of the 24 individuals < 35 mm caught at Southfield during the summer of 1973 and winter 1973 to 1974, 11 were males and 13, females.

FEEDING BEHAVIOR

Individual *valencienni* capture insect prey from the ground at the base of trees to the outer edges of leaves forty feet above the ground. They do so by searching slowly and carefully throughout the tree (or bush) in which they live. When a lizard first spots a prey item, the item is usually within 8 cm of the lizard's face and is usually captured once spotted. These findings emerge from 84 hours of systematic observation of unmarked *valencienni* in 1968 and are supported by numerous incidental observations made during the summers of 1969 and 1973.

In September, 1968, 36 feeding attempts were observed. An attempt at feeding was assumed to occur if an individual moved quickly for several inches and snapped its jaws. The feeding attempt was gauged to be a success if the jaw snap was followed by chewing (i.e., by jaw movements). In the majority of unsuccessful attempts, a small prey item (assumed to be an insect) fluttered away. Likewise, in the majority of successful attempts, an insect was seen in the lizard's mouth before being consumed.

The distance at which the lizard first spotted the prey item was recorded as the distance from which the lizard began its lunge. There is no evidence that individual *valencienni* ever creep up on prey.

TABLE 2. NUMBERS OF MALES AND FEMALES CAPTURED AT SOUTHFIELD.

	females (≥ 50 mm)	males (≥ 55 mm or ≥ 50 mm)
June 1971	44	35
Summer 1973	97	92
Winter 1973-1974	31*	24†

* Of these 31 females, 21 had been marked in the summer of 1973.

† Of these 24 males, 18 had been marked in the summer of 1973.

Usually, the lizard is moving slowly over an area, constantly searching it visually, when it interrupts the searching to lunge and snap, often at something hidden in the bark under its nose. Of the 36 feeding attempts, 27 were successful. Of the 34 for which the distance the prey item was spotted was recorded, all but three times, the prey item was less than 12 cm from the lizard when first spotted. The furthest a prey item appeared to be spotted was 45 cm. The feeding attempts ranged from ground level to 13 m up. Twelve took place 6 m above the ground or higher, but these data are strongly biased toward observations close to the ground, since lizards were more easily spotted and followed at low heights. Because *valencienni* takes prey at short distances with high success, once prey is spotted, the species is, in the terminology of Schoener (1971) a *searcher* (as opposed to a *percher*, such as *lineatopus*). The finding that *valencienni* takes food from throughout the tree is consistent with the data of Rand (1967a) and Schoener and Schoener (1971), namely, that *valencienni* has the most variable "perch" height of a Jamaican anole, i.e., it is sighted from the ground to the tree-tops.

In behavior, *valencienni* is clearly a searching species, in the sense that most individuals can be observed most of the time searching for prey. They do so in five different places: 1) on the ground; 2) on leaves; 3) on the trunk of a tree and its limbs; 4) in holes; and 5) on epiphytes growing on trees, epiphytes such as *Tillandsia recurvata*. The searching behavior itself consists of moving very slowly while frequently cocking the head so as to look at the substrate. The lizards are especially likely to search irregular places in the bark, large holes in a tree and places where limbs have broken off. Likewise, they search out all epiphytes very carefully and on broad-leaved trees such as mangos will go out onto leaves to search their surface.

Typical searching behavior of two dif-

ferent individuals are presented here, condensed from Trivers' field notebook (measurements converted to metric equivalent).

While drawing close to a tree to observe two *lineatopus* at 8:30 am on September 16, 1968, Trivers almost stepped on a *valencienni* (assumed to be a female) who was on the ground a foot from the tree. Trivers withdrew and watched through binoculars:

8:33 lizard jumps onto tree and climbs straight up to 5m.

8:35 stops at series of bromeliads (*Tillandsia recurvata*)

8:38 moves in among them, searching

8:40 carefully, slowly climbing through a bromeliad

8:43 has moved a foot higher since entering bromeliads

8:46 stealthily moves another three inches

8:49 another three inches, then suddenly moves 45 cm very quickly, as if it has spotted something. It then darts, snaps something off a bromeliad and eats.

8:50 moves several inches through bromeliad and stops

8:55 now 6 m up, turns to move out a horizontal branch which is about 7.6 cm thick

9:05 upside down in a large bromeliad, searching

9:10 same place

9:18 still upside down, searching, sometimes on a bromeliad, sometimes on the branch itself

9:25 upside down on a bromeliad when it seems to spot something on a neighboring bromeliad, also upside down. I too spot something on the second bromeliad. Starts to dart the 5 cm to the neighboring bromeliad but—as if forgetting it is upside down—it steps into thin air and falls 6 m to the ground. It appears to be uninjured.

In the second case, an individual was watched continuously for three hours and forty minutes. The individual was almost certainly a female as judged by her appearance, the size and coloration of her dewlap, and by the nonaggressive way she interacted with an adult male who appeared to be courting her. During the time she was observed, she moved from the foot of the tree to the foliage 11 m up and back down to the ground. She fed three times (once at ground level, twice at 11 m). All three prey items were spotted at distances of 15 cm or less. She

used her dewlap on six different occasions, on three of which the adult male was within a couple of meters of her. Observations on this animal are as follows:

At 9:40 on September 6, 1968 an adult *valencienni* was spotted upside down on a horizontal branch 5 m above the ground. Assumed to be a female, the lizard was searching an irregular area in the bark. She moved on to the trunk, and in the next ten minutes moved down to 1 meter above the ground. At 9:56 she moved down to 0.5 m, then down to 7.5 cm. She paused, dashed about 15 cm out onto the ground, caught a prey item, returned to 15 cm up the tree and ate what appeared to be a small, white moth.

10:13 a cat appears, circles the tree rapidly, and scares the female up to 5 m where she stops to search a warty, cracked area of the bark

10:10 1 m higher; a male who was also scared up by the cat is 1 m higher than the female, facing away from her and dewlapping repeatedly

10:14 male 1.5 m higher than female and still dewlapping; she jerks her head as if about to dewlap but no dewlap

10:23 she is now 10 m up going out a 2.5 cm thick branch

10:27 11 m up at end of branch, looking over a whorl of leaves

10:35 goes out another twig which ends in a whorl of over 20 leaves. Pulls itself into leaves and searches visually for over a minute, suddenly darts straight up 7.5 cm and catches a large insect, which she chews

10:40-10:57 searches other leaves in area

11:00 facing down on a branch 0.3 m below the leaves; male is 1 m above her dewlapping

11:04 female just dewlapped (small dewlap, many scales)

11:08 both male and female are 1.5 m lower. Male is dewlapping. Male moves rapidly down the branch, past where the female is and further down

11:13 female is 5 m up slowly searching the bark; for the next five minutes she does not move

11:28 she is 0.3 m lower, facing down, head raised, often looking around (at what?)

11:30 still looking around, moves sideways and dewlaps again, then moves to another branch

11:35 5.4 m up, slowly moving up

11:38 6 m up, moving up. At 11:42 she dewlaps several times (again, small dewlap, much white showing)

For the next 45 minutes she spent most of her time searching several clumps of

leaves (without success). At one point, a large wasp landed within 8 cm of her without eliciting any response. At 11:56 she dewlapped twice; no other lizard was visible near her. At 12:20 she fed on a small insect which was about 2 cm back of her head when she spotted it (10 m above ground on a twig). At 12:26 she dewlapped again and within a minute the large male was spotted about one meter above her, dewlapping. He moved to within a few cm of her and dewlapped repeatedly. Then he ran by her. For the next twenty minutes she and he descended to 5 m up, and the entire time he was within a meter of her, often dewlapping. She dewlapped at 12:53, and he moved rapidly up the tree away from her. For the next half hour she descended slowly to a height of less than a meter. Observations were discontinued at 1:25.

FEMALE-FEMALE INTERACTIONS

Two or more marked adult females were seen within centimeters of each other over 100 times during all visits to the two study areas, and no aggressive interaction was ever observed. Marked females were never seen to display to each other, nor to make any physical contact nor to show any clear avoidance behavior. On four occasions unmarked adults who appeared to be females displayed toward other adults assumed to be females. In three cases, a presumptive female dewlapped at a second presumptive female which was several centimeters away. There was no response nor any follow-up behavior. It is very likely that the dewlapping individual in these three cases was a female, but it is not certain that the recipient was also a female. In the fourth case a presumptive female bit at her own reflection in a mirror. (All other females ignored their mirror images.)

In virtually all interactions between marked females, the relations appeared to be neutral, but in certain situations, described below, females may have been

positively attracted to each other (or to some common stimulus). The neutral relations between adult female *valencienni* contrast strongly with the aggressive interactions that characterize female-female relations in *A. lineatopus* (Rand, 1967b), *A. garmani* (Trivers, 1976), *A. opalinus* (Jenssen, 1973) and *A. grahami* (Trivers, unpublished data). To illustrate the nonaggressive nature of *valencienni* female relations, we give here two examples.

1) On July 22, 1969, three adult females (snout-vent lengths: 60, 65, and 66 mm) were seen within centimeters of each other at a hole about 5 m up a mango tree. The three arrived at the hole within fifteen minutes of each other from three different directions, each stayed several minutes and left independently of the others. Two other adult *valencienni*, which were unmarked and assumed to be females, passed within centimeters of two of the marked females. At no time did any of the individuals clearly alter behavior in response to the others. The hole which attracted the females was one near which females were often seen and one which contained *valencienni* eggs. It is not known whether the sight of a female near such a hole attracts other females.

2) Females (like males) are reluctant to leave bushes or trees for open ground. They appear to be much less reluctant if another individual has preceded them. On August 6, 1969, at 2:15 pm an unmarked adult *valencienni* left a mango tree to climb among some rocks at the base of the tree. Within about 20 minutes, four other unmarked adults left the tree to search among the same rocks. At 2:45, all were caught. Two were then 4 m from the base of the tree but within centimeters of each other. Both were 66 mm females. Two others closer to the tree and within one meter of each other were a 64 mm female and a 62 mm female. And, finally, the individual nearest the tree was a 62 mm male. All appeared to be searching for food, and at least one fed successfully while among the rocks. No

interactions were apparent. The presence of an adult male is not typical, but other such cases have been observed: one male within a meter of one or more females, with no obvious interaction. For example, at 10:30 am July 6, 1969, four adults were caught while searching for food on the trunk of a royal poincianna tree, all within 1 m of the ground and of each other. Three were females (59, 60, and 65 mm), and one was a male (68 mm).

The above example is only atypical in that more than two individuals were involved. In the majority of female-female interactions, one female passes close to another while both are searching for food. It would be interesting to know if females tend to avoid searching through areas recently searched by others, but no good evidence exists one way or the other. Certainly females do not show strong avoidance, and we have often seen one female search the general area recently searched by another. Females may be actively attracted to each other 1) at holes containing eggs and 2) at the base of trees, but this is merely an impression based on the frequency with which we observed more than one female together at such places.

DAILY FEMALE MOVEMENTS AND DISPERSAL

Since females do not interact aggressively and since there is no evidence they avoid each other, it is of interest to know how extensively their home ranges overlap. The best evidence for degree of overlap comes from three large contiguous trees whose occupants were watched during the summer of 1969. (Data from other trees give similar, but much less detailed, results.) The trees were two mangos connected together by a royal poincianna. Each tree stood about 13 m tall and had extensive foliage. The three trees were connected to each other in the foliage but to no other trees. It was possible, then, for a female to wander

throughout the three trees. Distances between the trees and the number of adult females captured on each are given in Table 3.

Between June 16 and September 6, 1969, 43 adult females were caught and marked on the three trees. The great majority of these (37) were marked by August 6. Since the six females caught after August 6 had little opportunity to be resighted (only one of them was, in fact, resighted), the analysis here is limited to the 37 marked by August 6. Of these 37, 29 were resighted at least once for a total of 69 resightings, or almost two resightings per individual marked on or before August 6. Of these 69 resightings, 64 found the lizard on one of the three connected trees. (The other five resightings involved nearby trees and they are discussed below.)

The 64 resightings are analyzed according to each lizard's tree of origin in Table 3. Just as more females were captured on mango-1 than on the other two trees, more females were resighted on that tree as well. This may partly indicate a preference by the lizards for mango-1, but it may result entirely from the greater ease with which lizards could be resighted and caught on mango-1. The tree had a large hole containing over 50 *valencienni* eggs located only one meter above the ground, and females were often sighted near this hole or near a second egg hole 4 m above ground. (The poincianna was not known to contain an egg

hole and mango-2 was only known to have one, 6 m above ground.)

Of the 21 lizards caught on mango-1, 18 were resighted and 82% of the resightings found the females on that same mango. Of the five females caught on the poincianna, all were resighted, but only 22% of the resightings found the lizards on the poincianna. Of the eleven females caught on mango-2, only six were resighted and only 27% of these resightings occurred on that mango. By treating each resighting as an independent event, it is possible to test for heterogeneity in the data. The data almost show a significant tendency for lizards to be resighted more often on the tree of their capture than expected by chance ($\chi^2 = 8.13$; $0.05 < p < 0.10$). What is clear is that the females wander very widely. Only one female (60 mm) showed a marked tendency to remain on the tree of initial capture (mango-1): during a three month period, she was resighted seven times, all of them on mango-1. If data on her are removed from Table 3, no trend toward localized movement is apparent.

Movement from one tree to another can be rapid, taking place in less than two hours. Four cases of females moving between two of the three trees within a day are presented here. 1) On July 8 a 60 mm female was captured and released on mango-2. An hour and a half later, she was spotted at the base of the poincianna. The following day she was seen again on the poincianna, but two days later than this she was seen on mango-1. On July 14 she was again seen on mango-1. 2) On July 18 a 64 mm female was caught at 10:00 am on mango-1 and was resighted that afternoon at 4:15 at the base of mango-2, 29 m away. She presumably reached mango-2 by way of the poincianna. 3) On July 21 a 65 mm female was caught on the poincianna. The following day she was seen at the base of mango-1. 4) On July 24 a 61 mm female was caught on the poincianna and a day later was seen on mango-2.

It might be supposed that these rapid,

TABLE 3. THE NUMBER OF TIMES 37 FEMALES WERE RESIGHTED ON THREE TREES AS A FUNCTION OF THE TREE ON WHICH EACH WAS INITIALLY SIGHTED.

		M-2	POINCI	M-1	TOTAL
TREES FIRST CAUGHT ON (No. in paren- theses)	M-1 (21)	5	3	36	44
	Poinci (5)	2	2	5	9
	M-2 (11)	3	2	6	11
	TOTAL	10	9	47	

long-range movements are a response to the trauma of capture, but we doubt this for several reasons. 1) Similar movements have been recorded between resightings (where no capture was involved). For example, a 62 mm female was resighted on August 5 on the poincianna and two days later was resighted again on mango-1 (where it had originally been captured). Likewise, in the data above, the 60 mm female moved to a new tree on the day of capture, where she remained for at least a day, before moving on to the third tree. 2) By following individual unmarked females for several hours through binoculars, two such long-range movements were observed on the same trees in 1968, although no lizards were captured during that visit. 3) In the Maryfield study site, from which these data on movements come, lizards were caught only at ground level, so that a lizard could easily evade capture by remaining above 4 m yet the movements described involve moving to a height of 10 or more meters, crossing to a neighboring tree and sometimes returning to ground level. Within a half hour of capture, a female's behavior could not be distinguished from that of an uncaptured female; that is, a female recently captured rapidly returned to the slow, methodical search for food characteristic of the species. 4) Such long movements in response to capture have not been observed in highly territorial species (*A. lineatopus*, Rand, 1967b; *A. garmani*, Trivers, 1976; *A. grahami*, Trivers and Hicks, unpublished data).

In addition to the 64 resightings recorded in Table 3, five additional resightings were recorded in trees near (but not connected in the foliage to) mango-1. In one case a female was captured on mango-2 and resighted only once, nearly two months later, on a mango 30 m from mango-1. This may have been a permanent move. In the second case, a female moved a short distance (about 12 m) across open ground to a neighboring tree and returned to her tree of capture (mango-1) all within two weeks. The

third case involved a 66 mm female who was caught at the base of mango-2 on August 6. Ten days later she was resighted 56 m away on an avocado tree near mango-1. Thirteen days after this she was again seen on mango-2, but twelve days later (on September 10) she was seen back on the avocado tree (as she was on September 13). The female presumably moved from mango-2 onto the poincianna, from there onto mango-1 and then moved 10 m across open ground to some bushes which connected with the avocado tree. Although it is much more likely that the female crossed by way of the poincianna and mango-1 than that she moved 55 m across open ground, such inferential data have not been included in Table 3. (Similarly, one can safely infer presence on the poincianna when a lizard is sighted on mango-1 and then on mango-2, or vice-versa, but five such inferences were not included in Table 3).

Even these examples do not give an adequate picture of *valencienni* female movements. Observations of female movements within a given tree indicate that all females spotted low on a tree soon move high into the foliage. Observations of the same female on successive days reveal no tendency for a female to emerge from the same part of the foliage nor to return to the same part. Although it is likely that more detailed data will reveal some localization, it is clear that the overlap of female home ranges within a tree, or within contiguous trees, is enormous.

The three trees also contained at least 12 adult males. This is certainly a serious underestimate, since many unmarked adult males were seen but never captured, primarily because males stayed considerably higher in the trees than did the females. Based on several lines of evidence reviewed in the "Sex Ratio" section, we estimate that the trees contained at least 25 adult males. Of the 12 actually caught, eight were captured on or before August 6, but only one of these was resighted, so that almost nothing is

known about these males. It is clear, however, that even if males defended nonoverlapping territories, no female would live exclusively within one male's territory and most females would wander (in the space of about two weeks) through virtually every male territory. In the space of a single day a female would be expected to encounter at least five adult males.

In other Jamaican *Anolis*, the larger size of the adult male is associated with a larger territory or home range than seen in the adult female. In *A. valencienni*, we may expect that this relationship will not hold. Females are not territorial, while males, as we shall see, are repelled by each other. Thus, females may wander more widely than do males.

In the summer of 1973, we had a sufficient number of resightings to test this possibility. Lizards were watched for six weeks. The maximum distance between resightings was calculated for each individual who was observed more than one time. Forty-seven adult females were resighted an average of 3.1 times each, while 30 adult males were resighted an average of 4.7 times. Although males were sighted more often than were females, their average maximum distance between resightings, 26.8 m, was slightly shorter than that for females, 28.7 m. If we imagine that each resighting contributed equally to the maximum distance (which is unlikely), then for each resighting, males moved 4.7 m, while females moved 7 m. What seems clear is that adult females move somewhat greater distances during six weeks time than do adult males. These data certainly include some examples of dispersal to new areas, but these instances are few. Most of the data described movements typically made during a period of two or three days wandering.

Individual *A. valencienni* take very unwillingly to the ground. They are slower on the ground than any other Jamaican anole and are found there less often. Like other Jamaican anoles, they descend to

the ground to feed, but we have never seen an individual move more than 3 m from the base of its tree in search of food. We have only twice seen individuals on the ground who were not feeding. One had fallen accidentally out of its tree, and the other was in the process of dispersing 22 m to a new tree. Data on 257 marked individuals indicates that some individuals do move as much as 35 m over ground to reach a new tree. Of the 257 marked individuals, 49 were recaptured and, of these, eight had dispersed across ground to new trees.

Comparing those who dispersed with those who did not shows that those who did not disperse grew more than those who did. Of the 41 individuals who did not disperse, 34 showed measurable increases in size (2 mm or more) in periods ranging from one half month to two months, whereas only two of the nine who dispersed showed significant increases in size in similar time periods ($p = 0.01$). The average growth rate for nondispersers was 2.34 mm/30 days and for dispersers it was 1.06 mm/30 days ($p = 0.001$).

When growth rate is plotted as a function of female size, it is seen that dispersing individuals tend to have lower growth rates for two reasons. Dispersing females tend to be larger and to show smaller growth rates for a given size. Neither effect is in itself significant.

Each effect could be explained as follows. Larger females may be less vulnerable to predation and able to traverse more quickly the open space. Females with low growth rates may be selected to take a greater risk in finding a new feeding area. Of course, females who have low growth rates and disperse, may do so because dispersal causes a subsequent low growth rate in a new and unfamiliar environment. But several lines of evidence support the former interpretation. 1) On August 18, 1969, Trivers predicted that either no. 76 or no. 134 or both would soon disperse, as neither had grown in more than a month. No. 134 was never

found again, but no. 76 was next seen 11 days later on a tree 24 m across open ground from its original one. 2) Four of the eight dispersals were off of one tree which supported a large population of which those remaining behind showed a lower than average growth rate (1.67 mm/30 days). Six dispersals went to a mango, which had been almost empty until dispersing individuals reached it. These facts suggest that the dispersers may be leaving overcrowded trees for less populated ones. 3) The only disperser caught at least two weeks after dispersing showed no significant growth while dispersing, but a 3 mm growth during the six weeks after dispersal.

COPULATORY BEHAVIOR

Female and male *valencienni* appear to copulate wherever they find themselves. We cannot think of a single place (other than inside holes) where we have seen *valencienni* without also seeing them copulate there. They copulate along the thin outer branches of a bush, anywhere along the trunk of a tree, facing up or down, one centimeter off the ground to 10 m up a tree. We have even seen them copulating on the outer leaves of a mango tree 6 m off the ground. There is no evidence that females exert choice over place of copulation, as they appear to in *A. garmani* in which individuals almost invariably copulate face down on the exposed trunk of a tree (Trivers, 1976).

The most striking feature of female copulatory behavior is that females will copulate with more than one male on the same day and with the same male (and different ones) on successive days. Since it is unlikely that females are producing eggs at a rate of two or more per day, sperm competition is expected to be an important determinant of male reproductive success in *valencienni*. The key fact—that females appear to copulate more than once per egg fertilized—is supported by a number of observations, summarized here.

In the summer of 1969 only four copulations were observed involving marked females. Two of the copulations were performed on the same day, by the same female, with two different males. The female was no. 85 (58 mm). She was watched continuously from 10:35 am to 1:15 pm on July 5. For two hours she searched for food at the base of her tree, often in the company of two other marked females. At 12:25 male no. 66 (71 mm) rushed down from a branch and caught no. 85 on a small branch, where they mated. Shortly thereafter, male no. 72 (75 mm) appeared. He dewlapped at the smaller male, no. 66, who jumped on to a neighboring branch and moved up into the foliage. Although male no. 72 and female no. 85 began moving toward each other, no. 72 suddenly jumped on to a nearby branch and moved rapidly up the tree. Within 15 minutes he returned to within 30 cm of no. 85, but at 1:05 male no. 95 (81 mm) rushed down the tree and caught no. 85. Male no. 72 crouched and dewlapped at no. 95 but then jumped out of the way. No. 95 and no. 85 copulated, for her the second copulation in 40 minutes.

During the July-August, 1973 visit to the Southfield study site a special effort was made to observe copulations, and 10 females were seen to copulate more than once, usually twice within a week and sometimes twice within 24 hours. 1) Female no. 171 (60 mm) copulated on July 27 first with male no. 78 (83 mm) and then with male no. 134 (84 mm) and on the following day again with male no. 134. The first copulation took place on one tree, and the next two on a pimento (*Pimenta officianalis*) separated from the first tree by open space. 2) Female no. 24 (57 mm) copulated with male no. 45 on July 27 and on the following day with male no. 165 (73 mm). The copulations took place on contiguous, small trees. 3) Female no. 151 (60 mm) copulated on July 21 with male no. 88 (76 mm) and the following day copulated again with the same male on the same tree. 4) Female

no. LF (68 mm) copulated three days apart on the same tree with the same male (no. 134: 84 mm). 5) Two females copulated four days apart with different males on nearby trees. 6) Three more females accounted for eight more copulations, each separated by between six and nine days from a neighboring copulation. 7) Finally, one 69 mm female copulated 14 days apart on different trees with different males. In all, there were 23 multiple copulations out of a sample of 50 copulations (in which the female was marked).

How is the size of the female associated with her tendency to recopulate? The frequency with which females seen to copulate once copulated additional times was plotted as a function of size of female. Above 59 mm females tended to recopulate *less* the larger they became. In addition, the larger a female becomes the greater the span of time separating recopulations. For example, the four recopulations performed within 24 hours of an earlier copulation were all performed by females 60 mm in size or smaller. Since it is very unlikely that a female matures an egg more often than once a week, these additional copulations should be unnecessary to the female. It is tempting to suggest that the smaller a female is the less control she has over whether she copulates. Data on the percentage of females who copulate at least once (as a function of size) make it unlikely that smaller females are maturing eggs faster than large females (see Figs. 2 and 3). If these data are correct, then sperm competition is expected to be more intense in small females while female choice is expected to be a more important determinant of male reproductive success for large females.

We have timed copulations in nature and in our female choice experiments (see below), and these show remarkable consistency, averaging about 2 minutes, rarely less than 1.5 minutes or more than 2.5 minutes. There is no relationship between size of the lizards and length of copulations.

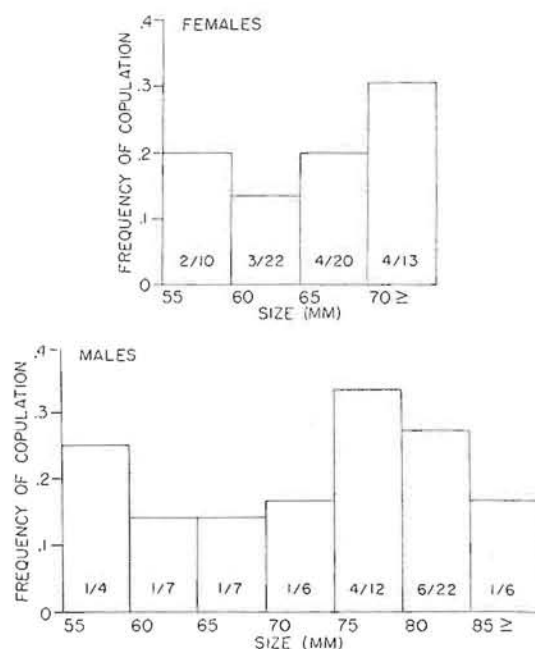


Figure 2. Frequency of copulation as a function of size (snout-vent length in mm) for females and males. These data were gathered during two weeks in June, 1971. Each fraction gives the number of copulations observed by members of the size class, divided by the number of individuals in that class.

Copulations sometimes appear to be somewhat aggressive. Males often bite females on the skinfold on the top of the neck. This may be done at the time of intromission, and the grip may be maintained during the entire copulation. Sometimes copulations are preceded by a very active stage, in which the male and female run a third of a meter or more while he attempts to cover her. These have the appearance of aggressive chases, in which the male adds an element of force to the persuasion.

Beyond this, in August 1973, Hicks observed an unusual pattern in one small adult male, which he entered in his notes under the title, "The bizarre behavior of Male no. 115, or rape and attempted forcible entry among the lower animals." No. 115 was a 57 mm male. On the 9th of August he copulated with a 50 mm female while they locked jaws. They con-

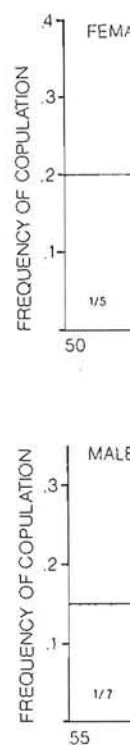


Figure 3. Frequency of copulation as a function of size (snout-vent length in mm) for females and males. These data were gathered during two weeks in June 1971. Each fraction gives the number of copulations observed by members of the size class, divided by the number of individuals in that class.

tinued to copulate. Hicks observed this behavior between the male and female. No. 115 was a 57 mm male. On the 9th of August he copulated with a 50 mm female while they locked jaws. They continued to copulate. Hicks observed this behavior between the male and female. No. 115 was a 57 mm male. On the 9th of August he copulated with a 50 mm female while they locked jaws. They continued to copulate.

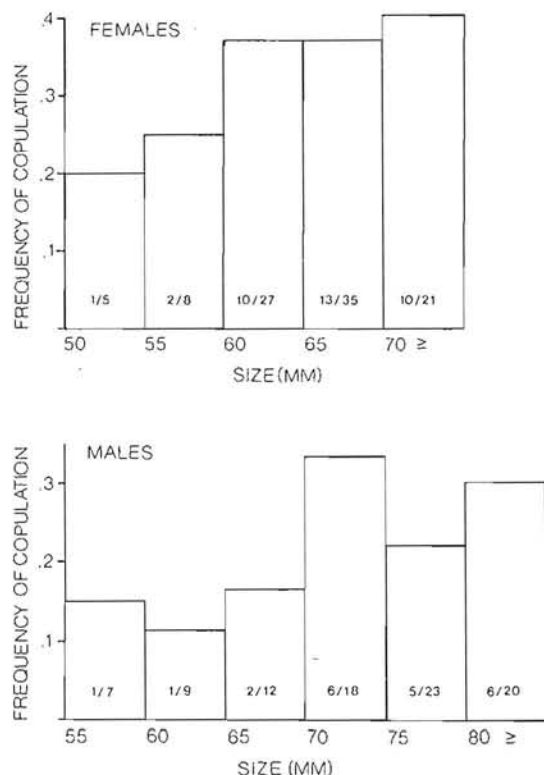


Figure 3. Frequency of copulation as a function of size (snout-vent length in mm) in females and males. Data for females include all copulations seen except those in June 1971. Data for males include all copulations except those seen in June 1971 and those seen while individual males were observed for three-hour periods.

tinued to lock jaws and fight after copulation was complete. Three days later, Hicks observed courting-fighting between the same male and a 66 mm female. No. 115 dewlapped at the female, but when he approached her closely, he would snap at her with his jaws. She chased him, he chased her. Chasing and dewlapping occurred around the trunk and up and down the tree. Finally, she half hid in a hole at the top of a dead branch. He approached within centimeters several times, once coming up right behind her. She did not move, and he seemed unable to do anything. Finally, he departed.

FEMALE CHOICE

In the highly territorial *A. garmani*, male courtship followed by female rejection has almost never been observed (Trivers, 1976). In *garmani*, females appear to choose the place to copulate and signal their accessibility by going to this place. In addition, the territorial system strongly reduces the opportunities for female choice. By contrast, female *valencienni* are exposed to many adult males each day and we have often observed male courtship and female rejection. In such a situation, a dewlapping male will typically approach a female who will move away from him. If he pursues her, she may run away from him, or she may dewlap back at him and attempt to keep her rear oriented away from him.

In the summer of 1973, we observed eleven cases of courtship and rejection involving marked *valencienni*. In four cases, the female who rejected the male was observed to copulate with that same male at some other time. In one case, she copulated with a male a day after rejecting him. In a second case, she copulated with a male two days after rejecting him. In a third case, a male courted the same female he had copulated with an hour and a half earlier, and she appeared disinterested in his second advance. Finally, a female ran from a courting male who had 16 days earlier copulated with her. These cases suggest that the female may be rejecting the time or the place as much as the male himself or that the female may succeed in rejecting some but not all of the advances of a particular male.

It seems certain that some cases of female rejection resulted because we were watching the lizards at very close quarters, but unambiguous cases of female rejection were also observed at considerable distances.

The most dramatic case of female avoidance took place on July 27, 1973. An 81 mm male was observed from 9:30 until 12:30 during which time he courted two females, both of whom appeared to reject

him. The male first courted a 61 mm female who ran from him. He did not pursue her. He then courted a 65 mm female who also ran from him. He chased the second female who continued to run from him. Finally, forced out on the end of a branch, she leapt from a height of 6 m to the ground in order to escape his attentions. He did not leap after her.

Our data on female rejection are too scanty to show whether there is any relationship between female size and tendency to reject, or between male size and tendency to be rejected, or between relative size of male and female and female tendency to reject.

To find out what criteria females use in choosing males, a series of experiments were run during the summer of 1976. At issue was whether females preferred males who differed by size or recent rate of growth. To ascertain the latter, nearly 300 lizards were captured between February and May. These individuals were then recaptured in June and July and used in choice experiments. Thus, for all individuals used size was known, and for many of these individuals, recent rate of growth to achieve that size was also known.

Initially the plan was to house each adult male in a 40-liter fish tank. All surfaces of the fish tank were painted opaque except one of the two large surfaces. The two tanks were placed next to each other, so that the males could not see each other, but so that a single female in a neighboring 80-liter fish tank could see each of the two males. The plan was then to measure the relative amount of time the female spent near each male. In actual fact, the fish tanks appeared far too confining on the individuals of both sexes. Most females spent the first hour trying to escape from the tank, moving from corner-to-corner. When they realized that they were not going to escape, they settled down in one corner and typically stayed there for dozens of minutes on end, sometimes for as long as two hours. It was difficult to convince

ourselves that females retained any interest in males under these conditions of confinement.

Two other experiments were attempted which were equally unsuccessful. In the first, females were released from a tin can onto a 3 m stick which separated at its end onto two sticks moving apart at a 90° angle. On each of these two sticks were tethered an adult male. Most females moved very slowly along the first 3 m, then chose which turn to make and ran very rapidly underneath the tethered male. Females often seemed to choose the smaller or less active of the two males, as if considering the male only as an obstacle to her own escape.

In the other kind of experiment, a series of eight small bushes were arranged in a row so that the vegetation of each bush connected its neighbors. On several of the bushes we tethered a single adult male per bush. In this experiment, females were provided a more natural and safe environment within which to choose a male. None of the females chose any of the tethered males. Most easily avoided them, and the males were rarely able to act in a natural way. Most moved as far as the tether would permit and strained against it. Some lost their grip on the substratum and hung from their tether. These had to be placed back on the bushes. In short, the females were exposed to the novel opportunity of meeting a series of restrained males, but this was of no use in discerning female choice.

In order to gain some value from our investment in capturing and recapturing the lizards, 108 experiments were run of the following sort. A female was released onto a bush which was placed in a large cleared area. Five minutes later an adult male was released onto the same bush. The two were permitted to remain together for an hour, or until they copulated, whichever came first. These experiments produced 36 copulations. It was clear from the behavior of the lizards that these experiments did not necessarily

females retained any under these conditions

periments were attempted equally unsuccessful. In were released from a tin k which separated at its s moving apart at a 90° these two sticks were male. Most females y along the first 3 m, turn to make and ran nderneath the tethered en seemed to choose s active of the two rring the male only as own escape.

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measure a female choice alone. Since the bush on which the lizards found themselves was isolated from neighboring vegetation, the female was reluctant to leave the bush, and the male had, in effect, a partly imprisoned female to court. Females often resisted the advances of males by moving away from them, by squirreling behind a limb so as to be out of sight, and by running rapidly when pursued, but females only rarely left the bushes under male duress. Larger males copulated significantly more often than smaller males, and larger females copulated more often than smaller females. Indeed, frequency of copulation for individuals of both sex varied as a function of size in the same way as observed in nature (Figs. 2, 3). The data relating size to frequency of copulation are as follows. For males ≤ 64 mm, 0.17; for successively larger 5 mm categories: 0.25, 0.31, 0.36, 0.38, and 0.42. For females ≤ 59 mm, 0.24; for successively longer 5 mm categories: 0.30, 0.37, 0.38, and 0.40.

Most copulations took place in the second half-hour of the experiment, but there was considerable variation. This allowed us to see whether size of the male, size of the female, or relative size of the two had any influence on the time elapsed until copulation. Relative size had no effect, but larger males copulated significantly quicker and larger females copulated quicker, though not significantly so (see Fig. 4). These data do not support the possibility that relatively larger males were forcing copulations. Instead, larger females appear more willing to copulate and do so more often, while the same is true of males.

For those wishing to pursue the problem, two suggestions are made. One is to build a large natural enclosure into which are released a number of adults of both sexes. A cage 5 m tall, 4 m wide, and 2 m deep enclosing small trees and bushes might permit a population of 10 or 20 adults to be observed simultaneously. Measurements could be taken of behaviors that correlate with female rejection

in order to see whether male characteristics can be correlated with these attempts at rejections. This kind of arrangement would have the virtue of enclosing the adults in a natural setting, but would have the disadvantage that females are not exposed to clear, binary choices. Thus it would be preferable to house adult females in naturalistic cages until their behavior had settled down and then to place two contiguous male cages next to the female cage for a period of time such as an hour, to see if the female will actively demonstrate a preference for remaining near one of the two males. Her behavior can be monitored to see whether this choice represents avoidance of the one male or choice of the other.

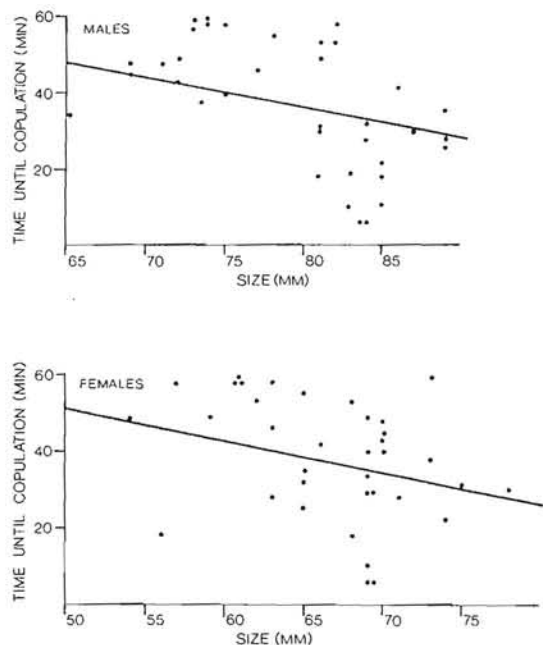


Figure 4. Time until copulations (minutes) as a function of size (snout-vent length in mm) for males and females during the mating experiments of 1976. The regression line fitting the male points is $y = 97.02 - 0.754x$ which yields an r of 0.397 with 35 degrees of freedom ($p < 0.05$). The regression fitting the female points is $y = 94.12 - 0.8454x$, $r = 0.302$ with 35 degrees of freedom ($0.05 < p < 0.10$).

THE USE OF THE FEMALE DEWLAP

It seems incongruous that female *valencienni* should possess a dewlap. The dewlap is normally found only on the more aggressive sex, i.e., on males, yet female *valencienni* are far less aggressive than female *grahami*, *garmani*, and *lineatopus*, all of whom lack the dewlap. Furthermore, female *valencienni* rarely use their dewlaps (in contrast to males of their own and other species). To resolve this anomaly, a special effort was made in the summer of 1969 to record all cases in which females dewlapped.

In addition to the case described under "Feeding Behavior," we twice observed a female dewlapping back at a male *valencienni* who approached the female closely. Both times the female was as large or larger than the male, and in both cases the male moved off without copulating. Except for three possible cases of a female dewlapping at another female (see "Female-Female Interactions"), all other observations show females dewlapping at members of other species. Females were observed three times to dewlap at adult male *A. grahami*, two of whom appeared to be courting the females; that is, the male *grahami* were dewlapping while approaching the female *valencienni*. In addition, female *valencienni* were observed to dewlap at 1) an adult male *lineatopus* who was about 30 cm away; at 2) a small female *grahami* who was centimeters away and who leapt over the dewlapping *valencienni* and ran away; and at 3) one of us when he approached the female to within a distance of one meter to photograph her.

These scanty observations do not permit firm conclusions, but it appears that females primarily employ their dewlap to discourage courting males, of their own and closely related species.

MALE-MALE INTERACTIONS

A male is rarely seen in the presence of another male, but when two are seen to-

gether, they are always fighting, displaying aggressively, or one is trying to hide from the other. In contrast to fights in *A. lineatopus* (Rand, 1967; personal observation), *A. grahami* (personal observation) and *A. garmani* (Trivers, 1976), *valencienni* fights appear tame. Males commonly dewlap toward each other and then one male darkens in color and attempts to hide. Movements are slow and chasing is rare. Of nine fights observed in the summer of 1973 (all involving marked males), only one involved actual contact, namely jaw-locking. Of the approximately ten male-male encounters observed in previous visits, none involved any body contact.

Data from eight fights observed in 1973 were reviewed. In only one of the six fights in which the two males were within 4 mm of each other in size did the larger of the two win. In four fights, the smaller appeared victorious (as judged by which male darkened and attempted to hide), and in one the outcome was unclear. Rand (1967) has shown in *A. lineatopus* that when the smaller of two lizards wins a fight it is usually because the smaller is the territory holder and the larger is an intruder.

Although male no. 92 was 4 mm larger than male no. 45, he lost to no. 45 on two separate occasions (separated by a week) (see Fig. 5). Both fights took place within the home range of no. 45, while no. 92 commonly occupied a neighboring home range. Indeed, the only two days no. 92 was spotted within no. 45's home range were the days he was seen fighting with no. 45 (see Fig. 8). It is worth emphasizing, however, that no. 92 copulated in no. 45's home range *after* one of the fights (see Fig. 5, black dot almost touching triangle). (No. 92 was only seen to copulate once in his own home range.) This is consistent with other observations of male-male encounters: a fight does not usually result in the ouster of one of the two males; instead, one male retreats and hides, remaining in the same area to feed and, sometimes, to copulate.

Male no. 45 also appeared to vanquish

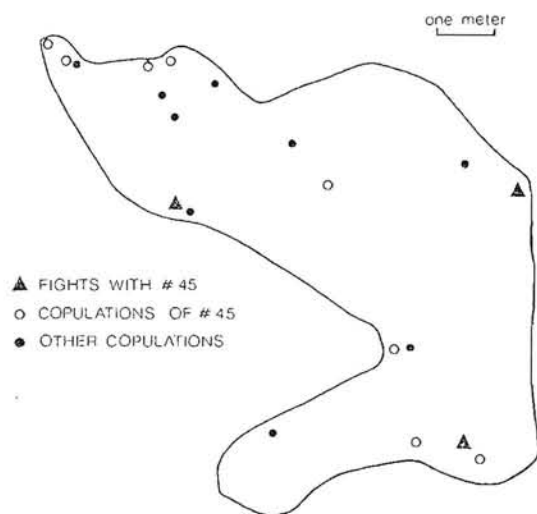


Figure 5. Male no. 45's territory during July and August, 1973. Pictured are the locations of fights (▲) and copulations of Male no. 45 (○), and copulations of other males within no. 45's territory (●).

another male who was larger than he was, no. 114 (79 mm). No. 114 was first seen in mid-July nearly 45 m from no. 45's home range; when sighted, no. 114 was copulating. No. 114 was next seen on August 10 in male no. 45's home range; he was seen there August 11 and 12 also but not seen anywhere afterwards. On August 11 he appeared to lose a long fight, involving jaw-locking, to male no. 45. Note that all three of no. 45's fights occurred at the edges of his home range (Fig. 5).

For the two other fights in which a smaller male appeared to vanquish a larger one, the relevant data are even less detailed. In both cases, the loser was seen only once, namely on the day of the fight. By contrast, one winner (male no. 172) was seen on seven different days on a set of eight neighboring trees. The second winner (male no. 107) was seen on eleven different days on two sets of trees. In both cases, the evidence suggests that the loser was either an outsider or sufficiently subordinate to be rarely sighted. Given the frequency with which many small males are resighted, we lean toward the former interpretation.

MALE HOME RANGE OVERLAP

In sharp contrast to more sexually dimorphic Jamaican anoles (*A. garmani*, Trivers, 1976; *A. lineatopus*, Rand, 1976; *A. grahami*, Trivers and Hicks, unpublished data), male home range overlap in *A. valencienni* is substantial. No male in either study area was known to occupy an exclusive area and several males were commonly seen within any one male's home range. To illustrate the extent of the overlap, we present detailed data on the home ranges of two males, one from each study area.

The Home Range of Male No. 72 (74 mm). Between June 25 and July 12 (1969) male no. 72 was seen eleven separate times on one of two connected small trees in the Maryfield study site. These two trees were part of a clump of four small connected trees. On six days, no. 72 was watched for at least an hour and seen to travel through a portion of one, or both, trees. On June 26 he copulated within his home range with female no. 46 (57 mm). Yet during this period of 17 days, five other adult males were seen within no. 72's home range and two of these males copulated with females resident within no. 72's home range.

Between July 1 and July 12 male no. 63 (73 mm) was seen seven times, each time on one of the two trees occupied also by male no. 72. On two of these occasions, no. 63 was watched for over two hours and each time he wandered throughout the two trees much as no. 72 did. On July 10 male no. 63 and male no. 72 encountered each other and no. 72 (although larger) appeared to be subordinate. Male no. 63 was about 4 m up on one of the trees when he spotted no. 72 on a stick 60 cm from the base of the tree. No. 63 dewlapped toward no. 72, then rushed down to a height of one meter and stood for several minutes looking in the direction of no. 72, who, meanwhile, had squirreled around on the stick so that the stick was between him and no. 63. No. 63 slowly started back up the tree dewlapping repeatedly. Fifteen minutes after

spotting no. 72, no. 63 had moved into the canopy out of sight, at which point no. 72 righted himself on the stick.

No. 63 was observed to court a female but was not seen to copulate before July 12. He alone of the males was seen after July 12 (although the trees were searched virtually daily). In the next two months no. 63 was seen six times on the same two trees, the last time of which he was copulating with an unmarked female.

Male no. 66 (71 mm) appeared to occupy one of the two trees contiguous with male no. 72's home range. That is, three of the four times male no. 66 was sighted, he was on this neighboring tree. The fourth time, he was seen on one of male no. 72's trees where he copulated with female no. 85 (58 mm) (see "Female Copulatory Behavior"). After the copulation, he walked onto a branch male no. 72 was sitting on. No. 72 dewlapped at him and no. 66 jumped to a neighboring branch and moved rapidly away.

Two males (63 mm and 81 mm) were seen only once each, and both were seen on one of the two trees that comprised no. 72's home range. The larger male copulated with female no. 85 on July 5 and appeared to frighten male no. 72 shortly afterwards (see "Copulatory Behavior").

In summary, for at least 16 days male no. 72 occupied a home range which he shared with a second male (no. 63) who, although smaller, appeared to be dominant over him. In addition, at least three other adult males were observed within this home range and two copulated within it. All interactions observed between the males were characterized by display and avoidance. Unfortunately, the difficulty of spotting *valencienni* in this study area does not permit us to infer anything from the absence of sightings after July 12. It is possible, for example, that after July 12 only male no. 63 remained within the two trees and that the high overlap observed prior to that day was merely temporary. Detailed data from the summer of 1973 render that an unlikely assumption, however. Throughout the

summer of 1973 the same degree of overlap was observed in all cases for which there were sufficient observations to plot home ranges. An example is the home range of male no. 45.

The Home Range of Male No. 45. Data on male no. 45 give a detailed picture of the overlap in male home ranges and the partly correlated overlap in access to females. Male no. 45 (77 mm) occupied a large home range containing nine small trees and many bushes and covering an area of about 25 square m (see Fig. 5, 6). First captured on July 7, 1973, he was watched throughout the summer visit to the Southfield study area and was last seen on August 18. He was seen on 16 different days and on five of these days his movements were followed for about three hours each day. On three of these three-hour watches, he wandered throughout about a third of his home range. On the other two three-hour watches, he restricted his movements to a corner of the home range.

Twenty-six adult females were seen at one time or another within no. 45's home

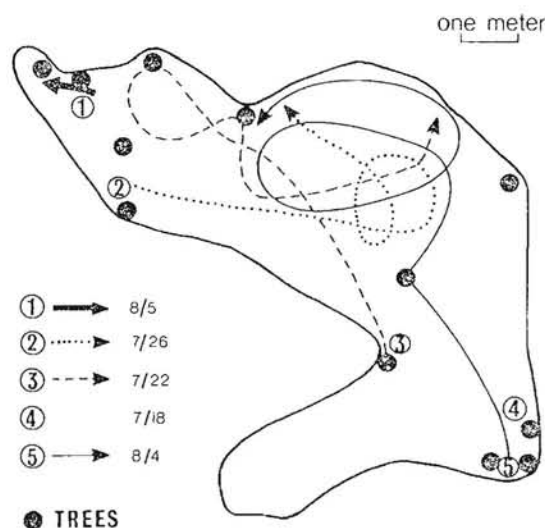


Figure 6. Male no. 45's movements in his territory during five days in which he was observed continuously each day. • = the trees in his territory. Note that in three days he travelled widely, while in two he moved little.

range. These females were sighted a total of 51 times within no. 45's home range and a total of 42 times outside his home range. Sixteen of the 26 females were seen to copulate, and they were seen to copulate a total of 24 times (only seven of which took place outside of no. 45's home range). Male no. 45 accounted for eight of these copulations, each with a different female (see Fig. 5). He twice copulated with two females on the same day. He copulated on five of the seven days in which his movements were followed for three hours. Indeed, six of his eight copulations were seen during these 21 hours of observation.

Five of the females with whom no. 45 copulated also copulated with other males. The five copulated seven other times with a total of five different males. Of the 16 copulations with males other than no. 45, nine took place inside no. 45's home range. A comparison of the location of these nine copulations with the location of no. 45's eight copulations shows broad overlap (Fig. 5).

The degree to which females seen in a male's territory will also be seen outside his territory is shown in Figure 7. The home ranges of six females, who were seen at least once in male no. 45's territory and were sighted at least five times in total, are shown in Figure 7. As we can see, even if male no. 45 maintained exclusive sexual access to these females when they were in his territory, which he does not, they would still wander widely outside of his territory.

The variety of copulations a male may enjoy in a short period of time are suggested by observations of male no. 134 (see Table 4).

Male no. 45 shared his home range with at least ten other adult males. The overlap was considerable. For example, on August 10 four adult males (in addition to no. 45 himself) were seen within no. 45's home range. The day before, three females copulated within no. 45's home range, only one of them with no. 45. The males overlapping with male no.

45 can be divided into four categories. Three were only sighted once or twice (if twice, both sightings were within no. 45's home range). Of those sighted more than twice, two lived entirely within no. 45's home range, two lived more within no. 45's home range than outside it, and three lived primarily outside no. 45's home range (see Fig. 8).

Males completely within no. 45's home range: 1) No. 96 (72 mm) was spotted on four different days on six separate trees within no. 45's home range. No. 96 copulated with three females (on different days) only one of whom was seen to copulate with no. 45. 2) No. 115 (57 mm) was spotted on ten different days and on four different trees, all within no. 45's home range. No. 115 copulated once with a female, and she was not seen to copulate with no. 45.

Males primarily within no. 45's home range: 1) No. 164 (73 mm) was seen eight different times, of which five sightings were within no. 45's home range and three were at its edge. He copulated three times—all of them in no. 45's home range. Only one of the females was also seen to copulate with no. 45. He fought once with male no. 115 (57 mm). 2) Male no. 114 (79 mm) was seen on three successive days in no. 45's home range (August 10–12). He was not observed to copulate there. The only other time he

TABLE 4. HISTORY OF COPULATIONS FOR MALE NO. 134 (84 MM) IN SUMMER, 1973.*

	DATE	FEMALE	SIZE OF FEMALE (mm)
1.	7/22	LF	68
2.	7/25	LF	68
3.	7/26	157	70
4.	7/27	171†	60
5.	7/27	97	67
6.	7/28	171	60
7.	7/29	182	70
8.	8/5	194	62

*All took place in the same pimienta tree.

†No. 171 copulated earlier that day with male no. 78 on a nearby achee tree.

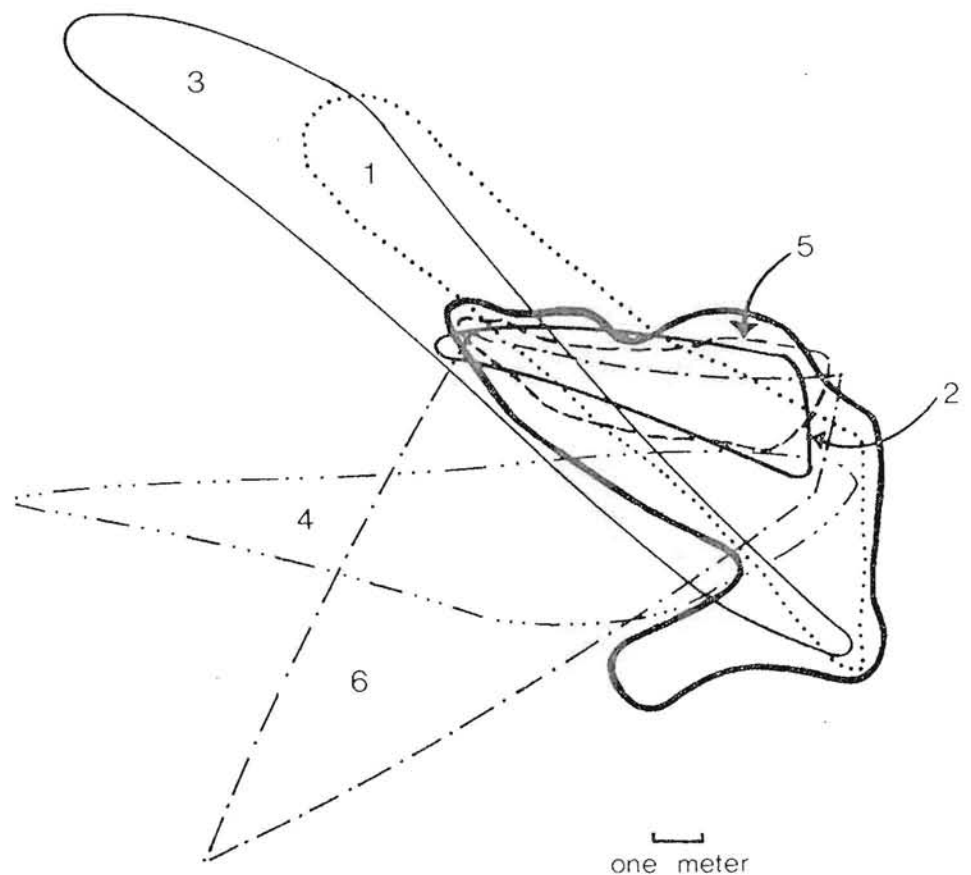


Figure 7. The overlap of Male no. 45's territory is pictured with the home ranges of six adult females observed at least once in his territory, for each of which there were at least five sightings. The mean number of sightings per female was 8.2.

was seen was nearly a month earlier, 43 m away, at which time he was seen copulating.

In summary, it is clear that adult males overlap with each other tremendously, both in space occupied (Fig. 8) and in access to members of the opposite sex (Figs. 5, 7). Commonly several males copulate with the same female and several males copulate with different females in the same space. Fights are short, mild and lead to withdrawal and hiding. Some males, at least, are highly variable in their movements, during some periods moving considerable dis-

tances, during others remaining mostly in one place (Fig. 6). Male-male competition must take an interesting and complex form in *A. valencienni* that would repay careful study.

FEMALE AGGRESSIVENESS IN A SEARCHING SPECIES

Why are female *valencienni* not aggressive? Imagine the contrary. Imagine that each female defends a territory within which to feed. Assume a female completes the search of her territory for food

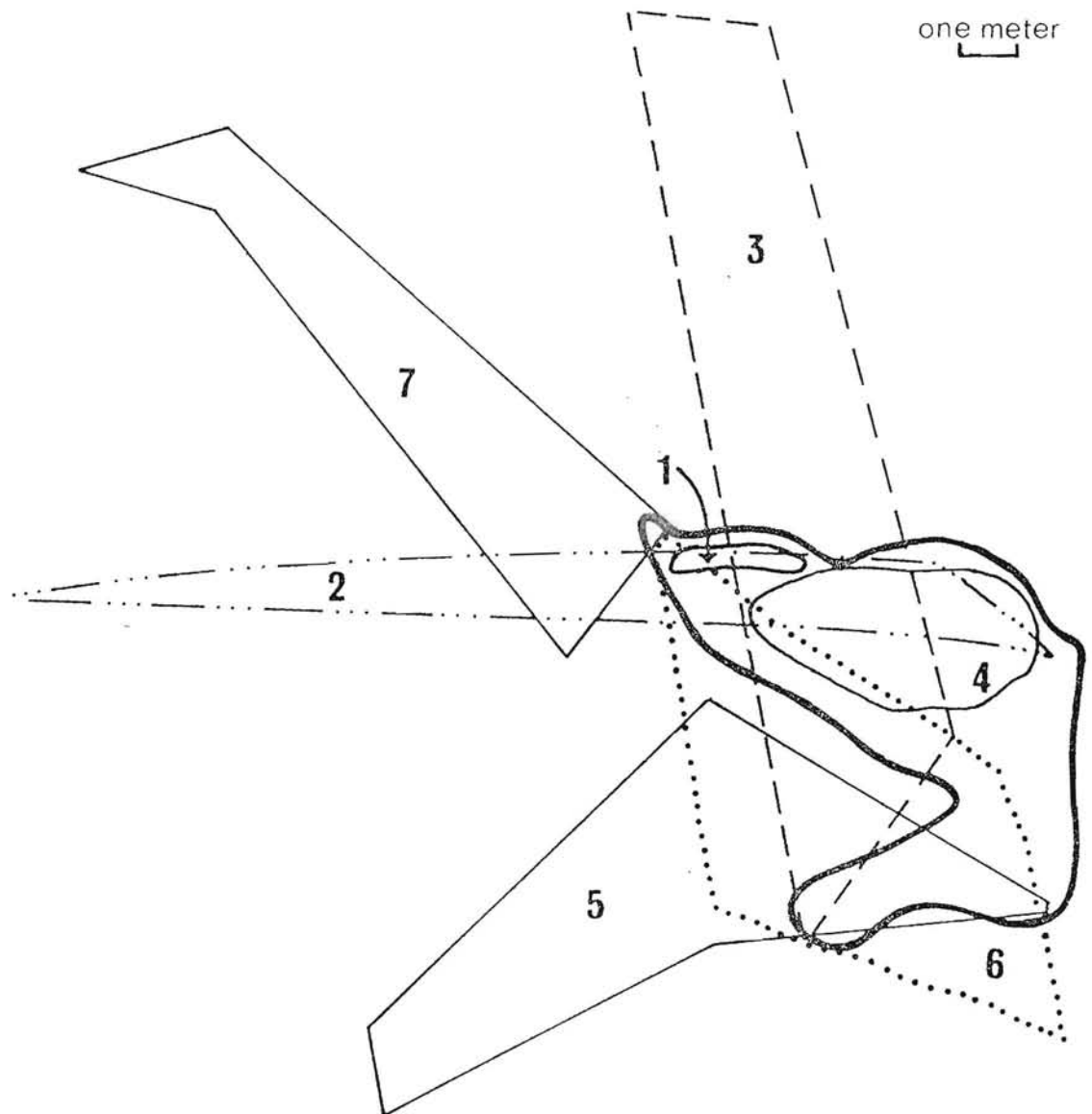


Figure 8. The overlap of Male no. 45's territory with those of seven other adult males seen at least once in his territory and sighted altogether more than two times. The mean number of sightings for these seven males is 6.7.

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in less than a day. She must now decide whether to research her own territory or to move into a neighbor's. To predict her behavior we should know the answers to three questions. 1) At what rate do resources within her territory renew themselves? 2) Have her neighbors completed

the search of their own territories? 3) Is she more likely to find items her neighbors missed or items she herself missed? What is the long-term variance in goodness of territory?

If resources renew themselves slowly (for example, overnight) then there will

be no strong incentive for a female to research her own territory. Indeed, under such conditions, there should be a stronger incentive to search her neighbors' territories, since 1) she knows she has completely searched her own territory and she does not know that her neighbors' territories have also been completely searched and since 2) it is more likely that she will find items her neighbors have overlooked than that she will find items she herself has overlooked (on the assumption that females show individual variability in searching behavior, e.g., in specific search images). Since the same arguments apply to other females, there is, under these assumptions, no incentive for females to guard territories once they have been searched.

FEEDING BEHAVIOR AND CRYPTICITY

For a series of reasons that stem from its feeding adaptation *valencienni* has (we believe) been strongly selected for crypticity. The fact that it is a searcher, means that individuals must constantly be on the move, thereby becoming more visible to predators. At the same time, however, they have not been selected for speed once they sight prey, so they are more vulnerable once sighted by a predator. In addition, they search by scanning very closely the surface centimeters in front of them. This narrows their field of vision considerably compared to perching lizards, making it less likely they will sight a predator early.

One could also argue that differential visibility toward potential prey may have selected for some of *valencienni*'s crypticity. If true, this should only apply to the face and neck and not to the dorsal surface of legs. It would also require that potential prey be able to respond to *valencienni* at distances of centimeters and this is not unlikely. The use of crypticity in social encounters is discussed below.

Our only actual data on predation are four observations of small *valencienni*

being eaten by other anoles. Two were hatchlings at Mayfield in August 1968, eaten apparently within an hour of hatching, one by an adult male *A. lineatopus*, the second by an adult male *A. grahami*. The others were eaten at Southfield 1) on July 21, 1973 by an 82 mm male *valencienni* and 2) on August 8, 1973 by a 56 mm male *valencienni*. In the first case of cannibalism the eaten lizard had been marked and was probably a 43 mm male. It was eaten head first. The second was unmarked and was eaten tail first, the head being bitten off without being swallowed.

COMMUNAL EGGLAYING, SEASONAL REPRODUCTION, AND PREDATION ON YOUNG

Anolis valencienni females lay eggs communally (Rand, 1976a). In Maryfield we found five communal egg deposits and in Southfield, one. These were located in holes in tree trunks from ground level to 6 m up. The number of eggs ranged from only two to well over 30. The largest was in a large hole one meter up the trunk of a mango tree. Although females often frequented this hole, and a mirror was arranged to view their activities inside the hole, egg laying was never observed. (Feeding attempts within the hole were observed, but never directed against the eggs.)

Anolis valencienni appears to breed seasonally. Although all five egg deposits contained eggs during the summertime, none contained eggs in late December and early January. Since the only egg hatched in captivity required 53 days from laying to hatching (Underwood and Williams, 1959), we conclude that no eggs are laid during at least November, December, and early January, but the periods of observation have been short enough so that copulations could have been overlooked by chance. (Except for seven days in December 1969, and eleven days in December 1973 to Jan-

uary 1974, *valencienni* has only been studied in the summertime). However, in two different summers of work at Southfield (June 1971, and July and August 1973) copulations were observed at a rate of slightly more than one per day, so that, at the very least, frequency of copulation must be strongly reduced in wintertime.

The size distribution of lizards caught strongly suggests that there is a peak in lizards hatching in the late summer and fall and that very few hatch between January and March. Of 231 lizards caught in July and August of 1973 (at Southfield) only thirteen (5.7%) were under 35 mm in size, while of 72 lizards caught in the same study site in December 1973 to January 1974, eleven (15.3%) were under 35 mm. The small lizards caught in the summer were probably laid as eggs as early as the beginning of April. A. S. Rand (personal communication) collected over 50 *valencienni* eggs during November and early December, and all of these hatched by mid-December (they are all the hatchlings on which Figure 1 is based).

Casual observations suggest that predation on hatchling *valencienni* is heavy and that hatching may be synchronous (perhaps to swamp predators). During a one hour and 40 minutes period on August 5, 1969, four hatchlings emerged from the large egg hole three feet up a mango tree at Maryfield. The first emerged at 1:50 pm, was captured and died while being measured (male = 25 mm). The second was eaten by an adult male *A. grahami* who had just entered the hole seconds before. It took the male two and a half minutes to swallow the hatchling. The third emerged at 3:10 and slowly (in short bursts of running) made its way up to 3 m up the trunk. During its last burst of running it was spotted by an adult male *A. lineatopus*, who seized it and ate it head first, requiring again two and a half minutes to consume the lizard. The fourth emerged from the hole, rested for ten minutes, then passed by an adult female *grahami* (47 mm). She saw the

hatchling but ignored it. In the next 20 minutes the hatchling made its way up to about 5 m, after which it could no longer be seen. When last seen, it was higher on the tree than where the male *lineatopus* was perched. (The male *grahami* was out of sight high in the tree.)

The synchrony of emergence (and presumably hatching) is striking. Although the hole was searched daily (before and after August 5), no other hatchlings were seen. Between August 4 and August 6, about 20 eggs appear to have hatched in this one hole. On August 6 there were no more eggs stuck to the wall but the bottom of the hole was littered with opened eggs.

One other instance of predation was seen at Maryfield. On August 9 in a different part of the study area a 62 mm adult male *grahami* caught and ate head first a very small *valencienni* who was 1.3 m above the ground on the tip of a one centimeter thick twig. One case of cannibalism was observed at Southfield. On July 21, 1973, an 82 mm male *valencienni* ate a small marked *valencienni* head first (probably no. 95, a 43 mm male).

THE EVOLUTION OF SOCIAL BEHAVIOR AND SEXUAL DIMORPHISM IN *A. VALENCIENNI*

In summary, we argue that the unusual features of *A. valencienni* probably evolved in the following fashion. At some point, individuals switched from perching to searching as a means of acquiring food. Since this new source of food was only slowly renewable within the day, females were no longer selected to maintain exclusive feeding territories, but were instead selected to wander widely and to interact nonaggressively with other females. This new style of movement rendered individuals more vulnerable to predation, since they were now continuously on the go and preoccupied with searching the substratum. Hence they became unusually cryptic.

Once a system of female territoriality had broken down, males were selected to tolerate much greater degrees of territorial overlap. This is because 1) in their search for food, males were also selected to wander widely; 2) excluding all males from a territory no longer gave exclusive access to the females residing in that territory; 3) the individuals of both sexes were more difficult to detect, thus aggressive control more difficult to impose; and 4) females, in their choice of mating partners, may have placed less emphasis on large male size than when they were a perching species.

We must confess, however, that we are ignorant concerning the role that female choice plays in generating male behavior and male size. Certainly *A. valencienni* seems, among lizard species, unusually suited to intense female choice, but we have been unable to design the proper experiment for measuring female preference. What evidence exists suggests that females may prefer larger than average males, but not strongly so. We do not know why sexual dimorphism is reduced in *A. valencienni*. In particular, we cannot discern the relative roles of male-male competition and female choice. We have been unable to penetrate the system of male-male competition. Do males move frequently, relatively large distances? Or do they patrol key crossing points, as if to waylay caravans?

ACKNOWLEDGMENTS

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Ernest E. Williams, and the Milton Fund (Harvard).

DEDICATION (TRIVERS)

Ernest E. Williams took me to Jamaica in 1968. He was on a collecting expedition; I was the driver. We arrived in Kingston in the evening and drove in a blinding rainstorm to the Maryfield Guest House, a decaying English great house set on three acres. The beautiful old trees and well-tended garden attracted a big population of lizards.

We began our field work over breakfast on the veranda watching *Anolis lineatopus*. The males warmed themselves in the sun and then engaged in display and aggressive encounters as they reoccupied their territories. These bright, active, little lizards reminded one almost of puppies or kids, enjoying a little social play in the early morning hours.

Ernest soon drew my attention to a more sinister species, which seemed to hide in the background. This was *Anolis valencienni*, which moved in a very distinctive fashion. Structurally, it was sufficiently aberrant to have appeared in earlier classifications as a separate genus *Xiphocircus* (Underwood and Williams, 1959). Individuals of this species seemed unusually abundant at the Guest House, and since an *Anolis* of this type had not been studied, I soon concentrated on figuring out its social system.

Ernest impressed me very warmly on that trip to Jamaica. He traveled in a very calm, quiet, unpretentious style. When we filled out our immigration cards and were asked to state our occupation, my natural impulse was to jack up the description as high as I could. I expected Ernest to do likewise. Nothing less than "Alexander Agassiz Professor of Zoology at Harvard University" seemed appropriate to the occasion. Instead he wrote, "Teacher." Simple, unpretentious, and

when need be, nonspecific or ambiguous. He also seemed fearless in his travels through Jamaica, and I much respected him for this. He neither swaggered nor scraped, but held himself calmly at all times.

In taking me to Jamaica, Ernest introduced me to more than *A. valencienni*. I have now lived nearly five years in Jamaica. I am married to a Jamaican and have four children by her. I own an acre of land and have planted 250 trees, mostly fruit. I have studied the butterflies of Southfield and collected data on an interesting symbiosis between a carpenter ant and a membracid. The trees I have planted are now beginning to attract anoles, including *A. valencienni*, and I look forward to many more years of watching.

I dedicate this paper to Ernest E. Williams with affection and respect. He was my graduate advisor and well loved at the time. Those were good years, now warmly remembered. What he introduced me to has become an enduring part of my life.

LITERATURE CITED

- HICKS, R., AND JENSSEN, T. A. 1973. New Studies on a montane lizard of Jamaica, *Anolis reconditus*. *Breviora Mus. Comp. Zool.* No. 404, pp. 1-23.
- LYNN, W. G., AND C. GRANT. 1940. The herpetology of Jamaica. *Bulletin of the Institute of Jamaica. Science Series*, No. 1.
- RAND, A. S. 1967a. The ecological distribution of the anoline lizards around Kingston, Jamaica. *Breviora Mus. Comp. Zool.* No. 272, pp. 1-18.
- . 1967b. Ecology and social organization in the iguanid lizard *Anolis lineatopus*. *Proceedings of the United States National Museum* 122 No. 3595: 1-79.
- SCHOENER, T. W. 1970. Size patterns in West Indian *Anolis* lizards. III. Sexual dimorphism in relation to differential resource utilization and sexual selection. Manuscript pp. 1-113.
- . 1971. Theory of feeding strategies. *Ann. Rev. Ecol. Syst.*, 2: 369-404.
- SCHOENER, T. W., AND A. SCHOENER. 1971. Structural habitats of West Indian *Anolis* lizards. I. Lowland Jamaica. *Breviora Mus. Comp. Zool.* No. 368, pp. 1-24.
- TRIVERS, R. L. 1976. Sexual selection and resource-acquiring abilities in *Anolis garmani*. *Evolution*, 30: 253-269.
- UNDERWOOD, G., AND E. E. WILLIAMS. 1959. The anoline lizards of Jamaica. Kingston, The Institute of Jamaica.