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SEXUAL SELECTION AND RESOURCE-ACCRUING ABILITIES IN *ANOLIS GARMANI*

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In 1969, I began a field study of the social behavior of two Jamaican lizards, *Anolis garmani* and *A. valencienni*. This study has developed into an attempt to measure how sexual selection has molded adult dimorphism in size and associated dimorphism in growth rates, mortality rates, and in sexual and aggressive behavior. Preliminary data for *Anolis garmani* were presented as part of a general theory for the evolution of sex differences (Trivers, 1972). Meanwhile, several important theoretical advances (Maynard Smith, 1971; Williams, 1975; Zahavi, 1975) have convinced me that female choice is a central factor molding male sexual dimorphism and systems of male-male competition. The data presented here for *Anolis garmani* tend to support the view that those males who do most of the mating are those who have tended to demonstrate the superiority of their non sex-linked genes.

METHODS

Social behavior was studied for eight months (between July, 1969 and January, 1972) during seven separate visits to a study area which eventually comprised 9 acres in Southfield, St. Elizabeth, Jamaica. (The study area was expanded during the 2nd visit and again during the 3rd; the last visit concentrated on only a portion of the study area.) The study area consisted of scattered fruit trees typical of Jamaica: *Mangifera indica*, *Blighia sapida*, *Pimenta officinalis*, *Cocos nucifera*, *Guazuma ulmifolia*, *Bursera simaruba* and three species of *Annona*, among others. During each visit to the study area an effort was made to catch all resident adults.

The lizards were captured, sexed, measured, marked and released where captured, usually within five minutes of capture. Toe-clipping gave a unique permanent mark to each individual, and, in addition, a number was painted on each individual's back for short-term identification without recapture. To reduce error in measurement, each individual was stretched by hand while being measured. A number of individuals were also weighed. Unless otherwise indicated, all measurements are snout-vent lengths given in mm.

During each visit the sighting of any marked lizard was recorded, as well as its behavior. Few lizards were observed for any length of time unless they were engaged in display or social behavior. A particular effort was made to spot copulating pairs. If one or both partners were unmarked the copulation was interrupted to catch the unmarked individuals. This was almost invariably successful in the case of males but often unsuccessful in the case of females (see below).

SEXUAL DIMORPHISM

Dissections of males and females in the collection of the Museum of Comparative Zoology, Harvard University, indicate that males reach sexual maturity at about 85 mm in size (based on the presence of seminiferous tubules), and females at about 70 mm in size (based on the presence of an egg). This accords well with field observations in which the smallest female seen copulating was 70 mm long, and the smallest male, 87 mm. The mean size of all adult males captured in the study area was 109.7 mm, and that of adult females, 83.5 mm. An analysis of weight vs. snout-

vent lengths showed, as expected, that weights varied as the cube of snout-vent lengths. Adult males weigh typically, therefore, 2.25 times as much as adult females. This degree of sexual dimorphism is unusual among anoles as large as or larger than *A. garmani*, but it is typical of several other Jamaican anoles.

Males also have proportionally larger jaws than females. Measuring the entire length of the lower jaw of animals in the field showed that males had jaws 1.06 times the size of jaws of females whose snout-vent length was identical. In addition, males have several external structures absent or poorly developed in females: a bright yellow dewlap used in display, a series of spikes along the back resembling the teeth of a saw (Fig. 1), and a stouter, more muscular neck and body.

I assume that males and females hatch at about the same size, and that the adult dimorphism is achieved by the male's faster growth rate, as documented below. In a small sample of the closely related and equally sized dimorphic *Anolis lineatopus*, hatchling males do not differ in size from hatchling females (A. S. Rand, unpublished data); and the same is true of a large sample of hatchling *A. valencienni* in the Museum of Comparative Zoology (Harvard) collection (Trivers and Hicks, in preparation). *Valencienni* is a closely related Jamaican anole in which adult males are 1.65 times as heavy as adult females. Both *lineatopus* and *valencienni* show the same sexual dimorphism in growth rates documented below for *garmani* (Rand, unpublished data; Trivers and Hicks, in preparation).

THE MEASUREMENT OF REPRODUCTIVE SUCCESS

Anolis lizards are ideally suited to the measurement of reproductive success because only a single egg matures at a time and females typically copulate only once in order to fertilize that egg (Crews, 1973). Thus, reproductive success can be mea-

sured by measuring frequency of copulation.

In all *Anolis* studied, females lay a single egg at a time (Smith, Sinelnik, Fawcett and Jones, 1973). I never saw a *garmani* female lay an egg, but dissection of ten females accidentally killed in the study area always showed one mature egg or none, although large females often showed one or two smaller eggs in earlier stages of development. For Puerto Rican anoles, each female caught copulating by George Gorman (personal communication) had one mature oviducal egg.

I assume that females typically copulate once in order to fertilize each egg. If a pair is permitted to copulate undisturbed ($N \cong 50$), the female (with one exception) is not seen to copulate again for at least one month. But if the copulation is interrupted (in order to catch one or both lizards), the female may copulate within a day with the same male. By interrupting successive copulations, I observed the same couple copulating as often as four times in one week. Once permitted an undisturbed copulation, however, at least a month elapsed before such a female was seen copulating again. (Only the first copulation of these interrupted series is counted in the data below.) These facts suggest that females copulate infrequently, presumably to fertilize an egg, and that fertilization inhibits further copulation within an ovulatory cycle (see Crews, 1973). The exceptional case referred to above concerns a large female (91 mm) who copulated eight days apart on the same tree, first with the territory holder, then with an interloper (the fourth copulation in Table 2) at a height of nearly 50 feet. (Both copulations are included in the data below.) The apparent tendency of *garmani* females to copulate once per egg contrasts sharply with the non-territorial female *valencienni* who often copulate more than once on the same day, usually with different males (Trivers and Hicks, in preparation).

Sperm storage has been demonstrated in *Anolis* (Fox, 1963) but if female *garmani*



FIG. 1. Male and female *A. garmani* engaged in a typical copulation face down four feet up the trunk of a coconut tree (photo: Joseph K. Long).

store sperm I assume they do so without regard to their own size (or to the size of the copulating male). If females copulate more than once to fertilize a single egg, I assume they do not do so as a function of their size (or that of the male). Finally, I assume that length of copulation is independent of the sizes of the participants.

Biases in sighting copulations are thought to be minimal for the following reasons. (1) *Garmani* appears to be unusual among lizards (and other animals) in that individuals choose highly conspicuous places in which to copulate. Although over $\frac{1}{2}$ of over 3000 observations of the lizards showed them to be in foliage where they are difficult to see, only one of 90 copulations took place in the foliage, and it was a homosexual copulation. (It and a second homosexual copulation are excluded from the data that follow.) All heterosexual copulations took place on highly

visible perches, the pair almost invariably facing down on the lower exposed trunk of a tree (Fig. 1). (2) In the congeneric Jamaican *A. valencienni*, by contrast, whose normal perch heights parallel those of *garmani* (Rand, 1967; Schoener and Schoener, 1971), copulations take place from the ground to the outer leaves of the foliage with no preferred orientation, facing up or down, and do not differ in height or visibility from typical non-copulating perches (Trivers and Hicks, in preparation). (3) *Garmani* copulations appear to last a considerable time. Only one was observed from beginning to end and it lasted 25 minutes. The median length of time of copulations first observed when already under way was about 10 minutes. Couples were extremely reluctant to disengage, even when approached, so that couples were sometimes noosed while still copulating. Individuals who had frequently been recaptured, however, would sometimes disengage when sighted or approached. Frequently recaptured individuals tend to be the largest, so the bias, if any, would tend to make copulations of large animals less frequently observed. (4) Once sighted, the male of a copulating pair was almost invariably marked, or, if not, was captured during or shortly after the copulation. Females were sometimes unmarked and remain uncaptured. The magnitude of this potential bias can be seen by comparing the number of marked females seen copulating (Table 1). The first, fourth and seventh samples are nearly unbiased in this respect and they differ in no obvious way from the other samples, so that the bias introduced, if any, appears to be trivial. (5) Smaller adult males (or females) copulate on perches which do not differ in either height or visibility from perches on which larger individuals copulate. (6) The bright green copulating pairs are so easy to spot against the brown trunks of trees that it is unlikely that many pairs were overlooked while a tree was being searched. All trees were searched regularly and thoroughly each day, but

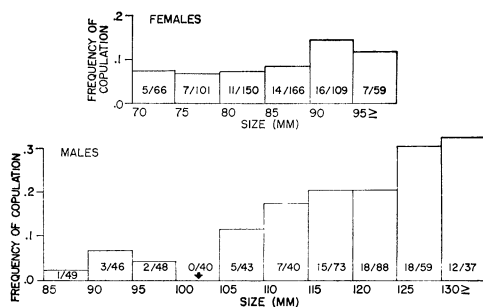


FIG. 2. Reproductive success in males and females as a function of size. Reproductive success is measured by the number of copulations observed per number of individuals (male or female) in each non-overlapping 5 mm size category. Data from all visits combined.

most work was done between 7:30 AM and 3:00 PM. In these data, there is no relationship between the time of day and the sizes of those who are copulating.

SIZE AND REPRODUCTIVE SUCCESS

Copulations in which one or both individuals were marked were recorded and the sizes of those seen copulating at least once were compared with the sizes of those

adults never seen copulating for five separate samples (Table 1; data from the first two visits were combined to form the first sample). In each sample the mean size of copulating males is significantly larger ($P < .05$) than the mean size of adult males never seen copulating. For each sample, the mean size of copulating females is also larger than the mean size of non-copulating females, but in only the last sample is this difference significant ($P < .05$). Ranking females by size, however, shows a significant tendency in all but the third sample for larger females to copulate more often than would be expected by chance (Kolmogorov-Smirnoff one-sample test; $P < .05$).

Taking all the data together and comparing the frequency of copulation for each non-overlapping 5 mm size category (Fig. 2), the tendency for females to copulate more often with increasing adult size is significant (t test; $P < .05$), and the tendency for males to copulate more often with increasing adult size is *significantly stronger* than that tendency for females (t test; $P < .05$). A male 110 mm or larger, for example, is 4.8 times more likely

TABLE 1. Mean size (\bar{x}) of individuals seen copulating (and standard error of the mean, s_x) compared to mean size of individuals never seen copulating, analysed by sex, for six separate samples. The first sample consists of data from the first two visits combined; all other samples represent separate visits.

	Summer '69 and Winter '69-70			Spring '70			Summer '70		
	\bar{x}	s_x	N	\bar{x}	s_x	N	\bar{x}	s_x	N
Copulating males	117.5	0.8	6	114.8	2.5	23	119.5	2.7	14
Non-copulating males	100.0	5.4	42	106.9	1.2	77	108.4	1.3	79
Copulating females	83.4	3.5	5	79.6	7.0	16	82.1	2.8	9
Non-copulating females	78.8	0.8	55	78.7	2.6	102	81.7	0.8	104
	Winter '70-71			Spring '71			Winter '71-72		
	\bar{x}	s_x	N	\bar{x}	s_x	N	\bar{x}	s_x	N
Copulating males	122.2	2.5	18	124.0	3.5	11	126.0	3.5	7
Non-copulating males	112.3	1.3	134	112.1	1.6	89	105.6	3.0	23
Copulating females	88.8	1.5	17	91.3	1.0	6	86.7	2.2	7
Non-copulating females	86.1	0.5	177	87.3	0.6	120	85.0	1.1	33

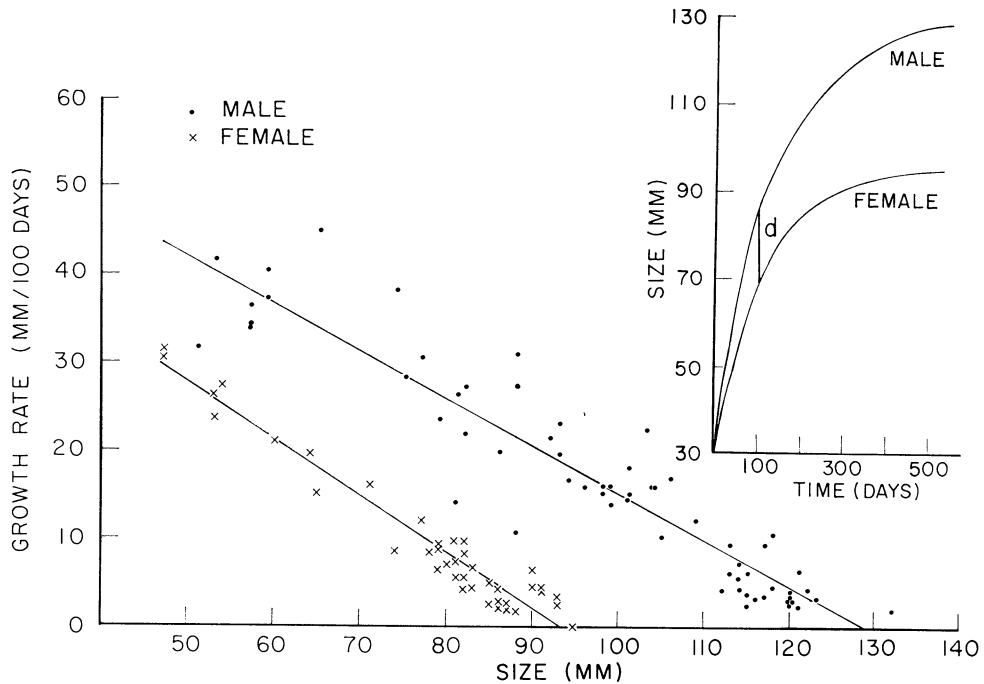


FIG. 3. Growth rate as a function of initial size for males and females originally captured in April-May 1970 and recaptured in August 1970. Inset shows size as a function of age for both sexes if individuals grew throughout the year at the summertime growth rates. The regression line fitting the male data is given by $y = -0.53x + 68.4$ and for the female data $y = -0.63x + 59.2$. The mean time between recapture for males was 107 days and for females, 103.7 days.

to copulate than a smaller adult male, while a female in a comparable category (85 mm or larger) is only 1.53 times more likely to mate than a smaller adult female. Large size is more important for male reproductive success than for female, and other things being equal, one would predict larger male adult size and higher growth rates for males when young in order quickly to reach the large sizes at which copulation becomes frequent.

Although there is an extremely regular tendency for frequency of copulation to increase with each increase of 5 mm in male size, this tendency is violated for males 95 mm–104 mm in size. In fact, the frequency of copulation for males 100 mm–104 mm in size is significantly lower than that predicted by a linear fit to the frequencies for the other categories (t test; $P < .005$). As shown below, this is a time

of transition in the lives of most males, a time in which they leave the territories of larger males and establish new ones of their own. A trough in male reproductive success at this time is not completely unexpected.

GROWTH RATES: AGE AND SIZE

In Fig. 2, size and age are confounded, the larger lizards tending to be the older ones. Indeed, in theory the entire correlation shown in Fig. 2 could result from the effects of age (and hence experience) on reproductive success. If this were true, however, then no sexual dimorphism in growth rates would be expected (unless, for some reason, size affected survival differently in the two sexes, which does not appear to be true: see Figs. 14 and 15). In short, higher male growth rate is

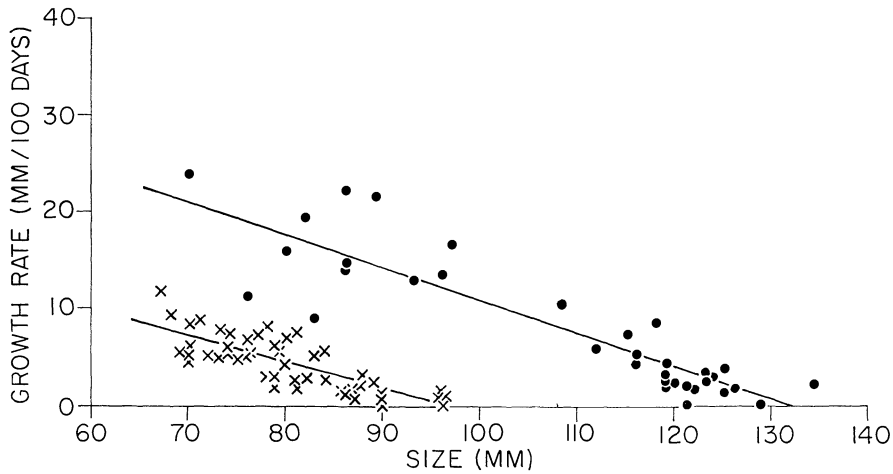


FIG. 4. Same as in Figure 3 except that initial capture took place in August 1970 and recapture in December-January 1970-71. Male data: $y = -0.35x + 46.2$; 144.6 days between captures. Female data: $y = -0.29x + 27.8$; 143.6 days between captures.

uniquely predicted by the assumption that large size is more important for male reproductive success than for female reproductive success.

To gather data on growth rates, animals were recaptured on successive visits to the study area, roughly at four month inter-

vals. At all seasons of the year males grow faster than similar-sized females, as documented in Figs. 3, 4, 5 and 6, in which are plotted growth rates as a function of size at initial capture for three different seasons. Note that during the two periods in which growth rates are greatest (summer,

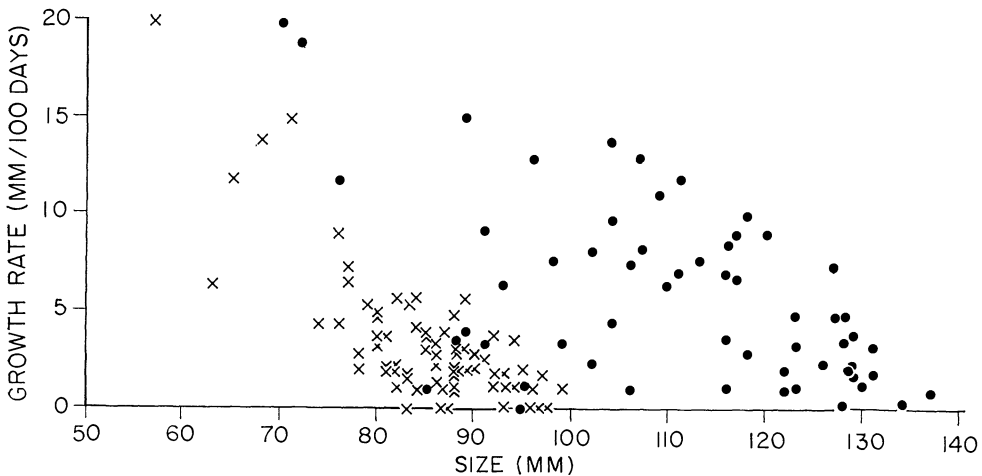


FIG. 5. Same as in Fig. 3 except that initial capture took place in December-January 1970-71 and recapture in April 1971. Average period between recapture: males, 95.0 days; females 96.8 days. Note that growth rates are strongly reduced compared to other seasons, that variance in male growth rates are increased and that there is overlap between male and female growth rates.

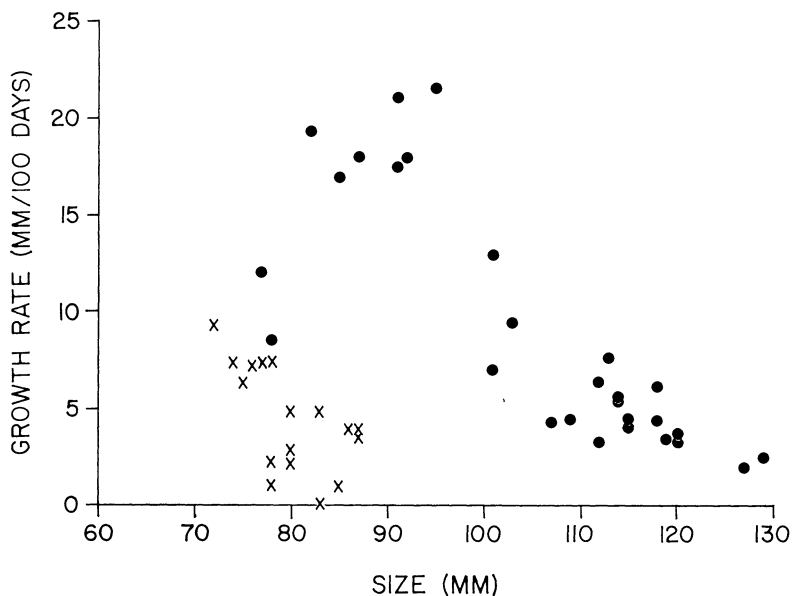


FIG. 6. Same as in Fig. 3 except that initial capture took place in December–January 1969–70 and recapture in April 1970. Mean time between recaptures for males, 107.5 days; for females, 100.3 days. Note that growth rates for the two males smaller than 80 mm are markedly lower than expected based on growth rates of larger individuals.

fall) there is no overlap between male and female growth rates. During the period of slowest growth rates, however (see Fig. 5) there is substantial overlap between the growth rates of males and females between 85 and 95 mm in size. Indeed, there is no evidence that males between 85 and 95 mm grow on average any faster than males 95 to 110 mm do.

These data appear to show that during the dry season (early spring) when growth rates, in general, are depressed, males who overlap the size of adult females suffer especially reduced growth rates (compared to larger males). Less numerous data from the spring of 1970 (Fig. 6) show some overlap in male and female growth rates, but less than in the spring of 1971, in which growth rates, in general, were much lower. In short, variance in male growth rates is greater in the poor growing season (the spring) and greatest when that season is especially harsh.

Ages of lizards were never exactly known because no lizards were marked as hatch-

lings so it is not possible to compare directly the effects of age and size on reproductive success. One can, however, compare the reproductive success of individuals who were the same size four months earlier but who are now of different sizes. One's interpretation will depend on whether one assumes that individuals who were once the same size are the same age or that the individual who grew more slowly afterward also grew more slowly earlier and hence was older when the two were the same size. In short, one must know how growth rates during one four month period are associated with growth rates in other periods.

When growth rates of the same individual in two successive periods are plotted together against size of the individual at the intermediate recapture, then it is clear that there is a strong, positive correlation between an individual's growth rate in the two successive periods: individuals who grew fast in the first period are more likely to grow fast in the second (Figs. 7, 8 and

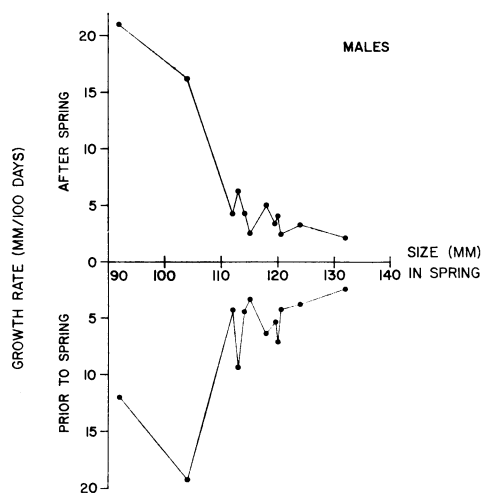


FIG. 7. Growth rates from winter 1969-1970 to spring, 1970, and from spring, 1970, to summer, 1970, are plotted for the same males as a function of their size in spring. Note that the lines have a tendency to be mirror images of each other.

9). This means that we can safely assume that of individuals initially the same size, the ones which subsequently grew more slowly are older. This, in turn, permits us to measure the effect, if any, of age on male

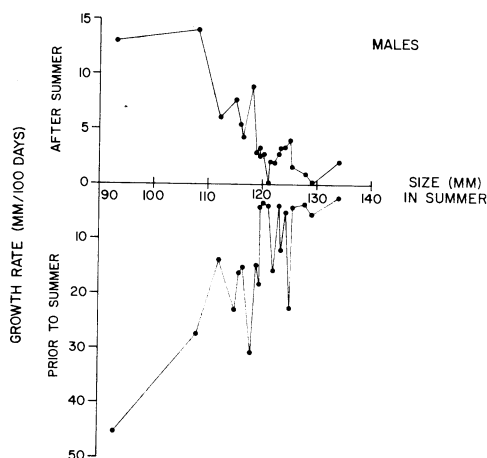


FIG. 8. As in Fig. 7, except that the growth rates are from spring to summer, 1970, and from that summer to winter, 1970-71, as a function of size at summer, 1970. Note that the lines have a tendency to be mirror images of each other.

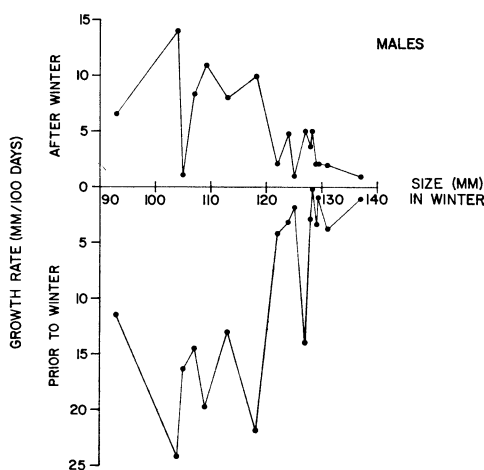


FIG. 9. As in Fig. 7, except that the growth rates are from summer, 1970, to winter, 1970-71, and from that winter to spring, 1971. Note the same mirror image as in Figs. 7 and 8.

reproductive success (frequency of copulation). If age makes an independent contribution, then there should be a tendency during any one visit for those males to copulate who later grew slowly (as corrected for body size). No such tendency is evident: in Figure 10 the males who copulate during a visit (open triangles) do not tend to have smaller growth rates thereafter. By contrast, in one of the three samples (after the lowest growth rates), those who grew fastest tended to copulate more often in the visit after these growth rates (open circles, Fig. 10).

MALE AGGRESSIVENESS

With the exception of the two homosexual copulations discussed below, two adult males were never seen near each other unless they were displaying aggressively (as described for *A. lineatopus* by Rand, 1967) or fighting. Only three fights were observed in the study area between adult males. In each case, both males attempted to bite the other on the jaw, neck or body. In one case, one male secured with his jaw a grip on the other's neck.

To confirm the part aggression may play in reducing territorial overlap, 37 experi-

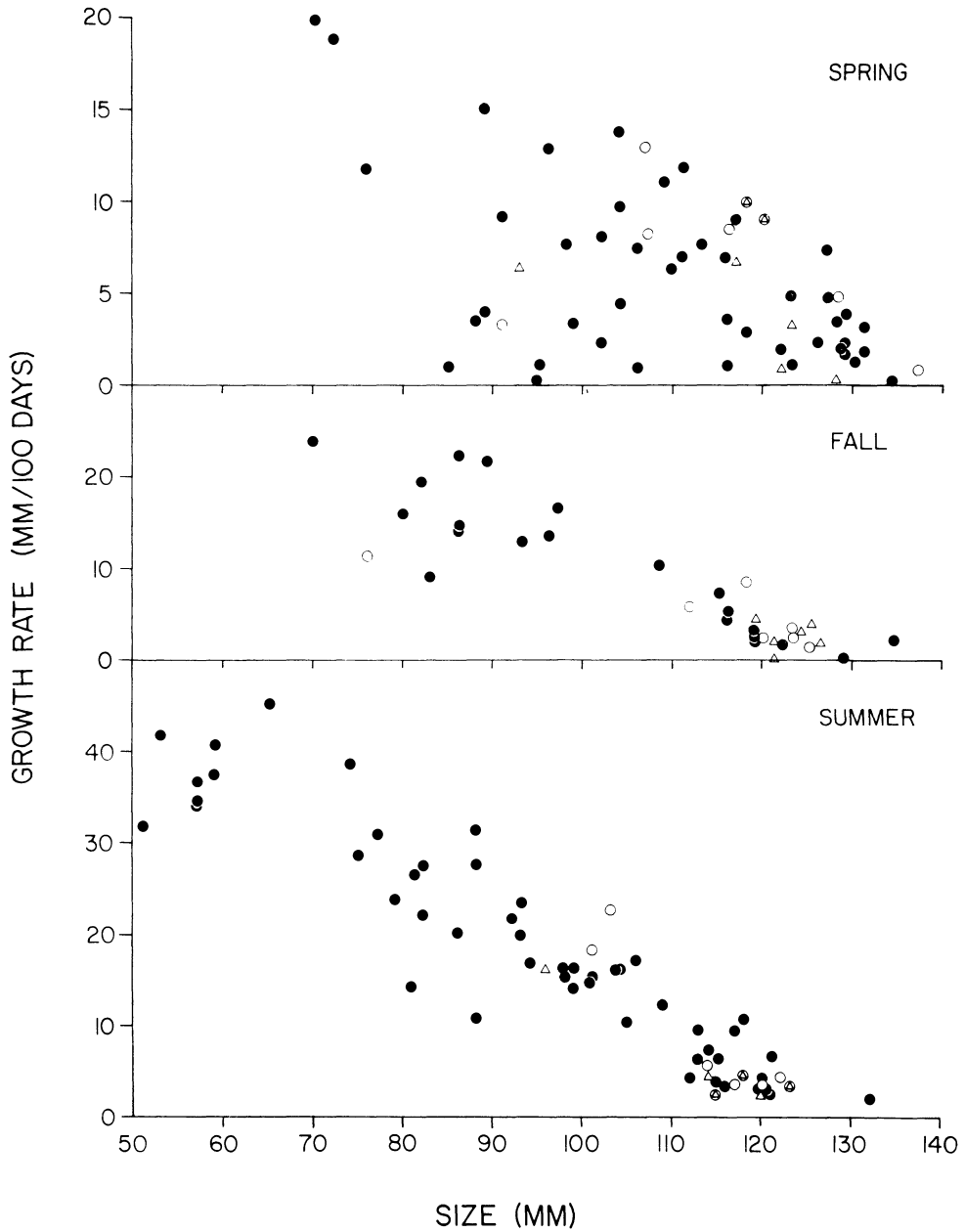


FIG. 10. Copulation as a function of growth rate in males for three separate periods. Open circles = males who copulated during the visit after the growth rate shown. Open triangles = males who copulated during the visit before the growth rate shown. Dark circles = males not seen to copulate during the visits before and after the growth rate shown. See text for interpretation.

ments were conducted in which a male, captured elsewhere, was tied down on a tree for at least 30 minutes or until a response was elicited. The tethered male was tied around his waist with nylon fishing line which was secured (with about a yard's free reign) to the tree, usually about 10 feet up the trunk. Five tethered males were used, ranging in size from 97 mm to 118 mm. None of the experiments was continually monitored; instead, each experiment was visited several times before being terminated. These experiments can be classified into those eliciting a strong, aggressive response, those eliciting a cautious response and those apparently eliciting no response at all. Twenty-four experiments elicited no reaction, but 13 of these were conducted on trees on which no male was ever seen during that visit (of four weeks) to the study area.

In six of the experiments, strong aggressive responses were elicited. Typically, within 30 minutes, a second male appeared, bright green, nuchal crests raised, throat area inflated, body fully extended, and approached the tethered male. If his approach was not interrupted (by an attempt to capture him) a fight soon broke out, the second male lunging repeatedly at the tethered male and attempting to bite him on the jaws, neck and side of the body.

Seven experiments elicited cautious responses. In these, a second male appeared but remained at some distance from the tethered male and approached only very slowly, if at all. For example, a 102 mm male was tethered on a thatch tree (*Cocos nucifera*) within sight of the resident (190 mm) who was perched down, fully green, on a brown frond, 17 feet from the ground. For the first several minutes the resident male responded only by eyeing the tethered male closely. He then moved onto the trunk and hid himself under a frond. Twelve minutes after the tethered male was introduced, the resident male had turned completely black and was nearly invisible under the frond. Meanwhile, the tethered male had moved part way around

the trunk away from the resident male. Although still green, some darkening had begun to appear. Several minutes later he escaped from his tether and abandoned the tree. Fifteen minutes after his escape, the resident male was bright green again and headed back up the tree.

One might suppose that the relative size of the tethered male would control the type of response (aggressive or cautious) shown by the resident male: if the resident is larger he should attack. The few data do not bear this out. The absolute size of the tethered male may be important in determining a cautious response in the resident, especially if the chance of serious injury is greater when larger males fight each other than when smaller males fight. I assume that in *garmani*, as has been shown in *A. lineatopus*, the larger of two males usually wins in a naturally occurring fight (Rand 1967).

To observe a more natural aggressive sequence two experiments were conducted in which males were released onto trees known to be occupied by other males. In the first, a 100 mm male was released onto a tree occupied by a 119 mm male. The smaller male slowly made his way to 10 feet up on the tree when he spotted the large male, who was perched two feet further up on the same branch. The larger male started toward the smaller one, who quickly turned and ran down to a height of six feet from which he leapt to the ground. He was never seen again. In the second experiment, a 109 mm male was released onto a tree occupied by a 114 mm male. The latter spotted him almost at once but reacted very cautiously, displaying in sight of the introduced male but not moving toward him. For an hour both moved cautiously within sight of each other, neither attacking, but the intruder moved out into the foliage while the resident remained low on the tree. Two hours later both were seen fighting on the trunk of the tree. Both fell to the ground, and the intruder then escaped back up the tree into the foliage. Later that day, the resi-

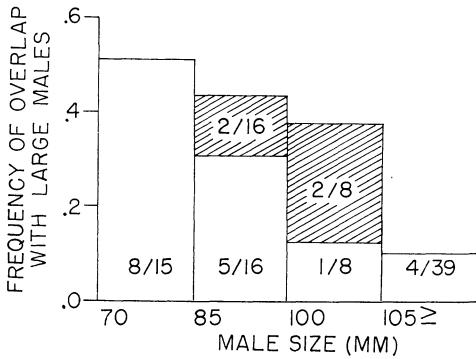


FIG. 11. Percentage of males in each size category known to be overlapping home ranges with large adult males (≥ 105 mm). Data taken from visits one, two and seven. Shaded areas refer to males who dispersed during the visit from the territory of a large male to a tree unoccupied by any other adult male. Two of the four cases of overlap in the ≥ 105 mm category were cases of temporary overlap which resulted in copulations with resident females.

dent was seen chasing the intruder through the foliage. After this, the intruder was never seen again while the resident was seen on successive days occupying the same tree.

MALE TERRITORIALITY

During the first, second and seventh visit to the study area, I attempted to map male territories by concentrating on a small portion of the study area. Males are sighted too infrequently to measure territory size in the usual way; that is, to construct a volume fitting such sightings. But fortunately males 105 mm and larger show a strong tendency to occupy trees which they may share with a male smaller than 105 mm but which they do not share with any other large male (105 mm and larger) (Fig. 11). Typically, during a given visit, a large male will be sighted between five and ten times in a large tree (or, in several smaller contiguous trees) without any other large male being sighted in that tree (or trees). When followed, such males wander throughout the tree (or trees). In the data presented here, a tree was assigned to a male if he was seen three or

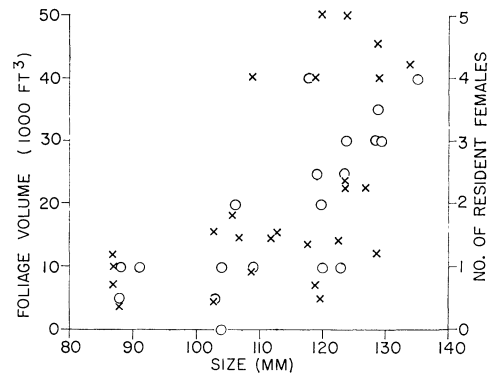


FIG. 12. Territory size (X) and the number of females resident within the male's territory (O) as a function of male size. Territory size was measured by estimating foliage volume (see text). One-half a female was arbitrarily assigned to each of two males if she overlapped both of their territories.

more times in it without any other adult male being seen therein. If, as happened several times, a large tree was also known to be occupied by a small adult male (85 mm–104 mm), both males were excluded from the data, since too few data were available to partition the tree between them. If a large male occupied several contiguous trees, of which one was also occupied by a small adult male, $\frac{1}{2}$ of that tree was arbitrarily assigned to each male.

Territory size was measured by foliage volume of trees exclusively occupied. The foliage volume of a tree was calculated by estimating the height of the tree and multiplying that by the area of a rectangle approximating the average horizontal dimensions of the foliage. This very crude estimate is obviously incapable of discriminating between very similar territories, but it is adequate to differentiate unambiguously between categories of trees (e.g. large, medium and small). A better way of estimating foliage volume was not devised partly because it soon became apparent that the lizards were not responding to foliage volume as such. Pimento trees (*Pimenta officianalis*), for example, never reach a large size but they are very at-

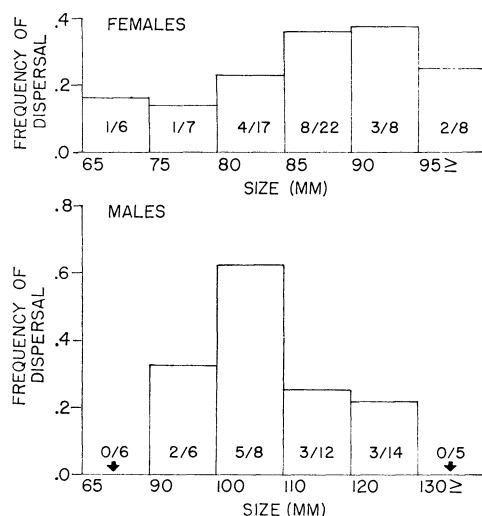


FIG. 13. Tendency to disperse across open ground 50 feet or more as a function of initial size in males and females. Animals were measured and marked in December 1970–January 1971 and recaptured in April 1971. The percentage of those recaptured who had dispersed is plotted against size of the animals in December–January. Mean distance of dispersal for the females, 123 feet; for the males, 119 feet.

tractive to the lizards, and a large adult male will often occupy a pimento tree containing several females. To prevent any subjective bias, the foliage volume of each tree in the study area was estimated at the beginning of the study *before* the sizes of any of the occupants were known.

There is a strong tendency for male ter-

ritory size to increase with the size of the adult male (Fig. 12). Furthermore, there is a strong tendency for the number of females resident within a male's territory to increase with the male's size (Fig. 12). Since about 90% of all copulations take place within the exclusive territory of the male observed copulating (see below), it is plausible to assume that the primary correlation between male reproductive success and male size results from the correlation between territory size and male size.

Males show a decreasing tendency to overlap with large males as a function of increasing size (Fig. 11). To avoid overlap growing males must usually disperse to an unoccupied tree, and five males were seen to do so *during the visit* in which they were first seen overlapping with a large male (shaded areas, Fig. 11). Likewise, dispersal data gathered from recapture work show a peak in dispersal for males 100–109 mm in size (Fig. 13).

MALE TERRITORIES AND COPULATIONS

For 49 of the observed copulations it is possible to say whether the male was copulating within his territory (in the sense of copulating in the tree in which he alone, among large males, was observed). Of these 49, 44 (or about 90%) were performed by the territory holder. Of the additional five, three were performed by temporary interlopers, and two by small

TABLE 2. Data on five copulations within the territory of a large male in which the territory owner (the large male) did not perform the copulation.

Date	Size of Territory Owner	Size of Copulating Male	Behavior of Copulating Male
9.7.69	124	116	Temporarily occupied one tree of 5-tree territory.
1.7.70	119	118	Seen only once on main tree of territory.
4.20.70	115	96	Resident within larger territory.
5.9.71	124	117	Entered from and quickly returned to his own neighboring territory.
8.6.71	121	91	Resident within territory; approached by owner.

males resident within a large male's territory.

In each of the three cases involving an interloper, the interloper was smaller than the resident male (see Table 2, copulations 1, 2 and 4). In the first case, the interloper occupied one corner of the larger territory for at least two days; he was not seen before or after. When first seen he was copulating with the one female known to be resident in that portion of the territory (a mango tree). Two hours later the larger male entered this portion of his territory, but no encounter was observed between the two males. It is possible that the large resident male was unaware of the copulation while it was going on. In the second case, the interloper was first seen while copulating and was never seen thereafter. The copulation took place on the main tree of the resident's territory (a pimento tree), and it seemed unlikely at the time that the resident could be unaware of the copulation. The resident was seen many times before and after in the same territory. In the third case, the interloper entered from his own territory 40 feet away and returned to it sometime after the copulation. It is very likely that the resident was not in this tree at the time but in one of eight small contiguous trees which he frequented (and in which he copulated).

Two of the 49 copulations were performed by small males regularly resident within a larger male's territory (Table 2, copulations 3 and 5). In the first case, the smaller male occupied a portion of the larger male's territory. In the second case, the larger resident male was observed approaching the copulating couple in a very aggressive posture: bright green, nuchal crests raised, body extended. Both the small male and his copulating partner had turned black, which in aggressive encounters seems to indicate fear. Unfortunately, the incident was interrupted in order to capture the copulating couple (who were unmarked).

The choice of the place to copulate appears to be the female's. I have only ob-

served the beginning of two copulations. In both cases, the female was already perched face down at the spot where the copulation took place while the male approached her from several feet away. In addition, I watched a female move down to the exposed trunk of a tree and remain perched nearly motionless for 40 minutes while a male repeatedly tried to approach her from about 20 feet further up the tree, but he was frightened back by passing humans (the male had been captured many times before). A local naturalist (Mrs. Dorel Staple) has often seen females perch at places where they soon copulate, and she believes that while they wait they adopt a special posture, with the rear slightly elevated. Crews (1973) has shown that female *Anolis carolinensis* have a copulation invitation pose.

If females choose conspicuous perches in which to copulate, why do they do so? It seems difficult to believe that the perches are safer than inconspicuous ones. It would be most interesting if, in this highly territorial species, females were advertising their availability in order to increase the number of males from which to choose. The only clear case of female rejection I observed involved a female who had been caught by the tail by a small adult male. For over a minute he attempted the impossible, that is, to copulate while maintaining a hold on her tail. He finally released the tail, moved quickly to cover her, but she moved even more quickly to escape him.

FEMALE AGGRESSIVENESS

No two adult females were ever seen near each other unless they were fighting or unless one was clearly hiding from the other. Only nine experiments were conducted with tethered females but two of these induced attacks from resident females. One induced an attack from a small resident male (91 mm) but none induced any sexual displays or any other response from any other male.

If adult females defend territories these

certainly overlap more than male territories. It was common to see as many as four different adult females at different times on the same part of the trunk of a large tree. Unfortunately, since females do not tend to occupy trees exclusively and since I have less than $\frac{1}{3}$ as many resightings per adult female as per adult male, I am unable to present any data on the sizes of female home ranges, their precise degrees of overlap, and whether they are sufficiently distinct to constitute territories, i.e., defended areas. Rand (1967) has shown for *A. lineatopus* that females do defend territories and that these show greater overlap than do male territories. T. Jennsen (unpublished data) has similar very detailed data for another Jamaican anole, *A. opalinus*.

HOMOSEXUAL COPULATIONS

Of the 62 copulations in which the individual underneath (see Fig. 1) was identified, two were homosexual copulations. The animal on top is invariably a male. The two males underneath were within the size range of adult females (83 and 76 mm in length), while the two males on top were large fully adult males (121 mm and 125 mm). One of the two copulations was unusual in that it took place on a small branch (less than two inches thick) high in the tree surrounded by foliage. The homosexual copulations differed in no other observable way from heterosexual copulations except that the small male underneath had turned partly black, which, in aggressive encounters, indicates fear. In only one heterosexual copulation had the female turned black, and that was one in which the male had also turned black, both animals being in the presence of a much larger male, who was approaching aggressively (see Table 2). Intromission appeared to have been achieved in both homosexual copulations.

The two males underneath were never seen again on subsequent visits to the study area, but one of the males on top was followed on two successive visits to

the study area, during which he was observed in two heterosexual copulations. These two and his homosexual copulation occurred on the same tree, a territory the larger male apparently occupied for at least eight months.

In the very similar *A. lineatopus*, Rand (1967) has shown that small adult males compete with adult females for territories within large male territories. There is no evidence of the large male ejecting a small adult male in order to open up space for an additional female. Arguing from natural selection, one would predict that large males ought to eject small males in order to open up space for additional adult females. Natural selection might favor small males remaining where they were, if their territories increased survival (or growth rate) above that expected elsewhere. An occasional buggery might be a small price to pay for the advantages of remaining within the large male's territory. Such a hypothesis can be tested by comparing the survival and growth rates of small males within large males' territories against the rates of small males found living on their own. Unfortunately, there were too few data from this study to make the appropriate test.

ADULT SEX RATIO

Biases in capture strongly favor males: they are larger, are more often found on conspicuous perches, and are easier to catch once spotted. During the first two visits a marked male was resighted more often than a marked female by factors of 3 and 3.8 respectively. Despite this bias, more adult females were captured than adult males for each of the visits (Table 3). As each is an independent sample, the difference is highly significant. The difference cannot result from males maturing at a greater age than females, since the sexes reach sexual maturity at about the same age (see Fig. 1).

If, as argued above, eggs destined to produce males are about the same size as eggs destined to produce females, then the cost

TABLE 3. *Adult sex ratio.*

	Males	Females	Sex ratio (M/F)
1	10	15	0.67
2	38	45	0.84
3	100	118	0.85
4	93	113	0.82
5	152	194	0.78
6	100	126	0.79
7	30	40	0.75
Total	523	651	0.80

to an adult female of producing a male will about equal the cost of producing a female. According to Fisher (1958), the sex ratio of conception should therefore be about 50/50. Natural selection would only favor a biased production of females if the population were strongly inbred (Hamilton, 1967), but dispersal data strongly argue against this assumption since in a typical three-month period approximately 28% of the adults of each sex disperse across ground 50 feet or more to new trees (Fig. 13). The alternate explanation is differential male mortality, something that data from other lizards, as well as theoretical considerations, would predict (Trivers, 1972).

SIZE AND SURVIVAL

Recapture data were used to test the relationship between size and survival or, chance of being recaptured within the study area for each of three four-month periods. If a lizard was not recaptured four months later but was known to be alive then (because of recapture still later), it was counted as being alive. Data on chance of survival four months later for lizards captured during three successive visits (winter 1969-70, spring 1970, summer 1970) showed no clear differences from visit to visit, and these data were aggregated to give a general view of chance of recapture as a function of initial size for both males and females (Figs. 14 and 15).

In order that such recapture data reflect actual chance of survival, one must know

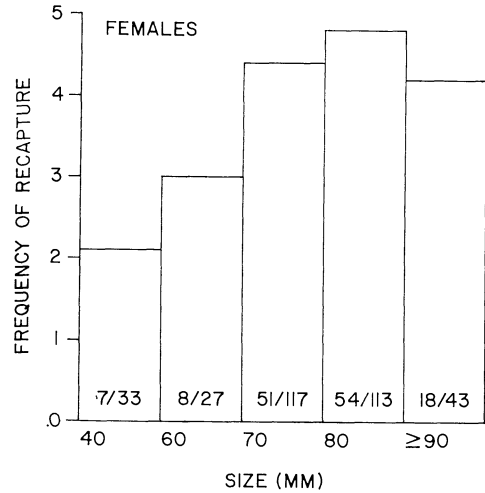


FIG. 14. Frequency of recapture four months later as a function of initial size for females captured in the winter 1969-70, the spring 1970 and the summer 1970. Females were counted as recaptured even if they were not recaptured four months later as long as they were known then to be alive because of later recapture.

how many lizards are dispersing out of the study area as a function of their size. Fig. 10 gives dispersal (within the study area) as a function of size. Since larger females appear to disperse slightly more often than smaller females, I conclude that at least up to 90 mm in size females appear to survive better with increasing size. For males, it appears safe to assume that they survive better with increasing size up to 110 mm but they show no increase in survival after this (and they may show a decrease). One must remember, of course, that size is confounded with age, and part of the relationships observed may be attributed to differences in age.

The relationship between size and survival appears to be similar for the two sexes, especially over the common size range of 40 to 90 mm in size.

There was no evidence that survival was correlated with growth rate. That is, there was no relationship between growth rate in one four month period and survival in the next. Likewise, the growth rate of

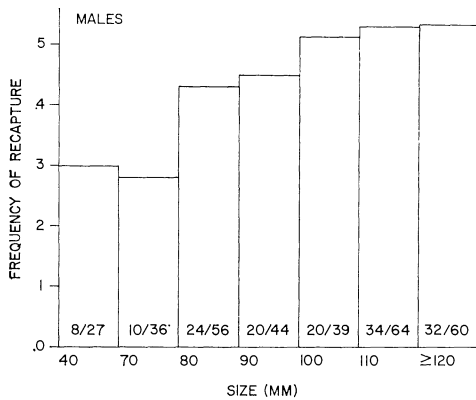


FIG. 15. Same as Fig. 14, except for males.

individuals who survived eight months (or twelve months) did not differ from the growth rate of comparable individuals who were only known to survive four months.

There was no relationship between weight at capture (as corrected by snout-vent length) and survival four months later.

SEXUAL SELECTION AND SEXUAL REPRODUCTION IN *ANOLIS GARMANI*

In species with no male parental investment (such as *A. garmani*) half the species investment is thrown away each generation on males (Fisher, 1958) so that there appears to be a constant two-fold advantage every generation in favor of asexual mutants (Maynard Smith, 1971). Williams (1975) has drawn the inference that the advantages of genetically diverse offspring must be far greater than hitherto imagined. Despite considerable success with specific life history models, Williams (1975) believes that sex must, in general, be at a disadvantage in low-fecundity organisms such as many vertebrates and insects. An attractive alternative is to imagine that female choice is sufficiently discriminating in such species so that those males actually mating each generation have genes which are about twice as good at producing successful daughters as are the genes of the mothers themselves. Because

only daughters invest, a block to the spread of asexual mutants exists only when the reproductive success of *daughters* is doubled by mating with preferred males (compared to asexual reproduction). In short, the advantage of genetically diverse offspring combined with a system of female choice could provide a block to the spread of asexual mutants in low-fecundity organisms.

Since environments are constantly changing, the ideal male genotype must also be changing. How can females come up with general criteria that work regardless of environment (see Zahavi, 1975)? A daughter is selected to maximize survival and resource accrual (where these resources are translated into investment) so that males who appear to have maximized this criterion are males whose genotype is preferable regardless of the environment within which this choice is being made. What is striking about our data on *A. garmani* is that those males who have maximized growth rates times survival are those who inseminate the adult females. Although I have no data on female choice, our other data suggest that females naturally mate with males whose daughters will have the best chance of maximizing resource accrual times survival. That there is a strong system of male-male competition for females does not imply that females are merely mating with males good at besting other males. Instead, systems of male-male competition are expected to evolve under the influence of female choice, so that males compete among themselves in such a way as to reveal to females that their genes are good at maximizing survival times resource accrual.

SUMMARY

1. The social behavior of *A. garmani* was studied for a total of eight months during seven separate visits to a study area of nine acres in Jamaica.

2. Adult males are 2.25 times larger by weight than adult females. At all times of the year and at all sizes for which there

are data males grow faster than females. Growth rates for the same individuals in different four month periods are positively correlated.

3. By measuring reproductive success as frequency of copulation, it was discovered that in adults of both sexes increasing size increases reproductive success, but that this tendency is *significantly stronger* in males than in females. There is no evidence that age makes an independent contribution to a male's frequency of copulation.

4. The steep slope of the function relating reproductive success to adult male size results apparently from sexual selection: males compete aggressively to occupy exclusive territories containing females. There is a strong tendency for large males to occupy correspondingly large territories which in turn contain large numbers of females. About 90% of copulations were performed by a territorial male within his territory.

5. As young males mature they tend to be found less frequently within the territories of large males. Males 105 mm and larger are almost never seen within the territories of other males in this category. Males 100–104 mm must disperse if they are still within a large male's territory and males within this size range show a significantly lower frequency of copulation than would be expected from the function relating size to reproductive success for other adult males.

6. Two homosexual copulations were observed and are described.

7. The adult sex ratio is biased in favor of females.

8. Recapture data appear to show that females survive better with increasing size up to 90 mm. Males appear to survive better up to 110 mm but probably not at larger sizes.

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