

The reproductive behaviour of the lizard, *Ameiva ameiva tobagana*

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THE common ground lizard of Trinidad, the zandolie, is identical with that of Tobago and is *Ameiva ameiva tobagana* (Brongersma, 1956). Its natural habitat is open and semi-open country, scrub land and light deciduous forest or secondary growth but since it frequently occurs in suburban gardens its behaviour can be easily observed. The following account of its reproductive behaviour is based on observations of nineteen matings made mostly during the period 1958 — 1963. The study is purely descriptive, no equipment of any sort other than field glasses having been used.

Courtship and mating

Phase 1. The male approaches the female in short spurts, jerking his head and shoulders at the end of each short forward movement. The head is pointed forward and slightly downward with the neck slightly arched and the minute throat fan expanded. As the forward motion stops the head and shoulders are jerked quickly upwards on extended forelegs and then allowed to fall back rather more slowly. On completing the jerk the lizard moves forward again. With this jerky, bobbing movement the

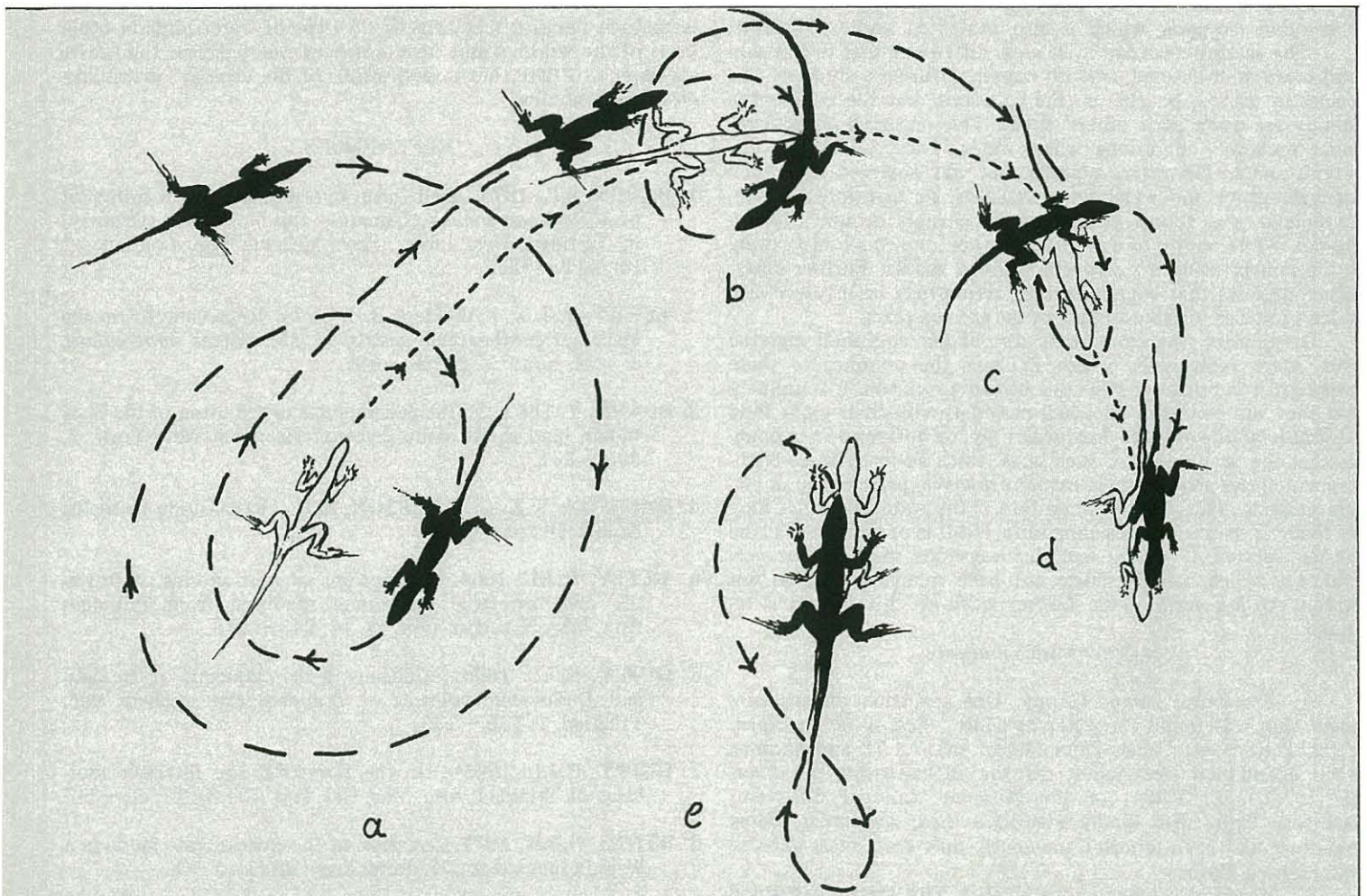


Fig. 1. Diagram of courtship behaviour in the lizard *Ameiva ameiva* to show the four phases (a — d) and the figure-of-eight movements of one male (e). See text. The male is shown in black

and the female in white. The path of the male is shown in large dashes and that of the female in small dashes.

male spirals in towards the female (see Fig. 1). The head jerk which is pronounced when the male is a metre or more away from the female may almost disappear when he is only a few centimetres away.

Phase 2. The female seems to pay no attention to the male's display but continues her quest for food. The early wide-circling stage of courtship in which there is no body contact soon gives way to a stage of closer circling in which the male pauses broadside across the female's path just in front of her so that in moving forward she crosses over the male's body, usually at the base of the tail. However, on one occasion, a female with her nose in the grass was so intent on the search for food that she passed below the male. On the female moving forward the male circles behind and around to cross her path once more.

Phase 3. Phase 2 eventually gives way to the third phase in which the male circles the female so closely that their bodies touch almost throughout the circle. At this stage there is little tendency for the female to move forward and eventually the male, coming to the base of her tail, mounts and straddles her instead of crossing over her.

Copulation does not necessarily follow immediately. The female may move forward from under the male who will then circle her and mount once more. My notes record copulation being effected on first mount on four occasions and after more than one mount on six occasions. On one occasion the female slid out from under the male six times and copulation took place only on the seventh mount. Sometimes, the male seems to restrain the female from moving forward.

Phase 4. In the final phase of courtship, the male rubs the female's back with a sideways movement, usually involving the cloacal region but on one occasion seeming to involve mainly

the chest. The female responds by arching the base of her tail, whereupon the male slips his tail below hers, opposes his cloaca to hers and copulates. That the male does not force himself below the female is shown by the fact that on one occasion the male rubbed the female three times before copulation succeeded. The first two rubbing movements apparently produced no response from the female.

Courtship is variable in the duration of each phase and the number of repetitions of each action in any one phase. But, there is also some other variation as well. One male, with cloaca pressed to the grass, performed distinct rubbing movements while at the female's side, touching her, and facing in the opposite direction and another male mounted and dismounted several times, moving in a figure of eight behind the female each time he dismounted. (Fig. 1e)

The act of inserting the hemipenis is very quick and the details almost impossible to see, but my impression is that the hemipenis is not everted until the cloacae are opposed and that the insertion is accomplished by quick thrusting movements. On one occasion when I was able to get really close after copulation had begun I did see unmistakable thrusting movements of the male's pelvis.

On fifteen occasions the duration of copulation was timed but, unfortunately, on only three of them did I have the use of a watch with a second hand and so in 12 of the times there is an uncertainty of about 15 sec. The mean of all the observations is 2 min 3 sec (with a standard deviation of 25 sec.) the shortest time being 1 min 5 sec and the longest 2 min 45 sec.

It has seldom been possible to see clearly the position in which copulation begins but apparently the male grips the fe-

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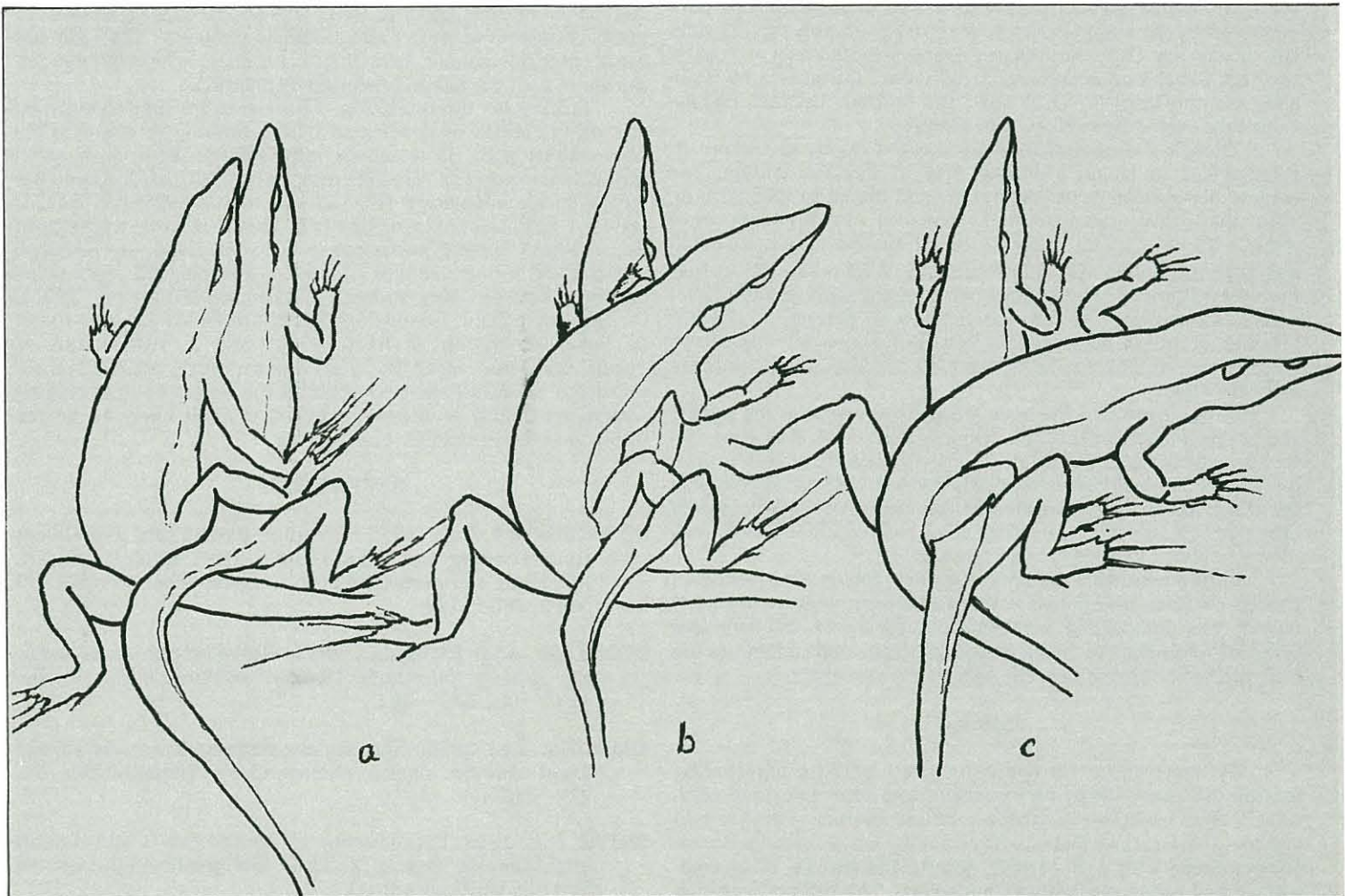


Fig. 2. The change of position observed in some copulations. Note the movement of the male over the female and the lowering of the female's tail.

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male near her pelvis with both legs of one side; the others support his weight. The female's tail is highly arched and, though the cloacal region of the male's body is at right angles to the axis of her body, the male lies above, parallel to and slightly to the side of her. In most of the copulations seen this position was held throughout except that the female lowered her tail gradually. As copulation ended the female simply moved from beneath the male. In the remaining five copulations the original position changed gradually after about 30 sec to 1 min. The male moved above and across the female's body as shown in Fig. 2 until the axis of his torso was more or less at right angles to hers. Copulation ended some 10 to 15 sec after the final position was attained.

After separation there has never been any of the grooming of the cloacal region that occurs in other lizards. On all but one occasion the pair has remained close together with the male almost immediately resuming his head jerking behaviour. On the exceptional occasion copulation occurred very late in the afternoon (5.20 p.m.) and on separation the female disappeared down a burrow almost immediately.

Most copulations were observed as single events but I have twice seen a pair copulate three times within a few hours and it is reasonable to suppose from the behaviour of the lizards that the copulations observed as single events were part of a series. On 7th December 1958 a courting pair was seen at 12.15 p.m. The first copulation occurred at 1.30 p.m. After an unnoted period of time when there was no courtship, courting began again and led to a second copulation at 2.15 p.m. Afterwards, courtship occurred sporadically until 2.40 p.m. when both lizards basked for 17 min with a 3 min interval in search of food. At 2.57 p.m. courtship began again leading to a third copulation at 3.07 p.m. On 1st January 1959 the courting couple was first seen at 10 a.m. the first copulation occurred at 10.05 a.m., the second at 10.25 a.m. and the third at 11.10 a.m. The intervals between copulations thus ranged from 20 min. to 52 min.

Though the observations are too few to be sure about it, there seems to be no preferred time of day for mating. The earliest observation is at 10.05 a.m. and the latest at 5.20 p.m. with the others spread out in between. In my experience *Ameiva* becomes active relatively late in the morning, about 8.30 and goes to ground well before sunset at 4.30 or 5 p.m. so that the observations of mating cover most of the daily period of activity. Observations are likewise too few to determine whether breeding occurs throughout the year. So far, the only months in which breeding has not been observed are May, June, October and November.

During courtship the male frequently protrudes his tongue and seems to be scenting the female's track and after some diversion which takes him away from the female he seems to find his way back to her at least partly by scent. The male has also been seen to taste the female but has never bitten her, though biting is common in the mating behaviour of other lizards. e.g. *Anolis aeneus*, *Cnemidophorus lemniscatus*.

During courtship the male may stop for no obvious reason though on some occasions I had the impression that my presence nearby was influencing his behaviour. However, he may also break off courtship to challenge another male and sometimes the male has been disturbed by passersby or motor traffic.

Fighting

My observations on fighting are few but worth recording for the light they throw on courtship behaviour. On three occasions a male broke off courtship to chase another male. On two of them the attacked male, before running off, adopted a threatening attitude with neck arched, nose to the ground, body compressed and raised on stiffly extended legs. This did not deter the attacker who simply charged the displaying male and chased him away. The chases are vigorous, the two lizards running many metres, and may end in physical contact. I have twice come

across two males locked in combat with one strenuously biting the other's head.

Discussion

The courtship of many animals is a series of activities in which the actions of each stimulate the other so that the actions follow a definite sequence. (Tinbergen 1971). But one of the outstanding features of courtship as described above is the apparent passivity of the female. Her only positive response to the male's series of movements is the arching of her tail immediately before copulation. Until this moment she seems utterly indifferent to the male's advances. This indifference may be more apparent than real for on two occasions the female arched her tail while the male was still in the close-circling phase. This shows that the male's behaviour in the earlier phase increased her "willingness to mate".

My interpretation is as follows:— Since I have seen the head jerk behaviour directed at both males and females, I regard this as a challenge to another individual. A female unwilling to mate retreats, a male either rapidly retreats or responds with the threat display after which a chase ensues. A female that is willing to mate however does not move away, at least not with any action faster than the normal progress in search of food. To the approaching male the female's seeming indifference is a positive act i.e. remaining in his presence, which gradually subdues the aggressive head jerk and finally eliminates it altogether for in the close circling phase the male does not show this behaviour.

The close circling of the male restricts the female's forward movement and induces passivity. The contact between male and female here is probably important. In the earlier part, the female crosses the male's tail and he hers and later there is extensive contact along the flanks as well. These contacts in a context of passivity repress aggression and stimulate sexuality. The final and most extensive contact is in the fourth phase which induces the female to arch her tail and facilitate copulation.

Such is my interpretation. I have seen no similar study on any other species of *Ameiva* so I have nothing to compare my observations with. It would be interesting to know how widespread is the peculiar "crossing over" behaviour that has been observed during copulation (Fig. 2) and what function, if any, it serves. I have seen nothing like it in any of the other species of lizard whose mating behaviour I have observed. In Ecuador, breeding of *Ameiva ameiva petersii* is seasonal with eggs being laid only between May and early December (Simmons, 1975). On the other hand, *Ameiva bifrontata* breeds all the year round in Venezuela (Leon & Ruiz, 1971) and *A. festiva* and *A. quadrilineata* also breed the year round (Smith, 1968). My observations are insufficient to establish the length of the breeding season in *Ameiva a. tobagana*, but it is more likely to be the whole year rather than part of the year.

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