Reproductive Behaviour of the Neotropical Gecko *Thecadactylus rapicauda* (Houttuyn)

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ABSTRACT
Data were obtained from 46 matings with the times of occurrence being noted for 38 of them. Copulation occurred in all months of the year. Fifteen of the copulations (39.5%) occurred between 0600 h and 1000 h, showing that *T. rapicauda* is not strictly nocturnal. Mating behaviour is described. The male bites the female before mounting. Copulation lasts on average 3 min. 25 sec. and separation is accompanied by violent shaking. Few eggs have been found and egg-laying behaviour is very incompletely known.

Key words: *Thecadactylus rapicauda,* reproductive behaviour, hemipenis, eggs.

INTRODUCTION

Thecadactylus rapicauda (Houttuyn) is common in Trinidad and Tobago and well-known to the people of these two islands who call it "woodslave", "twenty-four hours", "mabouia" or "checker-check". It is present in many habitats (Murphy 1997) and particularly in dwelling houses in country areas where it may be seen eating insects attracted by lights. When I moved into my new home near Talparo in June, 1982, a small population was already in residence. It is not the easiest of animals to study for several reasons. It is basically nocturnal and its activity cycle does not match that of humans. Its colour is a pattern of browns, greys and cream which changes with illumination and background and, apart from females with easily visible eggs, the sexes are similar and not determinable unless the lizard is in the hand. It does not invite investigation for its most common "activity" is waiting and the sense that guides action is just as likely to be scent as sight.

On the other hand, its action is not usually rapid and is usually easily followed. Furthermore, it can become habituated to humans, making close observation possible with the near certainty that the observed activity is not influenced by the observer. Over the years, most of the adult individuals in my house have become habituated to my presence and have allowed me to watch them close up, within 0.3 m. My passing to and fro has seldom caused any reaction and there is only one instance in the behaviour I shall describe when my coming on scene may have altered the course of events. The juveniles show avoidence behaviour while growing up but they lose their fear as they mature.

Study site and methods

For the vast majority of the observations presented here, the study site has been my present home in Leotaud Trace, Talparo, Trinidad. The house is a prefabricated one of greenheart timber with a total floor area of about 112 sq. m. It stands on pillars ranging from 56-96 cm tall because of the slightly sloping ground. A level ceiling, also of greenheart timber, 2.41 m above the floor separates an attic from the living area. There are some ill-fitting timbers and the odd knot-hole giving numerous connections for the lizards between the two levels. Lizards are almost never seen on the floor but mostly on the walls and ceiling where the adhesive scales of the feet give them adequate grip (Beebe 1944). Because the species is basically nocturnal, a torch is often required for seeing details. Habituated lizards do not react to this; unhabituated ones react by protruding the tongue and, perhaps, by trying to move away from the illuminated area. I estimate that the total population is about 20.

T. rapicauda is vocal. It makes three distinctly different calls. The one that gives it its name "checker-check" is a loud rattle of clucking sounds which in the literature is designated a multiple-click, or MC, call. The second call is a rasping hiss that I write as "shrrr" and think of as a prickly hiss. The third call is a soft "kek". All three have been heard in connection with reproductive behaviour, but the second is by far the most common. It became a signal to get up and investigate.

This study was begun on 8 December, 1982 and is ongoing. In the descriptions that follow "arm" means "front leg" and "leg" means "hind leg." Dates are given in the form day/month/year.

OBSERVATIONS

Courtship and mating behaviour

In most animals copulation is preceded by a series of movements by both the male and the female that prepare them for co-operation in performing the act. This phase is usually referred to as courtship. In some species it takes a relatively long time. In others, as in *Thecadactylus,* it

Table 1. Actions performed by *T. rapicauda* before, during and after courtship and mating.

	before copulation								copulation							after copulation									
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y
01					X	X			X															X	
02				X					X																
03				X					X																
04									X							X								X	
05		X	X	X	X	X		X	X	X				X		X				X	X				
06									X				X	X	X	X				X		X		X	
07																				X	X			X	
08		X	X	X	X				X								X							X	
10																				X	X	X	X	X	
12							X		X		X		X		X	X				X	X				
13																			X	X	X	X			
14							X		X				X	X		X		X	X	X	X			X	
15					X		X		X							X		X		X	X			X	
16										X										X				X	
17				X	X		X	X	X	X			X		X			X		X				X	
18									X								X			X				X	
19		X		X	X	X	X		X	X			X		X	X		X	X	X					
20																X				X	X				
21																X		X	X	X	X				
22											X					X				X	X				
23											X								X	X	X	X		X	
24																			X	X	X				
25																				X	X	X		X	X
26																				X	X				
27																				X	X	X			
33			X	X				X	X	X		X	X			X		X		X	X				
34				X						X										X	X			X	
35									X	X		X	X			X		X		X	X			X	
38	X			X			X		X		X		X	X		X		X	X	X	X	X		X	
41									X	X								X		X	X			X	
42											X									X	X				
43											X									X	X	X	X	X	X
44			X	X	X			X	X		X		X	X		X		X	X	X	X	X		X	
45										X										X		X			X
46										X										X	X			X	
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y

Table 1.
Observations. (Numbers in parenthesis refer to Carpenter and Ferguson 1977).

A. Male protrudes tongue (63).
B. Male bites female's tail (17).
C. Male bites female's flank (128).
D. Male bites female's neck (129).
E. Male mounts female (125).
F. Male wriggles, moves sideways on female's back (108).
G. Female attempts to move forward.
H. Female arches tail.
I. Male opposes his cloaca to hers. Copulation (13).
J. Copulation from female's left.
K. Copulation from female's right.
L. Crossover copulation.
M. Male thrusts. (137).
N. Male wraps tail around female's (132).
O. The female attempts to move forward.
P. Violent tremble accompanies separation (14).
Q. Separation not accompanied by violent tremble.
R. Female moves off.
S. Female's tail arched.
T. Male's tail arched.
U. Male licks hemipenis.
V. Male pursues female (19).
W. Female pursues male (19).
X. Hissing call heard (154).
Y. MC call heard (154).

is relatively short. It seldom happens that all of the possible preliminary movements are made and the inclusion or omission of them has a bearing on the duration of the courtship phase. In *T. rapicauda* the female is relatively passive, whereas the male makes several different movements before copulating. I have seen copulation with some or all of courtship 18 times and part or all of post-copulatory behaviour another 27 times. Table 1 summarises 36 of these observations, the remaining 10 being omitted because they add nothing. From this we can reconstruct the full repertoire of movements during courtship, copulation and the post-copulatory period as follows. Seemingly, following chemical cues (see Discussion) the male approaches the female who may or may not move away at his approach. He bites the female's tail and moves forward on one side of the female. When his head reaches alongside the female's pelvis, he transfers his bite to her flank and then her neck. He crawls on to her back, and briefly wriggles his body from side to side. During this phase the female often tries to move forward. The male restrains her with an arm gripping her near midbody and a leg gripping her near the tail. The female then arches the base of her tail (seemingly as a response to the biting and the rubbing) and keeping one leg pressed to the female's rump, the male slips his pelvis under the female's tail and presses his cloaca to hers. It has been impossible to see if the hemipenis is everted at this stage.

During copulation the male thrusts his pelvis against

the female. The thrusts start at the rate of about one per second, and are at first fairly gentle – pulses rather than thrusts. Later the thrusts are much more powerful, last 2-3 sec. and may have the effect of curling the male's body much more strongly. The thrusting seems not to involve prior partial withdrawal of the hemipenis. Throughout copulation the hemipenis is kept firmly within the female's cloaca. The female sometimes tries to move forward but is restrained by the male.

Separation usually comes abruptly and details are hard to see. There is a violent shaking or shivering which lasts a fraction of a second, and then the two are separate. The shaking is sometimes violent enough for one or both of the lizards to fall to the ground as a result; the rattle it produces is audible and recognizable for what it is when heard. After separation the female usually moves off a short distance with a slightly arched tail. The male usually stands still with a strongly arched tail and the reddish hemipenis partially everted. He will then curve around and lick the hemipenis, sometimes for many minutes, either in one uninterrupted session or in several sessions with movements in between. Occasionally, he may chase the female before licking the hemipenis, but in my observations he has always licked his hemipenis. Sometimes the chasing that follows copulation is accompanied by the sound I call a hiss (No. 2 above). This sound is made by both male and female.

It may be assumed that the shaking causes the separation of the two lizards. This may not be correct. To help in deciding the issue, I give descriptions of six different instances: No. 19 (7/5/97). A violent shaking of the pair occurred so quickly it was impossible to know exactly what happened. There may have been 6-9 oscillations and then the lizards separated with the male's hemipenis still partially everted. No. 33 (2/12/01). The male got off the female on her left side, shivered violently without shaking the female and then moved away. No. 35 (14/6/02). The male removed his leg from the female's rump and stood clear of her. He shivered violently shaking the female a little. No. 38 (24/7/03). At parting the male removed his leg from the female's rump while still biting her, shivered, released his bite on the female who then moved away. No. 44 (19/3/05). The male removed his leg from the female's rump and stood a little to her right. Still biting the female, he shivered violently shaking the female at the same time. He released his bite and she moved 20 cm away with a slightly arched tail. On one occasion there was a completely different type of separation and here there may have been some influence from the near presence of the observer. The lizards remained joined for l0 - l5 sec. after first observation. The male then got off the female and turned around to face the opposite direction. He then pulled himself free and ran off hissing. No. 18 (3/12/96). One other separation (No. 8) took place with almost no shaking, the female seeming to slip forward without difficulty.

On four occasions liquid containing white suspended matter flowed down the wall from the lizards during or at the end of copulation. This is thought to be a mixture of semen and urine from the female's cloaca. Ten copulations were timed accurately enough to be meaningful. The mean of these was 3 min. 2 sec. with the range 2 min. 18 sec. - 4 min .

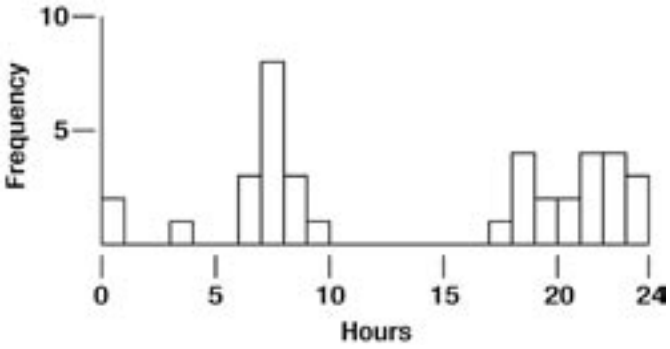

Fig. 1. Distribution of 36 copulations by hour.

Time of copulation

Figure 1 plots copulation as a function of time. There are only 38 observations, instead of 46, because the times at which eight copulations occurred were not recorded. During the period 1000-1800 h no copulation has been observed which is unsurprising for a nocturnal animal. For the next six hours (roughly sunset to midnight) 21 copulations were recorded, which is again unsurprising. Three observations for the next six hours is obviously low, but this coincides with the observer's period of sleep. The 15 observations (39.5%) in the period 0600-1000 h is remarkable for a nocturnal animal and points to a considerable amount of activity in these daylight hours. Figure 2 shows that the lunar cycle does not influence the timing of copulation.

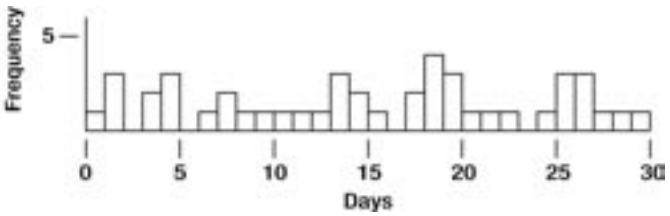

Fig. 2. Distribution of 46 copulations by day through the lunar cycle with Day 1 being the day of new moon.

Table 1 shows that the male usually chases the female after copulation, but there is in fact much variability. In case No. 10 the male bit the female twice while making the hissing sound and before running off. In No. 25 the male made the MC call just seconds after separation and

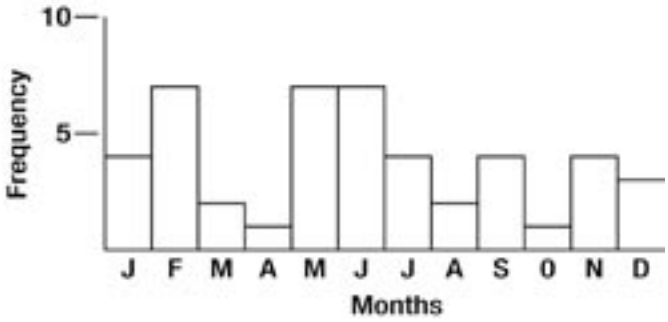

Fig. 3. Distribution of 46 copulations by month.

before licking his hemipenis. This same male, a minute or two later, caught his mate by the base of her tail and gave her a thorough shaking. Copulations 25 and 26 had taken place almost simultaneously with the two couples less than 2 m apart. One of the females ran close to male 25 when she was caught. It was probably his mate, but not certainly so, for I could not accurately keep track of what all four of the lizards were doing at the same time. After copulation 43 the female moved 3-4 m from the site with the male in pursuit. She eventually turned to face the male and tried to bite him. Then she gave the MC call and the male fled. She then uttered two "kek" calls before finally moving away. After copulation 45 the male remained at the site with his body turned around as though licking his hemipenis but I could not actually see this. The female, meanwhile, moved about 2 m off. After about 5 min. the male began tracking her, seemingly by scent, and came face to face with her. He fled behind a small electric oven and the female then gave the MC call. She later moved farther on with the male dallying about 50 cm behind for a while before ceasing to follow.

A failed attempt at copulation is also instructive. A male biting a tailless female on her neck came into view. He was trying to mount the female but kept slipping off as she moved forward. It seemed as though the absence of a tail deprived him of an anchor for his leg on her rump and he never made contact with her cloaca.

Which of his two hemipenes was licked by the male was noted for 22 of the 46 copulations. In 12 it was the left and in 10 the right. This means that on 12 occasions the male copulated from the female's right side and on 10 occasions from the left side. The difference is not statistically significant. ($x^2 = 0.18$, $P = 0.67$).There were only two occasions (33, 35) when the male adopted a "crossover" position, biting the female's neck just right of the mid-line but copulating from her left side.

Breeding Season

Fig. 3 shows that copulation has been recorded for all months of the year, so that there is no breeding season in the ordinary sense of the term. In other words, breeding is continuous.

Only one copulation has been recorded for October but there is other evidence of breeding in that month. On 18/10/02 a female was found on the floor obviously dying from injuries sustained in an accident of 2/10/02. Two hours later she was dead and examination showed she was gravid. The egg measured 16 x 11 mm, was still without a shell but probably close to laying. However, continuous breeding of the species does not mean that the female is always ready to accept the advances of the male. The following observation illustrates this. I heard the sound of a lizard falling to the floor and went to investigate. I found on the floor a dark individual I could recognize as Three-toed Sloth (TTS - named so because of missing fingers on his right hand) and known to be male. On the ceiling was another lizard I could recognize as White Patches (WP - so named for distinctive marks on the tail). TTS quickly ran up the wall and approached WP with the exaggerated, "humped up" stance I had assumed to be defensive. He then bit WP on the flank just rearward of the left arm and held on. WP was then off the ceiling and high up on the wall. He attempted to mount but WP would not co-operate. Together they moved down the wall and then, when near the bottom, up again. WP eventually struggled free and ran to a spot about 70 cm away. The time was 0626 h. I wrote up the observations and then went back to look for them. I found them again close together at the bottom of a nearby door. TTS bit WP, stepped back briefly and then bit her again and held on. He managed to transfer his bite to a point just right of the mid-line and rearward of the right arm. WP arched her tail and copulation followed (No. 33 in Table 1).

Egg deposition

Thecadactylus eggs are hard to find; I have found only one at the study site, on 19/2/90. It measured 14 x 13 mm and was buried in dry soil below the NE corner of the house. This site was searched again on 22/11/01 and 29/6/05. Neither eggs nor eggshells were found. Because I wanted dated eggs for determining the duration of incubation, I built a small retreat shaped like a Nissen hut that I thought might attract them as a laying site. They ignored it. Thinking they might lay in sand I got two circular biscuit tins and filled them with sand. On 26/1/01 I put them in the kitchen against the fridge where they would be seen. No egg was laid in them during the next 10 months. I tried again three years later with two plastic trays placed on the floor of the porch against the west wall on 1/7/05. To 6/2/06 no egg has been laid there.

On two occasions during the year 2005 the attic was

searched for eggs but none was found. Eggs of *Gonatodes ceciliae* have been found in large clusters in clefts in limestone boulders in the Heights of Aripo. In searches with Stephen Smith which resulted in these finds no *Thecadactylus* egg was ever found.

Back in 1955 on 12 February four eggs were found in light soil at the base of one tree and one more egg at the base of another tree at the side of Serpentine road, St Clair. On 22 May that year two more were found at the base of a tree in the same area. Although Beebe (1944) collected "dozens of these geckos" the only egg he had was one laid by a captive specimen.

DISCUSSION

Humans evolved in the tropics and they breed all the year-round so it is easy for them to believe that tropical animals breed year round. However, this is not the case. In Brasil the neotropical skink *Mabuya nigropunctata* breeds in the dry season, August - December (Vitt and Zani 1997) while in Trinidad it breeds in the period January - August (Quesnel 2005). The iguanid *Tropidurus plica* also breeds from February to August in Brasil (Vitt 1991). However, *Anolis trinitatis* (Gorman and Licht 1975) and the gecko *Gonatodes vittatus* (Quesnel 1957) in Trinidad breed year-round. The data presented above indicate that *Thecadactylus rapicauda* also breeds year-round. However, continuous breeding of the species does not mean that the female is always ready to accept the advances of the male, as the observation on TTS and WP illustrates.

It is clear from the final outcome that TTS made the correct assessment of WP's physiological condition in his initial bite. Why then did they not mate on his first try? One possibility is that WP may have been a virgin about to experience her first sexual encounter. She may simply have reacted to what was new. If she was not a virgin it may be that a certain amount of learning is required before events proceed smoothly. Van Lawick-Goodall (l97l) gives a vivid description of how different the first sexual encounter of a virgin chimpanzee can be from subsequent ones. Chimps are not reptiles but there may be something common to both in this situation. Anyway, the fact that this "experimental" bite is there in the male's repertoire suggests that the female's physiological state varies in a patterned way in each individual and provides each individual with its own breeding season.

In this species the clutch size is one. Of the four eggs collected on 12/2/55, two hatched on the same day (15/5/55) leading me to believe for a long time that the clutch size is two. This is disproved by the captive female that laid one egg in her vivarium (Beebe 1944) and by the presence of just one egg in the oviduct of the specimen I dissected on 18 October, 2002 (see above). It is likely that the female is unreceptive to the male during the early development of the egg. She would then become receptive as the optimum time for fertilization approached and remain so until the egg had acquired its shell. The 'experimental' bite of the male is his means of determining when this state has been achieved.

WP was described and named on 4/3/01 nine months before she was seen in the incident of 2/12/01 which was described earlier. On three subsequent occasions her post-copulatory behaviour was witnessed in copulations 36 of 2/2/03, 38 of 24/7/03 and 39 of 13/11/03. The last record of her was on 4/2/04 so she had been under observation for a period of 2 years 11 months. Not enough of her copulations were seen to establish a pattern of egg laying (assuming a close connection between insemination and egg laying), but it does seem very possible that the first of her copulations that was seen was actually her initiation to sex.

Table 1 records that the hiss sound was heard at some stage in 21 of the 46 copulatory encounters, one (No. 1) before copulation, three times both before and after and 17 times only after copulation. It is not always possible to know which lizard makes the sound. It is likely that the sounds made before copulation come from a reluctant female. The ones made after copulation can come from either sex. Of the eight calls where one could be sure of the author, two were from females and six from males. Of the two females, one called at separation, the other running away after separation. Of the males, one (No. 18 - see above) hissed on separation, the others all hissed while chasing females.

Animals that do not live in groups (flocks or herds) seem to find close contact with others of their kind stressful, and they avoid it. The fact that 21 of 46 matings generated hissing protests (cries of annoyance) suggests that in this species courtship does not suppress all aggressive behaviour. For the duration of copulation aggression is suppressed, but once that is over aggressive tendencies come flooding back stimulated by the proximity of the protagonists, hence the biting and hissing.

Ten of 22 males copulated from the female's left and twelve of them from the right showing no statistically valid preference for one or the other. Had I learnt much earlier what I recently learnt, that cats like humans are either left or right-handed (pawed), I would have paid much more attention to this aspect of the behaviour of *T. rapicauda.* Yehudah Werner (pers. comm.) has reported that handedness does in fact occur in reptiles. For two reasons, *T. rapicauda* would make a good candidate for the study of this phenomenon in lizards: 1). The hiss that occurs so often at the end of copulation alerts the observer to the fact that copulation may have occurred. 2). The licking

of the hemipenis which always occurs after copulation indicates from which side of the female it has taken place. The problem then boils down to collecting enough data on identifiable individuals to obtain a statistically significant result. For me the most surprising aspect of the behaviour is the violent shaking that accompanies separation of the mating animals. At first I considered that this was necessary to liberate the hemipenis from the female's cloaca, but the six variations described earlier argue against this simple postulate. It seems that sometimes the male removes his leg from the female's rump so that he stands to one side. In this case either the hemipenis is already free or it is still locked within the cloaca and stretches as the male gets off. I have found it impossible to see the hemipenis at this time and believe that a stretch of such a length may be impossible. If so, the hemipenis would already be released, so what then is the function of the violent shake? The shake always affects the male but not always the female. It usually (always?) occurs before he stops biting the female so it is an unlikely signal of release. So why does it occur? I have no satisfactory answer. Perhaps the "impossible" stretch is possible. The male of copulation 18 who pulled away without shaking (see above) did seem to be stretching something. Perhaps the shaking does shake loose the inserted hemipenis. This implies spines in the hemipenis such as some snakes have (Bellairs 1960), but it has not been possible to investigate this adequately.

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