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Food and Feeding Behaviour of the Nocturnal Neotropical Gecko *Thecadactylus rapicauda* (Houttuyn) in a Dwelling House in Trinidad, West Indies

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ABSTRACT
Thecadactylus rapicauda is a sit-and-wait predator. In ambush on a vertical surface it prefers a vertical orientation to a horizontal one. Its diet includes a wide variety of insects, at least one spider and some vertebrates. The insects come mainly from the orders Lepidoptera and Orthoptera. Three vertebrate species are recorded as prey for the first time. They are the frog *Scinax rubra* and the lizards *Gonatodes vittatus* and *Tropidurus plica*. Though basically nocturnal, *T. rapicauda* spends some time hunting by day and eats diurnal species as well as nocturnal ones. It prefers big prey to small prey and uses a head-down posture when battering its prey items to death before swallowing them. An argument is advanced to show that as the force of battering increased through the preferential selection of big prey, the need for a secure foothold on the vertical surface increased and led to the evolution of the highly effective adhesive pads on the digits. Only a few observations have been made on the feeding of the spider *Avicularia avicularia,* but from these it is deduced that it is a direct competitor of *T. rapicauda*. The two species eat each other.

Key words: *Thecadactylus rapicauda,* food, prey items, big prey, battering.

INTRODUCTION

This paper is the second of a short series describing the behaviour of *Thecadactylus rapicauda*. The first (Quesnel 2006) dealt with reproductive behaviour; this one deals with food, feeding and associated activities such as drinking and defecating. *T. rapicauda* is a sit-and-wait predator (Quesnel 2004) and is most often seen immobile. However, the frequent battering that takes place when a *Thecadactylus rapicauda* has caught relatively large prey attracts attention because of the sound it makes. Thus, by such means and by chance encounters with feeding individuals, a body of knowledge has gradually been built up over the past twenty-two years and is here presented.

STUDY SITE AND METHODS

The study site was my home on Leotaud Trace near Talparo, Trinidad. The house was described in the earlier publication and will not be described here. The lights, some of which are never switched off, attract a variety of insects, the therophosid spider *Avicularia avicularia* and other lizards such as *Gonatodes humeralis, Gonatodes vittatus*, *Hemidactylus mabouia*, and *Sphaerodactylus molei*. In the dry season the frog *Scinax rubra* is attracted by the water in the bathroom.

Because *Thecadactylus rapicauda* is nocturnal, a torch (flashlight) was often required for better observation of details. Most of the adults were habituated to human presence and allowed a sufficiently close approach that the prey could sometimes be identified to species while being eaten. However, in presenting the results in tabular form they are often assigned to orders and families. Times of capture were recorded and, later in the study, a short description of size and appearance. If the individual lizard could be identified from characteristic markings, its identity was also recorded. The behaviour was described as completely as conditions permitted. Prey items that appeared to be spat out because they were distasteful were not counted as food. Prey items that seemed to be lost accidentally when the predator was trying to subdue them were counted as food.

Butterflies of the genera *Caligo* and *Eryphanis* are important prey items for *Thecadactylus rapicauda* and the eyespots on the under surfaces of the wings frequently deflect attack to a non-vital part of the insect. Eighty-four individuals of the four species (three of *Caligo* and one of *Eryphanis*) were identified as victims of *T. rapicauda* attacks. Six of the victims perished and 78 survived at the cost of pieces of wing which were eaten by the lizards. These 78 individuals all qualified for inclusion in this study and appear in Table 1. For convenience the terms ‘arm’, ‘leg’, ‘hand’ and ‘foot’ are used with the same meaning as for human limbs. Dates are given in the form day/month/year.

OBSERVATIONS

Orientation of the Predator in Ambush

It has been mentioned already that *Thecadactylus rapicauda* is a sit-and-wait predator (Quesnel 2004). Casual observation suggested that it preferred vertical surfaces to horizontal ones when sitting in ambush. It seemed to use the floor only in pursuit of prey or to return to the wall after falling off. Though it occasionally lay in wait on the ceiling, it was much more often seen on the walls where individuals preferred an up-down orientation to a horizontal one. These ideas were tested in a series of 112 observations during the period 4/10/01 – 30/11/01. Observations were made only in the normal period of activity roughly between 1800 h and 0600 h and no more than one observation was made on one individual on any one day. At each observation the body axis was assigned visually to one quarter of a square according to the figure below. No observation was made on any lizard close enough to the floor or ceiling for its orientation to have been influenced by the near presence of the extra surface.

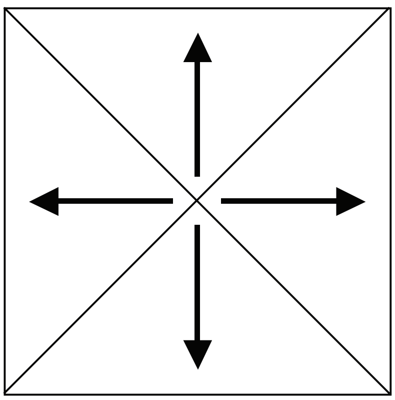


Fig. 1. Approach to description of body axis.

The distribution was as follows: head up 42, head down 35, head left 18, head right 17. Therefore, *T. rapicauda* does indeed seem to prefer a head-up stance in ambush. The counts revealed a population of at least eight individuals.

The Time of Feeding

Figure 2 is a frequency distribution of the time of capture of prey items by *Thecadactylus rapicauda* over 22 years of study. Four features are noteworthy: 1). most prey items (46, 58 %) were captured during the period 1800 h to midnight; 2). fewest (5, 6 %) were captured during the period midnight to 0600 h which coincides with the observer's usual period of sleep during which there were few observations; 3). twenty-nine (36%) were captured during the period 0600 – 1800 h indicating that *T. rapicauda* is not strictly nocturnal; 4). there is no peak in the numbers captured at 1800 h although sunset is the time of maximum activity for important prey items such as species of *Caligo* and *Eryphanis* (Quesnel 2003). The 78 individuals of these genera that are known to have been attacked (Table 1) are unrepresented in Fig. 2 because the time of attack of each is unknown but also because of the prey's ability to elude capture.

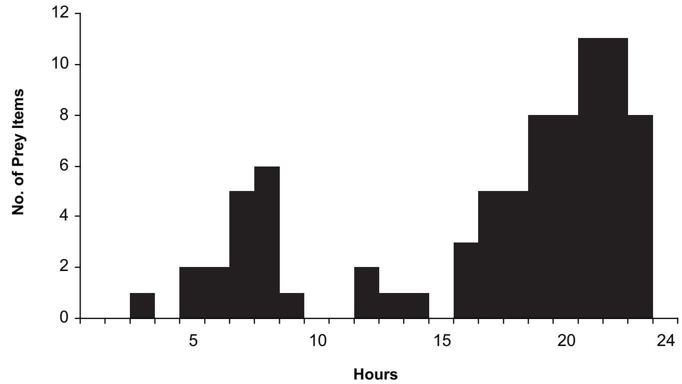


Fig. 2. Frequency distribution of the times of capture of prey by *Thecadactylus rapicauda* over the 22 years of the study.

Prey Consumed

Table 1 displays the range of prey attacked and consumed by *Thecadactylus rapicauda*. For the most part they are arranged by order and family in an order similar to that in Vitt and Zani (1997) so that the two tables may be easily compared. In a general way they follow the classification of insects by Kirkpatrick (1957). There are 22 categories of prey in all, in which six are families, four are single species and the other eight are groups ranging from orders to genera. Column 2 consists of items known to have been completely consumed whereas items in Column 3 escaped after capture or were eaten in part whether by accident or design. Thus 78 of the 96 items (81%) of those in Column 3 are individuals of *Caligo* or *Eryphanis* that were attacked as prey but escaped because the attack was directed at eyespots on the under sides of the wings and the butterflies escaped leaving a piece of wing for the lizard to eat. Four other brassolids similarly escaped capture, one sphingid moth was too large to be swallowed and was discarded, an *Avicularia avicularia* escaped after one leg was bitten and broken off and a young *Tropidurus plica* of S-V length 50 mm, was discarded as too big to swallow.

In Columns 5 - 7 the prey items have been classified by size in an attempt to show that *T. rapicauda* eats more big prey than small. This will be taken up again later but it may be stated here that strictly mathematical considerations are not appropriate. The animals in the large category have a body length (not counting the wings) of 36 mm and above. Those in the Small 2 category have a body length of 23 mm or less.

The category most often attacked (Col. 4) was that of the category *Caligo* plus *Eryphanis* with a total of 84 (28%). Taking the family Brassolidae as a whole for comparison with the other families, the number attacked rises to 95 (32%). The next largest category is the group Tettigoniidae plus Acridiidae followed by the group "other moths". Comparing the larger groupings such as orders

Table 1. Distribution of prey items by taxonomic status and size.

1	2	3	4	5	6	7
Orthoptera						
Tettigoniidae + Acridiidae	44	3	47	13		0
Gryllotalpidae	3	0	3	3	0	0
Blattodea	7	2	9	1	2	2
Mantodea	9	0	9	5	0	4
Isopterans	10	0	10	0	10	0
Homoptera (cicadas)	6	2	8	0	0	0
Coleoptera (beetles)						
Scarabiidae	11	0	11	0	7	7
Others	6	0	6	0	2	2
Lepidoptera						
Caligo + *Eryphanis*	6	78	84	84	0	0
Other brassolids	7	4	11	0	0	0
Hesperiids (skippers)	1	0	1	0	0	0
Saturniidae	4	2	6	1	0	0
Sphingidae (hawk moths)	20	3	23	4	0	5
Notodontidae	7	0	7	5	0	0
Other moths	38	0	38	1	15	31
Hymenoptera						
Formicidae (ant alates)	16	0	16	0	16	16
Odonata	2	0	2	2	0	0
Diptera						
Tabanidae (horseflies)	3	0	3	0	3	3
Arachnida						
Avicularia	0	1	1	1	0	0
Vertebrata						
Scinax rubra (frog)	1	0	1	0	0	0
Gonatodes vittatus	3	0	3	3	0	0
Tropidurus plica	0	1	1	1	0	0
	204	**96**	**300**	**124**	**55**	**70**

Col. 1. Edible species arranged taxonomically.
Col. 2. Number of prey items seen to be eaten.
Col. 3. Number of prey items attacked, but not known to be eaten.
Col. 4. The sum of Columns 2 and 3.
Col. 5. Number of individuals attacked above 35 mm long after connection for battering (see text).
Col. 6. Number of attacked individuals that were shorter than 20 mm. Small 1.
Col. 7. Number of attacked individuals that were shorter than 23 mm. Small 2.

the number consumed was largest in the Lepidoptera (82 - 40%), followed by Orthoptera (63 - 31%). Only one arachnid species appears in the table, and that only partially eaten, *Avicularia avicularia*.

Thecadactylus rapicauda does not eat everything that comes its way. Table 2 gives a summary of the species rejected as food with short descriptions of the behaviour observed with each. Some of the rejected items (assassin bugs, fire-flies, click beetles and *Apoica* sp.) were scrutinized at a distance of 3-10 cm before being rejected. Sometimes the scrutiny involved tongue flicks, at other times it seemed to be visual only. Other rejected items (cockroaches, stinkbugs, moths) were bitten or bitten and shaken before being rejected. It is assumed that the biting allowed the lizard to determine whether the object was distasteful or not.

Table 2. Insects rejected as food by *Thecadactylus rapicauda*.

Insects	Incidents	
	No.	Kind
Blaberus sp. (cockroach)	2 1	Touched with tongue; rejected Bitten, rejected; lizard wiped tongue
Pentatomidae (stink bug)	1	Bitten, shaken; lizard moved away
Reduviidae (assasin bug)	2	Scrutinized from ca. 3 cm; lizard moved
Lepidoptera (moths)	2	Both bitten and spat out
Cantharidae (fire-flies)	4	Scrutiny from about 5 cm, tongue flicks
Elateridae (click beetles)	1	Scrutinized close up
Apoica sp. (nocturnal wasps)	1	Scrutinized for 10 min. at about 3 cm

Capture and Ingestion of Prey

Since *Thecadactylus rapicauda* is a sit-and-wait predator, prey and predator most often meet when prey moves into the range of vision of the predator. When this has happened two different responses from the predator have been observed; a rapid run to attack and capture the prey or a period of scrutiny and slow approach. The former has occurred when the potential prey has kept on moving after attracting the predator's attention; the latter has occurred when the potential prey has ceased to move. Thus, when small active prey (ant alates, small beetles, small moths) have aroused the interest of the predator, the latter responded with a quick run to the prey which was then bitten, squeezed and swallowed at the site of capture. With large prey that has stopped moving the response has been different. The predator has stalked the prey with an advance so slow it was almost impossible to detect. This was the method used when hunting brassolid butterflies, moths and katydids. Table 3 gives some measurements of the speed of advance in such cases. The final move was either a quick run of two or three steps (impossible to see clearly) or a more carefully prepared strike in which the predator slowly moved one foot far forward to the armpit, anchored it to the substrate there and then lunged forward keeping the anchored foot in place. Head down now, squeezing the prey in its jaws, the lizard battered and scraped it on the substrate.

With the prey now subdued the lizard began the long process of swallowing it and early in the process turned head up. Then by adding two more movements to the two already described (scraping and battering) the lizards tried to engulf the inert prey. The first was a stretching upward with the mouth agape and the second the assumption of an S-shaped configuration of the body accompanied by a "pressing down" motion. On one occasion the lizard was first seen at 2255 h on 6/1/02 head down battering a species of *Crinodes* moth it had caught from behind. At 2309 h it turned head up and after 24 scrapes, 14 stretchings, 12 twists and three batterings the wing tips of the moth finally disappeared at 0055 h on 7/1/02. After more scrapes, stretchings, licking of the lips left and right, and licking of both eyes for another 10 minutes the meal was finally over. Clearly, the head up posture during the swallowing allows the force of gravity to aid the process.

Such is the usual course of events, but *Thecadactylus rapicauda* does not always have its way unspoilt. On at least 3 occasions prey has inadvertently shot out its mouth during the battering stage, presumably because it had not been held firmly enough. On one occasion it was a *Periplaneta* cockroach, on another it was a brassolid butterfly (*Opsiphanes cassiae*) and on the third occasion it was a sphingid moth. On every occasion the lizard paid no further attention to the prey on the floor below it even though it may have been in full view.

There have been at least two instances where an attacking *Thecadactylus rapicauda* has missed its target or barely touched it. In another similar occurrence a subadult individual approached a tettigoniid, closing the gap between them fairly quickly and flicking its tongue as it moved along. When still about 20 cm from the insect the lizard lunged towards it four times covering a distance of about 4 cm with each lunge. On the fifth lunge the lizard bit the insect, then let go and backed off as though afraid.

Table 3. Some measurements of the average speed of advance when *Thecadactylus rapicauda* stalks its prey.

Prey Item	Estimated distance mm	Time taken min.	Ave. rate mm/min.
Tettigoniid	50	12.5	4.0
Eryphanis automedon	81	60	1.35
Eryphanis automedon	200	60	3.3
Eryphanis automedon	125	50	2.5
Opsiphanes cassiae	140	15	9.3
Opsiphanes cassiae	80	225	0.36
Small moth	250	10	25

After two or three more ineffectual lunges the tettigoniid flew away. The whole incident was so unusual that it may have been a youthful lizard's first attack on a tettigoniid.

Table 1 records nine instances of *Tecadactylus rapicauda* eating mantids. In one or more the initial attack was unsuccessful. The mantis, thought to be a *Stagmatoptera septentrionalis,* was on my desk where it was noticed by a nearby *T. rapicauda* who approached it rapidly, bit it on the thorax, shook it 3-4 times and, surprisingly, let it go. The mantis then reacted with its full defensive display (see Fig. 32 in Crane 1952). The lizard fled but on the following day what seemed to be the same mantis, which had remained in the vicinity, was caught and eaten by a *T. rapicauda*.

Thecadactylus rapicauda and Brassolid Butterflies

Three species of *Caligo*, one of *Eryphanis*, two of *Opsiphanes* and one of *Catablepia* are often attacked by *T. rapicauda*. All of these species have eyespots on the under surface of the wings that are thought to deter or deflect a predator's attack. This study includes five individuals of the genus *Caligo* and one of *Eryphanis automedon* that were eaten by *T. rapicauda* (Table 1, Col. 2) and 78 individuals of the same genera with wing damage typical of *T. rapicauda* attack (Table 1, Col. 3). Unfortunately, the time of attack is not known for any of the individuals and they are thus unrepresented in Fig. 2.

T. rapicauda and *Avicularia*

Avicularia avicularia is the most common of several native theraphosid "tarantula" spiders and there may be as many as three or four of them in my home at any one time. From my limited observations it is clear that they eat moths, tettigoniids and cicadas as does *T. rapicauda* and the two species may be direct competitors. They even eat each other as the following observations will show. On 9/9/91 a *T. rapicauda* stalked and eventually grasped an *A. avicularia* by one leg. The lizard shook the spider, breaking off the leg it was holding while the spider fell to the floor. The lizard then ate the leg untroubled by the hairs. On 12/04/05 a scuffling sound attracted my attention to a calendar on the wall. Two *T. rapicauda* ran out from behind it and the leg of an *A. avicularia* appeared as well. Exposing the spider I could see that it was eating the tail of one of the lizards which was still wiggling. How the battle began I did not see, but it is certain that the spider's bite was strong enough to cause the bitten lizard to break off its tail and strong enough to cope with the spasms of the severed tail.

T. rapicauda and Vertebrate Prey

The only vertebrate previously listed as prey is *Sphaerodactylus molei* (Murphy 1997). This paper lists three more species; two lizards and a frog. My notes record *Gonatodes vittatus* as prey on three occasions with the added information on one occasion that *Thecadactylus rapicauda* swallowed it in only 2-3 min. The second lizard is *Tropidurus plica* whose S-V length is about 15% longer than that of *T. rapicauda*. Five hours and 20 mins after an adult *T. rapicauda* had captured a hatchling, the prey was discarded as too big to swallow. It had been seized from the rear and on ejection the entrails and most of the tail were missing, presumably digested. The corpse was measured and preserved in formalin. SVL = 59 mm, 49% of max *T. rapicauda* SVL.

The *Scinax rubra* was eaten on 19/4/03. As in the case above, the predator had caught its prey from the rear and its legs were sticking out from the side of the mouth when, attracted by the sound of battering, I arrived on the scene at about 2015 h. By 2032 h the swallowing was almost over. Murphy (1997) gives the SVL for males as 34 mm and for females 39 mm.

T. rapicauda and Big Prey

An adult male *Thecadactylus rapicauda* that had been preserved on 26/9/05 was measured and dissected: SVL = 88 mm, stomach = 42 mm long. A female that had been preserved on 1/1/02 after removal of the head for preparation of a skull was dissected and measured: stomach length = 39 mm. For easy calculation we can take 40 mm as the mean length of an adult stomach. Prey that can fill or nearly fill a stomach of this size is considered to be big prey. In the early years of the study attention was focused on what the lizards ate rather than the size of the prey, which was not measured. In any case the measurement of prey that was being consumed was impossible without interference. However, measurements of food items have been made more recently on insects caught or found dead in the study area or those in the collection at the University of the West Indies. A partial list of the measurements made is given in Table 4 as a guide in the process of determining to what size category prey should be assigned.

The problem now at hand is how to convert "can fill or nearly fill a stomach" into some more objective measurement. With insects like mole crickets, beetles and even short-horned grasshoppers whose shape is roughly the

Table 4. Prey size given in mm for some large to intermediate insects in the diet of *T. rapicauda*. Body length (Body L.) = length to tip of abdomen. Total length (Tot. L.) = length to tip of wings. For mole crickets and mantids these two are virtually identical. For Lepidoptera wing span is given instead of total length. %40 = % length of *Thecadactylus rapicauda* stomach.

Prey Items	Tot. L.	%40	Body L.	%40	Class	Source
Long-horned grasshoppers						
Unidentified	70	175	27	67.5	Large	VCQ*
	70	175	30	75	Large	VCQ*
	60	150	30	75	Large	VCQ*
	56	140	30	75	Large	VCQ*
Short-horned grasshoppers						
Unidentified	38	95	30	75	Inter	VCQ*
Mole crickets (Gryllotalpidae)						
Unidentified			38	95	Large	VCQ*
Cockroaches (Blattodea)						
Blaberus atropes	54	135	45	112	Large	R&W+
Periplaneta americana	31	77.5	28	70	Inter	R&W+
Mantids (Mantodea)						
Stagmatoptera septentrionalis			75	187	Large	Crane[x]
Vates lobata			60	150	Large	Crane[x]
Butterflies, moths (Lepidoptera)						
Caligo eurilochus	158	395	37	92.5	Large	VCQ*
Caligo illioneus	133	333	33	82.5	Large	VCQ*
Opsiphanes cassiae	81	203	32	80	Inter	VCQ*
Unidentified saturnid	107	267	39	97.5	Large	VCQ*
Unidentified sphingid	80	200	40	100	Large	VCQ*
Notodontidae (*Crinodes*)	37.5	93.7	35	87.5	Large	VCQ*
Odonata: *Anax junius*			58	145	Large	UWI[o]
Boyieria venosa			50	125	Large	UWI[o]

* Living or dead specimens measured by the author in the study area.
+ Size measured by the author from pictures in Roth and Willis (1960).
[x] Size stated in Crane (1952).
[o] Specimens in the UWI collection measured by the author. Similar in size to the ones eaten by *T. rapicauda*.

shape of the lizard's stomach, the decision was relatively easy: a length of 35 mm, 87.5% of 40 mm, was considered enough to put it in the large category. Below that, where wings were relatively large, the nearer to 30 mm the body became, the larger the wings would have to be to compensate for the smaller body size. The upper limit to small (Small 1 in Table 1) was set at 20 mm and with these guidelines a classification was made as follows: large 149, small 55, intermediate 96.

However, this calculation is biased in favour of large prey by the inclusion of the large prey brought to the notice of the observer by the sound of battering. The records were reviewed and all such instances removed. As a further countermeasure to bias the upper limit to the Small category (Small 2, Table 1) was raised to 23 mm. The total number of large is now down to 124 (Col. 5) and the small up to 70, but the number of large prey items is still 80% more than the number of small prey items.

However, this is not all the evidence. On two occasions *T. rapicauda* has tried to eat prey that was too big for it to swallow. On 26/5/04 a *T. rapicauda* tried to eat a large sphingid moth which it spat out after 35 minutes of battering and attempted swallowing. Unfortunately, this moth was not measured. The second occasion was the attempted eating of *T. plica* already described under the heading of '*T. rapicauda* and vertebrate prey'.

Drinking

Drinking has been observed 14 times. *Thecadactylus rapicauda* laps in the manner of a cat but without curling the tongue backward. Instead, it flattens the tongue against the wall of the container at the water level and alternately protrudes and retracts it. Eighty-three laps were counted on one occasion and 245 on another occasion. It would seem that *T. rapicauda* can stand dehydration for long periods, perhaps several weeks, and then rehydrate when the opportunity arises.

Defecation and Urination

It is well known that in lizards urination accompanies defecation, the urine appearing as a white blob of uric acid along with the faeces. This "double act" has been seen four times with the lizard hanging by its arms from a support with its legs swinging freely. During this the legs moved and the tailed arched as though the lizards had great difficulty in expelling the excreta. If this is true in fact, then it is not surprising seeing how much of the food consists of hard angular exoskeleton. A drop of liquid has often accompanied the excreta and, on one occasion, what seemed like a sort of sac such as some species of nestling birds produce, surrounded the excreta.

On one occasion the lizard hung from the ceiling by the arms and one leg with the other leg swinging free. On this occasion there were no faeces but uric acid alone. On two occasions urination alone has been seen, separate from defecation, and this may be much more common than previously thought.

Like *Gonatodes vittatus* (Quesnel 1957), *T. rapicauda* seems to have preferred sites for defecation.

DISCUSSION

Thecadactylus rapicauda has a wide distribution from Mexico southward to Ecuador and Brasil as far as the limit of Amazonia and from Necker in the British Virgin Islands through the Lesser Antilles to the Guianas (Peters and Donoso-Barros 1970; Vitt and Zani 1997; Maclean 1982). Donoso-Barros (1968) states that in Venezuela it "lives in all the habitats including arid, rainforest, cloud forest, savannas and human habitations." Vitt and Zani (1997) observe that it "appears to be the only primarily nocturnal lizard in lowland tropical forest of Central and South America, although occasional individuals have been reported active during the day." It is likely that in the area where it evolved vertical surfaces were present on tree trunks and rocky environment. Beebe (1944) has remarked that anywhere in the neotropical region "when human beings first occupy a house" *T. rapicauda* has already occupied it. So it was with me when I occupied my study site.

In buildings *Thecadactylus rapicauda* is more frequently found on the walls than on the ceiling and it is almost never found on the floor. The present study has shown that on vertical surfaces it is more often in an up-down orientation than a horizontal one. Possibly this preference evolved because it better suited the tree trunk habitat where the gecko's long axis is parallel to the long axis of the trunk. However, it may have evolved along with the head-down stance for battering and the head-up stance for swallowing large prey.

Vitt and Zani (1997) consider *Thecadactylus rapicauda* to be "strictly nocturnal." I have not found it to be so. As Fig. 1 shows, 29 prey items of a total of 80 (36%) were taken during daylight hours with two in the hour after mid-day. In the preceding paper in the series (Quesnel 2006) it was recorded in Fig. 1 that 16 copulations occurred in the same period, 15 between 0600 h and 0700 h and one between 1700 h and 1800 h, contributing 42.1% of the total. Thus, *T. rapicauda* is also reproductively active during daylight hours. (A correction needs to be made to Quesnel (2006) concerning Fig. 1. The figure itself is correct but the accompanying text is faulty. Where it reads "no copulation" it should read "one copulation" and where it reads "21 copulations" it should read "19 copulations.")

Vitt and Zani (1997) studied the diet of two populations of *Thecadactylus rapicauda* in Amazonia, an eastern site at Curuá-una near Santarem and a western site at Cuyabeno in eastern Ecuador. The former is approximately 1600 km SSE of Trinidad and the latter approximately 2000 km SW of Trinidad. The two Amazonian sites are approximately 1700 km apart so they are further apart than Santarem is from Trinidad. Both of these are areas of lowland forest probably not too different from the secondary forest and agricultural estates near my study site. At the eastern site (Curuá-una) *T. rapicauda* ate food falling into 18 categories (not counting its own shed skin) most of them being families of insects. At the western site (Cuyabeno) *T. rapicauda* ate food from only seven categories with 19 of the 30 items coming from what was the family Blattidae (cockroaches) and is now the order Blattodea.

My Table 1 above contains 18 insect categories plus one arachnid category and three vertebrate categories. There is more similarity in the diet of *Thecadactylus rapicauda* at Curuá-una and the Trinidad site than there is between the two Amazonian sites. Furthermore, the first five of the categories in Vitt and Zani's Table 2 correspond with the first five categories in my Table 1. Only two categories of those five occur at the Cuyabeno site. The Formicidae occur only at the Curuá-una and the Trinidad sites but not at the Cuyabeno site. Here the similarities end. Of six beetles in the diet at Curuá-una none was a scarab whereas in Trinidad 11 out of 17 (65%) were scarabs. Only one moth of 36 items (2.6%) occurred in the diet at Curuá-una whereas in Trinidad there were 74 in 300 items (24.6%). Perhaps some of the species in the Trinidad sample were attracted by fluorescent light but, more likely, the Amazonian collections were made when some species were not "in season". Vitt and Zani (1997) hint at this when they write "few researchers spend long enough time periods within the habitats of these lizards to collect adequate samples." It is particularly surprising that only one Lepidoptera was found in the stomachs of the lizards at each of the Brasilian sites when 170 lepidopterans were counted among the total of 300 food items (57%) of the lizards at the Trinidad site.

No vertebrates were found in the Brasilian lizards but three species are herein reported for the first time in the diet of Trinidadian *Thecadactylus rapicauda*: the frog *Scinax rubra* and the lizards *Gonatodes vittatus* and *Tropidurus plica*. Of the three *G. vittatus* seen to be eaten two were male and the sex of the third was not noted. In previous studies of *G. vittatus* (Quesnel 1957; Quesnel *et al*. 2002) populations have always had a preponderance of females. Is this the result of preferential preying on males by *T. rapicauda*? *G. vittatus* males have a vivid pattern which makes them more visible than females so there is a distinct possibility that *T. rapicauda* eats more males than females and is thus responsible for the uneven sex ratio.

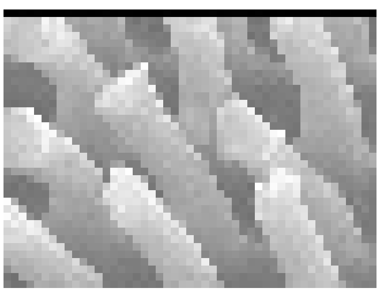
It was argued earlier that *Thecadactylus rapicauda* prefers big prey to small prey and it is time now to consider the consequences of this. Big prey is hard to swallow and can spend a long time (1-2 hours) in the throat of the predator. How does the lizard manage to breathe during this long period? The same problem is faced by snakes and their solution is "a special modification which allows the glottis (the opening of the windpipe) to be protruded and retracted" (Parker and Grandison 1977). When a bulky meal is being swallowed the glottis is protruded to the front of the mouth which allows breathing to continue. Does *T. rapicauda* have such a glottis?

Large meals imply that meals must be eaten sporadically with relatively long intervals between them. During these intervals the lizard's stomach must be empty and the lizard presumably hungry. I suggest that the individuals seen during daylight hours are hungry individuals extending their hours of hunting and, by being out in the open, extending the area under their surveillance. Presumably they can do this for long periods using the fat stored from the previous meal as the source of the little energy they need for this extra sitting and waiting. It was noted earlier that some individuals have expelled uric acid without expelling faeces at the same time. This is evidence that their digestive tracts were empty and a concomitant state of hunger highly likely. These ideas can be tested with captive specimens and should be tested if a more complete picture of feeding behaviour is to be acquired. The empty belly is known to affect foraging behaviour in the gecko *Goniurosaurus kuroiwae* (Werner *et al*. 2006).

The third consequence of eating large prey is the evolution of the highly effective pads on the feet of this species and it may have happened, I propose, in this way. *Thecadactylus rapicauda*, along with many other species, inherited the behaviour of battering its prey while standing head down on a vertical surface. There is no reason to believe that this behaviour is unique to it. In fact, I have seen the same behaviour in the much smaller *Gonatodes vittatus*. However, this behaviour was crucial to the evolution of the adhesive pads because it enlisted the force of gravity in subduing the prey. As the size of the prey increased, the power of the blows increased. This in turn put a premium on the ability of the lizard to hold on to its support, hence the evolution of the highly effective adhesive pads.

What happens when the lizard is not properly anchored to the substrate is illustrated by the difficulties encountered by Useless Leg. Some time prior to 20/11/00 this lizard had its left forelimb damaged. In time, the lower part rotted away leaving only the part above the elbow. He subsequently lost five digits on the remaining limbs. At 2230 h on 1/8/02 I found him on the kitchen floor trying to subdue a sphingid moth he had caught. He climbed the wall, turned head down and on beginning to batter the moth immediately fell off. He struggled back up, began battering again and promptly fell off again. He returned to the wall and managed to hold on until he turned head up at about 0105 h on 2/8/02. He had not managed to swallow the moth when by 0120 h observations ceased.

These observations indicate that the need for a tight hold on the vertical support when feeding, and not any imagined need to adhere to extraordinarily smooth surfaces, led to the evolution of the adhesive discs. While this paper was being prepared an article appeared in the Newsday of 7/12/06 announcing the development of a new adhesive "using light to etch three-dimensional patterns



Synthetic Gecko is composed of millions of mushroom-shaped hairs. (Photo taken from BBC.com world news story: **Geckos inspire 'super-adhesive'** http://news.bbc.co.uk/1/hi/sci/tech/5217240.stm)

on to the material. The resulting 'Synthetic Gecko' is made of layers covered with thousands of stalks with splayed tips made of a polyimide, a synthetic like Nylon." The article did not state what species of gecko had been used as a model nor did it give a scale to the accompanying illustration which I have copied above, but we have at last a plausible explanation for the adhesive power of the gecko's toes.

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