Field and Captivity Observations of the Lizard *Gonatodes vittatus* (Gekkonomorpha: Sphaerodactylini) in Trinidad and Tobago.

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ABSTRACT

Gonatodes vittatus was observed in Trinidad, both in the field and in captivity. In the field it occurred on trees and masonry walls, and on and inside wooden houses. At least some individuals showed great site fidelity to their retreats. Males and females were territorial; in captivity males required about twice the area that females did, and in the field the sex ratio (males:females) varied from 50:100 to 71:100. The natural life span was at least 3 years. In houses, the predators of *G. vittatus* included the larger gecko species; and in captivity, death sometimes accompanied faulty moulting (sloughing). The diel cycle was characteristically diurnal, and emergence was temperature-dependent. *G. vittatus* is a sit-and-wait forager, and individuals preferred a vertical perch posture with the head pointing down, irrespective of the height above the ground. At night, some individuals living in protected areas slept on the walls in the open. New locality records for *G. vittatus* include one in north-eastern Tobago at 11°18'50"N, 60°32'30" W.

INTRODUCTION

Gonatodes vittatus (Lichtenstein 1856) is a small gecko (Reptilia: diurnal Gekkonomorpha: Sphaerodactylini) with round pupils and slightly expanded toes. It attains an RA length (rostrum to anus, snout to vent) of 34mm in males and 33mm in females, the tail is 108 PERCRA (% of RA, Werner 1971). Its sexual dichromatism is striking and unambiguous: the vertebral band in males is white with a black border (Plate I. 1); in females it is brownish and lacks the black border (Plate I. 2). The species ranges from Colombia to Venezuela and to offshore islands (Peters & Donoso-Barros 1970; Boos 1977; Roesler 1995; Murphy 1996 & 1997). In Trinidad it is widespread, mainly on forestedge tree trunks, masonry walls, on, and even in, buildings (Quesnel 1957; Murphy 1997). When seized, its skin tears (Murphy 1997) in a sort of defensive autotomy. Like other sphaerodactylines, it lays singleegg clutches (Underwood 1954; Quesnel 1957; Murphy 1997). In Trinidad, egg laying occurs throughout the year (Quesnel 1957). Further background information on G. vittatus, including photographs, is found in Quesnel (1957), Boos (1977) and Murphy (1997). However, information on its behaviour and ecology in the field is limited mainly to the definition of the habitat at its sites of occurrence, and information on its biology is limited, because it has rarely been kept in captivity (Quesnel 1957; Seufer 1991).

This report derives from two sources: field and captivity notes accumulated by the senior author, VCQ, during decades of both casual and planned observations since 1954, and field observations made by NW and YLW in Trinidad and Tobago, incidental to studying the foraging behaviour of *Gonatodes* spp. (Persaud *et al.* in press) in May and June 2000.

MATERIAL AND METHODS Study Sites and Observation Times

Apart from incidental observations at various locations, most of our data derive from three study sites. The Talparo Site: The home of VCQ at Haven Hill Farm near Talparo, central Trinidad (10°31'15" N, 61°16'15" W, altitude 50m). This wooden house is raised on square concrete pillars, from 52 to 92cm high, of rectangular cross section, approx. 29 x 33cm. *G. vittatus* occurred both in the house and under it on the pillars. Observations of diel activity were conducted from 7 to 27 February 2001. On each day the geckos were counted three times.

The PGH Site: *G. vittatus* was observed near the Pax Guest House (Plate I. 3) on Mt. St. Benedict, Tunapuna, northern inland Trinidad (10°39'38.6" N, 61°23'49.8" W, altitude 160m), living in crevices of south-facing masonry retaining walls, constructed of

assorted stone types, along the mountain road. The walls we observed were about 100m long and 50-200cm high and comprised four distinct sections. The major one was the "black wall" (Plate I. 4), which was not sheltered, except for some agaves and bushes growing above it and protruding over it; the "brown wall," which comprised a series of shallow niches roofed by arches resting on protruding buttresses; the "cemetery area," where some low wall sections were largely sheltered by the umbrella of a broad-canopy tree; and the "upper section," leading uphill from the Guest House, which was not studied systematically except for repeated checks on a few specific retreats. In these walls the geckos used as retreats either the roomy drainage holes created by the leaving-out of a stone, or small crevices in the mortar between stones.

The UWI Site: on the campus of The University of the West Indies, St. Augustine, northern inland Trinidad (10° 38' 20" N, 61° 24'5" W, altitude 15m), *G. vittatus* inhabited the trunks of some of the 15 large *Samanea* saman trees scattered sparsely over the campus lawns (Plate I. 5 & 6).

Additionally some observations were made on unidentified trees on Toco Beach.

Focal observations at the PGH and UWI Sites were carried out on 14 days during the period 22 May to 13 June 2000, with emphasis on the Mt. St. Benedict masonry walls. Observations were made on four days between 05:50 and 07:40, totalling 4.5 hours; on 9 days between 08:40 and 12:50, totalling 12 hours; on ten days between 15:00 and 18:40, totalling 16 hours; and on three nights between 20:45 and 22:00, totalling 2.5 hours. About half of these 35 hours of observation were performed by a single observer, the other half by two observers.

During the observation period at the PGH and UWI Sites the daily maximum temperature on Trinidad averaged 32°C (May), 31°C (June) and the daily minimum averaged 24°C (both months). The averages for the actual study days were similar. The total monthly rainfall on Trinidad was 137 and 201mm (May, June). On the study days at the PGH and UWI Sites the daily rainfall averaged 7 mm. All these values are typical for the time of year.

Observation in the Field

At the Talparo Site the outward and inward faces of both the pillars and the low connecting walls were examined (VCQ) from a distance with 8x40 binoculars. The number of males, females, juveniles and those of uncertain classification were recorded. Beginning on the seventh day, air temperature was recorded at the start and end of each census to an estimated tenth of a degree Celsius.

At the PGH and UWI Sites we (NW and YLW) scanned likely spots from maximum reasonable distances, depending on illumination, sometimes using 10x25 binoculars (which focuses as close as 2.8m). When a gecko was located and appeared undisturbed, we endeavoured to observe it from a distance of 3-6m, again depending on illumination. Observations, comprising environmental and behavioural data, were recorded on tape and later transcribed to paper. Documentation was augmented by photography. Air temperature and sometimes substrate temperature were taken at the end of an observation near the gecko's location, using a Miller-Weber quick-responding smallanimal mercury thermometer. Illumination was measured by a Gossen Lunasix-F photographic exposure meter graded in lux.

In this project we did not catch and mark the observed animals, and took no body temperature, in part because the skin of G. vittatus might tear (see Seifan et al. 2002). However, we mapped and photographed the PGH and UWI Sites, and marked used retreats on the former, thus defining repeated observations of the same individual, to the extent that these geckos show site fidelity, as discussed below.

Captivity

Most behavioural observations were made on individuals living in two wooden cages (VCQ). The larger cage measured 92x30x38cm (LxWxH). Both ends had wire mesh screens and the front was glass. The back was strengthened inside with two wooden posts, and at the bottom of each there was a square tray with dry leaf mould and a stone of suitable shape to provide a perch above and a cavity below where the lizards could hide. There were 13 potential retreats made by halving the trays of matchboxes and sticking these halves in place with sticking plaster. Six of them on the back wall were covered with flaps of paper to improve privacy. This was an attempt to provide the kind of hiding place G. vittatus uses behind peeling bark on tree trunks. The smaller cage measured 35x23x26cm (LxWxH). Its front was a movable sheet of glass, and the back a wire mesh screen. The furniture was like that in the larger cage.

Fourteen observations were conducted (VCQ) be-

tween 21 October 1957 and 19 January 1958 and between 13:30 and 18:45. The observational periods lasted from 30 to 70 minutes. A plan of the cage was drawn and the changing positions of the animals were marked on it using the letters identifying each animal and connecting them by arrows to indicate the direction of movement. Comments written on the plan described what happened in encounters between two animals. As far as could be determined, the observer, only a metre away, did not influence their behaviour.

Statistics

In addition to the tests used and explained by Seifan *et al.* (2002), we tested the significance of parallel variation of a behavioural parameter (e.g. the number of retreats with an active occupant outside) and an environmental factor (e.g. temperature in steps of 1° C) by simple linear regression using an analysis of variance (ANOVA) procedure. This method compares the variances among and between groups, and distinguishes which of several factors of interest contribute significantly to the variance differences (Sokal and Rohlf 1997).

We also investigated which one of several environmental factors was most influential in affecting behaviour by applying stepwise multiple regression analysis. This is a method to decide which of several independent (explanatory) factors best explains a dependent variable. The procedure chooses the best explanatory factor and then adds to it the next best factor, until the addition of factors ceases to significantly improve the explanatory ability of the function (Sokal and Rohlf 1997).

OBSERVATIONS

Penetration into Houses

Although not a "house gecko" G. vittatus occasionally occurs in inhabited houses. Our observations are listed in Table 1. On the Talparo Site, the mature female long occupying the windows near the desk became tame, running on the desk to catch insects at the desk lamp, sometimes approaching but never running on to VCQ's hand.

At the PGH Site two additional sightings inside were also of females. At least three different individuals were probably involved and most indoor encounters seemed to be one-time occurrences.

Site Fidelity and Population Density

Observation at the PGH masonry walls (NW and

YLW) yielded 382 records pertaining to 50 retreats occupied at one time or another, which we marked along 100m of the walls. There were 221 gecko sightings,

Table 1. Observations of G. vittatus indoors.

Number and sex	Location	Date	Time of day	Comments (Observer/s)
1m	Living room, Roberts Street, Port of Spain.	25 June 1965	21:30 - 22:30	Perhaps a temporary "invader". (VCQ)
1m & 1f	Window near desk, Talparo Site.	2000- 2001	Stable	Apparently resident. See under Longevity. (VCQ)
1f	E window of bedroom, Talparo Site.	2000- 2001	Stable	Apparently resident. (VCQ)
1m & 1f	NW corner of bedroom & nearby corridor, Talparo Site.	2000- 2001	Stable	Apparently resident. (VCQ)
1m & 1f	Sill of the kitchen louvres, Talparo Site.	2000- 2001	Stable	Apparently resident. (VCQ)
1f	Bedroom floor, PGH.	23 May 2000	18:20	Dusk Running. (W)
1f	Door-post of door leading to the outside, PGH.	28 May 2000	18:20	This or a similar fe- male was in the same place and position on at least two further occasions. (W)
1f	Corridor wall of natural stone, PGH.	9 June 2000	20:30	Artificial light. 120 cm up wall meters away from doors to the out- side. (W)

usually with known sex, position and posture; 118 "no show" observations at marked retreats, and 43 separate weather descriptions. Some individual geckos, identifiable by a combination of sex, size, and tail state (complete or regenerated and proportion of the latter) appeared to show complete site fidelity (Plate I. 7 & 8 and retreats #4 and #15 in Table 2). However, some retreats appeared to serve animals of both sexes (e.g. retreat #3 in Table 2). On no occasion were two individuals (of any sex) seen together in one retreat. Hence it seems probable that there is some interchange in the use of retreats. From the number of occupancy changes revealed by a sex difference, we calculated that the distribution of the animals over the retreats is far from random (c^2 test, p<0.001), presumably due to site fidelity.

Sightings on the trees (mainly on the UWI Site but including a day visit to Toco Beach, north-eastern Trinidad), where retreats were not marked and observation time was shorter, are fewer (n=20, and one

Table 2. Sur	nmary of observations	made at some retro	eats inspected
often.			

Retreat	Description	Total visits	Numbers and types of observations		
			Number	Туре	
#4	Drainage hole, "brown wall".	34	13	Male inside, usually in it's upper right cor- ner, sitting on a little shelf. Male outside, usually right next to the hole, only once >10cm away. Occupant not found	
			0	Occupant not lound.	
#15	Horizontal crevice be- tween stones, "cem- etery area".	13	7 2 2 2 2	Male inside, only his head visible, pointing out and downwards. Male lying along the opening, his body fully visible (Plate I. 8). Occupant not found. Record unclear.	
#3	Small crevice be- tween stones, "black wall".	25	12 2 9 2	Occupied by female. Occupied by male. Occupant not found. Occupant sex not recorded.	

additional description of weather). We saw 1 to 4 geckos, of the same or both sexes, per tree but others could have eluded us; they were seen at elevations of 0.3 to 3.0 m above ground.

Social Behaviour in Captivity

G. vittatus never used the cage ceilings and could not cling to the glass fronts, so the usable area in the small cage was about $0.3m^2$ and in the large cage about $0.9m^2$, including the strip of wood between the two glass panes in the front. In the small cage one male and one female could be kept indefinitely. No attempt was made to keep two pairs or two females in this cage. Young hatched, but if left long with the adults were killed.

When in October 1957 systematic observations were begun (VCQ), the large cage was populated with two males, M1 and M2, and two females, F1 and F2. Of these, F1 had been in the large cage for 21 days, and before that in the small cage (with a male) for a few months; M2 had been in the cage for 14 days; however, M1 and F2 were newly caught. On day 6, M2 was found dead with torn skin in several places. He was replaced with M3 on day 8. (M1 had been removed for these two days and was housed separately before being reintroduced with M3.) On day 9, M3 had large areas of skin missing and was moved to another cage. A new female F3 was introduced on day 12 and M3 was reintroduced but almost immediately removed and excluded from the experiment because of fierce fighting. Observations continued on male M1 with females F1, F2 and F3.

In addition to "attack" behaviour (a quick charge at another) and "retreat" (a movement away from another), three types of display were observed. (1) In the raised body display (RB), G. vittatus stands on stiffly extended legs with the tiny throat fan (or dewlap) expanded and the tail extended stiffly behind with, perhaps, a slight upward tilt. This is delivered broadside to the individual it is meant to influence. Sometimes the forelegs are bent slightly and immediately straightened again to produce a "bob" of the head. Occasionally, added to this display, the tail waves in a plane perpendicular to both the substrate and the long axis of the body. (2) In the side to side display (S-S) the body is pressed to the ground. The head and shoulders are moved from side to side. accompanied by a slight step forward with each turn of the head. This may involve tail twitching, a wave motion in a plane parallel to the substrate. (3) Tail waving in the absence of the raised body or side to side displays.

The raised body display seems like threat (and sometimes was followed by an attack) and the side to side display seems like appeasement. In order to test this, we sought to correlate these to objective measures of aggressiveness. The data were analysed by tabulating the number of times the different types of behaviour occurred in the individuals in a pair of "confrontees". F3 was the least aggressive individual; because she exhibited neither the RB display nor the S-S display, she can contribute nothing to this inquiry, so we ignore her when ranking the individuals by their degree of aggressiveness. Attack/retreat (A/R) ratios were calculated for each combatant in the pairs M1:F1, M1:F2, F1:F2, and from these the total A/R score for each individual was computed (Table 3). Hence their rank in terms of aggressiveness is F1>F2>M1.

Table 3. Summary of the number of times each display was ob-served from each of the three geckos F1, F2 and M1 in the groupcage.

Individual	F1	F2	M1
Attack / retreat score	6.5	2.0	0.31
Number of RB displays	10	8	5
Provoked	3	3	2
Unprovoked	7	5	3
Number of S-S displays	1	0	14
Number of tail-waving displays	0	3	3

Longevity

On the Talparo Site one free-living mature female was recognizable by the three missing middle toes of her front left foot. She was first recorded on 30 November 1995 and was last seen on 9 February 1998 (after 2.2 years). Her total life span would have been at least one year more. Another female (F1) lived in captivity from 23 June 1956 to 2 February 1958 (1.6 years) and was gravid at the time of death. She was gravid when caught and would have been at least 0.9 years old then, so her total life span was at least 2.5 years (VCQ).

In captivity, death was sometimes associated with moulting (sloughing). One male died 3 days after moulting; a second during protracted, 5 day long moulting and a female a day after moulting (VCQ).

On three occasions at the Talparo Site, we observed *G. vittatus* being eaten by syntopic, larger geckos: twice by *Thecadactylus rapicauda* (8 September 1986; 4 October 1990) and once by *Hemidactylus mabouia* (31 May 2000) (VCQ).

Diel Cycle and Behaviour

In general and at all three sites, *G. vittatus* was seen in the shade. Only very rarely were *G. vittatus* observed in early, hazy, or spotty sunlight, and never basking in midday sun.

At the Talparo Site the averages (± 1 SD) of the census were as follows: at 07:30, 5.8 \pm 4.06; 12:30, 9.7 \pm 4.19; 17:30, 15 \pm 2.42. The corresponding mean air temperatures were: 07:30, 22.0°C; 12:30, 26.7°C; 17:30, 25.3°C. Ratio males:females = 54:100.

At the PGH Site, in the morning when we began observations at 05:55, with the air temperature on different days between 23.6 and 25.8°C and light intensity between 2,780 and 3,420 lux, we did not find



Fig. 1. The percentage of active retreats (with the occupant seen outside) of *Gonatodes vittatus* as a function of air temperatures, on the PGH Site.

G. vittatus; the first individuals appeared at 06:00. Sunrise at the location was at 06:20. Until 06:45, when air temperature was 23.6-25.8°C, sightings were few, and 50% of the individuals seen had only the head protruding from a crevice. From 06:00 to 06:45 there were 8 sightings from 40 known and visited retreats (20% of known retreats showing animal presence). In contrast, from 06:46 to 15:36, with air temperature between 25.8 and 31.4°C, and light intensity at 9,000-108,000 lux, against 119 sightings, there were only 20 no-show observations (85.6% presence). Thereafter the activity waned and from 16:22 to 18:45, with air temperature between 23.7 and 28.2°C, against 88 sightings there were 57 no-shows (60.7% presence). The differences between these periods, in terms of animals seen per hour, were significant (ANOVA, P<0.05). As shown in Figure 1, with rising air temperature the percentage of retreats whose occupant was visible outside rose significantly (ANOVA, P<0.005). Indeed, the emergence was more closely dependent on air temperature than on time of day, light, or substrate temperature (stepwise multiple regression analysis, P<0.005).

Air temperature (AT) closely correlated with substrate temperature (ST) (AT= 0.83xST+4.1; R²=0.85), the maximum differences being -0.8 and 2.2°C.

The end of daytime activity was between 18:00 and 18:45, when on nine occasions animals were observed retreating into crevices. Often they had shortly before emerged from a protected position to the outside, as if following the fading light. Two extreme cases were noted on 12 June 2000 between 18:25 and 18:35, two males, each on the relatively well illuminated front face of a buttress of the brown wall, when approached, escaped and ran a distance of about 2m into their retreats. This behaviour differed from the usual situation in which G. vittatus, when outside, remains close to its retreat. At other times, we never saw G. vittatus on these masonry buttresses, which protrude towards the roadway with its pedestrians and occasional vehicles. Despite the tendency of G. vittatus to "go to sleep" at 18:00 to 18:45, on two occasions individuals emerged from crevices at 18:20.

The effects of rain and wind could not be measured as both varied too gradually even for qualitative assessment. Early in the morning when the south-facing masonry walls were illuminated from the east, the majority of individuals inside the drainage holes (in the black



Fig. 2. The numbers (in %) of male (black columns) and female (grey columns) *Gonatodes vittatus* observed at different elevations above ground, pooled for the PGH and UWI Sites. The elevations are pooled in steps of 25 cm, with the upper limits of the ranges indicated along the abscissa.

wall) were usually sitting on the inner eastern wall. This position may have been preferred because either the western wall was better illuminated, and there it would be easier to see prey, or because the wind was blowing from the east, so that this position was less exposed to the wind. Whenever the drizzle became stronger, *G. vittatus* were outside only in rain-sheltered places: sections of the walls under a masonry overhang, or shielded by bushes protruding from above the wall, and especially the "cemetery" area, widely roofed over by a large tree.

On each of three nights, (26 and 29 May and 13 June 2000, between 20:45 and 22:00; air temperature 24.8-26.7°C), inspecting the masonry walls on Mt. St. Benedict, we found 4 or 5 individuals, of both sexes, completely exposed on the surface of the walls (Plate I. 9 & 10). These were found in the cemetery area and nowhere else. Probably seven individuals were involved. Their postures were horizontal or vertical with the head up. In most cases, they did not respond when closely approached. For example, on 26 May at 21:53, a male on a concrete gate-post, resting vertically with the head up, did not respond to the thermometer, taking substrate temperature 5mm in front of his snout. He was easily caught, but lost some skin, and was released. Most of these sleeping individuals did not respond to close-up flash photography; only direct touch caused them to wake up and take refuge. However, in three cases an individual behaved as if it woke up because of our approach, or was already awake, and ran away. However, there occurred also some nocturnal activity under electric lights, as described above (see Penetration into Houses).

At the UWI Site, our observations on the trees were made between 09:16 and 18:21 (n=21 sightings), with



Fig. 3. The numbers (in %) of *Gonatodes vittatus* observed in horizontal postures (grey column) or vertical postures, regardless of head direction (black column), as a function of air temperatures, on the PGH Site.

air temperature between 25.8 and 30.7°C (substrate temperature was up to 0.7°C higher) and light intensity, 5,540-44,000 lux. As there were no statistical differences between our observations on the trees and on masonry (PGH Site), the results are pooled in the following.

The orientation of 68 individuals, seen outside on masonry and trees with posture recorded, was either vertical, with head up (n=5), vertical with head down (n=44), or horizontal (n=19). Similarly, the orientation of 50 individuals in drainage holes or other protected situations were vertical, with head up (n=4), vertical with head down (n=33), or horizontal (n=13); the predominance of vertical postures was significant in both cases (c² test, p<0.001), and within these, the predominance of the head-down direction was significant (c^2 test, p<0.001). In both cases the posture and direction were not related to the elevation above the ground (K-S tests, in both cases P>0.35). However, as shown in Figure 2, the height of perching differed significantly (K-S test, p<0.001) between the sexes, the males perching higher. Further, as shown in Figure 3, the proportion of vertical postures (vs. horizontal) significantly rose with air temperature (K-S test, P<0.05) but not with light intensity (K-S test, P>0.35). Additionally, 44 sightings were of individuals hidden inside crevices, or under tree bark, with only the head visible, often pointing down.

Another variable of the perching posture was the elevation of the head with respect to the substrate. Regardless of whether the individual was oriented with its head down or up, the head was often tilted away from the substrate. Unfortunately this detail was not recorded in the field, but it is seen in some of our photographs.

Location	Coordinates	m	Date	Comments
Petit Valley (Palm Avenue)	10°42'N, 61°32'W	30	29 March 1961	
Mandalay, Moruga	10°05'N, 61°16'W	1	24 Sept. 1961	Extremely common on walls and around house.
Manzanilla Bay (Road to Hell)	10°31'N, 61°01'W	1	28 Nov. 1976	Swampy ground.
Paria Springs, Brasso Seco	10°44'N, 61°16'W	310	7 August 1998	In cocoa house.
Talparo Junction	10°31'N, 61°16'W	30	6 February 2001	Ruined building, four individuals.
Chaguaramas	10°41'N, 61°37'W	15	2 January 1998	On tree trunk.
Avocat, Blanchisseuse	10°46'N, 61°19'W	65	13 October 1999	Around building, three individuals.
Bush Bush Trinidad Regional Virus Laboratory Field Station.	10°24'N, 61°03'W	1	25 March 2001	Absent or overlooked when the same building was inpsected in 1973.

Table 4. New locality records for G. vittatus on Trinidad.

As to social life, in the field we saw neither mating nor other physical contact between individuals. A few times a male chased a female, once a female chased away a considerably larger male. We also saw no small juveniles.

New Locality Records

On Trinidad *G. vittatus* is widespread and known from many localities (Murphy 1997). Additional localities are given in Table 4 (VCQ). As evidence for its presence on Tobago Murphy (1997) quotes two records from Scarborough (11°11'N, 60°45' W) where we (VCQ), too, observed it, 20 October 1976. We (NW) observed a female at the Flagstaff road junction, on the Charlotteville to Speyside main road (11°18'50"N, 60°32'30" W altitude 198m, 4 June 2000). The animal was not in one of the damp culverts inhabited by *Gonatodes ocellatus* but about 150cm above ground, on an old crate, which had some vegetation growing on it. The animal was seen once and observed carefully but could not be photographed.

DISCUSSION

Penetration into Houses

The issue of geckos, especially *Gonatodes*, penetrating houses is briefly discussed elsewhere (Seifan *et al.* 2002). In Trinidad, *G. vittatus* has been observed in houses by Quesnel (1957), Underwood (1962) and Murphy (1997). The latter saw them in rooms of the Simla Station, where we too, saw them on the buildings (31 May 2000, Y.L. Werner & N. Werner, unpublished). At the Talparo site some individuals may have been attracted to the house by the artificial light, but windows have advantages. Insects in trying to get out of rooms get obstructed by the panes and become easy prey. Furthermore, G. vittatus would probably be a little safer there from the attentions of the much larger gecko Thecadactylus rapicauda which seems to prefer the darker parts of the house (see section on Longevity). All but one of the individuals that we encountered inside the Pax Guest House seemed to be intruders, possibly on extended foraging forays. But on several occasions a female was observed perched near the bottom of the same doorpost; presumably this was the same individual, which could therefore have been a regular inhabitant.

Site Fidelity and Population Density

Site fidelity is not well known in geckos, and presumably it varies among and within species. However, it is important to distinguish between fidelity to the retreat and fidelity to the foraging ground or perch, because, in geckos these may be separated by tens of metres (Stanner et al. 1998; Bogin 1999). During our observations (21 May to 13 June, 2000) of G. vittatus at the PGH Site, some individuals, of both sexes, showed great retreat fidelity, while others appeared to switch retreats. As individuals could not be marked, it remains unknown whether or not each was using a consistent set of retreats. However, two other behaviours could have caused the occasional use by a gecko of one sex, of a retreat usually occupied by a gecko of the other sex. First, the rarer user could have possessed its own retreat elsewhere, and momentarily occupied another while on a long-range expedition and suddenly in need of a refuge (see under Foraging Behaviour). Second, a given retreat could have been inhabited by a pair and always only one partner at a time emerged, though we have no supporting evidence. Hence, it is not certain that site fidelity is not general.

Since the number of individuals seen during inspections varied, and indeed it is common for lizards not to emerge on each climatically suitable day (Regal 1974; Rose 1981), it is hard to estimate the number of individuals along the observed 100m of masonry walls.

The number of observed retreats (n=51) may ex-

ceed the number of individuals but as new retreats continued to be found till the end of the observation period, it is possible that not all the individuals inhabiting the designated walls had been counted. A reasonable estimate would be about 50 individuals for the 100m length of walls. In order to estimate the biomass of *G. vittatus* per unit area we used the area that is ecologically significant, that is, the surface area of the wall. The height of the walls is very variable but because most retreats were at elevations of 5 to 100cm, and only nine retreats were at elevations of 110 to 175cm, we arbitrarily took a height of 120cm. This yields an estimate of 2.4m² per individual (0.4 gecko per m²) but the distribution of *G. vittatus* was noticeably uneven.

Our observations of 1 to 4 *G. vittatus* per campus tree agrees with Stamps's (1977: p. 291-292) observation in the Botanical Gardens, Trinidad, "...one male and one or more females are usually found per tree [trunk]; a large tree had two males, one on each side."

Longevity and Causes of Death

The maximum life span of a free-living *G. vittatus* reported here, 3.2 years, supports the 3 to 4 year estimate of Quesnel (1957). Werner *et al.* (1993) surveyed the longevity of Gekkonomorpha and found that in captivity the maximum correlated (r = 0.78) with the maximum rostrum to anus length of the species. From their data, a species of the size of *G. vittatus* would be expected to have a maximum life span of 2 years. Considering our findings and that of a male *G. albogularis* that exceeded 5.6 years (Slavens 1993), it would seem that *Gonatodes* live longer than other small geckos.

The association of death with moulting for G. vittatus in captivity has also been observed in G. humeralis (VCQ) and is discussed by Seifan *et al.* (2002).

Predation by *H. mabouia* was, to our knowledge, previously unreported. Further, the only vertebrate material in the stomach contents of specimens of *T. rapicauda* from Brazil was shed skin (Vitt and Zani 1997); 64 stomachs were examined, of which 44 contained prey (Vitt, personal communication, 22 March 2002). Predation of the smaller diurnal gecko *Sphaerodactylus molei* by *T. rapicauda*, which is both diurnal and nocturnal (Valdivieso & Tamsitt 1963, Vitt & Zani 1997) is documented (see Murphy 1997). *G. vittatus* coexists with both *H. mabouia* and *T. rapicauda* in and around Pax Guest House. We saw no predation during the short time of our observation.

Activity, Diel Cycle and Sleeping Behaviour

Our observations of the diel cycle of G. vittatus at the Talparo and PGH Sites agree with those of Quesnel (1957) and Underwood (1962), in that the species is diurnal. However, the details differ in that in Port of Spain, Quesnel (1957) found a midday dip in activity (or emergence), whereas we found that at the Talparo Site activity gradually rose throughout the day till 17:30, and at the PGH Site it rose in the morning but dropped off after 16:00. It seems that G. vittatus does most of its foraging in the afternoon. Explanation of the differences between the sites is limited because the observations and temperature recordings were made on different days and at different times. Still, the midday dip in activity reported by Quesnel (1957) suggests that G. vittatus avoids the mid-day sun and that activity in shaded areas was under-reported. The decrease in activity at the PGH Site occured after 16:00 and probably resulted from the drop in temperature on the hill, which we found to be decisive for activity.

That some individuals of G.vittatus sleep in the open at night has apparently not been reported previously. However, it occurs in some other diurnal forest lizards, for example, G. humeralis habitually sleeps on leaves and branches (Avila-Pires 1995) and Japalura polygonata (Agamidae) also sleeps in the open on Okinawa (unpublished observation). However, while in J. polygonata and other lizards with normal eyelids, it is easy to recognise sleep by the synchronous eye closure accompanying the prostrate or adpressed posture (Mathews & Amlaner 2000), in brilled geckos the definition of sleep is problematic. In our observations, sleep was verified by the lack of response to visual, and presumably also acoustic, stimuli at threateningly close range. The individuals of G. vittatus that we did find sleeping in the open occurred only in the "cemetery area" within the PGH Site, where, unlike the other wall sections, no cars and very few people were passing.

Foraging Behaviour

G. vittatus and some congeners are strict sit-andwait, or ambush, foragers (Persaud *et al.* in press). Yet the occasional appearance of *G. vittatus* females in the house at the PGH Site seems to indicate that they may venture on relatively long-range expeditions. Because these expeditions were undertaken by females into rooms lacking other individuals of *G. vittatus* and sometimes occur at night under artificial lighting, their function is probably foraging rather than social. The preference of *G. vittatus* for a vertical headdown perching posture, already noted by Persaud *et al.* (in press), was statistically verified here and is discussed by Seifan *et al.* (2002).

Social Behaviour and Sex Ratio

Our concentration on quantifying the foraging behaviour of *G. vittatus* may account for having so few field observations of its sexual and social behaviour. We only saw males chasing females and a female chasing a male, whereas Stamps (1977: 291-292) only reports males chasing males and females chasing females.

The social behaviour of *G. vittatus* from Trinidad was observed in one-versus-one encounters staged in an arena (Demeter & Marcellini 1981). Our results from a group cage generally accord with theirs. They term the S-S display "lateral head-sway" and describe its performance by the male while approaching a female. If this display is in fact appeasement as well as part of courtship, it would explain why the male M1, which was aggressive towards other males, used it in encounters with females. We did not observe copulation and it may be a rare event since the female stores sperm (Quesnel 1957).

Table 3 shows the association of the different displays with the individuals differing in aggressiveness. The most RB displays came from the most aggressive individual, the least from the least aggressive, whether considered as all RB displays or unprovoked displays. In contrast, S-S displays are associated with the least aggressive individual. Therefore, it seems correct to regard RB displays as threat and S-S displays as appeasement. Tail waving by itself is too rare for any assessment at the present time.

The results from the group cage show that males require more space than females and are fiercely aggressive to each other. In a confined space the stronger male will kill the weaker. The females are aggressive to each other more than to males. From the results, males seem to require >0.88 m² each and females about 0.44 m². Assuming overlapping use of the area by males and females, this should give a male to female sex ratio in the field of about 1:2. In the field, this ratio has been found to be 50:100 by Quesnel (1957), 71:100, at the PGH Site (Persaud *et al.* in press) and between 54 and 71:100 at the Talparo Site depending on the time of day.

New Records

Our record on Tobago of a new locality for G. vittatus

may be due to an expanding range (Murphy 1997), or to the additional search effort.

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LEGENDS FOR PLATE I

1. *G. vittatus* male perching head-down, partly protected, on masonry wall on Mt. St. Benedict, Tunapuna, Trinidad (21 May 2000, 10:40, air temperature 29.4°C).

2. *G. vittatus* female on masonry wall on Mt. St. Benedict, Tunapuna, Trinidad (21 May 2000, 10:20, air temperature 31°C).

3. Habitat and study site of *G. vittatus*: The Pax Guest House on Mt. St. Benedict, Tunapuna, Trinidad. Note the forested slopes in the background (right) and the black masonry retaining wall with drainage openings in the foreground (left), inhabited by many *G. vittatus* and some *Hemidactylus mabouia* (23 May 2000).

4. Section of the black masonry wall with two drainage openings and another crevice, marked as regular retreats of *G. vittatus*, Mt. St. Benedict, Tunapuna (13 June 2000). Scale: the lower marked hole is 50cm above the road.

5. Habitat and study site of *G. vittatus: Samanea saman* trees, UWI campus, St. Augustine, Trinidad (22 May 2000).

6. *G. vittatus* male, on *Samanea saman* tree trunk, UWI campus, St. Augustine, Trinidad (30 May 2000). Note that in this situation, even the colourful male is not very conspicuous.

7. *G. vittatus* male above his regular drainage opening (# 30) in masonry wall, "upper section", Mt. St. Benedict, Tunapuna (10 June 2000, 18:40).

8. G. vittatus male in his regular crevice (#15) in masonry wall near the cemetery, Mt. St. Benedict,





















Tunapuna, Trinidad (26 May 2000).

9. *G. vittatus* male sleeping exposed, head-up, on concrete wall in the cemetery area, Mt. St. Benedict, Tunapuna, Trinidad (26 May 2000, 22:00).

10. *G. vittatus* female sleeping exposed on masonry wall in the cemetery area, Mt. St. Benedict, Tunapuna, Trinidad (26 May 2000, 21:45).

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