

## OBSERVATIONS ON THE ECOLOGY OF THE ARRHYTHMIC EQUATORIAL GECKO *CNEMASPIS KENDALLII* IN SINGAPORE (SAURIA: GEKKONINAE)

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**ABSTRACT.** - Brief observations on the little-known 'rock-gecko' *Cnemaspis kendallii* in the Bukit Timah Nature Reserve, Singapore, in November-December 1999, augmented by examination of museum specimens, have increased the knowledge of its behaviour, biology and ecological morphology. It inhabits both tree trunks of assorted types up to 2.5 m and granite rocks. It is active abroad both day and night, with a foraging mode that is an extreme sit-and-wait strategy (moving 0.28% of the time). Its small eye, with spectacle diameter of 5.25 percent of head and body length, is typical of diurnal scansorial geckos. The circular pupil of the eye differs from that of other diurnal geckos. The tail (when complete), 125.5 percent of head and body length, is unexpectedly long for an extreme sit-and-wait gecko. Clutches of two hard-shelled eggs are laid, the eggs, approx. 9.25 mm in diameter, stick to each other and to the substrate. The oviposition season extends at least over September-December, and possibly over the whole year.

**KEY WORDS.** - *Cnemaspis kendallii*, gecko, south east Asia, foraging mode, diel cycle, reproduction, eye size, pupil shape, tail length, tail regeneration.

### INTRODUCTION

*Cnemaspis kendallii* (Gray, 1845) is a somewhat enigmatic gecko. Its eye, as typical of the genus, has a circular pupil (Fig. 1A) (Boulenger, 1885, 1912; De Rooij, 1915) as is usual in diurnal Gekkonoidea, yet its diel activity was recently described as crepuscular or

nocturnal, at least partly (Lim & Lim, 1992). Indeed, most of its congeners in India are considered by some to be nocturnal despite their round pupils (Murthy, 1990; Tikader & Sharma, 1992), although Das (personal communication) has reported that all or most species are diurnal. Some other congeners are considered to be active both day and night (Manthey & Grossmann,

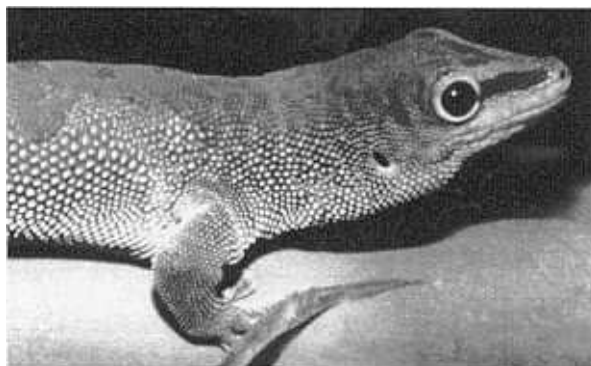
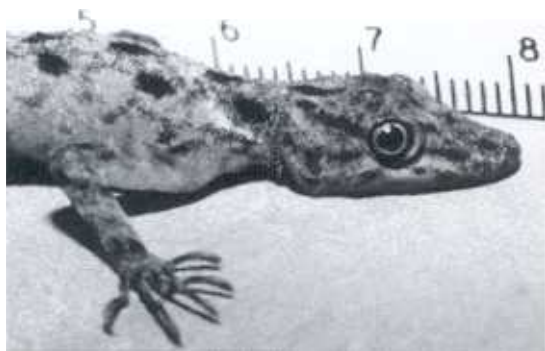


Fig. 1. - Comparison of the shape of the eye pupil in geckos. A, in *Cnemaspis kendallii* (female HJ-R-19,388 in life; ruler, cm and mm); B, in *Phelsuma madagascariensis grandis* (in Wilhelma Zoo, Stuttgart, 5 July 2000; adult animal).

1997; Cox et al., 1998). At another level, at least locally in Singapore, while its vernacular name is “rock gecko” and it is often regarded to be confined to, or primarily inhabiting, rocks, such as granite outcrops (De Rooij, 1915), it has also been described as a forest species usually seen on tree trunks and rocks (Lim & Lim, 1992; Teo & Rajathurai, 1999). In Singapore it has been considered to be uncommon (Lim & Lim, 1992) and the National Parks Board of Singapore has regarded its population as small (Sharon Chan, personal communication). The species, perhaps the genus, is hard to keep in captivity, as individuals will refrain from eating (Hidetoshi Ota, personal communication; Kelvin Lim, personal communication).

We conducted field observations on *Cnemaspis kendallii* in the Bukit Timah Nature Reserve, Singapore, with two aims. First, generally to advance the understanding of the biology and ecology of this gecko. Second, specifically to define and quantify its foraging mode.

Foraging mode is species-specific, and for most predatory animals, such as insectivorous lizards, it can be classified as either “sit-and-wait”, i.e. passive ambush, or “widely foraging”, i.e. active search. Related to this distinction, lizard species (and usually whole families) of these two ecological types differ in many traits - morphological, e.g., tail length; physiological, e.g., metabolic rate; behavioural, e.g., prey detection and escape tactics; and biological, e.g., relative clutch mass (Huey & Pianka, 1981; Perry et al., 1990; Cooper, 1995). However, species of the Gekkonoidea tend to show a complex pattern of intermediate, alternating, or fluctuating foraging mode and this situation is poorly understood (Werner et al., 1997a). Within a wider comparative investigation into a possible relation of the foraging mode of geckos to their prevalent nocturnality (Werner et al., unpublished), it seemed of particular interest to examine the foraging mode of *Cnemaspis*, with its presumably diurnal eye and alleged nocturnal habits. We relate our field observations to relevant data obtained from museum material and we discuss the results in the perspective of the biology of geckos in general.

## MATERIAL AND METHODS

**Definitions and Abbreviations.** - CV, coefficient of variation (standard deviation as percentage of mean); HUI, Hebrew University of Jerusalem; percra, percents of ra length (Werner, 1971); ra, rostrum-anus (snout-vent) length (Werner, 1971); MPM, moves per

minute, the computed number of times, during 1 minute, that a gecko switched from “stationary” to “locomoting”; PTM, percent time moving, the number of seconds the gecko was locomoting, as percent of observation time; PTS, the reciprocal of PTM-, percent time stationary; ZRC, Zoological Reference Collection (now Raffles Museum of Biodiversity Research) of the Department of Biological Sciences, National University of Singapore, formerly USDZ (Leviton et al., 1985).

**The Species.** - *Cnemaspis kendallii* was originally described by Gray (1845) from Borneo as *Heteronota kendallii*, then listed by Boulenger (1885) as *Gonatodes kendallii*. Its present name-combination originated when McCann (1955) included it in the genus *Cnemaspis* of Strauch (1887). This is a small gekkonine gecko without clinging toe-pads; in the data of Das & Bauer (1998) the largest of 7 males measured 56.8 mm from rostrum to anus, while the largest of 3 females reached 79.5 mm. Eye-catching in the definition of the genus and in the morphological description of this species, although Gray (1845) did not mention the point, is the “round” pupil of the eye, as shown in Fig. 1A (Boulenger, 1885, 1912; De Rooij, 1915; Lim & Lim, 1992; Roesler, 1995; Manthey & Grossmann, 1997; Das & Bauer, 1998). Ecologically the species has indeed been described as diurnal by De Rooij (1915) and Manthey & Grossmann (1997) but as crepuscular or nocturnal by Lim & Lim (1992).

The scant information on this gecko was recently thoroughly reviewed by Das & Bauer (1998), who redescribed the lectotype, summarised the pholidotic variation (apparently on the basis of 30 specimens from throughout the range) and the sexual size dimorphism (from 10 specimens from unspecified localities), and reviewed the literature data on taxonomy, distribution, habitat and food. Hence we need to comment here only on selected aspects of ecological relevance.

**Material Examined** (n=25). - From Singapore (n=10): HUI-R-19388, ZRC 2.1107-8, 2.3014, 2.3520, 2.3544, 2.4647; live individuals examined on the study site - FL2,3, FL4, FR3. From the Anamba and Natuna Islands. (n=5): ZRC 2.1109-13. From Malaysia (n=10): ZRC 2.1101, 2.1103-6, 2.3015, 2.3501-3, 2.3546.

**Study Site.** - The Bukit [=hill] Timah Nature Reserve in inland Singapore, 01°21'N, 103°46' E, is typical of the latitudinal distribution of *Cnemaspis kendallii*, from 05°00'N in West Malaysia to 00°12'S on the Natunas Islands (Das & Bauer, 1998). Annual

precipitation in the Reserve averages 2353 mm; the annual temperature overall average is 26.7°C. The reserve comprises 164 hectares of hills up to 163m a.s.l. (Foo & Kwok, 1999), covered with primary forest, old secondary forest and young secondary forest (Corlett, 1997). Our observations were conducted in a small area of steep slopes, 70-140m a.s.l. with primary and old secondary vegetation in the south-eastern part of the reserve. The trees, mostly with straight bare trunks, comprise a considerable variety of species and are of extremely heterogeneous sizes (Fig. 2). In the mixed undergrowth assorted ferns and thorny 'rattan' palms are conspicuous, and the ground was at the time heavily overlain with leaf litter, predominantly of huge leaves. There are a few small granite outcrops, some flat and affording little shelter and some comprising boulders with deep crevices. The rock habitat is greatly augmented by three man-made tunnels, the entrances of which are surrounded by bared granite; these are known locally as a major domicile of *Cnemaspis kendallii* and also *Cyrtodactylus* sp., perhaps *C. quadrivirgatus*. The area is traversed by named and sign-posted paths, often consisting of stairs.



Fig. 2. - Typical habitat of *Cnemaspis kendallii*: forest of the study site, Bukit Timah Nature Reserve, Singapore, 21 Dec. 1999.

#### **Methods - Field observations and foraging mode. -**

We preliminarily visited the study site for orientation and planning five times during 18 Nov. -3 Dec.1999, always over the late afternoon and early evening hours. On the three first occasions heavy rain hindered observation of geckos. Foraging mode was thereafter observed along selected sections of established paths by 2-3 observers, on 7 Dec.99 from 0930 to 2230, and on 10 Dec.99 during 1530-2230 h, totalling 41 observer hours. In daytime we scanned rocks and tree trunks from a 2-3 m distance. When a gecko was discovered and identified, we retreated to at least 3 m and observed it (if possible) for 30 min, recording the observations into a mini-cassette recorder. For observation at night, geckos were caught in daytime (after or without observation) by a noose on a 62 cm stick, sexed, measured, and toe-clipped for both future identification (Paulissen & Meyer, 2000) and future DNA study. The toes in 95% ethanol are deposited in ZRC. Finally we placed on the gecko's back, dorso-laterally, a pair of patches (5x5 mm) of reflecting tape (3M model Skotchlite 8850), according to the method used by Werner & Bouskila (1995). On the "reflector" we wrote a serial number with a black fine felt pen, and released the animal where it had been caught. In the evening the place was revisited and the gecko spotted from tens of meters by the reflected head-torch light. We then observed it as above, usually from >5 m, in marginal white torch-light. We recorded only air temperature at 1 m (Miller-Weber thermometer).

**Thermoregulation. -** We improvised a thigmothermal gradient from a 90x45x45 cm glass aquarium floored with coarse shingle. Near one end we placed a flat round metal box (diameter 19, height, 7.5 cm) containing a 40W incandescent lamp; sand was heaped up around the box and thinly covered it, forming a "hill" with hot top (>50°C) and slopes with decreasing heat. Two females were caught on 10 Dec.99 at night, kept for 2 days in open-air temperature (26-28°C), two more days at room temperature (23-25°C) then tested in the gradient. They were given a water dish and offered mealworms, metamorphosed *Tenebrio* beetles and baby hissing cockroaches (*Grophadorhina portensa*) but did not eat. In daytime, a gecko would be noosed out, and rectal temperature taken by a Miller-Weber thermometer.

**Morphology. -** In the field geckos were measured by ruler to nearest mm, and weighed by a Pesola 10-g spring balance to nearest 0.5 g; eggs were measured by plastic Vernier callipers, to nearest 0.1 mm. Measurement of museum specimens was with dial

Vernier callipers, to 0.1 mm, if necessary - under a dissecting microscope. Sex and the regenerated portion of the tail were only assessed externally. In this species the original tail is cross-banded dark-and-light (Fig. 3), and this pattern seems not to reappear on the regenerated tail.



Fig. 3. - One of the foraging postures of *Cnemaspis kendallii* (Bukit Timah study site, Singapore): Adpressed posture of an individual with complete tail (21 Dec. 1999 at 1600h).

## OBSERVATIONS

**Habitat and Population.** - During the search on 7&10 December, we scored 26 sightings which apparently pertained to 14 individual geckos. Six geckos were on tree trunks and eight geckos were on rocks. Seven geckos were seen again with certainty, at least once, on the same or the next visit, on the same tree or on the same rock outcrop (within few meters). The identification of the individual on the

second occasion was absolute for four geckos (three on rocks, one on tree) due to marking, and assumed on other occasions due to circumstances (e.g., same tree trunk, sometimes on its same side and in same posture, and never two individuals on same tree).

The geckos occurred only on dry granite rocks, not on those green with moss; and only on boulders or rock-walls with deep crevices, not on the flat smooth outcrops. They were on vertical rock faces, or clinging to negative inclines or to ceilings of overhanging rocks, never on the upper surface. The inhabited trees were of assorted species, with the bark ranging from very smooth to very rough, and the diameter from approx. 10 cm to approx. 1 m. On the trunks most geckos when first sighted were 25-200 cm above ground, only one was at approx. 2.5 m. On the rocks their postures were varied. On the tree trunks they were almost always vertical, six records with head-up and four records with head-down. The direction was not related to the height above ground. Their posture was sometimes adpressed (Fig. 3) but usually almost semi-erect (Werner & Broza, 1969) with the belly barely resting on the substrate, and both the neck and the tail inclined "up", away from the substrate (depicted by Lim & Lim, 1992: 122). In this posture they appear rather alert. None were noted on the ground.

Parts of the study site were briefly inspected on two additional, final occasions. On 13 Dec.99 during 1730-2000h, a targeted search for three individuals left in the field three days earlier, bearing reflectors, failed to find any geckos. On 21 Dec.99 during 1500-1630 (AT=25.7, rainy) we observed two geckos on familiar sites and two more on trees earlier searched without results, both with the head down.

**Diel Activity Cycle.** - Geckos were seen abroad at any hour during the full range of observation time, from 0930 to 2230, hence in full daylight of a sunny (lightly hazy and part-cloudy) day; in twilight; and in the darkness of a moonless forest night. All were seen only in full shade, even if a patch of sunlight was near. The range of air temperatures of all observations (day and night) was confined to 25.2-27.8°C. Interestingly, the geckos usually seemed not to respond to the many park visitors who were passing within 2 m of them (often noisily, sometimes running). At least five marked individual geckos were each seen abroad in both daytime and night-time.

**Foraging Mode.** - We did not see any interactions among individuals; all observations were of geckos which in our judgement could not see others, the

Table 1. The foraging behaviour (time budget) of *Cnemaspis kendallii* at Bukit Timah, Singapore, in December 1999, as based on 30 min observation periods. MPM, moves per minute; PTM, percent time moving; PTS, percent time stationary. The difference between day and night data could only be tested for PTS; the probability that these two averages represent the same population, was  $p=0.688$  (T-test, 2-tailed, unequal variances), so the data are pooled as 'total' which includes an eleventh observation, taken in twilight.

	Observation time (seconds)	n (of animals)	MPM	PTM	PTS
<b>Day mean</b>	1818	5	<b>0.02</b>	<b>0.40</b>	<b>99.6</b>
S D	26.8		0.04	0.89	198.9
CV	1.48		200.0	222.5	199.7
<b>Night mean</b>	1825	5	<b>0.03</b>	<b>0.22</b>	<b>99.8</b>
S D	25.6		0.04	0.35	0.35
CV	1.4		133.3	159.1	0.35
<b>Total mean</b>	1820	11	<b>0.02</b>	<b>0.28</b>	<b>99.7</b>
S D	24.6		0.04	0.62	0.62
CV	1.35		200.0	221.4	0.62

proximate occurrence of which was rare anyway. On a few occasions geckos escaped when approached within approx. 1.5 m for photography. Otherwise most geckos discovered could be observed for the full sampling period of 30 min, as summarised in Table 1. Normally each observation was of a different individual. Only one gecko did we observe first in the morning and then in the evening, to verify that the behaviour was identical. Hence the 11 observations in Table 1 were derived from 10 animals. On 7/11 occasions the gecko remained stationary during the 30 min observation time, at mast turning the head, adjusting the posture without locomotion, or sometimes making some movements which could have indicated feeding on the spot. Those geckos that did locomote during the observation, mostly did so with distances of 10-60 cm covered at a rapid pace which probably is not compatible with foraging on the move (Cooper et al., 1999). When the move was over too long a distance to be reasonably interpreted as going for discovered prey, they were probably either changing the location of ambush or escaping from a disturbance (not identified). Nevertheless all these moves are included in the statistics of the observations, summarised in Table 1.

**Thermoregulation.** - The two females were introduced into the gradient on 14 Dec. 99 at 1200 h; substrate temperature was  $>50^{\circ}\text{C}$  in the hottest area, top of the "hill", decreased steeply down the slopes, and was  $19^{\circ}\text{C}$

throughout most of the tank. At 1415 h (rectal) BTs were  $22.8^{\circ}\text{C}$  in female FR2 and  $23.0^{\circ}\text{C}$  in female FR3. Thereafter female FR2 suddenly died. On 15 Dec. Female FR3 had at 1845 h  $\text{BT}=22.5^{\circ}$ ; and on 16 Dec. (with gradient temperatures from  $19.5^{\circ}\text{C}$  to  $>50^{\circ}\text{C}$ ), at 0830 h,  $\text{BT}=24.5^{\circ}$ ; and at 0930 h,  $\text{BT}=23.6^{\circ}\text{C}$ . Thereupon this animal, too, suddenly died. An informal average of these five readings brings  $23.3^{\circ}\text{C}$ . It must be stressed that before their sudden death these animals did not seem moribund; they were agile.

**Ecological Morphology.** - All the individuals of *Cnemaspis kendallii* which we detected in Bukit Timah in November-December 1999 were adults, although the search was thorough enough to reveal, at night, several tiny juveniles of a skink. The largest of all the 10 individuals of *Cnemaspis kendallii* seen from Singapore (most were from Bukit Timah), combining field and museum data, measured 52 mm ra; 7 others were in the range 49-50 mm. In the whole material in the ZRC the largest of 11 males measured 62 mm ra and the largest of 7 females, 68 mm.

Eye size (more precisely, spectacle size - Werner, 1969) in adult animals of at least 49 mm ra, from throughout the examined material, averaged 5.2 percra ( $n=13$ ). In life, at least in *C. kendallii*, the pupil is not as perfect a circle as in some other genera of geckos, e.g., *Gonatodes*, *Lygodactylus*, *Phelsuma* or *Pristurus*, which are reputedly and also actually diurnal

(e.g., figures in Werner, 1969). As seen in Fig.1, the iris is slightly notched dorsally and ventrally. Such notching is also shown in the drawing of the holotype of *Cnemaspis yercaudensis* (Das & Bauer, 2000).

The tail was incomplete, i.e. part missing, in 10 museum specimens (40%) so that its condition in life is unknown. Of the 15 live and preserved specimens with (externally) ascertained tail condition, only 5 (33%) had complete tails; these tails were on average 125.5 percra long (range 118-132 percra). The other 10 (67%) had some part of the tail (most or little) regenerated; among these, the combined length of the tail was 119-120 percra in 3 specimens, and 90-111 percra in the remaining 7. Interestingly the specimens with complete tail comprise 5/8 of Singapore geckos with known tail state, whereas in the material from Malaysia and the Anamba and Natuna islands, all the 7 specimens with known tail state, had partly regenerated tails.

**Reproduction.** - On 18 Nov.99 we found a clutch of two white, rigid-shelled, spherical eggs, sticking together and to the rock substrate, in a shallow niche of a rock-wall at the entrance to one of the tunnels (at which we have observed *Cnemaspis kendallii*), approx. 1.5 m above ground. Due to their position only their combined diameter (parallel to the substrate) could be accessed and measured, 18.5 mm. We inspected the place on subsequent visits, and on 7

Dec.99 we found that they had hatched (Fig. 4A); their previous inspection had been on 3 Dec.99.

On 21 Dec.99 we visited the peat swamp forest near the Upper Peirce Reservoir in the Upper Catchment Reserve, and inspected the above-ground sections of a concrete water pipeline. In a corner between the underside of the pipeline and one of its concrete supports we found a cluster of 5 clutches of *Cnemaspis* eggs, each comprising 2 eggs at equal stage. One clutch had hatched (from its appearance, this year), one clutch was grey (with developed embryos), and 3 clutches were white to pinkish (early development), to judge from experience with *Ptyodactylus* (Werner, 1986)(Fig. 4B).

The female (FR2) which died on 16 Dec.99 was obviously ovigerous. Upon its dissection (freshly dead) each ovary (the right-hand one cranial to the left-hand one) contained one large spherical egg of 5.3 mm diameter, and on it a group of three medium-sized flat follicles, the largest of 1.5 mm diameter, and a cluster of at least three small follicles.

Female ZRC 2.1111 collected on 16 Sep.1925 (on Pulau [=Island] Siantan, Anamba Islands) was obviously ovigerous and was radiographed, revealing two eggs, one appeared shelled and intact and measured 8x5.9 mm; the other appeared damaged and was not measured.

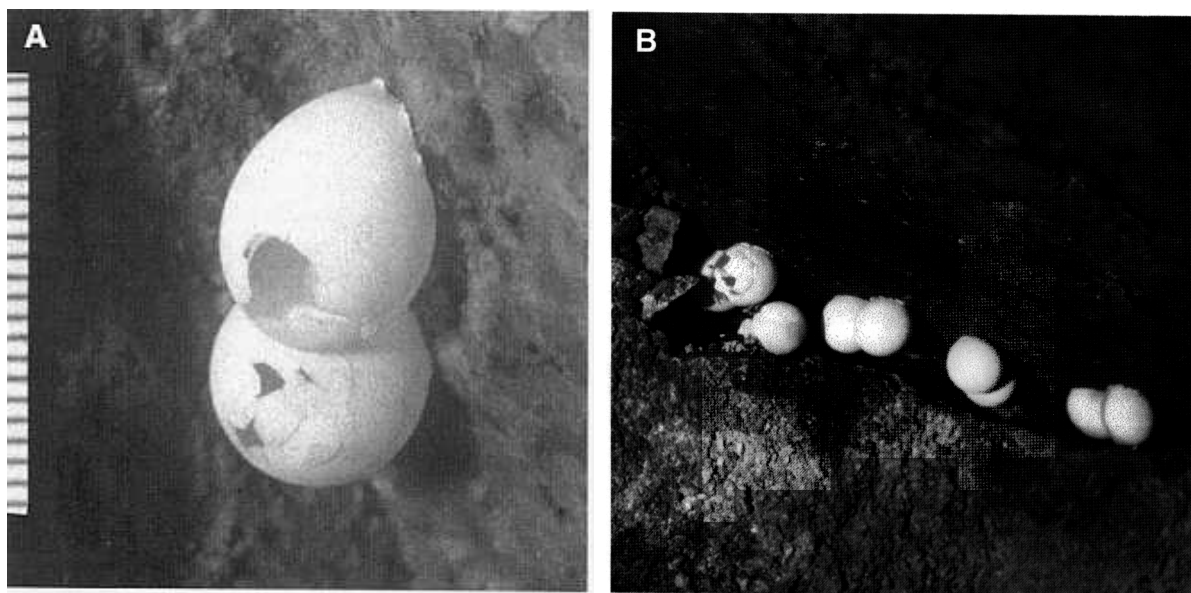


Fig. 4. - Eggs of *Cnemaspis kendallii* in Singapore. A, Egg clutch near the entrance to one of the tunnels, Bukit Timah reserve, recently hatched, 7 Dec.1999 (ruler with mm). B, Cluster of five clutches in different stages, under the concrete water pipeline in the peat swamp forest, near the Upper Peirce Reservoir in the Upper Catchment Reserve, 21 Dec. 1999.



Juvenile ZRC 2.1108, collected at Bukit Timah on 4 Sep. 1898 by S.S. Flower, measured 20.4 mm ra (tail too contorted to measure).

## DISCUSSION

This brief study somewhat increases the knowledge of the ecology of *Cnemaspis kendallii* which had been scant (Manthey & Grossmann, 1997; Das & Bauer, 1998) and enables some comparative comments.

**Habitat, Population and Conservation.** - Gekkonid species may be either cursorial or scansorial. These two types are gradually being shown to differ in an increasing number of aspects, beyond the obvious ones of habitat use and the frequent possession of digital clinging pads by the scansorial species. Some of these aspects will be discussed here.

Scansorial geckos may use two types of substrate for accessing a three-dimensional environment (as compared with that of cursorial species): tree trunks, rocks, or both. For example, in central Israel, *Cyrtopodion kotschy* lives on tree trunks, *Ptyodactylus guttatus* on rocks and their substitutes, and *Hemidactylus turcicus* on both (Werner, 1995). *Cnemaspis kendallii* is locally named "rock gecko" but our observations of eight individuals on rocks and eight on trees confirm the statements of Lim & Lim (1992) and Manthey & Grossmann (1997) that it occurs on both tree trunks and rocks. We cannot identify a "primary" or "preferred" substrate for lack both of a sharper definition of "suitable tree trunks" and "suitable rocks" and then of a survey of their relative availability, besides a more extensive census of their occupation by the gecko. Regardless of preference, this species, in using the two substrates at the same place and time, resembles some other scansorial geckos, such as *Hemidactylus turcicus* in the Mediterranean (op.cit.), or *Pachydactylus turneri* in the Namib Desert (Werner, 1977, as *P. laevigatus*). Such truly wide niche-breadth should be distinguished from that of species which are stated to occupy both substrates while actually these occur in different places, each population being limited to one substrate, e.g., *Gehyra variegata* and *Oedura marmorata* across Australia (Cogger, 1992).

Our observations enable only a crude guess about the population density of *Cnemaspis kendallii* at Bukit Timah. We have seen at least 16 individuals along the approx. 1070m of paths that we inspected repeatedly and which in principle contained geckos

(along some paths we found no geckos, presumably because of forest type). Because usually we did not inspect the "back side" of trunks and rocks, we may conservatively multiply the number of geckos by a factor of 1.5, thus averaging one individual gecko per 44.6 meters of path length. If from this we surmise an average diameter of 44.6 m of hypothetical mutually exclusive contiguous territories, or 1561.5 m<sup>2</sup> per territory, we arrive at an estimated 6-7 adult geckos per hectare of correct habitat. This value ignores the general tendency of lizards not to come out every day even in suitable weather (Pianka, 1970; Rose, 1981), which appeared to apply also in our case. If therefore we roughly guess a double value of 13 adult geckos/hectare, this will be within the lower extreme of the range estimated for diurnal lizards (Turner, 1977). Little comparative information exists from other arboreal geckos. Much higher values were found by Kitchener et al. (1988) in Western Australia: for the somewhat smaller *Gehyra variegata* an average of 66.4/ha and for the somewhat larger *Oedura reticulata* an average of 46.8/ha. Including juveniles, the respective values were 118.9/ha and 113.9/ha. However, while the expression of the population density per ground area is relevant for assorted human considerations, the area biologically relevant to the geckos should probably be measured in terms of the surface of inhabitable tree trunks.

Our having seen only adults is open to many interpretations but the simplest would be that on the one hand this gecko matures in less than a year, and on the other hand the juveniles have a more reclusive behaviour, as known from some other reptiles (Blair, 1960). But a combination of heavy predation on juveniles and long life span of surviving adults can also not be ruled out, and none of these factors are mutually exclusive. The reproductive (oviposition) season, from the scant evidence collected here, must extend at least from August through December; in some other tropical lizards it is known to operate throughout the year.

These observations are too scant to provide an estimate of the conservation status of *Cnemaspis kendallii* at Bukit Timah. One key point which remains an open question is whether the species occurs throughout the forest or is limited to certain types of patches, perhaps primary forest. Among the assorted potential gecko predators which occur in the park, one which could have a marked detrimental effect is the macaque *Macaca fascicularis*, of which about a hundred live there (Lucas, 1996; Teo & Rajathurai, 1997).

**Arrhythmic Activity Cycle.** - Usually species of geckos have been described as diurnal, crepuscular or nocturnal, and Werner (1969) has introduced the term diurno-nocturnal for the species, that, while foraging at night, perform their diurnal thermoregulation by exposed basking out of cover. The nocturnal activity of geckos may be further constrained by the environmental temperature (Bustard, 1967, 1968) but at least some tropical nocturnal geckos limit their main activity to part of the night without such a thermal cause (Bustard, 1970; Chou & Leong, 1984).

As said above, *Cnemaspis kendallii* was previously considered crepuscular or nocturnal (Lim & Lim, 1992). Our observations show that individual *Cnemaspis kendallii* are abroad day and night, presumably foraging. Both the amount of spontaneous movement (Table 1) and the animals' wariness appeared to be similar day and night. The species (or genus) is unique in this, although its activity during the later part of the night remains unknown. As described above, the exposure in daytime cannot be interpreted as basking. Such day-and-night active animals have been termed arrhythmic (Walls, 1942). Thus *C. kendallii* contrasts sharply with the common house gecko species in Singapore, *Cosymbotus platyurus* and *Hemidactylus frenatus*, which clearly are crepuscular and nocturnal (Chou & Leong, 1984). Our observations are limited to November-December and the diel activity cycle of geckos may vary seasonally (Frankenberg, 1978) but such variation is not very expected in the relatively stable equatorial climate of Singapore. Some other *Cnemaspis* species, too, are considered to be active both day and night (Manthey & Grossmann, 1997; Cox et al., 1998). Other congeners have generally been described as diurnal (Roesler, 1995). Nevertheless, congeners in India are reported by Murthy (1990) and Tikader & Sharma (1992) as nocturnal despite their round pupils, although Das (personal communication) considers that all or most species are diurnal. Interestingly, of two new species recently described by Das & Bauer (2000) from southern India, the holotype of *Cnemaspis otai* was found at 1730h on 6 January and that of *C. yercaudensis* at 2129h on 13 January, both out in the open (but it is unknown whether awake).

**Foraging Mode.** - The foraging mode of *Cnemaspis kendallii* is more extremely SW than in most other geckos studied (Table 2). This could be related to its arrhythmic diel cycle: The danger of being predated is proportional to the duration of exposure but reduced by immobility. *C. kendallii* may be eating

mainly prey that comes its way at its perch: (a) At least two stationary individuals were observed making movements which could have been due to feeding. (b) No individuals were seen on the ground as observed in some other scansorial (arboreal and saxicolous) geckos (Werner et al., 1997b). (c) In only four of ten observations on trees did the *C. kendallii* have the head pointed towards the ground, and only one was seen in such posture near the bottom (25 cm) of its tree trunk, as often seen in *Gekko hokouensis* (Werner & Takahashi, unpublished). But feeding on the ground cannot be entirely excluded, since of six stomachs examined (on the Tioman and Tulai islands), one contained a small scarabeid beetle and a small polydesmoid millipede, another contained an earthworm, a third - two ants and soil, and two others - only soil, indicating terrestrial foraging that is concentrated more on the soil layer than on the [leaf] litter (Bullock, 1966).

It is noteworthy that the CV is very high, as in most geckos (Table 2), in difference from that seen in other lizards, e.g. Lacertidae (Werner et al., 1997a).

**Ecological Morphology.** - The sexual size dimorphism intimated in the data of Das & Bauer (1998), wherein the largest of 7 males measured 56.8 mm SL, and the largest of 3 females reached 79.5 mm, appears confirmed in principle by the material in ZRC, the largest of 11 males having measured 62 mm and the largest of 7 females, 68 mm. This dimorphism accords with the conclusion of Fitch (1981), that in small species of lizards the female is larger than the male, although in many geckos the contrary is true (Chou, 1978).

Eye size varies among geckos in relation to two ecological factors (Werner, 1969; Pianka & Pianka, 1976). As in other animal groups, the eye is larger in nocturnal than in diurnal species of similar body size (Walls, 1942). But within the nocturnal group, and again within the diurnal group, eye size is larger in the cursorial than in the scansorial species. The eye of *Cnemaspis kendallii* has been described as "large" (Boulenger, 1885; De Rooij, 1915; McCann, 1955; Das & Bauer, 1998). In fact according to the data of Werner (1969) the eye size of 5.25 percra, as found here, unambiguously falls within the group possessing the smallest eyes, the diurnal scansorial species (n=6, 3.7-5.9 percra). The eyes of scansorial species that are diurno-nocturnal or nocturnal are larger (n=11, 5.4-7.0 percra), and so are the eyes of cursorial species, of any diel cycle (n=12, 5.8-8.7 percra).



Table 2. The foraging mode of *Cnemaspis kendallii* compared with those of other gekkonine geckos. Abbreviations as in Table 1.

Species	Location		MPM	PTM	Source
<i>Cnemaspis kendallii</i>	Singapore	Mean	<b>0.02</b>	<b>0.28</b>	Present data
		CV	200.0	221.4	
<i>Gehyra mutilata</i>	Tahiti	Mean	<b>0.6</b>	<b>1.6</b>	Werner, 1998
		CV	65	71.25	
<i>Gehyra oceanica</i>	Tahiti	Mean	<b>0.27</b>	<b>2.03</b>	Werner et al., 1997b
		CV	5.18	57.63	
<i>Gekko gecko</i>	Thailand	Mean	<b>0.04</b>	<b>5.8</b>	Stanner et al., 1998
		CV	n. a.	n. a.	
<i>Gekko hokouensis</i>	Japan: Okinawa	Mean	<b>0.35</b>	<b>25.5</b>	Werner et al. 1997b
		CV	42.9	57.6	
<i>Gekko japonicus</i>	Japan: Fukuoka	Mean	<b>0.15</b>	<b>8.9</b>	Werner et al., 1997b
		CV	133.	107.5	
<i>Hemidactylus frenatus</i>	Tahiti	Mean	<b>0.28</b>	<b>0.57</b>	Werner, 1998
		CV	n. a.	n. a.	
<i>Lepidodactylus lugubris</i>	Tahiti	Mean	<b>1.15</b>	<b>4.81</b>	Werner, 1998
		CV	120.8	108.1	
<i>Pachydactylus turneri</i>	NW Namibia	Mean	<b>0.16</b>	<b>0.00</b>	Cooper et al., 1999
		CV	145.1	0.00	
<i>Afrogecko porphyreus</i> (as <i>Phyllodactylus porphyreus</i> )	Stellenbosch	Mean	<b>0.04</b>	<b>1.0</b>	Cooper et al., 1999
		CV	223.6	223.6	
<i>Rhoptropus afer</i>	Namibia	Mean	<b>0.00</b>	<b>0.00</b>	Cooper et al., 1999
		CV	0.00	0.00	
<i>Rhoptropus barnardi</i>	NW Namibia	Mean	<b>0.28</b>	<b>1.0</b>	Cooper et al., 1999
		CV	137.02	0.00	
<i>Teratoscincus roborowskii</i>	China: Turfan	Mean	<b>0.44</b>	<b>8.8</b>	Werner et al., 1997b
		CV	186.0	167.8	

The notched round pupil of *Cnemaspis kendallii*, which differs in shape details from that of other diurnal geckos (and most reptiles), deserves study. If it is representative of the genus, it probably evolved from a vertical pupil separately of other gekkonid round pupils; if the notching is species-specific, it could either be a primitive remnant of such an evolutionary process, or secondarily derived within the genus from a round pupil. Either way, the notching seems to indicate recent or incomplete conversion to full diurnal-eye structure, and this may relate to the arrhythmic diel cycle. The structure of the retina of *Cnemaspis* is unfortunately unknown (Garth Underwood, pers. com.).

Tail length has been found to vary in correlation with foraging mode. When compared among closely related species, it is relatively longer in the widely foraging species than in the sit-and-wait foragers (e.g., in Lacertidae - Huey & Pianka, 1981; Perry et al., 1990). We cannot embark here on a full comparison of tail length and foraging mode in geckos. But it is interesting that while *Cnemaspis kendallii* is an extreme sit-and-wait strategist, its complete tail, averaging 125.5 percra, is longer than in many other geckos (Boulenger, 1885).

The frequency of regenerated tails varies among species (Arnold, 1984) and sometimes seems to differ between species according to their ecological type (Werner, 1968; Pianka & Huey, 1978; but see Bauer & Russell, 1994). It is thus logical that it should sometimes vary intraspecifically, among populations (Pianka, 1970; Tinkle & Ballinger, 1972). The small sample examined here seems to indicate that this may well be the case in *Cnemaspis kendallii*, with tail breakage and regeneration much rarer in Singapore than elsewhere in the species' range. A similar situation was recently observed in *Gekko hokouensis*: on Okinawa regenerated tails are rare but they are very frequent on some other islands (Werner et al., unpublished). The ecological interpretation of such variation invokes predation pressure but is ambiguous. A low rate of tail loss and regeneration may reflect the absence of heavy predation pressure but it may also reflect expert predation by saurophagous specialists, that leave no tail-less lizards behind (Pianka, 1970; Pianka & Huey, 1978; Seligmann et al., 1996).

**Reproduction.** - As has been pointed out by Manthey & Grossmann (1997), previously nothing had been known about the reproduction of this species. Our identification of the eggs found in the field relies on the combination of circumstances that at least five

congeners (*C. affinis*, *flavolineatus*, *nigridius*, *siamensis*, *kumpoli*) oviposit clutches of two eggs stuck together and to the substrate (W. Grossmann, pers. comm. 14 Dec. 1999); and that the syntopical species of the other genus with this oviposition habit, *Gekko*, are too large for the eggs seen (Werner, 1989).

Repeated oviposition of multiple clutches during the season is known in *C. nigridius* and *C. siamensis*, and this probably is the practice of *C. kendallii*. The presence together of several clutches, some at different developmental stages, is probably due to a number of females returning to the same site for repeated oviposition, as is suspected in other Singapore geckos (Chou, 1979), and known in *Ptyodactylus* (Werner, 1986). In *Cnemaspis* (*Ancylodactylus*) *africanus* reproduction seems to occur throughout the year (Fitch, 1970). Reproduction throughout most of the year has been reported from some other tropical geckos, e.g., *Gonatodes vittatus* (Quesnel, 1957), *Lepidodactylus lugubris* (Roesler, 1998). Considering the fragmentary data collected here, this may also be the habit of *C. kendallii* but more complete evidence is necessary. Meanwhile we only have evidence of oviposition during September-December, although the juvenile found in September makes oviposition in July or August a probability.

## CONCLUSIONS

1. Brief observations on the little-known 'rock-gecko' *Cnemaspis kendallii* in the Bukit Timah Nature Reserve, Singapore, in November-December 1999, augmented by examination of museum specimens, materially increased the knowledge of its behaviour, biology and ecological morphology.
2. It inhabits both tree trunks of assorted types up to 2.5 m above ground, and granite rocks.
3. It is active abroad both day and night.
4. Its foraging mode is a sit-and-wait strategy most extreme among geckos, shared only by one or two other gecko species, among a total of thirteen species studied in this respect.
5. Its eye (spectacle diameter), 5.25 percent of head and body length, is as small as in other diurnal scansorial geckos.
6. The round pupil of the eye differs from those of other diurnal geckos in being notched dorsally and ventrally.
7. Its tail (when complete), 125.5 percent of head and body length, is unexpectedly long for an extreme sit-and-wait foraging gecko.
8. It lays clutches of two hard-shelled eggs, each

approx. 9.25 mm in diameter, sticking to each other and to the substrate.

9. The oviposition season extends at least over September-December, probably over July-December, and possibly over the whole year.

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## LITERATURE CITED

- Arnold, E. N., 1984. Evolutionary aspects of tail shedding in lizards and their relatives. *Journal of Natural History*, **18**: 127-169.
- Bauer, A. M. & A. P. Russell, 1994. Is autotomy frequency reduced in geckos with "actively functional" tails? *Herpetological Natural History*, **2**: 1-15.
- Blair, W. F., 1960. *The Rusty Lizard, a Population Study*. University of Texas Press, Austin. XIV+185 pp.
- Boulenger, G. A., 1885. *Catalogue of the Lizards in the British Museum (Natural History)*. 1, *Geckonidae, Eublepharidae, Uroplatidae, Pygopodidae, Agamidae*. Trustees of the British Museum, London. XII+497 pp.
- Boulenger, G. A., 1912. *A Vertebrate Fauna of the Malay Peninsula. Reptilia and Batrachia*. Taylor and Francis, London. 294 pp.
- Bullock, J. A., 1966. Observations on the fauna of Pulau Tioman and Pulau Tulai: 7. The food of the amphibians and reptiles. *Bulletin of the National Museum (Singapore)*, **34**: 85-96.
- Bustard, H. R., 1967. Activity cycle and thermoregulation in the Australian gecko *Diplodactylus vittatus*. *Copeia*, **1968**: 606-612.
- Bustard, H. R., 1968. Temperature dependent activity in the Australian gecko *Gehyra variegata*. *Copeia*, **1967**: 753-758.
- Bustard, H. R., 1970. Activity cycle of the tropical house gecko, *Hemidactylus frenatus*. *Copeia*, **1970**: 173-176.
- Chou, L. M., 1978. Some bionomic data on the house geckos of Singapore. *Malayan Nature Journal*, **31**: 231-235.
- Chou, L. M., 1979. Eggs and incubation period of three gekkonid lizards. *Copeia*, **1979**: 552-554.
- Chou, L. M. & C. F. Leong, 1984. Activity cycles of the house geckos, *Cosymbotus platyurus* and *Hemidactylus frenatus*. *Malayan Nature Journal*, **36**: 247-252.
- Cogger, H. G., 1992. *Reptiles and Amphibians of Australia*. 5th edition. Reed, Chatswood, NSW. 775 pp.
- Cooper, W. E., Jr., 1995. Foraging mode, prey chemical discrimination, and phylogeny in lizards. *Animal Behavior*, **50**: 973-985.
- Cooper, W. E., Jr., M. J. Whiting, J. H. Van Wyk & P. le F.N. Mouton, 1999. Movement and attack-based indices of foraging mode and ambush foraging in some gekkonid and agamine lizards from southern Africa. *Amphibia-Reptilia*, **20**: 391-399.
- Corlett, R. T., 1997. The vegetation in the nature reserves of Singapore. *Gardens' Bulletin (Singapore)*, **49**: 147-159.
- Cox, M. J., P. P. van Dijk, J. Nabhitabhata & K. Thirakhupt, 1998. *A Photographic Guide to Snakes and Other Reptiles of Peninsular Malaysia, Singapore and Thailand*. New Holland Publishers, London. 144 pp.
- Das, I. & A. M. Bauer, 1998. Systematics and biogeography of Bornean geckos of the genus *Cnemaspis* Strauch, 1887 (Sauria: Gekkonidae), with the description of a new species. *Raffles Bulletin of Zoology*, **46**: 11-28.
- Das, I. & A. M. Bauer, 2000. Two new species of *Cnemaspis* (Sauria: Gekkonidae) from Tamil Nadu, Southern India. *Russian Journal of Herpetology*, **7**: 17-28.
- De Rooij, N., 1915. *The Reptiles of the Indo-Australian Archipelago. I. Lacertilia, Chelonia, Emydosauria*. E.J. Brill, Leiden. XIV+384 pp.
- Fitch, H. S., 1970. Reproductive cycles of lizards and snakes. *University of Kansas Museum of Natural History Miscellaneous Publications*, **52**: 1-247.
- Fitch, H. S., 1981. Sexual size differences in reptiles. *University of Kansas Museum of Natural History Miscellaneous Publications*, **70**: 1-72.
- Foo, S. L. & T. C. Kwok (eds.), 1999. *Singapore 1999*. Ministry of Information and the Arts, Singapore. 363 pp.
- Frankenberg, E., 1978. Interspecific and seasonal variation of daily activity times in gekkonid lizards (Reptilia, Lacertilia). *Journal of Herpetology*, **12**: 505-519.
- Gray, J. E., 1845. *Catalogue of the Specimens of Lizards in the Collection of the British Museum*. Trustees of the British Museum, London. XXVII+289 pp.
- Huey, R. B. & E. R. Pianka, 1981. Ecological consequences of foraging mode. *Ecology*, **62**: 991-999.
- Kitchener, D. J., R. A. How & J. Dell, 1988. Biology of *Oedura reticulata* and *Gehyra variegata* (Gekkonidae) in an isolated woodland of Western Australia. *Journal of Herpetology*, **22**: 401-412.
- Leviton, A. E., R. H. Gibbs, Jr., E. Heal & C. E. Dawson, 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia*,

- 1885: 802-832.
- Lim, K. K. P. & F. L. K. Lim, 1992. *A Guide to the Amphibians and Reptiles of Singapore*. Singapore Science Center, Singapore. 160 pp.
- Lucas, P., 1996. Why the monkeys must not be fed. In: Lum, S. & I. Sharp (eds.), *A View from the Summit - The Story of Bukit Timah Nature Reserve*. Nanyang Technological University, Singapore and National University of Singapore, Singapore, pp. 69-71.
- Manthy, U. & W. Grossmann, 1997. *Amphibien & Reptilien Suedostasiens*. Natur und Tier Verlag, Muenster. 512 pp.
- McCann, C., 1955. The lizards of New Zealand. Gekkonidae and Scincidae. *Dominion Museum Journal, Wellington*, 17: i-viii, 1-127.
- Murthy, T. S. N., 1990. A Field Book of the Lizards of India. *Records of the Zoological Survey of India*, Occasional Paper No. 115. VII+116 pp., 8 pls.
- Paulissen, M. A. & H. A. Meyer, 2000. The effect of toe-clipping on the gecko *Hemidactylus turcicus*. *Journal of Herpetology*, 34: 282-285.
- Perry, G., I. Lampl, A. Lerner, D. Rothenstein, E. Shani, N. Sivan & Y. L. Werner, 1990. Foraging mode in lacertid lizards: variation and correlates. *Amphibia-Reptilia*, 11: 373-384; 13: 96.
- Pianka, E. R., 1970. Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. *Ecology*, 51: 703-720.
- Pianka, E. R. & R. B. Huey, 1978. Comparative ecology, resource utilization and niche segregation among gekkonid lizards in the southern Kalahari. *Copeia*, 1978: 691-701.
- Pianka, E. R. & H. D. Pianka, 1976. Comparative ecology of species of nocturnal lizards (Gekkonidae) in the Australian desert. *Copeia*, 1976: 125-142.
- Quesnel, V. C., 1957. The life history of the streak lizard, *Gonatodes vittatus*. *Journal of the Trinidad Field Naturalists' Club*, 1957: 5-14.
- Roesler, H., 1995. *Geckos der Welt, alle Gattungen*. Urania, Leipzig. 256 pp.
- Roesler, H., 1998. Bemerkungen zur Fortpflanzungsbiologie von Geckonen - Aufzeichnungen aus den Jahren 1993 bis 1996 (Sauria: Gekkota). *Gekkota (Quedlinburg)*, 1: 64-175.
- Rose, B., 1981. Factors affecting activity in *Sceloporus virgatus*. *Ecology*, 62: 706-716.
- Seligmann, H., A. Belles & Y. L. Werner, 1996. Tail loss frequencies of lizards and predator specialization. In: Steinberger, Y. (ed.), *Preservation of our World in the Wake of Change*, vol.6 A/B, ISEEQS Publ., Jerusalem, pp. 520-522.
- Stanner, M., Kumthorn Thirakhupt, N. Werner & Y. L. Werner, 1998. Observations and comments on the tokay in Thailand and China as predator and as prey (Reptilia: Sauria: Gekkonidae: *Gekko gecko*). *Dactylus*, 3: 69-84.
- Strauch, A., 1887. Bemerkungen ueber die Gekkonidan-Sammlung im Zoologischen Museum der Kaiserlichen Akademie der Wissenschaften zu St. Petersburg. *Mémoires de l'Académie des Sciences Impériales de Saint-Petersbourg*, 7: I-II, 1-72.
- Teo, R. C. H. & S. Rajathurai, 1997. Mammals, reptiles and amphibians in the nature reserves of Singapore - diversity, abundance and distribution. Proceedings of the Nature Reserves Survey Seminar, *Gardens' Bulletin (Singapore)*, 49: 353-425.
- Tikader, B. K. & R. C. Sharma, 1992. *Handbook of Indian Lizards*. Zoological Survey of India, Calcutta. X11+250 pp., 42 pls.
- Tinkle, D. W. & R. E. Ballinger, 1972. *Sceloporus undulatus*: A study of the intraspecific comparative demography of a lizard. *Ecology*, 53: 570-584.
- Turner, F. B., 1977. The dynamics of populations of squamates, crocodilians and rhynchocephalians. In: Gans, C. & D. W. Tinkle (eds.), *Biology of the Reptilia* vol. 7, Academic Press, London, pp. 157-264.
- Walls, G. L., 1942. The vertebrate eye and its adaptive radiation. *Bulletin of the Cranbrook Institute of Science*, 19: 1-785.
- Werner, Y. L., 1968. Regeneration frequencies in geckos of two ecological types (Reptilia: Gekkonidae). *Vie et Milieu*, 19C: 199-221.
- Werner, Y. L., 1969. Eye size in geckos of various ecological types (Reptilia: Gekkonidae and Sphaerodactylidae). *Israel Journal of Zoology*, 18: 291-316.
- Werner, Y. L., 1971. Some suggestions on the standard expression of measurements. *Systematic Zoology*, 20: 249-252.
- Werner, Y. L., 1977. Ecological comments on some gekkonid lizards of Namib desert, south west Africa. *Madoqua*, 10: 157-168.
- Werner, Y. L., 1986. Ecology of eggs and laying sites of *Ptyodactylus* geckos. In: Rocek, Z. (ed.): *Studies in Herpetology*. Charles University, Prague, pp. 441-444.
- Werner, Y. L., 1989. Egg size and egg shape in Near-Eastern gekkonid lizards. *Israel Journal Zoology*, 35: 199-213.
- Werner, Y. L., 1995. *A Guide to the Reptiles and Amphibians of Israel*. Nature Reserves Authority, Jerusalem (in Hebrew with English captions for figures). 86 pp.
- Werner, Y. L., 1998. Preliminary observations on foraging mode in a community of house geckos on Tahiti and a comment on competition. *Tropical Ecology*, 39: 89-96.
- Werner, Y. L. & A. Bouskila, 1995. Foraging at night: do geckos sit and wait? *Abstracts 2nd Asian Herpetological Meeting, Ashgabat 6-10 Sep. 1995*, p. 59.
- Werner, Y. L. & M. Broza, 1969. Hypothetical function of elevated locomotory postures in geckos (Reptilia: Gekkonidae). *Israel Journal Zoology*, 18: 349-355.
- Werner, Y. L., S. Okada, H. Ota, G. Perry & S. Tokunaga, 1997a. Varied and fluctuating foraging modes in nocturnal lizards of the family Gekkonidae. *Asiatic Herpetological Research*, 7: 153-165.
- Werner, Y. L., A. Bouskila, S. J. J. F. Davies & N. Werner, 1997b. Observations and comments on active foraging in geckos. *Russian Journal of Herpetology*, 4: 34-39.