

Varied and Fluctuating Foraging Modes in Nocturnal Lizards of the Family Gekkonidae

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Abstract. -Heliothermic lizards have been used as model organisms in studies of foraging mode, although their behavior is generally complicated by thermoregulation. Tropical nocturnal gekkonid lizards could be better models than temperate diurnal lizards. In several recent reviews, gekkonids have been considered to be sit-and-wait (ambush) predators. Observation of *Gekko hokouensis*, *G. japonicus* and *Teratoscincus roborowskii* in the field on warm nights revealed that by the measure of moves-per-minute they are sit-and-wait (SW) predators but by the measure of percent-time-moving *G. hokouensis* is widely-foraging (WF), as is *Coleonyx variegatus*, according to the literature. The behavior of individuals of all three species combines to varying extent both SW and WF modes. This observation accords with recent reports of foraging behavior in *G. gecko* and *Stenodactylus doriae*. Reexamination of the original literature sources quoted in recent reviews showed that these sources had already qualitatively described many geckos as either WF or mixed strategists. The fluctuating foraging mode of geckos presumably enables these nocturnal visual predators to locate stationary prey and, without wasting locomotor energy, to locate mobile prey. The option to employ both SW and WF modes may depend on the absence of competition. Although geckos as a group had been believed to be SW predators, their relative clutch mass (RCM) had often been believed to be as small as in WF lizards. More recently, several geckos were shown to have larger RCMs. Hence geckos, rather than having a paradoxically low RCM, are in fact intermediate between SW and WF lizard groups in both RCM and foraging mode.

Key words: Reptilia, Lacertilia, Gekkonidae, *Gekko hokouensis*, *Gekko japonicus*, *Teratoscincus roborowskii*, China, Japan, foraging mode, nocturnality, relative clutch mass.

Introduction

Ever since they were first coined by Pianka (1966), the terms "sit-and-wait" (SW) and "widely foraging" (WF) have been used extensively to describe foraging behavior. Often they have been considered alternative states of a dichotomy (Pianka, 1986; McLaughlin, 1989; Etheridge and Wit, 1993; and references in Pietruszka, 1986), while some authors have viewed them as extremes of a continuum (Pianka, 1974:203; Pietruszka, 1986; Perry et al., 1990). Although Vitt and Congdon (1978) and Vitt (1990) recognized the possibility of a continuum of foraging modes, their papers highlight differences between SW and WF lizards. Implicit in the use of these terms (or the equivalent "ambush" and "active" foragers) are the

assumptions that there is little intraspecific or intra individual variation in foraging behavior.

Lizards have been used often as models for studying the foraging behavior of animals in the field. The two commonest coins for quantification and comparison have been the "percent time moving" (PTM) and "movements per minute" (MPM, see below) (Huey and Pianka, 1981; Perry et al., 1990).

Going by such yardsticks, the foraging mode, either SW or WF, is usually considered typical of a whole lizard family. Thus, Agamidae, Anguidae and Iguanidae (s.l.), unless herbivorous, are SW foragers, whereas almost all Lacertidae, Scincidae, Teiidae and Varanidae are WF (Huey and Pianka, 1981; Dunham et al., 1988; Green and King, 1993; Cooper, 1994a, b).

The studies underlying this classification obviously presuppose that the observations quantified had been free of socially-motivated (Regal, 1983:116) and of thermoregulation-related (Anderson, 1993) behavior. Whereas it is relatively easy to account for the former (Kingsbury, 1989), it is often difficult to completely exclude the latter when observing diurnal poikilotherms such as lizards. Nocturnal lizards such as geckos can thus provide superior models of foraging mode if observed in a climate with stable night temperatures approximating those preferred by the lizards.

The Gekkonidae have traditionally been considered SW predators (Pianka, 1986:48; Dunham et al., 1988:513), and this view appears somewhat supported by recent observations on *Gekko gekko* (Stanner et al., in press). However, *Coleonyx variegatus* employs an intermediate strategy (Kingsbury, 1989) and some others have recently been counted as active foragers (Cooper, 1994a,b). Thus it remains unclear whether the Gekkonidae are characterized by a given foraging mode, as are other lizard families, and, if so, what that foraging mode is.

This issue is of particular interest because whereas SW lizards usually have greater relative clutch masses (RCMs) than WF lizards (Vitt and Congdon, 1978), geckos tend to have RCMs similar to those of WF lizards (Vitt and Price, 1982: figs. 1 and 3). This putative paradox cannot be explained fully as an adaptation of geckos to life in crevices (Vitt, 1981); small RCMs occur also in cursorial, arenicolous species of geckos (Vitt and Price, 1982; Werner, 1989); in some of these this could be a phylogenetic constraint (Vitt, 1986; Stearns, 1992) but presumably at least in the primitive group of Eublepharinae (Kluge, 1967; Werner, 1972) this would not be the case. Hence additional data on the foraging modes of geckos are needed.

Therefore, we report here on the foraging behavior of three nocturnal geckos in the eastern Asian summer, *Gekko hokouensis*, *G. japonicus*, and *Teratoscincus roborowskii*. We pay particular attention to intraspecific variation, which has been reported in the foraging behavior of some other lizards (Pianka et al., 1979; Kingsbury, 1989; Perry, 1996), and to intra-individual variation, a topic which has not been addressed previously.

Materials and Methods

Abbreviations and Definitions

CV, coefficient of variation (standard deviation as percent of mean); FM, foraging mode; MPM, "move-

ments per minute", the average number of times, during one minute, that a lizard changed its locomotory state from "stationary" to "moving"; PTM, "percent time moving" percentage of the total time, that the animal spent locomoting; perera, percents of ra; ra, rostrum-anus ("snout-vent") length (Werner, 1971); RCM, relative clutch mass, ratio of total clutch mass to total maternal mass, including the clutch (Vitt and Price, 1982); SD, standard deviation; SW, "sit-and-wait" predator; WF, "widely ranging forager".

Data Collection

Environmental factors such as illumination can affect the activity of nocturnal geckos (Frankenberg, 1979; Frankenberg and Werner, 1979; Bouskila et al., 1992; Petren et al., 1993). We therefore detail the circumstances of the observations.

Observations were made at night by one observer carrying an electric torch with a removable cover of red cellophane paper (two layers). When the torch was held on the observer's forehead, *Teratoscincus* could be located on the ground by their reflecting reddish eyeshine. With both *Gekko* species, which were observed mainly on walls, this method was superfluous. Searching began at a distance (>20 m for *Teratoscincus*; less for the *Gekko* species) with white light. The main observations were made from 3-10 m, depending on species and situation, with red light. We endeavoured to observe each individual for 30 minutes; finally the gecko was approached and examined. In all three species, some of the locomotion of the individuals was towards the observer, hence presumably the observer did not affect them (following Anderson, 1993).

To enable prompt photography, the observer carried a ready camera (Leica M3 with 135 mm lens) with flash and mostly Agfachrome Professional 200 ASA film. Air temperature was recorded with a Miller-Weber mercury thermometer ("Schultheis" type) 1 m above ground (for *Teratoscincus* also 1 cm above ground, and substrate temperature was also taken). Illumination was recorded with a Lunasix-3 (Gossen) light meter.

Observations and environmental data were recorded into a microcassette recorder (Panasonic RN-102). When the information was transcribed on paper, detailed time data were derived from a clock synchronized with recorded times. Because the speeds of recording and playback varied with battery strength, care was taken to use equivalent batteries.



Figure 1. Study site for *Gekko hokouensis* at the Chinen Castle ruins, near Chinen, Okinawa Island, Japan (4 August 1992).

Data Processing and Presentation

Geographical grid references of towns, for macro-ecological evaluation, are from the Times Atlas of the World (1967).

Observations suspected of reflecting social interactions or observer effect were excluded. The proximity of an observer may suppress the activity of lizards (Sugerman and Hacker, 1980) or stimulate excessive activity (Regal, 1983).

To enable comparison with previous data (Huey and Pianka, 1981; Perry et al., 1990), we use MPM and PTM to assess FM. These depend on the definition of discrete locomotor states, although the activity of the animals may constitute a continuum of patterns (Regal, 1983:115). We coarsely classified all postures and actions as "stationary" or "moving". "Stationary" included the time during which the gecko remained in the same place, perhaps moving its head, jaws, tongue, limbs or tail, or even shifting its posture by 180°, as long as it did not move towards another location. "Moving" included crawling, walking, running, jumping and jerking forwards.

A complication arose from frequent brief pauses during locomotion in *Gekko hokouensis*. We found a precedent in Avery et al. (1987a, b), who analyzed the locomotion of four lacertid species by videotape. "Standard" locomotion (neither fleeing nor chasing), presumably representing foraging behavior, comprised 88-143 bursts of movement per minute, each of 0.25-0.56 sec. The intervening pauses lasted 0.12-0.17 sec, and occupied 18-40% of the time. In the FM of female *Podarcis sicula* in nature, Avery (1991) defined as 'movement' a bout of locomotion separated from others by pauses of >1 second. Thus defined, movement duration in *P. sicula* averaged 10.9 sec; pause duration averaged 22.4 sec (MPM= 1.8; PTM=

32.7). We followed this methodology for approx. half the data of *Gekko hokouensis*, which included appropriate time statements.

In the remainder of *G. hokouensis* data, the observations had been grouped per half-minute periods, leaving precise durations unknown. These records were scanned automatically by the NOTITA computer program (N. Werner & H. Dreher, in MS) which constructed a quantitative table, from which some summarising statistics were derived by the Microsoft Excel program.

We do not use velocity as a descriptor of FM (Huey and Pianka, 1981; Magnusson et al., 1985; Anderson, 1993) because velocity is generally affected by body size (Avery et al., 1987b).

Species, Environments and Observations

***Gekko hokouensis* Pope, 1928.** *Gekko hokouensis* males attain 59.8 mm ra (mean 53.9) and females 65.4 mm ra (mean 54.8) on Okinawa Island (Ota, unpublished data).

Study site. *G. hokouensis* was studied at the Chinen Castle ruins near Chinen (26° 07'N, 127° 49'E), southern Okinawa Island, Japan (. 1). Most observations were made on geckos on and in a small modern but uninhabited concrete-block building among large trees (fig. 1); few observations were made on geckos on the trees. None of the other gecko species occurring on Okinawa (Ota, 1989) was encountered in the study site.

Procedure and conditions. On five nights between 28 July and 4 August 1992, observations started between 1850 h (at which time the illumination was down to 700 lux) and 2015 h (sunset was approx. at 1915 h), and lasted as long as geckos were active on the building. Throughout the observations, the sky was mostly at least half overcast, hiding the moon which was waxing, in its first quarter. Air temperature varied only between 26.0 and 28.1° C. On the first night, observations were made by a team of two; on the later nights, the two observers functioned as separate teams. Observations were made from distances of 3-5 m, so that behaviour was seen in detail. Observation time totalled 27.25 team-hours.

Observations. Of 63 geckos recorded, only 12 could be followed for >30 min. These showed varied movement patterns.

Bouts during which the geckos were stationary, lasted from <1 min to >15 min. While stationary, geckos often turned their head (to one side or another, or back to the straight position, up to twice per minute).

Table 1. Measures of foraging mode in the geckos studied. Species means are based on samples described or quoted in the text.

Species	Minutes observed		Moves/minute		% of time moving	
	X	SD	X	SD	X	SD
	(Range)		(Range)		(Range)	
<i>Gekko hokouensis</i> n=12	37.8	7.15	0.35	0.15	25.5	14.7
	(30.5-53.5)		(0.18-0.65)		(5.1-51.5)	
<i>G. japonicus</i> n=12	25.44	12.32	0.15	0.2	8.94	9.7
	(4-43)		(0.00-0.75)		(0.0-50.0)	
<i>Teratoscincus roborowskii</i>	11.97	8.81	0.44	0.8	8.83	14.8
	(1.5-36.03)		(0.00-2.82)		(0.0-50.0)	
	<i>Duration (seconds) of a single-</i>					
	<i>Stationary pause</i>		<i>Move</i>			
<i>Gekko hokouensis</i> n=12	150.2	74.1	50.2	29.9		
	(5-1050)		(1-375)			
<i>G. japonicus</i> n=12	856.6	818.7	34.7	38.6		
	(2-2580)		(1-150)			
<i>Teratoscincus roborowskii</i> n=11	385.0	296.3	13.2	23.0		
	(1-1800)		(1-150)			

turned the whole body to another direction (up to once per four minutes), or waved or vibrated the tail (up to once in seven minutes). Licking the lips could occur at any time (usually up to once per minute).

Gecko movements between stationary bouts took three major forms: (a) Normal walking or running, usually for a distance of 5-100 cm at a time.

(b) Crawling: the geckos sometimes advanced, with or without pauses, by a slow "crawl", at a speed of about 1 cm/min. We saw no evidence that this was consistently related to the gecko having detected a prey item.

(c) Interrupted locomotion: a sequence of forward movements by 1-2 cm each ("micromoves"), at a rate of usually 2-12 (rarely up to 72) "micromoves" per

minute. Following Avery et al. (1987a, b; see Materials and Methods) we classify each sequence of locomotion by "micromoves", including its brief pauses, as one bout of moving, or "move". But "micromoves" could also occur singly or widely spaced, and then were reckoned separately.

On the basis of these definitions of "moves", their statistics are summarized in Table 1.

The sex of twelve females was verified by capture or was evident due to obvious gravidity but the sex of only four males was ascertained by capture. Males appeared to be a little more active than females but the difference was not statistically significant (MPM: males, $X=0.46$; females, $X=0.32$; t-test $p=0.06$).

Gekko japonicus (Duméril et Bibron, 1836). *Gekko japonicus* males reach 65 mm ra (mode 60 mm), and females reach 70 mm ra (mode 61 mm) (Tokunaga 1984:fig.1).

Study site. *G. japonicus* was studied on the Hakozaki campus of Kyushu University, Fukuoka (33° 39'N, 130° 21'E), Kyushu Island, Japan, where the investigations of Tokunaga (1984) had been conducted. The geckos were on various buildings and sheds, especially in portions of walls or passage ceilings lit by incandescent or fluorescent lamps or by nearby street lamps. *G. japonicus* is the only gecko species in this study site (Nakamura and Uéno, 1963; Tokunaga, 1984), and no other reptiles were encountered during the observations.

Procedure and conditions. During three nights, 9-11 August 1992, observations by one observer started between 1915 h, when the illumination was 44 lux, and 2030 h (sunset, approx. 1910 h; end of twilight, approx. 2040 h), but had to be ended for logistic reasons by 2300 h, while geckos were still active. Throughout the observations the sky was overcast; sometimes a slight drizzle rained. The mostly-hidden moon was waxing in its second quarter. Light intensities where most geckos were observed ranged from 0.35 to 1000 lux. Some geckos were in the lit areas and others in nearby shaded situations. At the times the daily observations were conducted, air temperatures ranged from 27.2°C down to 24.5°C. These three nights followed two very rainy nights, when the site had been on the margin of a typhoon. The geckos were observed from distances of 5-8 m, so that fine details were missed. Observation time totalled 7.5 h.

Observations. Of 20 geckos recorded, only 7 could be followed for >25 min; the 12 observed for >4 min behaved variably: three remained stationary throughout (up to 43 min) whereas others alternated moving and pausing, usually moving less frequently than once every ten minutes, and spending up to 10% of their time in locomotion; but one spent 50% of the time moving (Table 1). There appeared to be some intra-individual variation; for example gecko no. 13 was once stationary for 15 min, whereas its other 7 stationary bouts all lasted <4 min.

The individuals were not sexed because most were high on walls.

Comment. The geckos may have been less active than usual during these observations due to the rainy weather and the cool season - in summer 1992 the mean daily temperatures were 2-3°C below the 30-year average (Fukuoka Meteorological Observatory records).

Teratoscincus roborowskii Bedriaga, 1905

Teratoscincus roborowskii was synonymized by Pope (1935:458) with *T. scincus* but is in the process of being validated by J. R. Macey et al. (see Autumn and Han, 1989). The species is arenicolous and its toes lack adhesive pads; males up to 87 mm ra, females up to 80 mm ra (from 30 adults in the California Academy of Sciences, courtesy J. Vindum).

Study site. *T. roborowskii* was studied near Turpan (42°55'N, 89°06'E), Xinjiang Uygur Autonomous Region, People's Republic of China (on the Turpan-Jiaohe road, approx. 4.5 km W of the Turpan Six Minarets Mosque; 3 km E of Jiaohe Ancient City).

Located on the margin of the Turpan Depression (-150 m), this area has a total annual precipitation average of 16.6 mm (Turpan Weather Bureau data). The daily maximum air temperature ranged up to 45°C in September 1987 (Autumn & Wang, 1988) but averaged only 40°C during the study period.

The study site comprised long-abandoned fields of blackish sand at the foot of hills with undisturbed vegetation described by Autumn & Wang (1988). The sand was soft in some places, hard packed in others, and retained remnants of furrows, ditches and wells. Plant coverage comprised only two small shrub species and by estimate varied between patches from 2% to 80%. Rainfall had exceeded the average - during the first half of the year (I.I.-9.VII.92), 21.8 mm had already accumulated (Turpan Weather Bureau data). In addition to the trees lining the road, some small stands of small *Tamarix* sp. trees occurred in the area.

Other than the *Teratoscincus* encountered at night, the only reptiles seen on the site were the diurnal lizards *Phrynocephalus axillaris* (Agamidae) and *Eremias velox* (Lacertidae). Some individuals of both species, especially of *Eremias*, were still active in the last daylight after sunset. According to Autumn & Wang (1988) *Psammophis lineolatus* (Colubridae) may also occur on the site. These authors pointed out the simplicity-in-principle of flora and herpetofauna on the site and in Chinese deserts in general.

Procedure and conditions. On four nights, 6-10 July 1992, observations (by one observer) started at 2125-2200 h (Beijing time; sunset, 2135 h), i.e., before the geckos emerged for their nocturnal activity on the surface; but had to be ended for administrative reasons at 0001-0030 h, while the geckos were still active. The moon was about 1/2 full (waxing), the sky mostly 4/8 cloudy; when gecko activity was high, the illumination was of the order of magnitude of 1 lux. Temperature differed little between sand surface, air 1 cm above ground and air 1 m above ground; the over-



Figure 2. *Teratoscincus roborowskii*, half-grown individual, scouting from the entrance of its burrow (Turpan, 2235 h, 8 July 1992).

all range during observations was 26.5–34.4°C. The wind varied from absent to fairly strong for short times, commonly blew from the north, and sometimes was noticeably warm. In the darkness, at distances of mostly approx. 10 m, gecko behavior was assessed from their returned eyeshine. Observation time totalled 10h 20' but as the torch became effective only at approx. 2210 h, the effective observation time approximated only 8h 20'.

Observations. On each night, the earliest gecko was spotted 40–65 min after sunset, after a search of 10–60 min. Thereafter, the finding of each successive individual usually required 0.5–5 min.

One individual, caught at 2310h on 9.VII.92 with sand temperature 30.5°C and air temperature (1 cm) 31.3°C, had a rectal temperature of 30.2°C.

Time budgets were calculated for the 11 animals observed (despite the vegetation) for > 90 sec and not suspected of having been affected by the observer (Table 1). Of 28 individuals discovered at a distance, only three were moving when spotted. This value of 10.7% of the animals moving when discovered is close to the 8.8 PTM calculated for the species (Table 1).

Individual foraging behavior was highly variable but two extreme patterns appeared to be dominant: several animals remained stationary throughout an observation period of 10–15 min; others kept alternating between standing and walking at intervals of 1–7 sec (rarely <1 or >60 sec).

Two individuals (a half-grown individual spotted on 8.VII at 2231 h and a subadult spotted on 9.VII at 2327 h) were sitting with only their fore-parts out of the openings of their burrows (fig. 2). One retained this position for 36 min, then ran out and away (the other was disturbed by the observer after 14 min, and retreated down its hole). When looking out from the burrow, these geckos may have been SW scouting like *Ptenopus* (Huey and Pianka, 1981).

Individuals were not sexed because this species autotomizes the skin when held, as described for *Teratoscincus scincus* by Bauer et al. (1993).

Comment. Thus these geckos are not simply "active foragers" as has been described for *Teratoscincus przewalskii* (Semenov and Borkin, 1992).

Discussion

The Foraging Mode of Gekkonid Species

For lizards, SW and WF appear to be the extremes of a FM continuum: (1) Both SW and WF are practiced differently by different lizard species, which combine different MPM and PTM values; (2) Some lizard species vary their FM during the day or during the year (Pietruszka, 1986); (3) the intermediate FM, repeatedly shifting the position for stationary scanning for prey, called "cruising" by Regal (1983:113–114), or, more aptly, "saltatory" by O'Brien et al. (1989), occurs also in lizards (Moremond, 1979). Nevertheless, SW and WF are definite foraging techniques: *Sceloporus merriami* and *Urosaurus ornatus* (Iguanidae) switched from distinct WF to distinct SW when food was scarce (Dunham, 1983). Indeed, generally SW is the optimal strategy for motile prey, and WF the optimal strategy for stationary prey (Gerritsen and Strickler, 1977).

In lacertid lizards the two FM measures, MPM and PTM, usually yield the same verdict as to whether a species is SW or WF, i.e., MPM values of <1–2 and PTM values of <15 indicate SW; MPM of >1.5–2 and PTM of >30 indicate WF (Huey and Pianka, 1981; Perry et al., 1990). By either index the species averages of *Gekko japonicus* and of *Teratoscincus roborowski* (Table 1) indicate that these geckos are SW foragers. The observations of Stanner et al. (in press) of *Gekko gecko* also are compatible with the suggestion of this species being a SW predator (0.04 MPM, 4.37 PTM). However, the third species studied here, *Gekko hokouensis*, is SW only in its MPM mean, and is WF, or nearly so, in its PTM. The situation in *Coleonyx variegatus* is very similar, with 0.57 MPM but 34 PTM (Kingsbury, 1989).

Thus by the index of MPM, all five gecko species for which at least some quantitative data exist, are SW predators. But the index of PTM is probably ecologically more significant, because it partly reflects energy investment in foraging, and by this index three species are SW, whereas two are WF. Moreover, the diet of *Ptyodactylus guttatus* indicates that this species forages more widely than previously believed (Perry and Brandeis, 1992), and Semenov and Borkin (1992) have stated that *Teratoscincus przewalskii* is a

Table 2. Coefficients of variation (CV) of measures of foraging mode in some lizards.

Family and Species	FM	CV of MPM	CV of PTM	Source
Lacertidae				
<i>Acanthodactylus boskianus</i>	WF	72.6	89.2	Perry et al., 1990
<i>Acanthodactylus schreiberi</i>	WF	56.5	67.5	Perry et al., 1990
<i>Acanthodactylus scutellatus</i>	SW	74.3	92.5	Perry et al., 1990
<i>Eremias lineoocellata</i>	SW	105.8	81.1	Huey and Pianka, 1981
<i>Eremias lugubris</i>	WF	36.4	25.6	Huey and Pianka, 1981
<i>Eremias namaquensis</i>	WF	55.7	48.6	Huey and Pianka, 1981
<i>Ichnotropis squamulosa</i>	WF	10.0	32.4	Huey and Pianka, 1981
<i>Lacerta laevis</i>	WF	84.5	81.0	Perry et al., 1990
<i>Meroles suborbitalis</i>	SW	40.4	45.9	Huey and Pianka, 1981
<i>Nucras tessellata</i>	WF	42.4	10.4	Huey and Pianka, 1981
Gekkonidae				
<i>Gekko hokouensis</i>	SW/WF	42.9	57.6	This report
<i>Gekko japonicus</i>	SW	133.3	107.5	This report
<i>Teratoscincus roborowskii</i>	SW	186.0	167.8	This report

WF species. This situation prompted us to trace some of the sources for the generalization that geckos are SW predators.

Dunham and Miles (1985) listed three gecko species, *Gehyra variegata*, *Heteronotia binoei* and *Oedura ocellata*, as SW predators, and quoted Vitt and Price (1982) as the source. Vitt and Price (1982) indeed listed 18 species of geckos, all as SW; this list included *G. variegata* and *H. binoei* but no *Oedura*. As sources for 16 species Vitt and Price (1982) quoted Pianka and Pianka (1976) and Pianka and Huey (1978) who, however, had described their stomach contents and not their FM. For the 17th species, *Coleonyx variegatus*, Vitt and Price (1982) quoted Tinkle and Hadley (1975) who had not dealt with FM, and Vitt and Congdon (1978), who had in fact listed the species, from their observations, as "sit and wait, limited foraging". The source for Vitt and Price's (1982) 18th species, *Lepidodactylus lugubris*, was an undated personal communication of Tinkle; he could have observed this species in trees, in rocks, or on houses having lights at night (Werner, 1990).

Dunham et al. (1988) gave the FM for nine species of geckos as SW, "based on literature descriptions": For three species they quoted Bustard (1968a, "1969" (=1968b), 1970, 1971), who, however, had said of *Gehyra variegata* (1968a), "Orthoptera ... fourth and fifth in numerical importance ... are the only items not found in the microhabitat. Presumably these are taken at night by foraging geckos when the grasshoppers are asleep;" of *Heteronotia binoei* (1968b), "grasshoppers ... most are presumably taken at night by foraging geckos when the grasshoppers are asleep;" and of *Oedura ocellata* (1971), "Most food eaten does not occur in the homesite and must be captured on the ground", indicating WF tendencies for all three (Bustard (1970) did not mention food or feeding). For two *Lygodactylus* species, Dunham et al. (1988) quoted Greer (1967) who, however, had intimated WF behavior, with ambushing only on opportune occasions. For the four remaining species they quoted How and Kitchener (1983) and Vitt (1986), though neither paper had dealt with FM.

Recently Arnold (1993) listed the foraging modes of seven gecko taxa: he considered four species of *Pristurus* and *Quedenfeldtia trachyblepharus* passive feeders, *P. celerrimus* a cruising forager, and *Gonatodes* active foragers, although he provided no quantitative data by either of the two indices mentioned above. Hence by the criteria developed for other lizards (especially Lacertidae), of the seventeen gekkonoid species whose FMs have been quantified or described, only eight are strict SW predators; nine tend in varying degree to WF strategies. This agrees in principle with the recent survey of Cooper (1994a,b) who counted 52 species as SW and 8 as having WF or mixed strategies.

The Structure and Sources of the Variable FM of Geckos

Previous studies of lizard FM have found intraspecific variation, which varied in extent even among the species within a family in one region. Among Lacertidae in the Kalahari, the CV of MPM ranged from 10.0% in *Ichnotropis squamulosa* to 105.8% in *Eremias lineoocellata* and that of PTM ranged from 10.4% in *Nucras tessellata* to 81.1% in *Eremias lineoocellata* (Table 2; Huey and Pianka, 1981). In the gecko *Coleonyx variegatus*, males in an enclosure moved a greater distance per hour (17.6 m/hr) than did females (9.4 m/hr), although MPM were equal (0.57) (Kingsbury, 1989). In *Anolis polylepsis*, Perry (1996) found significant differences in foraging behavior between males, females and juveniles. But we are unaware of any attention given to intraindividual variation in FM.

The three species reported here share great behavioral variability, as shown also (in two of them) by the high CVs of MPM and of PTM (Table 2). In each species, some individuals appeared to be very stationary, sometimes throughout the whole observation time (Table 1). Other individuals were so active that they could not be observed throughout the intended period. Single consecutive movement (or bouts of rapid alternations of standing and moving) lasted several minutes at the most (Table 1) but the maximum PTM observed in individuals approximated 50% in two of the species (Table 1).

Similar variability occurs in three other geckos for which some data are available. (1) The arenicolous *Stenodactylus doriae* in the 'Arava Valley, Israel: during 30 min observation periods, some individuals remain stationary throughout, whereas others move about actively (Werner, pers. obs.; Bogin, 1993). (2) The adult *Gekko gecko* individual briefly observed by Stanner et al. (in press) near Bangkok also behaved variably: In the first night it perched itself on a van-

tage point in the dark, and during 280 min of observation moved only 8 times, within only 40 cm (0.03 MPM, 2.5 PTM). In the second night it stationed itself at an illuminated window and was more active: during 640 min it moved 29 times (10 of these, eating); by these movements, which totalled 40 min, it locomoted nearly 50 meters (0.05 MPM, 6.25 PTM). (3) Preliminary observations of *Hemidactylus turcicus* (Perry, unpublished) also show great variability in FM.

No similar variability has been reported by Kingsbury (1989) from *Coleonyx variegatus*, so currently the combination of SW and WF behaviors is known only from gekkonine geckos.

This heterogeneity resembles that reported in *Lacerta laevis* (Lacertidae), in which during observation periods of five minutes, most individuals were either completely stationary or rather active (Perry et al., 1990).

Unless random, such heterogeneity could result from three factors, which are not mutually exclusive. (1) FM may change with age: in two species of *Ichnotropis* (Lacertidae), as well as in *Varanus komodoensis*, the juveniles are WF whereas the adults partly adopt SW behavior (Broadley, 1979; Auffenberg, 1981). But all the data discussed above were derived from adults and subadults.

(2) There are precedents for a sexual difference in the FM of lizards of other families, usually with males more active than females, by one measure or another (Pietruszka, 1986; Anderson, 1993; Perry, 1996). In *Coleonyx variegatus*, Kingsbury (1989) found that, although males and females moved equally frequently, males moved longer distances each time. This confirmed the earlier observation by Cooper et al. (1985), that males were more active (exposed) than females.

A reverse sexual difference occurs in *Phrynocephalus mystaceus* (Agamidae): males scout SW while perched in presumably territory-guarding situations, whereas females are WF (Polynova and Lobachev, quoted by Ananjeva and Tsellarius, 1986). Perry (1996) found a similarly reversed sexual difference in *Anolis polylepsis*.

Of the geckos reported here, *Gekko hokouensis* males may have been a little more active than females. As explained above, *G. japonicus* and *Teratoscincus roborowskii* individuals were not sexed. In *Lacerta laevis* it is likewise unknown whether the different behavior patterns were related to sex (Perry et al., 1990).

(3) Species averages of MPM and PTM always mask intraspecific variation. With the usual short

observation bouts per individual, it remains unknown whether the variation is inter- or intra-individual. The longer observation bouts applied here, revealed individuals that switched from stationary to active behavior or vice versa. Because of the variations in the style and speed of the active behaviour, it seems that the animals were then foraging and not shifting to new SW stations; i.e., this was not saltatory foraging (O'Brien et al., 1989). But conceivably the brief pauses during WF in *G. hokouensis*, and also in the *Lacerta* spp. (Avery et al., 1987a, b; Avery, 1991), indeed serve for "snapshot scanning" as suggested by O'Brien et al. (1989), so that in these species the WF periods are actually saltatory foraging. As the data now stand, the three species reported here, as well as *G. gecko* and *S. doriae*, seem to methodically practice a fluctuating FM, alternating SW and WF bouts.

Function of the Fluctuating FM in Geckos

Huey and Pianka (1981) summarized theoretical predictions and observations to the effect that an increase in food availability should result in an increase in foraging velocity, in SW as well as WF species. Moreover, Dunham (1983) found that *Sceloporus merriami* and *Urosaurus ornatus* switched from a WF to a SW foraging tactic during periods of low resource abundance.

If this principle were applicable to the fluctuating FM of geckos, a reversed "giving-up time" principle (Green, 1987) would be indicated: a gecko forages actively, till the lack of prey causes it to switch to the energetically cheaper SW strategy. When its patience is rewarded with prey, it "can afford to try its luck" and resumes the WF strategy.

We suggest that some geckos fluctuate between the two FMs irrespective of momentary success. Geckos are visual hunters despite the poor light in which most operate. They seem to cope with this handicap by (1) having larger eyes if nocturnal and also (2) if foraging cursorially, without scouting from vantage points (Werner, 1969); (3) by foraging in erect, stretch-limbed, posture (if cursorial), the better to view their surroundings (Werner and Broza, 1969); and (4) by being more active, WF, in the better-illuminated times of night (at least in some species) (Frankenberg and Werner, 1979; Bouskila et al., 1992). The last phenomenon seems to parallel the observation of Dunham (1983) quoted above: when food is more apparent, foraging becomes more active.

We hypothesize that (5) by alternatingly employing SW and WF strategies, some geckos, foraging when the range of vision is short, increase their probability of encountering stationary as well as mobile

prey while reducing the costs associated with locomotion (e.g., energy expenditure and detection by predators). This would parallel the behavior of other animals which vary their foraging tactics at times of food shortage or increased food requirements (Curio, 1976:20, 27).

The employment of both SW and WF modes by these geckos may be related to lack of competition: The segregation of diurnal lizards in a community into SW and WF species presumably aids in resource partitioning (Pianka et al., 1979:87-88; Huey and Pianka, 1981:995). This dimension of resource partitioning comes in addition to the many reviewed by Schoener (1974). The species reported here, *Gekko hokouensis*, *G. japonicus* and *Teratoscincus roborowskii*, were each the sole nocturnal lizard species observed in the area. Where *G. gecko* was observed (Stanner et al., in press) it was associated only with *Hemidactylus frenatus*, two orders of magnitude smaller (>100g and <10g, respectively). Where *Stenodactylus doriae* was observed (Bogin, 1933) the area carrying its dense population (Bouskila, 1987) contains very few individuals of other cursorial geckos. It would be instructive to observe FM where a number of gecko species forage together. The comparison should be made within the Gekkonidae so as to minimize the confusion of ecological and phylogenetic factors (Dunham and Miles, 1985; Huey and Bennett, 1986).

FM and Relative Clutch Mass

It has been stated that geckos, believed to be SW predators, have small RCM, compared to SW lizards of other families (Vitt and Price, 1982; Vitt, 1986). However, on the one hand, Werner (1989) has already pointed out that the RCM of geckos is actually somewhat larger than generally believed, being intermediate between those typical of WF and SW lizards. On the other hand, we have shown here that the FM of geckos is not as strictly SW as generally stated but contains WF components to varying extent. Hence geckos, rather than having a paradoxically low RCM, are in fact intermediate between SW and WF lizard groups in both their FM and RCM.

Werner and Frankenberg (1989) have shown that among lizard species, the correlation of the RCM to the relative body size of the female (female ra as percent of male ra), depends on the FM of the species: in SW predators (Agamidae, Chamaeleonidae, Iguanidae), the larger the female is compared to the male, the greater the RCM. But in WF species (Lacertidae, Scincidae), the larger the female (relative to the male), the smaller the RCM. Interestingly, the relationship among gekkonidae tends to be as among

WF species (Werner, 1996). Moreover, Vitt (1990) has pointed out that among sympatric caatinga lizards, geckos differ from typical SW species in possessing continual rather than seasonal reproduction. The last two observations seem to further support the notion that geckos should not be considered strict SW predators.

Conclusions

By the statistical measure of MPM (as used for lacertids), the geckos *Coleonyx variegatus*, *Gekko gecko*, *G. hokouensis*, *G. japonicus* and *Teratoscincus roborowskii* are SW predators.

Gekko gecko, *G. japonicus* and *Teratoscincus roborowskii* are SW predators also by the statistical measure of PTM (as used for lacertids); but by this measure *Coleonyx variegatus* and *G. hokouensis* are WF. Most other gekkonine species, whose foraging has been verbally described in literature, also appear to have at least partial WF tendencies.

The foraging behavior of *Gekko gecko*, *G. hokouensis*, *G. japonicus*, *Stenodactylus doriae* and *Teratoscincus roborowskii* is sometimes SW and sometimes WF; at least in *G. hokouensis*, *G. japonicus* and *T. roborowskii* individuals appear to fluctuate between these two predation tactics.

The variable, often fluctuating, FM of these gekkonines probably serves to increase the variety of accessible prey for these nocturnal visual hunters.

The employment of both SW and WF tactics by these gekkonines may depend on the absence of other, competing nocturnal lizards.

Geckos are intermediate between SW and WF lizards, in both foraging mode and relative clutch mass.

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