Factors affecting foraging behaviour, as seen in a nocturnal ground lizard, *Goniurosaurus kuroiwae kuroiwae*

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**Abstract**

In most lizards foraging behaviour is either ‘widely foraging’ or ‘sit and wait’ but in geckos it varies and fluctuates, providing an opportunity to examine potential factors modulating the foraging mode. In an endeavour to identify these, marked individuals of *Goniurosaurus kuroiwae kuroiwae* (Gekkonidae: Eublepharidae) were observed during July to October 1999 on Okinawajima, Japan. The subtropical and nocturnal conditions presumably reduced the number of intervening factors. Statistical analyses, including stepwise regression analysis, attributed relative responsibilities to individual factors. Using reflecting adhesive tape, 66 individuals were individually marked. These yielded 60 observation bouts of 30 min, including 28 individuals observed on more than one night. The foraging behaviour was active, relatively ‘widely foraging’ compared to the ‘sit-and-wait’ behaviour of most other geckos, and variable both within and between individuals. Individuals with empty stomachs showed increased activity. Various components of the foraging behaviour and the factors affecting them radically differed between the sexes. The body temperature of females averaged 1°C higher than that of males. Female activity exceeded that of males and increased during July to October, being highest after cessation of oviposition. In both sexes activity correlated negatively with the duration of observation bouts and positively with ambient temperature, receding around midnight. Under a full moon males were more active but fewer females emerged from shelters. The effect of tail regeneration differed sexually. These innovative results dictate caution in the manufacture of foraging behaviour data for comparative purposes.

**Keywords:** Foraging mode, geckos, lunar phase, sex, tail regeneration, temperature

**Introduction**

Several recent behavioural-ecological researches have been aimed at the elucidation of the behavioural strategies evolved by animals for the efficient gathering of food (Krebs 1978; Perry and Pianka 1997). Predatory animals can either invest energy in actively searching for
prey (WF, widely foraging), or conserve energy sitting in ambush and waiting for approaching prey (SW, sit-and-wait foraging). These two foraging modes (FMs) have been studied extensively in lizards. In this model group, most of the species consistently employ one of the two FMs, although temporal variation may occur (Huey and Pianka 1981). This stability has enabled the identification of morphological, physiological, behavioural and ecological correlates (sometimes considered ‘consequences’) of the two FMs (Werner and Frankenberg 1989; Perry 1999; references in Werner et al. 2004). Moreover, usually all or most species of a family share a similar FM. Thus the lizard families Scincidae, Teiidae, and Varanidae are considered WF strategists, and the families Agamidae, Chamaeleonidae, and Iguanidae (sensu lato) are considered SW strategists. This consistency has enabled linking the evolution of FM to the higher-level phylogeny of the saurians (Cooper 1995; Perry 1999).

In the families of geckos, collectively comprising the infraorder Gekkonomorpha (Rösler 1995), however, the FM shows variation at all levels. The serpentinomorph geckos, subfamily Pygopodinae, include both SW and WF strategists (Patchell and Shine 1986; Webb and Shine 1994; Wall 2005). The quadrupedal geckos, as a group, were long considered SW predators. However, Werner et al. (1997) argued that many gecko species of the subfamily Gekkoninae show mixed FMs. Werner and Bouskila (1995) similarly observed mixed or intermediate foraging behaviour in each of three diplodactyline gecko species. In contrast, Cooper (1995) defined the Gekkonidae exclusive of the Eublepharidae (Underwood 1954) as SW, and the Eublepharidae as WF. This last conclusion remained unproven until Werner et al. (2001, 2004) showed that Goniurosaurus kuroiwae orientalis was, compared to other geckos, quite WF. However, definition of this species as WF resulted from statistical summation of extremely heterogeneous behaviour. Marked individuals had such varied foraging regimes that during a 30-min observation bout one could either remain immobile, or actively locomote up to 84% of the time (Werner et al. 2004).

The within-individual variation in Goniurosaurus kuroiwae orientalis suggests that this species is a good model for examining factors affecting foraging behaviour. Here we endeavoured to test a series of obvious hypothetical factors through observation of marked, free-living individuals of Goniurosaurus kuroiwae kuroiwae in the southern part of Okinawajima, Japan. Observing marked animals enabled us to record numerous potentially relevant variables of the animals and of the environment, and to test their correlation with the main measures of FM. The strict nocturnality of the species and its subtropical humid environment (Ota 1989; Grismer et al. 1994) excluded such confounding factors as thermoregulatory shuttling. Thus beyond defining the FM of the species and identifying factors modulating it, this project constitutes an appraisal of the methodology of FM observation. Secondarily, the study was hoped to improve our understanding of the biology of this rare, endangered, and protected animal (Ota 2000). At another level, we shall minimise the repeated discussion of points treated sufficiently in Werner et al. (2004).

**Material and methods**

**Abbreviations and definitions**

The following abbreviations are used in the text and tables: RA, rostrum–anus (snout–vent) length (Werner 1971); PERCRA, percentage of RA (Werner 1971); FM, foraging mode; SW, sit-and-wait foraging, ambushing prey from a stationary perch; WF, widely foraging, actively scouting for prey during locomotion; MPM, moves per minute, the computed
number of times, during 1 min, that a gecko switched from ‘stationary’ to ‘locomotion’
(initially this is computed per observation bout); PTM, percentage time moving, the
percentage of time during the observation bout that the gecko spent locomoting—crawling,
walking, running, or jumping; SM, duration of a single move; SP, duration of a single
stationary pause; ATC, air temperature 1 cm above ground; PD, the number of days that
passed from the beginning of observations (1=7 July 1999); NS, not significant.

Subject species

Goniurosaurus kuroiwae kuroiwae (Namiye, 1912) is a medium-sized eublepharid, endemic
to Okinawajima Island and some neighbouring islands of the central Ryukyus, Japan.
Unlike conspecific subspecies, the colour pattern is longitudinally striped (rather than
cross-banded; Grismer et al. 1994). This cursorial gecko occurs around and in limestone
caves and rocks (Ota 1989). It is strictly nocturnal (Tanaka and Nishihira 1987; H. Ota,
unpublished observations). The preferred body temperature is relatively low: according to
Dial and Grismer (1992), 21.7°C, compared to 23.8–32.8°C of eight other eublepharids;
according to Werner et al. (2005), 16.6°C, compared with 25.8°C of Eublepharis macularius
Blyth, 1854. On Okinawajima it seldom emerges at temperatures below 16–17°C (Tanaka
and Nishihira 1987; H. Ota, unpublished data). Reproduction and growth were studied by
Tanaka and Nishihira (1989).

Study site

Sefa Utaki is a National Historical Monument at Kudeken, Chinen Village, southern
Okinawajima (approximately 26°09′N, 127°49′E, 50 m a.s.l.). This is a hilly park, with
localised limestone cliffs and boulders, some of which are places of worship (Utaki),
forested with evergreen broad-leaf trees forming patches with closed canopy. Lower
vegetation, mostly sparse, occurs mainly in the clearings. Along the gullies stretch about
375 m of stone-paved walks, and in order to minimise the danger from the aggressive
viperid habu, Trimeresurus flavoviridis (Hallowell, 1860), we primarily moved along these
walks. Our search for animals extended to 10–15 m to each side, covering an area of
approximately 7500 m². For orientation we marked trees along the walks.

Okinawajima Island lies in the subtropical zone. At Naha (26°10′N, 127°40′E), 15 km W
of the study site, the annual rainfall averages 2142 mm, and monthly average temperatures
range from 16.0 (January) to 28.1°C (July) (Japan Meteorological Association Okinawa
Branch 1989).

Data collection

Two observers (rarely more) visited the site for 53 shifts spread between 7 July and 8 October
1999. We operated from the time of expected abundant surface activity 21:00 h (Tanaka and
Nishihira 1987), until the decline of activity, onset of daylight. Alternating observation shifts
covered either the first half (from 20:00–21:00 to 24:00–01:30 h) or the second half (from
01:00–01:30 to 05:00–06:00 h) of the night, totalling 450–500 man-hours.

We visually scanned the habitat with electric torches. Each captured gecko was labelled
on the flanks with a pair of 4 × 4 mm stickers of adhesive reflecting tape (3M: Scotchlite
8850) carrying its serial number. One or two toes were also clipped for permanent
identification, and stored in ethanol for DNA analysis (H. Ota et al., in preparation). This
toe clipping should not affect locomotion (Middelburg and Strijbosch 1988; Paulissen and Meyer 2000). Geckos were released where captured.

Gecko behaviour was recorded when a marked gecko was rediscovered on a later night. In the light of a head-torch the reflecting stickers were conspicuous at great distance (Figure 1). Initially, we searched with white light but observed in red light (Semenov and Borkin 1992; Werner et al. 1997). Later, we observed with white light, because we learned that geckos see in red light as well as man does (Denton 1956). We directed the weak outer rim of the circle of torchlight at the gecko, and the reflecting patches revealed its movements. We mostly observed from a distance of 8–10 m. Sometimes we used binoculars to read the number on the reflecting patches. We endeavoured to observe each gecko for 30 min. This unconventionally long observation bout, reducing the number of observations and decreasing statistical power, enabled discovery of temporal variation in the foraging behaviour (Werner et al. 1997; Stanner et al. 1998). Observation was sometimes truncated through the gecko escaping out of view. Some observations erroneously exceeded 30 min. All data were dictated into a tape recorder (Sony m-430 Microcassette recorder or Aiwa HS-JS195 cassette recorder) and later transcribed to paper (adjusting with a clock showing seconds).

Individual data recorded included the gecko’s initial location relative to marked trees, serial number, sex, RA, tail length (original and regenerated portions separately), and body mass. Lengths were measured to the nearest 0.1 mm by dial callipers and mass was taken to the nearest 0.1 g by portable electronic balance. For females, presence or absence of externally visible eggs in abdomens was also examined.

Figure 1. *Goniurosaurus kuroiwae kuroiwae* (a juvenile with complete tail) marked with numbered reflecting labels, on the study site, Okinawajima Island (6 August 1999, ca 02:30 h), after release following the process of measuring and marking.
The behavioural data included mainly the basic FM markers ‘moving’, ‘stopping’, ‘running’, and ‘crawling’, as related to time, because little else was seen. Shifting body parts, or reshuffling position without translocation, were not counted as movement. When such movements seemed to represent feeding this was noted but no food items could be identified. Observations suspected of social effects were excluded.

We recorded cloud coverage, moon phase and conspicuous wind or rain at the beginning and end of each observation shift, or for a prominent change.

Environmental data for each observation included the location, substrate, elevation above ground, relation to cover, and air temperature at 1 m above ground. Humidity and illumination data were discarded due to equipment failure. Upon termination of the observation bout, we caught the gecko again and recorded its body temperature, mass, and air temperature 1 cm above ground and substrate temperature near the gecko’s location. All temperatures were taken to the nearest 0.1°C using a Miller-Weber quick-responding small-animal mercury thermometer or a Takara Digimulti D611 thermometer calibrated against it.

Finally, we flushed the stomach (method to be reported separately), collecting any contents, but we refrained from flushing the stomach of the same gecko on two successive nights. Thereafter the gecko was released where captured.

Statistics

We discarded no observation (other than those suspected of social effects) and gave equal weight to observations of any duration, to maximise the representation of the population. For each observation bout we calculated the average of each of four descriptors of FM: PTM, MPM, SM, and SP.

Before performing univariate tests we applied a two-tailed variances-ratio test for homogeneity of variances. Thereafter we tested the significance of differences between samples, by the parametric Student’s t test for equal variances or Aspin–Welch’s t test for unequal variances, and by the non-parametric Mann–Whitney U test for equal variances or the Kolmogorov–Smirnov (K-S) two-sample test for unequal variances. We analysed the effects of potential factors by simple linear regression analysis, calculating Pearson’s correlation coefficient, \( r \), and its probability, as well as the related regression (Zar 1999). We accepted a significance value of \( P \leq 0.05 \) without correcting for the multiple testing but relied on the parallel results of parallel tests.

Finally, we assessed for each of the FM descriptors (dependent variables) the relative responsibility of the various potential factors (independent variables), by applying stepwise regression analysis (Draper and Smith 1998) using the REG procedure (SAS 1999). In selecting descriptors we excluded independent variables with \( P > 0.15 \). Where required we tested the interaction between two factors by two-way factorial ANOVA.

Results and comments

General and nature of the data

During the observation period, 19:30–06:00 h of the nights of 7 July to 8 October 1999, air temperature (1 m above ground) varied only within 24.2–27.5°C. The daily (nocturnal) averages of this temperature, of air temperature at 1 cm above ground (where a gecko was caught), of substrate temperature there, and any given gecko’s rectal temperature, all
clustered within a half-degree range. The same was true of their minima and maxima. Rain that exceeded a light drizzle and strong wind occurred only occasionally.

We marked 66 individual geckos (32 males, 31 females, and three juveniles of uncertain sex). Of these we encountered again, at least once, at least 28 individuals (10 males, 16 females, and two juveniles). Including repeated encounters, these yielded 55 observations, 17 of males, 34 of females, and four of juveniles; and five additional observations derived from geckos observed but not marked (Table I).

The females (n=16) exceeded the males (n=10) a little in both RA (mean 83.4 versus 79.8 mm) and mean mass (11.5 versus 10.1 g) (Table I); these differences were not statistically significant (U tests and K-S tests ranged from P=0.67 to P>0.99). In G. k. orientalis the same trends were significant (Werner et al. 2004). Relative total tail length was a little greater in males (mean 64.9 PERCRA, n=8) than females (62.7 PERCRA, n=16); and so was the original tail portion (30.7 versus 25.5 PERCRA) but the opposite was true of the regenerated portion (34.2 versus 37.2 PERCRA). These differences only appeared to be significant when calculated on the basis of observations (n=13, 31; K-S test, P=0.06, 0.02 and 0.04, respectively).

During August the proportion of visibly ovigerous females declined and the last was encountered on 26 August. This accords with earlier information that the oviposition season in southern Okinawajima Island often lasts till August (Tanaka and Nishihira 1989).

A visual review of the results, i.e. the four foraging descriptors, of the 55 observations from identified individuals and their spread across the 28 individuals, revealed huge inter-observation variation, with PTM ranging from 0 to 52.3, and MPM ranging from 0 to 4.8. This variation was at least in part due to within-individual variation. For example, male no.

| Sub-sample | Minutes per observation | PTM | MPM | SM (s) | SP (s) | Size (RA, mm) | Tail length (PERCRA) | Mass (g) |
|------------|------------------------|-----|-----|--------|--------|---------------|----------------------|---------|
| Males (n=17) | Mean 23.8 9.4 0.4 15.4 611.6 79.2 67.6 10.1 | SD 10.1 11.1 0.5 19.1 728.3 11.4 23.2 4.5 | Minimum 6.0 0.0 0.0 0.0 28.1 57.2 27.2 5.0 | Maximum 35.0 35.4 1.6 63.7 1860.0 89.5 94.4 13.4 |
| Females (n=34) | Mean 25.8 17.0 1.0 10.7 196.7 83.6 63.6 11.6 | SD 7.9 15.5 0.9 9.4 428.7 4.5 13.0 2.2 | Minimum 4.5 0.0 0.0 0.0 6.8 74.3 19.9 7.2 | Maximum 34.0 52.3 4.8 53.4 1860.0 92.0 83.1 14.4 |
| Juveniles (n=4) | Mean 28.7 6.6 0.3 13.9 208.7 48.0 67.8 2.2 | SD 4.0 6.0 0.1 9.9 86.1 10.4 29.1 1.5 | Minimum 23.0 2.0 0.2 2.9 131.1 38.1 42.2 1.2 | Maximum 32.4 15.1 0.4 26.1 314.7 57.0 93.0 3.9 |
| Alla (n=60) | Mean 24.7 15.2 0.9 12.3 301.2 79.4 65.0 9.8 | SD 9.0 14.3 1.0 12.7 536.6 12.2 17.3 4.3 | Minimum 3.5 0.0 0.0 0.0 6.8 38.1 19.9 1.2 | Maximum 35.0 52.3 4.8 63.7 1860.0 92.0 94.4 14.4 |

*Included are five observations on unidentified marked geckos.*
6, observed twice, showed PTM values of 8.0 and 35.4; female no. 8, observed three times, showed PTM values of 1.5, 14.7, and 31.0. Therefore we tested the correlation between all second and first observation bouts of the same individuals, in terms of MPM, move duration and pause duration (PTM would arithmetically result from these). The absence of any such correlation (pooled sexes, $n=27$, $-0.155<r<0.159$, $0.427<P<0.441$) justifies viewing the results in terms of single observations, yielding sample sizes that warranted separation by sex. In Table I, the units are the observation bouts, disregarding whether some of them derived from the same individual. Accordingly, the duration of observation bouts is averaged per observation in Table I.

The foraging mode in general

Overall PTM averaged 15.2; MPM averaged 0.9; SM averaged 12.3 s; and SP averaged 301 s (Table I). These values differ from those for the small sample of G. k. orientalis (Werner et al. 2004), which had higher PTM (23.1), lower MPM (0.4), much longer SM (77 s) and longer SP (745.8 s).

The behaviour of the geckos varied such that at any time we could see some individuals exploring actively while others were stationary for a long period. The active geckos were often walking in semi-erect posture (Werner and Broza 1969) (Figure 2). At another level, we discovered that additional to walking on the ground and climbing on stonewalls and rock cliffs, the geckos occasionally ascended tree trunks, up to a height of 1m. They sometimes lingered there (Figure 3) but sometimes appeared to explore one tree trunk after the other.

Figure 2. Goniurosaurus kuroiwae kuroiwae (female with complete tail) encountered (untouched) walking semi-erect on the study site, Okinawajima Island (13 August 1999, ca 22:30 h).
Goniurosaurus k. kuroiwae resembled G. k. orientalis in the high intra-subspecific, inter-individual, and intra-individual variation of the FM descriptors. Our results explain parts of this variation. The inter-individual variation in FM begins with a sexual diergism, the females being more active with higher PTM and MPM (Table I).

Endeavouring to understand the variation within individuals and among individuals, we tested the correlation of FM descriptors with potentially causative factors, separately for pooled sexes and for each sex. Attributing importance to hunger, we present the results of flushing the stomach first.

**Effect of the empty belly**

Only 16 stomach flushings were available from the 60 observations, and all 16 indicated empty stomachs. Our flushing technique is dependable, and a few geckos did contain food, but unfortunately all of these lacked relevant behavioural data. This result excludes the stomach condition from participating as a factor in stepwise regression. We can only
compare the FM values between those recorded with empty stomach and those recorded with stomach condition unknown (Table II). The effect of the empty belly differed somewhat between the sexes. In the males it greatly elevated PTM and MPM and shortened the stationary pauses. In the females, the only significant effect was the extension of single moves. However, both PTM and the duration of single moves seem to have similarly increased in males and females.

We tested by two-way factorial ANOVA for interactions of sex with stomach condition for each of the four FM measures. The only interaction between the two factors occurred for SP ($P=0.02$), which with empty stomach was shortened in males but lengthened in females (Table II).

Because stomach condition could not be incorporated into the stepwise regression, we performed the stepwise regression also separately for the sub-sample of animals with empty stomachs, and for that of animals with unknown stomach condition, and these two are compared in Table III.

The finding that all 16 applicable stomach flushings indicated empty stomachs may perhaps be explained as follows. Huey et al. (2001) have surveyed how often different lizards ‘run on empty’ and concluded that empty stomachs are frequent in nocturnal lizards, in widely foraging species, and in members of the Gekkonomorpha. *Goniurosaurus k. kuroiwae* fits all three categories and may sustain their combined effects. Additionally, the frequency of empty stomachs could have been enhanced in roving geckos because both PTM (Tables II, IV) and digestion rate (Huey 1982) are correlated with temperature.

If, as it seems, the geckos responded to hunger by increasing their foraging activity, they followed the model expected of ectotherms (Helfman 1990), exemplified in the lacertid *Aporosaura* (Robinson and Cunningham, in Huey and Pianka 1981). This is of interest because the response, theory notwithstanding, is not uniform; the normally SW iguanids *Sceloporus merriami* Stejneger, 1904 and *Urosaurus ornatus* (Baird and Girard, 1852) switched to WF when food became particularly abundant (Dunham 1983). Perhaps mathematically relating foraging activity to food item density is an unrealistic simplification because of the multitude of factors involved.

**Organismal factors hypothetically affecting foraging mode**

**Body size.** Both PTM and MPM were significantly positively affected by body size (approximately 18% of the variation with sexes pooled, stomach condition unknown, and

| Sample    | Stomach condition | No. of observations | PTM Mean | PTM SD | MPM Mean | MPM SD | SM (s) Mean | SM (s) SD | SP (s) Mean | SP (s) SD |
|-----------|-------------------|---------------------|---------|--------|----------|--------|-------------|----------|-------------|----------|
| Males     | Unknown           | 11                  | 6.1     | 10.4   | 0.21     | 0.31   | 14.6        | 19.8     | 893.2       | 774.7    |
|           | Empty             | 6                   | 15.5    | 10.3   | 0.73     | 0.54   | 17.0        | 19.5     | 95.5        | 56.0     |
|           | $P$ for difference|                     | 0.04    |        | 0.02     |        | 0.48        |          | 0.03        |          |
| Females   | Unknown           | 24                  | 13.7    | 12.5   | 1.04     | 1.00   | 8.2         | 4.9      | 168.2       | 367.2    |
|           | Empty             | 10                  | 25.0    | 19.4   | 0.95     | 0.76   | 16.7        | 14.3     | 265.2       | 567.3    |
|           | $P$ for difference|                     | 0.19    |        | 0.89     |        | 0.02        |          | 0.82        |          |
| All       | Unknown           | 44                  | 12.9    | 12.7   | 0.89     | 1.06   | 10.7        | 11.1     | 337.4       | 565.5    |
|           | Empty             | 16                  | 21.4    | 16.8   | 0.87     | 0.68   | 16.8        | 15.8     | 201.6       | 448.7    |
|           | $P$ for difference|                     | 0.09    |        | 0.54     |        | 0.05        |          | 0.39        |          |

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PD not excluded; Tables III, IV). The other descriptors of FM were not significantly correlated with RA or body mass. In G. k. orientalis none of the descriptors of foraging mode was significantly affected by any parameter of body size (Werner et al. 2004). In lizards size reflects age but the precedents for age-related shifts of FM are from WF to more SW (references in Werner et al. 1997) and our results are among adults. Perhaps the more active individuals are more successful and grow larger.

Sex. The females (Table I) were more active than the males, having higher PTM (U test, \(P=0.03\); K-S test, NS) and MPM (U test, \(P=0.003\); K-S test, \(P=0.01\)), and shorter stops (U test, \(P=0.005\); K-S test, \(P=0.02\)). They may have had shorter moves (U test and K-S test, NS). Similar sexual diergism was observed in G. k. orientalis but was not statistically significant, perhaps due to insufficient sample sizes (Werner et al. 2004). The sexual foraging diergism in G. k. kuroiwae likely derives in part from the females’ higher body temperature, which would enhance activity (Huey 1982) but extends beyond a temperature effect, as the FMs of the sexes differ in their responses to such factors as empty stomach (see above), tail condition, and moonlight (see below).

Sexual foraging diergism has also been reported in other lizards and either sex may be the more active (references in Werner et al. 1997). In Anolis spp. the males are larger but eat less, and move around much less than the females, which presumably need greater energy intake for reproduction (Andrews and Asato 1977; Parmelee and Guyer 1995; Perry 1996). This consideration could apply here too, despite the decline of the reproductive season

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**Table III.** Relative responsibility of the foraging mode factors in Goniurosaurus kuroiwae kuroiwae on Okinawajima Island, according to stomach condition (sexes pooled), from stepwise regression analysis (for each factor the direction of its effect is given in parentheses).

| Stomach condition | PTM | MPM | SM | SP |
|-------------------|-----|-----|----|----|
|                   | Factors % | \(P\) | Factors % | \(P\) | Factors % | \(P\) | Factors % | \(P\) |
| Unknown (n=32)    | RA (+) 18.23 0.008 | OS (−) 16.72 0.020 | PM2 (+) 23.02 0.002 | OS (+) 0.09 0.094 |
| Unknown* (n=32)   | ATC (+) 10.81 0.066 | OS (−) 16.72 0.020 | PM1 (+) 16.96 0.019 | OS (+) 9.07 0.094 |
| Empty (n=13)      | PD (+) 57.78 0.003 | PD (+) 65.73 0.001 | * | TOP (+) 23.14 0.074 |
| Empty* (n=13)     | MOS (−) 10.92 0.059 | MOS (−) 9.66 0.076 | * | RA (+) 20.36 0.055 |
|                   | OS (+) 10.27 0.103 | ST (−) 6.36 0.111 | * | PM1 (+) 18.74 0.139 |
|                   | ST (−) 9.09 0.039 | * | |
| Empty (n=13)      | MOS (−) 33.85 0.037 | MOS (−) 37.56 0.026 | * | TOP (+) 23.14 0.074 |
|                   | ST (−) 22.89 0.044 | PM1 (−) 12.54 0.144 | * | RA (+) 20.36 0.055 |
|                   | * | PM1 (+) 18.74 0.139 |

Abbreviations and list of independent variables (see text for other abbreviations): %, percentage responsibility for variation; ATC, air temperature 1 cm above ground; MOS, moon phase; OS, seconds observed (duration of observation bout); PD, the number of days that passed from the beginning of observations (1-7 July 1999); PM1, time from sunset to recording environmental data, in minutes; PM2, time from sunset to beginning of the observation, in minutes; RA, rostrum–anus length; ST, substrate temperature; TAP, length of whole tail, PERCRA; TD, relative degree of tail development; TOP, tail, length of original part, PERCRA; TRP, length of regenerated part of tail, PERCRA; *, all variables disqualified from stepwise regression analysis due to \(P > 0.15\). Note that in all tests RM [relative mass = (mass in g/RA\(^3\))] was excluded. *Different results after exclusion of PD.
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Table IV. Relative responsibility of assorted factors on the measures of foraging mode in male and female Goniurosaurus kuroiwae kuroiwae on Okinawajima Island, revealed by stepwise regression analysis on the basis of field observations (for each factor the direction of its effect is given in parentheses).

| Sample     | PTM   | MPM   | SM    | SP    |
|------------|-------|-------|-------|-------|
| Males      |       |       |       |       |
| \((n=12)\) | OS \((-)\) 65.99 0.001 & OS \((-)\) 58.10 0.004 & PM1 \((-)\) 25.99 0.090 & MOS \((-)\) 51.68 0.008 |
|            | PM2 \((-)\) 14.69 0.028 & TOP \(+)\) 10.52 0.116 & TD \(+)\) 17.72 0.127 & TRP \(-)\) 21.67 0.024 |
|            | TD \(+)\) 8.02 0.044 &       | OS \(-)\) 13.58 0.149 & RA \(+)\) 18.52 0.003 |
|            | MOS \(+)\) 4.06 0.088 &       |       |       |
| Females    |       |       |       |       |
| \((n=29)\) | PD \(+)\) 48.84 0.0001 & PD \(+)\) 28.58 0.003 & TD \(-)\) 8.39 0.127 & TAP \(+)\) 13.66 0.048 |
|            | PM1 \((-)\) 9.70 0.021 & OS \(-)\) 20.20 0.004 &       |       |
|            |       |       |       |       |
| Females\(^b\) | ATC \(+)\) 17.12 0.017 & TAP \(-)\) 23.15 0.008 &       |       |
| \((n=29)\) | TAP \(-)\) 14.86 0.039 & ATC \(+)\) 11.82 0.028 &       |       |
|            | OS \(+)\) 6.88 0.106 & OS \(-)\) 10.73 0.050 &       |       |
|            |       | RA \(+)\) 9.17 0.037 &       |       |
|            |       | PM2 \(+)\) 6.89 0.040 &       |       |
| All        |       |       |       |       |
| \((n=45)\) | PD \(+)\) 26.14 0.0003 & PD \(+)\) 12.21 0.019 & MOS \(+\)\) 10.04 0.034 & OS \(+)\) 7.81 0.063 |
|            | RA \(+)\) 18.10 0.0006 & RA \(+)\) 17.64 0.002 & PM1 \(-)\) 10.04 0.027 &       |
|            | OS \(+)\) 6.06 0.031 & OS \(-)\) 10.90 0.009 & PM2 \(+\)\) 7.98 0.039 &       |
|            | MOS \(+)\) 3.24 0.103 & MOS \(-)\) 7.35 0.022 &       |       |
|            | TOP \(+)\) 2.55 0.140 &       |       |       |
| All\(^b\)  |       |       |       |       |
| \((n=45)\) | ATC \(+)\) 13.53 0.012 & OS \(-)\) 11.97 0.020 & MOS \(+)\) 10.04 0.034 & OS \(+)\) 7.81 0.063 |
|            | OS \(+)\) 9.55 0.028 & ATC \(+)\) 12.38 0.012 & PM1 \(-)\) 10.04 0.027 &       |
|            | PM1 \(-)\) 6.67 0.049 & TOP \(-)\) 8.18 0.031 & PM2 \(+\)\) 7.98 0.039 &       |
|            | TOP \(+)\) 5.27 0.090 & PM2 \(-)\) 4.08 0.116 &       |       |

See Table III for abbreviations of independent variables. Note that in all tests RM \([\text{relative mass} = \text{mass in g/RA}^3]\) was excluded. \(^a\)When PD was excluded the results remained the same. \(^b\)Different results after exclusion of PD.

during our observation period. Clearly, if the FM of a lizard species is quantified in ignorance of the sexual composition of the sample, the data may be inadequate for comparative purposes.

**Physical condition.** While mass \((\text{g})\) is correlated with RA, relative mass, the ratio of mass to cubic RA \((\text{g mm}^{-3})\), may express the nutritional condition of the animal and conceivably affect the FM. But stepwise regression analysis for the pooled sexes, which in addition to the potential factors listed in Table IV, included also relative mass \((n=18)\), failed to ascribe to this factor a significant effect on any FM descriptor. This remained true when only the females \((n=12)\) were tested and also when (for the \(n=18\)) the effects of only RA, relative mass, and four measures of tail condition were tested. In \(G. \ k. \ orientalis\) the situation was identical (Werner et al. 2004).

**Tail condition.** Loss of the tail, with subsequent regeneration, affects the life and behaviour of lizards, and especially their locomotion patterns (Martin and Avery 1997, 1998; Seligmann 1998; references in Seligmann et al. 2003). Previous information on the effect of tail loss on movement patterns of lizards concerns mainly lacertids, without sex distinction, where tail loss depresses PTM (Martin and Salvador 1997) and the depression may persist despite regeneration (Seligmann 1998). In our material only three of 33 individuals had retained complete original tails. The rest had tails composed to varying extents of an
original stump and a regenerated portion. The frequent tail breakage in this population is hard to interpret ecologically in terms of predation pressure (Seligmann et al. 2003) but it must in part reflect longevity because the probability for accidents accumulates over time (Bustard and Hughes 1966; Schall and Pianka 1980). It does give an opportunity to check the effect of tail loss on FM in a gecko.

Therefore, we considered three parameters of the tail (in PERCRA): length of the ‘original’ tail (the entire intact tail or the original stump of a regenerated tail), length of the regenerated portion of the tail, and total tail length (original plus regenerated portions). The correlations of the FM descriptors with each of these measures were explored on the basis of individuals (using per-individual averages of the FM measures). Among males, MPM correlated with the length of the original tail \((r=0.85, P=0.007, n=8)\) and with the total length of the tail \((r=0.82, P=0.014, n=8)\); and SM correlated with the length of the regenerated portion of the tail \((r=0.72, P=0.046, n=8)\). In contrast, among females, PTM marginally appeared negatively correlated with total tail length \((r=-0.48, P=0.06, n=16)\); while SP was weakly correlated with total tail length \((r=0.5, P=0.04, n=16)\) and with the length of the original tail portion \((r=0.5, P=0.048, n=16)\). For the pooled total sample none of these correlations was significant. To some extent these trends were reflected in the stepwise regression analysis (Table IV).

Additionally, we tested whether energy requirements for tail regeneration affected FM. We devised an index showing to what extent the regenerated tail already replaces the autotomised part (in PERCRA) as below:

\[
\text{‘Degree of tail regeneration’} = \frac{\text{Length of the regenerated portion of the tail}}{\text{Desired length of the regenerated portion of the tail}}
\]

\[
\text{‘Desired length of the regenerated portion of the tail’} = \text{(Typical length of intact tail)} - \text{(Length of the original tail stump)}
\]

We derived the ‘Typical length of intact tail’ from the three individuals with intact tails encountered in this project (this may not represent the species but served only for comparisons within the project). This computed index had little effect: in males (viewed as individuals) only SM marginally appeared correlated with this tail-regeneration index \((r=0.68, P=0.066, n=8)\). The stepwise regression analysis (Table IV) ascribed to this effect 18% responsibility for the variation in SM without statistical significance, and to the resulting effect on PTM 8% responsibility with \(P=0.044\). In the females a negative effect on SM was indicated, but without statistical significance.

Consequently, in males \((n=8)\) tail completeness enhanced mobility as in lacerids, while in females \((n=16)\) there may have been a weak opposite effect. The relatively moderate level of the effects may be ascribed to the relatively extensive regeneration of the broken tails. In \(G.\ k.\ orientalis\) there were no effects of tail condition on FM (Werner et al. 2004). The probable rationale for the sexual difference is that during tail regeneration the males but not the females locomoted less, saving their energy for regeneration in view of the social importance of the tail (references in Seligmann et al. 2003). In summary, when recording the FM of lizards for comparative purposes, it would be prudent to note the condition of the tail, as well as the gender.

**Environmental factors hypothetically affecting foraging mode**

**Temperature.** The temperatures associated with females exceeded those for males by about 1°C (per observation). The body temperature of females \((n=24)\) averaged 26.4°C and that
of males \((n=8)\), 25.5°C \((U\text{ test, } P=0.01; \text{ K-S test, } P=0.03)\). The parallel air temperatures at 1 m and at 1 cm above ground and substrate temperature were similar.

Despite the limited scope in this study for temperature effects, the FM varied firstly with temperature, and especially with air temperature at 1 m above ground, but only in the females (on the basis of \(n=32\) observations, \(r=0.44, P=0.012\); after removal of the seasonal effect, 17% responsibility). We assumed that the lack of similar correlation in the males (and in the whole sample) derived from variation introduced by the males having their activity depressed during the dark half of the month (see below). Therefore, we repeated the test adding to the females only the males in the full-moon half of the month. The enlarged sample yielded higher significance \((n=38, r=0.44, P=0.005)\), implying that the temperature effect applies also to the males. Indeed, in \(G. k.\ orientalis\) it was mainly in the males that the SM increased with the ambient temperature (Werner et al. 2004).

A temperature effect on activity is of course expected in reptiles (Huey 1982). We attribute the lesser correlation of activity with body temperature, substrate temperature, and air temperature at 1 cm, to the fact that these values vary with the spatial environmental mosaic across which the animals move, while air temperature at 1 m is a more stable and representative parameter. The observation that in the empty-stomach sub-sample PTM was depressed by the substrate temperature remains to be explained by more detailed research.

**Season.** The FM of the females varied with the season, as quantified by the number of days elapsed since the beginning of the project (PD): the correlation of PTM with the date was clear and significant \((34\) observations, \(r=0.6, P=0.0002)\); the stepwise regression credited the date with responsibility for 49% of the variation in PTM and 29% in MPM. In the animals with empty stomachs the effect of PD was even greater \((Table\ III). The other FM descriptors showed no distinct effects of the date. In the males there was no seasonal effect \((e.g. for PTM, n=17\) observations, \(r=-0.02, P=0.9)\) \((Table\ III). This sexual difference was not due to the timing of observations, because the observation period of the females ranged over days 1–57 \((mean=19.2)\) and that of the males over days 1–66 \((mean=22.1)\). In correlation with the time elapsed since the beginning of the project there occurred a small but significant rise in air temperature at 1 m \((r=0.6, P=0.0001, n=54)\). But as only the females increased their activity, probably this was not a temperature effect. Since oviposition ceased in the middle of the study period, it seems likely that after oviposition the females intensified their search for food to replenish energy stores. Because the season was a stable factor that strongly affected only the females, we performed a second version of all stepwise regressions excluding this factor \((PD)\), which thus more reasonably presented comparable data for the two sexes \((Tables\ III, IV)\).

Not much was previously known of seasonal shifts in the FM of lizards, although for lacertids the possibility has been implied \((Nemes 2002)\) and for geckos the observation of seasonal shifts in food composition \((Perry and Brandeis 1992; Gil et al. 1994)\) has indicated the possibility. The seasonal shift observed herein dictates caution in the compilation of databases with surmisedly comparative values of FM descriptors.

**Hour.** According to the univariate correlation tests, the foraging activity did not seem to be affected by the time of night, measured in minutes elapsed since sunset. But the stepwise regression revealed in both sexes a negative effect of the time of night on the PTM and MPM during the first half of the night \((PM1 in Table IV)\); this may well have been a
temperature effect. The apparent increase in activity towards morning could be a response to increases in temperature, illumination (see below), or both.

Moon phase. Generally on bright moon nights visual predators intensify their foraging (which is more rewarding) while their prey animals suppress their locomotion in the open (Frankenberg and Werner 1979). A gecko faces a trade-off: is it more predators or more prey? We sorted the observation nights into the two halves of the lunar month, centred around the full moon versus centred around the new moon. The activity of the males, but not of the females, was markedly depressed during the dark half-month (Table V). The males in the new-moon half-month significantly differed both from the females in the same half-month and from the males in the full-moon half-month, in PTM, MPM, and SP (Mann–Whitney and K-S tests, \( P < 0.05 \)). During the full-moon half-month there was no sexual difference, and for the females there was no moon-phase effect. By the stepwise regression (Table V), too, the effect of moonlight was substantial in males (for PTM 4% responsibility, positive, and for SP 52%, negative) but insignificant in females, after discounting the effect of the season.

Among nocturnal cursorial desert geckos both possible outcomes of this trade-off occur. Moonlight enhances the locomotor activity of *Stenodactylus doriae* (Blanford, 1874) (Bouskila et al. 1992), but suppresses that of *Teratoscincus scincus* (Schlegel, 1858) (Werner 2001; Y. L. Werner et al., unpublished data). The effect on *G. k. kuroiwae* in the dark

| Sub-sample | PTM  | MPM  | SM (s) | SP (s) |
|------------|------|------|--------|--------|
| **Full-moon half of the month** | | | | |
| Males \((n=6)\) | Mean | 18.9 | 0.6 | 26.5 | 82.6 |
| | SD | 10.8 | 0.3 | 24.0 | 27.9 |
| | Minimum | 6.4 | 0.3 | 5.2 | 41.5 |
| | Maximum | 35.4 | 1.1 | 63.8 | 119.4 |
| Females \((n=7)\) | Mean | 16.0 | 0.7 | 14.3 | 354.3 |
| | SD | 14.0 | 0.7 | 16.5 | 618.1 |
| | Minimum | 0.0 | 0.0 | 0.0 | 21.6 |
| | Maximum | 21.4 | 1.9 | 53.4 | 1860.0 |
| **New-moon half of the month** | | | | |
| Males \((n=11)\) | Mean | 4.3 | 0.3 | 9.4 | 900.2 |
| | SD | 6.3 | 0.5 | 10.7 | 731.6 |
| | Minimum | 0.0 | 0.0 | 0.0 | 28.1 |
| | Maximum | 21.4 | 1.7 | 32.3 | 1860.0 |
| Females \((n=27)\) | Mean | 17.3 | 1.1 | 9.8 | 155.9 |
| | SD | 15.5 | 1.0 | 5.6 | 342.8 |
| | Minimum | 0.0 | 0.0 | 0.0 | 6.8 |
| | Maximum | 52.3 | 4.8 | 20.1 | 1800.0 |
| **Difference between moon phases, K-S test** | | | | |
| Males, \( P \) | 0.033 | 0.033 | 0.198 | 0.011 |
| Females, \( P \) | 0.862 | 0.273 | 0.999 | 0.273 |
forest, depression of activity during the dark half of the month only in the males, seems puzzling.

To examine whether the moon phase affected the frequency of emergence of the geckos from their shelters (holes in the ground and rock crevices; Tanaka and Nishihira 1987; H. Ota, unpublished data), we also estimated the search effort for each night as (number of observers) \times (number of hours), calculated the number of geckos encountered per unit search effort, and compared the results between the two halves of the month (Table VI). For the males the count of geckos relative to search effort was equal in the two month-halves. The count of females resembled that of the males in the full-moon half-month but in the new-moon half-month (when the males reduced their locomotor activity), the females were more abundant by about a third. Can a gecko in its retreat respond to the lunar phase? The locomotor activity of *Ptyodactylus guttatus* von Heyden, 1827 maintained in a shielded chamber varied significantly with the lunar phase (Frankenberg and Werner 1979), raising the possibility of an endogenous cycle. Nevertheless, in *Stenodactylus doriae*, despite the lunar effect on locomotion, emergence was unaffected (Bouskila et al. 1992). The sexually diergic situation in *G. k. kuroiwae* calls for behavioural observation with non-intrusive optical equipment and behavioural experimentation.

**Effect of the duration of the observation**

An artificial factor that could potentially have affected the data was the very duration of the observation. Table VII shows that PTM, MPM, and SM were negatively correlated with observation time, and SP was positively correlated, though these correlations varied somewhat between the sexes. Stepwise regression confirmed the role of extended observation time in depressing the statistics of mobility, especially in the males (Table IV and to a lesser degree Table III). Obviously the early disappearance of an observed gecko, truncating the observation, is due to its being active, not to its being stationary, and extended observations included longer sitting pauses, depressing the values of PTM and MPM. This result parallels that in *G. k. orientalis* (Werner et al. 2004). This artefact, previously unexplored, clearly has implications for cross-project comparisons of FM

| Sub-sample                        | No. of nights (per half-month) | Search effort (man-hours; one night, on average) | Ratio: No. of geckos/effort (one night, on average) | Significance \( (P) \) of the difference between sexes or between moon phases |
|-----------------------------------|--------------------------------|-------------------------------------------------|--------------------------------------------------|--------------------------------------------------|
|                                   |                                |                                                 |                                                  | By \( U \) test | By K-S test |
| Full-moon half of the month       |                                |                                                 |                                                  |                    |            |
| Males                            | 22                             | 6.83                                            | 0.26                                             | 0.3235            | 0.2156     |
| Females                          | 22                             | 6.83                                            | 0.27                                             |                    |            |
| New-moon half of the month       |                                |                                                 |                                                  |                    |            |
| Males                            | 28                             | 6.80                                            | 0.26                                             | 0.0573            | 0.3475     |
| Females                          | 28                             | 6.80                                            | 0.36                                             |                    |            |
| Males                            |                                |                                                 |                                                  |                    |            |
| Full moon                        | 22                             | 6.83                                            | 0.26                                             | 0.4342            | 0.6451     |
| New moon                         | 28                             | 6.80                                            | 0.26                                             |                    |            |
| Females                          |                                |                                                 |                                                  |                    |            |
| Full moon                        | 22                             | 6.83                                            | 0.27                                             | 0.0308            | 0.0020     |
| New moon                         | 28                             | 6.80                                            | 0.36                                             |                    |            |
statistics. There is no easy way to eliminate this artefact, as excluding the incomplete observations would bias the data in favour of inactive individuals, and truncating all observations in line with the shortest would abolish the advantage of long observations.

**Discussion**

*Defining the specific foraging mode*

To our knowledge, this project, together with the pilot study of *G. k. orientalis* by Werner et al. (2001, 2004), constitutes a first effort to examine multiple factors responsible for variation in the FM of a lizard. The selection of a subtropical and strictly nocturnal gecko with no strict phylogenetic constraint in this character as a model, obviously moderates the number of factors (Werner et al. 2004). The quest for factors affecting the FM is intimately connected with the problem of defining the FM.

Werner et al. (1997) have discussed the varied FM of geckos and its deviation from the classical dichotomy, whereby each lizard species was defined as either WF or SW. They proposed that a lizard able to use both modes, perhaps due to the absence of competition, could glean a wider spectrum of insects. Perry (1999) has regarded this hypothesis as widely accepted. However, there has been little evidence as to whether the intraspecific variation in FM derives from variation within or between individuals, or both. Only recently did Werner et al. (2004) discover, through the repeated observation of marked individuals of *G. k. orientalis*, that much of the variation occurs within individuals. They also discussed possible causes for this variation but the limited data provided little proof.

Here we explored factors that may affect the FM of the related *G. k. kuroiwae*. As explained earlier (Werner et al. 2004), we accept PTM as the summarising descriptor of foraging activity. Huey and Pianka (1981) defined the threshold of PTM, above which a lizard species would be considered WF, as 30%, whereas <15% would indicate SW. Perry (1995, 1999) has reviewed the subsequent literature and using data from 83 species (of 12 families) concluded that although WF and SW types exist among lizards, in general FM is not a dichotomy but varies continuously. In contrast, Cooper et al. (2001) found in a sample of 16 American lizards that in the 10 SW species PTM was under 5% but in the six WF species PTM exceeded 60%.

As explained above, the variety of FMs within the Gekkonidae is extreme in the saurian scenario. The majority of gekkonids examined in assorted locations had PTM<5%, and most of the rest, PTM<10% (Werner et al. 1997; Stanner et al. 1998; Werner 1998; Cooper 1999; Cooper et al. 2001; Werner and Chou 2002; Persaud et al. 2003). In contrast, the eublepharids *G. k. orientalis* and *G. k. kuroiwae* have overall PTMs of 23.1 and 15.2% and thus, compared to other gekkonids, seem to be WF strategists. These PTM values are underestimates due to the effect of the duration of

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**Table VII.** The descriptors of foraging mode of *Goniurosaurus kuroiwae kuroiwae* as correlated with observation duration (seconds).

|        | PTM | MPM | SM | SP |
|--------|-----|-----|----|----|
|        | \( r \) | \( P \) | \( r \) | \( P \) | \( r \) | \( P \) |
| **Males (n=17)** | | | | | | |
| \(-0.76\) | 0.0004 | \(-0.36\) | 0.1502 | \(-0.55\) | 0.0217 | 0.51 | 0.0363 |
| **Females (n=34)** | | | | | | |
| \(-0.19\) | 0.2708 | \(-0.17\) | 0.3220 | \(-0.09\) | 0.9585 | 0.19 | 0.2704 |
| **All (n=60)** | | | | | | |
| \(-0.37\) | 0.0029 | \(-0.34\) | 0.0077 | \(-0.24\) | 0.0623 | 0.29 | 0.0222 |
observations (see above), but it is unclear to what extent the same may apply to some of the comparative values from SW gekkonomorphs. We suggest that the FM dichotomy may exist with different numerical PTM values in different groups, and within one group in different places (Perry et al. 1990). It is not biologically justified to impose on all lizards a uniform cut-off between the SW and WF modes.

The two sexes

In G. k. kuroiwae, the females were insignificantly larger and heavier than the males, and had only a slightly higher body temperature. Thus these differences seem only partly to explain the extent to which the geckos were sexually diergic in their responses to most of the environmental variables. Overall, the females were more active than the males in both PTM and MPM and had shorter pauses. The effect of the empty belly, though tending to elevate PTM in both sexes, considerably differed in details between the sexes. Tail loss affected the sexes very differently, increasing the activity of females but depressing that of males.

Elevated temperature increased the activity of both sexes but the extension of move duration occurred mainly in the males. The season affected only the females. Most dramatic was the difference in the effect of moonlight—its absence depressed the activity of the males but increased the emergence of females.

Factors affecting foraging mode

Besides by sex, the numerical values in the WF strategy of the G. kuroiwae subspecies are modulated by parameters of the individuals—body size or age, tail condition (but not general physical condition)—and by variables of the physical environment—temperature, season, time of day, and moon phase—besides the methodological artefact of the duration of observation bouts and, of course, hunger versus satiation. For most of these foraging-modulating factors and interactions it remains unclear to what extent they are unique to the species, to the family, to the infraorder, or more widespread. At this point, although most of these phenomena require further study by experimental methods, a caveat already emerges that the creation of FM data for comparative purposes should consider more variables than has hitherto been conventional. Especially, while environmental variables can be standardised, the organismic parameters require checking.

Missing factor

The assemblage of significant or probable ($P<0.15$) causative factors discussed here, organism-dependent, observer-dependent and abiotic environmental, accounts in different sub-samples for 24–93% of the variation in PTM and 36–82% of the variation in MPM (Tables III, IV). Part of the deficit from 100% is presumably due to factors that although tested failed to attain the threshold for inclusion in the stepwise regressions. All these, however, still fail to explain why an individual gecko would behave so differently on two temporally close occasions (e.g. Werner et al. 2004; Figure 2), or why two individuals should behave so differently at the same time on adjacent locations, within one observer’s visual field. The most likely factor that we could not assess but has been documented on other occasions is temporal and spatial fluctuations in food abundance (Huey and Pianka 1981). This missing factor could best be tested experimentally in arena conditions where food quantity can be manipulated. However, although variation in this resource must be
common, most other lizards show much more consistent behaviour. Therefore, even such future examinations will probably not falsify the hypothesis that fluctuating foraging behaviour is a built-in strategy in geckos (Werner et al. 1997).

Conclusions

1. Compared with most other geckos, Goniurosaurus kuroiwae kuroiwae is an active forager, though possibly a little less so than G. k. orientalis.
2. The FM of G. k. kuroiwae shows remarkable intra-individual variation, which may explain much of the great apparent inter-individual variation.
3. Individuals with empty stomachs forage significantly more actively.
4. Although female G. k. kuroiwae are insignificantly larger than males, and their body temperature is significantly but only 1°C higher, the FM and the factors affecting it show strong and manifold sexual diergism.
5. Tail loss affects the sexes differently, increasing the activity of females but depressing that of males.
6. In general, foraging activity as expressed by PTM is correlated with ambient temperature.
7. Foraging activity (PTM) of the females varies seasonally, increasing from July to September, being highest after the cessation of oviposition.
8. In both sexes the locomotor activity recedes in the middle of the night, probably as a temperature effect.
9. The effect of the phase of the moon differs sexually. During the darker half-month centred on the new moon, compared with the half-month centred on the full moon, the males have a lower PTM but the females have a higher rate of emergence from shelters.
10. The duration of an observation bout constitutes an artefact statistically reducing the observed activity (PTM, MPM, and SM) while increasing SP.
11. All the factors discussed here, organismic, artificial and abiotic environmental, fail to fully explain the behavioural variation observed. The behavioural fluctuations may reflect a built-in strategy.
12. The occurrence of significant organism-dependent (size, sex, tail condition) and observer-dependent (duration, and daily and annual timing of observation bouts) effects on FM descriptors, and the sexually diergic response to abiotic variables, which in other taxa remain largely unexplored, dictates caution in the manufacture and comparative use of FM data.

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