



## Analysis of the locomotor activity of a nocturnal desert lizard (Reptilia: Gekkonidae: *Teratoscincus scincus*) under varying moonlight

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### Abstract

1. This project seeks to identify determinants of the variation observed in the foraging behavior of predatory animals, especially in moonlight, using a lizard as a model.
2. Moonlight generally enhances the foraging efficiency of nocturnal visual predators and often depresses the locomotor activity of prey animals. Previous evidence has indicated for three different nocturnal species of smallish gecko lizards that they respond to moonlight by increasing their activity.
3. In this study some aspects of the foraging activity of the somewhat larger nocturnal psammophilous *Teratoscincus scincus*, observed near Repetek and Ashgabat, Turkmenistan, were significantly depressed by moonlight, while several confounding factors (sex, maturity, size, sand temperature, hour, prior handling and observer effect) were taken into account.
4. This behavioral difference may relate to the eye size of the various species.
5. Additionally, a novel method of analyzing foraging behavior shows that in this species the duration of moves increases the duration of subsequent stationary pauses. Measurement of locomotor speed, yielding an average speed of 220% of the maximum aerobic speed, indicates a need for these pauses. Secondarily, pause duration decreases the duration of subsequent moves, precluding escalation of move duration.
6. The results of this and related projects advocate the taking into account of physiological and environmental factors that may affect an animal's foraging behavior.

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### Introduction

The locomotor activity of foraging lizards, as an example of predatory animals (Huey et al., 1983; Reilly

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et al., in press), is constrained by many factors, and some of these are best explored in nocturnal species, operating without the complications of basking and overheating (Werner, 2001; Werner et al., 2001, 2004, 2006).

Moonlight may affect the locomotor foraging activity of nocturnal animals, especially in open sandy desert. Bright moonlight improves the ability of visual predators to detect prey. Many studies of reactions of prey animals to moonlight were conducted on granivores or herbivores, and are thus biased towards prey that does not need to consider variations in the availability of its food (e.g., Kotler et al., 1991, 2002; Daly et al., 1992). The results of these studies indicated that in most cases prey animals reduce their amount of locomotion, at least in the open, and the increase in predation risk has been implicated (exceptions reviewed in Bouskila, 1995). The situation for a prey animal that is also a predator is more complicated because it has to consider the reactions of its prey as well (Skutelsky, 1996), and both its predators and its prey may be involved in a game situation (Bouskila, 2001; Blinder, 2001). Thus, in moonlit nights nocturnal geckos, small insectivorous lizards, face a trade-off: should they respond to the increased risk from visual predators, to their own increased ability to detect prey or to the availability of prey, which is often reduced (Reichmann, 1998)?

Hypothetically, the outcome of this trade-off is difficult to predict, because it depends on the magnitudes of the costs and benefits, which may be affected by the game situation. But so far, all of the few relevant reports have indicated one direction. The full-moon phase enhances the locomotor activity of *Stenodactylus doriae*, a psammophilous convergent of *Teratoscincus*, in nature (Bouskila et al., 1992; Bogin, unpubl. data; Reichmann, 1998) and also that of the rupicolous *Ptyodactylus guttatus* in a shielded laboratory chamber without any light stimulus (Frankenberg and Werner, 1979). Moreover, moonlight seems to enhance the activity (of the males only) of *Goniurosaurus kuroiwae kuroiwae* (Eublepharidae) even in the dark subtropical forest (Werner et al., 2006).

On the occasion of the 2nd Asian Herpetological Meeting in Turkmenistan, 1995, we observed the locomotor activity of the nocturnal desert gecko *Teratoscincus scincus* in order to describe its foraging mode (FM). During the observation period moonlight varied sufficiently to allow an analysis of the direction and degree of correlation of the gecko's locomotor behavior with the variation in lunar illumination. In this article we investigate the effects of two factors on the locomotor activity of *T. scincus*: the external, abiotic, factor of the moon's illumination at night, and the internal, organismic, factor of resting pauses during locomotion. The potentially confounding effects of prior handling, body size, age, sex (intrinsic factors),

observer effect, temperature and time of night (extrinsic factors) are also investigated to the extent possible. The effect of season (Klauber, 1939; Werner et al., 2006) is not considered, as the project lasted only eleven days.

The percentage of the time that lizards are on the move in the field positively correlates, in interspecific comparisons, with their specific level of endurance in laboratory tests (Garland, 1999). By induction, this raises the possibility that in the field, physiological constraints may relate the duration of single locomotion bouts (moves) to the duration of stationary pauses. Indeed, analysis of observations on the foraging behavior of lacertid lizards (Perry et al., 1990) has long ago indicated that such relations may exist (Hervé Seligmann, unpublished data). Therefore, here we also explore (a) whether in this species the duration of moves correlates with the duration of preceding stationary pauses, or (b) the duration of pauses correlates with that of preceding moves; (c) the directions of any such correlation; (d) the possible effects of moonlight on such correlations, and (e) the possible individual physiological background of such correlations. Note that this analysis offers the rare opportunity to identify the causal relationships in correlations from non-manipulative observational data, i.e., to identify which variable is cause, and which is effect (Pfister, 1995).

## Material and methods

### Species and environment

*Teratoscincus scincus* (Schlegel, 1858) is a psammophilous cursorial desert gecko widely distributed in central Asia (Anderson, 1999). Males and females attain a head-and-body length of up to 90 mm, and the tail approximates 66% of that. In daytime it hides in burrows in the sand, leaving them after dark to forage outside. After 0100 h the activity decreases though some forage till dawn (Szczerbak and Golubev, 1996).

The Repetek desert research station in the Karakum ("black sand") desert of Turkmenistan, at 38° 34' N, 63° 10' 40" E (this and other locations are from a "Trimble Scoutmaster GPS"; according to the Times Atlas (1997) the Repetek station is at 38° 36' N, 63° 11' E), 120 m above sea level and gives direct access to a sand-dune habitat. The sparse vegetation is climaxed by small *Ammodendron* trees in patches and bushes of *Haloxylon persicum*, *Salsola richteri* and some *Ephedra*. During the observations, on 30.VIII–4.IX.1995 (data for statistics till 2.IX), mainly between 2000 and 0100 h (sunset was approx. 1920 h), the sky was clear (no rain), and from 2000 h to around midnight air temperature dropped from 25–29 °C to 15.5–22 °C, and sand surface temperature from 24–28 °C to 15–22 °C. Temperature was

recorded with a Miller-Weber mercury thermometer ("Schultheis" type).

Some observations were also made in the sands east of Ashgabat, at approx. 37° 52' 20" N, 58° 43' E, 150 m above sea level, on 5.IX.1995 between 1900 h and 2330 h, while air temperature dropped from 26.8 °C to 20.4 °C and sand surface temperature from 29 °C to 18.8 °C. Finally, cursory observations were made in the sands north of Ashgabat, at approx. 38° 14' 40" N, 58° 27' 25" E, 120 m above sea level, on 9.IX.1995. All three habitats were essentially similar, bare sands with sparse shrubs.

### Moonlight ranking

Moonlight was occasionally assessed with a Gossen Lunasix photometer but for calculating correlations its relative ranking was calculated for each observation from data available at [http://aa.usno.navy.mil/data/docs/RS\\_OneYear.html](http://aa.usno.navy.mil/data/docs/RS_OneYear.html) as follows: new moon occurred on 25.VIII.1995 and full moon on 9.IX.1995. From this we derived a "percent moon fullness" for each day, indicating how full the moon was (0%—no moon, 100%—full moon). We next assigned to each observation a "relative moon elevation" at the central hour of the duration of that observation (0%—not in the sky, 100%—at zenith), derived from the given daily rise and setting times. Finally we multiplied: "percent moon fullness"  $\times$  "percent moon elevation", yielding the moon rank (relative ground brightness) of the observation. This simplified calculation overestimates the effect of moon elevation on ground brightness, compensating for the effect of elevation on bush-shade area.

### Data collection

Observations of foraging mode (locomotor activity) were mostly made by two observers, one carrying an electric torch with a removable cover of red cellophane paper (Werner et al., 2006). With the torch held on the observer's head, *Teratoscincus* could be located by their reflected eye-shine. Searching began at a distance (>20 m) with white light (Werner et al., 1997). Observations were then made from a smaller distance, depending on the situation, with red light, and dictated to the second operator. We endeavored to observe each individual for at least 30 minutes; finally the gecko was approached and examined. Some of the locomotion of the geckos was towards the observers; hence presumably observer presence did not affect gecko behavior (Anderson, 1993).

Some of the observed animals (5 out of 22) were caught before the observation and marked with reflecting stickers. Before analyzing the data we verified by T-tests and Mann Whitney tests that the handled

animals did not significantly differ from the others in locomotor activity ( $P > 0.05$  for the various statistics).

Data were formulated in terms of the conventional four descriptors (measures) quantifying the locomotor activity of lizards and describing their FM (Werner et al., 1997): (1) Moves per minute (MPM)—the number of times the animal moved during the observation bout, divided by the duration of the observation bout in minutes. (2) Percent time moving (PTM)—the total moving time as a percentage of the total duration of the observation bout. (3) Average move—the average duration (in seconds) of the animal's moves. (4) Average pause—the average duration (in seconds) of the animal's stationary pauses. Although these four foraging mode measures are interdependent, it is interesting to know of each one separately whether it differs between subsamples. For example, animals that have a high PTM may attain this in many short bouts or in a few long bouts, and only by measuring MPM as well can we separate the cases.

The speed of locomotion could not be recorded routinely but was addressed separately in four focal individuals of *T. scincus*. We used an infrared CCD surveillance camera connected to a Hi-8 camcorder recording at 30 frames (60 fields) per second. A military-spec infrared filter covering a 35 watt halogen lamp provided IR illumination to a distance of approx. 30 m. One day prior to observation, we captured the focal individuals and fixed reflective tape dots 6 mm in diameter to the upper hind limbs. The dots were brilliantly visible under IR illumination to a distance of approx. 30 m. As focal individuals moved, an alternating pattern of left and right reflective dots was evident, permitting measurement of stride frequency at a resolution of 60 Hz by examination of the video fields in a video editing system. We measured stride length in selected movement bouts in the four focal individuals using footprints in the sand. We estimated running speed as the product of stride frequency and stride length.

### Statistics

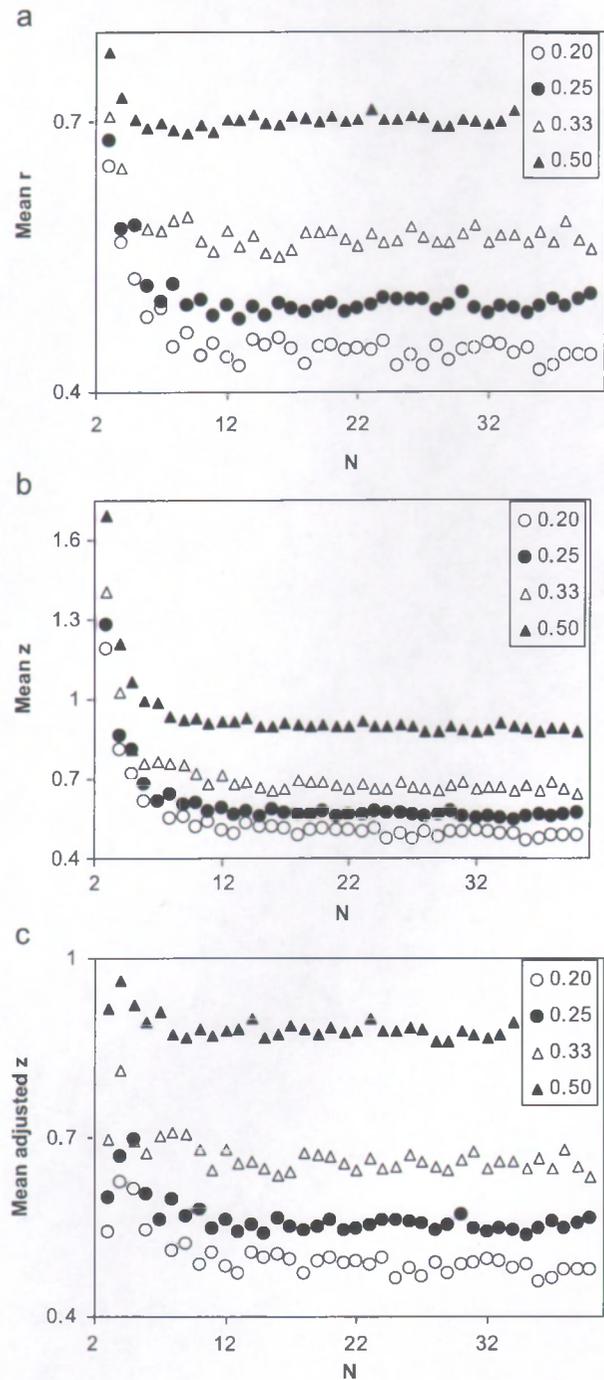
All the variables mentioned in the Introduction may be inter-related but as the data were inadequate for multivariate analyses since not all variables were known for each observation, we analyzed them separately (as in separate projects), without applying the Bonferroni procedure for multiple testing (Moran, 2003; Nakagawa, 2004). For data processing and statistics SPSS (Version 14.0, SPSS Inc.) and Excel (Version 2003, Microsoft) were used. For tests concerning moonlight, we crudely divided them into two groups, "without any moonlight" and "with some moonlight", because the number of observations was small. Between these two groups

we compared the four FM descriptors. We tested equality of means by T-tests for equal or for unequal variances as determined by the Levine-test, equality of medians by the non-parametric Mann Whitney test, and correlations by parametric (Pearson) and non parametric (Spearman rank) methods. For the latter two, we used the individual moon rank, not the pooled category “with some moonlight”. In some cases, we used partial correlation analyses to control for the confounding effects of some factors on movement patterns, as well as multiple regression analyses (limited to two independents due to the small sample sizes). The combination of these two methods indicates, by qualitative comparison between their respective results, to what extent associations are due to effects of single factors (despite confounding effects), or interactions between factors (implicitly included in multiple regression, explicitly excluded in partial correlation analysis).

For exploring the interactions between move and pause durations, we used the Pearson correlation coefficient,  $r$ . The use of  $r$  as an estimate of the association between move and pause durations, in order to compare the strengths of  $r$  found in different individuals, encounters two problems. First, the scale of  $r$  is not linear but logarithmic. Therefore the difference between  $r = 0.2$  and  $r = 0.3$  is not equivalent to the difference between  $r = 0.7$  and  $r = 0.8$ . The correlation coefficient requires transformation to a linear scale. We used the  $z$  transformation: individual correlation coefficients were first transformed to  $z$  values by the formula  $z = 0.5 \cdot \ln((1+r)/(1-r))$  where  $r$  is the Pearson correlation coefficient (Amzallag, 2001). Accordingly,  $r = 0.2$  becomes  $z = 0.202$ ;  $r = 0.3$  becomes  $z = 0.31$ ;  $r = 0.7$  becomes  $z = 0.87$ ; and  $r = 0.8$  becomes  $z = 1.10$ . Hence distances that in terms of  $r$  appear as equivalent, are revealed after linearization of the scale by  $z$  transformation as different.

Second, the absolute value of  $r$  is affected by the number of degrees of freedom of the sample: for small samples the absolute value of  $r$  tends to represent an overestimate, and the lower the real absolute value of  $r$

of the sampled population, the greater this overestimation for low  $N$  values. In other words, in small samples (especially  $N < 40$ ) correlation coefficients decrease as a function of the number of degrees of freedom, but this effect depends on the level of  $r$ . For example, Fig. 1a plots the mean  $r$  of 250 simulations (in which the value of  $r$  was inserted using the method of Chambers, 1991) for each  $2 < N < 41$  as a function of  $N$ , sampling populations in which  $X$  explains 20, 25, 33 and 50%



**Fig. 1.** Demonstration of the change of  $r$  as a function of  $N$ , the dependence of this function on the basic level of  $r$ , and the moderation of these effects by transformations. See also the text. (a) The mean  $r$  of 250 simulations for each  $2 < N < 41$ , as a function of  $N$ , sampling four populations in which  $X$  explains 20, 25, 33 and 50% of the variation, respectively, in  $Y$  (corresponding  $r$ 's: 0.45, 0.50, 0.58 and 0.71). (b) The same data as in Fig. 1a but after  $z$  transformation. (c) The same data as in Figs. 1a and b, but after  $z_a$  transformation [ $z_a = z - (r/(2n-5))$ ], where  $z_a$  is the adjusted  $z$ ] in order to decrease the effect of sample size on the estimate of the strength of the correlation. This transformation of  $z$  allows for the bias introduced by low sample sizes.

of the variation in  $Y$  (corresponding  $r$ 's: 0.45, 0.50, 0.58 and 0.71). For the last, the decrease in  $r$  ceases near  $N = 5$ , but for  $r = 0.45$ , the decrease of  $r$  with  $N$  levels off near  $N = 12$ . The leveling off occurs at a greater  $N$ , the lower the 'real'  $r$ . But this results from an erroneous analysis, overlooking the nonlinearity of the scale of  $r$ . Correct analysis requires a  $z$  transformation of  $r$  values before averaging them. The results are shown in Fig. 1b, for identical data as in Fig. 1a, but after  $z$  transformation. Here, for sampling a population of points with 'real'  $r = 0.70$ , mean  $z$  values level off near  $n = 8$ , and with  $r = 0.45$ , near  $n = 13$ .

Fig. 2 plots the absolute values of the  $z$ -transformed correlation coefficients as a function of the number of degrees of freedom. It shows that the estimated strength of the correlation is affected by the number of degrees of freedom in our sample. Our  $z$  values for observed data reflect  $r$ 's that are frequently below  $r = 0.45$ . This means that effects of sample size before leveling off as shown in Figs. 1a and b on the estimation of  $r$  (and  $z$ ) for actual lizard behavior data may be stronger than in the above simulation examples. Below we propose an imperfect method to handle the effects of sample size on the absolute value of  $r$ .

In order to decrease the effect of sample size on the estimate of the strength of the correlation, we apply a transformation of  $z$  that allows for the bias introduced by the low sample size:  $z_a = z - (r/(2n-5))$  where  $z_a$  is the adjusted  $z$  (Sokal and Rohlf, 1981, p. 590). Despite this adjustment,  $z_a$  still decreases with  $n$  (Fig. 1c), but the extent of the bias is weaker than for  $z$ . Nevertheless, the

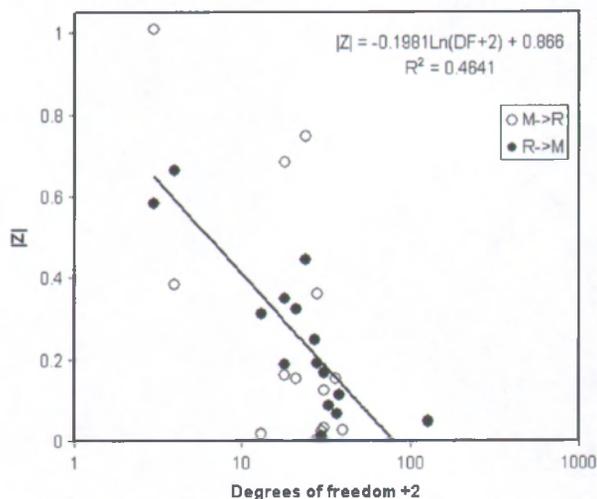


Fig. 2. Absolute values of  $Z$ -transformed correlation coefficients of both the durations of pauses with the durations of preceding moves (open symbols) and the durations of moves with the durations of preceding pauses (solid symbols), as a function of the number of move-pause cycles in each correlation (degrees of freedom,  $DF + 2$ ).

fact that results are qualitatively similar whether analyzing the actual  $z$  values or these adjusted  $z$  values, suggests that results reflect a biological principle (see Discussion), rather than one due to sample size (for uncorrected  $z$  values) or to random sampling effects (for adjusted  $z$  values).

## Results

### Homogeneity of the observations

First we checked whether all the observations ( $N = 22$ ) constitute one homogeneous group regarding locomotor activity, or vary according to prior handling, sex, maturity or body length (Werner et al., 2006). We segregated the known adult animals into males ( $N = 5$ ) and females ( $N = 10$ ). There was no significant difference between the sexes in any of the four FM descriptors (Mann Whitney tests,  $P > 0.37$  for all). Next, dividing the animals into juveniles ( $N = 5$ ) and sexed adults ( $N = 15$ ), again there was no significant difference between subgroups ( $P > 0.39$  for all descriptors). Finally we tested for correlation between each of the descriptors and body length of the animals (range: 41–90 mm, head and body) using Spearman rank correlation tests. There was no significant correlation ( $P > 0.16$  for all descriptors). Consequently, we analyzed the effects of moonlight for the whole sample, pooling sexes and ages.

Nevertheless, there seemed to be a behavioral age difference. When juvenile *T. scincus* walked, they commonly held the contrastingly black-and-white cross-banded tail bent upwards (Fig. 3), a stance rarely observed in the duller-colored adults (Anderson, 1999, Plate 10B). In *T. roborowskii* this posture has been interpreted as mimicry of scorpions by the cross-banded juveniles (Autumn and Han, 1989); it has also been observed in *T. przewalskii* (Semenov and Borkin, 1992).

The overall locomotor behavior of *Teratoscincus scincus* as observed is summarized in Table 1. Segregating the results according to moonlight reveals its effect on the behavior.

### Observer effect

We explored whether the behavior of individual lizards changed during the observation bout, perhaps due to either disturbance by, or habituation to, the observer. For each individual with  $> 3$  move-rest cycles ( $N = 16$ ) we calculated the correlations of (a) move duration, (b) pause duration, (c) move duration divided by the next pause duration, and (d) move duration divided by the preceding pause duration, with the serial number of the cycle within that observation.

There emerged little evidence for any "observer effect": (1) No analyses showed differences between



**Fig. 3.** Photograph of young *Teratoscincus scincus*, walking with the tail raised (Repetek, Turkmenistan, 1 September 1995, midnight).

individual lizards handled prior to observations, and those not handled. (2) For analyses (a) and (b) these correlations were statistically significant ( $P < 0.05$ ) only in one individual. Pooling results from all individuals, the signs of the correlation coefficients were not systematically in one direction (the numbers did not deviate from 50:50).

Analyses (c) and (d) showed opposite tendencies: (c) was negative in 11 out of 16 individuals, and (d) was positive in 12 out of 16 individuals (this difference was significant at  $P < 0.05$  by sign test). The  $R^2$  of (c) was greater than that of (d) in 11 out of 16 cases. Although this difference was not in itself significant, it is compatible with the results reported below, that move duration determines the next pause duration, rather than the opposite.

### Speed of locomotion

Mean stride frequency in *T. scincus* was 5.5 hz ( $\pm 2.1$  SD;  $n = 56$ ). Speeds ranged from 0.11 to 1.1 km h<sup>-1</sup>, and averaged 0.74 km h<sup>-1</sup> ( $\pm 0.28$  SD). Thus, most of the speeds measured were above the predicted capacity of a diurnal lizard of similar size at 25 °C (Autumn, 1999).

However, the lizards averaged speeds approx. 220% of their maximal aerobic speed (MAS; Autumn et al., 1994, 1999). This suggests that intermittent locomotion may play a major role in the locomotor behavior of this species.

### Effects of moonlight

After assigning to each animal a 'moon rank' approximately reflecting the relative amount of moonlight when the animal was observed (Materials and methods), we performed two tests to check the effects of moonlight on locomotion.

- (1) We divided the animals into a subgroup that was observed without any moonlight, and another that had some moonlight, regardless of rank. Table 2 presents the results of Mann Whitney tests for the four descriptors between the subgroups. While the average duration of a single move was unaffected by moonlight, the three other FM descriptors indicated a depression of activity under moonlight. Pause duration was doubled, significantly, accompanied by a decrease of MPM to 16.7%, significantly; PTM,

**Table 1.** A summary of the locomotor activity descriptors of the pooled observed animals,  $N = 22$ ; SD, standard deviation; CV, coefficient of variation ( $100 \times \text{SD}/\text{Mean}$ )

Variable	Mean $\pm$ SD	Range	CV
Duration of observation (min)	58.4 $\pm$ 16.1	19.5–91.4	27.6
MPM (moves/minutes)	0.4 $\pm$ 0.5	0–2.1	126.5
PTM (%)	8.8 $\pm$ 12.7	0–50.6	144.3
Average move (seconds)	10.1 $\pm$ 8.9	0–31	88.6
Average pause (seconds)	915.4 $\pm$ 1375.2	23–5485	150.2

**Table 2.** Comparison of locomotor activity measures and internal correlations ( $z$ -adjusted) between animals observed without moonlight ( $N = 15$  but for the correlations  $N = 12$ ) and those observed with some moonlight ( $N = 7$  but for the correlations  $N = 3$ ); SD, standard deviation;  $P$ , from the Mann Whitney test for equality of medians, two-tailed

	No moon mean $\pm$ SD	With moon mean $\pm$ SD	$P$
MPM	0.6 $\pm$ 0.6	0.1 $\pm$ 0.1	0.039
PTM	11.5 $\pm$ 14.1	3.1 $\pm$ 7.0	0.078
Average move	10.5 $\pm$ 8.0	9.1 $\pm$ 11.3	0.535
Average pause	725.5 $\pm$ 1449.3	1322.3 $\pm$ 1197.7	0.032
Pause with preceding move, adjusted $z$	0.07 $\pm$ 0.26	0.30 $\pm$ 0.34	0.30
Move with preceding pause, adjusted $z$	-0.09 $\pm$ 0.25	-0.14 $\pm$ 0.18	0.84

**Table 3.** Correlation of the measures of locomotor activity with moon rank ( $N = 22$ ;  $r$ , Spearman rank correlation coefficient) and with sand temperature ( $N = 17$ ;  $r$ , Pearson correlation coefficient);  $P$  values are two-tailed

Environmental variable	MPM		PTM		Average move		Average pause	
	$R$	$P$	$r$	$P$	$R$	$P$	$r$	$P$
Moon rank	-0.465	0.029	-0.404	0.062	-0.180	0.423	0.481	0.023
Sand temp.	-0.196	0.452	-0.056	0.831	0.472	0.056	-0.208	0.422

suggested to be the best indicator of FM when lacking direct observations of eating (Cooper et al., 1999, 2001), was reduced to 27% (though only with  $P = 0.078$ ). Simultaneously, MPM was significantly reduced to only 16.7%.

- (2) We tested for correlation (Spearman-rank) of the different locomotor activity descriptors with moon rank (Table 3). The results similarly showed that move duration was unaffected but otherwise moonlight depressed the activity (though for PTM only at  $P = 0.062$ ). Thus, by both tests, under the shining moon the animals moved less frequently and paused for longer periods.

Because moon rank was negatively correlated ( $r = -0.70$ ;  $P < 0.001$ ) with the time of night (hour), we calculated the (parametric) partial correlations of behavioral variables with moon rank, adjusting for effects of the hour (Table 4). The results confirm a major effect—moonlight increases pause duration (partial  $r = 0.69$ ,  $P = 0.006$ ), and less clear negative effects on mobility.

Observations on 5.IX.1995 in the sands east of Ashgabat accorded with this trend. The 72%-full moon rose at 1442 h and set at 0017 h, so that in the middle of the observation period, 2130 h, it was high in the sky. By 2130 h nine *T. scincus* were seen (by BST): seven were sitting with only the anterior part of the body protruding from the burrow (Werner et al., 1997; Fig. 2), the eighth had been approx. 30 cm from the burrow and dodged inside, and the ninth was a juvenile found under a shrub. On 9.IX.1995 in the sands north of Ashgabat the full moon rose at 1722 h

and set at 0445 h. During 1630–2100 h we saw assorted reptiles, reptile tracks and invertebrates but recorded no *T. scincus*.

When *T. scincus* walked on the sand, they often left conspicuous tracks from which the extent of their roaming could be followed (Fig. 4). On several occasions when observations were terminated after several hours of moonshine, we found convoluted tracks around the burrow, confined within a radius of 30–50 cm from it; for example, on 3.IX.1995 at 2300 h (15 °C).

Additionally, there arises the question whether emergence from the burrows changes with the lunar phase (Bouskila et al., 1992; Werner et al., 2006). Taking the search effort into account, the numbers of individual

**Table 4.** Partial parametric correlations of the behavioral variables with moon rank, adjusting for effects of the hour; and vice versa, of the behavioral variables with the hour, adjusting for the effects of the moon rank

	Moon rank		Hour	
	$R$	$P$	$r$	$P$
MPM	-0.37	0.20	-0.11	0.72
PTM	-0.48	0.085	-0.45	0.11
Mean move	-0.21	0.48	-0.40	0.16
Mean pause	0.69	0.006	0.30	0.30
$M \rightarrow R$	-0.08	0.80	-0.50	0.07
$R \rightarrow M$	-0.13	0.67	-0.26	0.37

$M \rightarrow R$ , correlation of pause durations with preceding move durations;  $R \rightarrow M$ , correlation of move durations with preceding pause durations.  $P$  values are two-tailed.



Fig. 4. Photograph of an example of the conspicuous footprints of *Teratoscincus scincus* in the soft sand, with a 10cm ruler (Repetek, Turkmenistan, 1 September 1995, 0730 h).

*T. scincus* encountered in any night were negatively correlated with their mean moon-rank (Spearman rank correlation analysis,  $r = -0.75$ ;  $P = 0.026$ , one-tailed, because we expected the lunar effect on emergence to parallel its effect on locomotion).

### The effect of temperature

We tested whether the correlations observed between some FM descriptors and moonlight rank were not in fact caused by coinciding temperature variation. We found no significant correlation between moon rank and sand temperature ( $P = 0.671$ , Spearman rank correlation test). Next we tested for correlation of the four FM descriptors with sand temperature for those 17 observations accompanied by sand temperature data (Table 3). Only average move duration appeared correlated with sand temperature ( $r = 0.47$ ;  $P = 0.056$ ); the other FM descriptors decidedly were not ( $P > 0.4$ ). Note that move duration is the one FM descriptor not affected by moonlight.

### Correlations among FM descriptors

Because we examined different measurements for FM, we tested whether these are correlated (Spearman rank method) with each other (Table 5). As expected, PTM, MPM and move duration were significantly positively correlated with each other, and significantly negatively correlated with pause duration. Note that the FM descriptor with the strongest all-round correlation (also termed connectance; Amzallag, 2000) with the other variables ( $r > 0.7$ ;  $P < 0.001$ ) was PTM, which is the arithmetic outcome of the three others.

Table 5. Correlations among the four descriptors of locomotor activity ( $N = 22$  for all correlations);  $r$  is the non parametric Spearman rank correlation coefficient;  $P$  values are two-tailed

	MPM	PTM	Average move
<i>PTM</i>			
<i>R</i>	0.931		
<i>P</i>	0.000		
<i>Average move</i>			
<i>R</i>	0.498	0.717	
<i>P</i>	0.018	0.000	
<i>Average pause</i>			
<i>R</i>	-0.984	-0.937	-0.506
<i>P</i>	0.000	0.000	0.016

### The detailed interrelations of moves and pauses

The unadjusted correlations of durations of pauses with the preceding moves were positive for 9 out of those 15 observations that contained more than 3 activity cycles. These results were significant ( $P < 0.05$ ) for only two or three individuals, according to two-tailed or one-tailed tests. This number of cases with  $P < 0.05$  is more than twice the 0.75 cases (5% of 15 cases) that would be expected due to the number of tests performed. This difference is not significant by the binomial test, so we see only an occasional individual phenomenon. Fig. 5 plots the duration of stationary pauses as a function of the duration of the preceding moves for one specific individual.

The unadjusted correlations of move duration with the duration of the preceding stationary pause, however, varied among individuals. They appeared negative for 10 out of 15 individuals, but the only correlation that was statistically significant ( $P < 0.05$ , two-tailed) was a positive one. For the individual presented in Fig. 5, pause durations Pearson-correlated with preceding move durations ( $r = 0.59$ ;  $P = 0.009$ ), but move durations failed to correlate with preceding pause durations ( $r = -0.19$ ;  $P = 0.45$ ).

In order to gain a more general picture of the move-pause correlations and their possible causal background, we examined the adjusted  $z$  values of correlations between pause duration and move duration, in both directions, for all individuals. Fig. 6 shows that the adjusted  $z$  values of correlations of pauses (dependent variable) with the preceding moves (independent variable) are more positive, and tend to be stronger in absolute values, than the correlations of moves (dependent variable) with the preceding pauses (independent variable). The  $z$  values are negative for only six individuals in the former, but for 10 in the latter group

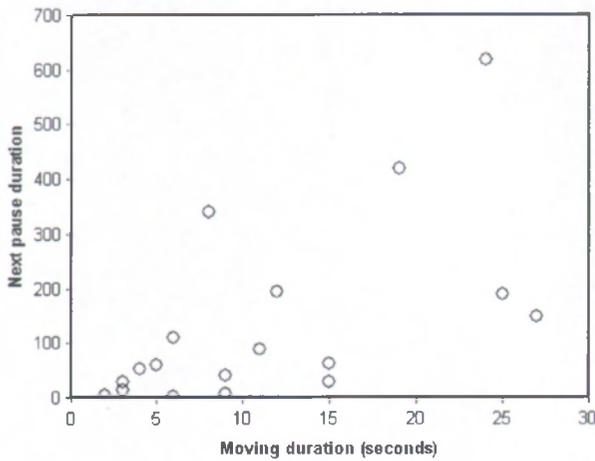


Fig. 5. Duration (sec) of stationary pauses as a function of the duration of the preceding moves, in one moon-exposed adult male as example (moonlight rank = 10.75; Spearman rank correlation,  $r = 0.644$ ;  $P = 0.004$ ).

of correlations. The slope and intercept of the regression line in Fig. 6 show that the regression significantly differs from  $y = x$  (the slope is significantly greater than unity, and the intercept significantly greater than zero).

The two effects seem to balance each other: move duration significantly increases the duration of the next pause, but pause duration (more moderately) decreases the duration of the next move.

Aiming to explain these results, we also checked for correlations of move duration with that of the previous move, and of pause duration with that of the previous

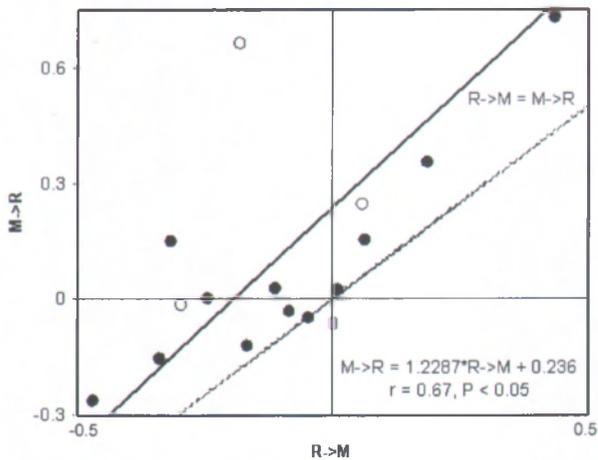


Fig. 6. Move-pause correlations and the effect of moonlight. Adjusted z values of the correlation coefficients of durations of stationary pauses with the duration of the preceding moves as a function of adjusted z values of the correlation coefficients of durations of moves with the duration of the preceding stationary pauses. Open symbols, animals observed in moonlight ( $N = 3$ ); solid symbols, animals observed without moonlight ( $N = 12$ ).

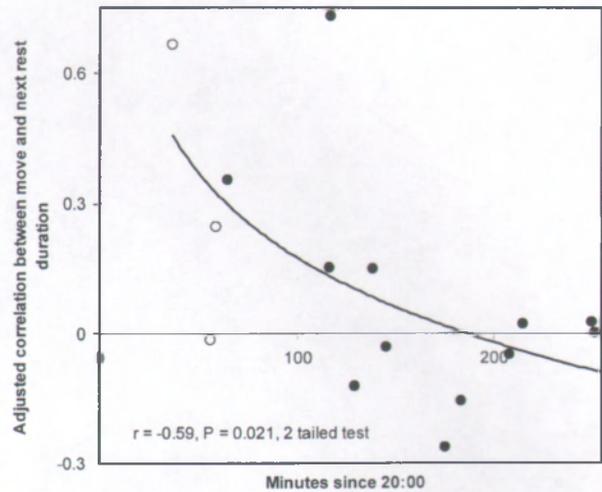


Fig. 7. Adjusted move-pause correlations as a function of hour of observation. The x axis is the number of minutes after 20:00h for the mid-time of an observation, the y axis is the adjusted z of the correlation coefficients between durations of move and next pause. Open and solid symbols as in Fig. 3. The line is the exponential regression ( $\ln y = ax + b$ ).

pause. These correlations were positive for 11 out of 14 individuals for the former, and 7 out of 15 individuals for the latter. They were generally weaker than those for pause duration with the preceding move (10 out of 14 individuals in the case of move-with-previous-move, and 7 out of 14 individuals in the case of pause-with-previous-pause), and much weaker than those for move duration with the preceding pause (12 out of 14 individuals in the case of move-with-previous-move, and 14 out of 15 individuals in the case of pause-with-previous-pause). Thus, the correlations are stronger between the durations of adjacent contrasting phases of the activity cycle than between those of the nearest same-phase components of the cycle.

**The effect of the time of night**

The finding that the parameters of FM varied among individuals (or among observations) to the extent that even the direction of the correlations among them varied, led us to check the effect of the time of night. The effect of the hour of observation on the four FM descriptors was variable and insignificant (Spearman-rank, 2-tailed tests, all  $P > 0.05$ ). But the effect of the hour on the correlation of pause with preceding move was significant ( $r = -0.55; P = 0.034$ ); its effect on the correlation of move with preceding pause was not ( $r = -0.23; P = 0.40$ ). Note that as the night progressed, the correlation of pause-with-preceding-move weakened and finally became reversed (Fig. 7). This effect was not due to temperature.

**Table 6.** Multiple regressions of each of the six behavioral variables (as the dependent variable) and moon rank and mid-hour of observation (as simultaneous independent variables)

	Multiple R	Hour	Moon rank
MPM	0.42	-1.14	-2.04, 0.056
PTM	0.49, 0.077	-1.97, 0.064	-2.25, 0.036
Mean move	0.53, 0.046	-2.53, 0.02	-2.14, 0.046
Mean rest	0.49, 0.073	2.23, 0.038	2.05, 0.054
<i>M</i> → <i>R</i>	0.55	-1.98, 0.07	-0.26
<i>R</i> → <i>M</i>	0.26	-0.93	-0.47

Presented are the *t* statistics for the slopes (for hour and moon) and, separated by comma, the *P* value (two-tailed) in each column. *M*→*R*, correlation of rest (pause) durations with preceding move durations; *R*→*M*, correlation of move durations with preceding rest durations.

Because of the strong negative correlation between hour and moon rank ( $r = -0.70$ ;  $P < 0.001$ ) we also calculated the partial parametric correlations of the behavioral variables with the hour, adjusting for the effects of moon rank (Table 4). The results confirm that there is little effect on the four FM descriptors but some depressing effect on the correlation of pause-with-preceding-move ( $r = -0.50$ ;  $P = 0.07$ ).

Finally, we calculated multiple regressions between each behavioral variable, as dependent variable, and moon rank and hour of observation, as simultaneous independent variables (Table 6). Hour and moon had parallel effects (significant or nearly significant) on the four FM descriptors, as well as on the two types of internal correlations.

## Discussion

### The effect of moonlight on the FM descriptors

The depressant effect of moonlight on the foraging activity of *Teratoscincus scincus* is shown by both the statistics of movement at Repetek (Tables 2, 3, 4 and 6) and the direct observation of individuals immobile under moonlight near Ashgabat. There also exist reports of other species of this small and compact genus (Szczerbak and Golubev, 1996; Macey et al., 1997, 1999), sometimes considered a separate subfamily (Han et al., 2004). Observations of *T. roborowskii* in western China (Werner et al., 1997) resemble the present ones: observed on 6–10.VII.1992, between 2125–2200 and 0001–0030 h, under a half-full moon and 4/8 cloud cover, *T. roborowskii* averaged PTM = 8.8, MPM = 0.44, and was defined as a SW forager. In contrast, Semenov and Borkin (1992) concluded that *T. przewalskii* was an active forager. Unfortunately, the absence of lunar data annuls the comparative value of that project, which thus places only a minor question mark on the behavioral uniformity of the genus.

As mentioned above, the few previous reports on other geckos indicated the opposite effect. Moonlight enhanced the locomotor activity of the cursorial psammophilous *Stenodactylus doriae* (Bouskila et al., 1992; Reichmann, 1998) and the cursorial forest-dwelling *Goniurosaurus kuroiwae kuroiwae* (Werner et al., 2006). Moreover, so far inexplicably, the rupicolous *Ptyodactylus guttatus*, experimentally isolated from moonlight, was more active during full moon (Frankenberg and Werner, 1979). One cannot explain this divergence of response to moonlight (or to the lunar cycle) without knowing the circumstances, including the local predators. For example, the species composition of the predators can affect the percentage of tail injury (Bouskila, 1995; Seligmann et al., 1996) and presumably also the behavior of the lizards. But one relevant factor may be eye size. The function of the eye depends on its absolute size (Walls, 1942), and *T. scincus*, being larger than those other gecko species, has larger eyes (Werner, 1969; Werner and Seifan, 2006: Table 1). Its eye size thus enhances the uniquely sensitive night vision of geckos (Roth and Kelber, 2004) that presumably enables their visual foraging on night-active prey. Conceivably, other factors being equal, its better vision could reverse the outcome of the trade-off: it may not need to risk locomotion under illumination and away from the burrow as it may detect enough food from its ambush. This speculation is supported by the observation that in *Stenodactylus doriae* only juveniles increase their activity under moonlight (Bogin, unpubl. data).

The possibility that gecko species differ in their response to moonlight helps to evaluate some earlier reports. Klauber (1939) encountered 203 live snakes while traveling at night 2500 km in the desert. He regarded his results—a reduction of activity to 68.6% on full-moon nights—as inconclusive. Indeed, we now see that multi-species samples could be heterogeneous.

Geckos are paralleled by nocturnal snakes in the trade-off whether to respond to moonlight with respect to their predators' reactions or their prey. Several reports indicate a reduced activity of nocturnal snakes under moonlight or other illumination: captive habu, *Trimeresurus flavoviridis* (Yamagishi, 1974); snakes in Ecuadorian tropics, despite cloud cover, suggesting an endogenous rhythm (Duellman, 1978, as quoted by Gibbons and Semlitsch, 1987); nocturnally fish-eating *Lycodonomorphus bicolor* (Madsen and Osterkamp, 1982); adult but not juvenile *Crotalus viridis* (Clarke et al., 1996).

What seems clear from our analyses is the relative strength of moonlight effects on *Teratoscincus* behavior, particularly conspicuous against the background of our having detected in our small sample no statistically significant effects of factors such as age, size, sex, temperature or observer effect, all factors classically

known for affecting many biological phenomena, including activity patterns.

### Defining the foraging mode

Despite the great difference between moonlit and dark times in the activity of *Teratoscincus scincus*, it is debatable whether one can say that the level of illumination causes *T. scincus* to shift between the two much-studied contrasting FMs, ambush or sit-and-wait (SW) versus widely (active) foraging (WF; Huey and Pianka, 1981; Cooper et al., 2001). On the one hand, under Huey and Pianka's (1981) criterion for Lacertidae both  $PTM = 3.1$  and  $11.5$  would be within the SW range, even according to the refined analyses of FM modes in Lacertidae (Seligmann, 2005), and so would  $MPM = 0.1$  and  $0.6$  (Huey and Pianka, 1981). On the other hand, even if WF and SW are not part of a continuum (Perry, 1999; Perry et al., in press) but discrete modes with resource division between them (Huey and Pianka, 1981), they need not be characterized by uniform quantitative values for all the world's lizards. They could exist separately in different guilds and at different places, with different local discriminating quantitative values, because only among related animals coexisting in one place does the issue of resource partitioning arise. However, discussion of this issue is premature because most available data on lizard FMs have been obtained with insufficient consideration of the multitude of factors that can modulate the FM descriptors (Werner et al., 2006).

In this project we could not test for effects of sex (Perry, 1996; Werner et al., 2006) and of age (Huey and Pianka, 1981; Perry, 1996) because of the small sample size; nor for the effects of tail regeneration (Seligmann, 1997; Martin and Avery, 1998; Seligmann et al., 2003; Werner et al., 2006) since regenerated tails are difficult to discern in *Teratoscincus* (Werner, 1967).

### The internal structure of the foraging mode and its causation

A given PTM value may result from a few long or many short bursts of locomotion; its structure is clarified by the remaining FM descriptors—MPM, move duration and pause duration. But what determines the duration of moves and pauses? This paper introduces the innovation of analyzing their mutual relationships. The analysis is complicated by the need to adjust correlation coefficients to the varying number of degrees of freedom in order to avoid artefacts that could affect the results shown in Fig. 6. Results from Fig. 6 closely resemble those from similar analyses with unadjusted data (the slope and intercepts of the regression are also significantly greater than 1 and 0, although to a lesser

extent). Hence the conclusions from Fig. 6 are probably robust.

Our results show that the durations of alternating moves and pauses are not random; rather, within many individuals (or observation bouts) and as an overall phenomenon, the duration of pauses is to some extent correlated with the duration of the preceding moves. Long moves apparently stimulate long pauses, as expected when average speed is 220% of the MAS. Long pauses enable, but do not require, short moves. Indeed, as reported above, correlations of pauses with preceding moves are stronger than correlations of moves with preceding pauses, which have a negative trend.

Note that the strength of the correlation reflects the accuracy of process, not the strength of its effects (slope of the regression function). We conclude that the internal structure of the foraging mode is largely dictated by move duration. We speculate that move duration may be determined physiologically and modulated by interventions such as food discovery. We further interpret that the opposite polarity of the two directions of correlation (pause with move versus move with pause) has a balancing function, preventing "run-away escalation" of the duration of locomotion bursts.

### The effect of moonlight and of the time of night on the internal structure of the foraging mode

Explanation of the gradual breakdown of the correlation of pause duration with preceding move duration towards the end of the nightly activity period awaits further investigation. Conceivably, a gecko pressed for food while time runs out could increasingly recruit anaerobic metabolism, or perhaps locomote more slowly, and either of these may be less risky while the gecko gradually approaches its burrow. However, moonlight was negatively correlated with hour ( $r = -0.70$ ;  $P < 0.001$ ). Partial correlation analyses (Table 4) show that the temporal decline in the correlation between pause duration with preceding move duration (Fig. 7) was mainly correlated with hour, not moonlight (Table 6), but multiple regression analyses (Table 6) suggest the possibility of a weaker effect of moonlight, too, on the association between pause and move duration. The difference between results from partial correlation and multiple regression analyses may be due to interaction components between independents which each method handles differently.

Generally, the locomotion of nocturnal geckos is energetically cheap; however, nocturnal activity at low temperatures dramatically reduces the maximal rate of aerobic metabolism, and thus the MAS (Autumn et al., 1994, 1997, 1999; Autumn, 1999). It is conceivable that proportionate pauses may be imposed on *Teratoscincus* only when it exerts itself through running at speeds above its MAS, and that this is how it tends to locomote

under moonlight. Unfortunately, we could not generally record distances, hence speed, so that this question must await future investigation.

### The implications of speed

There is a growing body of evidence revealing some geckos as mobile predators (Cooper, 1995, Werner et al., 1997, 2001, 2004). However, the thermal sensitivity of aerobic metabolism limits the speed that geckos can sustain at low night temperatures. Indeed, the average speed of *T. scincus* in our focal observations was 0.74 km/h, or 220% of their maximal aerobic speed. This is slow speed relative to that of diurnal lizards near their thermal optima (35–40 °C), yet is a substantial aerobic challenge for a gecko at 25 °C.

In animal movement intermittent locomotion is the rule, not the exception (Kramer and McLaughlin, 2001). Although intermittent locomotion could increase energetic costs, perceptual benefits in vision and detection avoidance by predators could outweigh those costs (Kramer and McLaughlin, 2001). Intermittent locomotion may increase or decrease endurance capacity relative to locomotion at the same constant average speed (Weinstein and Full, 1992). For example, a 15 sec exercise, 30 sec pause protocol at speeds above MAS doubled endurance capacity in *T. przewalskii* (Weinstein and Full, 1999). Most other combinations of exercise and pause intervals decreased endurance capacity. Our results suggest that intermittent locomotion (Weinstein and Full, 1999) may play a major role in the locomotor behavior of this species. It is possible that individuals of *T. scincus* select exercise/pause durations that maximize endurance capacity, but this may not be possible because recovery time after exercise at speeds above MAS may be greatly increased at low temperatures (Wagner and Gleeson, 1997). Pause durations much greater than exercise intervals may be required for complete recovery, which could explain our observation that pause duration was approx. 690% of exercise duration in the absence of moonlight.

The physiological and performance consequences of intermittent locomotion are difficult to model a priori because no metabolic steady states are attained (Gleeson and Hancock, 2001). While it is in theory possible to predict strategies (i.e., exercise intensity, exercise duration, and pause duration) that will increase performance limits for intermittent activity, this requires laboratory measurements (Weinstein and Full, 1991). Two important next steps will be necessary to determine what proportion of physiological performance capacity is actually used in nature: (1) continuous measurement of frequency, speed, and duration of locomotion in the field, and (2) measurement of oxygen consumption in the laboratory while applying observed exercise/pause durations during controlled treadmill locomotion.

### Conclusions

1. Some parameters of the locomotor activity of a foraging nocturnal desert lizard, the psammophilous gecko *Teratoscincus scincus*, observed near Repetek and Ashgabat, Turkmenistan, were significantly depressed by moonlight. In this behavior this species resembled herbivorous prey animals rather than some other predatory insectivores.
2. The behavioral discrepancy to three other gecko species that are known to be more active in moonlight is tentatively attributed to the larger size of *Teratoscincus*. Its larger eye may enable it to see prey from the safety of ambush.
3. A novel method of analyzing foraging behavior shows that the duration of moves increases the duration of subsequent stationary pauses, and, secondarily, pause duration decreases the duration of subsequent moves, so that the duration of moves is stabilized.
4. The effect of move duration on subsequent pause duration is attributable to the fact that the gecko's average locomotion speed is 220% of maximum aerobic speed, requiring timely pauses.
5. A fuller description and deeper understanding of the foraging behavior of lizards may perhaps be achieved through the future application of additional descriptors and modes of analysis.
6. Because lizards serve as model organisms for ecological research, the results of this and other recent projects cited constitute a caveat that endeavors to quantify foraging behavior should consider many potential physiological and environmental determinants.

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### References

- Amzallag, G.N., 2000. Connectance in *Sorghum* development: beyond the genotype-phenotype duality. *BioSystems* 56, 1–11.
- Amzallag, G.N., 2001. Data analysis in plant physiology: are we missing the reality? *Plant Cell Environm* 24, 881–890.
- Anderson, R.A., 1993. An analysis of foraging in the lizard, *Cnemidophorus tigris*. In: Wright, J.W., Vitt, L.J. (Eds.), *Biology of Whiptail Lizards (Genus Cnemidophorus)*.

- Oklahoma Mus. Nat. Hist., Norman, Oklahoma, USA, pp. 83–116.
- Anderson, S.C., 1999. The Lizards of Iran. Society for the Study of Amphibians and Reptiles, Ithaca, NY, USA.
- Autumn, K., 1999. Secondly diurnal geckos return to cost of locomotion typical of diurnal lizards. *Physiol. Biochem. Zool.* 72, 339–351.
- Autumn, K., Han, B., 1989. Mimicry of scorpions by juvenile lizards, *Teratoscincus roborowskii* (Gekkonidae). *Chinese Herpetol. Res.* 2, 60–64.
- Autumn, K., Weinstein, R.B., Full, R.J., 1994. Low cost of locomotion increases performance at low temperature in a nocturnal lizard. *Physiol. Zool.* 61, 238–262.
- Autumn, K., Farley, C., Emshwiller, M., Full, R.J., 1997. Low cost of locomotion in the banded gecko: a test of the nocturnality hypothesis. *Physiol. Zool.* 70, 660–669.
- Autumn, K., Jindrich, J., Denardo, D., Mueller, R., 1999. Locomotor performance at low temperature and the evolution of nocturnality in geckos. *Evolution* 53, 580–599.
- Blinder, P., 2001. Foraging games: a stochastic dynamic game model for a predator-prey system. M.Sc. Thesis, Ben Gurion University of the Negev, Beer Sheva.
- Bouskila, A., 1995. Interactions between predation risk and competition: a field study of kangaroo-rats and snakes. *Ecology* 76, 165–178.
- Bouskila, A., 2001. A habitat selection game of interactions between rodents and their predators. *Annales Zoologici Fennici* 38, 55–70.
- Bouskila, A., Ehrlich, D., Gershman, Y., Lampl, I., Motro, U., Shani, E., Werner, U., Werner, Y.L., 1992. Activity of a nocturnal lizard (*Stenodactylus doriae*) during a lunar eclipse at Hazeva (Israel). In: Proceedings of the First Argentinian and First South American Congress of Herpetology, Tucumán, Argentina. *Acta Zoologica Lilloana* vol. 41, pp. 271–275.
- Chambers, W.V., 1991. Inferring formal causation from corresponding regressions. *J. Mind Behav.* 12, 49–69.
- Clarke, J.E., Chopko, J.T., Mackessy, S.P., 1996. The effect of moonlight on activity patterns of adult and juvenile prairie rattlesnakes (*Crotalus viridis viridis*). *J. Herpetol.* 30, 192–197.
- Cooper Jr., W.E., 1995. Foraging mode, prey chemical discrimination, and phylogeny in lizards. *Anim. Behav.* 50, 973–985.
- Cooper Jr., W.E., Whiting, M.J., Van Wyk, J.H., Mouton, F.N.P., 1999. Movement- and attack-based indices of foraging mode and ambush foraging in some gekkonid and agamine lizards from southern Africa. *Amphibia-Reptilia* 20, 391–399.
- Cooper Jr., W.E., Vitt, L.J., Caldwell, J.P., Fox, S.F., 2001. Foraging modes of some American lizards: relationships among measurement variables and discreteness of modes. *Herpetologica* 57, 65–76.
- Daly, M., Behrends, P.R., Wilson, M.I., Jacobs, L.F., 1992. Behavioural modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. *Anim. Behav.* 44, 1–9.
- Duellman, W.E., 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. *University Kans. Mus. Nat. Hist. Misc. Publ.* 65, 1–352.
- Frankenberg, E., Werner, Y.L., 1979. Effect of lunar cycle on daily activity rhythm in a gekkonid lizard, *Ptyodactylus*. *Israel J. Zool.* 28, 224–228.
- Garland, T., 1999. Laboratory endurance capacity predicts variation in field locomotor behaviour among lizard species. *Anim. Behav.* 58, 77–83.
- Gibbons, J.W., Semlitsch, R.D., 1987. Activity patterns. In: Seigel, R.A., Collins, J.T., Novak, S.S. (Eds.), *Snakes: Ecology and Evolutionary Biology*. Macmillan, New York, pp. 396–421.
- Gleeson, T.T., Hancock, T.V., 2001. Modeling the metabolic energetics of brief and intermittent locomotion in lizards and rodents. *Amer. Zool.* 41, 211–218.
- Han, D., Zhou, K., Bauer, A.M., 2004. Phylogenetic relationships among gekkotan lizards inferred from c-mos nuclear DNA sequences and a new classification of the Gekkota. *Biol. J. Linn. Soc.* 83, 353–368.
- Huey, R.B., Pianka, E.R., 1981. Ecological consequences of foraging mode. *Ecology* 62, 991–999.
- Huey, R.B., Pianka, E.R., Schoener, T.W. (Eds.), 1983. *Lizard Ecology: Studies of a Model Organism*. Harvard University Press, Cambridge, Massachusetts.
- Klauber, L.M., 1939. Studies of reptile life in the arid southwest. Part I. Night collecting on the desert with ecological statistics. *Bull. Zool. Soc. San Diego* 14, 7–64.
- Kotler, B.P., Brown, J.S., Hasson, O., 1991. Owl predation on gerbils: the role of body size, illumination, and habitat structure on rates of predation. *Ecology* 71, 2249–2260.
- Kotler, B.P., Brown, J., Dall, S., Gresser, S., Ganey, D., Bouskila, A., 2002. Foraging games between gerbils and their predators: temporal dynamics of resource depletion and apprehension. *Evolutionary Ecology Research* 4, 495–518.
- Kramer, D.L., McLaughlin, R.L., 2001. The behavioral ecology of intermittent locomotion. *Amer. Zool.* 41, 137–153.
- Macey, J.R., Ananjeva, N.B., Wang, Y., Papenfuss, T.J., 1997. A taxonomic reevaluation of the gekkonid lizard genus *Teratoscincus* in China. *Russian J. Herpetol.* 4, 8–16.
- Macey, J.R., Wang, Y., Ananjeva, N.B., Larson, A., Papenfuss, T.J., 1999. Vicariant patterns of fragmentation among gekkonid lizards of the genus *Teratoscincus* produced by the Indian collision: a molecular phylogenetic perspective and an area cladogram for Central Asia. *Mol. Phylogenet. Evol.* 12, 320–332.
- Madsen, T., Osterkamp, M., 1982. Notes on the biology of the fish-eating snake *Lycodonomorphus bicolor* in Lake Tanganyika. *J. Herpetol.* 16, 185–188.
- Martin, J., Avery, R.A., 1998. Effects of tail loss on the movement patterns of the lizard, *Psammmodromus algirus*. *Funct. Ecol.* 12, 794–802.
- Moran, M.D., 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* 100, 403–405.
- Nakagawa, S., 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behav. Ecol.* 15, 1044–1045.
- Perry, G., 1996. The evolution of sexual dimorphism in the lizard *Anolis polylepis* (Iguania): evidence from intraspecific variation in foraging behavior and diet. *Can. J. Zool.* 74, 1238–1245.

- Perry, G., 1999. The evolution of search modes: ecological versus phylogenetic perspectives. *Am. Nat.* 153, 98–109.
- Perry, G., in press. Movement patterns in lizards: measurement, modality, and behavioral correlates. In: Reilly, S.M., McBrayer, L.D., Miles, D.B. (Eds.), *Foraging Behavior in Lizards*. Cambridge University Press, Cambridge.
- Perry, G., Lampl, I., Lerner, A., Rothenstein, D., Shani, E., Sivan, N., Werner, Y.L., 1990. Foraging mode in lacertid lizards: variation and correlates. *Amphibia-Reptilia* 11, 373–384 and 13, 96.
- Pfister, C.A., 1995. Estimating competition coefficients from census-data—a test with field manipulations of tidepool fishes. *Am. Nat.* 146, 271–291.
- Reichmann, A., 1998. The effect of predation and moonlight on the behavior and foraging mode of *Stenodactylus doriae*. M.Sc. Thesis, Ben-Gurion University of the Negev, Beer Sheva.
- Reilly, S.M., McBrayer, L.D., Miles, D.B. (Eds.), *Foraging Behavior in Lizards*. Cambridge University Press, Cambridge, In press.
- Roth, L.S.V., Kelber, A., 2004. Nocturnal colour vision in geckos. *Proc. R. Soc. Lond. B*, 271 (Suppl.), S485–S487.
- Seligmann, H., 1997. Tail injury alters activity patterns in *Podarcis muralis* (Lacertidae). *Israel J. Zool.* 44, 87.
- Seligmann, H., 2005. Three distinct foraging modes among lacertid lizards. *Israel J. Zool.* 51, 76.
- Seligmann, H., Beiles, A., Werner, Y.L., 1996. Tail loss frequencies of lizards and predator specialization. In: Steinberger, Y. (Ed.), *Preservation of Our World in the Wake of Change*, Vol. 6. A/B, ISEEQS Publ., Jerusalem, Israel, pp. 520–522.
- Seligmann, H., Beiles, A., Werner, Y.L., 2003. Avoiding injury or adapting to survive injury? Two coexisting strategies in lizards. *Biolog. J. Linn. Soc.* 78, 307–324.
- Semenov, D.V., Borkin, L.J., 1992. On the ecology of Przewalsky's gecko (*Teratoscincus przewalskii*) in the Trans-altai Gobi, Mongolia. *Asiatic Herpetol. Res.* 4, 99–112.
- Skutelsky, O., 1996. Predation risk and state-dependent foraging in scorpions: effects of moonlight on foraging in the scorpion *Buthus occitanus*. *Anim. Behav.* 52, 49–57.
- Sokal, R.R., Rohlf, F.J., 1981. *Biometry: The Principles and Practice of Statistics in Biological Research*, 2nd Edition. Freeman, New York.
- Szczerbak, N.N., Golubev, M.L., 1996. Gecko Fauna of the USSR and Contiguous Regions. *Contributions to Herpetology*, Vol. 13. Society for the Study of Amphibians and Reptiles, Missouri, USA.
- Times Atlas, 1997. *The Times Atlas of the World, Comprehensive Edition*. Times Books, London.
- Wagner, E.L., Gleeson, T.T., 1997. The influence of thermoregulation on behavioural recovery from exercise in a lizard. *Funct. Ecol.* 11, 723–728.
- Walls, G.L., 1942. The vertebrate eye and its adaptive radiation. *Bulletin of the Cranbrook Institute of Science* 19, 1–785.
- Weinstein, R.B., Full, R.J., 1991. Intermittent locomotion increases distance capacity at low temperature in the ghost crab. *Am. Zool.* 31, 141A.
- Weinstein, R.B., Full, R.J., 1992. Intermittent exercise alters endurance in an eight-legged ectotherm. *Am. J. Physiol.* 262, R852–R859.
- Weinstein, R.B., Full, R.J., 1999. Intermittent locomotion increases endurance in a gecko. *Physiol. Biochem. Zool.* 72, 732–739.
- Werner, Y.L., 1967. Regeneration of specialized scales in tails of *Teratoscincus* (Reptilia: Gekkonidae). *Senck. Biol.* 48, 117–124.
- Werner, Y.L., 1969. Eye size in geckos of various ecological types (Reptilia: Gekkonidae and Sphaerodactylidae). *Israel J. Zool.* 18, 291–316.
- Werner, Y.L., 2001. Enigmas of the manifold foraging behavior of gekkonomorph lizards. Abstracts, 4th World Congress of Herpetology, Sri Lanka, 2001, pp. 127–128.
- Werner, Y.L., Seifan, T., 2006. Eye size in geckos: asymmetry, allometry, sexual dimorphism, and behavioral correlates. *J. Morphol.* 267, 1486–1500.
- Werner, Y.L., Okada, S., Ota, H., Perry, G., Tokunaga, S., 1997. Varied and fluctuating foraging modes in nocturnal lizards of the family Gekkonidae. *Asiatic Herpetol. Res.* 7, 153–165.
- Werner, Y.L., Takahashi, H., Yasukawa, Y., Ota, F., Ota, H., 2001. Variation in the foraging behavior of a nocturnal gecko, *Goniurosaurus kuroiwae orientalis* (Reptilia: Gekkonomorpha). Abstracts, 4th World Congress of Herpetology, Sri Lanka, 2001, pp. 128–129.
- Werner, Y.L., Takahashi, H., Yasukawa, Y., Ota, H., 2004. The varied foraging mode of the subtropical eublepharid *Goniurosaurus kuroiwae orientalis*. *J. Nat. Hist.* 38, 119–134.
- Werner, Y.L., Takahashi, H., Yasukawa, Y., Ota, H., 2006. Factors affecting foraging behaviour, as seen in a nocturnal ground lizard, *Goniurosaurus kuroiwae kuroiwae*. *J. Nat. Hist.* 40, 439–459.
- Yamagishi, M., 1974. Observations on the nocturnal activity of the habu with special reference to the intensity of illumination. *Snake* 6, 37–43.