Foraging mode of the Moorish gecko *Tarentola mauritanica* in an arid environment: Inferences from abiotic setting, prey availability and dietary composition

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Abstract

Predators, particularly those living in deserts, use two main foraging strategies, namely sit-and-wait or wide foraging. The Moorish gecko *Tarentola mauritanica*, a gecko frequently inhabiting humanized habitats, has been repeatedly classified as a sit-and-wait predator. However, previous data on dietary composition in natural habitats suggest a wide foraging strategy for this species. This study seeks to elucidate the foraging mode of the Moorish gecko in a natural, arid zone of southeastern Spain, from data of diel temperature cycling, prey availability and dietary composition. In this zone, the Moorish gecko has almost no prey availability in the cliffs where it retreats during the day, low and scattered prey availability on the ground near the cliffs, and lives in an environment that severely restricts foraging at night because of the low ambient temperatures. However, as shown by dietary analysis, the Moorish gecko captures prey belonging to diverse taxonomic groups, mainly ground-dwelling arthropods, as observed in other rupicolous geckos inhabiting arid zones in the Mediterranean area. These results suggest that, in these arid, natural habitats, the Moorish gecko forages widely on the ground, as previously proposed for other gekkonids from arid habitats.
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Keywords: Diel temperature cycling; Iberian peninsula; Foraging mode; Moorish gecko; Prey availability

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1. Introduction

Deserts are known for having fluctuating productivity (Louw and Seely, 1982; Pianka, 1986), and animals living in arid areas have to cope with this uncertainty in trophic resources. The scant, scattered, and unpredictable food resources represent a main factor determining the kinds of organisms able to survive in deserts. For predators, the necessity of finding live prey may force them to become generalist predators (e.g. Polis, 1991a–c). To gain enough food from these uncertain resources, predators have to optimize the way in which they forage.

The two main strategies of foraging used by predators are classified as sit-and-wait or wide foraging. In the former, the predator remains motionless in one place and attacks prey that pass nearby; in the latter, the predator moves and attacks the prey encountered during movement trips (Huey and Pianka, 1981; Cooper, 1995, 1997; Perry and Pianka, 1997). For a desert predator, living in zones with low prey availability and wide temperature fluctuations, both strategies have advantages and drawbacks. Although foraging widely is energetically expensive, species that use this mode of feeding appear to capture more prey per unit of time than do sit-and-wait species (Pianka, 1986). This could be an advantage for a nocturnal ectotherm, since the low temperatures during night may reduce the foraging period and the animal would therefore need to maximize its capture efficiency. The advantages of the sit-and-way strategy, in turn, are basically energy savings and reduced predation risk (Pianka, 1986).

We have chosen the Moorish Gecko, *Tarentola mauritanica*, to examine the advantages and drawbacks of these two foraging modes. This species is a good subject study for several reasons. This reptile, rock-dwelling with broad digits and is distributed throughout the Mediterranean region; shows a marked anthropophilous behaviour, being common in human constructions (e.g. Martínez-Rica, 1997; Hódar, 2002). As a consequence, some features of its biology, such as diet and feeding habits, have been studied mainly in human habitats (Martínez-Rica, 1974; Seva, 1988; Gil et al., 1993, 1994; Capula and Luiselli, 1994; Pérez-Mellado, 1994). However, the species is also found in varied natural habitats, from rock cliffs in relatively wet and woody zones, to true deserts, where parallel studies are lacking (but see Mellado et al., 1975; Salvador, 1978; Hódar and Pleguezuelos, 1999). In fact, because it thrives in human habitats (towns, farms, agricultural landscapes), the typical vision of the Moorish gecko hunting close to artificial lights has given this species a widely accepted image of sit-and-wait predator (Seva, 1988; Gil et al., 1994; Pérez-Mellado, 1994), despite that this situation is not at all comparable with the wild.

In a previous study, we analysed the diet of the Moorish gecko in a natural, arid zone of southeastern Spain (Hódar and Pleguezuelos, 1999). In consideration of the diet composition, we suggested an ambush foraging mode for the species in these habitats (see also Perry and Brandeis, 1992; Werner et al., 1997, for other gekkonid species in similar habitats). The abiotic setting of the zone, with wide fluctuations in temperature from day to night during the gecko's activity season implies that the foraging period for a nocturnal ectotherm like the Moorish gecko must be very narrow. In this work, our aim is to test whether, as previously proposed, the Moorish gecko behaves as an ambush forager in this arid zone. Since the species is nocturnal, the possibility of studying the foraging behaviour by direct observations without altering the natural behaviour of the animal is difficult. Hence, we have made a detailed study of both the diet of the gecko and the prey availability in several different microhabitats, in which the gecko could potentially acquire

its food. The relationship between diet and prey availability can thus offer valuable information about the foraging mode of the gecko. Because of the particular diel activity of the Moorish gecko (nocturnal) and the extreme climate of the study area, all findings on foraging ecology of the species have been interpreted under the perspective of the environmental setting.

2. Study area and methods

2.1. Study area

The study area is located in the Guadix-Baza region (SE Spain), a Neogene basin at 700–1100 m a.s.l. surrounded by mountains (1700–3000 m a.s.l.). The climate is continental Mediterranean, with warm, dry summers and cold winters (average temperature 26.6 °C in July and 7.2 °C in January), and roughly 300 mm of average annual rainfall, sparsely distributed between autumn and spring, although the study site, in the lower part of the basin is drier (30-year standard meteorological averages, Castillo-Requena, 1989). Field work was carried out in a rambla (a seasonal watercourse) named Barranco del Espartal (UTM 30sWG2754, 750 m a.s.l.). The sampling site is a badlands landscape, with a substrate of silt with gypsum sediments. The vegetation is rather sparse, 46% bare ground, 21% grassland and 33% shrub cover, and a mean shrub height of 80.5 cm (see Hódar et al., 1996; Hódar and Pleguezuelos, 1999 for details). The main plant species included *Salsola vermiculata*, *Artemisia herba-alba* and *Gypsophila struthium*, with scattered shrubs of *Retama sphaerocarpa* and *Tamarix gallica*.

2.2. Temperature measurements

Temperature was recorded in April, the beginning of the gecko's activity period in the study area, and July, the hottest month, by means of data loggers and temperature probes (Onset Computer Corporation, Pocasset, Massachusetts, USA). On both the silt cliff and on the ground 3 m from the cliff, three thermistors were placed during a registering period of 7 days, with registers every hour. Thermistors were placed on the soil and cliff surface, to mimic places where a gecko could thermoregulate.

2.3. Diet analysis

Diet analysis was based on faecal samples, collected every 2 weeks between April and September 1996. Faecal analysis provides accurate information on the diet of the gecko (see Hódar and Pleguezuelos, 1999, and references therein). Feces were collected by surveying two marked walls in silt cliffs (20 m long × 4.5 high and 35 m long × 15 m maximum high; the surface surveyed was the lower 2 m of the walls, ca. 110 m^2). Geckos take refuge during the day in fissures of these walls, while nocturnal observations revealed that during night they move on ground a few meters from the walls, but these reptiles were in general scant and shy (pers. obs.). During each visit, we collected all the feces found, but only complete feces were preserved. No other gecko species is present in the zone, and the feces of other lizard species in the zone clearly differ from those of geckos (Hódar and Pleguezuelos, 1999). Since sampling was conducted consistently on the same area of the cliffs, and all excrements were collected, we assumed that every gecko living in

the cliffs had the same probability of being sampled, thereby eliminating the risk of pseudoreplication.

Feces were dispersed in water and examined under a $10-40 \times$ binocular microscope equipped with a micrometer (0.1 mm precision). Prey remains were identified, sorted and measured. Prey were determined to the finest taxonomic level possible, and later assigned to Operational Taxonomic Units (OTUs, sensu Sneath and Sokal, 1973). Measurements of characteristic body parts provided an estimate of the prey's body size and dry mass by means of regression equations previously developed by using arthropods collected in the study area (Hódar, 1996, 1997). Statistical analyses of prey size and mass were made only with those prey for which body length or dry mass was either measured or estimated. However, for prey with no estimated biomass, we assigned the average biomass for its OTU and month in order to get a better estimate of the importance of that OTU.

2.4. Prey availability

Prey availability was estimated in cliff wall and ground by means of two different capture methods. Sampling periodicity was fortnightly during the 6 months of the study, and the capture period was from sunset to sunrise (i.e. one night). The two methods were:

(a) Sticky traps, polyvinyl boards of 310 cm^2 surface, covered with glue RataStop®. Eight traps were fixed to the wall, four at 0.5 m height and four at 1 m height, 2 m apart from each other. The second fortnight of September traps were not placed, resulting in a total of 88 traps for the entire sampling period.
(b) Pitfall traps (6.4 cm in diameter), half filled with water and detergent. Eight traps were placed 1 m apart of the cliff and other 8 placed 3 m apart of the cliff, 2 m apart from each other. Pitfalls were placed at the same time and sampling period as the sticky traps, making a total of 192 traps.

Both the pitfall as well as the sticky traps are methods widely used for sampling arthropods (see e.g. Cooper and Whitmore, 1990; Marquet et al., 1990; Ausden, 1996), and are usually considered a biased estimator of availability, being strongly dependent on the mobility pattern of arthropods. Certainly, no method of trapping insects gives an accurate idea about how the predator perceives availability, and several studies expound upon this problem (e.g. Cooper and Whitmore, 1990; Andersen, 1991). In view of the above, capture data in traps were modified for a better adjustment with diet data (Hutto, 1990; Wolda, 1990): we removed Diptera below 2 mm in length in wall samples, and Collembola and Acarina in both wall and ground, from the availability data. This represented 64 out of 102 captures in sticky traps, and 800 out of 939 in pitfall traps, but these arthropods are not eaten by geckos and constitute 0.1% of the arthropod biomass collected in the traps.

2.5. Data analysis

Temperature data were analysed with repeated-measures ANOVA, in which micro-habitat (wall vs. ground) and month (April vs. July) were the between-subject factors and

the hour of the day the within-subject. Dietary data were computed on a monthly basis, and summarized as percentages of both numerical frequency and estimated biomass (Rosenberg and Cooper, 1990). For vegetal remains, only occurrence was recorded. Differences in dietary composition were analysed with contingency tables, whereas prey sizes and masses were analysed with the Kruskal–Wallis test (Zar, 1996). In the same way, differences between diet and availability in the different microhabitats were analysed with contingency tables, whereas the prey-size distribution was compared with the Kolmogorov–Smirnov test. Nonparametric tests were applied because of the non-normal distribution of variables (Shapiro-Wilk test). All tests were carried out by using the JMP statistical package (SAS Institute, 2000).

3. Results

3.1. Abiotic setting

Temperatures were significantly higher for July than for April ($F_{1,1840} = 1739.08$, $p < 0.0001$), and for the ground than for the wall ($F_{1,1840} = 192.42$, $p < 0.0001$, rmANOVA). The wall had a higher thermal inertia—that is, the soil warmed up quickly (and reached higher absolute values) but also cooled quickly, resulting in higher night-time temperatures for the wall than for the ground (Fig. 1). In April, the temperature at noon was 18 °C and at midnight around 12 °C, but around 31 and 23 °C, respectively, in July. That is, although temperatures were high in July at noon, they fell sharply to cold levels at night, especially in April, severely reducing the night period with temperatures that allow gecko activity.
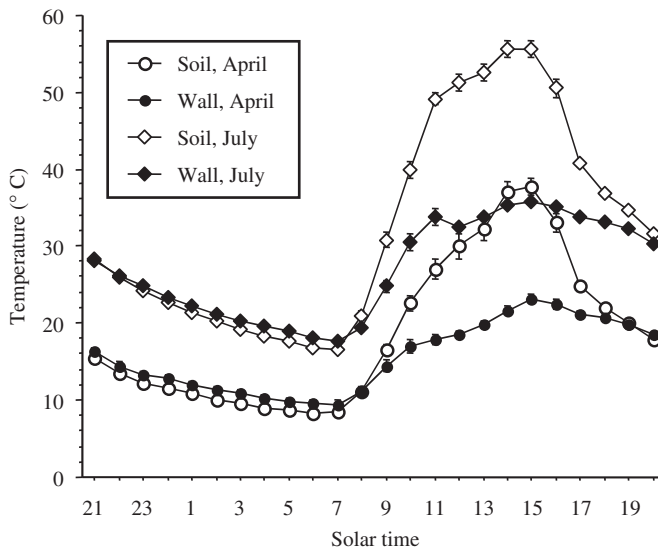

Fig. 1. Diel temperature cycle (mean±SE) in the study area (Barranco del Espartal, SE Spain). The cycles are shown for the coldest month, April, and the hottest, July, as well as for walls, where geckos retreat during the daytime, and ground, where geckos forage at night.

3.2. Diet analysis

A total of 144 feces were collected during the study period, containing a total of 386 identified animal prey, all arthropods (Table 1). Vegetal remains were found in five scats, but the nature of the records (dry leaves and debris) suggests that they were ingested accidentally. The more important prey groups in terms of numerical frequency were Araneae (spiders), Lepidoptera larvae (caterpillars), Carabidae (ground beetles) larvae, Curculionidae (weevils), and other Coleoptera, which comprised roughly two-thirds of the diet. In terms of biomass, Araneae, Onyscidae, Lepidoptera and Carabidae larvae, and Coleoptera others, pooled represented 75% of the diet of the Moorish Gecko in our study area (Table 1).

Dietary composition showed significant monthly changes throughout the study period ($\chi^2 = 188.29$, d.f. = 55, $p < 0.0001$). Araneae was the overall main group, while Lepidoptera and Carabidae larvae were important during the first half the study period, and from July onwards were surpassed by Onyscidae, other Arachnida, and Coleoptera. In general this represents a shift from less sclerotized, and hence highly profitable groups such as larvae in spring, to hard and sclerotized species, adapted to the harsh conditions of drought in summer; it also means a more diverse diet in summer months than in spring ones (Table 1). The shift also produced significant changes in prey length ($H = 17.93$, d.f. = 5, $p < 0.003$) and prey mass ($H = 29.78$, d.f. = 5, $p < 0.0001$, Kruskal–Wallis test) during the active period, the prey being longer and heavier during the spring than during the summer season (Table 1). Most of the prey (78.4%) were 2–12 mm in body length.

Table 1

Taxonomic composition and biomass of the Moorish gecko (*Tarentola mauritanica*) diet in the Barranco del Espartal (SE Spain)

Group	April % N	April % B	May % N	May % B	June % N	June % B	July % N	July % B	August % N	August % B	September % N	September % B
Araneae	30.3	62.4	15.8	24.5	14.9	39.8	10.4	22.9	11.7	17.2	28.6	35.0
Arachnida others	—	—	4.0	0.1	—	—	2.1	13.0	8.3	22.8	7.1	17.0
Onyscidae	—	—	4.0	12.4	3.2	10.0	4.2	15.5	3.3	9.5	7.1	19.0
Homoptera	3.0	0.5	—	—	3.2	0.3	12.5	2.3	20.0	2.9	9.5	1.0
Heteroptera	—	—	1.3	0.7	1.1	0.7	2.1	8.9	3.3	6.4	—	—
Lepidoptera larvae	24.2	16.5	6.6	6.6	11.7	6.1	4.2	1.3	6.7	11.2	4.8	8.5
Lepidoptera imago	—	—	1.3	2.3	3.2	7.4	6.3	9.5	5.0	10.9	—	—
Carabidae larvae	12.1	4.05	29.0	24.9	41.5	26.5	12.5	11.7	6.7	5.3	2.4	0.1
Curculionidae	15.2	7.65	23.7	14.0	3.2	1.6	—	—	3.3	2.9	4.8	3.1
Coleoptera others	7.6	3.2	6.6	6.2	6.4	3.0	10.4	4.5	6.7	8.1	14.3	13.9
Formicidae	1.5	0.03	1.3	0.5	4.3	0.1	25.0	7.2	11.7	0.7	9.5	0.5
Insecta others	6.1	5.7	6.6	8.3	7.5	4.5	10.4	3.3	13.3	2.5	11.9	2.0
Vegetal (%P)		6.1		—		4.0		—		7.7		—
No. identified prey		66		76		94		48		60		42
No. measured prey		51		59		75		33		44		21
Diversity *H'*		1.78		1.96		1.89		2.17		2.33		2.09
No. feces analysed		33		22		25		16		26		22

% N, numerical frequency; % B, percentage of biomass; in vegetal remains, % P indicates percentage of occurrence.

3.3. Diet–availability relationship

The capture rate in the availability traps was low, both in sticky and in pitfall traps. Captures were extremely low in sticky traps (average 1.16 ± 0.16 captures/trap/night, Fig. 2). Pitfall traps averaged 4.88 ± 1.02 captures/trap/night through the study period, but around 7–8 captures/trap/night at the beginning and at the end of the activity period, when most of the captures were Collembola and Acarina, abundant in this period when there is some moisture in the soil, and were scarcer in the hottest months. When these prey were eliminated (see Methods) and only taxonomic groups that take part in the diet of the Moorish gecko were considered, the capture rate fell well below 1 capture/trap/night (0.43 ± 0.07 on the wall, 0.72 ± 0.10 on the ground, Fig. 2).

Both the taxonomic composition and the prey-size distribution of the captures in the traps differed from those found in the gecko's diet (Table 2). Furthermore, some of the main groups present in the diet never (Carabidae larvae) or rarely (Lepidoptera larvae)
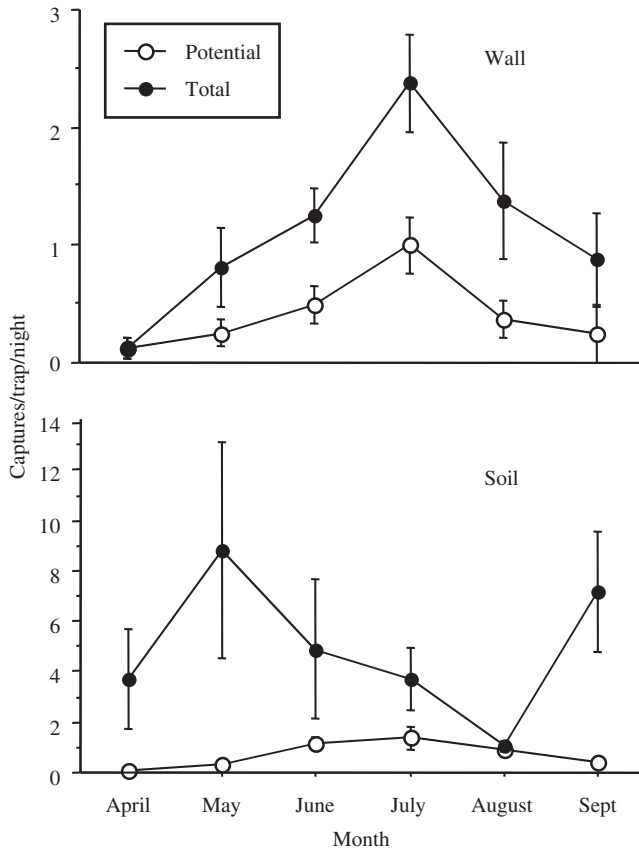

Fig. 2. Capture rates (number of prey per trap and per night, mean $\pm$ SE) for sticky traps (on the wall) and pitfall traps (on the ground) during the activity period of the Moorish gecko (*Tarentola mauritanica*) in the Barranco del Espartal (SE Spain). The figure separates the total capture rate from the capture of prey that, because its size and taxonomic identity, are true potential prey for the Moorish gecko (see Methods for details).

Table 2

Taxonomic composition of the Moorish gecko (*Tarentola mauritanica*) diet in the Barranco del Espartal (SE Spain), prey availability according to captures in sticky traps (cliff) and pitfalls (soil 1 and 3 m), and comparison between diet and availability in the three microhabitats sampled

Group	Diet	Cliff	Soil 1 m	Soil 3 m
Araneae	70	6	2	7
Arachnida others	12	0	0	1
Onyscidae	13	0	6	4
Homoptera	27	1	1	0
Heteroptera	5	0	0	0
Lepidoptera larvae	40	0	1	2
Lepidoptera imago	10	15	0	0
Carabidae larvae	80	0	0	0
Curculionidae	35	0	0	2
Coleoptera others	31	0	23	22
Formicidae	29	4	23	21
Insecta others	34	0	16	8
Collembola + Acarina	0	74	443	357
Prey vs. *availability*				
Taxonomic composition, G		37.23	83.25	71.61
$p <$		0.0001	0.0001	0.0001
Prey size, K–S test		0.704	0.272	0.227
$p <$		0.0001	0.0004	0.0075

Collembola and Acarina were not included in the comparison.

appeared in traps, either on the wall or on the ground, reflecting that the Moorish gecko and traps differ in the way that capture their prey.

4. Discussion

The diet of the Moorish gecko in the Barranco del Espartal agrees with the dietary composition found in similar studies on this species in natural habitats; it is also quite similar to the diet found at the same site and for this species in the year 1995 (Hódar and Pleguezuelos, 1999), despite that 1995 was a very dry year (133.6 mm) and 1996 was a wet one (522.3 mm, data from a meteorological station 25 km apart of the study area). The diet is almost exclusively based on arthropods, as in other gekkonids (Avery, 1981; Bauer and deVaney, 1987; Marquet et al., 1990; Valakos and Polymeni, 1990; Perry and Brandeis, 1992; Saenz, 1996; Szczerbak and Golubev, 1996). Previous studies on the diet of the Moorish gecko in Mediterranean peninsulas (Valverde, 1967; Martínez-Rica, 1974; Gil et al., 1994; Capula and Luiselli, 1994) and islands (Salvador, 1978; Seva, 1988; Gil et al., 1993) show that dietary composition, although invariably based on arthropods, varies widely between zones. In any case, there is a clear contrast between studies conducted in human environments and those carried out at natural sites. The diet of the Moorish gecko in humanized and/or urban habitats includes flying groups such as Diptera and adult Lepidoptera, which may represent a major part of the diet (up to 24% in Cabrera, Balearic Islands, Salvador, 1978, or 36.1% in Rome, Capula and Luiselli, 1994), corresponding with the typical image of the gecko capturing prey near the public lighting, while in our

case the flying groups (Lepidoptera imago, Diptera, Formicidae winged and Neuroptera) are minor, and the most important dietary groups live mainly on low shrubs and the ground (see also Hódar and Pleguezuelos, 1999). Human lights attract several groups of insects and, in this way, a sit-and-wait behaviour can be optimal for a gecko. However, in natural environments prey are scattered and there are no permanent patches of high prey availability, as shown by the low capture rate in the two types of traps used in our study area. Furthermore, cities and other anthropic habitats usually maintain warmer temperatures than do natural ones, and in this sense are better for the gecko activity. The temperatures registered in our study area, even in July, are well below the preferred body temperature for Moorish gecko in the laboratory (31.6 °C, Gil et al., 1994; see also Brown, 1996; Arad et al., 1997), and in general below the activity body temperatures recorded in the field, around 25 °C (Gil, 1992). Although geckos can remain active well below this temperature (the critical thermal minima is 5.3–9.3 °C for *Tarentola boettgeri* in Canary Islands; Brown, 1996), and most of nocturnal lizards have developed the capacity of work at low temperatures (Autumn et al., 1994, 1997), this is an important difference to consider when analysing the way in which geckos get their food in natural versus human habitats.

In summary, the Moorish gecko in the Barranco del Espartal has almost no prey available on the cliffs, to which it retreats only during day; it has low and scattered prey availability on the ground near the cliffs, living in an environment that severely constrains night-time foraging due to the ambient temperatures for most of the activity period. However, as indicated by dietary analysis, and the fact that the species survive and reproduce in the study area, the Moorish gecko captures sufficient prey from diverse taxonomic groups, mainly ground-dwelling arthropods, as observed in other rupicolous geckos inhabiting arid zones in the Mediterranean area (Perry, 1981; Perry and Brandeis, 1992; also Hódar and Pleguezuelos, 1999). Although other factors may also be of importance in determining the foraging behaviour of the gecko, such as predation risk (Gil et al., 1993), this does not appear to apply in our zone, where nocturnal and potential predators for the Moorish Gecko are varied (Hódar and Pleguezuelos, 1999). The single conclusion that can be drawn from the above is that, in these arid, natural habitats of southeastern Spain, the Moorish gecko forages widely on the ground, as previously proposed for other gekkonids from arid habitats (Werner et al., 1997). This agrees with the opinion that reptile species tend to forage actively when food availability is low, despite their usual sit-and wait foraging strategy (Ananjeva and Tsellarius, 1986; Pianka, 1986), and that species engaged in this mode of feeding appear to capture more prey per unit of time than do sit-and-wait species (Pianka, 1986). Our work did not enable a fine-tuning insight on prey selection by the Moorish gecko, but at least indicated the places where a rupicolous gecko forages when in natural environments, both under a prey-availability and environmental-temperature cues. This contrasts with ideas widely accepted until now on the feeding habits of Moorish gecko and cliff-dwelling Gekkonidae in general, and stresses the need for more detailed studies on this group (Werner et al., 1997).

Acknowledgements

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