

SHORT NOTES

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**REPRODUCTIVE
CHARACTERISTICS OF THE
INSULAR LACERTID *TEIRA DUGESII***

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The endemic lizard of the Madeiran Archipelago (Portugal), *Teira dugesii*, was recently separated from the lacertid genus *Podarcis* after the phylogenetic revisions of Böhme & Corti (1993) and Mayer & Bischoff (1996), but has close affinities with this genus (Richter, 1980). Therefore, a close phylogenetic relationship with the other two species included by Mayer & Bischoff (1996) in the genus *Teira*, *Teira perspicillata* (formerly included in the genus *Podarcis*) and *Teira andreanszkyi* (which belonged before to the genus *Lacerta*) must be taken into account. Nevertheless, more recent studies show that these species do not form a strongly monophyletic clade (Oliverio *et al.*, 2000), although *T. dugesii* and *T. perspicillata* seems to be sister species (Harris & Arnold, 1999).

As in other species of insular lacertid, little information is available on the reproductive characteristics of *Teira dugesii* (Richter, 1986; Malkmus, 1995; Bosch & Bout, 1998), although studies on other aspects of its biology have been published (e.g., diet: Sadek, 1981; Davenport & Dellinger, 1995). The species presents a high level of polymorphism both within and between islands, mostly in pigmentation (Cook, 1979; Crisp *et al.*, 1979), but also in body size, body proportions and scalation (Báez & Brown, 1997). Three subspecies have been described, the one that lives on the island of Madeira being the nominal form, and also the most robust and largest one (Bischoff *et al.*, 1989).

Teira dugesii is distributed throughout the archipelago, with very high densities over most of the island of Madeira (Dellinger, 1997). It occupies a great range of habitats, from sea level (including the intertidal zone: Davenport & Dellinger, 1995) to high areas in the

mountains (up to 1861 m), and from uncultivated areas, with "laurisilva" (laurel woods), to the interior of the towns. It is more abundant in rocky areas, without dense or tall vegetation (Dellinger, 1997). Recently an introduced population has been detected in the city of Lisbon, Portugal (Sá-Sousa, 1995). *Teira dugesii* is omnivorous, feeding on invertebrates, leaves, nectar and fruits (Elvers, 1977, 1978; Sadek, 1981; Beyhl, 1990; Davenport & Dellinger, 1995).

The purpose of this note is to present and discuss data on some reproductive traits of this species, especially the relationships between female size and the number and size of eggs and hatchlings. This study was carried out with live animals that mated, laid eggs and produced hatchlings under controlled, captive conditions.

Lizards were captured by hand and with a noose in areas around the city of Funchal (island of Madeira : 17° 0' W, 32° 45' N) in May 1995. These animals were transferred to terraria at La Coruña (Spain), where they were kept throughout the period of reproduction. The island of Madeira enjoys a very diverse climate, mainly conditioned by wind direction and altitude. La Coruña, located at sea level, has a distinctly Atlantic climate, very similar to the climate of the Madeiran coast (Carballeira *et al.*, 1983).

The study of captive animals was performed in three outdoor, open-air terraria measuring 60 × 40 × 40 cm, under natural conditions of light and temperature. These terraria were exposed to direct sunlight, so shade was provided over approximately one third of their surface, to allow the lizards to thermoregulate. The floors of the terraria were covered with 2 cm of gravel, over which stones and bark pieces were placed to provide shelter. Lizards were fed small pieces of fruit daily (banana, tomato, apple and figs) and live insects twice a week (*Tenebrio molitor* larvae, ant pupae and grasshoppers – nymphs and imagos of various acridid and tettigoniid species). Water was supplied *ad libitum*.

Twenty-six female lizards, which were individually marked by toe clipping, were introduced into the terraria on 5 May 1995, and observed daily thereafter. Sex, snout-vent length (SVL: to 0.1 mm, checked by double measurements), body mass and tail length were recorded for each animal. The reproductive state of each female was determined periodically by ventral palpation in order to detect the presence of eggs in the oviducts. When eggs were detected, females were removed and placed individually in 10 × 10 × 20 cm plastic boxes, filled to a depth of about 15 cm with soil, where eggs were laid. Immediately after laying, the female and each egg were weighed to 0.001 g precision. The number of eggs and their lengths and widths were also recorded. Egg volume was estimated as $V=4/3\pi a^2b$, where $a=1/2$ width and $b=1/2$ length. Egg characteristics were in all cases determined within 8 hr of laying. Each clutch could be unequivocally assigned to an individual female, allowing calculation of relative clutch mass (RCM) as the mass of the clutch (immediately after laying) divided by the mass of the spent female.

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TABLE 1. Reproductive traits and adult female body size (snout-vent length, SVL) of *Teira dugesii* from Funchal, Madeira island. These traits were obtained from vivarium-laid eggs and from hatchlings hatched in a vivarium. Hatchling data correspond to the mean value for each clutch.

	Mean±SD	Min.	Max.	<i>n</i>
Female SVL (mm)	60.8±5.4	49.9	69.5	25
Female body mass (g)	4.84±1.63	2.72	8.40	21
Female condition	7.90±2.02	4.72	12.09	21
Clutch size	2.44±0.77	2	5	25
Clutch mass (g)	1.464±0.334	1.050	2.100	16
RCM	0.338±0.077	0.205	0.489	16
Egg mass (g)	0.658±0.103	0.525	0.925	16
Egg volume (mm ³)	552±106	395	814	18
Hatchling SVL (mm)	30.9±1.3	29.1	33.4	11
Hatchling condition	2.06±0.35	1.53	2.65	11
Hatchling mass (g)	0.641±0.133	0.454	0.885	11

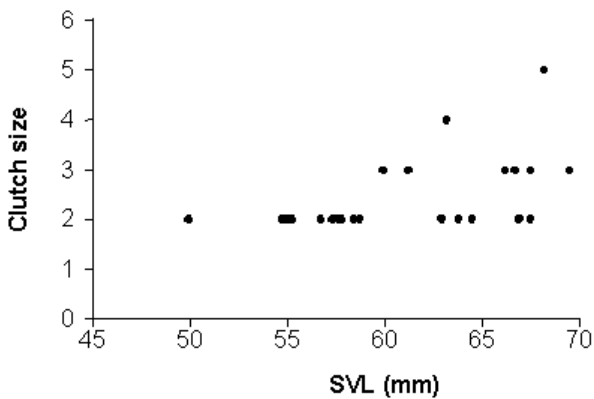


FIG. 1. The relationship between clutch size (number of eggs) and female snout-vent length (SVL) in *Teira dugesii*.

Each clutch was incubated in its plastic box near an open, south-facing window (see Galán, 1997). After hatching, the SVL, mass and sex of the hatchlings were recorded. Sex could be determined on the basis of dorso-lateral lines, which are evident at hatching in females but not in males. Sex was confirmed when animals reached sexual maturity.

Reproductive traits observed in the sample of *Teira dugesii* are summarized in Table 1. Clutch size (Fig. 1), mean egg size (volume and mass) and total clutch mass (Fig. 2) were all heavily dependent on female body size

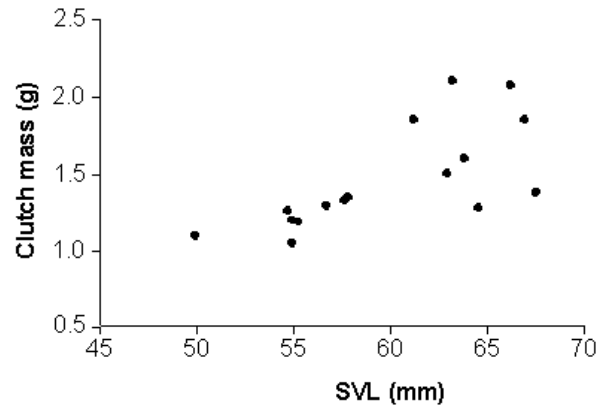


FIG. 2. The relationship between total clutch mass and female snout-vent length (SVL) in *Teira dugesii*. The mass of each egg mass was measured immediately after oviposition.

(Table 2). However, there was not a significant relationship between female SVL and RCM. Larger eggs gave rise to larger hatchlings (Fig. 3), but neither the SVL nor the body mass of hatchlings was significantly correlated with female size (Table 2). There was no significant difference between the mean sizes of male and female hatchlings (Table 3).

The mean RCM observed in *Teira dugesii* is similar to that of several continental populations of *Podarcis* species, which have a larger clutch size (Braña *et al.*, 1991). This is in accord with the idea of a relative stabil-

TABLE 2. Summary of linear regression analyses of reproductive traits on female snout-vent length (mm) in *Teira dugesii*.

Reproductive trait	<i>R</i> ²	<i>F</i>	df	<i>P</i>	intercept	slope
Clutch size	0.29	9.30	1,23	0.006	-2.18	0.08
Clutch mass (g)	0.49	13.54	1,14	0.002	-1.18	0.04
Mean egg volume (mm ³)	0.24	4.94	1,16	0.041	-3.35	9.16
Mean egg mass (g)	0.37	8.18	1,14	0.013	-0.05	0.01
Relative clutch mass	0.18	3.17	1,14	0.097	0.71	-0.01
Mean hatchling SVL (mm)	0.02	0.21	1,9	0.660		
Mean hatchling mass (g)	0.01	0.09	1,9	0.773		

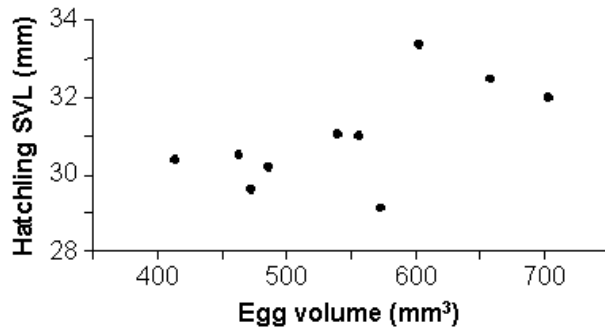


FIG. 3. The relationship between the mean snout-vent length (SVL) of hatchlings and mean egg volume in 10 clutches of *Teira dugesii* ($r=0.62$, $P<0.05$).

ity of RCM among lizards (Vitt & Congdon, 1978; Vitt & Price, 1982).

Rykena & Bischoff (1992) found a positive correlation between female body mass and clutch mass in *Teira andreanszkyi*, and a positive correlation between RCM and clutch size. We found no significant relationship between RCM and clutch size in *Teira dugesii* ($R^2=0.07$; $F=1.09$; $df=1,14$; $P=0.314$).

We observed double-clutching in three large *T. dugesii* (SVL: 63.8, 66.2 and 66.9 mm respectively), which laid for the first time in May and for the second time in July (two) or August (one). The average period between two consecutive layings was 64.3 days (range: 53–71 days). Matings were observed in these females 20 to 28 days (mean = 24.7 days) after the first laying and 41 to 50 days (mean = 46.0 days) before the second laying. The characteristics of each female's first and second clutch were similar: the clutch size was the same (3 eggs in one case and 2 in the other two) and the characteristics of the eggs and of their hatchlings did not differ significantly. In captive, fully-grown females of *Teira andreanszkyi*, Rykena & Bischoff (1992) detected up to six clutches in one breeding season.

The few published data on the reproduction of *Teira dugesii* are from Richter (1986), according to whom the laying period is May-August, with a clutch size of two or, exceptionally, three eggs. The laying period we observed was similar. It lasted for four months in 1995, from May to August. Clutch size varied significantly among these months ($F_{3,25}=3.73$, $P=0.026$; Table 4), though the size (SVL) of reproductive females did not ($F_{3,25}=1.97$, $P=0.15$). This laying period is longer than for the majority of temperate lacertid species, in which

TABLE 3. Summary statistics of snout-vent length (SVL) and body mass of male and female hatchlings of *Teira dugesii*. Measurements were in all taken within 24 hr of hatching.

	Mean±SD	Min.	Max.	<i>n</i>
<i>Hatchling SVL (mm)</i>				
male	30.9±1.8	28.7	33.6	12
female	30.9±1.0	29.1	33.4	21
<i>Hatchling body mass (g)</i>				
male	0.645±0.158	0.436	0.891	12
female	0.598±0.099	0.471	0.871	21

laying usually lasts for three months, ending in July (Bauwens & Díaz-Uriarte, 1997). However, another insular lacertid, *Podarcis pityusensis*, was reported to have a laying period coincident with that which we observed in *Teira dugesii*, i.e. May-August (Carretero *et al.*, 1995).

In *T. dugesii*, the clutches consisted of few, large-sized eggs. At the moment of laying, the eggs were elongate, the width of the largest reaching only 40% of the length (mean = 51.7 %, range: 40%–60%, $n=32$). In *Teira perspicillata* (Doumergue, 1901; Richter, 1986; Schleich *et al.*, 1996), as in *Teira andreanszkyi* (Rykena & Bischoff, 1992), eggs are also cylindrical and elongate. Such a large egg size in a relatively small-sized lizard may constrain the eggs to have a cylindrical shape, differing considerably from the usual oval shape in the lacertids (e.g. Arnold & Burton, 1978; Bruno, 1986). This cylindrical shape arises from the morphological constraint imposed by the female's pelvic girdle (Sinervo & Licht, 1991).

The most frequent clutch size in *Teira dugesii* was two (17 cases in 25), and this number was observed in smaller adult females as well as in the larger ones, although some of the latter had clutches of up to five eggs (Fig. 1).

Very small clutch sizes and large eggs have been observed in insular species or populations of the closely related genus *Podarcis* (Vicente, 1989; Carretero *et al.*, 1995; Castilla & Bauwens, 2000a,b). Thus, in *Podarcis pityusensis* from the Mediterranean island of Ibiza, average clutch size is 2.3 eggs (range: 1–4) and average egg volume is 394 mm³ (Carretero *et al.*, 1995). *Podarcis carbonelli berlengensis* from Berlenga Island

TABLE 4. Female snout-vent length (SVL, in mm) and clutch size of *Teira dugesii* in each of the four months of the laying period (SEM = standard error of the mean).

Month	Female SVL (mean±SEM)	Range	Clutch size (mean±SEM)	Range	<i>n</i>
May	63.0±1.9	55.0–69.5	2.37±0.18	2–3	8
June	63.7±1.5	58.7–68.2	3.14±0.40	2–4	7
July	59.6±2.2	54.7–66.9	2.14±0.14	2–5	7
August	57.0±2.8	49.9–63.8	2.00±0.00	2	6

(Portugal) has an average clutch size of 2.01 eggs (range: 1-4), and average egg and clutch masses of 0.43 g and 0.88 g, respectively (Vicente, 1989). *Podarcis atrata* from the Columbretes Islands (Spain) has an average clutch size of 2.8 eggs (range: 1-5), and average egg and clutch masses of 0.37 g and 1.04 g (Castilla & Bauwens, 2000a). The average size of the reproductive females in these lacertids is similar to that observed in *Teira dugesii*.

Teira perspicillata and *Teira andreanszkyi* also have very small clutch sizes, in spite of the fact that these are not insular species. Thus, *Teira perspicillata* lays two to three eggs (Doumergue, 1901; Richter, 1986; Schleich *et al.*, 1996) and *Teira andreanszkyi* lays one to three: Busack (1987) has detected two to three (mean = 2.1) while Rykena & Bischoff (1992) observed one to two (mean = 1.6) varying between 0.264 g and 0.340 g.

Our sample of *Teira dugesii* had similar clutch sizes to some insular *Podarcis* populations, but the average size of *T. dugesii* eggs was much larger. The large size of the eggs was also related to the large size of the hatchlings (Fig. 3), suggesting a tendency towards maximization of size at hatching (see also Sinervo, 1990; Frankenberg & Werner, 1992). In this process, the lizard of Madeira seems to have advanced much further than insular populations of *Podarcis*, excepting *P. lilfordi* (Table 5).

The high level of morphological polymorphism described in *Teira dugesii*, as well as the wide range of habitats that it occupies in the Madeiran Archipelago (Cook, 1979; Báez & Brown, 1997; Dellinger, 1997) may lead to some variability in reproductive traits. The present paper deals only with populations in the Funchal area, although it is probable that the general reproductive traits observed – such as long laying period, small clutch size and large eggs and hatchlings – occur in other populations of this archipelago.

The data of the present paper point towards two alternative explanations for the reproductive characteristics of *T. dugesii*. If the genus *Podarcis* is used as a basis for comparison, then the data provided by this work suggest that the reproductive traits of the studied population are an adaptation to insularity. On the other hand, if we accept as true the close phylogenetic relationship between the lizards of the island of Madeira and the genus *Teira* (*sensu* Mayer & Bischoff, 1996), and we compare its reproductive characteristics with the two species of *Teira* from North Africa, then the present results suggest that phylogenetic relationships rather than mere adaptations to insular conditions may account for the relatively small clutch size. However, as far as egg size is concerned, *Teira dugesii* could be viewed as an insular *Teira*.

TABLE 5. Reproductive traits of some continental and insular lacertid lizards (*Podarcis* spp. and *Teira* spp.). SVL: mean or range of female snout-vent length (mm); Clutch size: number of eggs [range (mean)]; Egg vol.: mean egg volume (mm³); Egg mass: mean egg mass (g).

Species	Location	SVL	Clutch size	Egg vol.	Egg mass	Reference
(A) CONTINENTAL						
<i>P. muralis</i>	Asturias	59.8	4-7(5.6)	-	0.27	Braña <i>et al.</i> (1991)
<i>P. muralis</i>	Basque Country	60.0	3-7(4.9)	-	0.28	Braña <i>et al.</i> (1991)
<i>P. bocagei</i>	Galicia	53.3	2-7(4.1)	236	0.26	Galán (1997)
<i>P. bocagei</i>	Asturias	55.4	3-4(3.3)	-	0.26	Braña <i>et al.</i> (1991)
<i>P. hispanica</i>	Asturias	51.8	1-3(2.3)	-	0.30	Braña <i>et al.</i> (1991)
<i>P. hispanica</i>	Salamanca	61.3	(3.6)	-	0.34	Castilla & Bauwens (2000a)
<i>T. perspicillata</i>	Morocco	50.6	-	283	-	Schleich <i>et al.</i> (1996)
<i>T. perspicillata</i>	Morocco	59.8	2-3	-	-	Richter (1986)
<i>T. perspicillata</i>	-	-	-	351	0.38	Bosch & Bout (1998)
<i>T. andreanszkyi</i>	Morocco	40-48	1-2(1.6)	256	0.30	Rykena & Bischoff (1992)
<i>T. andreanszkyi</i>	Morocco	44-53	2-3(2.1)	-	-	Busack (1987)
<i>T. andreanszkyi</i>	-	-	-	276	0.31	Bosch & Bout (1998)
(B) INSULAR						
<i>P. carbonelli berlengensis</i>	Berlenga	57.0	1-4(2.0)	389	0.43	Vicente (1989)
<i>P. atrata</i>	Columbretes	63.1	1-5(2.8)	346	0.37	Castilla & Bauwens (2000a)
<i>P. pityusensis</i>	Ibiza	57.5	1-4(2.3)	394	-	Carretero <i>et al.</i> (1995)
<i>P. lilfordi</i>	Cabrera	61.9	2-4(2.5)	550	0.63	Castilla & Bauwens (2000b)
<i>T. dugesii</i>	Madeira	60.8	2-5(2.4)	552	0.66	This work

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REFERENCES

- Arnold, E. N. & Burton, J. A. (1978). *Guía de campo de los reptiles y anfibios de España y Europa*. Barcelona: Ed. Omega.
- Báez, M. & Brown, R. P. (1997). Testing multivariate patterns of within-island differentiation in *Podarcis dugesii* from Madeira. *J. Evol. Biol.* **10**, 575-587.
- Bauwens, D. & Díaz-Uriarte, R. (1997). Covariation of life-history traits in lacertid lizards: a comparative study. *Am. Nat.* **149**, 91-111.
- Beyhl, F. E. (1990). Observations on the flower-visiting lizards of the island of Madeira, Portugal (Reptilia: Sauria: Lacertidae). *Courier Forschung-Institut Senckenberg* **129**, 153-158.
- Bischoff, W., Osenegg, K. & Mayer, W. (1989). Untersuchungen zur subspezifischen Gliederung der Madeira-Mauereidechse, *Podarcis dugesii* (Milne-Edwards, 1829). *Salamandra* **25**, 237-259.
- Böhme, W. & Corti, C. (1993). Zoogeography of the lacertid lizards of the western Mediterranean basin. In *Lacertids of the Mediterranean region*, 17-33. Valakos, E. D., Böhme, W., Pérez-Mellado, V. & Maragou, P. J. (Eds). Athens, Bon & Alicante.
- Bosch, H. A. J. in den & Bout, R. G. (1998). Relationships between maternal size, egg size, clutch size, and hatchling size in European lacertid lizards. *J. Herpetol.* **32**, 410-417.
- Braña, F., Bea, A. & Arrayago, M. J. (1991). Egg retention in lacertid lizards: relationships with reproductive ecology and the evolution of viviparity. *Herpetologica* **47**, 218-226.
- Bruno, S. (1986). *Guida a tartarughe e sauri d'Italia*. Firenze: Giunti.
- Busack, S. D. (1987). Notes on the biology of *Lacerta andreanszkyi* (Reptilia: Lacertidae). *Amphibia-Reptilia* **8**, 231-236.
- Carballeira, A., Devesa, C., Retuerto, R., Santillán, E. & Uceda, F. (1983). *Bioclimatología de Galicia*. La Coruña: Ed. Fundación Pedro Barrié de la Maza.
- Carretero, M. A., Llorente, G., Santos, X. & Montori, A. (1995). Características reproductoras de una población introducida de *Podarcis pityusensis*. *Rev. Esp. Herp.* **9**, 93-102.
- Castilla, A. M. & Bauwens, D. (2000a). Reproductive characteristics of the lacertid lizard *Podarcis atrata*. *Copeia* **2000**, 748-756.
- Castilla, A. M. & Bauwens, D. (2000b). Reproductive characteristics of the island lacertid lizard *Podarcis lilfordi*. *J. Herpetol.* **34**, 390-396.
- Cook, L. M. (1979). Variation in the Madeiran lizard *Lacerta dugesii*. *J. Zool., Lond.* **187**, 327-340.
- Crisp, M., Cook, L. M. & Hereward, F. V. (1979). Color and heat balance in the lizard *Lacerta dugesii*. *Copeia* **1979**, 250-258.
- Davenport, J. & Dellinger, T. (1995). Melanism and foraging behaviour in an intertidal population of the Madeiran Lizard *Podarcis (=Lacerta) dugesii* (Milne-Edwards, 1829). *Herpetol. J.* **5**, 200-203.
- Dellinger, T. (1997). *Podarcis dugesii* (Milne-Edwards, 1829). Lagartija de Madeira, Lagartixa da Madeira. In *Distribución y biogeografía de los Anfibios y Reptiles en España y Portugal.*, 415-417. Pleguezuelos, J. M. (Ed). Monografías de Herpetología, nº 3. Granada: Editorial Universidad de Granada & A. H. E.
- Doumergue, F. (1901). *Essai sur la faune erpétologique de l'Oranie*. Oran: Imp. Typogr. Fouque.
- Elvers, I. (1977). Flower-visiting lizards on Madeira. *Botaniska Notiser* **130**, 231-234.
- Elvers, I. (1978). The Madeiran lizard-flower connection observed in a natural habitat. *Botaniska Notiser* **131**, 159-160.
- Frankenberg, E. & Werner, Y. L. (1992). Egg, clutch and maternal sizes in lizards: intra- and interspecific relations in near-eastern Agamidae and Lacertidae. *Herpetol. J.* **2**, 7-18.
- Galán, P. (1997). Reproductive ecology of the lacertid lizard *Podarcis bocagei*. *Ecography* **20**, 197-209.
- Harris, D. J. & Arnold, E. N. (1999). Relationships of wall lizards, *Podarcis* (Reptilia: Lacertidae) based on mitochondrial DNA sequences. *Copeia* **1999**, 749-754.
- Malkmus, R. (1995). *Die Amphibien und Reptilien Portugals, Madeiras und der Azoren: Verbreitung, Ökologie, Schutz*. Magdeburg: Westarp Wissenschaften.
- Mayer, W. & Bischoff, W. (1996). Beiträge zur taxonomischen Revision der Gattung *Lacerta* (Reptilia: Lacertidae) Teil 1: *Zootoca*, *Omanosaura*, *Timon* und *Teira* als eigenständige Gattungen. *Salamandra* **32**, 163-170.
- Oliverio, M., Bologna, M. A. & Mariottini, P. (2000). Molecular biogeography of the Mediterranean lizards *Podarcis* Wagler, 1830 and *Teira* Gray, 1838 (Reptilia, Lacertidae). *J. Biogeogr.* **27**, 1403-1420.
- Richter, K. (1980). *Lacerta dugesii* Milne-Edwards, 1829 und *Lacerta perspicillata* Dumeril et Bibron, 1839 gehören zur Gattung *Podarcis* Wagler, Subgenus *Teira* Gray, 1838. (Reptilia, Lacertidae). *Zool. Abh. Mus. Tierk. Dresden* **36**, 1-9.
- Richter, K. (1986). *Podarcis dugesii* (Milne-Edwards, 1829) - Madeira Mauereidechse. In *Handbuch der Reptilien und Amphibien Europas*, Band 2, Echsen (Sauria) III: *Podarcis*, 388-398. Böhme, W. (Ed). Wiesbaden: Aula Verlag.
- Rykena, S. & Bischoff, W. (1992). On reproductive biology of the High Atlas Mountain lizard *Lacerta andreanskyi* Werner, 1929. In *Proc. Sixth Ord. Gen. Meet. S. E. H.*, 399-402, Korsós, Z. & Kiss, I. (Eds). Budapest.

- Sadek, R. A. (1981). The diet of the Madeiran lizard *Lacerta dugesii*. *Zool. J. Linn. Soc.* **73**, 313-341.
- Sá-Sousa, P. (1995). The introduced Madeiran lizard, *Lacerta (Teira) dugesii* in Lisbon. *Amphibia-Reptilia* **16**, 211-214.
- Schleich, H. H., Kästle, W. & Kabisch, K. (1996). *Amphibians and Reptiles of North Africa*. Koenigstein: Koeltz Scientific Books.
- Sinervo, B. (1990). The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effects on offspring performance. *Evolution* **44**, 279-294.
- Sinervo, B. & Licht, P. (1991). Proximate constraints on the evolution of egg size, number, and total clutch mass in lizards. *Science* **252**, 1300-1302.
- Vicente, L. A. (1989). *Sobre a história natural dos répteis da ilha Berlenga a síndrome de insularidade*. PhD Thesis. University of Lisbon.
- Vitt, L. J. & Congdon, J. D. (1978). Body shape, reproductive effort and relative clutch mass in lizards: resolution of a paradox. *Am. Nat.* **112**, 595-608.
- Vitt, L. J. & Price, H. J. (1982). Ecological and evolutionary determinants of relative clutch mass in lizards. *Herpetologica* **38**, 237-255.

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