

# Non-synergistic sexual and geographical morphological variation in the lacertid lizard *Psammodromus algirus* (Linnaeus, 1758) from North Africa

Farouk Khelifaoui<sup>1,\*</sup>, Idriss Bouam<sup>2</sup>, Messaoud Saoudi<sup>2</sup>, Oussama Saadi<sup>3</sup>, and Larbi Tahar-Chaouch<sup>4,5</sup>

**Abstract.** Broadly distributed lizard species may exhibit significant variation in the direction and magnitude of morphological dimorphism. The Algerian *Psammodromus*, *Psammodromus algirus*, is a common and widely distributed lacertid lizard in the Western Mediterranean region and research on sexual and geographical morphological variation in this species is uneven across clades, with the North African populations being overlooked. In this study we investigated the sexual and geographical dimorphism in two populations of *P. algirus* from Algeria. Although no morphological variation in SVL was detected in our study, we observed that males had larger heads and longer hind limbs than females. Additionally, the two populations differed in terms of pileus width, forelimb length, and hind limb fourth toe length, regardless of sex. We discuss the potential reasons for these observed patterns in relation to selective pressures, such as predation, competition, or sexual selection. The findings of this study suggest an intraspecific stability in morphological patterns across the geographic range of the species and emphasize the need for further research to unravel the underlying mechanisms responsible for the observed patterns of sexual and geographical morphological variations.

**Keywords.** Algeria, Mediterranean, morphology, Sauria, sexual dimorphism

## Introduction

Sexual dimorphism refers to the differences in physical characteristics between males and females of a given species. These differences may be observed in multiple phenotypic traits, including body size, which is referred to as sexual size dimorphism (hereafter SSD) (Mori et al., 2022). SSD has been widely documented in various animal taxa, including lizards (Braña, 1996; Cox et al., 2003). Interestingly, sexual dimorphism in lizards can exhibit significant variation in direction and magnitude within the same species. This is particularly evident in species with wide geographical ranges,

where dimorphic traits may display strong phenotypic plasticity and varying patterns of sexual dimorphism (Cruz-Elizalde et al., 2020; Glavaš et al., 2020; Muraro et al., 2022). Such variation makes lizards ideal models for investigating the extent and nature of sexual dimorphism across different populations.

The Algerian *Psammodromus*, *Psammodromus algirus* (Linnaeus, 1758), is a medium-sized lacertid lizard with a Western Mediterranean chorotype; it is found throughout the Iberian Peninsula, along the Mediterranean coast of France, on Conigli Islet (Sicily, Italy), and in North Africa, ranging continuously from southern Morocco to the northern half of Tunisia (Uetz et al., 2022). It is pervasively found across its range and occurs in a broad array of habitat types (e.g., agricultural lands, coastal sandy areas, open forests, maquis) and at varying elevations from sea level up to 2600 m (Salvador, 2014; Martínez et al., 2019). Although six subspecies were previously recognized along the species' wide distribution, primarily based on coloration differences, these are now typically regarded as morphotypes (de Faria, 2019). Phylogenetic analyses revealed that the species consists of three distinct clades, namely the African, the Iberian Northwestern, and the Iberian Southwestern clades (Verdú-Ricoy et al., 2010; Mendes et al., 2017, Faria and Harris, 2020).

<sup>1</sup> Department of Biology, Faculty of Sciences, Badji Mokhtar Annaba University, 23005 Sidi Amar, Annaba, Algeria.

<sup>2</sup> Department of Ecology and Environment, Faculty of Natural and Life Sciences, University of Batna 2, 05078 Fesdis, Batna, Algeria.

<sup>3</sup> Department of Biology, Faculty of Natural and Life Sciences, Chadli Bendjedid University, 36000 El-Tarf, El-Tarf, Algeria.

<sup>4</sup> Department of Biology, Faculty of Natural and Life Sciences, Ibn Khaldoun University, 14000 Tiaret, Tiaret, Algeria.

<sup>5</sup> Forest Conservation of Batna Province, 05000 Batna, Algeria.

\* Corresponding author. E-mail: farouk.khelifaoui@yahoo.fr

Despite the evident phylogeographic structure in *P. algirus* and being one of the most commonly encountered reptiles across much of its range, knowledge about intraspecific morphological variation in this species is currently uneven across clades and geographical regions. Studies were exclusively conducted in the Iberian Peninsula (Iraeta et al., 2011; Zamora-Camacho et al., 2014; Salvador, 2015), while North African populations remained unstudied. However, significant intraspecific morphological divergence between Iberian and North African lineages in other lacertid species (e.g., wall lizards, genus *Podarcis*) has been substantiated (Kaliontzopoulou et al., 2012), highlighting the need to explore the potential morphological variation in the Algerian *Psammotromus* across its North African range.

In view of the above, we undertook a heuristic study to analyse and compare SSD in two populations of *P. algirus* from Algeria. Our study aims to assess whether there is variability in SSD at a regional scale in this widely distributed lacertid lizard. Additionally, the obtained results are discussed in the context of the previously published studies on Iberian clades.

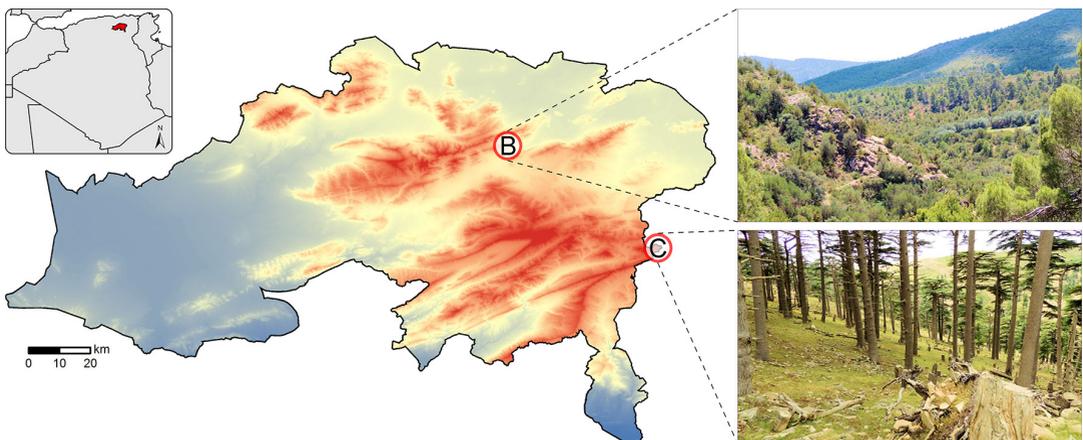
## Materials and Methods

**Study area.** This study was carried out at two locations in Batna Province, northeastern Algeria (Fig. 1). The first site, hereafter referred to as Belezma, is situated within the Belezma Biosphere Reserve at an elevation of 1070 m (35.61°N, 6.20°E). It is a closed maquis type forest, characterized by dense thickets of evergreen shrubs and trees, mainly Aleppo Pine (*Pinus halepensis*), Mastic Trees (*Pistacia lentiscus*), Rosemary (*Rosmarinus officinalis*), and Holly Oak (*Quercus ilex*), and dense

understorey vegetation (Bouam et al., 2016). The second site, hereafter referred to as Chélia, is nested within the Aurès Massif on Mount Chélia, approximately 51 km southeast of Belezma (35.31°N, 6.62°E). It is located at a higher elevation of 2090 m and is an open forest primarily consisting of pure stands of Atlas Cedars (*Cedrus atlantica*) and sparse mid- and understorey vegetation (Saoudi et al., 2017). Climate data for the two sites were retrieved from WorldClim v2.1 at a spatial resolution of 30 arc-seconds (Fick and Hijmans, 2017). Based on these data, we derived the Emberger Quotient for each site (Daget, 1977), which indicates that Belezma has an inferior semi-arid climate while Chélia is characterized by a sub-humid climate.

**Sampling protocol.** Sampling was performed during favourable meteorological conditions (i.e., warm sunny weather) in spring and summer, by walking slowly in a single direction along random transects with relatively homogeneous vegetation. The transects were spaced more than 100 m apart, and each was surveyed only once to avoid sampling the same lizards twice. We noosed or hand-captured adult *P. algirus* (SVL > 55 mm, the size for sexual maturity in both sexes; Carretero, 2002). Sex was determined by visual examination of colour patterns and femoral pore morphology following Díaz et al. (1994) and Carretero (2002). Overall, 61 adult specimens were examined (eight males and 11 females from Belezma, 16 males and 26 females from Chélia). The relatively low sample size from Belezma was due to the dense vegetation structure and the anti-predatory escape tactics of *P. algirus* in this habitat (Martín and López, 1995).

**Morphometrics.** We measured seven morphological traits on each lizard to the nearest 0.01 mm using a



**Figure 1.** (a) Map of the sampling sites (red circles) for *Psammotromus algirus* in Batna Province, northeastern Algeria, with sample habitats views of (B) Belezma and (C) Chélia.

digital calliper. The traits included SVL, pileus length (PL), pileus width (PW), head height (HH), hind limb length (HLL, measured from the end of the most distal toe to the point of connection with the body), forelimb length (FLL, measured from the tip of the most distal toe to the shoulder joint), and the length of the fourth hind limb toe (HLT, measured from the end of the toe to the point where it connects to the limb). Measurements were taken on the right side of the specimens for bilateral traits. Following measurements, lizards were released at their initial capture locations.

**Data analyses.** A Principal Component Analysis (PCA) was performed on all morphological variables to explore patterns of morphological variation between sexes and sites. Prior to performing PCA, all measurements were scaled to unit variance to account for substantial differences in mean and standard deviation among them (Groth et al. 2013). Only components with eigenvalues  $> 1.0$  were retained, following the Guttman-Kaiser criterion (Yeomans and Golder, 1982). Subsequently, we investigated the variation of each trait individually between sexes and sites, while also considering interaction terms. The variation in SVL was analysed using a two-way analysis of variance (ANOVA) while a two-way analysis of covariance (ANCOVA) was used for the other morphological traits to control for the effect of body length by including SVL as a covariate. HLL and HLT were  $\log_{10}$ -transformed prior to analysis to fulfil the assumptions of parametric tests. All statistical analyses were performed in the RStudio interface (v2023.3.0.386) (Posit Team, 2023) in R software v4.2.3 (R Core Team, 2023).

## Results

The results of the PCA indicated a relatively significant overlap in morphospace between males and females within each site, while showing less overlap between populations (Fig. 2A). All head traits (PL, PW, HH) together with HLL contributed significantly to PC1, which accounted for 65.18% of the variance, with males being the larger sex. PC2 explained 16.70% of the variance, and HLT was the most prominent loading of that component, suggesting this trait may differ between the two sites. SVL did not exhibit high contribution values (Fig. 2B, Table 1), suggesting that SVL is not a relevant variable in sex- or geography-based morphological variation in *P. algirus*. These findings are reflected in the results of the two-way ANOVA and ANCOVA (Table 2). More specifically, the two-way ANOVA showed no evidence of SSD in

SVL, as there were no significant differences between males and females nor between populations. However, the two-way ANCOVA indicated a significant male-biased SSD in all head dimensions (PL, PW, HH) and HLL. Additionally, the effect of locality was significant for PW, FLL, and HLT, but PW and FLL explained less of the variation than HLT (Table 1). Populations from Belezma had greater PW and FLL, while populations from Chélia had greater HLT. No significant effect of the interaction between sex and site was detected for any of the morphological traits.

## Discussion

The present study is one of the first to address geographical and sexual dimorphism patterns in *P. algirus* in North Africa. Results from regional scale studies, such as the one presented here, are crucial for understanding spatial patterns in morphological variation of widespread lizard species (Muraro et al., 2022). Our study revealed no geographical or sexual dimorphism in SVL, which is consistent with the findings of Carretero and Llorente (1997) and Iraeta et al. (2011) from different regions of Spain. Interestingly, *P. algirus* does not adhere to either the female-biased sexual dimorphism in SVL reported in three of its congeners (namely *P. hispanicus*, *P. edwardsianus*, *P. occidentalis*; San-Jose et al., 2012), nor to the male-biased sexual dimorphism in SVL that common among lacertid lizards (Cox et al., 2007). A detailed study of pre- and post-maturational processes in *P. algirus* would be useful for understanding the lack of SSD in SVL in this species (Stamps, 1993).

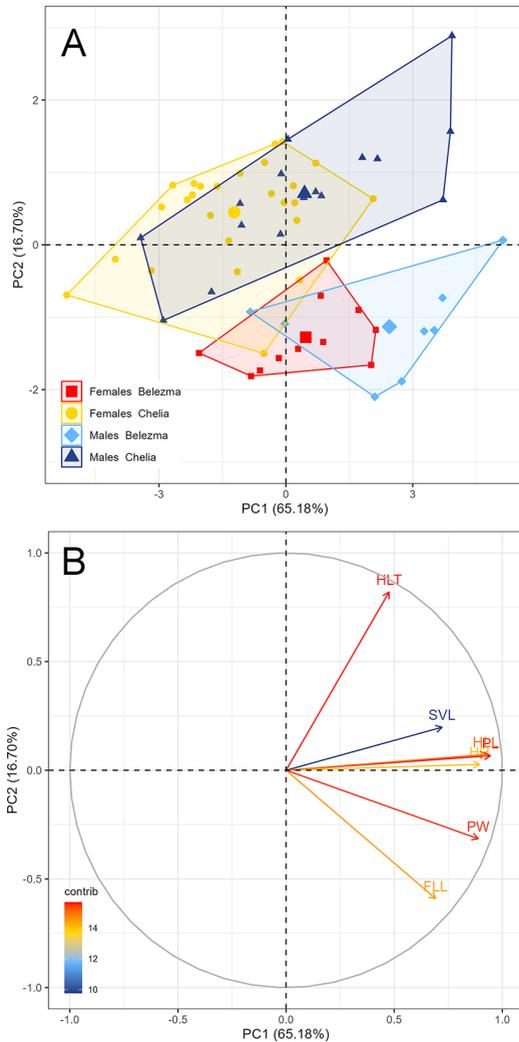
Our results showed a similar trend to previous studies, in that *P. algirus* males had larger head dimensions than females (Iraeta et al., 2011; Zamora-Camacho et al., 2014). Male lacertids typically have relatively larger heads than females (Braña, 1996; Kaliontzopoulou et al., 2008; Liang et al., 2022). This has been interpreted as a result of sexual selection providing benefits in intrasexual duels, through enhanced fighting ability, and/or intersexual encounters, through improved grasping ability (e.g., Gvoždík and Van Damme, 2003; Huyghe et al., 2005). Alternatively, other studies have suggested that head size differences could contribute to preventing intersexual competition when feeding (e.g., Herrel et al., 1999; Verwaijen et al., 2002). Salvador and Veiga (2001) demonstrated that male *P. algirus* engaged in intense intrasexual competition to access larger females, and that morphological traits, including larger heads, increased pairing success.

This fact, coupled with the absence of any observed sex differences in the dietary habits of *P. algirus* (Moreno-Rueda et al., 2018), could suggest that sexual selection, rather than trophic segregation, may shape the evolution of head size in male *P. algirus*. While Iraeta et al. (2011) did not observe interpopulational variability in head dimensions in this species, our study found that individuals from Belezma had wider heads than those from Chélia. Vanhooydonck and Van

Damme (1999) and Kaliontzopoulou et al. (2010) provided empirical evidence for an association between head shape and the use of structurally different habitats both at the inter- and intraspecific levels in lacertid lizards. This has been explained by the hypothesis of mechanical constraints related to refuge use (Arnold, 1973). However, behavioural studies are necessary to interpret the functional significance of the observed patterns in *P. algirus*.

Our findings support the previously reported SSD in *P. algirus*, where males have longer hind limbs than females (Iraeta et al., 2011; Zamora-Camacho et al., 2014). In *P. algirus*, there seems to be a consistent pattern of positive association between longer hind limbs and functional implications for locomotion. While Zamora-Camacho et al. (2014) found a positive relationship between hind limb length and sprint speed, Martín and López (2001) and Iraeta et al. (2011) did not find such a relationship. Instead, Iraeta et al. (2011) proposed an alternative perspective, suggesting an association with endurance or manoeuvrability rather than sprint speed. Male *P. algirus* occupy larger home ranges than females, engage in prolonged periods of territorial patrolling and courtship behaviours (Díaz, 1993; Salvador et al., 1995), and display brighter colouration during reproductive activity (Carretero, 2002). However, this increased activity and conspicuousness also make males more vulnerable to predation, which may necessitate higher sprint speed, endurance, or manoeuvrability.

The absence of statistically significant SSD in forelimb length in our data contrasts with the findings of Zamora-Camacho et al. (2014), who reported longer forelimbs in males. This disparity could be due to methodological differences, such as discrepancies in measurement



**Figure 2.** (A) Ordination plot of the first two principal components for an analysis of adult male and female *Psammodromus algirus* from two populations in northeastern Algeria. Polygons with shading show the convex hull of males and females in each of the two sites. (B) Contribution in percentage of each morphological variable to the principal component analysis; blue colour indicates low contribution while red colour indicates high contribution.

**Table 1.** Factor loadings (eigenvectors), explained variance, and eigenvalues for the first two axes of a Principal Component Analysis (PCA) of adult male and female *Psammodromus algirus* of two populations in northeastern Algeria.

Trait	PC1	PC2
SVL	0.72	0.19
PL	0.94	0.06
PW	0.88	-0.31
HH	0.89	0.02
HLL	0.92	0.07
FLL	0.69	-0.59
HLT	0.47	0.81
Variance (%)	65.18	16.63
Eigenvalue	4.56	1.16

**Table 2.** Mean values ± standard deviation and range of the morphological traits (measurements in mm) for adult male and female *Psammodromus algirus* of two populations in northeastern Algeria (Belezma and Chélia), and ANOVA (for SVL) or ANCOVA (rest of the morphological traits) results for the factors of sex, site, and their interaction. Significant differences are indicated by an asterisk (\*).

Trait	Belezma		Chélia		AN(C)OVA (sex, site, sex×site)	
	Males (n = 8)	Females (n = 11)	Males (n = 16)	Females (n = 26)	F <sub>DFn,DFd</sub>	p-value
SVL	70.69 ± 4.67	70.94 ± 7.44	68.63 ± 7.19	67.27 ± 5.81	0.255 <sub>1,57</sub>	0.616
	(64.86–76.96)	(57.11–84.66)	(55.24–83.28)	(55.83–78.29)	2.906 <sub>1,57</sub>	0.094
PL	18.13 ± 1.12	16.15 ± 0.98	16.83 ± 1.61	15.57 ± 1.25	0.201 <sub>1,57</sub>	0.655
	(16.39–19.71)	(14.64–18.02)	(14.27–19.23)	(13.20–18.69)	28.866 <sub>1,56</sub>	< 0.001*
PW	10.48 ± 1.02	9.45 ± 0.63	8.85 ± 0.85	8.22 ± 0.70	2.886 <sub>1,56</sub>	0.095
	(8.68–11.78)	(8.47–10.46)	(7.13–10.40)	(7.00–9.43)	2.902 <sub>1,56</sub>	0.094
HH	9.40 ± 0.90	8.60 ± 0.96	8.85 ± 1.07	7.94 ± 0.95	16.634 <sub>1,56</sub>	< 0.001*
	(8.09–10.56)	(7.45–10.10)	(6.94–10.74)	(5.95–9.85)	41.856 <sub>1,56</sub>	< 0.001*
HLL	40.23 ± 4.28	37.04 ± 1.86	38.00 ± 3.37	35.00 ± 2.29	1.997 <sub>1,56</sub>	0.163
	(31.73–46.06)	(33.91–39.56)	(32.25–43.52)	(28.58–38.83)	15.065 <sub>1,56</sub>	< 0.001*
FLL	23.37 ± 1.63	22.22 ± 1.59	18.79 ± 1.45	17.91 ± 1.74	2.266 <sub>1,56</sub>	0.138
	(20.52–25.33)	(19.78–24.94)	(16.82–21.65)	(13.48–20.97)	0.010 <sub>1,56</sub>	0.585
HLT	20.26 ± 1.83	19.04 ± 0.83	21.76 ± 2.17	20.70 ± 1.47	19.655 <sub>1,56</sub>	< 0.001*
	(17.90–23.48)	(17.56–20.27)	(18.29–26.37)	(17.65–23.77)	4.003 <sub>1,56</sub>	0.05
				0.185 <sub>1,56</sub>	0.669	
				4.885 <sub>1,56</sub>	0.031	
				89.419 <sub>1,56</sub>	< 0.001*	
				0.200 <sub>1,56</sub>	0.657	
				7.144 <sub>1,56</sub>	0.01	
				26.283 <sub>1,56</sub>	< 0.001*	
				0.302 <sub>1,56</sub>	0.585	

accuracy between our study (0.01 mm) and that of Zamora-Camacho et al. (2014) (0.5 mm). Additionally, while we controlled for statistical difference in forelimb length based on SVL, Zamora-Camacho et al. (2014) used occiput-vent length.

Interestingly, we observed that individuals from Chélia had significantly longer hind limb fourth toes and shorter forelimbs than those from Belezma. Although information on lacertids is lacking, toe length has been positively correlated with stride length in *Anolis* lizards (Irschick, 2002). Martin and Avery (1998) demonstrated that *P. algirus* increases speed by increasing the stride length of the hind limbs. Our results make sense in this context, as lacertids from open habitats should run faster and tend to have shorter forelimbs as the latter may prevent interference with the locomotor cycles of the hind limbs (Vanhooydonck and Van Damme, 1999). Future studies on *P. algirus* may benefit from including data on hind limb toe length,

particularly in populations from different habitats, as it may reveal interesting relationships with regard to locomotor performance and adaptation to varied environmental conditions.

Because our study was limited by a relatively small population and sample size, particularly in Belezma, the results should be treated as indicative rather than conclusive. Nevertheless, our findings corroborate those of previous studies on Iberian populations (Carretero and Llorente, 1997; Iraeta et al., 2011; Zamora-Camacho et al., 2014), which lend further weight to the validity of our study. Our findings imply an apparent intraspecific stability in morphological patterns across the geographic range and the different clades of the species. Furthermore, our study highlights several intriguing questions that warrant further investigation to better understand the underlying functional and evolutionary implications of this variation in this widespread lacertid species.

**Acknowledgements.** We would like to thank Abbas Bouteghriout and Chemseddine Benbouda for their tremendous help with the fieldwork. Thanks are also due to Arnaud Badiane and three anonymous reviewers for their insightful and constructive feedback, which contributed to enhancing the quality of this work.

## References

- Arnold, E.N. (1973): Relationships of the Palearctic lizards assigned to the genera *Lacerta*, *Algyroides* and *Psammadromus* (Reptilia: Lacertidae). *Bulletin of the British Museum (Natural History) Zoology* **25**: 289–366.
- Bouam, I., Necer, A., Saoudi, M., Tahar-Chaouch, L., Khelifaoui, F. (2016): Diet and daily activity patterns of the lacertid lizard *Psammadromus algirus* (Sauria: Lacertidae) in a semi-arid Mediterranean region. *Zoology and Ecology* **26**: 244–252.
- Braña, F. (1996): Sexual dimorphism in lacertid lizards: male head increase vs female abdomen increase? *Oikos* **75**: 511–523.
- Carretero, M.A. (2002): Sources of colour pattern variation in Mediterranean *Psammadromus algirus*. *Netherlands Journal of Zoology* **52**: 43–60.
- Carretero, M.A., Llorente, G.A. (1997): Reproduction of *Psammadromus algirus* in coastal sandy areas of NE Spain. *Amphibia-Reptilia* **18**: 369–382.
- Cox, R.M., Butler, M.A., John-Alder, H.B. (2007): The evolution of sexual size dimorphism in reptiles. In: *Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism*, p. 38–49. Fairbairn, D.J., Blanckenhorn, W.U., Székely, T., Eds., New York, USA, Oxford University Press.
- Cox, R.M., Skelly, S.L., John-Alder, H.B. (2003): A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution* **57**: 1653–1669.
- Cruz-Elizalde, R., Ramírez-Bautista, A., Pacheco, L.F.R., Lozano, A., Rodríguez-Romero, F.D.J. (2020): Sexual dimorphism in size and shape among populations of the lizard *Sceloporus variabilis* (Squamata: Phrynosomatidae). *Zoology* **140**: 125781.
- Daget, P. (1977): Le bioclimat Méditerranéen: analyse des formes climatiques par le système d'Emberger [The Mediterranean bioclimate: analysis of climatic forms by the Emberger system]. *Vegetatio* **34**: 87–103.
- de Faria, J.F.P. (2019): Unravelling evolutive histories from the Maghreb: two comprehensive studies on the lacertids *Podarcis vaucheri* and *Psammadromus algirus*. Unpublished MSc thesis, University of Porto, Porto, Portugal.
- Diaz, J.A. (1993): Breeding coloration, mating opportunities, activity, and survival in the lacertid lizard *Psammadromus algirus*. *Canadian Journal of Zoology* **71**: 1104–1110.
- Díaz, J.A., Alonso-Gómez, A.L., Delgado, M.J. (1994): Seasonal variation of gonadal development, sexual steroids, and lipid reserves in a population of the lizard *Psammadromus algirus*. *Journal of Herpetology* **28**: 199–205.
- Faria, J.F., Harris, D.J. (2020): Phylogeography of *Psammadromus algirus* (Linnaeus, 1758) in Morocco. *Herpetology Notes* **13**: 1055–1061.
- Fick, S.E., Hijmans, R.J. (2017): WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* **37**: 4302–4315.
- Glavaš, O.J., Počanić, P., Lovrić, V., Derežanin, L., Tadić, Z., Lisičić, D. (2020): Morphological and ecological divergence in two populations of European glass lizard, *Pseudopus apodus* (Squamata: Anguillidae). *Zoological Research* **41**: 172–181.
- Groth, D., Hartmann, S., Klie, S., Selbig, J. (2013): Principal Components Analysis. In: *Computational Toxicology. Methods in Molecular Biology*, p. 527–547. Reisfeld, B., Mayeno, A., Eds., Totowa, New Jersey, USA, Humana Press.
- Gvoždík, L., Van Damme, R. (2003): Evolutionary maintenance of sexual dimorphism in head size in the lizard *Zootoca vivipara*: a test of two hypotheses. *Journal of Zoology* **259**: 7–13.
- Herrel, A., Spithoven, L., Van Damme, R., De Vree, F. (1999): Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. *Functional Ecology* **13**: 289–297.
- Huyghe, K., Vanhooydonck, B., Scheers, H., Molina-Borja, M., Van Damme, R. (2005): Morphology, performance and fighting capacity in male lizards, *Gallotia galloti*. *Functional Ecology* **19**: 800–807.
- Iraeta, P., Monasterio, C., Salvador, A., Díaz, J.A. (2011): Sexual dimorphism and interpopulation differences in lizard hind limb length: locomotor performance or chemical signalling? *Biological Journal of the Linnean Society* **104**: 318–329.
- Irschick, D.J. (2002): Evolutionary approaches for studying functional morphology: examples from studies of performance capacity. *Integrative and Comparative Biology* **42**: 278–290.
- Kaliontzopoulou, A., Carretero, M.A., Llorente, G.A. (2008): Head shape allometry and proximate causes of head sexual dimorphism in *Podarcis* lizards: joining linear and geometric morphometrics. *Biological Journal of the Linnean Society* **93**: 111–124.
- Kaliontzopoulou, A., Carretero, M.A., Llorente, G.A. (2010): Intraspecific ecomorphological variation: linear and geometric morphometrics reveal habitat-related patterns within *Podarcis bocagei* wall lizards. *Journal of Evolutionary Biology* **23**: 1234–1244.
- Kaliontzopoulou, A., Carretero, M.A., Llorente, G.A. (2012): Morphology of the *Podarcis* wall lizards (Squamata: Lacertidae) from the Iberian Peninsula and North Africa: patterns of variation in a putative cryptic species complex. *Zoological Journal of the Linnean Society* **164**: 173–193.
- Liang, T., Wang, L., Shi, L. (2022): Sexual and natural selection interplay in sexual head shape dimorphism of two sympatric racerunners (Squamata: Lacertidae). *Frontiers in Ecology and Evolution* **10**: 1016885.
- Martin, J., Avery, R.A. (1998): Effects of tail loss on the movement patterns of the lizard, *Psammadromus algirus*. *Functional Ecology* **12**: 794–802.
- Martín, J., López, P. (1995): Influence of habitat structure on the escape tactics of the lizard *Psammadromus algirus*. *Canadian Journal of Zoology* **73**: 129–132.
- Martín, J., López, P. (2001): Hindlimb asymmetry reduces escape performance in the lizard *Psammadromus algirus*. *Physiological and Biochemical Zoology* **74**: 619–624.
- Martínez, M.M.G., Harris, D.J., Geniez, P., de Pous, P., Salvi, D. (2019): Amphibians and Reptiles of Morocco. Frankfurt am Main, Germany, Edition Chimaira.

- Mendes, J., Harris, D.J., Carranza, S., Salvi, D. (2017): Biogeographical crossroad across the Pillars of Hercules: evolutionary history of *Psammodromus* lizards in space and time. *Journal of Biogeography* **44**: 2877–2890.
- Moreno-Rueda, G., Melero, E., Reguera, S., Zamora-Camacho, F.J., Álvarez-Benito, I. (2018): Prey availability, prey selection, and trophic niche width in the lizard *Psammodromus algirus* along an elevational gradient. *Current Zoology* **64**: 603–613.
- Mori, E., Mazza, G., Lovari, S. (2022): Sexual dimorphism. In: *Encyclopedia of Animal Cognition and Behavior*, p. 6389–6395. Vonk, J., Shackelford, T.K., Eds., Switzerland, Springer Nature.
- Muraro, M., Sherpa, S., Barzaghi, B., Bombi, P., Borgatti, D., Di Canio, V., et al. (2022): Condition- and context-dependent variation of sexual dimorphism across lizard populations at different spatial scales. *Scientific Reports* **12**: 16969.
- Posit Team (2023): RStudio: Integrated Development Environment for R. Boston, Massachusetts, USA, Posit Software.
- R Core Team (2023): R: A language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing.
- Salvador, A. (2014): Fauna Ibérica, Volume 10, Reptiles. Madrid, Spain, Museo Nacional de Ciencias Naturales.
- Salvador, A. (2015): Lagartija colilarga – *Psammodromus algirus* (Linnaeus, 1758). In: *Enciclopedia Virtual de los Vertebrados Españoles*. Salvador, A., Marco, A., Eds., Madrid, Spain, Museo Nacional de Ciencias Naturales.
- Salvador, A., Martin, J., López, P. (1995): Tail loss reduces home range size and access to females in male lizards, *Psammodromus algirus*. *Behavioral Ecology* **6**: 382–387.
- Salvador, A., Veiga, J.P. (2001): Male traits and pairing success in the lizard *Psammodromus algirus*. *Herpetologica* **57**: 77–86.
- San-Jose, L.M., Gonzalez-Jimena, V., Fitze, P.S. (2012): Patterns of phenotypic variation reveal substantial differentiation in sexual dimorphism of three *Psammodromus* (Squamata, Lacertidae) species. *Contributions to Zoology* **81**: 181–197.
- Saoudi, M., Necer, A., Bouam, I., Khelifaoui, F., Saadi, O. (2017): Daily activity, biometry and diet of the North African ocellated lizard *Timon pater* in mount Chélia, north-eastern Algeria. *African Journal of Herpetology* **66**: 1–11.
- Stamps, J.A. (1993): Sexual size dimorphism in species with asymptotic growth after maturity. *Biological Journal of the Linnean Society* **50**: 123–145.
- Uetz, P., Freed, P., Aguilar, R., Hošek, J. (2022): The Reptile Database. Available at <http://www.reptile-database.org>. Accessed on 4 April 2023.
- Vanhooydonck, B., Van Damme, R. (1999): Evolutionary relationships between body shape and habitat use in lacertid lizards. *Evolutionary Ecology Research* **1**: 785–805.
- Verdú-Ricoy, J., Carranza, S., Salvador, A., Busack, S.D., Díaz, J.A. (2010): Phylogeography of *Psammodromus algirus* (Lacertidae) revisited: systematic implications. *Amphibia-Reptilia* **31**: 576–582.
- Verwajen, D., Van Damme, R., Herrel, A. (2002): Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. *Functional Ecology* **16**: 842–850.
- Yeomans, K.A., Golder, P.A. (1982): The Guttman-Kaiser criterion as a predictor of the number of common factors. *The Statistician* **31**: 221–229.
- Zamora-Camacho, F.J., Reguera, S., Rubiño-Hispán, M.V., Moreno-Rueda, G. (2014): Effects of limb length, body mass, gender, gravidity, and elevation on escape speed in the lizard *Psammodromus algirus*. *Evolutionary Biology* **41**: 509–517.