

Western Sand Racer – *Psammodromus occidentalis*
Fitze, González-Jimena, San-José, San Mauro y Zardoya, 2012

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Synonyms

Psammodromus edwardsii (Barbosa du Bocage, 1863, p. 333); *Psammodromus hispanicus* (López Seoane, 1877, p.352; Lataste, 1878, p. 694; Boscá, 1880, p. 273); *Psammodromus hispanicus hispanicus* (Mertens, 1925, p. 81 – 84; 1926, p. 155).

Common Names

Catalan: Sargantana occidental ibèrica; French: Psammodrome occidental; German: Westlicher Sandläufer; Portuguese: Lagartixa-do-mato occidental; Spanish: Lagartija occidental ibérica.

History of Nomenclature

Up until 2010, *P. occidentalis* had been classified as belonging to *P. hispanicus*. In 2010, this species was characterized by Fitze et al. (Fitze et al., 2010; San Jose Garcia et al., 2010) based on molecular, phenotypic, and ecological analyses (Fitze et al., 2011, 2012).

Type Locality

Terra typica is central Spain; Colmenar del Arroyo, Madrid (Fitze et al., 2012), where both the holotype and paratypes were captured. The holotype was deposited at the National Natural History Museum of Spain (MNCN-CSIC, Madrid) and the paratypes at MNCN-CSIC and at the British Natural History Museum (NHM, London) (Fitze et al., 2012).

Origin and Evolution

Psammodromus occidentalis belongs to the genus *Psammodromus*, the sister taxa of *Gallotia*. Both taxa form the subfamily Gallotiinae (Harris et al., 1998), which belongs to the family Lacertidae (Harris et al., 1998).

The *Psammodromus* genus consists of six species: *P. algirus* (Linnaeus, 1758), which is the oldest species (estimated split at 25 ± 0.27 Mya) (Carranza et al., 2006); *P. blanci* (Lataste, 1880) (estimated split at 20 ± 0.2 Mya) (Carranza et al., 2006); *P. microdactylus* (Boettger, 1881), whose phylogenetic relationship is unknown; *P. occidentalis* (Fitze et al., 2012) (estimated split at 8.3 Mya, range: 2.9 – 14.7); and *P. edwardsianus* (Dugès, 1829) and *P. hispanicus* (Fitzinger 1826), whose split is estimated at 4.8 Mya (1.5 – 8.7) (Fitze et al., 2011). The split between *P. occidentalis* and the ancestor of *P. edwardsianus* (Dugès, 1829) and *P. hispanicus* (Fitzinger 1826) dates back to the Miocene, during which a progressive uplift began to close the east of the Betic Straits, thereby forming the Guadalquivir basin (Early Messinian: 7.2 – 5.5 Mya). Phylogenetic relationships and the spatial distribution of molecular diversity suggest that a barrier between Málaga and the Guadalquivir River may have given rise to the divergence of *P. occidentalis* and the ancestor of *P. edwardsianus* and *P. hispanicus* (Fitze et al., 2011, 2012). *P. occidentalis* exhibits decreasing molecular diversity with increasing latitude (Fitze et al., 2011), indicating northward range expansion during Pleistocene glacial and interglacial periods (Fitze et al., 2011). No *P. occidentalis* populations consist of *P. hispanicus* or *P. edwardsianus*, suggesting that the mechanisms that gave rise to speciation continue to prevent population mixing and range expansion.

Description of the adult

Psammodromus occidentalis is a Lacertid of small body size. Compared with other species (*P. algirus*, *P. blanci*, *P. microdactylus*), its skull is relatively elevated and robust (Salvador, 1981) and pterygoid teeth are absent (Pérez-Mellado, 1998). Its dorsal coloration ranges from greyish to grey-brown to greenish, and it displays four dorsal longitudinal lines ranging in colour from cream to grey. The belly is generally white. Nuptial coloration is a conspicuous green. No supralabial scales are found below the subocular scale. *P. occidentalis* exhibits 4 superciliar

scales, 4 supraocular scales, 18.9 ± 0.3 (mean \pm se) gular scales (range: 15 – 23), 0.7 ± 0.2 (0 – 3) collar scales, 25.1 ± 0.4 (21 – 29) ventral scale rows, 11.2 ± 0.2 (8 – 13) femoral pores, and 2.0 ± 0.4 (0 – 5) ocelli (Fitze et al., 2011, 2012). Adults have a SVL of 48.31 ± 0.72 mm (38 – 58 mm) and a body mass of 1.866 ± 0.07 g (1.077 – 2.75 g) (Fitze et al., 2011). Other authors have reported similar values (Table 1).

Table 1. Average \pm se (or sd) snout-to-vent length (SVL) and body mass measured in different populations.

Locality	SVL (mm)	maximal SVL (mm)	Body mass (g)	reference
Salamanca	48.4	56		Bauwens and Díaz Uriarte (1997)
Salamanca	40.27 ± 1.05 se		1.43 ± 0.08 se	Bauwens et al. (1995)
Huelva	40.05 ± 5.5 sd		1.1 ± 1.1 sd	Mellado et al. (1975)

Hind limb and tail lengths of 15.75 ± 0.54 mm (mean \pm se) and of 64.82 ± 2.38 mm, respectively, have been recorded in Salamanca (Bauwens and Díaz Uriarte, 1997). In Huelva, head width is on average 5.54 mm \pm 4.0 sd and head length is 9.8 mm \pm 1.4 sd (Mellado et al., 1975). In the Central System, *P. occidentalis* has a body condition of 0.05 g/mm, with 19.5 ± 2.12 (mean \pm sd) throat scales (range: 18 – 21), 31.6 ± 1.43 (30 – 34) dorsal scales, 26 ventral scales, 10.83 ± 0.83 (10 – 12) femoral pores, and 21.18 ± 1.47 (19 – 24) subdigital lamellae below the fourth toe of the right posterior foot (Pérez-Mellado, 1981). While the estimates from Salamanca and Huelva are based on a sample size of >30, those of the Central System are based on very small sample sizes, and caution is thus advised when interpreting the data.

Identification

P. occidentalis can be easily distinguished from *Psammotromus edwardsianus* by the absence of a supralabial scale below the subocular scale. In comparison with *Psammotromus edwardsianus* and *Psammotromus hispanicus*, *Psammotromus occidentalis* has a more pointed snout. The number of femoral pores and throat scales lies between that of *Psammotromus edwardsianus* and *Psammotromus hispanicus*. *P. occidentalis* has more ocelli than *Psammotromus hispanicus*, and a more pointed head and more extensive nuptial coloration than *Psammotromus edwardsianus* (Fitze et al., 2011).

Sexual dimorphism

Little research has been conducted on sexual dimorphism and the few published studies suggest that males are generally smaller than females. In Huelva, (Lepe and El Asperillo, Doñana) adult males are smaller (SVL = 46.2 ± 6.0 mm (mean \pm sd), range: 32.5 – 51.4 mm) than adult females (47.8 ± 4.7 mm, 36.6 – 53.7 mm) (Pérez-Quintero, 1996). A similar pattern is observed in the eastern Central System (SVL males: 42.7 ± 1.7 mm, 41.2 – 44.7 mm; SVL females: 46.5 ± 1.6 mm, 45 – 48.6 mm) (Pérez-Mellado, 1981). Males have lower body mass than females (males: 1.97 ± 0.15 g, 1.75 – 2.1 g; females: 2.13 ± 0.3 g, 1.8 – 2.5 g) (Pérez-Mellado, 1981).

Femoral pore secretions

No information exists regarding femoral pore secretions.

Karyotype

As the karyotype for *Psammotromus sp.* has been described without additional specifications, it is unclear whether this description pertains to *P. occidentalis*, *P. edwardsianus*, or *P.*

hispanicus. The karyotype may consist of $2n = 38$ chromosomes, 2 of which are microchromosomes (Matthey, 1939), 2 metacentric, and the remaining 34 acrocentric (Calera González and Cano Pérez, 1979).

Description of the juvenile

In Salamanca the first hatching juveniles appear in July and the majority of the juveniles hatch in August (Pascual Gonzalez and Perez Mellado, 1989; Pollo and Pérez Mellado, 1990), while in Huelva the first juveniles hatch in mid June (Pérez-Quintero, 1995b, 1996) and peak hatching is as well in July / August (Pérez-Quintero, 1996). In Huelva, the last juveniles hatch in September (Pérez-Quintero, 1996) and Salamanca in in October. In both months hatching is generally rare (Pascual Gonzalez and Perez Mellado, 1989). At hatching juveniles have on average a body size (SVL) of 22.9 mm and a body mass of 0.31 g (Bauwens and Diaz Uriarte, 1997), while other authors reported 23 – 24 mm for SVL and 55 mm for total length (Pascual Gonzalez and Perez Mellado, 1989). These measures are in line with those reported from captivity (SVL: $22.9 \text{ mm} \pm 1.2 \text{ sd}$ (range: 19 – 23 mm); body mass: $0.31 \text{ g} \pm 0.06 \text{ sd}$ (0.25 – 0.43 g); tail length: $35.2 \text{ mm} \pm 3.2 \text{ sd}$ (30 – 42 mm)) (in den Bosch, 1986). At hatching no prominent sex differences are visible (in den Bosch, 1986). Juveniles grow in size mainly in August and September when temperatures are optimal (Pascual Gonzalez and Perez Mellado, 1989) and no important sex differences in growth exist (Pascual Gonzalez and Perez Mellado, 1989). Juveniles may reach adult size already before the start of the winter (Pascual Gonzalez and Perez Mellado, 1989; Pollo Mateos and Perez-Mellado, 1989). There exists variation in the proportion of juveniles that attain adult size before winter, probably as a consequence of variance in climatic parameters before egg laying, during incubation, and during juvenile growth. In some cases few juveniles of adult size (i.e. few mature individuals) have been reported before the start of hibernation (Pollo Mateos and Perez-Mellado, 1989) and in other cases the majority of the juveniles reach adult body size (SVL at maturity: $\geq 37 \text{ mm}$ males and $\geq 41 \text{ mm}$ females) (Pascual Gonzalez and Perez Mellado, 1989). Growth accelerates with increasing spring temperatures and is high in April/ May. Growth estimates of 4.03 mm/month (0.134 mm/day) for males to 6.36 mm/month (0.212 mm/day) for females have been reported (Pascual Gonzalez and Perez Mellado, 1989), although these values may be overestimated as they are not based on individual-based growth and individual-based growth estimates reported by the same authors are in fact much lower (0.035 – 0.096 mm/day; i.e., 1.3 – 6-fold lower) (Pascual Gonzalez and Perez Mellado, 1989). In their first spring, captive juveniles reach a body size of 41 mm, a tail length of 74 mm, and a body mass of 2.3 g. In their second year (second spring) captive individuals reach a SVL of 50 mm and a body mass of 3.5 g (in den Bosch, 1986).

Recently-hatched offspring are darker than adults and in some cases are almost dark brown, but display the same colour pattern as adults. Recently-hatched juveniles lack ocelli. The first moult occurs 3 – 4 weeks after hatching, after which coloration changes continuously until adult coloration is attained before the start of winter. Blue ocelli are produced in the first spring, and undergo a temporal change from blue to greenish. In summer, the typical green nuptial coloration is fully developed (in den Bosch, 1986). The size of the coloured axillary patches increases with age (in den Bosch, 1986).

Maturity is generally reached during the first spring at the age of 8 – 9 months (Pascual Gonzalez and Perez Mellado, 1989), although some authors have reported that maturity is reached at 5 months (excluding hibernation) and a body size of 42 mm (Bauwens and Diaz Uriarte, 1997). The vast majority of the juveniles reach sexual maturity by the first spring after hatching (Pascual Gonzalez and Perez Mellado, 1989) and survive on average 11 months (Bauwens and Diaz Uriarte, 1997).

Geographic variation

Genetic diversity of *P. occidentalis* differs between populations. Southern populations form a paraphyletic assemblage with respect to northern populations, and analyses of molecular diversity have demonstrated a recent northward population expansion of southern and northern populations. This pattern is supported by the haplotype diversity observed in three different known genes (cytochrome *b*, *nad4*, and suppressor of SWI4 1). Southern populations consist of

several haplotypes, while northern populations consist of a single haplotype in codifying genes (cytochrome b, nad4, and suppressor of SWI4 1; Figure 5 in Fitze et al., 2011). Statistical analyses suggest that northward post-glacial range expansion may underlie these observed patterns (Fitze et al., 2011). It remains unknown whether phenotypic differentiation parallels the observed genetic differentiation.

Habitat

P. occidentalis is mainly found in open areas with loose soil, especially areas with sparse Mediterranean-type scrub. It inhabits oak tree landscapes containing Lavender (*Lavandula*), Cistus plants (*Cistus*), Spanish Gorse (*Genista*), *Thymus*, and Broom (*Lygos*) (Barbadillo, 1987). *P. occidentalis* can also be found in coastal dunes and grassland (Pleguezuelos et al., 2009), fallow lands, pine forests (Guillaume, 1997), and sandy or stony sites lacking vegetation, such as riverbeds and quarries (Guillaume, 1997). In general, it inhabits sparsely-covered shrub land and open, shaded, grassy areas (Pollo and Perez-Mellado, 1990). *P. occidentalis* selects microhabitats containing herbs and shrubs, the densest parts of which are found between ground level and 10 cm above the ground, and it avoids wooded areas and areas with tall bushes (Carrascal et al., 1989; Fitze, P. S., personal observations).

In Galicia, *P. occidentalis* inhabits forests with Mediterranean influence, typical of the Orense district, which consist of Bournemouth Pine (*Pinus pinaster*), Italian Stone Pine (*Pinus pinea*), Cork Oak (*Quercus suber*), Strawberry Tree (*Arbutus unedo*), Lavender (*Lavandula*), Heath plants (*Erica*), Broom (*Sarothammus*), and *Pterospartium tridentatum* (Chouza Mata and Cid Gonzalez, 1982).

In León it inhabits partially degraded areas, oak forests, and heath land (Delibes and Salvador, 1986).

In Salamanca, *P. occidentalis* lives in areas dominated by Holm Oak (*Quercus rotundifolia*) forests, which belong to the *Quercion (broteroi) fagineae* Br. It as well inhabits areas with sparsely distributed tree species that include Cork Oak (*Quercus suber*), Portuguese Oak (*Quercus faginea*), and Raywood (*Fraxinus angustifolia*). The shrub land cover usually comprises the *Cistion laurifoli* Rivas Goday (1949) Alliance, with the following characteristic species: French Lavender (*Lavandula stoechas*), Spanish Marjoram (*Thymus mastichina*), *Halimium viscosum*, and White Spanish Broom (*Cytisus multiflorus*) (Pollo and Perez-Mellado, 1990).

In the central system, *P. occidentalis* is found in the *Quercus ilex* Schmid (Rivas-Goday, 1955) Alliance (Pascual Gonzalez and Pérez Mellado, 1987) and in areas containing Holm Oak (*Quercus rotundifolia*), Pyrenean Oak (*Quercus pyrenaica*), Portuguese Oak (*Quercus faginea*), and Cork Oak (*Quercus suber*), and with very reduced bush cover due to grazing and ploughing (Pascual Gonzalez and Pérez Mellado, 1987). According to some authors, Foxglove (*Digitalis thapsis*) is important for *P. occidentalis*, and this abundant species is used preferentially as a refuge (Pascual Gonzalez and Pérez Mellado, 1987). This may however be specific to the area studied rather than a general pattern, as this plant has not been observed in any of the populations studied by Fitze et al. (2011).

In Huelva, zones with little or no plant cover are preferred by *P. occidentalis* (Mellado et al., 1975), which primarily inhabits sandy areas with naked soil.

In Portugal, *P. occidentalis* is found in Macchia, Garrigue, and in agricultural regions. It is frequently found on eroded land, land that has been altered by humans, and land with short and sun-exposed grass (Thero –Brachypodietea) that may be sparsely populated by Broom (*Cystus*) (Malkmus, 2004).

P. occidentalis is almost exclusive to the thermo- and meso-Mediterranean zones, but may penetrate into supra-Mediterranean regions (Malkmus, 2004). It lives in regions that receive less than 1000 mm of annual precipitation and can be found from sea level up to altitudes of 1050 m above sea level (a.s.l.) (Serra da Nogueira), although most sightings have been recorded below 300 m a.s.l. (Malkmus, 2004).

Abundance

Population densities are low across the entire geographic distribution and densities as high as those reported for *P. edwardsianus* or *P. hispanicus* have not been described to date. In Huelva (e.g., Doñana National Park), Extremadura, and the mountains surrounding Salamanca, densities are low (Mellado Camacho, 1980; Pérez-Mellado, 1982; Fitze, P. S., personal observations). In Fresno Alhániega and Sieteiglesias de Tormes (Salamanca), densities reach 6.25 individuals per hectare (García and Mateos, 2009). The highest reported densities (12.5 individuals per hectare) were observed in the Cantabrian mountains (Delibes and Salvador, 1986).

Conservation status

P. occidentalis is not indexed in the IUCN Global categories (2009), but its conservation status corresponds to “of least concern” (LC), given its wide distribution and because its potential population decline is not sufficiently rapid to qualify for listing in a more threatened category (Pleguezuelos et al., 2009).

Similarly, *P. occidentalis* is not indexed in the IUCN categories for Spain (2002), but can be considered as LC (Carretero et al., 2004).

Threats

P. occidentalis may be locally threatened by the disappearance of scrubland. Direct threats include intensive agriculture, fires, and urbanization of suitable habitat (especially in coastal areas). Another reason why it may be locally threatened are the low population densities that may hinder rapid recolonization of locally extinct areas. However, globally, it is not significantly threatened and its population trends are stable (Blanco and González, 1992; Pleguezuelos et al., 2012).

Conservation measures

The species benefits from the protection of habitats with Mediterranean shrub land and prevention of the total elimination of small bushes (Carretero et al., 2004). A very important conservation measure is the protection of open areas with naked soil, i.e., the prevention of rapidly advancing natural succession, which closes open areas and renders habitats unsuitable.

Geographic distribution

P. occidentalis is found on the western Iberian Peninsula. Its presence has been recorded from Huelva in the south to Galicia, Cantabria and León in the north (Carretero et al., 2002; Chouza Mata and Cid Gonzalez, 1982; Fitze et al., 2011, 2012). It inhabits the western part of the Iberian Peninsula from Extremadura, Madrid and León in the east to Portugal in the west. The eastern limit of its distribution includes Doñana National Park (Huelva), Trujillo, and Madrid (Fitze et al., 2011, 2012). Its altitudinal limit may be at 1'700 m a.s.l. (Sierra de Guadarrama) (Carretero et al., 2002), although it is unclear whether this observation pertains to *P. occidentalis* or *P. hispanicus*. The confirmed altitudinal limit of this species is 1330 m a.s.l. (Lizana et al., 1995), although the precise geographic and altitudinal distribution is unknown.

The most important variable predicting its distribution is mean temperature of the driest months (Fitze et al., 2011)

Trophic Ecology

P. occidentalis principally consumes small prey and flightless terrestrial arthropods such as spiders, wingless ants, and nymphs of Orthoptera (Mellado et al., 1975; Pascual Gonzalez and Pérez Mellado, 1987; Pérez-Mellado, 1981, 1982; Pollo and Perez-Mellado, 1990). The most

frequently consumed taxa are spiders, followed by Coleoptera, Formicidae, Homoptera, Heteroptera, Curculionidae, and Orthoptera (average frequency: > 5 % of ingested prey). No significant differences exist between males and females in terms of ingested prey types (Table 2; exact Wilcoxon-signed rank test: $V = 102$, $P = 0.49$).

Table 2. Food composition of *P. occidentalis* according to three independent studies conducted in Huelva (Mellado et al., 1975), Central System (Pérez-Mellado, 1981, 1982), and Salamanca (Pascual Gonzalez and Pérez Mellado, 1987). The proportion of items ingested per locality, study, sex, age, and taxa is indicated.

	Huelva	Central System	Salamanca			
			total	males	females	juveniles
Arachnidae						
Aranea	24.8	22.4	27.1	26.7	28.4	26.8
Opiliones	1.1	2	0.4	0.8		0.3
Solifugae			1.1	1.7	0.5	0.9
Acari			2.4	1.7	2.4	3.3
Insecta						
Curculionidae		18.4				
Homoptera		16.3	8.6	6.6	12.5	8.4
Orthoptera		10.2	7.4	11	8.2	3
Coleoptera	23.9	8.2	2.4	2.8	4.8	0.6
larvae		6.1	1.8	1.9	2.9	0.9
Heteroptera		2	19.5	13	11.5	31.6
Hemiptera	0.5					
Dictyoptera			1.3	0.3	2.9	1.5
Lepidoptera		2	1	1.4	1.4	0.3
larvas	5.9		2.9	3.3	5.8	0.6
Diptera	2.3		1.7	1.7	1.4	1.8
Hymenoptera	1.1		1.4	0.3	2.9	1.8
Formicidae	15.3		17.5	23.1	11.1	15.4
Phasmatodea			0.1		0.5	
Miriapoda	2.3	2	1.4	1.9	0.5	1.5
Crustacea						
Isopoda	9.4					
Collembola			0.2	0.3	0.5	
Mollusca						
Gasteropoda			0.1		0.5	
fruits		6.1				

The most notable difference between sexes concerns the proportion of ingested Formicidae and Homoptera; females consume less Formicidae (-12 %) and more Homoptera (+ 6 %) than males. In males, Formicidae and Homoptera are the second and fifth most common prey types, respectively, while in females Formicidae are the fourth and Homoptera the second most common prey type. The juvenile diet does not differ significantly from that of the male (Table 2; exact Wilcoxon-signed rank test: $V = 134$, $P = 0.12$) or female (Table 2; $V = 91$, $P = 0.52$). Heteroptera are the main prey type of juveniles (18 – 20 % more frequent in juvenile vs male and female stomachs; Table 2), followed by Araneae, Formicidae, Homoptera and Orthoptera, the latter of which are consumed at a lower frequency than in adults (-5 % vs adult females and -8 % vs adult males). No significant differences in the proportion of ingested prey types consumed by adults exists between studies conducted in the same geographic region (Table 2: $V = 123$, $P = 0.81$) (Pascual Gonzalez and Pérez Mellado, 1987; Pérez-Mellado, 1981, 1982), or in different geographic regions (Huelva versus Central System: Wilcoxon-signed rank test: V

= 81, $P = 0.85$ (Mellado et al., 1975; Pérez-Mellado, 1981, 1982); Huelva versus Salamanca: $V = 158$, $P = 0.15$ (Mellado et al., 1975; Pascual Gonzalez and Pérez Mellado, 1987).

Spiders are consumed throughout the year (Pascual Gonzalez and Pérez Mellado, 1987) and are the main prey type in all months (25 – 45 % of consumed prey) except August and October (Pascual Gonzalez and Pérez Mellado, 1987), during which Heteroptera (39.2 % of prey items) and Formicidae (57.9 %) dominate (Pascual Gonzalez and Pérez Mellado, 1987). The number of prey per stomach was 5.94 in Salamanca (Pascual Gonzalez and Pérez Mellado, 1987), 3.5 in Huelva (Mellado et al., 1975), and 3.77 in the west of the Central System (Pérez-Mellado, 1981, 1982).

Prey size is generally between 2 and 5 mm (58 % of prey items) in the Central System (Pérez-Mellado, 1982, 1998), while the biggest individuals may be up to 18 mm (Pérez-Mellado, 1981, 1982). In Salamanca prey size ranged from 0.5 – 20.5 mm (Pascual Gonzalez and Pérez Mellado, 1987), with 85.5 % < 8 mm. In Huelva prey sizes range from 0 – 10 mm (91.2 %) with the largest prey ranging from 30 to 35 mm in size (Mellado et al., 1975).

The most abundant prey (> 6 % of prey items) range in size from 2 to 8 mm for males, 1 to 7 mm for females and 1 to 6 mm for juveniles (Pascual Gonzalez and Pérez Mellado, 1987). The average prey size of females (5.9 mm \pm 4.79 sd) is larger than that of both males (5.46 mm \pm 3.4 sd) and juveniles (3.99 mm \pm 2.76 sd) (Pascual Gonzalez and Pérez Mellado, 1987). These results suggest the absence of trophic segregation for prey size or prey type (see above analyses) between sexes (but see opposing conclusions: Pascual Gonzalez and Pérez Mellado, 1987; Pérez-Mellado, 1998; Pollo and Perez-Mellado, 1988). Trophic segregation may exist between age classes, both for prey type (juveniles vs males; see above analyses) and prey size (juveniles vs adults) (Pascual Gonzalez and Pérez Mellado, 1987).

The hunting strategy of *P. occidentalis* consists of active foraging, during which prey is located in a defined area/territory (Pascual Gonzalez and Pérez Mellado, 1987). This may be the reason why the prey of *P. occidentalis* is mainly terrestrial or has limited flying skills.

Reproduction

In the west of Salamanca, the reproductive season begins in March (Pollo and Perez-Mellado, 1990) while in the southern Iberian Peninsula reproduction can begin as early as January (Pérez-Quintero, 1996). Copulation activity peaks in April/May and lasts until June (Pascual Gonzalez and Perez Mellado, 1989; Pollo and Perez-Mellado, 1990). In captivity (in the Netherlands), the copulation period begins in mid-March and lasts until July (in den Bosch, 1986).

Males are territorial and fight with one another (in den Bosch, 1986). Fights begin with 'head wrestling' and end with biting (in den Bosch, 1986). After a successful fight, hierarchies are established and fights become rare (in den Bosch, 1986).

The minimum body size (SVL) of reproductive males is 38 mm, while that of reproductive females is 39 mm in Huelva (Pérez-Quintero, 1996) and 42 mm in Salamanca (Bauwens and Diaz Uriarte, 1997).

Copulation commences with the male biting the female's tail, followed by progressive biting of the tail upwards towards the cloacae, biting on the flank, and a final skin bite in the middle of the back (in den Bosch, 1986). In *P. occidentalis*, the flank bite observed during the copulation of other Lacertids (e.g., *Zootoca vivipara*) is only an intermediate behaviour, and copulation only occurs after biting of the female's back skin. After the dorsal bite, the male bends his body around the female's tail. The female then raises her tail to facilitate copulation, after which copulation commences (in den Bosch, 1986). No noises are made during copulation. Females signal that they are not interested in copulation by rapidly moving the head from side to side. This behaviour has been observed during the entire pre-copulatory process, from the initiation bite up to the start of the copulation (in den Bosch, 1986). Females can also resist male copulation attempts by biting the males or refusing to collaborate. In captivity, reproduction coincides with male femoral pore secretions and several sequential copulations have been observed (in den Bosch, 1986).

Male reproductive cycle

In the west of Salamanca, the reproductive period starts at the beginning of March when testicle size is maximal (Pollo and Perez-Mellado, 1990). In Salamanca, the testicles of *P. occidentalis* are fully developed in April and reach their maximum volume one to two months later (Pascual Gonzalez and Perez Mellado, 1989). From July onwards, testicle size decreases sharply to reach its annual minima in August (Pascual Gonzalez and Perez Mellado, 1989; Pollo and Perez-Mellado, 1990). Testicle size then progressively increases from September to October (Pascual Gonzalez and Perez Mellado, 1989; Pollo and Perez-Mellado, 1990). In the southern Iberian Peninsula (Huelva) maximal testicle size (length and volume) is observed in March/April, and subsequently decreases until August when it reaches its minima. Thereafter, testicle size increases gradually until November and in February reaches a size slightly smaller than its maximal size (Pérez-Quintero, 1996). These data contrast with those of another study conducted in the same region (Huelva), which reported maximum and minimum testicular volumes in February – May and September, respectively (Pérez-Quintero, 1995b). According to this author, maximum testicular size is reached 2 – 3 months earlier in south-eastern Spain than in Salamanca, suggesting that this parameter is influenced by the harshness of the winter (Pérez-Quintero, 1996).

In the west of the Central System testicular size in males without nuptial coloration is $4.2 \text{ mm} \pm 0.6 \text{ sd} \times 2.3 \text{ mm} \pm 0.2 \text{ sd}$ (range: $3.5 - 5.2 \text{ mm} \times 2.1 - 2.8 \text{ mm}$) in April and $3.9 \text{ mm} \pm 0.74 \text{ sd} \times 2.4 \text{ mm} \pm 0.2 \text{ sd}$ ($2.8 - 4.5 \text{ mm} \times 2.1 - 2.6 \text{ mm}$) in July (Pérez-Mellado, 1982).

In Salamanca, adult males display nuptial coloration in April and May (Pascual Gonzalez and Perez Mellado, 1989; Pérez-Mellado, 1981), *i.e.*, during the proposed main copulation season. However, no studies have systematically analyzed the temporal pattern of nuptial colour expression.

Female reproductive cycle

Females start reproducing at the age of 8 – 9 months (Pollo Mateos and Perez-Mellado, 1989). According to Pollo and Perez-Mellado (1990), females start reproducing at the age of 9 – 10 month (same locality) or 5 months (not counting hibernation) (Bauwens and Diaz Uriarte, 1997). In captivity sexual maturity is reached at a similar age (in den Bosch, 1986).

In Salamanca, the female reproductive cycle lasts from March until July (Pollo and Perez-Mellado, 1990). Maximal female sexual activity is observed between April and July, and coincides with that of males (Pascual Gonzalez and Perez Mellado, 1989). The populations of the northern meseta (west of Salamanca) (Pollo Mateos and Perez-Mellado, 1989) commence reproduction slightly earlier than the more continental populations of Salamanca (Pascual Gonzalez and Perez Mellado, 1989), most likely due to the warmer microclimate in the areas inhabited by the western populations (Carretero and Llorente, 1991).

The duration of the copulation process has only been described in captivity, where copulation lasts approximately 40 seconds, during which the male does not relax its hold on the dorsal skin of the female (in den Bosch, 1986).

In southern populations the first vitellogenic eggs appear in March (Pérez-Quintero, 1995b, 1996). In Salamanca, the majority of follicles are vitellogenetic in April and only a few follicles are atretic (in the process of degeneration) (Pascual Gonzalez and Perez Mellado, 1989). In Salamanca vitellogenic follicles appear one month later than in Huelva (Pérez-Quintero, 1996), while in the west of Salamanca vitellogenic follicles appear from April to June (Pérez-Mellado, 1981).

The number of vitellogenic follicles ranges from 1 – 4 (3.06 ± 0.09 ; mean \pm sd) in Salamanca (Pascual Gonzalez and Perez Mellado, 1989), 2 – 5 (2.66 ± 0.94) in Huelva (Pérez-Quintero, 1996), and 2 – 5 in the West of Salamanca (Pérez-Mellado, 1981). A study of several populations by Fitze et al. (2011) reported 1 – 4 vitellogenic eggs (3.33 ± 1). In Salamanca, vitellogenic follicles have a maximum diameter of 7.25 mm (Pascual Gonzalez and Perez Mellado, 1989), a length of $4.43 \pm 1.48 \text{ mm}$ (mean \pm sd) ($2.06 - 7.41 \text{ mm}$) and a width of $3.63 \pm 1.19 \text{ mm}$ ($1.61 - 6.14 \text{ mm}$) (Pollo and Perez-Mellado, 1990). In the South, egg lengths and widths of $5.51 \pm 1.6 \text{ mm}$ ($3.3 - 7.5 \text{ mm}$) and $4.54 \pm 1.77 \text{ mm}$ ($2.0 - 6.7 \text{ mm}$) have been reported (Pérez-Quintero, 1996).

The first oviductal eggs appear in March in the South (Pérez-Quintero, 1996) and between May and July in Salamanca (Pascual Gonzalez and Perez Mellado, 1989). In the South the number of oviductal eggs ranges from 2 – 5 (3.6 ± 1.01 ; mean \pm sd) (Pérez-Quintero, 1996). Egg length is 11.79 ± 1.92 mm (7.9 – 13.9 mm) and egg width is 6.37 ± 0.47 mm (5.2 – 7.3 mm) (Pérez-Quintero, 1996). In northern populations egg length is 10.26 ± 1.18 mm (8.82 – 14.28 mm) and egg width is 5.65 ± 0.73 mm (4.67 – 6.92 mm). Oviductal eggs of 14.28 mm in length have been described in Salamanca (Pollo and Perez-Mellado, 1990).

Gestation is estimated to last 45 – 50 days (Pollo and Perez-Mellado, 1990) and the first clutches are laid at the end of May (Pollo and Perez-Mellado, 1990).

It has been proposed that *P. occidentalis* produces up to two clutches per year, both in the South (Huelva, Pérez-Quintero, 1996) and in the North (Salamanca, Bauwens and Diaz Uriarte, 1997). In the South, the first clutch is produced between April and June, and the second between July and September (Pérez-Quintero, 1996), while in Salamanca the first clutches are produced between May and July (Pascual Gonzalez and Perez Mellado, 1989). In captivity, 3 – 7 clutches are produced per year (in den Bosch, 1986).

Laying lasts 1 – 2 hours and eggs are deposited at the end of a 15-cm long curved or spiral tube excavated in moist sand (in den Bosch, 1986).

Clutch size is 2 – 5 in Huelva and in the west of Salamanca (Pérez-Mellado, 1981; Pérez-Quintero, 1995b), with an average clutch size of 3.6 ± 0.99 sd in Huelva and 4 in the west of Salamanca (Pérez-Mellado, 1981; Pérez-Quintero, 1995b). According to different studies conducted in Salamanca, average clutch size varies between 3.2, 3.14, and 2.57 (Bauwens and Diaz Uriarte, 1997; Pascual Gonzalez and Perez Mellado, 1989; Pollo Mateos and Perez-Mellado, 1989). The interval between two clutches is 20 days (in den Bosch, 1986).

Both the presence and absence of a significant correlation between SVL and clutch size have been reported by different authors (Pérez-Quintero, 1995b, 1996). Despite these conflicting results, a significant positive and quadratic correlation between female SVL and clutch size was observed in a study of females from several populations ($F_{1,7} = 23.44$, $P = 0.002$, $R^2 = 0.88$) (Fitze et al., 2011); clutch size consistently increased with SVL for SVLs between 44 mm and 49 mm, and all females with an SVL ≥ 49 mm produced 4 eggs.

During gestation the body mass of pregnant females increases by 1 g (in den Bosch, 1986). Egg colour is whitish/white (in den Bosch, 1986). The average egg mass recorded in Salamanca was 0.256 g (Bauwens and Diaz Uriarte, 1997), while in the west of Salamanca clutches laid in July contained eggs measuring $10.3 \text{ mm} \pm 0.6 \text{ sd} \times 6.0 \text{ mm} \pm 0.3 \text{ sd}$ ($n = 4$ eggs of the same clutch; range: 9.6 – 11.1 mm \times 5.6 – 6.2 mm) (Pérez-Mellado, 1981). In captivity, the egg size recorded immediately after laying was 6.2 ± 0.6 mm (mean \pm se) (range: 5.0 – 7.0 mm) \times 10.2 ± 0.6 mm (9.5 – 11.8 mm), and egg mass 0.19 ± 0.05 g (0.14 – 0.28 g) (in den Bosch, 1986). After oviposition, fertilized eggs 'grow' to a size of 10.5 ± 0.7 mm (9.6 – 11.2 mm) \times 14.0 ± 1.4 mm (11.8 – 16.6 mm) and a mass of 0.75 ± 0.11 g (0.63 – 0.93 g) (in den Bosch, 1986).

After oviposition, females actively cover the eggs with sand. This egg-burying behaviour can continue for several days (in den Bosch, 1986). In captivity the eggs of the last clutches to be laid were sterile, indicating that females can store sperm for a limited time only (or not at all), or can store only a limited quantity of sperm (in den Bosch, 1986).

Egg incubation is estimated to last approximately two months in Salamanca (Pascual Gonzalez and Perez Mellado, 1989) and 60 – 65 days in the west of Salamanca (Pollo and Perez-Mellado, 1990). The duration of incubation (from laying to hatching) is temperature-dependent, and thus was 56 (53 – 66) days at 25°C and 38 (37 – 41) days at 29°C (in den Bosch, 1986).

From August onwards in Salamanca and from September onwards in Huelva, most females exhibit atretic follicles (Pascual Gonzalez and Perez Mellado, 1989; Pérez-Quintero, 1996) and are reproductively inactive from October onwards (Pérez-Quintero, 1996).

Population structure and population dynamics

Between the emergence from hibernation and the hatching of juveniles in August, populations consist of the adult age class only. Two age classes are observed in the period between hatching and hibernation: juveniles of 23.9 – 33.44 mm and adults with an SVL of 42.5 – 51.65 mm (Pascual Gonzalez and Perez Mellado, 1987, 1989). The number of adults decreases in the period between reproduction and the point at which juveniles attain adult body size. The juvenile age class predominates in autumn.

Population densities have been estimated annually in Fresno Alhániega and Sieteiglesias de Tormes (Salamanca) from 2002 using the same methodology and research personnel. Densities of 6.25 individuals/ha were recorded in 2002, 2003, and 2008, but no individuals were detected between 2004 and 2007, suggesting strong inter-annual population fluctuations (García and Mateos, 2009). As *P. occidentalis* occupies a narrow niche within the ecological succession (see habitat section), large temporal population fluctuations can occur and temporally stable populations only exist in climax communities or in habitats that are temporally maintained by humans (e.g., habitats with annual sheep and goat grazing).

Interactions between species

P. occidentalis may live in the presence of other lizards such as *Psammodromus algerus*, *Acanthodactylus erythrurus*, *Podarcis hispanica*, and *Podarcis carbonelli* (Pollo and Perez-Mellado, 1990; Fitze, P. S., personal observations). Moreover, considerable spatial niche overlaps with *P. bocacei* (82 – 97 %), *L. Schreiberi* (97 %), *T. lepidus* (84 %), and *A. erythrurus* (71 – 73 %) have been described (Pérez-Mellado, 1981), although the actual overlap is very small and at the microhabitat level only a minimal overlap exists with *Podarcis carbonelli* and juveniles of *Psammodromus hispanicus* and *Acanthodactylus erythrurus* (Carrascal et al., 1989; Fitze, P. S., personal observations). No information exists regarding behavioural interactions among species.

Antipredator strategies

When presented with an actual or perceived threat *P. occidentalis* accelerates explosively seeks cover at the base of thick bushes, where it abruptly stops and remains motionless to avoid detection (moving prey is more easily detected), aided by its cryptic coloration and dorsal colour pattern. Once the predator begins to move, attempting to locate its prey from the side or from above, it loses its ability to detect fine movements in the bush, at which point the Western Sand Racer creeps slowly to the edge of the bush, and again accelerates explosively to reach the next nearest bush. This escape behaviour is usually undetected by the predator (or by humans) and the Sand Racer either stays in the bush or repeats this behaviour to move on to other bushes. Moreover, this escape behaviour can occur in all possible directions, and the Sand Racer may return to a bush in which it has previously hidden. *P. occidentalis* rarely hides in holes. However, it frequently walks around stones, suggesting that it hides in a hole, and simply passes through the gap between stone and vegetation in order to exit via a route that is not visible to the predator (Fitze, P. S., personal observations).

Predators

Predators include the Montpellier Snake (*Malpolon monspessulanus*) (Díaz Paniagua, 1976; Valverde, 1976), probably the Ladder Snake (*Rhinechis scalaris*), Cattle Egret (*Bubulcus ibis*) (Mateos and Lázaro, 1986), Common Kestrel (*Falco tinnunculus*) (Valverde, 1976), Lesser Kestrel (*Falco naumanni*) (Franco and Andrada, 1976), Black Kite (*Milvus migrans*) (Garzón Heydt, 1974), Montagu's Harrier (*Circus pygargus*) (Garzón Heydt, 1974), and Common Buzzard (*Buteo buteo*) (Garzón Heydt, 1974).

Parasites

No specific information exists regarding parasites of *P. occidentalis*. Potential parasites include those described for *P. edwardsianus*.

Activity

At least in the South, *P. occidentalis* can be active during the winter (Barbadillo, 1987), while in the North it undergoes a lethargic period in the winter (Pérez-Mellado, 1982). However, according to Pérez-Quintero (1996), *P. occidentalis* is inactive in the winter in the Province of Huelva, where it emerges from hibernation in January/February. In Salamanca it is active from March until October (Pollo and Perez-Mellado, 1990; Pollo Mateos and Perez-Mellado, 1989) and in the west of Salamanca from April to September (Pérez-Mellado, 1982).

The periods of greatest activity of *P. occidentalis* are in spring and autumn, with the highest level of activity in autumn due to the presence of juveniles (Pollo Mateos and Perez-Mellado, 1989). Corresponding activity maxima have been described in the South (Pérez-Quintero, 1995a).

Daily activity patterns switch from a unimodal pattern in spring to a bimodal pattern in summer in both southern and northern populations (Pérez-Mellado, 1981, 1982; Pollo Mateos and Perez-Mellado, 1989; Pollo and Perez-Mellado, 1990). In spring and autumn, *P. occidentalis* is active around midday if minimum temperatures are reached, and in the summer it is active early in the morning (until 12 a.m. solar time) (Pérez-Mellado, 1981) and in the afternoon (15 – 17 h), although significantly less so than in the morning (Barbadillo, 1987; Pérez-Mellado, 1981). In the summer, no activity is observed around midday (Pollo Mateos and Perez-Mellado, 1989), if temperatures are $\geq 26^{\circ}\text{C}$ (Pérez-Quintero, 1995a). Similar patterns of summer activity have also been described in captivity, where *P. occidentalis* is active in the morning, but not in the afternoon due to excessively high temperatures (in den Bosch, 1986).

Some authors have suggested that *P. occidentalis* may estivate during the hottest months of the year (Barbadillo, 1987), but no conclusive evidence exists to support this assertion. Diurnal activity is significantly increased after a period of bad (cloudy and rainy) weather.

Thermal biology

The body temperature of active individuals ranges from 19 to 38°C, and temperatures are significantly higher in juveniles (Pollo and Perez-Mellado, 1988). Body temperatures differ significantly between sexes and age classes (Pollo Mateos and Perez-Mellado, 1989). Females have an average body temperature of $30.09 \pm 3.22^{\circ}\text{C}$ (mean \pm sd) (range: 22.5 – 36°C), which is higher than that of males ($28.94 \pm 4.31^{\circ}\text{C}$; 19 – 38°C), while juveniles exhibit the highest body temperatures ($31.06 \pm 1.87^{\circ}\text{C}$; 21 – 34.5°C) (Pollo Mateos and Perez-Mellado, 1989). Body temperatures measured in a thermal gradient average 35.94°C, which likely reflects optimal body temperature (Bauwens et al., 1995). In comparison with these temperatures recorded in individuals in Salamanca, the average annual body temperature of active individuals in the South (Huelva) is higher (32.6°C; 28.8 – 36.6°C).

Several thermoregulatory phases exist in spring. The first daily thermoregulatory phase is during the first hours of the morning, and the second phase occurs around 12.00 solar time (Pollo Mateos and Perez-Mellado, 1989). Maximum body temperature is reached early in the morning (8 – 9 a.m.), probably due to active thermoregulation, and body temperature during the day reaches around 30°C. During the main activity period (9 – 10 a.m.), body temperature drops by up to 5°C, and thereafter increases slightly until the end of the day (Pollo Mateos and Perez-Mellado, 1989).

Body temperature is dependent on both air and substrate temperature (Pérez-Quintero, 1995a; Pollo Mateos and Perez-Mellado, 1989), and diurnal activity is only observed if air temperatures are lower than 26°C (Pérez-Quintero, 1995a).

Home range

No specific information exists regarding the home range of *P. occidentalis*, although it may be similar to that described for *P. edwardsianus*.

Behaviour

Noise/Sound Production

P. occidentalis emits high-pitched squeaking noises when manipulated (von Bedriaga 1879; Fitze, P. S., personal observation). These vocalizations may also be emitted in the presence of a predator or during reproduction (Barbadillo, 1987). Females may emit a long squeak when approached by a male, but no sound is produced during copulation (in den Bosch, 1986). Phonographic recordings have demonstrated that the frequency of the emitted sound is 1.5 – 16 kHz, with a duration is 700 – 900 ms (Böhme et al., 1985). However, it is unclear whether these sound recordings pertain to *P. hispanicus*, *P. edwardsianus*, or *P. occidentalis*.

Sprint speed

The maximum sprint speed of *P. occidentalis* is 149.9 ± 34.5 cm/s (mean \pm sd) (Bauwens et al., 1995) and an optimal sprint speed of 135.9 ± 27.5 cm/s is attained at $35.94 \pm 0.42^\circ\text{C}$ (Bauwens et al., 1995). Thermal-performance breadth, *i.e.*, the body temperature range at which speed is at least 80 % of its maximum, is $6.41^\circ\text{C} \pm 1.08$ se and occurs between 33 and 40°C (Bauwens et al., 1995). The critical thermal maximum is at 45.5°C , while the preferred temperature is 35.1°C (Bauwens et al., 1995).

Movement and Hibernation

P. occidentalis is largely terrestrial and is mainly observed on the ground (>80 % of observations), although it can also climb small bushes (Pérez-Mellado, 1981). It hibernates in the embankments of paths, in forest lynchets, and beneath small stones (Pérez-Mellado, 1981).

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