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Edward's Sand Racer – *Psammodromus edwardsianus* (Dugès, 1829)

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Synonyms

Lacerta Edwardsiana Dugès 1829, p. 337 – 339; *Aspistis Edwardsiana* Wagler 1830, p. 156; *Notopholis Edwardsiana* Wagler 1830, p. 342; *Notopholis Edwardsiana* Wiegmann 1834, p. 10; *Psammodromus cinereus* Bonaparte 1839, p. 62; Gray 1838, p. 274; *Psammodromus edwardsii* Duméril & Bibron 1939, p. 253; *Lacerta cinerea* Schinz 1840, p. 28; *Notopholis cinereus* Schinz 1840, p. 28; *Psammodromus hispanicus* Steindachner 1869, p. 41; *Psammodromus hispanicus edwardsianus* Mertens 1925, p. 81 – 84.

Common names

Catalan: Sargantana Cendrosa; French: Psammodrome d'Edwards; German: Edwards Sandläufer; Portuguese: Lagartixa-do-mato de Edwards; Spanish: Lagartija de Edwards.

History of Nomenclature

In 1829, Dugès described a new species *Lacerta edwardsiana* captured in Southern France and named it 'Lézard d'Edwards', in honor of the French/Belgium zoologist Henri Milne Edwards (Dugès, 1829). In the table of his original publication (page 339), he erroneously wrote *L. Edwarsiana* instead of *L. Edwardsiana*, resulting in some confusion. In 1839 Duméril classified *L. Edwardsiana* as a synonym of *Psammodromus hispanicus* (Duméril and Bibron, 1839). In the same year Bonaparte described a new species *Psammodromus cinereus* captured in Southern France, which was also observed in Spain (Boscá, 1880; Boscá, 1881; Gray, 1838), and whose main difference, compared to *P. hispanicus*, was its homogeneous dorsal coloration. Boettger described individuals from Almería and Cartagena and concluded that one individual was an intermediate form between *Psammodromus hispanicus* and *Psammodromus cinereus* (Böttger, 1881). Confusion persisted for some years, during which Schreiber (1875) and Gogorza (1883) expressed doubts that the individuals classified as *P. cinereus* were different from *P. hispanicus*, given the few morphological differences and the highly overlapping habitat. Boulenger (1885) ended the confusion by establishing that *P. cinereus* was a color abberation of *P. hispanicus* and not an independent species. This classification is supported by contemperary genetic analyses, which have demonstated no obvious differences between lizards belonging to *P. edwardsianus* and those with the coloration described for *P. cinereus* (*P. cinereus*: PF76, PF80; intermediate individuals: PF89, PF91) (Fitze et al., 2011).

For some time the existence of two subspecies was discussed (*P. hispanicus hispanicus* and *P. hispanicus edwardsianus*), as the phenotypic differentiation was ambiguous (this was due to the existence of three species, rather than two subspecies; Fitze et al., 2012). In 1925 Mertens described *Psammodromus hispanicus edwardsianus* (inhabiting the Eastern Iberian Peninsula and the Catalan semi-deserts) (Mertens, 1925) as a subspecies of *Psammodromus hispanicus* Fitzinger, 1826 (inhabiting the Western Iberian Peninsula). His conclusions were based on the number of scales present around the body (*edwardsianus:* 34 – 42 (Boulenger) and 36 – 43 (Mertens); *hispanicus*: 30 – 34 (Boulenger)), the number of femoral pores (*edwardsianus:* 10 – 15 (Boulenger) and 10 – 17 (Mertens); *hispanicus*: 9 – 12 (Boulenger)) and the number of lamella below the fourth toe (*edwardsianus:* 19 – 23 (Boulenger) and 19 – 24 (Mertens); *hispanicus*: 16 – 20 (Boulenger)). He also noted that in *edwardsianus* the subocular scale is separated from the margin of the mouth by 1 – 2 small supralabial scales, while in *hispanicus* the subocular scale directly contacts the margin of the mouth (*i.e.,* no supralabial scales exist) (Mertens, 1925).

In 2010, *Psammodromus hispanicus edwardsianus* was elevated to the species level *Psammodromus edwardsianus* (Fitze et al., 2010; San Jose García et al., 2010) based on molecular, phenotypic, and ecological analyses (Fitze et al., 2011, 2012).

Terra typica

Terra typica is the south of France (Guillaume, 1997b; Mertens and Müller, 1928), more precisely the 'Bas - Languedoc' (Dugès, 1829), which is the Mediterranean region of the old province of Languedoc (*i.e.,* the lowlands of the province, which include the coastal areas and their surroundings) and nowadays includes the departments of Hérault, Gard, and Aude, and the towns of Carcassonne, Narbonne, Montpellier, and Nîmes.

Origin and Evolution

The *Psammodromus* genus consists of six species: *P. algirus* (Linneaeus, 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, 2012) (estimated split at 8.3 Mya, range: 2.9 – 14.7), *P. edwardsianus* (Dugès, 1829), and *P. hispanicus* (Fitzinger 1826), whose split is estimated at 4.8 Mya (1.5 – 8.7). The split between *P. edwardsianus* (Dugès, 1829) and *P. hispanicus* (Fitzinger 1826) dates back to the Miocene/Pliocene boundary and thus coincides with the Messinian salinity crisis and the opening of the Strait of Gibraltar. Phylogenetic relationships and the spatial distribution of molecular diversity suggest that *P. edwardsianus* conserved the niche of its ancestor and that a barrier between Málaga and the Guadalquivir River may have been the origin of speciation (Fitze et al., 2011, 2012). *P. edwardsianus* exhibits decreasing molecular diversity with increasing latitude, indicating northward range expansion during the Pleistocene glacial and interglacial periods (Fitze et al., 2011). None of the *P. edwardsianus* populations include *P. occidentalis* or *P. hispanicus*, suggesting that the barriers that gave rise to speciation continue to prevent population mixing and range expansions.

Identification

P. edwardsianus can be distinguished from *P. hispanicus* and *P. occidentalis* by the presence of a supralabial scale below the subocular scale (Boulenger, 1921; Fitze et al., 2011; Mertens, 1925; Pérez-Mellado, 1998). In addition, it has a more pointed head, much less extensive greenish nuptial coloration, and more femoral pores and throat scales than its two sister species (Fitze et al., 2011, 2012). *P. edwardsianus* also has more ocelli, less ventral and collar scales, and a lower body mass than *P. hispanicus*. Its mouth is more pointed than that of *P. hispanicus* but less pointed than that of *P. occidentalis* (Fitze et al., 2011, 2012).

Description of the adult

Psammodromus edwardsianus is a Lacertid of small body size. Compared to other species (*P. algirus, P. blanci, P. microdactylus*) its skull is relatively elevated and robust (Salvador, 1981) and it has no pterygoid teeth (Pérez-Mellado, 1998). Its dorsal coloration ranges from greyish to grey-brown to yellowish/greenish, and it exhibits four dorsal longitudinal lines and greyish interlines, although these are absent in some individuals. The back may also exhibit a homogenous chestnut brown colouration, which in the past has resulted in erroneous classification of such individuals as another species (*Psammodromus cinereus*) (Bonaparte, 1839).The belly is generally white and in rare cases yellowish. The nuptial coloration is yellowish/greenish. Nuptial coloration is present on the head, neck, belly, supralabial scales, and to a lesser extent, on the flank, but is absent on the back. *P. edwardsianus* exhibits 12.1 ± 0.1 (mean ± se) femoral pores (range: 9 – 15), 20.4 ± 0.2 throat scales (15 – 26), 1.9 ± 0.1 ocelli (0 – 5), and 24.6 ± 0.3 ventral scales (20 – 29). Body length is on average 46.39 ± 0.33 mm (snout-to-vent length (SVL), 34 – 56 mm) and body mass 1.69 ± 0.03 g (0.96 – 2.51 g) (Table 3 in Fitze et al., 2011).
Growth rates of adults with an SVL of 35 – 41 mm of 0.2 – 0.0083 mm/day (Seva Román, 1982) and 0.04 mm/day (Carretero et al., 1992) have been recorded in Alicante and Catalonia, respectively.

Sexual dimorphism

Sexual dimorphism in phenotypic traits is observed, albeit to a lesser extent than in other Lacertids (Carretero, 1993; Carretero, 1994). The head of the male is more robust and wider than that of the female (Barbadillo, 1987; San José García et al., 2010). Males also have more pronounced femoral pores than females and the base of their tail is slightly broader, while the tail of the female narrows progressively from base to its tip. Males exhibit more extensive nuptial coloration, and the coloration behind the forelegs is yellower than that of females (San José García et al., 2010).

In El Prat de Llobregat the average SVL recorded was 37.05 mm in adult males and 38.7 mm in adult females (Carretero, 1994).

The numbers of ventral scales and femoral pores differ between sexes (Carretero, 1994). Males have less ventral scales (mean ± sd: 27.2 ± 1.1, range: 24 – 31) and more femoral pores (11.9 ± 0.8, 10 – 14) than females (ventral scales: 29.0 ± 1.3, 25 – 32; femoral pores: 11.3 ± 0.9, 10 – 14). Males also have larger heads, which are longer (distance from snout to posterior orbital margin: males, 10.4 ± 0.7 mm, 8.7 – 12; females: 9.6 ± 0.6 mm, 8.8 – 11.3), wider (males: 6.5 ± 0.4 mm, 5.5 – 7.5; females: 5.9 ± 0.3 mm, 5.3 – 6.9) and higher (males: 5.5 ± 0.5 mm, 4.6 – 6.9; females: 5.0 ± 0.3 mm, 4 – 6.8) as compared with females. Males also have longer tails and larger feet than females (Carretero, 1993, 1994).

Little sexual dimorphism in coloration is observed (Carretero and Llorente, 1991b). It is generally agreed that males have more ocelli and more prominent nuptial coloration (including ocelli) during the reproductive period. However, sexually active males lacking greenish ocelli and sexually inactive juveniles and adults (of both sexes) with ocelli have both been observed. Males occasionally exhibit a yellowish patch that extends from the head and neck towards the belly, but it remains unclear whether this is a sexually dimorphic trait (Blasco, 1975; Carretero and Llorente, 1991b; Fitze, P. S. unpublished results).

Karyotype

The karyotype for *Psammodromus sp.* (belonging to *Psammodromus hispanicus*) has been described without specifying the origin of the studied individuals. It is thus unclear whether these analyses pertain to *P. edwardsianus*, *P. occidentalis*, or *P. hispanicus*. The karyotype of *P. edwardsianus* may consist of 2n = 38 chromosomes, two of which are microchromosomes (Matthey, 1939), two metacentric and the remaining 34 acrocentric (Calera Gónzalez and Cano Pérez, 1979).

Description of the juvenile

Juveniles hatch from July onwards, with the majority hatching from mid-July to August (Carretero, 1993; Carretero and Llorente, 1991b). Hatching rarely occurs in September and has not been reported in October (Carretero, 1993; Carretero and Llorente, 1991b). Recently hatched individuals have a SVL of 20 mm (Barbadillo, 1987), 20 – 22 mm (Carretero and Llorente, 1991b). Juveniles of a reintroduced population in Aiguamolls de l'Empordà (Girona) hatched with a SVL of 23 – 25 mm (Carretero et al., 1992), while a SVL of 22 – 23 mm and a total length of 53 – 54 mm was recorded for juveniles hatched in captivity (von Fischer ,1884a). Juveniles grow at a rate of approximately 0.16 mm/day (Carretero et al., 1992), and subadults (SVL of subadults: 28 – 34 mm) at approximately 0.1 – 0.058 mm/day (Seva Román, 1982).

In their first spring, all juveniles reach sexual maturity and most attain adult body size (Carretero ,1993; Carretero, and Llorente, 1993).

Recently hatched juveniles have a darker coloration than adults, and in general juveniles exhibit duller colours and less contrasted colour patterns than adults. Coloration and colour contrast thus becomes more pronounced with age (Carretero, 1993).

Geographic variation

Southern populations form the basal sister group of the Northern populations. Most genetic variation exists between Northern and Southern groups, and significant differences exist among populations and within groups. Haplotype diversity is higher in the South than in the North, where populations are dominated by a single haplotype (both in mitochondrial DNA and the suppressor of SWI4 1). Statistical analyses suggest that recent northward range expansion may be the result of post - glacial range expansion from Southern refugia (Fitze et al., 2011).

Mertens and Müller (1928) cited individuals with intermediate traits between those of *P.*

hispanicus and *P. edwardsianus,* which were also listed by Boulenger (1921). These individuals were observed in a potential contact zone between the two species and have been used as evidence of the existence of hybrids. However, these observations should be interpreted with caution, as no definitive evidence exists to support the existence of hybrids (Fitze et al., 2011, 2012).

Little information is available regarding phenotypic differences among populations, and it remains unknown whether phenotypic differences reflect genetic patterns. However, individuals from Islas del Barón appear to be smaller, probably due to depredation by *Malpolon monspessulanus* (Mateo, 1990).

Individuals with homogeneous dorsal coloration (previously classified as *Psammodromus cinereus*) (Bonaparte, 1839) have been observed predominantly in Valencia, as well as in other geographic locations. These phenotypes were sampled by Fitze et al. (2011), but were genetically indistinguishable from *P. edwardsianus* of other populations and coloration, and did not cluster together (see History of Nomenclature) (Fitze et al., 2011), suggesting that they may reflect smaller point mutations.

Geographic distribution

The species is present on the Iberian Peninsula and in southern France. Its presence has been confirmed from Málaga in the South to the Rhone valley (France) in the North (Bons, 1989; Fernandez-Cardenete et al., 2000; Fitze et al., 2011, 2012). Sightings have been reported from Cuenca in the west and Hyères Salines (France) in the east (Bons, 1989; Fitze et al., 2011, 2012). While sightings in the east of St. Raphaëlle (*e.g.,* Fréjus, Alpes - Maritimes, Francia) have been reported (Bons, 1989), these have not been corroborated since 1961 (Bons, 1989). The meridional and the occidental limits are currently unknown.

In Spain, the altitudinal distribution ranges from sea level to 1700 m above sea level (asl) in Sierra Nevada (Barranco de las Casas de Don Diego), Granada (Carretero et al., 2002; Fernández-Cardenete et al., 2000; Fitze et al., 2011, 2012). In Alicante, *P. edwardsianus* is mainly found between 0 and 400 m asl (65 % of observations) and has been observed with lower frequency between 400 - 800 m asl (20 % of observations) (Escarré and Vericad, 1981; Seva, 1989).

In France it is found from sea level to 750 m asl in the Sainte-Victoire massif (Bons, 1989) and exceptionally at altitudes of up to 1130 m asl at Lagarde d'Apte (Vaucluse) (Olioso, 1993).

P. edwardsianus has been observed on two islands; 'Isla de Barrón' and 'Isla de Perdiguera' in the Mar Menor (Murcia) (Guillaume, 1997a; Mateo, 1990).

It has been introduced in a military area at Melilla and an individual was captured at Sidi Ifni, Morocco (Bons and Geniez, 1996; Carretero et al., 2002) and deposited at the Estación Biológica de Doñana (EBD-CSIC). Beside these point observations no confirmed sightings outside of the European continental shelf have been reported.

Habitat

P. edwardsianus inhabits dry, open, and mainly flat habitats, *i.e.,* terrain with a gradual inclination and vegetation rarely higher than 30 cm (Seva, 1989). It occupies degraded Mediterranean vegetation and vegetation mosaics that contain naked soil and maximal vegetation density between 0 – 20 cm (80 % of observations) (Carretero, 1993). It principally inhabits areas with early ecological succession (Carretero and Llorente, 1997 – 1998). *P. edwardsianus* can be found in wastelands, steppes, Mediterranean bush land, vegetation of coastal sand pits (Pleguezuelos et al., 2009), understorey of open pine and oak forests (Guillaume, 1997a), and in fallow and cultivated land (Carretero et al., 1997a, 2002). It has been observed in forests with compact substrate and even in sandy or stony sites lacking vegetation, such as riverbeds and quarries (Carretero et al., 2002; Guillaume, 1997a). It depends on naked soil and scattered bushes, the densent parts of which lie close to the ground (Carretero et al., 2002). The densest populations live in dry and open habitats with loose vegetation (Carretero et al., 2002).

In El Prat de Llobregat, *P. edwardsianus* inhabits herbaceous vegetation dominated by *Echinophora spinosa* (Carretero and Llorente, 1993). This habitat is characterized by a

Mediterranean coastal climate, *i.e*., moderate temperatures, reduced temperature range, and a long period of summer dryness (Carretero and Llorente, 1993). In Alicante, it inhabits very flat regions with little relief, including muddy areas and their contact zones with fixed dunes, soils with a moderate level of humidity, and soils with sparse vegetation (Seva Román, 1982). It mainly inhabits streams and rivers (55 % of observations), followed by coasts, channels and ditches (± 20 % of observations) (Escarré and Vericad, 1981). In France, its distribution is limited to the floral Mediterranean region. In costal areas, it inhabits fixed dunes, covered by halophilic vegetation, while in inland regions it inhabits degraded bush land (Bons, 1989).

P. edwardsianus selects microhabitats containing herbs and shrubs with maximum vegetation density between ground level and 10 – 15 cm above ground (Fitze, P. S., personal observation).

P. edwardsianus is a thermophile species, and in El Prat de Llobregat inhabits areas with an average annual temperature of 16.5°C and an annual precipitation of 598 mm (Carretero and Llorente, 1993). More generally, it inhabitats areas with average annual temperatures above 12° C and annual precipitation < 700 mm (according to Carretero et al., 2002, who cites an area inhabited by *P. algirus* and *A. erythrurus*, but not necessarily by *P. edwardsianus*).

No significant differences in preferred substrate type or substrate coverage between sexes and age classes have been described (Carretero, 1993). However, differences have been reported between age classes as regards the height of vegetation selected for hiding; juveniles generally hide in smaller plants than adults (Carretero, 1993). Moreover, the ecological niche of juveniles is generally smaller than that of adults, and is contained within the adult niche (Carretero and Llorente, 1997 – 1998).

Abundance

Population densities of *P. edwardsianus* of 17.5 ± 9.5 individuals/hectare (range: 26 – 9; measured at El Prat de Llobregat in 1989) (Carretero, 1992; Carretero, 1997 – 1998) and 23 individuals/hectare (24.8 – 13.4; measured at El Prat de Llobregat in 1997) (Carretero 1997 – 1998) have been described. Carretero (1997 – 1998) suggested that population densities are temporally stable, although subsequent sampling demonstrated the contrary. In 2006 – 2007 extremely low population densities were recorded in El Prat, with the population on the verge of local extinction (Llorente, G. A., personal communication; Fitze, P. S., personal observation) due to ecological succession, which was a consequence of the introduction of a protection plan for the Kentish Plover (*Charadrius alexandrinus*) (Breton et al., 2000; Llorente, G. A., personal comunication). These observations demonstrate that significant and rapid fluctuations can occur in *P. edwardsianus* populations.

Conservation status

The conservation status of *P. edwardsianus* is classified as "of least concern" (LC), according to the IUCN Global Categories (2009), given its wide distribution and large populations, which presumably are not declining fast enough to qualify for listing in a more threatened category (Pleguezuelos et al., 2012).

P. edwardsianus has not been indexed according to the IUCN categories for Spain (2002), and its status can be considered as "of least concern" (Carretero et al., 2002).

Threats

The species may be locally threatened by the loss of scrubland, due to intensive agriculture and fires, and the urbanization of suitable habitat and coastal areas. Ecological succession represents another local threat, which eliminates preferred habitat and prevents the creation of new habitat (see Population Structure and Population Dynamics section). It has also been proposed that populations in Northern Iberia lack connectivity and may be at risk due to local extinctions (Carretero et al., 1992, 1997b, 2002). However, no global threat to the population exists, given its wide distribution (see Blanco and González, 1992; Pleguezuelos et al., 2012).

Conservation measures

Several measures to conserve *P. edwardsianus* populations have been applied in the past. At the beginning of the 20th century *P. edwardsianus* was abundant in 'los Aiguamolls de l'Empordá' (Girona), but subsequently became extinct (Carretero et al., 1992). In 1990, individuals from the Ebro delta population were successfully reintroduced to this region (Carretero and Bartralot, 2000).

It has been proposed that preventing complete bush removal and protecting Mediterranean bush land may aid the conservation of the species (Carretero et al., 2002). However, allowing ecological succession to progress unchecked may lead to rapid population decline and even to eventual extinction (see Population Structure and Population Dynamics section). It is therefore very important to maintain open areas with naked soil, *i.e.,* to limit the progress of ecological succession.

Trophic Ecology

P. edwardsianus is a euryphagous or generalist species (Carretero and Llorente, 1991a). It can also be classifed as opportunistic, as its diet varies with prey abundance (Carretero, 1993).

P. edwardsianus mainly consumes spiders (Aranea), Hymenoptera (ants: Formicidae), and beetles (Coleoptera) (Table 1) (Carretero and Llorente, 1991a; Escarré and Vericad, 1981; Pérez-Mellado, 1998; Seva, 1989).

In Catalonia, in the north of its geographic distribution, true bugs (Heteroptera) form an important part of its diet, while in the South (Alicante) bugs (Hemiptera) are a major component of the diet (Table 1). No significant differences have been observed between populations in the proportion of ingested taxa (Table 1, exact Wilcoxon-signed rank test: $V = 91$, $P = 0.88$). A large proportion of the Hymenoptera consumed are ants (Formicidae), while leaf beetles (Chrysomelidae) and ladybirds (Coccinellidae) represent the most commonly consumed beetles (Escarré and Vericad, 1981). *P. edwardsianus* also eats miriapods, moluscs and crustaceans (Carretero and Llorente, 1991a; Escarré and Vericad, 1981). The most commonly ingested taxa are spiders (Aranea was present in 48.8 % of the stomachs analysed), followed by beetles (36.5 %), Heteroptera (24.1 %), butterfly larvae (Lepidoptera larvae: 31.8 %), ants (24.6 %), imagi of flies (Diptera 22.3 %), Orthoptera (18 %), Hymenotpera (16.6 %), Homoptera (15.6 %), beetle larvae (13.7 %), and isopods (10.4 %) (Carretero and Llorente, 1991a).

Males consume more Orthoptera and butterfly larvae than females and juveniles (Table 1) (Carretero, 1993; Carretero and Llorente, 1991a). As compared with males, females consume more ants while juveniles consume less Orthoptera and more ants and true bugs (Tabla 1) (Carretero, 1993; Carretero and Llorente, 1991a). Females consume a higher diversity of prey types and more units of prey than males (Carretero, 1993), while juveniles have the lowest prey diversity (Carretero, 1993). Nonetheless, frequency differences between sexes and age classes are small and non-significant (sex: $V = 143$, $P = 0.85$, age class: $V \geq 135$, $P \geq 0.78$).

Diet changes with season (Carretero and Llorente, 1991a); spiders and beetles are consumed throughout the year, while true bugs and winged ants are principally eaten in spring and autumn (Carretero, 1993), when they are most abundant.

Consumed prey ranges in size from 2 – 3 mm up to 27 – 30 mm in Alicante (Escarré and Vericad, 1981), and from 0.5 mm up to 30 mm in Catalonia (Carretero, 1993; Carretero and Llorente, 1991a). The majority of ingested prey is less than than 8 mm in size. In general, the prey size of adults is larger and more variable than that of juveniles (Carretero, 1993). Predator and prey size are positively correlated, i.e., large individuals eat large prey while small individuals eat small prey (Carretero and Llorente, 1991a).

In summary, juveniles ingest smaller prey than adults and only slight differences are observed in the frequency of ingested taxa between age classes and between sexes (Carretero and Llorente, 1991a). Females consume more prey of slightly higher taxonomic diversity than males, and prey size does not differ among sexes (Carretero and Llorente, 1991a). It has been suggested that the higher prey number ingested by females is due to their greater reproductive investment (Carretero and Llorente, 1991a).

No alimentary bottleneck exists in winter (Carretero, 1993), which allows for early reproduction and the production of up to two clutches per year (Carretero, 1993).

Table 1. Dietary composition of *P. edwardsianus* according to two studies conducted in El Prat de Llobregat (Catalonia) (Carretero, 1993; Carretero and Llorente, 1991a) and Alicante (Escarré and Vericad, 1981). The proportion of the ingested prey per taxa is indicated, and is broken down according to locality, sex, and age class where possible.

	El Prat de Llobregat (Catalonia)				Alicante
	total	males	females	juveniles	total
Arachnidae					25.4
Aranea	15.61	13.94	16.76	16.58	
Opiliones	1.49	1.88	1.73	1.36	
Acari	0.47		0.58	0.82	
Pseudoescorpiones	5.21	0.54	1.73	1.36	
Insecta					
Homoptera	4.55	4.83	6.94	2.17	
Orthoptera	4.18	7.24	4.05	1.36	2.9
Coleoptera	10.69	8.85	14.16	10.33	22.5
larvae	3.35	2.95	4.05	2.99	
Heteroptera	14.22	16.89	40	17.95	
Hemiptera					10.9
Dictyoptera	1.58	2.15	10	0.82	
Lepidoptera	1.49	2.15	3.33	1.63	0.7
larvae	7.9	8.58	35	7.88	
Diptera	5.41	6.7	23.33	5.71	4.3
larvae	0.84	0.54	6.67		
Hymenoptera	5.58	4.02	3.18	9.24	23.9
Formicidae	13.2	10.46	13.01	16.03	
Microcoryphia	1.3	1.07	1.16	1.63	
Dermaptera	0.19		0.29	0.27	2.2
Neuroptera	0.65	1.07		0.82	
Thysanura					2.2
Embioptera					0.7
Miriapoda					
Lithobimomorpha	0.19	0.27		0.27	
Crustacea					
Isopoda	4.18	4.83	3.47	3.8	
Collembola					0.7
Mollusca					0.7
Stylommatophora	0.19		0.58		
others	0.56	1.07	0.58		2.9

Male fat reserves are minimal during the reproductive period (April – June), but increase in August and reach a maxima in winter (January), when they account for 1.8 % of body mass. From January onwards, fat reserves shrink to reach minimum levels in April.

Female fat reserves are minimal in May – July, and increase thereafter, peaking in January when they account for 2.8 % of the body mass. Fat reserves shrink from February onwards to reach minimum levels in May (Carretero, 1993; Carretero and Llorente, 1991b).

Lipid consumption in males is thought to begin early in the year, and earlier than in females (February – March), probably due to the demands of pre-reproductive activity (Carretero and Llorente, 1991b).

The first clutch is fuelled by lipid reserves accumulated the previous autumn (Carretero and Llorente, 1991b), which corresponds to a capital breeder strategy. Second clutches are fuelled by lipids ingested during the previous months (May – June), corresponding to an income breeder strategy. This may explain why female fat reserves do not increase before the end of the reproductive season (Carretero and Llorente, 1991b).

Reproduction

The reproductive period begins in March (Carretero, 1993) and lasts until July (Carretero, 1993; Carretero and Llorente, 1991b; Escarré and Vericad, 1981). It is not known when copulation occurs, but it likely occurs within the same time frame as that described for *P. occidentalis* (Fitze, 2012).

The SVL of egg laying females is 37.5 – 47.5 mm (Escarré and Vericad, 1981). The SVL at which males attain sexual maturity is unknown.

Male reproductive cycle

Males attain sexual maturity at the age of one year (Carretero and Llorente, 1991b).

Testicle size and volume develop following a seasonal pattern (Figure 1 in Carretero and Llorente, 1991b), increasing slightly from January to March (Carretero and Llorente, 1991b) to remain more or less constant until the end of the reproductive period. Testicular size declines sharply thereafter (from July onwards), reaching a minimum in August. From then on testicular size increases, peaking in January (Carretero, 1993; Carretero and Llorente, 1991b). The progression of testicular size is similar in both testicles (Carretero and Llorente, 1991b).

The epididymis only develops during the reproductive period and remains small for the rest of the year. It begins to grow from January onwards to reach its maximum size in May, and subsequently shrinks until August to remain at a constant size until the following January (Carretero, 1993; Carretero and Llorente, 1991b).

Little or no relationship exists between the nuptial coloration and the testicular cycle. Sexually active males with no greenish ocelli have been observed, as well as juveniles and adults (both sexes) with greenish ocelli outside the reproductive period (Blasco, 1975; Fitze, P. S., personal observations).

Reproductive cycle of females

Females attain sexual maturity during their first spring (Carretero and Llorente, 1991b).

Ovaries increase in size from February onwards, and are well developed by March (Carretero and Llorente, 1991b), when reproduction begins, and stays the same until the end of the reproductive period in July (Carretero and Llorente, 1991b).

Ovary size shows two maxima, which occur during the reproductive period (Figure 3 in Carretero and Llorente, 1991b), the first in April and the second, which is the annual maximum, in June/July. Ovary size appears to decrease slightly in May (Carretero and Llorente, 1991b). During the non-reproductive period, ovary mass is significantly decreased (Carretero, 1993; Carretero and Llorente, 1991b).

Vitellogenic follicles have a diameter of 2 mm (Table 2a) and are present throughout the entire reproductive season (March – July) (Carretero and Llorente, 1991b; Escarré and Vericad, 1981), and number 2 – 4 (mean± sd: 2.76 ± 0.72) (Carretero and Llorente, 1991b). Oviductal eggs (Table 2b) have been observed in May and July, varying in number from 3 – 4 (3.60 ± 0.54).

Table 2. Dimension of vitellogenic follicles and oviductal eggs according to Carretero (1993) and Carretero and Llorente (1991b):

	vitellogenic follicles			oviductal eggs		
	mean	± sd	range	mean	± sd	range
length (mm)	4.16	1.5	2.05 – 7.10	10.38	1.18	8.30 – 12.80
width (mm)	3.47	1.33	1.4 – 5.80	5.66	0.45	4.95 – 6.70
volume (mm^3)	37.2	33.96	2.1 – 124.17	176.89	45.48	130.21 – 282.04

A study by Carretero and Llorente (1991b) reported no oviductal eggs in June in two consecutive years, although all females were gravid and exhibited vitelogenic follicles This observation suggests that the first clutch is produced before June (at least in the specific population studied) and the second clutch from July onwards.

Results from studies conducted in Spain (Pleguezuelos et al., 2009) and France (von Fischer, 1884b) suggest that females produce two clutches, while other authors have proposed that only large females can produce a second clutch (Carretero et al., 1992; Carretero and Llorente, 1991b, 1993). Females rarely reproduce in their second year (Carretero, 1993), although evidence suggests that individuals may live longer than one year (Carretero, 1993; Fitze, P. S. personal observations).

Clutches are laid between April and July in France (Cheylan, 1972; von Fischer, 1884b), and between early May and and late July in Spain (Carretero and Llorente, 1991b).

Females lay clutches of 2 – 4 eggs in Catalonia (mean clutch size ± sd: 2.92 ± 0.68) (Carretero, 1993; Carretero and Llorente, 1991b), 2 – 5 eggs in Alicante (average clutch size: 3) (Escarré and Vericad, 1981), and 2 – 6 eggs in France (wild individuals: 4 eggs; Cheylan, 1972; captive individuals: 2 – 6 eggs; von Fischer, 1884b; 3 – 4 eggs; Naulleau, 1980; 2 – 4 eggs; Sautureau, 1980). In two independent studies, no significant correlation between SVL and clutch size was observed (r_{Spearman} = 0.221, N = 21, Prat de Llobregat, Carretero y Llorente, 1991b; r_{Spearman} = 0.321, N = 32, P = 0.073, females from several populations, Fitze, P. S., personal observations).

Egg size in France is 12.7 x 7 mm (measured in captivity) (von Fischer, 1884b), while that recorded in Alicante ranges from 2.5 x 2.5 mm to 13.5 x 6.5 mm (Escarré and Vericad, 1981). Gestation and incubation last around 110 days and hatchlings appear from the first week of July (Carretero and Llorente, 1991b). The estimated length of the incubation period (*i.e.,* the time between the laying of the first clutch (at the start of May) and the emergence of the first hatchlings (start of July)) is ± 2 months (Carretero and Llorente, 1991b), although shorter incubation periods have been proposed for second or final clutches (those laid at the end of July), given that the last juveniles hatch in mid-September (Carretero and Llorente, 1991b). In captivity the incubation period ranges from 48 – 65 days (von Fischer, 1884b).

Population structure and dynamics

From spring until the hatching of juveniles in August, populations consist exclusively of adults; juveniles reach sexual maturity and adult body size during their first spring, thus no subadults exist when juveniles hatch (Carretero and Llorente, 1991b). Between the hatching of the first juveniles (in August) and November, the population consists of two age classes (juveniles and adults) (Carretero and Llorente, 1991b; Carretero and Llorente, 1993). The number of adults decreases progressively after the reproductive period until juveniles attain adult size (Carretero and Llorente, 1991b; Carretero and Llorente, 1993), and very few adults survive the first winter (Carretero, 1993; Fitze, P. S., personal observations). A reintroduction study reported that introduced adult animals had disappeared by July, within three months after reintroduction, further demonstrating that the majority of adults die in summer, after the reproductive period (Carretero et al., 1992). A near-complete renovation of the populations occurs annually (Carretero and Llorente 1991b; Carretero and Llorente, 1993). The highest numbers of individuals is observed in the autumn, due to the presence of recently hatched juveniles (Carretero and Llorente, 1993), and in spring due to reproductive activity (Carretero and Llorente, 1993). In El Prat de Llobregat , sex ratios of 0.56 (1.25 males/female) and 0.57 (1.33 males/female) were recorded (Carretero, 1992).

Carretero (1997 – 1998) suggested that the high population densities recorded in El Prat de Llobregat were temporally stable, although subsequent studies have demonstrated the contrary. In 2006 – 2007 the population density in El Prat was extremely low and the population was close to extinction (Llorente, G. A., personal communication; Fitze, P. S., personal observations) due to ecological succession, as a consequence of the implementation of a protection plan for the Kentish Plover (*Charadrius alexandrinus*) (Breton et al., 2000; Llorente, G. A., personal communication). These observations demonstrate that significant and rapid fluctuations in the abundance of *P. edwardsianus* do occur. Similar patterns have been observed in a population located in Playa de Pals (Girona) where a very high-density population was recorded in 2006 in an area that had been recently cleared by humans (approx. 60 individuals were recorded in 60 minutes of intensive sampling). In 2008, a high population density was once again recorded (approx.15 individuals detected in 60 minutes), while in 2009 and 2010 less than 2 individuals were sighted in one hour of sampling (Fitze, P. S., personal observations). These observations demonstrate that population fluctuations are highly dependent on the persistence of specific stages of ecological succession. As *P. edwardsianus* occupies a narrow niche within the ecological succession (see habitat section), large temporal population fluctuations occur, and temporally stable populations exist only in climax communities or in habitats that are temporally maintained by humans (*e.g.,* habitats with annual sheep and goat grazing). It has been suggested that significant migratory relocations occur from one year to the next (Seva Román, 1982), usually when the habitat becomes less attractive.

Interactions between species

P. edwardsianus sometimes lives in the presence of other lizards such as *Psammodromus algirus* and *Acanthodactylus erythrurus*, but little overlap exists at the microhabitat level (Carrascal et al., 1989; Fitze, P. S., personal observation). *P. algirus* prefers bushy areas while *P. edwardsianus* exhibits a preference for open areas (Carretero and Bartralot, 2000), and the main niche overlap exists between *P. edwardsianus* and juveniles of *P. algirus* and *A. erythrurus*. Little microhabitat overlap with other species (Carrascal et al., 1989; Fitze, P. S., personal observation) exists because *P. edwardsianus* lives in early ecological succession stages, where no other lizard can live (Carretero and Llorente, 1997 – 1998).

Antipredator strategies

When at risk *P. edwardsianus* usually flees and hides at the base of dense bushes, and in Alicante at the base of dense *Hyparrhenia hirta* and *Paronychia suffruticosa* (Seva Román, 1982). *P. edwardsianus* accelerates explosively (von Fischer, 1884b) and stops abruptly upon reaching cover, where it remains motionless to avoid detection (moving prey is more easily detected), aided by its cryptic coloration and colour pattern. Once the predator begins to move, attempting to detect the Sand Racer from the side or from above, it can no longer detect fine movement in the bush, at which point the 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 and the Sand Racer either stays in the bush or repeats this behaviour to move on to other bushes. This escape behaviour can occur in all possible directions, and the Sand Racer may return to a bush in which it has previously hidden (von Fischer, 1884b; Fitze, P. S., personal observation). *P. edwardsianus* rarely hides in holes (Fitze, P. S., personal observation). However, it frequently passes through gap between stones and vegetation in order to exit via a route that is not visible to the predator, suggesting that it hides in a hole (Fitze, P. S., personal observation).

Another anti-predator strategy attributed to *P. edwardsianus* involves rapid burrowing in the sand by moving the body from side to side (von Fischer, 1884b), although this behaviour is rare (Fitze, P. S., personal observations) and only observed where loose sand is present (*e.g.,* on sand dunes). In these conditions, *P. edwardsianus* can even creep for several meters beneath the cover of the sand without being spotted (von Fischer, 1884b; Fitze, P. S., personal observation). Another escape tactic is the simulation of death (von Fischer, 1884b). When captured it emits a short squeak, the purpose of which is unknown (Barbadillo, 1987).

Predators

Confirmed predators include *Malpolon monspessulanus* (Díaz Paniagua, 1976; Valverde, 1984), *Coronella girondica* (Vericad and Escarré, 1976), with very likely *Elaphe scalaris*, *Chamaeleo chamaeleon* (Pérez-Mellado, 1998), *Psammodromus algirus* (von Bedriaga, 1879), and *Tyto alba* (Martín and Vericad, 1977). While other avian and mammalian predators exist, published evidence is lacking.

Parasites

Encountered parasites include Nematodes: *Parapharyngodon psammodromi* (frecuency: 1.5 % of the individuals analysed) (Roca and Lluch, 1986) and *Parapharyngodon echinatus* (Nematoda: Pharyngodonidae; frecuency: 6 % of the individuals analysed), which is a parasite of the large intestine of *P. edwardsianus* (Roca and Lluch, 1986). Other parasites include

Cestodes: *Oochoristica agamae* (frequency: 6.1 % of individuals analysed), *Mesocestoides* sp. (frequency: 1.5% of the individuals analysed) (Roca et al., 1986; Roca et al., 1985), and *Oochoristica gallica*, which has been found in the intestine (Dollfus 1954) and which can reach body sizes of 15 – 30 mm.

P. edwardsianus can also be infested by Acarians, which usually attach to the side of the neck and at the point where the front legs meet the trunk (Arnold, 1986; Fitze, P. S., personal observations).

Activity

The activity of *P. edwardsianus* varies seasonally (Mellado and Olmedo, 1987). In the majority of its geographic range, *P. edwardsianus* is active throughout the entire year (Carretero and Llorente, 1993). In winter it is active in southern Levante (Barbadillo, 1987; Mellado and Olmedo, 1984, 1987) and in Catalonia (Carretero and Llorente, 1991b). In Alicante, *P. edwardsianus* is active from February to October and is probably inactive from November to January (Escarré and Vericad, 1981), suggesting that it may hibernate. Some authors have suggested that estivation may occur (Barbadillo, 1987), although solid evidence is lacking.

In Catalonia, the activity of *P. edwarsianus* decreased from December to January. In February, the number of sightings increases, peaking in April, coinciding with the reproductive period (Carretero, 1993). Thereafter, activity decreases until June, and remains low in July. Maximum activity (highest number of sightings) occurs from August to October (Carretero, 1993), probably due to the high number of hatching juveniles (Carretero, 1993; Carretero and Llorente, 1993). In Alicante, maximum activity is observed in spring, and decreases in summer (Barbadillo, 1987; Seva Román, 1982).

Daily winter activity follows a unimodal pattern and is restricted to the hours of 9 am to 1 pm, and limited to 3 – 4 hours per day (maximum duration of daily activity: 12 hours). Daily activity is higher in spring, and remains unimodal, but is bimodal in summer (Carretero and Llorente, 1993), with activity observed early in the morning (7 – 10 am, peak at 9 am) and some activity in the afternoon (1 – 4 pm) (Barbadillo, 1987; Carretero, 1993; Seva Román, 1982). In the autumn, *P. edwardsianus* activity is unimodal, beginning as early as 6 am, with maximum activity between 9 am and 3 pm (Carretero, 1993).

Similar activity patterns are observed in males, females, and juveniles (Carretero, 1993), both in terms of the daily activity pattern and the point of maximum activity (Mellado and Olmedo, 1984). However, slight differences in the duration of activity are observed between age classes. Compared to adults, juveniles exhibit an opportunistic activity pattern and maximize their activity period (Carretero and Llorente, 1993). In general, small sized individuals exhibit more uniform daily activity and an increased range of daily activity (Carretero and Llorente, 1993). The activity of males, females, and juveniles increases after adverse meteorological conditions.

Thermal biology

P. edwardsianus displays thermo-conformity (Carretero and Llorente, 1993) and can also adjust body temperature via thermoregulation (Carretero, 1993), which plays an important role in the winter. Average body temperature (cloacae temperature) is 30.7 ± 4.43°C (mean ± sd) (range: 18.3 – 38.4°C) (Carretero and Llorente, 1993). Body temperature is normally higher than air or substrate temperature, with the exception of the summer, when substrate temperatures are higher than body temperatures (Carretero and Llorente, 1993). Male body temperature (31.6 ± 3.86°C; 23.1 – 37.6°C) is higher than that of females (30.9 ± 4.42°C; 20.9 – 38.4°C) and juveniles (30.0 ± 4.7°C; 18.3 – 37.8°C) (note that these juvenile values correspond to those reported for juveniles by Carretero, 1993), and for females by Carretero and Llorente (1993). It is thus unclear whether females have higher body temperatures than juveniles, or *vice versa*). Body temperature is positively correlated with air and substrate temperature in both males and females, and depends more importantly on the former (Carretero and Llorente, 1993). No differences are observed between sexes or age classes in terms of the effect of air or substrate temperature on body temperature (Carretero, 1993). In winter, the difference between body temperature and air or substrate temperature is greater than in summer or autumn (Carretero, 1993). Preferred body temperatures (as measured in the laboratory) differ among seasons. The preferred body temperature is 30.6 ± 1°C in spring, 32.6 ± 1.2°C in summer, 32.3 ± 0.7°C in autumn, and 29 ± 1.5°C in winter (Patterson and Davies, 1984). Preferred body temperatures are thus lower in spring and winter than in summer and autumn (Patterson and Davies, 1984). Thermoregulation occurs in response to cold air temperatures and is mainted for the entire day in winter. In summer, thermoregulation is observed early in the morning and at the end of the day (Carretero and Llorente, 1993). Because air humidity is higher during thermoregulatory hours in the summer, it remains unclear whether low humidity, high temperatures or both are responsible for the reduced thermoregulatory activity in the middle of the day (Carretero and Llorente, 1993).

The increased thermoregulatory activity of juveniles may be a consequence of reduced thermal selectivity, rather than decreased thermoregulatory efficiency. Juveniles display more opportunistic thermoregulatory activity and maximize the period of thermoregulation, which may permit increased food consumption (Carretero and Llorente, 1993).

Metabolic rates range from 14.52 $\mu l\ O_2\ g^{-1}h^{-1}$ ± 1.33 (mean ± sd; measured in non-gravid females in winter at 5°C) to 465.8 $\mu l\ O_2\ g^{-1}h^{-1}$ ± 127.3 (measured in males in summer at 35°C) (Patterson and Davies, 1984). No differences in metabolic rate are observed between males and females, although differences in resting metabolic rate are observed between seasons. In winter, the resting metabolic rate at low temperatures is significantly lower than that observed in any other season (Patterson and Davies, 1984), suggesting that the winter resting metabolic rate may be the result of reduced activity.

The metabolic rate at 20°C is higher for gravid females compared to non-gravid females and males (Patterson and Davies, 1984), which may be a consequence of increased activity or reproductive investment.

Home range

The territory size of *P. edwardsianus* is estimated at 25 m^2 (estimate based on 8 captures) (Seva Román, 1982). No additional data are available.

Behaviour

Noise/Sound Production

*P. edwardsianus p*roduces high-pitched squeaking noises when manipulated (von Fischer, 1884a; Fitze, P. S., personal observation). These noises may also be emitted in the presence of a predator and during reproduction (von Fischer, 1884a). When a male approaches a female, females can emit a long squeak, but no sound is produced during copulation (in den Bosch, 1986). Phonographic recording have demonstrated that the frequency of the emitted sound is 1.5 – 16 kHz and the duration 220 – 750 ms (Böhme et al., 1985). However it is unclear whether these sound recordings pertain to *P. hispanicus, P. edwardsianus,* or *P. occidentalis*.

Movement

P. edwardsianus is mainly terrestrial and can climb small bushes. In coastal areas climbing appears to be absent (Carretero, 1993), while individuals have been seen to climb bushes in inland regions (Fitze, P. S., personal observations). *P. edwardsianus* has no fixed refuges (Carretero, 1993), which may favour the colonization of new pioneer habitats. Snake-like tail movements have been observed during male-male encounters and when frightened (Fischer 1884a).

Tongue flicking

The rate of tongue flicking increases in the presence of visible prey (Verwaijen and Van Danune, 2007), but does not differ from control situations in the presence of chemical cues originating from potential prey. The tongue flicking rate is highest when potential prey is both visible and chemically perceived (Verwaijen and Van Danune, 2007). The normal tongue flicking rate is 3.6 times per minute ± 0.5 se. This increases to 3.7 times per minute ± 0.5 upon detection of prey scent, 6.5 times per minute ± 0.8 when prey is visible, and 7.7 times per minute ± 1 when prey is visible and chemically perceived (Verwaijen and Van Danune, 2007).

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