Species Review 11:

Lestes macrostigma (Eversmann), the Dark Spreadwing

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Summary

Lestes macrostigma (Dark Spreadwing) occurs across the southern Palearctic from the Atlantic coast as far east as Mongolia. It is locally common in the central part of its range, including Greece and Bulgaria, but becomes increasingly rare in the western parts of the region where, with notable exceptions, it is essentially coastal. It is very much associated with temporary, brackish and saline habitats and, very often, with *Bolboschoenus maritimus* (Sea Club Rush). Many of its coastal habitats are under threat, especially from wetland transformation schemes of various types and, for that reason, the species is listed as Endangered in the European Red List.

Phylogeny

The family Lestidae comprises approximately 150 species (Bridges, 1994; Dijkstra *et al*., 2013). In the western Palearctic, it comprises three genera:

- *Sympecma* – (Winter Damseflies- 2 species) – dull brown patterned species providing camouflage for the overwintering adults. The only genus in western Europe with this behaviour.

- *Chalcolestes* – (Willow Emeralds- 2 species) – large metallic green damselflies without blue pruinosity. These species usually oviposit in green wood above their breeding habitat.

- *Lestes* – (Emerald Damselflies or Spreadwings - 5 species) – medium to large metallic damselflies with blue pruinosity.

The genus *Lestes* is one of the most widely distributed, with species ranging over all continents (except Antarctica) from the tropics almost up to the Arctic Circle. They are medium to large damselflies, mainly inhabiting open, stagnant and often temporary waters. In the western Palearctic, the genus can be further classified into two phylogenetic groups (Dijkstra and Kalkman 2012):

- Northern *Lestes* – *Lestes sponsa* (Hansemann, 1823) and *L. dryas* Kirby, 1890. Both species occur in the UK. The males of both species have extensive blue pruinescense on both the thorax and the abdomen.

- Southern *Lestes* – *Lestes barbarus* (Fabricius, 1798), *L. virens* (Charpentier, 1825) and *L. macrostigma* (Eversmann, 1836). Of these only *L. barbarus* has been recorded in the UK. The males of *L. barbarus* and *L. virens* have limited blue pruinescense.

Lestes macrostigma (Dark Spreadwing) is the largest species in the genus and the sexes are very similar, exhibiting little sexual dimorphism. Males and females are both metallic black with extensive blue pruinosity and conspicuously large pterostigmas, making them unmistakeable.

Description

Egg

Eggs in all Lestidae are laid endophytically (inserted into plant shoots) and are therefore elongate. Eggs are approximately 1.4 mm long (Matushkina & Lambret, 2011), which is similar to other species of the genus with the exception of *Lestes dryas*, where they are rather larger at 1.8 mm long (Jodicke, 1997). Eggs of all species are approximately 0.3mm diameter.

Larva

Lestid larvae are quite distinctive, with long legs and often with patterned or almost black caudal lamellae. In *Lestes macrostigma* the patterning of the lamellae is rather indistinct (Plate 1). The colour of the exuviae may vary in different places, those collected at Laguna de Petrola in Spain, for example, appearing lighter coloured than those from France and Lesbos.

The shape of the caudal lamellae can be useful in identification to species level, although *L. macrostigma* can be more easily identified by the shape of the labial mask (Nielsen, 1954). Indeed, the labial mask of all species of *Lestes* is very distinctive and is worthy of some discussion. In general, the total length

Plate 1. Final instar larva of *Lestes macrostigma*. Photograph by P. Lambret.

of the extended mask (i.e. prementum + postmentum) almost always exceeds 40% of the overall length of the larva (excluding the lamellae) (Table 1, Plates 2A, 3A). This is greater than that in other genera of damselflies (Plate 2B,C). The advantage of the long extension is presumably to facilitate catching prey but this advantage can only be achieved by streamlining of the prementum as otherwise it would become unwieldy, resulting in loss of control. However, uncharacteristically, the length of the extended mask in *L. macrostigma* is only about 31% (Table 1, Plate 3B), which is considerably less than in the other species of the genus. The shape of the prementum reflects this (Plate 3) and the 'hourglass' shape of the prementum in *L. macrostigma* (Plate 3B) is probably the most important diagnostic feature for the larvae of this species.

Adult

At the teneral and post-teneral stage (*sensu* Corbet, 2004), immediately after emergence, when the cuticle has not completely hardened and when flight is clumsy, the majority of damselflies can be hard to identify as they lack colour and identification markings. However, this is not the case with *Lestes macrostigma,* which, even at this early stage, is an unmistakable and striking metallic black. This coloration develops approximately two hours after the beginning of final ecdysis (i.e. when the adult dorsum breaks through the thorax of the larva, at which stage it is uncoloured (Plate 4A) (Lambret, 2013). The change to the post-teneral black adult is striking (Plate 4B). Even if the adult is trapped in its exuvia it still develops its black colouration (Plate 4C). In certain light conditions,

Table 1. The total length of the extended mask (pre and post mentum) compared with the total length of the body, excluding the lamellae, in zygopteran families. From specimens of exuviae in the first author's collection.

	Length of extended labial mask (mm)	Body Length (excl. lamellae) (mm)	Length of mask as a percentage of body length
Lestidae			
L. dryas	8.3	19.5	43%
L. sponsa	7.1	17.0	42%
L. barbarus	7.7	16.8	46%
L.v.virens	6.9	16.0	43%
L. macrostigma	5.3	17.0	31%
Calopterygidae			
C. haemorrhoidalis	6.7	17.5	38%
C. virgo	6.7	20.0	34%
Coenagrionidae			
E. najas	4.1	17.0	24%
E. cyathigerum	3.1	13.0	24%
I. elegans	3.2	12.0	27%
Platycnemidae			
P. pennipes	4.0	14.0	29%

the teneral adults can look bluish with bottle-green hues on the abdomen (Plate 4D). The eyes at this stage are dull brown.

The day following emergence, the adults of both sexes start developing a blue pruinosity over the entire body, with the exception of the five median segments of the abdomen (Lambret, 2013). When mature, the eyes become cobalt blue in the male, and half teal - half navy blue in the female. The metallic black base and extensive pruinescence (Plate 5) renders these insects unmistakeable in the field at any stage in their development and is particularly useful when studying populations where other *Lestes* species are present. When fully adult the individuals, like all species of the genus, rest with their wings open (Plate 5). However, in periods of bad weather or when young, they rest with all four

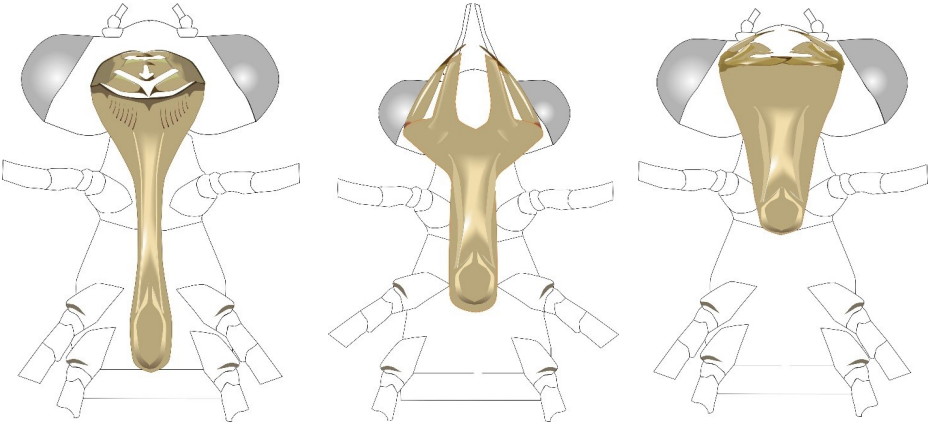

Plate 2. The various shapes of the prementum (viewed from below) of three species which represent three western Palearctic damselfly families. (A) In *Lestes barbarus* the spoon shaped prementum is greatly narrowed for much of its length, (B) In *Calopteryx haemorrhoidalis* the prementum is both narrowed and extended forward, (C) *Erythromma najas* has a typical triangular prementum. The total length of the labial mask compared to the overall length of the larva is 46% in *Lestes barbarus*, 38% in *Calopteryx haemorrhoidalis* and 24% in *Erythromma najas*.

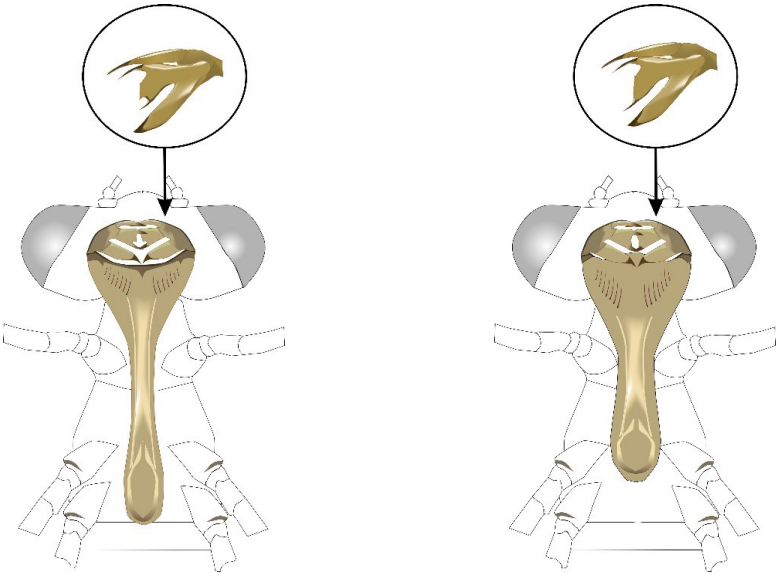

Plate 3. Comparison of the labial mask of (A) *Lestes barbarus* and (B) L*estes macrostigma*. The total length of the labial mask compared to the overall length of the larva is 46% in *Lestes barbarus* but only 31% in *Lestes macrostigma*.

A

B

C

D

Plate 4. The neutral colour of the emerging adult *L. macrostigma* (A) quickly changes to the striking and diagnostic black of the newly emerged adult (B), even when the adult remains trapped in its exuvia (C), with developing colours as the insect matures (D). A, photograph P Lambret; B & C, photographs by D.Chelmick; C, photograph by Isidro Frutos.

wings closed along the sides of their body (Plate 4D). This is characteristic of all European Lestidae, except in the genus *Sympecma*, which always holds its wings in this closed manner.

Distribution & Abundance

Boudot & Raab (2015) stated that *Lestes macrostigma* has a very extensive, albeit fragmented, distribution. It ranges from Iberia across Europe, Kazakhstan and Southern Russia to Siberia, China and Mongolia, extending north as far as the 49th degree of latitude. It is locally common in the eastern part of its range up to the 13th degree of longitude, beyond which it becomes increasingly rare. In Italy and the Mediterranean Islands the colonies are essentially coastal (Boudot & Raab, 2015).

Annual abundance is highly variable with strong populations in one year but virtually disappearing the next (Borisov, 2005; Cano-Villegas & Conesa-García, 2010; Berquier & Andrei-Ruiz, 2019). Local weather conditions are largely responsible for this variability due to problems of egg viability on the one hand, and fitness of larvae on the other:

- Egg mortality from dessication increases the longer the egg is not flooded. If flooding does not occur until late spring the year after oviposition, the egg is no longer viable (Lambret *et al*., 2018).

- From data in Southern France, larval densities are greatly reduced if flooding takes place too early in the year of oviposition (late summer/early autumn) (Lambret *et al*., in prep. a).

- Although increasing salinity enhances survival of larvae, it has sub-lethal costs on larval fitness, even affecting the adult insect (Lambret *et al*., in prep. b).

In summary, optimum populations are produced in western Europe only when the drought period is ended in late autumn/early winter and flooding persists until the adult insects appear in Spring.

Its distribution in southwest Europe is very restricted. In France it is found in only two areas. The southwest Atlantic coast, where it is generally rare and sporadic, although quite common in the southwest corner of Poitou-Charentes (Grand & Boudot, 2006; Jourdes, 2009). The second area is the southeast Mediterranean coast centred upon the Camargue. It is also found in Corsica (Berquier & Andrei-Ruiz, 2019). In Spain there are also two centres of distribution - along

A

B

Plate 5. Adults of L. macrostigma. (A) male, (B) female. Photographs by D. Chelmick.

the southern coast of Andalucia and in the recently discovered colonies in the central uplands of Castilla La Mancha (Plate 6).

In France it breeds regularly in the Camargue along the Mediterranean coast. It also breeds in the Olle d'Oleron and in the Marais de Rochefort et Marennes area of the Poitou-Charentes region (Jourde, 2009). In Spain, breeding has been confirmed in both the main centres of distribution. However, the populations are highly variable. To illustrate how variable populations can be, and by kind permission of Florent Prunier, we have extracted records from ROLA (la Red de Observadores de Libélulas en Andalucía), which includes all Spanish data for this species.

There have been considerable fluctuations this century (Table 2). There were no records on the database from 1995 and 2005, then occasional good years (i.e. 2011 and 2018) separated by years of near absence. The huge increase in 2018 is most encouraging but perhaps only indicates the increase in dragonfly

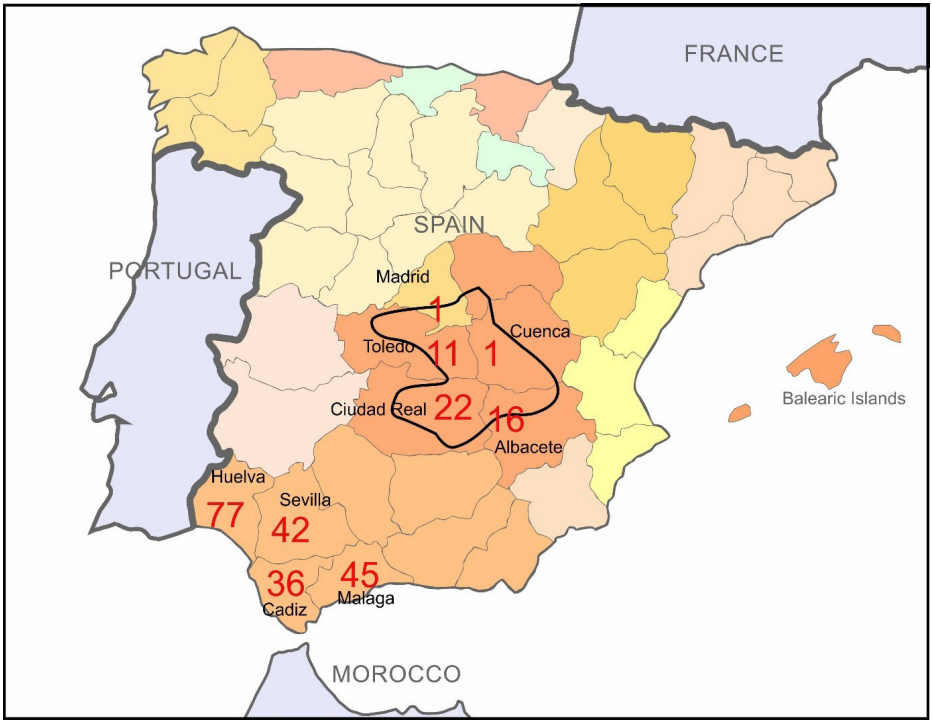

Plate 6. Map of Spain showing all records by Province for *L. macrostigma*, except for isolated historical records. The region bordered by the black line was described by Lorca et al. (2008) as La Llanura Manchega, which shows remarkable parallels with the Pannonian Basin in terms of its mean May temperature and its mean annual temperature range.

Table 2. The Spanish provincial records for *L. macrostigma.* The total and by year for this century are shown.

Region	Total (all years)	2006-2009	2010	2011	2012	2013	2014	2015	2016	2017	2918	2019
ANDALUCIA												
Cadiz	36	1	5	5	1			3		4	10	
Huelva	77	3	8	20	2	3	1	4		4	18	
Sevilla	42	1	7	4		3	2	1	1	4	11	
Málaga	45	3				1	1	5			24	
CASTILLA LA MANCHA												
Albacete	16										10	6
Ciudad Real	22					1		1	3		7	9
Cuenca	1										1	
Madrid	1											
Toledo	11										3	2
Total	**251**	**6**	**20**	**29**	**3**	**8**	**4**	**14**	**4**	**12**	**84**	**17**

recording in Spain. In 2019 there were no records from Andalucia, whilst the recently discovered central Spain (Castilla La Mancha) sites continued to flourish. At the time of writing there is little information concerning 2020, although Cecilia Diaz Martinez (pers.com.) reports sightings of two mating pairs on one of the Central Spain sites that was dry for the whole of 2019.

Habitat

Lestes macrostigma is restricted to temporary, brackish (oligohaline) waters (Grand & Boudot, 2006; Boudot & Raab, 2015), although the species appears to breed much more extensively in fresh water in the eastern parts of its range (Kosterin, 2015). Such warm, shallow waters contribute to its rapid larval development in the western Palearctic (Schiel & Buchwald, 2015). Although this species oviposits in various plant species, it is closely associated with *Bolboschoenus maritimus* (Sea Club Rush) and, to a lesser extent, with *Juncus maritimus* (Sea Rush) and *Schoenoplectus lacustris* (Common Club Rush) (Matushkina *et al*., 2016; Lambret *et al*., 2018). Such habitats invariably dry out in summer and rely upon spring rainfall for successful development of the larvae. Typical important sites for this species are the marismas of the Coto Doñana in Spain (Plate 7) and Marais du Vigueirat, Tour du Valat Natural Reserve in

the Camargue, France (Plate 8). The Laguna de Petrola, one of the recently discovered sites in Central Spain, can be quite dry in the autumn (Plate 9).

Life Cycle

Egg

Lestes macrostigma lays its eggs preferentially in the stems of *Bolboschoenus maritimus* (Plate 10A), although other narrow leaved plants such as *Juncus* sp. are used (Plate 10B) (Lambret *et al*., 2015a,b). Each visiting female lays her eggs in a vertical line (Plate 10A) and it is therefore possible to see how stems have been used by many females (Matsushkina & Lambret, 2011). Lambret *et al*. (2018) demonstrated that, because *B. maritimus* grows in deeper parts of temporary ponds, after the drought period they are flooded before other plants, thereby enhancing hatching success and early larval development. The eggs are highly resistant to desiccation and are able to delay hatching during prolonged periods of drought (Lambret, 2018).

Lambret *et al*. (2017) recalled that wintering damselfly eggs are divided into two types:

- Type 1 which winter at an early development stage before katatrepsis (embryo development – (Corbet, 2004)).

- Type 2 which winter in an almost fully completed embryonic stage after katatrepsis.

Different *Lestes* species belong to different types. *Lestes macrostigma* eggs belong to Type 1, which Lambret *et al*. (2017) suggested is adaptative to a typically unpredictable environment, thereby avoiding hatching too early when ponds may dry prematurely during late winter in certain years. Due to their earlier embryonic stage, Type 1 eggs are less sensitive to environmental changes. This strategy also allows for freezing and ice bound conditions, commonly found in the upland habitats of central Spain and parts of central Europe. This late hatching is combined with rapid larval development and growth (Schiel & Buchwald, 2015) so that it can be completed before the habitat dries out. Lambret (2018) stated that egg survival rates do not extend beyond one year, which means that *L. macrostigma* is unable to cope with prolonged drying of habitat over a number of years.

Eggs are always laid above the water and are typically flooded by rainfall in autumn and winter. Flooding is necessary for initial embryo development

Plate 7. June in the marismas of the Coto Doñana, which is the most important area for *L. macrostigma* in Spain. Photograph by D. Chelmick.

Plate 8. Close up of breeding habitat for *L. macrostigma* at Tirasses, Tour du Valat Natural Reserve, Camargue, France. Photograph by P. Lambret.

Plate 9. Laguna de Petrola. One of the recently discovered breeding sites for *L. macrostigma* in Central Spain, showing it dry in September. Photograph by D. Chelmick.

(Lambret *et al*., 2018). Post-winter, when average daily water temperatures reach approximately 14°C, embryo development is recommenced in all eggs simultaneously and lasts approximately two weeks (Martynov & Martynov, 2008). This results in synchronized hatching (Lambret *et al*., 2017) with up to 50% of eggs developing to larvae during a two week period at the end of March. As a result, *L. macrostigma* hatches later than other lestid species but has the shortest development time and highest growth rate (Schiel & Buchwald, 2015).

Larva

Lambret (2016) found that larvae in Southern France were 22 times more abundant amongst aquatic vegetation than over exposed mud. In the Lagunas of central Spain, where breeding populations of *Lestes macrostigma* have recently been discovered, there is very little aquatic vegetation other than emergent plants such as *Juncus spp* (rushes) and *Bolboschoenus maritimus*. In such cases, the larvae live amongst the bases of the emergent plants making them difficult to observe and concealing them from predators. Lasting approximately 2 months, larval life is short even compared to other lestid species and successful completion can be a race against time before the habitat dries out. One of us (DC) visited the Salinas de Pinilla in central Spain in Spring 2019. The water was very shallow (circa 15 cm) and its temperature was 19°C. There was no aquatic vegetation but the water was a soup of clearly visible tiny invertebrates.

A

B

Plate 10. Egg cuts made by a female *L. macrostigma* in (A) *Bolboschoenus maritimus* and (B) *Juncus maritimus*. Photographs by P. Lambret.

Adult

Dispersal *Lestes macrostigma* inhabits temporary shallow waters, which are by their very nature unreliable; the current year's breeding habitat may or may not be suitable for coming generations. In order to find suitable new sites and expand its range, the species exhibits dispersive behaviour, especially where large numbers emerge (Papazian, 1995). Vagrants are regularly found far from the nearest reproductive site (Kuhn, 1998; Marinov, 2007). As an example of the spectacular dispersal of this species, in late May and early June 2018 one male and one female were recorded from Quintana de la Serena in the province of Badajoz in Spain (Frutos Cuadrado *et al*., 2019). This site is some 200 km north of Coto Doñana and 300 km west of the recently discovered Central Spain sites, although it is possible that some overlooked breeding sites may exist in between.

Fons Peels (pers com.) photographed a cloud of maturing *L. macrostigma*

Plate 11. Post-teneral and maturing *L. macrostigma* during a massive emergence in Greece in May 2019. Photograph by F. Peels.

in Greece in 2019 (Plate 11). The large numbers present would dictate that they would overwhelm the available breeding habitat and would be looking to disperse.

Reproduction Lambret (2010) stated that sexual maturity (tandems observed) is achieved approximately 15 days after emergence. This accords with other *Lestes* species (Sawchyn & Gillott, 1974a,b). Lambret & Stoquert (2011) described the species daily pattern of activity, and especially reproduction. Males actively search out females from early morning and, once found, the females are held in tandem.

The male then transfers sperm from the genital pore at the end of his abdomen to the bursa copulatrix (Plate 12A). This usually takes place when a tandem is formed immediately before copulation. On completion, the male encourages the female to mate by curving his abdomen upward (Plate 12B). If the female is ready she will then form the copula (Plate 12C). Copulation lasts from 10 to 50 minutes. In most cases, the female will already have copulated with another male and is, therefore, ready to oviposit. When forming the initial tandem, it is essential that the new male prevents the female from reaching plant stems in which she will lay eggs. The new male will usually land on a leaning shoot,

A

B

C

Plate 12. Stages in mating in *L. macrostigma*. (A) Sperm transfer during tandem (the penis can clearly be seen), (B) Pre-copula, (C) Copula. A & C, photographs by D. Chelmick; B, photograph by P. Lambret.

A

B

Plate 13. (A) A tandem pair of *L. macrostigma* with the hanging female unable to lay eggs, (B) Detail of a 'hanging' female. A, photograph by P. Lambret; B, photograph by D. Chelmick.

Plate 14. Oviposition in *L. macrostigma,* which is almost always carried out in tandem. Photograph by D. Chelmick.

thereby preventing oviposition and encouraging copulation (Plate 13). It is noted that, in most Zygoptera, removal of any previously placed sperm forms part of the copulation process (Corbet, 2004; Adolfo Cordero-Rivera, pers. com.).

Once copulation has been completed, oviposition commences immediately. The pair remains in tandem and search out suitable oviposition plants (Lambret, 2015b). Oviposition is often in areas that have dried out; however, where water is present the egg laying is always between 10 and 30 cm above the surface (Plate 14). When the female has completed oviposition, she grooms her ovipositor with her hind legs (Plate 15) and, after the male has, unsuccessfully, suggested further flight by repeated slight wing beats, the pair separates.

Flight Season *Lestes macrostigma* is generally considered to be an early flying species. However, adult emergence timing is very much dependent upon water temperature, flooding and the commencement of post-diapause embryo development. Lambret (2010) summarised the flight period, which varies with latitude, starting in March in Turkey and as late as August in Romania, Austria

Plate 15. A female *L. macrostigma* grooming her ovipositor post oviposition. Photograph by P. Lambret.

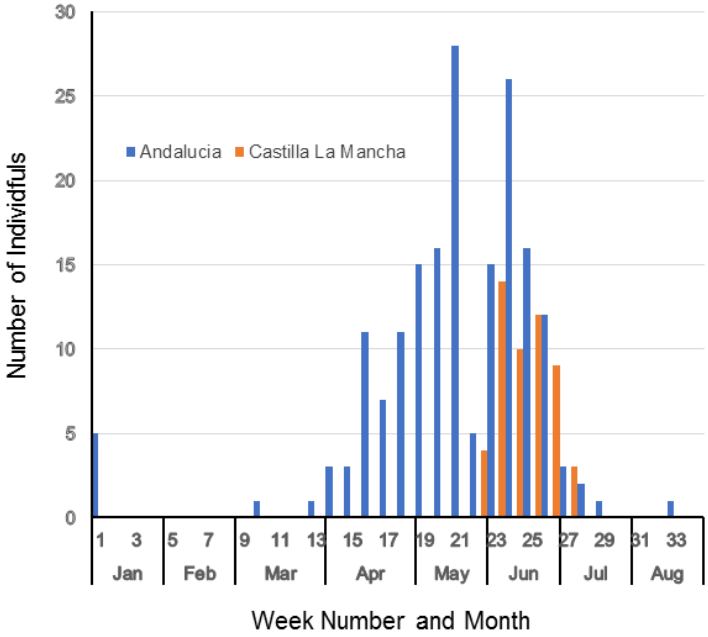

Figure 1. Records of *Lestes macrostigma* from Spain showing the numbers recorded in Andalucia and Castilla La Mancha by week number and by month (ROLA Database). Week 1, 1 January; Week 33, 12 August.

and the French Atlantic Coast. However, there are some anomalies, J-P Boudot (pers.com.) recording emergence in Sardinia on 29 July in 2008.

The flight period in southwest France has been noted as from 18 May to at least the end of July (Grand & Boudot, 2006; Jourde, 2009), with the peak of emergence being in the first two weeks of June (Jourde, 2009). In Andalucia (which is primarily the Coto Doñana), if weather conditions are right, very early appearances are possible. In normal years, where egg hatching occurs in mid March (Lambret *et al*., 2017), the main adult season commences in early May, peaking during June (Lambret, 2010) (Fig. 1). In central Spain, in the cooler upland conditions, June is the most important month (Fig. 1), although records for this area are fewer and the complete time-frame may be greater. The duration of the flight season depends on the beginning of the drought period, a longer flooded phase of the habitat allowing late larvae to achieve their development and to emerge successfully, which lengthens the flight period. In southern France, because of this and given that adults can live up to 50 days (Lambret, unpub. obs.) explains why the flight period can last until the end of July (Lambret & Papazian, 2017).

Climactic Influence – could *Lestes macrostigma* become a UK species?

Boudot & Raab (2015) provided a map of the European distribution of *Lestes macrostigma*. Analysis shows that 57% of the records are lowland and within 20 km of the coast.

Taking this map and overlaying it digitally with climatic variables (Steinhauser, 1970) then:

- 88% of all records occur where the mean May temperature is ≥15°C.
- 93% of inland records are to be found where the mean annual range of temperature is ≥20° C.

An analysis of the inland records shows that approximately 40% of these are concentrated in an area of eastern Austria and Hungary known as the Pannonian Plain or Basin, which fulfils both temperature criteria.

Much of western Europe is outwith the mean annual temperature difference highlighted here. However, there is an area of central Spain where such conditions prevail. This region (bordered by the black line in Plate 6) is described by Lorca *et al*. (2008) as La Llanura Manchega, which shows remarkable parallels with the Pannonian Basin and is where almost all recent Central Spain discoveries of *L. macrostigma* have been made. Chelmick (in prep) provides a detailed comparison of the two regions.

The newly discovered sites in Central Spain could imply that *L. macrostigma* is expanding its range. However, the possibility that this poorly recorded area has simply been overlooked is perhaps more likely. Does this mean that it will eventually become part of the UK fauna? One of the key temperature criteria is the mean May temperature of **≥** 15°C. Steinhauser (1970) shows this contour south of the Alps in France, entering Spain near Barcelona and crossing immediately to the north of Madrid. Such conditions are unlikely to prevail in the UK in the forseeable future. However, there are coastal colonies in France which are clearly outwith this variable. The Vendee is a region of France north of La Rochelle with lowland coastal marshes in which *L. macrostigma* thrives; indeed Benoit Guillon (Guillon 2020) posted photos of a population of more than 500 individuals on 2 June 2020. This region is contained within a mean annual range of temperature of **≥**15°C, which includes much of eastern England. Lowland coastal habitat is certainly available as is *Bolboschoenus maritimus*. A further positive indicator is that the damselfly with which *L. macrostigma* is most often associated in Spain is *Lestes barbarus*, which has in recent years established a number of colonies along the south and east coasts of England

(e.g. Parr, 2020). It is hoped that this paper will encourage UK field observers to be diligent in their coastal searches and that yet another lestid species can be added to the UK list.

Conservation

Lestes macrostigma is a species requiring warm spring habitats with flooding lasting from late autumn through to late Spring in order to successfully complete its larval development. With the inevitable warming of our climate, does this bode well for its future? The recent discovery of populations in central Spain is encouraging. However, more importantly, the warming climate brings unpredictability of weather and, if dry springs become more common, then the future of this insect, particularly in western Europe, is uncertain.

The temporary nature of the habitats on which *L. macrostigma* relies render it very vulnerable to weather conditions, primarily rainfall. Many of the habitats are coastal, of which most have already disappeared and many others are still threatened by industrial and urban development. In the Marennes Oleron basin (Poitou-Charentes) the habitat is seriously threatened by intensification of oyster cultivation (Jourde, 2009). Fortunately most of the key western European sites: the Coto Doñana in Spain, the Camargue and the Neusiedl Lake in the Pannonian Basin all have a reasonable degree of protection. In the Camargue, during unfavourably dry years, the core populations are in seasonal habitats where water levels are controlled by conservation management systems. The situation in central Europe and, in particular, the Pannonian Basin of Austria and Hungary, which contains many historical records (Boudot & Kalkman, 2015), is not known. Whether the species has declined here or is simply under recorded, is not known. Recently, several pilot programs of species habitat restoration or adaptive management have been initiated (Lambret *et a*l., 2016) and should be extended to other regions across Europe.

Acknowledgments

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Website

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