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Cover illustration: Male *Calopteryx splendens* compete for prominent perches at a prime breeding site. Photograph by Steve Cham.

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Observations of male aggression in *Calopteryx splendens* (Harris) (Banded Demoiselle) and territorial behaviour at high population density

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Summary

Calopteryx splendens (Harris 1782) (Banded Demoiselle) favours slow to medium flowing rivers and streams, where males can be observed defending territories in areas that are most likely to attract females. At high population densities, male territorial behaviour changes and becomes more aggressive, with biting used in an attempt to displace tandem males. This paper describes territorial behaviour and male strategy observed during the summer of 2018, when high numbers of *C.splendens* were increasingly concentrated into small areas of a stream due to lowering water levels.

Introduction

Male *Calopteryx splendens* defend strategic areas of stream or river which females are likely to find attractive for ovipositing. These comprise areas with suitable perches for males just above the water's surface and a suitable oviposition substrate, such as floating and submerged leaves of aquatic macrophytes, for females. Adult males defend these areas by chasing intra and interspecific intruders at the water's surface (Zahner, 1960; Plaistow, 1997) and will typically display to other rival conspecific males by flashing their heavily pigmented wings at each other while in flight (Plate 1). Under normal situations, with low or medium population density, males will perch on prominent objects just above the water's surface and will fly out to intercept potential rival males with little if any physical contact. Females visit water when they are ready to mate or oviposit and single males will typically display to a female as she approaches the water by wing whirring while flying low over, or just on, the water's surface (Plate 2). The male also raises the distal segments of the abdomen to reveal the prominent light cream coloured underside, to signal to the female that this is a suitable place to oviposit. Where a number of males are present in the same area a passing female will attract their attention and they will pursue her by flying after her. Such processions are a regular occurrence at breeding

Plate 1. At low to medium population densities, male *Calopteryx splendens* display to conspecifics by wing flashing to defend prime areas of water.

Plate 2. A male *Calopteryx splendens* settles on the water trying to attract passing females by wing whirring.

sites. There are indications that males adopt two sets of behaviour depending on population density – a territorial male strategy and a non-territorial male reproductive strategy at suitable locations (Golab *et. al.,* 2017) and these will be discussed in this paper.

After a male has successfully formed a tandem the pair leave the water and copulation promptly takes place on bank-side vegetation. They return to water after mating with the female ovipositing, either in tandem or alone, in areas of underwater plants (Plate 3). At low population densities this will often go undisturbed with the female going on to oviposit alone after release from tandem. At higher densities, tandem pairs will encounter repeated and aggressive attacks from rivals in an attempt to displace the tandem male. This behaviour was observed frequently during the summer of 2018, when high numbers of *C.splendens* males were increasingly concentrated into a small area of stream due to exceptionally warm weather, low rainfall and subsequent lowering of water levels.

The study site

The Elstow Brook flows west to east across central Bedfordshire (VC30),

Plate 3. When undisturbed, female *Calopteryx splendens* will typically oviposit alone.

flowing into the River Great Ouse at Willington. The study site is a length of stream near Willington (TL105502) which is approximately 3 metres wide with a depth in summer in most years in the range of 0.5 to 1 metre. *Ranunculus fluitans* (River Water-crowfoot) grows in the shallower parts of the stream and it is these areas that are attractive to *Calopteryx splendens* (Plate 4A). The area is well recorded and *C. splendens* is present each year in moderate numbers (recorded according to BDS convention as C: 6-20). Higher numbers (recorded according to BDS convention as E: 101-500) can also be observed along the nearby River Great Ouse. The summer of 2018 was notable for long, warm and sunny periods throughout. The low rainfall and warm temperatures were noted as a heatwave in Bedfordshire, where temperatures in July reached in excess of 30ºC over a number of days (Bucknall, 2020). As the summer progressed, the lowering water levels in the stream created areas with an average depth of <0.2m, shallow enough to walk across. As the population of *C. splendens* increased, individuals became more concentrated in close proximity to areas of crowfoot in these shallow areas, where the leaves were exposed at, or just below, the surface of the water (Plate 4A).

Methods

Regular observations were made over five days, between 23 and 27 July 2018, at the peak of numbers during the flight period. The improved access to the stream areas due to the low water levels enabled a close approach so that mating behaviour could be studied and photographed (and videoed) with relative ease (Plate 4B). Still photographs and videos of behaviour were recorded using a Canon 7D digital camera fitted with a Canon 100-400mm f/4.5-5.6L IS II USM lens mounted on a tripod. This enabled the setup to be positioned in the stream with good visibility of any activity. Observations in the field, made by eye, do not always 'see' the detail of rapid behavioural events. Only by taking sequences of photographs or videos can the nature of the interactions between individuals be revealed. In this study, details of mating and aggressive behaviour, including biting, were recorded that would normally be difficult to evaluate directly in the field.

Observations

Throughout each site visit, males were observed competing for perching sites, with multiple males occupying prominent perches in prime areas (Plate 5). At their peak the number of males was estimated in the range of 70-100 individuals (recorded according to BDS convention as D: 21-100) along this short stretch (approximately 20m) of the Elstow Brook. Females, both alone and in tandem,

A

B

Plate 4. The study site at Elstow Brook (A) the area of River Water-crowfoot growing in the shallow water attractive to *Calopteryx splendens*, (B) The exceptional low water levels in 2018, allowing close observation of mating behaviour. Richard Revels and Stan Saunders accompany the author.

Plate 5. At prime breeding sites multiple males compete for prominent perches. Wing flashing helps to space them out.

were frequently observed arriving to oviposit into the fine floating or submerged leaves of crowfoot. Single, mated females would try to 'sneek' into the area in an attempt to oviposit alone. They would fly in rapidly and attempt to go underwater as quickly as possible, occasionally successfully (Plate 6). On a number of occasions they were quickly intercepted by males, resulting in new tandem formation. Males would then attempt to leave the water with the females in tandem. Rival males would immediately engage and try to displace the tandem male, leading to a scrum on the water surface (Plate 7). Males initially use wing flashing in an attempt to deter rivals (Plate 8) but at these higher densities this is rarely effective. Tandem pairs returning to water would also be attacked by rival males. Initial attempts would try to knock or push the other onto the water surface with their legs (Plate 9A,B). This would attract the attention of other males, resulting in up to four males directly competing for one female with physical contact (Plate 10). During these aggressive encounters competing males would resort to biting, particularly to the distal end of the tandem male's abdomen, in an attempt to release the female (Plate 11A,B).

The heightened activity triggered responses from other males perched nearby,

Plate 6. Females 'sneek' in and try to go underwater to oviposit before they attract the attention of males.

Plate 7. An ovipositing female attracts the attention of males, where one forms a tandem and others form a scrum on the water.

Plate 8. A tandem male initially uses wing flashing in an attempt to deter a rival male.

with rapid patrolling flights made around the tandem pair. At times there were many males flying over the crowfoot areas, making it impossible to count them (Cham, 2020 – see video link under references). During these bouts of intense activity, same sex tandems between males were observed on a number of occasions. Rival males often formed a tandem with tandem pairs (Plate 12A,B) as well as with single males (Plate 13A,B). Same sex male-male tandems occasionally led to attempts to copulate with the other male (Plate 13A,B). This also included observations of intra-male sperm transfer by the leading male (Plate 14).

Observations over the study period revealed many males with parts of their wings missing or damaged (Plates 15,16). Some males exhibited holes in their wings, others had tears and some had relatively large pieces of wing missing or hanging off (Plate 17). While abrasion can occur during these aggressive encounters, leading to tattered wings, the main cause appeared to be the result of repeated biting (Plate 18). Male wing parts were observed floating on the water in areas where these encounters had been observed (Plate 19). The wings of *C. splendens* are easily distinguished from those of most other species (NB. *Calopteryx virgo* does not occur in this area). One video recording showed a rival male using its mandibles to repeatedly bite across the wing of a male in tandem, severing the distal part (Cham, 2020 - video link). In addition, males were observed with legs missing, presumably also as a result of inter-male

A

B

Plate 9. Aggression by rival males. (A) Males initially try to knock or push the tandem male onto the water surface with their legs, (B) Rival males are attracted and fly towards the tandem pair with their legs lowered ready for attack.

Plate 10. Up to four males may directly compete for one female by attempting tandem formation.

aggression.

Other stretches of the Elstow Brook, upstream and downstream for approximately 1km, were investigated but only in this one area were these conditions found.

Discussion

Territorial behaviour in *Calopteryx splendens* allows males to defend an area that encompasses the oviposition substrate required by females. Resident males are more likely to obtain higher mating success by defending a territory compared to non-territorial males, which are expected to fail in obtaining copulation under these conditions (Plaistow, 1997). Securing a territory is a major determinant of copulatory success and territorial interactions are a common feature in other calopterygids, described as wars of attrition, where success or failure in defending territories is based on fat reserves (Marden & Waage, 1990; Marden & Rollins, 1994; Plaistow & Siva-Jothy, 1996). Observations of *Caloptyeryx haemorrhoidalis asturica* by Córdoba-Aguilar (2000) showed that non-territorial males avoided fighting and that they obtained a lower number of

A

B

Plate 11. (A,B) If initial attempts at dislodging the tandem fail, the males use biting directed at the distal end of the tandem male's abdomen.

A

B

Plate 12. Rival males forming tandems with the tandem male. (A) The imperative to mate is so high that mistaken identity is commonplace. NB the missing leg of the tandem male, (B) The rival male tries to pull the tandem male in the opposite direction.

A

B

Plate 13. (A,B) In the foreground a male forms a tandem with another male and tries to achieve copulation. NB in the background behind the male-male tandem is a female ovipositing in tandem.

Plate 14. During a same sex tandem the leading male transfers sperm from its primary to its secondary genitalia in anticipation. Inset, detail of sperm transfer.

Plate 15. Oviposition quickly follows copulation. The male contact guards the female. Note the missing parts on each wing resulting from biting by rival males.

Plate 16. A rival male attempts forced tandem formation. Note that both males show parts of their wings missing.

Plate 17. A male showing large areas of wing missing. Note the similarity of the major missing wing part to that in plate 19.

Plate 18. A rival male bites at the wing of a tandem male. This can result in holes and tears in the wing thus reducing male fitness.

Plate 19. Parts of male wings resulting from biting by rival males were observed floating on the water.

matings compared to territorial males because, although they courted females, they were chased away, and the courtship was interrupted by the territorial male. Another reason why they may have received a lower number of matings was that females preferentially mated with territorial males in order to secure a place for oviposition. In circumstances, such as in the drought conditions at the Elstow Brook in 2018, lack of available territories and increased density of males led to behaviour changes where non-territoriality becomes the preferred strategy. Defending a territory when numbers are at high density becomes so energetically expensive that the resident males are more likely to have lower reproductive success than non-territorial males (Córdoba-Aguilar & Cordero-Rivera, 2005).

Gołab and Sniegula (2012) reported a reduction in the availability of potential territories to male *C. splendens* as a result of a decrease in aquatic macrophytes after flooding events. This was regarded to be the main cause of a change in male behaviour towards a more non-territorial strategy, resulting in more fights and damaged wings compared with the pre-flood year. They also observed frequent male–male tandems, a behaviour which they regarded at the time to be uncommon in *C. splendens*. The observations at the Elstow Brook in the drought year of 2018 support these findings, but in this case the reduced availability of territories for males resulted from exceptionally low water levels rather than the effects of a flooding event removing macrophytes. Each of these two differing situations resulted in more intense competition and a greater numbers of males showing behaviour related to a non-territorial strategy.

At low to mid-range densities, males threaten each other with wing displays, with one male typically giving way. Generally, male *C. splendens* do not engage in contact fights, with aerial contests consisting of chasing intruders, which usually do not result in body or wing damage (Marden & Waage, 1990; Plaistow & Siva-Jothy, 1996; Corbet, 1999). In the closely related *Calopteryx maculata*, territorial males normally expel intruders and neighbours with brief (< 15 s) pursuit flights (Waage, 1988). At higher densities the normal territorial system breaks down, leading to increased physical aggression between males (Hilfert-Ruppell & Ruppell, 2007; Rüppell & Hilfert-Rüppell, 2013). Gołab & Sniegula (2012) observed males crashing into each other or even biting conspecifics, while trying to mate with the same female, and argue that this behaviour followed the availability of a relatively small area of vegetation, which caused extremely high competition. Rüppell *et. al.* (2005) observed body injuries and aggressive behaviour among *C. splendens* males in the Oker River in Germany. They observed that most males in this population adopted aggressive behaviour, mainly because of long periods of unfavourable weather which subsequently resulted in high numbers of already mature males. However, the observations at Elstow Brook followed weeks of exceptionally favourable weather conditions

which presumably allowed numbers to build up during this time. As water levels in the stream dropped, males were increasingly more concentrated in a smaller area of prime resource, resulting in an increase in aggressive behaviour.

Gołab & Sniegula (2012) also considered sex ratio, with a lack of females being a factor causing changes in male behaviour and population dynamics of *C. splendens*. In the post-flood year of their study, sex ratio changed drastically compared to the pre-flood year. It has been reported that the sex ratio in Zygoptera at emergence and in the adult stage is only slightly male-biased (Corbet, 1999; Córdoba-Aguilar, 2008). The summer of 2018, with extended warm and sunny conditions, was especially favourable to dragonflies in the UK. Female *C. splendens* were much in evidence in the areas surrounding the Elstow Brook site during 2018 and there was no reason to suggest that the sex ratio at the site deviated from the expected near parity. Sex ratio and lack of females does not therefore satisfactorily explain a change of male behaviour.

Male *C. splendens* are attracted to the movement and silvery reflections of females when they arrive at the breeding site, either ovipositing alone or with males in tandem. Males would immediately fly from their perches and attempt to displace the tandem male. A female or tandem pair would quickly be surrounded by many flying males (Plate 20). Gołab & Sniegula (2012) regarded the most common way to obtain mating by a male was by forced copulation during observations of the post-flood population. This was also reported in *Calopteryx haemorrhoidalis haemorrhoidalis* in Central Italy, where rival males forcibly took ovipositing females in tandem (Cordero & Andrés, 2002). Despite numerous observed attempts at the Elstow Brook site, on no occasion was a rival male seen successfully displacing a tandem male.

Ruppell & Hilfert-Ruppell (2013 and undated DVD) stated that biting is the most important weapon used by males of *Calopteryx* species, although rarely succeeding in displacing the tandem male. Biting is directed to various parts of the body, with observations of biting directed at the abdomen, wings and legs of other males (Plate 21). Direct biting leading to release of a female was not recorded at the Elstow Brook. It is likely that, as density increases, the population of males comprises a combination of males that were previously holding territories as well as non-territorial, or floating males. Biting of wings that results in the loss of wing parts may lead to a progressive weakening of male fitness that gives an advantage to other males with less damage. Biting may be a tactic used by less fit, non-territorial males as a means to compete.

The loss of wing parts in Odonata has been widely reported and is often associated with bird attack. Gołab & Sniegula (2012) judged wing damage visually in their study but did not classify the degree and cause of injuries.

Plate 20. Mating behaviour elicits a response from nearby males that home in on the tandem pair.

Plate 21. A male and a female in tandem under attack from three other males. One male has formed a tandem with its anal claspers at the head end of the tandem male. A second male attempts to displace the tandem male by biting the distal part of its abdomen, while at the same time attempting to form a tandem with the female. A third male bites the wings of the tandem male.

However, they considered that increased yet unsuccessful bird attacks, due to more conspicuous male behaviour, should be taken into account. Whilst not observed in this study, bird predation of *C.splendens* has been observed along the nearby River Great Ouse resulting in small piles of wings found on the river bank. Here the wings are bitten off cleanly at the base leaving the whole wing intact (Plate 22). *Motacilla cinerea* and *M. alba* (Pied and Grey Wagtails respectively) are the main culprits. Unlike bird predation, the small sections of wing observed at the Elstow Brook resulted from inter-male aggression and match well with observations of males with holes and tears. Biting has also been observed in other species, such as *Enallagma cyathigerum* (Common Blue Damselfly), when densities are high (Cham, 2008) and is probably more prevalent, yet unobserved, in other species.

The sexual imperative at high densities results in mistaken tandem formation with other males, some of which are already in tandem with females and these were frequently observed at Elstow Brook over the period of study. Male–male tandems on a large scale were also observed in the post-flood year by Gołab and Sniegula (2012) and they argue that this male–male mating behaviour occurred because of scarcity of females (Bagemihl, 1999). However, observations at Elstow Brook gave no indications to suggest a scarcity of females. Females were relatively abundant in the hinterland and frequently observed along the stream and therefore some other explanation is needed for the observed

Plate 22. Male wings left on the bank as a result of bird attack show complete wings (compare with the wing part resulting from biting by rival males in Plate19).

behaviour and breakdown in sexual recognition.

Conclusions

The summer of 2018 was notable for a combination of long warm periods and low water levels, which resulted in high numbers of *Calopteryx splendens* at Elstow Brook. Observations made during the time of the study would support the view that males adopt a non-territorial mating strategy when population density is high. These observations also indicate that a reduction in the availability of a suitable oviposition substrate, leading to increased congregation of males into smaller areas of prime microhabitat, can result from different environmental factors.

Males frequent areas attractive to females and, at times of high population density, will perch in close proximity to each other. The weeks leading up to the time of the study at Elstow Brook in 2018, and indeed the following summer of 2019, would pass as 'normal' conditions with average population density, yet at some point in 2018 the threshold density was reached at which a change of male strategy occurred. As density increases and resources decrease, males would find that defending a territory would be energetically expensive or stressful and need to adopt the alternative non-territorial strategy. Furthermore, this supports the theoretical argumentation that the number of non-territorial males should increase with increasing population density, due to the lack of vacant territories (López-Sepulcre & Kokko, 2005). If lowering water levels and potential drought conditions could be forecasted accurately in advance this would make an interesting basis for further study to understand the underlying physiological mechanism for the change of territorial strategy.

Acknowledgements

I would like to thank Richard Revels for drawing my attention to the high numbers of *C. splendens* in the area of the Elstow Brook in July 2018 and the opportunities for close up study.

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Video Links

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Migrant and dispersive dragonflies in Britain during 2019

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Summary

The year 2019 was a truly impressive one for migrant dragonflies in the UK, featuring alongside the heady days of 1995 and 2006. It was thus a record year for sightings of both *Anax ephippiger* (Vagrant Emperor) and *A. parthenope* (Lesser Emperor). The former species saw three separate influxes – during late winter/early spring, during summer and again during the autumn. The summer influx was notable for the presence of multiple individuals at several sites, and breeding behaviour was reported on several occasions, though no progeny were positively identified later in the season. *Anax parthenope* appeared at over 80 sites in the UK during summer, these sightings including only the third- and fourth-ever records for Scotland. Although there was clearly a major influx, records were received from many sites that had also recorded the species over the previous few years, and it seems that breeding populations in Britain may now at last be becoming more widespread. In addition to the impressive arrivals of *A. ephippiger* and *A. parthenope*, *Sympetrum fonscolombii* (Red-veined Darter) also appeared in near-record numbers, with reports from almost 150 sites during the year. At Drift Reservoir in Cornwall, some 120 individuals were present during the second week of July, though most of these then rapidly moved on. Successful breeding was noted at a number of sites, with emergences occurring from late August onwards. However, given the size of the early season influxes, the number of such breeding sites seemed smaller than might perhaps have been expected.

Other highlights of 2019 included the sighting of two male *Crocothemis erythraea* (Scarlet Darter) along the south coast during high summer. One site – Longham Lakes in Dorset – had also recorded the species in 2017, which could just be a coincidence, but might hint at the presence of an undiscovered breeding colony nearby. Good numbers of *Aeshna affinis* (Southern Migrant Hawker) were seen away from their Thames Estuary strongholds for the second year in succession, with records coming from many of the areas that had reported the species during 2018, as well as from new areas such as coastal south Wales. This species now seems to be becoming increasingly widespread in southern

Britain. *Aeshna isoceles* (Norfolk Hawker) also continued its range expansion in south-east England, with a record even from Medmerry RSPB Reserve in West Sussex. The expansion of both *A. affinis* and *A. isoceles* may be linked to a combination of both internal dispersal and immigration from the Continent.

Amongst our recent colonist damselflies, both *Chalcolestes viridis* (Willow Emerald Damselfly) and *Erythromma viridulum* (Small Red-eyed Damselfly) showed substantial range expansion during 2019, particularly along the east coast. The most northerly site in Britain for *C. viridis* is now in North-east Yorkshire, while *E. viridulum* was recorded as far north as County Durham.

Account of species

Notable sightings reported to the BDS Migrant Dragonfly Project during 2019 are detailed below; for information on events during 2018, see Parr (2019).

Chalcolestes viridis (Vander Linden) – Willow Emerald Damselfly

This species has been steadily expanding its range in the UK since its first appearance in 2007 (Cham *et al*., 2014), and the reporting year saw this trend continue. Important new westerly records were received from Wytham Woods, Berkshire/Oxfordshire on 10 September (SBr) and from near Coventry, Warwickshire, on 21 September (KPR). The highlight of the year was, however, a major push northwards that became apparent during late August. During this period, and over the following weeks, there were thus a number of sightings as far north as the Humber Estuary (both the North Lincolnshire and South-east Yorkshire sides, e.g. Alkborough Flats and Hull, respectively). There was, in addition, a record from Harwood Dale Forest in North-east Yorkshire on 26 August (SBe). This sighting is almost 150 km further north than the most northerly sightings made during 2018, and clearly represents a major range extension.

Lestes barbarus (Fab.) – Southern Emerald Damselfly

It was another relatively good year for the species in the UK. While there was little evidence for any significant immigration, records were received from most of the recently active breeding sites. This included the inland one near Beaconsfield in Buckinghamshire, though this site suffered substantial habitat degradation over the 2018/19 winter, and whether breeding here will continue remains to be seen. Around the Greater Thames Estuary, reports were received from both Cliffe in Kent and Canvey Island in Essex. Sightings, including records of mating pairs, from Little Belhus Country Park, Essex, during late July (EH),

also add weight to the suggestion that the species may well breed more widely in the Thames Estuary area than is currently appreciated. At the well-known site at Winterton Dunes, Norfolk, an immature male was spotted on 27 June 2019 (JHa) and records of 1–2 mature individuals were made there over 7–21 August (DRo *et al*.), with oviposition being noted on 21 August (SC). Despite there having been no records at all from the site during 2018, this rather suggests that *L. barbarus* does indeed breed there, but populations are small and easily overlooked.

Coenagrion scitulum (Rambur) – Dainty Damselfly

After having become extinct in Britain back in the early 1950s, *Coenagrion scitulum* reappeared in Britain in the Isle of Sheppey area of Kent during 2010 (Cham *et al*., 2014). This bridgehead population appears broadly stable, but has shown only limited signs of expanding. During 2019, a new site for the species was discovered in East Kent (JGB). Although several individuals were present, no exuviae or other signs of local emergence were noted, and it was thought possible that this new colony results from a fresh influx from the Continent. Especially with general access to areas currently favoured by the species being very limited, and our understanding of the species' precise population structure thus being incomplete, it is however difficult to be sure.

Erythromma viridulum (Charp.) – Small Red-eyed Damselfly

As with its fellow recent colonist *Chalcolestes viridis*, this species experienced a major push northwards along the east side of England during late summer, though signs of dispersal became apparent rather earlier than for that species. From early August onwards, records were received from new areas in North-east Yorkshire, from North-west Yorkshire and even from County Durham. The most northerly site for the species in the UK is now at West Boldon, Co. Durham, where records of small numbers were made throughout much of August (DFo, JHg *et al*.). In the west of the UK, significant further range expansion was also noted. A sighting at Panty Bedw fishery in Carmarthenshire on 6 August (RS) is a good record for Wales, and the first records for Staffordshire were made at Highgate Common (DJ) and at Belvide Reservoir (SN). More spectacularly, the species also appeared for the first time in the south Lancashire region. Small numbers were spotted at Towneley on 9 & 25 August (AH), there were reports from the Festival Gardens in Liverpool throughout much of August (PB, PK *et al*.), four were seen on the Leeds-Liverpool Canal near Leigh on 23 August (JSu) and three were at Worsley on 26 August (WJ).

In line with the species' apparently enhanced mobility during 2019, a number of interesting records of *E. viridulum* were also made within the main UK range.

One was attracted overnight to a UV moth trap at Walberswick, Suffolk, on the night of 30 July (HW) and one was noted near the shoreline at Sandwich Bay, Kent, on 8 August (AL). Elsewhere, a teneral seen at Trewoon in Cornwall on 27 June (ITJ) probably relates to arrivals noted in the county during 2018 (Parr, 2019).

Ischnura pumilio (Charp.) – Scarce Blue-tailed Damselfly

This species is very rare in most of eastern England, but 2019 saw small-scale arrivals along the East Anglian coast. The first record for Suffolk was made when three were seen and photographed at Kessingland Beach on 2 July (TA), while 1–2 were reported from Winterton Dunes, Norfolk, over 22–26 August (SC, RG).

Aeshna affinis (Vander Linden) – Southern Migrant Hawker

The Thames Estuary populations of this recent colonist species are now well-established, but 2018 saw many individuals reported from elsewhere in southern and eastern England (Parr, 2019). The current reporting year again saw a wide spread of records away from the Greater Thames Estuary (Fig. 1), with the species being recorded from no less than 18 counties during the period 20 June–12 September. Further sightings were made at many sites that first recorded the species during 2018, such as Southease (DSa) and Winchelsea (MHa) in East Sussex, Lytchett Bay in Dorset (IB), Quy Fen in Cambridgeshire (AM), Hempsted in Gloucestershire (MHb) and Spurn in East Yorkshire (DO, SBO). In addition, records were sometimes also received from further localities in the same general areas as these key sites. In Cambridgeshire, for example, records from Quy Fen were supplemented by sightings at Ditton Meadows (DM) and Wicken Fen (DRu), both of which lie within 10 km of Quy. The extent of these 'repeat' sightings strongly suggests that they result from successful local breeding having taken place, though relatively few obvious immatures were positively reported. Such immatures were, however, noted in Suffolk near Felixstowe on 17 June (DH) and at Walberswick on 5 July (CM), as well as in East Sussex near Fairlight on 27 June (MU). In addition to these records from previous areas, a number of sightings came from entirely new regions for the species, implying that significant fresh migration and/or internal dispersal also took place during the year. Particularly notable sightings included the first records for Wales. Single male *A. affinis* were thus seen at both Llandegfedd Reservoir (13 August; GV) and Goldcliff Wetlands (1 September; SD) in Monmouthshire, as well as at Kenfig NNR in Glamorgan (24 August; TW). During 2019, mating or oviposition was reported from at least five sites away from the Thames Estuary strongholds, and probably went unobserved at others. *Aeshna affinis* now seems well on its way to becoming quite widely established in southern

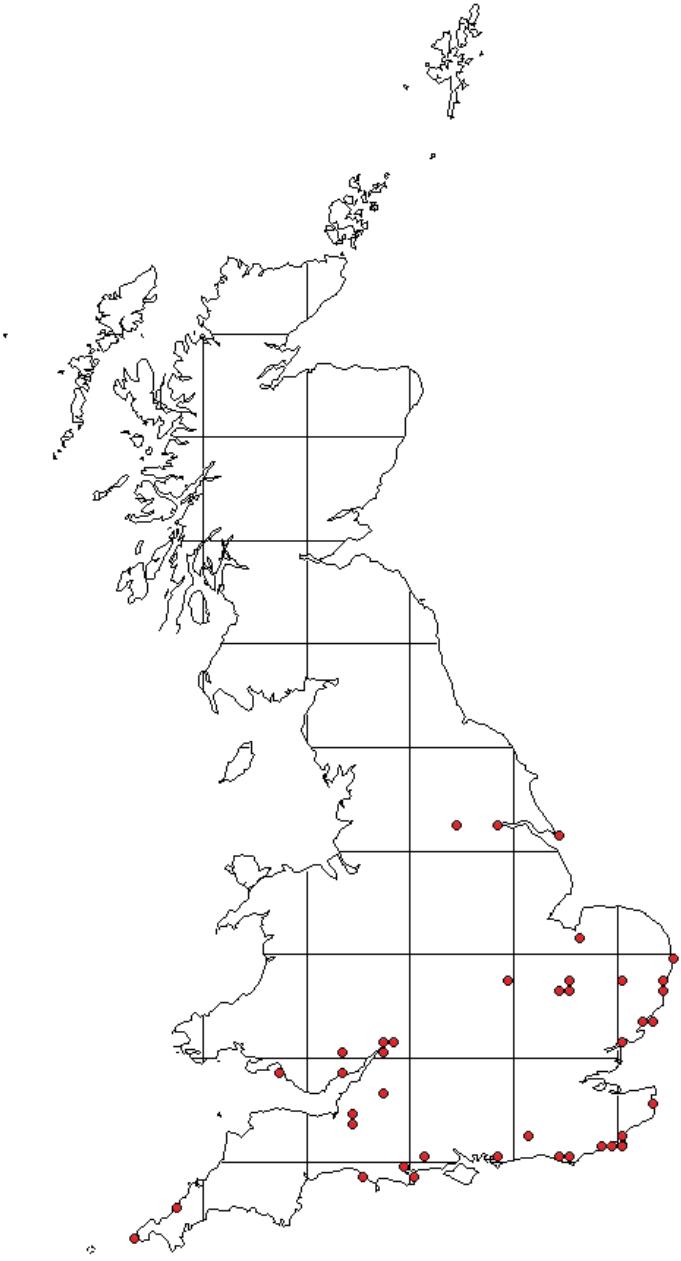

Figure 1. Sightings of *Aeshna affinis* made during 2019 at sites away from their Greater Thames Estuary strongholds.

Britain, though, with a few notable exceptions, most sites are still relatively near the coast. Coastal grazing marshes do seem to provide particularly favourable habitat for the species, and incoming migrants also typically first settle in coastal areas.

Aeshna isoceles (Müller) – Norfolk Hawker

This species has been increasing its range in the UK over recent years and is no longer restricted to just Norfolk and Suffolk. It seems likely that the trend is climate driven, and range expansion may involve both internal dispersal and a degree of immigration from the Continent. After a series of unexpected records in southern England during 2018 (Parr, 2019), yet further unusual sightings were made during the current reporting year. At the London Wetlands Centre, Surrey/Greater London, the first-ever records of *A. isoceles* were made in 2018, but the species reappeared in 2019 when up to two were regularly reported over the period 11 June–2 July (PSm *et al*.). Sightings of *A. isoceles* were also made at a number of entirely new locations in south-east England, several of which were well away from known breeding sites; these included records from Wildmoor Heath, Berkshire, on 29 June (RK) and at Medmerry RSPB Reserve, West Sussex, on 5 July (PJA). Although the species does breed relatively nearby, the discovery of up to ten individuals right on the Suffolk coast at Kessingland Beach and nearby Kessingland Sluice on the morning of 30 June (LBC), at the same time as several migrant *Anax ephippiger* appeared in the area, is also of interest. These individuals had mostly moved on by the afternoon, and it is tempting to speculate that they could have been of Continental origin.

Aeshna mixta Latreille – Migrant Hawker

This species had a comparatively quiet year in 2019, though up to 200 were noticed at Ipswich Golf Course, Suffolk, on 30 July (NS). One was attracted to a UV moth trap at Bengeo, Hertfordshire, on the night of 26 July (SK), while another was similarly attracted to a trap near Oxford on the night of 2 August (BS). Later in the season, 100 were at Hartlepool Power Station, Teesside/County Durham, on 11 September (GH), 70+ were at Sandwich Bay, Kent, on 12 September (SBBOT) and “a noticeable arrival” was seen at Dawlish Warren, Devon on 15 September (DWRG).

Anax ephippiger (Burmeister) – Vagrant Emperor

This species appeared in unprecedented numbers during 2019, with no less than three major influxes being noted – in late winter/early spring, summer and again in autumn. Most records were from coastal areas (Fig. 2), and included a few individuals as far north as Scotland, though the precise pattern of events

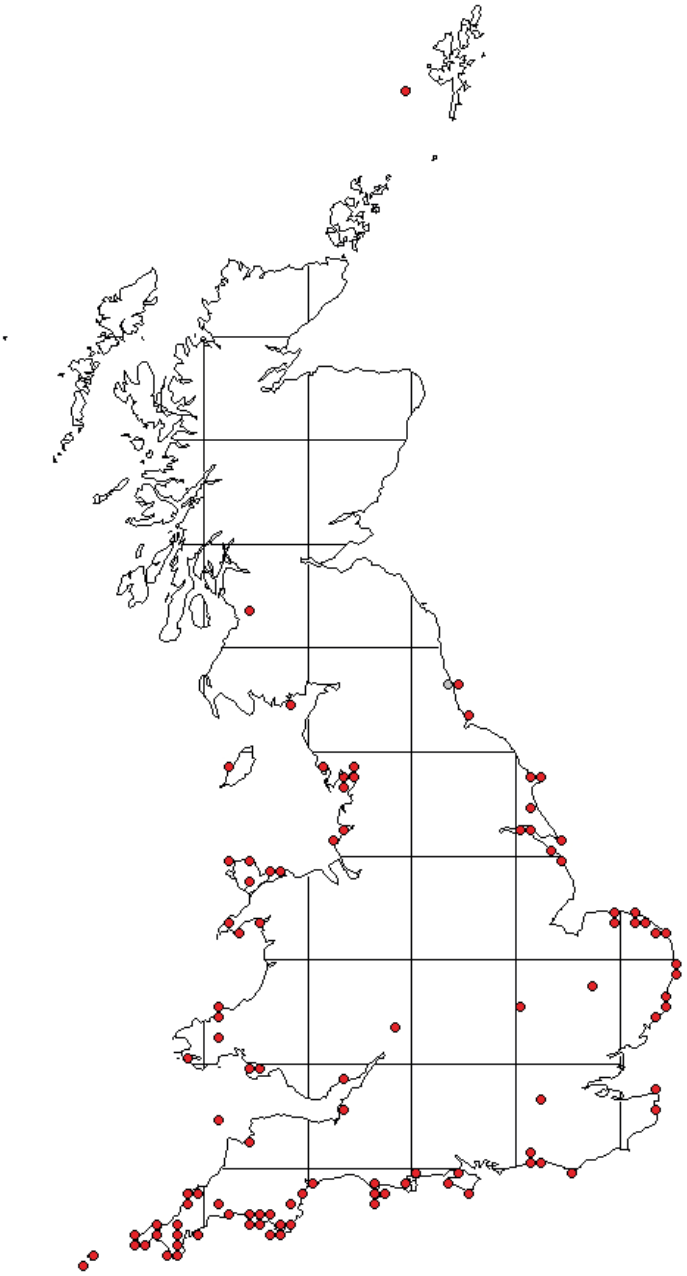

Figure 2. Sightings of *Anax ephippiger* made during 2019. Winter records of 'unidentified dragonflies' are also included (see text). The grey dot indicates a plausible but unconfirmed summer record.

Plate 1. *Anax ephippiger* (male) attracted to a UV moth trap at Steyning, West Sussex, on the night of 13 October 2019. Photograph by O. Ellis.

differed significantly between influxes.

The first influx of the year began on 15 February and lasted for about six weeks, with a noticeable peak of sightings around 24–27 February. During this period some 55 dragonflies were reported either by members of the general public or by dragonfly enthusiasts and, although only 20% of the individuals were photographed or were seen well enough for their identity to be confirmed as *Anax ephippiger*, it seems likely that all sightings relate to this species since it is the only one reasonably to be expected on the wing in the UK at this time of year (Cham *et al*., 2014). Most records during this early influx came from western areas of England and Wales, with a few reports as far north as the Isle of Man, Cumbria and even Rascarrel Bay in Kirkcudbrightshire (26 February; RBM). A very small number of more easterly sightings were also made; these were, somewhat atypically, mainly from inland sites. Unidentified dragonflies were, for instance, reported from Salph End, Bedfordshire, on 24 February (RDS) and Beddington Farmlands, Surrey, on 26 February (PA).

The early season sightings came to an end in the second half of March, though there was a later report of a single individual at Kenidjack, Cornwall, on 14 May (JVP). During the second week of June another surge of new records then

began. On 9 June, individuals of *A. ephippiger* were photographed at three sites on the east coast of England (in Suffolk, Lincolnshire and East Yorkshire), and during the period up until the end of July the species was noted at some 30 localities. These were principally on the east coast of England, though a few sightings were also made near the west coast of Britain, as far north as Kilmarnock, Ayrshire (11 July; JSt). Several sites held multiple individuals simultaneously, with no less than 28 being reported from the Holkham/Wells area of Norfolk on 29 June (JMC). Very large numbers of *A. ephippiger* were also seen in Belgium and the Netherlands around this time (Observation.org, 2019). In general, individuals did not linger long, and moved on within at most a few days. At certain sites, the dragonflies however seemed more settled, and there were sightings at Carlton Marshes in Suffolk for over six weeks (GD *et al*.), though this could, of course, involve more than one immigration event. Mating and/or oviposition were recorded from a few favoured sites during the summer, most notably at Holkham, Carlton Marshes, and at Windmill Farm in Cornwall. *Anax ephippiger* has a short larval development time (Dumont & Desmet, 1990), but no locally-bred second-generation individuals were to be noted in Britain later in the year. Successful breeding could, however, have easily been overlooked. It is now known that emergences generally take place overnight, with the adult dragonflies then immediately leaving the natal area (Nederlandse Vereniging voor Libellenstudie, 2019). Proof of breeding is thus heavily reliant on finding exuviae.

Summer records started to tail off in the middle of July, though a few 'stragglers' were reported along the east coast of England during late July, and sightings continued at Carlton Marshes, Suffolk, until 29 August. Amazingly, a third influx was, however, then to occur. On 22 September, a female was attracted overnight to a moth trap in Pembrokeshire (RR), and between this date and mid-November, records of *A. ephippiger* were received from over 30 sites. These sites were principally on the south coast of England, but there were also a few records on the east coast, including even two sightings in County Durham (Whitburn Coastal Park (DFo) and Hartlepool (MM), both on 15 October). The last record of the year was from Sandwich Bay in Kent, where an individual was found perched up and torpid during poor weather on 17 November (SBBOT); it finally succumbed to the cold some 5 days later.

The unprecedented arrivals of *A. ephippiger* seen in the UK during 2019 have been analysed in more detail by Parr (2020). The summer and autumn peaks in activity were also widely noted on the Continent, where the species similarly appeared in dramatic numbers. The late winter/early spring influx was, however, more restricted to Britain and Ireland (Parr, 2020).

Anax imperator Leach – Emperor Dragonfly

A series of unexpected records from eastern coastal areas rather suggests that considerable dispersal or longer-distance migration took place during the year. Scottish records of *A. imperator* are still very scarce (Parr, 2019), so sightings at Forvie NNR, Aberdeenshire, on 31 July (DPi) and from near Morton Lochs, Fifeshire, on 6 August (JC) are of note even in themselves. They do, however, also represent the most northly Scottish records ever made. Intriguingly, a bright blue and green dragonfly was also seen on Papa Stour in the Shetland Isles around 1 August (NT), though unfortunately its identity could not be confirmed. Further south, in England, a female *A. imperator* was caught in a moth trap at Landguard, Suffolk, on the night of 18 July (NO), while another female was attracted to UV light at Bacton, Norfolk on the night of 13 August (PW). Dragonflies attracted to light often seem to involve migrants (Parr, 2006).

Anax parthenope Sélys – Lesser Emperor

Following on from a good showing in 2018 (Parr, 2019), this species had a record year in the UK during 2019, with reports from 80+ sites in 34 counties over the period 1 June–5 September. Multiple immigration waves were clearly involved, with records from new sites being broadly spread throughout much of the summer, though there were noticeable surges in sightings around 4–6 July and 23–26 July. This latter peak corresponds with a period of record-breaking heat in much of Britain (Met Office, 2020a). Unlike *A. ephippiger*, which turned up primarily at coastal sites during the year, records of *A. parthenope* were widely spread (Fig. 3). Most reports came from southern and central England, but sightings included only the third- and fourth-ever records for Scotland – at Mire Loch in the Scottish Borders on 3 July (CH) and at Kinloch on the Isle of Rum on 25 July (SA). Other more northerly records included a male at the Silverlink Biodiversity Park, Northumberland, on 22 June (CB), another male at the Sunderland Academy Pools, Co. Durham, on 16 July (DFo) and a female that was attracted overnight to a UV moth trap at Flamborough, East Yorkshire, on the night of 30 July (MP). In addition, a long-staying individual was present at a site on the Isle of Man during mid July–early August, with an ovipositing pair even being seen there on 1 August (PH). Mating and/or egg-laying (typically done in tandem) were indeed quite widely reported in the UK during 2019, with at least 16 documented instances (in Cornwall, Dorset, East Sussex, Essex, Suffolk, Norfolk, Cambridgeshire, Worcestershire, Glamorganshire and on the Isle of Man).

While major immigration clearly occurred during the summer, it seems likely that a significant number of records also referred to locally-bred individuals, as a result of growing colonisation of the UK. Many records thus came from sites

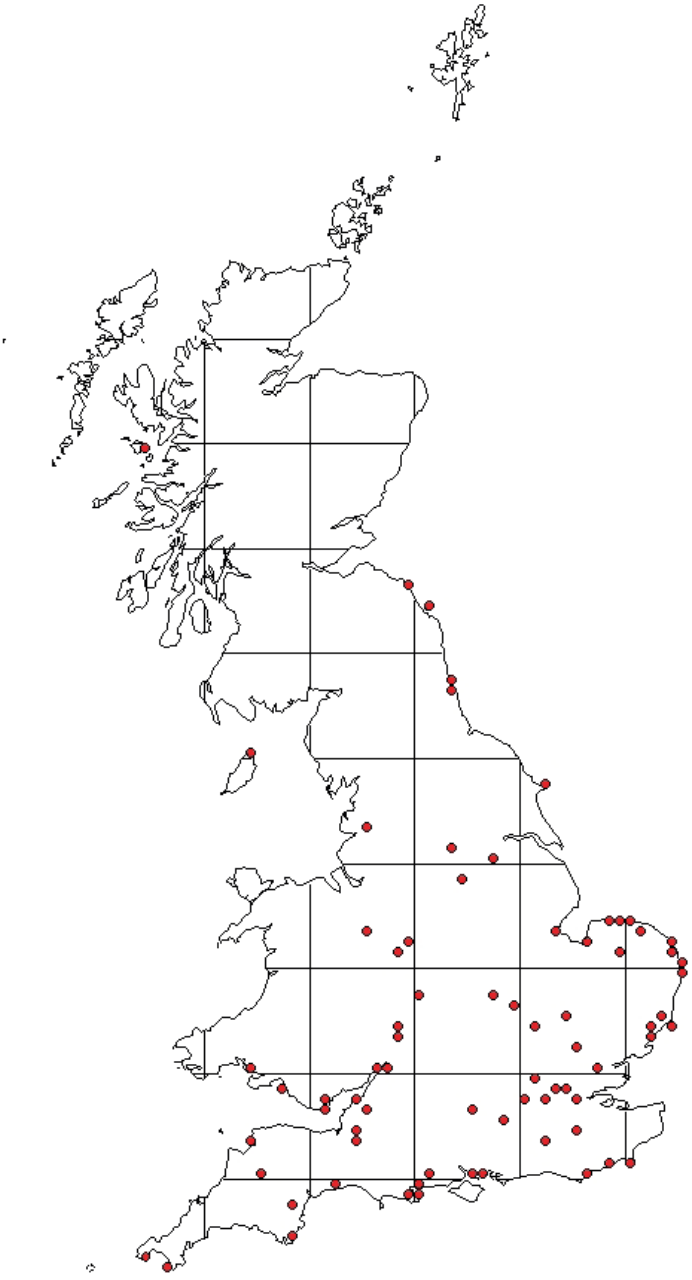

Figure 3. Sightings of *Anax parthenope* made during 2019.

that had also recorded the species in 2017 or 2018 (though of course it could be that sometimes migrants were simply re-finding particularly favourable habitat). A few of these sites also hosted the species for a considerable length of time, rather suggestive of continuing emergences rather than a specific influx. At Loompit Lake in Suffolk, sightings for instance covered the period 24 June–19 August (WB). Rather surprisingly, with the exception of Longham Lakes in Dorset, where up to 10 individuals were claimed on 28 July (PSa), numbers reported from 'traditional sites' were, however, always very small. Clearly much still remains to be learnt about the precise status of *A. parthenope* in Britain. In our area, the species does seem to favour larger waterbodies or multi-waterbody complexes, which can make detailed study difficult.

***Crocothemis erythraea* (Brullé) – Scarlet Darter**

Two records were received during the year; both have been accepted by the Odonata Records Committee. These sightings constitute only the tenth and eleventh confirmed British records.

28–29 June	Male at Longham Lakes, Dorset (photographed); P. Ritchie *et al*.
21 July	Male at Pannel Valley Ponds, East Sussex (photographed); A. Kitson.

Significant movement of *Crocothemis erythraea* was noted in northern Europe during summer 2019, with the first-ever record for Sweden coming during mid July (M. Billqvist, pers. comm.) and with four records from Denmark doubling their previous total (Fugle og Natur, 2019). The British record from Pannel Valley fits in with this main migration wave. However, that from Longham Lakes is just a little early. An individual was also seen at Longham Lakes back in 2017 (Parr, 2018), and that such a rare dragonfly should be recorded at the same site twice in three years seems a little unexpected. Perhaps the recent sighting hints at the presence of an, as yet, undiscovered breeding site in the nearby area? Whatever the exact situation, the species' continuing good fortunes on the near Continent mean it certainly remains a potential colonist of the UK.

***Libellula quadrimaculata* L. – Four-spotted Chaser**

One was photographed at Porth Hellick on St Mary's, Scilly Isles, on 2 August (VS), with it, or another, also reported from the island the following day (JHe). These are the first records for the Scilly Isles.

Sympetrum danae (Sulzer) – Black Darter

The species is normally absent from much of south-eastern England, but a small-scale immigration apparently took place on the east coast during late summer. A male was thus photographed at Carlton Marshes in Suffolk on 25 August (GD), while one was reported from Aldborough Hatch, Essex, on 26 August (MHg).

Sympetrum fonscolombii (Sélys) – Red-veined Darter

After a relatively quiet year in 2018, *Sympetrum fonscolombii* arrived in Britain in near record numbers during 2019, only the events of 2006 (Parr, 2007) being as, or more, dramatic. The first well-documented sightings came on 9 June, when records were received from Norfolk (PWs), Lincolnshire (2 sites; JSm, CA) and East Yorkshire (SBO), coincident with arrivals of both *Anax ephippiger* and the butterfly *Vanessa cardui* (Painted Lady) along the east coast of England. Over the following three months, records of mature adults were received from over 130 sites in the UK, as far north as Lindisfarne in Northumberland (JF) and Millar's Moss in the Scottish Borders (DG). Such sites, covering some 35 counties, were widely spread but, with the exception of a few clusters such as those in the West Midlands and wider London area, they were predominantly coastal (Fig. 4). Several waves of migration were clearly involved during the year. Following the early June arrivals there was a big surge in reports during the last 10 days of June and first 10 days of July, but the species continued to be reported from new sites throughout most of the summer. A small peak in sightings was, for instance, also noted during the hot weather at the end of July. Although records not infrequently referred just to singletons, a number of sites reported counts into double figures, and a few very high counts were also received. At Drift Reservoir, Cornwall, some 120 individuals were thus present on 8–9 July (DFl, DPa), though most of these then rapidly moved on. Good numbers (20+) were also reported from Windmill Farm, Cornwall, during the first half of July (AB, CM).

Worn, ageing, mature adults continued to be seen in Britain until 15 September (Carlton Marshes, Suffolk; PR), which is quite a late date by normal standards – presumably reflecting the wide temporal spread of immigration waves seen during summer. By 17 August (Vanbrugh Pits, Kent/Gtr. London; JB), records were also being supplemented by newly emerged second-generation individuals. Breeding sites were identified in Kent, Dorset, Suffolk, Norfolk, Worcestershire and County Durham (Oakenshaw Wildlife Reserve; KW) though, given the magnitude of the early summer arrivals, this seems a relatively small list. Perhaps early season immigrants did not always stay around long enough to breed extensively, or maybe some emergences will not take place until spring

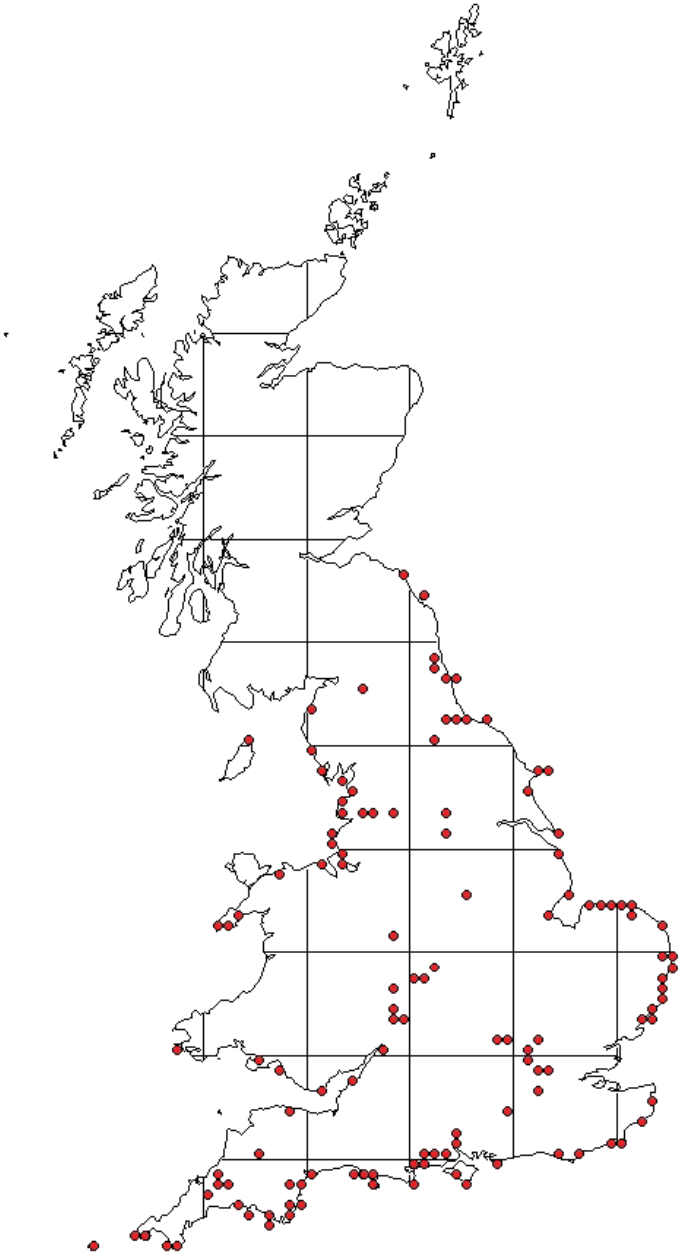

Figure 4. Sightings of 'first-generation' *Sympetrum fonscolombii* made during spring and summer 2019.

2020. In addition to records from breeding sites, several second-generation *S. fonscolombii* also turned up during early autumn at sites where breeding was unlikely, these presumably being dispersing individuals from elsewhere in the UK or farther afield. Of particular note was a sub-mature male attracted to a UV moth trap at Church Cove on the Lizard, Cornwall, during the night of 21 September (MT). A few interesting, later season records were also received, most notably of fully mature females seen at Hengistbury Head, Dorset, on 10 October (OF) and at Cuckmere, East Sussex, on 23 October (AK). These individuals might well be associated with the arrivals of *A. ephippiger* that were also taking place at the time.

***Sympetrum striolatum* (Charp.) – Common Darter**

It was seemingly a quiet year for migration by this species, though movements involving only small numbers can often be difficult to detect. A male was attracted to a UV moth trap near Orelston Forest, Kent, on the night of 9 September (JL); such records of dragonflies at light frequently seem to involve migrants (Parr, 2006).

Discussion

The 2019 reporting year was characterised by some truly spectacular migration events, involving several species and multiple arrival waves. Both *Anax ephippiger* and *A. parthenope* were seen in record numbers, and some of the largest arrivals of *Sympetrum fonscolombii* ever seen in the UK were also noted. During the summer, a few localities indeed held all three of these southerly migrant species at the same time. In addition to these events, *Crocothemis erythraea* – still a great rarity in the UK – turned up at two sites. As well as immigration of species whose strongholds lie in southern Europe, some apparently more local migration was also noted. A few *Ischnura pumilio* and *Sympetrum danae* for instance appeared in East Anglia, and some *Libellula quadrimaculata* were also on the move. This aspect appeared small in comparison to the appearances of 'southern' migrants, but the arrival of familiar species can often go under-reported.

Some of the various migration waves seen during the year could be tied to specific meteorologically events. The arrivals of *A. ephippiger* seen in February were thus linked to periods of unseasonal winter warmth and southerly winds originating from North Africa (Met Office, 2020b). The abnormally hot weather of late July (Met Office, 2020a), which saw a new UK maximum temperature of 38.7°C being recorded in Cambridgeshire on 25 July, was also associated with a degree of enhanced immigration. Other, more prolonged migration events

could also be identified, these perhaps reflecting generalised movements in response to high population levels in the dragonflies' source areas. Of particular note were the arrivals of *A. ephippiger* and, to a lesser degree, *S. fonscolombii* seen on the east coast of England during June. These arrivals were frequently accompanied by large-scale immigration of Lepidoptera such as *Vanessa cardui* (Painted Lady) (Butterfly Conservation, 2019) and *Plutella xylostella* (Diamondback Moth) (Warwick Crop Centre, 2019), and were clearly part of some very spectacular insect migrations indeed.

As well as facilitating long distance migration, weather conditions during the summer also seemed to enhance local dispersal. A number of resident species thus showed significant range expansion during the year. In particular, our recent colonist *Chalcolestes viridis* produced records up to 150 km north of its previous range boundary, whereas in previous years the average rate of annual range expansion had been almost an order of magnitude less than this. *Erythromma viridulum* also showed significant northwards movement during the year.

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T. Wright (TW).

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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

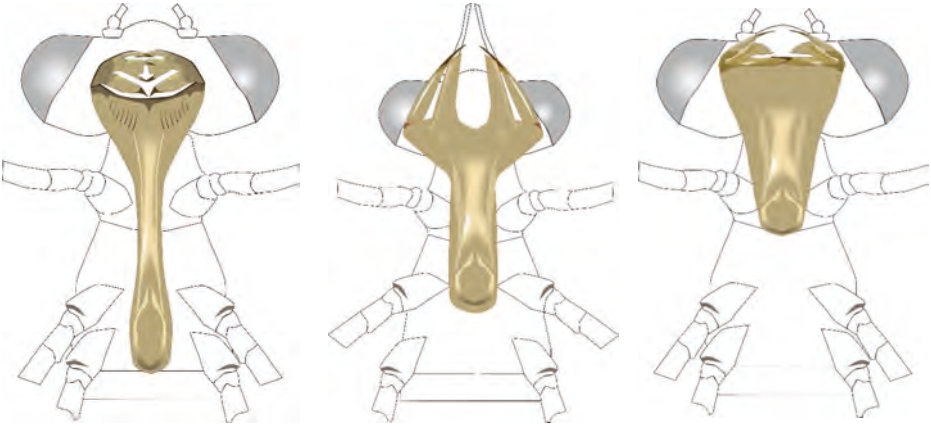

Plate 2. The various shapes of the prementum (viewed from below) of three species which represent three western Palearctic damselfly families. (A) In *Lestes barbarus* the spoon shaped prementum is greatly narrowed for much of its length, (B) In *Calopteryx haemorrhoidalis* the prementum is both narrowed 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*.

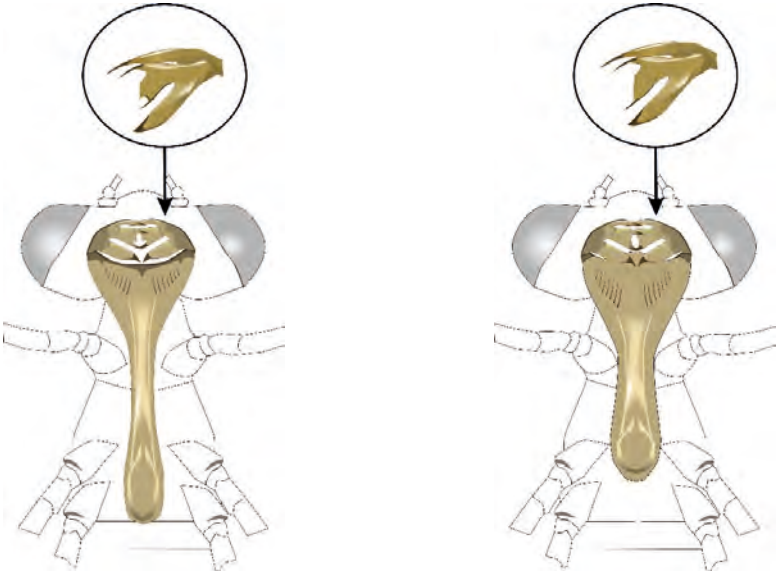

Plate 3. Comparison of the labial mask of (A) *Lestes barbarus* and (B) L*estes macrostigma*. The total length of the labial mask compared to the overall length of the larva is 46% in *Lestes barbarus* but only 31% in *Lestes macrostigma*.

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

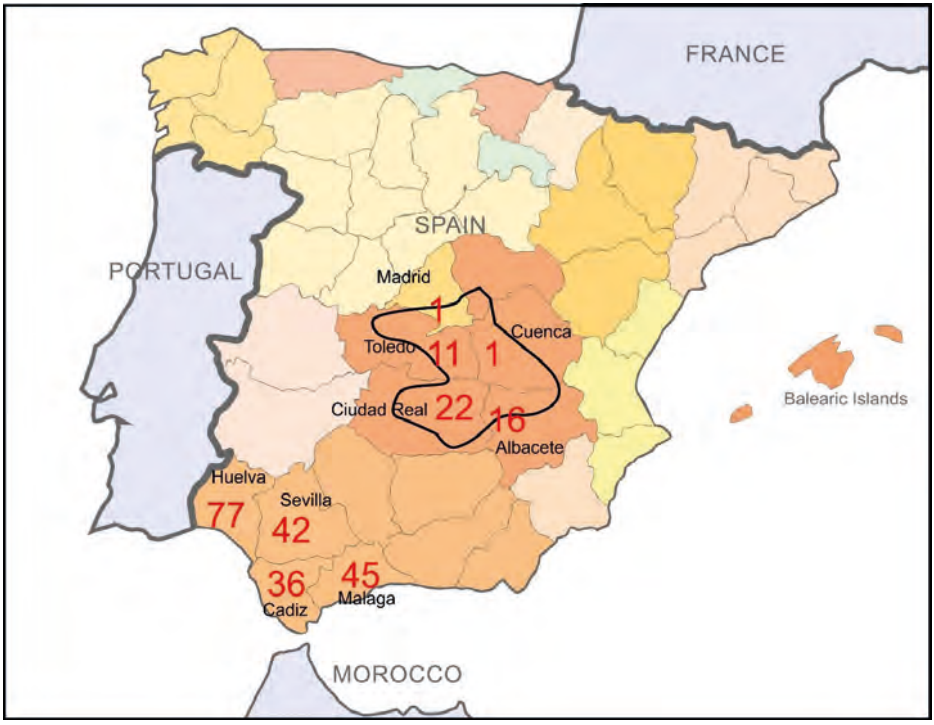

Plate 6. Map of Spain showing all records by Province for *L. macrostigma*, except for isolated historical records. The region bordered by the black line was described by Lorca et al. (2008) as La Llanura Manchega, which shows remarkable parallels with the Pannonian Basin in terms of its mean May temperature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

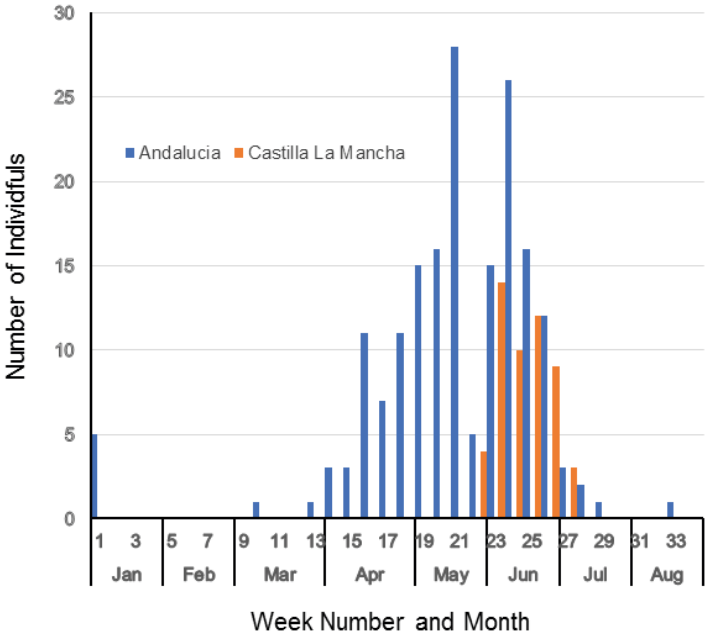

Figure 1. Records of *Lestes macrostigma* from Spain showing the numbers recorded in Andalucia and Castilla La Mancha by week number and by month (ROLA Database). Week 1, 1 January; Week 33, 12 August.

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.

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Emergence of seven odonate species, based on exuviae collection, from four small artificial ponds at Ghadira Nature Reserve, Malta

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Summary

The Ghadira Nature Reserve, Malta is a saline marshland. The construction of three small fresh water ponds in the early nineteen nineties, together with the addition of a fourth in 2017, attracted a number of odonate species. Seven species reproduce regularly in them, with another two ovipositing sporadically. The regular collection and counting of exuviae provides an accurate count of the numbers and species emerging. For this purpose, in 2019, exuviae were collected twice weekly from mid-March to mid-December. The most numerous species emerging from each of the four ponds was *Crocothemis erythraea* (Scarlet Darter). Most, if not all, of the seven species had two (in some cases three) generations annually. Birds were the main predators of larvae, both during the growth period and at emergence, and of tenerals. Spiders and possibly Painted Frogs took what appeared to be an insignificant number of tenerals.

Introduction

The Ghadira Nature Reserve was established in the early nineteen eighties and is situated in the northern and narrowest part of Malta. It is a small wetland flanked by the sandy beach of Mellieha bay on its north-eastern side and by the low sea-cliffs of Ic-Cumnija on its south-western side. The area was used as a salt-pan in the medieval period and as a hunting reserve in more recent times, before being declared a bird sanctuary in 1979. In the early eighties the area was engineered to create areas of open water with several islands where wading birds could feed and breed. Being below sea level, the water in the reserve is saline and, in the early nineteen nineties, three small freshwater ponds were built to attract more birds and other wildlife. A fourth pond was added in 2017 (Plate 1).

Plate 1. Aerial view of the study site showing the location of the four ponds (1-4).

These ponds were immediately patronized by dragonflies but it was not until 2008 that an odonate sightings log started being kept at the reserve. Since then 13 species have been recorded (Gauci, 2018b), seven of which regularly breed in the four freshwater ponds and two of which have, on very rare occasions, been observed ovipositing in Pond 1 but without exuviae ever being found (Table 1).

Site

The study area comprised four ponds (Plate 1), the water level in which is maintained by water pumped from a tank.

Pond 1 (Plate 2)

This is situated on the north-western side of the reserve along the service road, with a line of *Tamarix africana* (Tamarisk) bushes on one side and an embankment harboring mixed shrubs on the other. Rectangular in shape, with an area of about 10m^2 and a depth of 25cm, it was constructed on a concrete base in the early nineteen nineties. The patch of emergent vegetation, consisting

Table 1. The confirmed breeding species, those which have been observed ovipositing but for which no exuviae have been found and those in which breeding activity has not been observed.

Regularly breed in the four ponds – exuviae found	
Ischnura genei	Island Bluetail
Anax imperator	Emperor Dragonfly
Anax parthenope	Lesser Emperor
Orthetrum cancellatum	Black-tailed Skimmer
Orthetrum trinacria	Long Skimmer
Sympetrum fonscolombii	Red-veined Darter
Crocothemis erythraea	Scarlet Darter
Oviposited rarely in Pond 1 – no exuviae found	
Trithemis annulata	Violet Dropwing
Selysiothemis nigra	Black Pennant
Breeding not recorded	
Anax ephippiger	Vagrant Emperor
Aeshna mixta	Migrant Hawker
Orthetrum chrysostigma	Epaulet Skimmer
Orthetrum coerulescens	Keeled Skimmer

of *Juncus* sp. (rush), is regularly grazed by wild rabbits. The pond is frequented by several species of birds. Due to the surrounding bushes the sun reaches the pond only from mid-morning.

Pond 2 (Plate 3)

Also built on a pre-existing concrete base in the early nineties this pond is roughly circular in shape with an area of about 15m^2 and an average depth of 25cm. It is situated on the north-eastern edge of the reserve at the edge of a small, degraded sand dune which is now being rehabilitated. Although it is surrounded by bushes and trees, it receives sunlight from early morning. In its centre there is a clump of *Carex extensa* (Giant Sedge) covering about 2m^2. Birds visiting this pond consist mainly of small insectivores but it is also occasionally visited by waders.

Pond 3 (Plate 4)

This is another pond built on a concrete base. It has an area of about 18m^2

Plate 2. Pond 1 at Ghadira Nature Reserve.

Plate 3. Pond 2 at Ghadira Nature Reserve.

Plate 4. Pond 3 at Ghadira Nature Reserve.

Plate 5. Pond 4 at Ghadira Nature Reserve.

Originally built in the early nineties it was abandoned a few years later. In 2017 it was repaired and a wooden photography hide built next to it. It has an average depth of 25cm. On two sides it is surrounded by *Limbarda crithmoides* (Golden Samphire) and *Juncus acutus* (Sharp Rush), with Tamarisk bushes on the other sides. It is situated on the south-eastern side of the reserve, 5m away from the edge of the main, saline, pool. Two small clumps of *Carex extensa* were introduced when it was repaired. It is frequented by various species of bird.

Pond 4 (Plate 5)

This pond consists of two interconnected, small, prefabricated structures. It is situated on the south-western side of the reserve and was constructed in 2017. It has a maximum depth of 50cm but it is only 4m^2 in area. On its northern side it is flanked by an embankment and on its southern side by a nature trail leading to a bird-watching hide a few metres away. It receives sunlight from mid-morning. The emergent vegetation consists of *Juncus* sp. but this is heavily grazed by rabbits during the drier months. It is frequented by *Discoglossus pictus* (Painted Frog).

Methods

Being able to collect all of the exuviae left behind by dragonflies emerging from a habitat offers a powerful method of quantifying the seasonal pattern of emergence (Corbet, 1999). Ideally, exuviae should be collected every day, as some may be blown off by strong winds or washed away by heavy rain. However, daily collection was not possible in this study.

Exuviae collection started in mid-March 2019 and went on until mid-December 2019. As far as possible exuviae were collected, in separate containers for the four ponds, twice weekly – on Wednesdays and Saturdays about two hours after sunrise. Wissinger (in Corbet, 1999) found that when anisopteran exuviae were collected every three days instead of daily, about 15% became lost by attrition. In the case of this study this might have applied to the early part of the season when the weather was still unsettled but it was unlikely that there was such a loss later in the season. On the few occasions when I was away from the Islands Ray Vella collected the exuviae.

To collect the exuviae, the emergent vegetation in the ponds, as well as the surrounding vegetation, were first scoured with close focusing binoculars so as not to disturb any odonates still in the emergence process. Due to the relatively low night temperatures between mid-March and mid-May and again towards the end of the season, except for the *Anax* species, some tenerals would still be

Plate 6. Exuviae of the seven breeding species collected from the ponds at Ghadira Nature Reserve. 1, *Ischnura genei;* 2, *Anax imperator*; 3, *Anax parthenope*; 4 *Orthetrum cancellatum*; 5, *Orthetrum trinacria*; 6, *Sympetrum fonscolombii*; 7, *Crocothemis erythraea.*

emerging at the time of collection. In these cases the exuviae (with tenerals still resting on them) were counted and then deducted from the number collected on the following visit. During collection, Ray Vella helped by locating exuviae with binoculars since, despite the small size of the ponds, it was often quite difficult to locate all the exuviae hidden among the vegetation.

Ischnura genei exuviae were easy to identify as this species is the only damselfly inhabiting the Maltese Islands. *Sympetrum fonscolombii* and *Crocothemis erythraea* are distinctive enough to separate with relative ease. Despite using the criteria in Brochard *et al*. (2012), Cham (2012a) and Carchini (2016) it was not always possible to reliably separate females of *Anax imperator* and *Anax parthenope*. Only 58% of *Anax* species collected could positively be identified to species level, with *A. imperator* outnumbering *A. parthenope* in a ratio of 5:1. For this reason the two species have been treated together. *Orthetrum cancellatum* and *Orthetrum trinacria* exuviae also closely resemble each other. Brochard & van der Ploeg (2012) gave a range of 19 to 29mm for final instar larvae of *O. cancellatum* while Cham (2012) gave the length range as 23 to 25.5mm for final instar larvae and exuviae. (*O. trinacria* is not treated by either Brocard & van der Ploeg or Cham since it is neither on the north-western European list nor on the British list). Carchini (2016) gives the length of *O.*

cancellatum exuviae as 25mm and that for *O. trinacria* as 25-30mm. The mean length of 48 *O. cancellatum* exuviae collected from Ghadira Nature Reserve in August 2018 was 27mm with a range of 20 to 29mm. The mean length of 28 *O. trinacria* exuviae collected from Ta' Qali, Malta by the author in August-September 2019 was 27.1mm, with a range of 25.0 – 29.6mm. The abdominal appendages, measured on the exuviae, were marginally longer in *O. trinacria* than in *O. cancellatum*. In the former the mean was 3.2mm with a range of 2.8 to 3.7mm (n=28). From 48 O. cancellatum exuviae collected from Ghadira Nature Reserve in August 2018 the mean was 2.7mm with a range from 2.0 to 2.9mm. It was thus possible to separate these two species by measuring overall and abdominal appendage lengths (Plate 6).

The maximum number of adults counted at the reserve on any one day was recorded for each of the seven species for which exuviae were found. Larval sampling was carried out on three occasions, once each in November and December 2018 and in January 2019.

Results

The most adults recorded flying at the reserve on any one day belonged to *Crocothemis erythraea*, followed by *Ischnura genei*, *Anax imperator*, *Anax parthenope*, *Orthetrum trinacria* and *Orthetrum cancellatum* (Fig. 1). No individuals of *Sympetrum fonscolombii* were observed.

A total of 1,450 exuviae was collected during the study period (Table 2). *Crocothemis erythraea*, with 1,227 (84.6% of the total) exuviae was by far the most numerous. Exuviae collection from Pond 1 had to be missed on six occasions between 20 March and 11 May so as to avoid disturbance to migratory birds resting and feeding at the reserve during that period. However, it seems probable that the number of exuviae potentially lost on the six days in question was negligible, as most of the 318 exuviae collected from this pond took place in the latter part of the season.

The first species to emerge was *I. genei*, with the first exuvia collected on 16 March. There was a peak of emergence in May, followed by a gap until the second half of June, with a second peak occurring in August (Fig. 2). A single exuvia, with a freshly emerged teneral on it, was found in Pond 1 on 6 November (not shown on Fig.2) – this was the latest emergence I ever recorded for this species in the Maltese Islands. Most *I. genei* emerged from Pond 2 where there is a large clump of *Carex extensa*. The exuviae were found on sedge blades arching into the water, just above the water surface; the exuviae were often

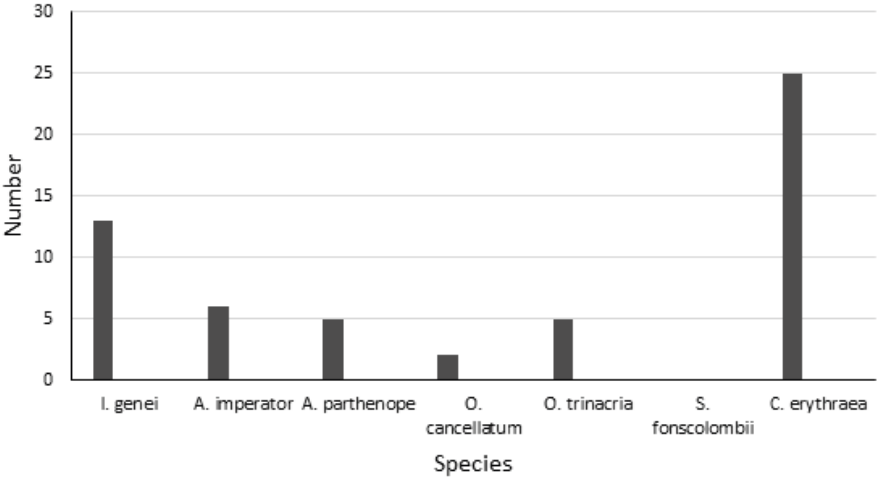

Figure 1. The maximum number of adults of the seven species confirmed as breeding, counted at Ghadira Nature Reserve on any one day.

Table 2. The total number of exuviae for each of the confirmed breeding species collected from the four ponds.

Species	Pond 1	Pond 2	Pond 3	Pond 4	Total
Ischnura genei	1	28	6	0	35
Anax imperator/parthenope	4	70	29	9	112
Orthetrum cancellatum	16	6	4	0	26
Orthetrum trinacria	9	0	0	1	10
Sympetrum fonscolombii	2	1	37	0	40
Crocothemis erythraea	286	473	445	23	1,227
Total number of exuviae	318	578	521	33	1,450

difficult to locate.

The second species to emerge was *S. fonscolombii*, with four exuviae collected on 20 March but no more until April. The main peak of emergence was in May and early June but there was a second, smaller emergence in August (Fig. 3). Nearly all exuviae belonging to this species were collected from Pond 3. The

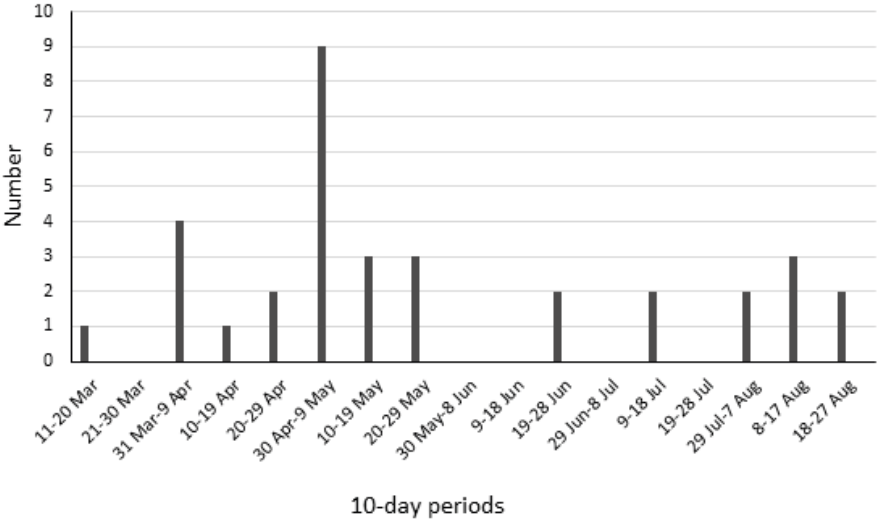

Figure 2. The total number of *Ischnura genei* exuviae collected in 10-day periods.

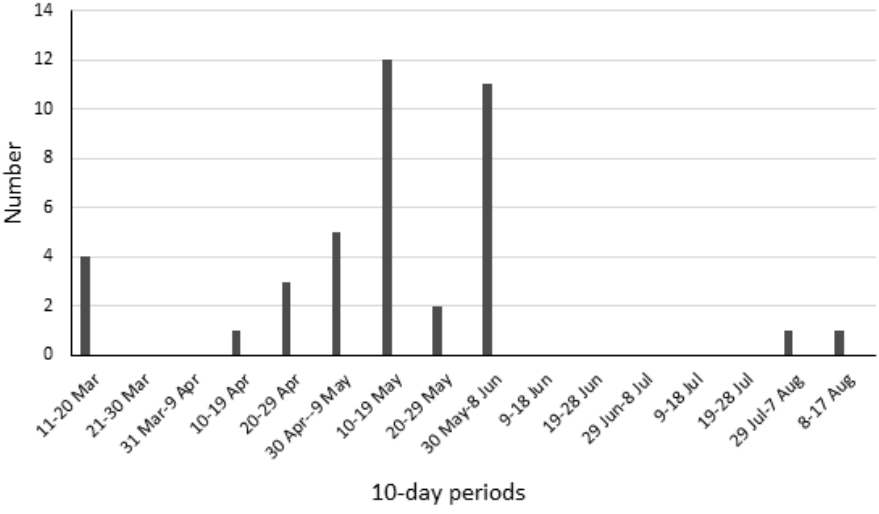

Figure 3. The total number of *Sympetrum fonscolombii* exuviae collected in 10-day periods.

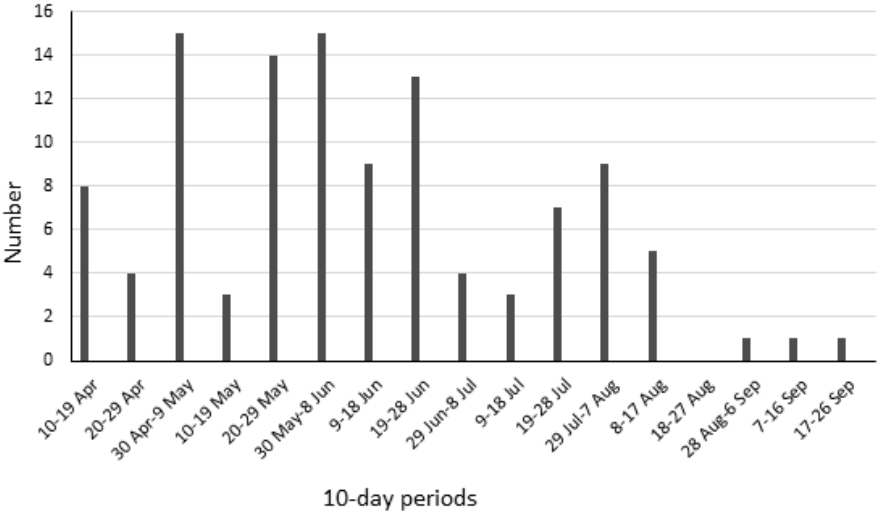

Figure 4. The total number of *Anax imperator/Anax parthenope* exuviae collected in 10-day periods.

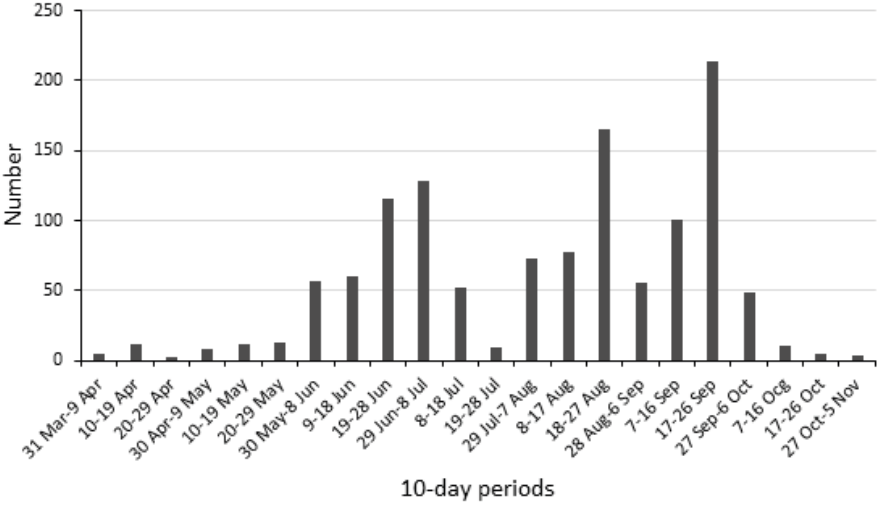

Figure 5. The total number of *Crocothemis erythraea* exuviae collected in 10-day periods.

first *Anax imperator/A. parthenope* exuvia was collected on 11 April (Fig. 4). However, the first mature adults had been seen on 24 March for *A. imperator* and on 25 March for *A. parthenope*. These had probably emerged from a few small agricultural cisterns found along the periphery of the reserve. There appeared to be two peaks, one in May/June, the second in late July and the first half of August. There was then a further, small emergence at the end of August and into September.

Despite eight teneral *C. erythraea* being seen between 23 and 30 March, the first exuviae were only collected on 3 April. There were two clear emergence peaks, one at the end of June and the beginning of July, the other in August/ September (Fig. 5). In the case of this species it is very likely that the tenerals seen near Ponds 2 and 3 in late March had emerged from these ponds and that their exuviae had been blown off by the strong winds and rain prevalent during that period. This theory is further strengthened since most *C. erythraea* and *S. fonscolombii* emerging from Pond 3 in the early part of the season used the SW facing wall of the wooden photography hide at heights ranging from 10cm to 2m. This site is totally exposed to the elements (Plate 7) but the strong to gale force winds prevailing at the time were mostly blowing from the NE.

Orthetrum cancellatum was not encountered flying before the first teneral and exuvia were found on 6 April. No further exuviae were found until the peak of emergence in May/June. Later emergences were recorded in the second half of July and in the second half of August (Fig 6). For *O. trinacria* the first adult

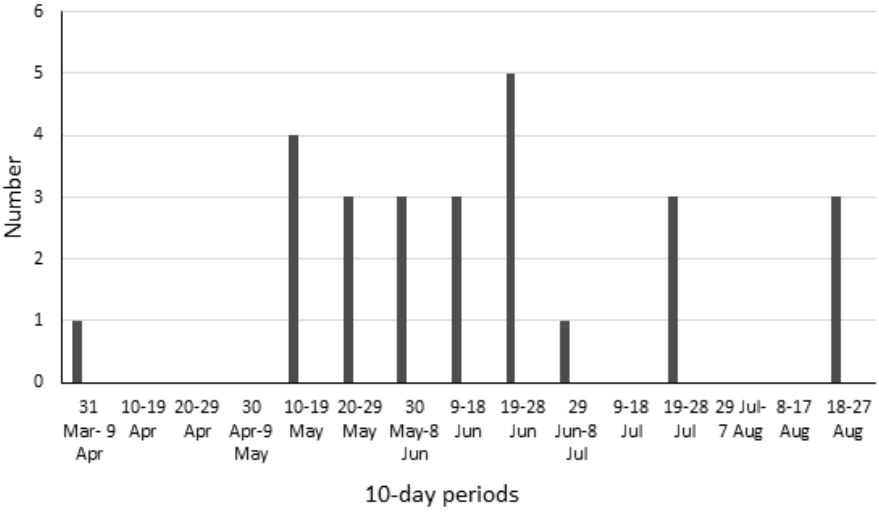

Figure 6. The total number of *Orthetrum cancellatum* exuviae collected in 10-day periods.

Plate 7. Exuviae on the SW-facing wooden face of the photography hide next to Pond 3.

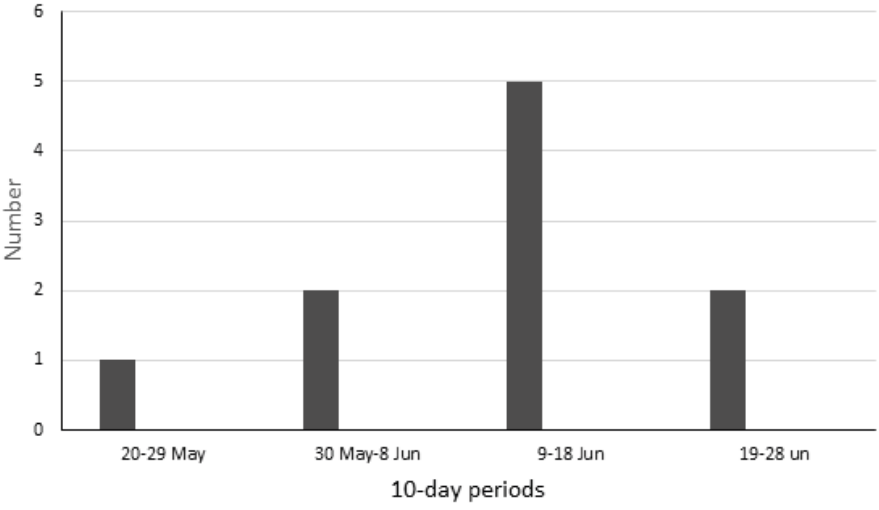

Figure 7. The total number of *Orthetrum trinacria* exuviae collected in 10-day periods.

was seen on 8 May and the first exuvia was collected on 22 May. Only 10 exuviae of this species were found, with a peak of emergence in the first half of June and the last exuviae collected towards the end of that month (Fig. 7).

The larval sampling produced larvae of *I. genei*, *Anax* sp., *S. fonscolombii* and *C. erythraea* in various stages of growth. While most of the *S. fonscolombii* larvae were in their penultimate and final instar, larvae of the other species varied from larval instar 2 to the final instar. No larvae of *O. cancellatum* and *O. trinacria* were found but, to avoid too much disturbance, the bottom sediment of the ponds was not searched.

Pond 1

All seven species that breed in the four ponds were regularly observed ovipositing during the 2018 and 2019 flight seasons, with *C. erythraea* being the most numerous. Just 28 (8.8%) of the 318 exuviae from this pond were collected between March and mid-June, with the rest being collected between mid-June and early December. This is probably due to heavy avian predation on larvae in the spring (D. Cachia, pers. com.), both by residents (mostly *Gallinula chloropus* (Moorhen) and by birds overwintering, as well as those on spring migration (particularly *Alcedo atthis* (Kingfisher)*, Rallus aquaticus* (Water Rail)*, Rallidae* (crakes)*,* and *Motacillidae* (wagtails)). Despite a few *I. genei* larvae being found during the pond survey, only one exuvia was found – on 6 November. Kingfishers and both *Motacilla alba* and *M. flava* (White and Yellow Wagtails) have also been seen and photographed preying on tenerals, mostly *C. erythraea* (D. Cachia, pers. com.) (Plate 8). Since the patch of rushes in the middle of the pond is heavily grazed by wild rabbits, *C. erythraea* larvae had to emerge very close to the water surface and three tenerals were found with the posterior half of their abdomen bitten off. Unlike in Ponds 2 and 3 (see below), no *C. erythraea* exuviae were found out of the water on vegetation surrounding the pond. Of the four *Anax* spp. exuviae collected, one was found on *L. crithmoides* across the service road 2m away from the water and the others on rushes close to the water surface. Except for one *O. cancellatum* exuvia found in the middle of the patch of rushes, all the other *O*. *cancellatum* and *O. trinacria* exuviae were found on *L. crithmoides* shrubs along three sides of the pond, mostly 0.5m away from the water's edge (Plate 9). This pond has always been the most favoured one for reproduction by the two *Orthetrum* species.

Pond 2

At 578, this was the highest number of exuviae collected from any of the four ponds. Most *I. genei* emerged from this pond, with the 28 exuviae collected constituting 80% of the total for this species for the four ponds. It was also the

Plate 8. A Kingfisher preying on a teneral C*rocothemis erythraea* at Pond 1. Photograph by Denis Cachia.

Plate 9. Teneral *Orthetrum trinacria* just emerged on *Limbarda crithmoides* shrub next to Pond 1.

main breeding ground for the two *Anax* species, with 70 exuviae (62.5% of the total number) recovered. All *I. genei* and *Anax* spp. larvae emerged on blades of *Carex extensa* in the middle of the pond. Of the 473 *C. erythraea*, just over 30% left the water and emerged on vegetation on the south-west and south-east of the pond, with the rest mostly on the clump of *Carex extensa*. Most of those leaving the water emerged about 15cm away but 25% of them travelled over a 1m sandy stretch and emerged on the dry stalks of annual plants. All *C. erythraea* exuviae were found at heights ranging between 3cm and 20 cm, both over water as well as over dry land.

Avian predation is thought to be less severe at this pond, although in past years kingfishers were regularly photographed taking well-grown *Anax* larvae. The main predators preying on tenerals were various species of spider which adorn the *Carex extensa* clump with cobwebs, with the main victims being *C. erythraea* (Plate 10).

Pond 3

521 exuviae were collected from pond 3, with *C. erythraea* again being the predominant species, with 445 exuviae (85.4% of the total number from this pond). Despite the fact that all seven species were regularly observed ovipositing, the number of exuviae collected was low except for *C. erythraea*. *S. fonscolombii* tandems were found ovipositing in good numbers in late autumn 2018 but only 37 exuviae were collected. 29 *Anax* spp. exuviae were found but only 4 *O. cancellatum* and no *O. trinacria.* This pond is frequented by several species of bird and undoubtedly there was heavy predation on larvae by resident and wintering birds in January – March and by spring migrants in March – May.

In the early part of the season, when emergence usually started in the early hours of the morning, *S. fonscolombii, C. erythraea* and, on one occasion, *O. cancellatum* mostly used the exposed south-west facing wooden wall of the photography hide as an emergence support (Plate 7). From June onwards *C. erythraea* exuviae were mostly collected from vegetation surrounding the pond at heights of 5 – 20 cm. Smaller numbers emerged on the two *Carex extensa* tufts in the pond, on stones and on a branch present in the water, as well as on the wooden face of the photography hide. Two tenerals which emerged close to the water surface on rocks were found with the posterior section of the abdomen bitten off.

Several species of bird were recorded and undoubtedly there was heavy predation on larvae by resident and wintering birds in January-March and by spring migrants in March-May. The following have all been seen to take larvae: *Alcedo atthis* (Kingfisher), *Gallinula chloropus* (Moorhen), *Porzana parva*

Plate 10. A teneral *Crocothemis erythraea* which fell victim to a spider at Pond 2.

Plate 11. A migrant Sedge Warbler preying on a final instar libellulid larva at Pond 3. Photograph by Ray Vella.

(Little Crake), *Gallinago gallinago* (Common Snipe), *Tringa ochropus* (Green Sandpiper), *Actitis hypoleucos* (Common Sandpiper), *Tringa glareola* (Wood Sandpiper), and *Acrocephalus schoenobaenus* (Sedge Warbler) (Plate 11) (R. Vella, pers. com.). Tenerals have most frequently been seen to be predated by White and Yellow Wagtails but also by other species including kingfishers (R. Vella, pers. com.).

Pond 4

Despite all seven species breeding in the ponds being recorded ovipositing on several occasions in Pond 4, only 33 exuviae were found. These comprised 23 *C. erythraea*, nine *Anax* spp. and one *O*. *trinacria*. Most *C. erythraea* exuviae were found in the latter part of the season, between late August and early October. All were found very low on the heavily grazed rushes, and two tenerals were found to have part of their abdomen bitten off. Avian predation was thought to be very low at this pond, possibly because of its close proximity to the bird-watching hide. Moorhens were sometimes seen scurrying away as people entered the hide. However, this pond is heavily patronized by Painted Frogs, with as many as 13 large specimens and many smaller ones being counted on several days, and these may be the main predators at this pond (see Discussion).

Discussion

Raebel *et al*. (2010) found that surveys based on flying adults cannot be compared with surveys based on larvae/exuviae, with results from the former often being misleading. Their study showed that pond surveys based on exuviae provide a reliable assessment of presence (or absence) of odonates. Indeed, the presence of exuviae or tenerals is the only definitive proof of breeding. Cham (2012b) also came to the conclusion that "the recording of flying adult dragonflies represents an ineffective method for determining the total population of a large dragonfly such as *Aeshna cyanea*". The present study further confirms that the recorded number of flying adults does not truly represent the total population of the species or indicate in which bodies of water they are breeding successfully. The number of flying adults recorded is highly dependent on various factors, such as weather, time of day and duration of observation.

Indeed, although all seven species treated here plus *Trithemis annulata* and *Selysiothemis nigra* have on occasion been noted ovipositing (*Sympetrum fonscolombii* and *Selysiothemis nigra* regularly oviposit in relatively large numbers) in the area at the south-west end of the reserve, known as the West Lake, which is less saline, no exuviae have ever been seen there, despite

regularly searching emergent vegetation through binoculars. The importance of the four fresh-water ponds for the odonate population at the reserve is thus self-evident.

While *Ischnura genei* and *Crocothemis erythraea* tenerals can usually be found within a radius of 10-20m of their emergence point (depending on the vegetation in the area), *Anax* spp. tenerals move long distances away and are seldom, if ever, encountered. Teneral *S. fonscolombii* emerging in spring also tend to move away as immature adults. In the two *Orthetrum* species the immature adults seem to stay close at Ghadira (although this does not seem to be the case in other sites that I regularly monitor).

Avian predation appears to be the main cause of mortality. Most larval predation is caused by waders (especially sandpipers), moorhens, rails, crakes, kingfishers and wagtails but also, rather surprisingly, by other small passerines such as Sedge Warblers (Plate 11). Tenerals have most frequently been seen to be predated by White and Yellow Wagtails, but also by other species, including kingfishers (Plate 8). Spiders appear to be the second biggest threat to tenerals, especially at Pond 2 (Plate 10), although the numbers predated in this way seem to be insignificant. Painted Frogs, the only amphibian species present locally, probably take larvae as they climb up to initiate emergence. The few *C. erythraea* tenerals which emerged very close to the water surface and were found with the posterior part of the abdomen missing are indeed thought to have been predated by Painted Frogs. Indeed, *Rana temporaria* (Common Frog) were thought to represent a significant threat to emerging adult *Aeshna cyanea* (Southern Hawker) at a garden pond (Cham, 2012b). At Pond 3, *S. fonscolombii* and *C. erythraea* were mostly emerging on the wooden face of the photogaphy hide in the early part of the season but stopped using it when the weather had warmed up. This could be due to the presence of *Tarentola mauritanica* (Moorish Gecko*),* which I have seen taking larvae climbing up to emerge, as well as pre-maiden flight tenerals, at other sites. Although ants have also been seen to predate both larvae leaving the water and newly-emerged tenerals, none were recorded during this study. Cham (2012b) also recorded a few instances of predation by wasps on emerging tenerals. Although no instances of attacks by wasps on emerging tenerals were observed during this study, on one occasion in past years I had observed *Polistes* sp. (Paper Wasp) attack a teneral *Orthetrum cancellatum* which had its wings still folded. They were only interested in its shiny wings, out of which they were cutting chunks. The teneral eventually fell to the ground, where the wasps continued to take pieces of its wings, and it later died.

In this study it was impossible to quantify accurately the magnitude of predation by birds, as most instances were witnessed by D. Cachia and R. Vella (and

other bird watchers/photographers in previous years), although it appears to be substantial. As it was impossible for me to visit the ponds every day, even predation by spiders could not be accurately gauged. It is quite probable that, besides *C. erythraea, I. genei* also suffered predation by spiders at Pond 2.

Corbett (1999) gave another two causes of mortality during emergence – failure to moult and failure to expand and harden the wings. During the present study, mortality due to these two causes appeared to be small. Only one *A. imperator* which failed to moult (incomplete ecdysis) and three *C. erythraea* with damaged wings, having failed to expand properly, were found.

Few studies have attempted to quantify the different causes of mortality at emergence. Gribbin & Thompson (1990) reported an overall mortality of 27.9% for *Pyrrhosoma nymphula* (Large Red Damselfly). Predation accounted for 21.8%, with birds topping the list with 7.4%. Climatic factors accounted for 6.2% of the mortality. Strong winds, heavy rain, and low temperatures are the three principal climatic factors responsible for mortality caused by failure to moult and failure to expand and harden the wings, the latter often leading to extreme distortions. Conversely, a study by Bennett & Mill (1993) over a three year period, recorded a mortality of emerging *Pyrroshoma nymphula* of just 3.0% to 5.2%. Most cases of failure resulted from incomplete ecdysis and failure to expand wings, with only 0.8% to 1.1% being attributable to predation by spiders and unknown predators. Despite their daily presence at the ditch the authors did not come across any predation by birds but attributed this to the dearth of birds, perhaps because of their presence. In the present study, the three cases of *C. erythraea* with damaged wings concerned individuals which had emerged in the middle of sedge clumps and been buffeted by strong winds. I had also often come across the same phenomenon with emerging *S. fonscolombii* at Chadwick Lakes (Malta), during the same period.

Corbett (1999) defined those species in which larvae overwinter in their final instar, and thus have a closely synchronized emergence, as ‘spring’ species and those that overwinter in one or more earlier stadia, thus having a less synchronized, more protracted emergence as ‘summer’ species. The results of this study point to *Sympetrum fonscolombii* and *Orthetrum trinacria* as being ‘spring’ species (Figs 3, 7). However, at Ta’ Qali, a stronghold of *O. trinacria* in Malta, I observed a strong emergence of *O. trinacria* between mid-August and mid-September in 2019, suggesting that the species is bivoltine. As regards *S. fonscolombii*, breeding numbers are also closely associated with the autumn rainfall pattern. When rains arrive early (end-August - early September), a second generation is produced and emerges in October and early November, the larval period being as short as 4-5 weeks (Gauci 2014, 2018a).

Ishnura genei is bi-voltine but the emerging teneral on 6 November suggests the possibility of a third generation. The two *Anax* species (Fig. 4) are also possibly bivoltine. The drop in emerging numbers of the *Anax* species in September is likely to be attributable to higher predation on final instar larvae by kingfishers. Larvae hatching from oviposition in late September have been found to emerge by the end of February and early March (personal observation). It is presumed that larvae resulting from oviposition in spring and early summer would have an even shorter larval period due to the higher temperatures and more abundant food supply. *Orthetrum cancellatum* is a 'summer' species and is also likely to be bivoltine (Fig. 6). Both *O. cancellatum* and *O trinacria* numbers were very low at the reserve in 2019. *Crocothemis erythraea* numbers were highest between mid-August and the end of September (Fig.5). The low numbers of this species emerging in April-May are probably the result of heavy avian predation by resident and wintering species as well as by spring migrants. Larval growth during the hot summer months is accelerated and the spectacular surge in emergence from June to September, with a dip in the second half of July, can be attributed both to the progeny resulting from the high number of ovipositing females as well as the dearth of avian predators during that time of year. It seems likely that this species is trivoltine, with populations emerging in April–early July, August, and September.

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Distinguishing early larval instars of Britain's two commonest damselflies, *Ischnura elegans* (Blue-tailed Damselfly) (Vander Linden) and *Coenagrion puella* (Azure Damselfly) (Linn.)

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Abstract

A simple plot of hind tibia length against head width gives a clear distinction between the early larval instars of *Ischnura elegans* (Blue-tailed Damselfly) and *Coenagrion puella* (Azure Damselfly), Britain's two commonest damselflies.

Introduction

Johannsson (2018) recently published a key for separating early larval instars of four common damselfly species in the UK, *Ischnura elegans* (Blue-tailed Damselfly) *Erythromma najas* (Red-eyed Damselfly), *Coenagrion pulchellum* (Variable Damselfly) and *Enallagma cyathigerum* (Common Blue Damselfly). This key seems to be based on her PhD thesis (Johannsson, 1976) and the species she encountered in the Norfolk Broads. It is surprising that she omitted *Coenagrion puella* (Azure Damselfly) since it commonly occurs at her two principal study sites of Alderfen and Upton Broad and did so in the 1970s. Nevertheless, attempts to distinguish early larval instars are to be welcomed as the first keys to British damselfly larvae (Fraser, 1949; Gardner, 1954) concentrated solely on the final larval instar. In more recent times Cham (2009) has delved deeper into important features of earlier larval instars that enables their identification to be determined and this work is the one most often used in the UK.

The aim of this paper is to present a simple method to distinguish between early larval instars of the two commonest British damselflies likely to be encountered in ponds and canals, *I. elegans* and *C. puella*. Much of the work on larval damselflies published by my research group has depended on being able to make this distinction (e.g. Banks & Thompson, 1987; Pickup & Thompson,

1990).

Methods

Larvae were collected from five ponds in the Liverpool area over the winter of 1981-2. In the laboratory their head widths (maximum distance across the eyes) and hind tibia lengths were measured under a microscope using a micrometer eyepiece. Those larvae whose head widths fell between 0.9 and 1.7 mm were maintained separately at 16°C in plastic cups containing about 75ml of dechlorinated water, a cocktail stick on which they could perch and an *ad libitum* food supply of *Daphnia magna* or *D. pulex*, both of which were maintained in culture. The larvae were allowed to feed and moult until they reached the final instar, when they could be identified using the available keys.

Results

There is a linear relationship between hind tibia length and head width. Based on the species identifications determined when the larvae reached their final instar, there is a good separation between the points for the two species, with very little overlap (Fig. 1). In terms of their general size (body length) *Ischnura elegans* larvae have narrower heads and longer legs than *Coenagrion puella* larvae.

Discussion

The distinction identified between these two common species (*Ischnura elegans* and *Coenagrion puella*) reflects what those experienced at looking at damselfly larvae of intermediate size might refer to as the 'jizz', to use a bird-watching term. The instars measured in this report are probably stages 6 to 9 (of 12) for *Ischnura elegans* and similar stages for *Coenagrion puella*. Smaller larvae are generally not captured in surveys because they escape through the mesh of nets conventionally used in sampling. However, the results (Fig. 1) suggest that the relationship would probably hold for smaller larvae.

There are two other useful visual clues for distinguishing between this pair of species. However, these only become completely reliable as the larvae approach later instars. *C puella* (and *Coenagrion pulchellum*) develops spots on its head behind the eyes. These are always present in the last two instars but not necessarily in the instars reported here. They are never present in *I. elegans*. The tips of the caudal lamellae of *I. elegans* are more pointed than

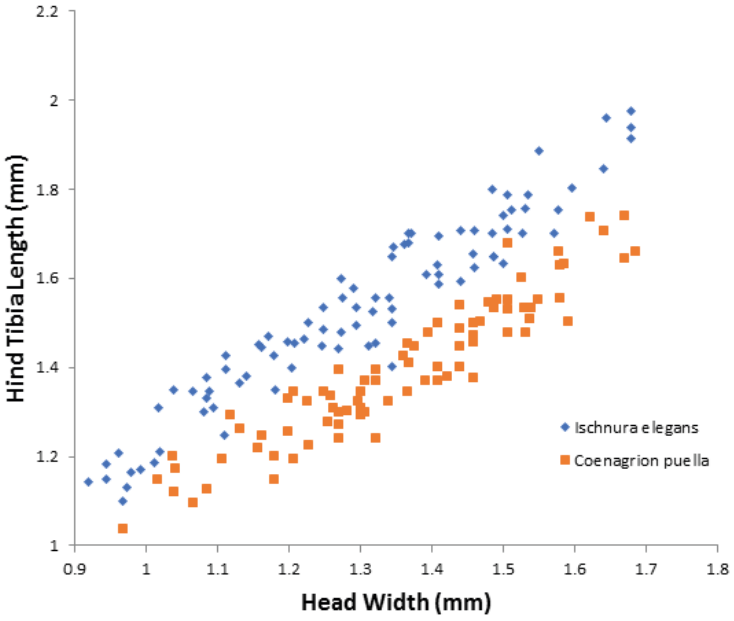

Figure 1 The relationship between Hind Tibia Length and Head Width in *Ischnura elegans* and *Coegnarion puella.*

those of *C. puella*, which can appear rounded. Furthermore, the stout setae on the caudal lamellae reach about the mid-point on both sides of the lamellae in *C. puella* but only on one side in *I. elegans*, those on the other side only reaching about a third of the length. This feature is not always easy to see in early instars.

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