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Cover illustration: Pruinescence on a female of *Libellula depressa*. Photograph by John Horne.

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Authors are asked to study these instructions with care and to prepare their manuscripts accordingly, in order to avoid unnecessary delay in the editing of their manuscripts.

- Word processed manuscripts may be submitted in electronic form either on disk or by e-mail.
- Manuscripts should be one and a half spaced, on one side of the page only and with margins at least 25mm on both sides and top and bottom. Footnotes should be avoided.
- Use of these terms is acceptable: 'exuvia' for cast skin (plural: 'exuviae'); 'larva' (instead of 'naiad' or 'nymph'); 'prolarva' to designate the first larval instar.
- Dates in the text should be expressed in the form: 24 July 2010.
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- Titles of journals should be written out in full.
- Figures, plates and tables should be presented on separate, unnumbered pages.
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Please refer to a recent issue of the journal for further style details.

SCIENTIFIC AND ENGLISH NAMES OF BRITISH ODONATA

ZYGOPTERA	DAMSELFLIES	<i>Aeshna juncea</i>	<i>Common Hawker</i>
<i>Calopteryx splendens</i>	<i>Banded Demoiselle</i>	<i>Aeshna mixta</i>	<i>Migrant Hawker</i>
<i>Calopteryx virgo</i>	<i>Beautiful Demoiselle</i>	<i>Anax ephippiger</i>	<i>Vagrant Emperor</i>
<i>Lestes barbarus</i>	<i>Southern Emerald Damselfly</i>	<i>Anax imperator</i>	<i>Emperor Dragonfly</i>
<i>Lestes dryas</i>	<i>Scarce Emerald Damselfly</i>	<i>Anax junius</i>	<i>Green Darner</i>
<i>Lestes sponsa</i>	<i>Emerald Damselfly</i>	<i>Anax parthenope</i>	<i>Lesser Emperor</i>
<i>Lestes viridis</i>	<i>Willow Emerald Damselfly</i>	<i>Brachytron pratense</i>	<i>Hairy Dragonfly</i>
<i>Sympetma fusca</i>	<i>Winter Damselfly</i>	<i>Gomphus flavipes</i>	<i>Yellow-legged Clubtail</i>
<i>Coenagrion armatum</i>	<i>Norfolk Damselfly</i>	<i>Gomphus vulgatissimus</i>	<i>Common Club-tail</i>
<i>Coenagrion hastulatum</i>	<i>Northern Damselfly</i>	<i>Cordulegaster boltonii</i>	<i>Golden-ringed Dragonfly</i>
<i>Coenagrion lanulatum</i>	<i>Irish Damselfly</i>	<i>Cordulia aenea</i>	<i>Downy Emerald</i>
<i>Coenagrion mercuriale</i>	<i>Southern Damselfly</i>	<i>Somatochlora arctica</i>	<i>Northern Emerald</i>
<i>Coenagrion puella</i>	<i>Azure Damselfly</i>	<i>Somatochlora metallica</i>	<i>Brilliant Emerald</i>
<i>Coenagrion pulchellum</i>	<i>Variable Damselfly</i>	<i>Oxygastra curtisii</i>	<i>Orange-spotted Emerald</i>
<i>Coanagrion scitulum</i>	<i>Dainty Damselfly</i>	<i>Leucorrhinia dubia</i>	<i>White-faced Darter</i>
<i>Erythromma najas</i>	<i>Red-eyed Damselfly</i>	<i>Leucorrhinia pectoralis</i>	<i>Large White-faced Darter</i>
<i>Erythromma viridulum</i>	<i>Small Red-eyed Damselfly</i>	<i>Libellula depressa</i>	<i>Broad-bodied Chaser</i>
<i>Pyrrhosoma nymphula</i>	<i>Large Red Damselfly</i>	<i>Libellula fulva</i>	<i>Scarce Chaser</i>
<i>Enallagma cyathigerum</i>	<i>Common Blue Damselfly</i>	<i>Libellula quadrimaculata</i>	<i>Four-spotted Chaser</i>
<i>Ischnura elegans</i>	<i>Blue-tailed Damselfly</i>	<i>Orthetrum cancellatum</i>	<i>Black-tailed Skimmer</i>
<i>Ischnura pumilio</i>	<i>Scarce Blue-tailed Damselfly</i>	<i>Orthetrum coerulescens</i>	<i>Keeled Skimmer</i>
<i>Ceriagrion tenellum</i>	<i>Small Red Damselfly</i>	<i>Crocothemis erythraea</i>	<i>Scarlet Darter</i>
<i>Platycnemis pennipes</i>	<i>White-legged Damselfly</i>	<i>Sympetrum danae</i>	<i>Black Darter</i>
		<i>Sympetrum flaveolum</i>	<i>Yellow-winged Darter</i>
		<i>Sympetrum fonscolombii</i>	<i>Red-veined Darter</i>
		<i>Sympetrum pedemontanum</i>	<i>Banded Darter</i>
		<i>Sympetrum sanguineum</i>	<i>Ruddy Darter</i>
		<i>Symptetrum striolatum*</i>	<i>Common Darter*</i>
		<i>Sympetrum vulgatum</i>	<i>Vagrant Darter</i>
		<i>Pantala flavescens</i>	<i>Wandering Glider</i>
ANISOPTERA	DRAGONFLIES		
<i>Aeshna affinis</i>	<i>Southern Migrant Hawker</i>		
<i>Aeshna caerulea</i>	<i>Azure Hawker</i>		
<i>Aeshna cyanea</i>	<i>Southern Hawker</i>		
<i>Aeshna grandis</i>	<i>Brown Hawker</i>		
<i>Aeshna isosceles</i>	<i>Norfolk Hawker</i>		

* Includes dark specimens in the north-west formerly treated as a separate species, *Sympetrum nigrescens* Highland Darter.

Species list in accordance with Davies, D.A.L. & Tobin, P. (1984 & 1985) The Dragonflies of the World: A systematic list of the extant species of Odonata. Vols 1 & 2.

A study of Southern Hawker *Aeshna cyanea* emergence from a garden pond.

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Summary

The construction in 2001 of a garden pond in close proximity to the author's house provided an opportunity for close study of emergence patterns, behaviour and predation of Southern Hawker *Aeshna cyanea*. This study discusses the impact of weather conditions and predation on emergence success over a period of several years. Exhaustive daily exuviae counts reveal differences in patterns of emergence in each year, influenced by larval development as well as periods of heavy rain and low temperatures. Predation by birds and wasps had a significant effect on the survival of emerging adults in some years

Introduction

Garden ponds represent an important habitat for dragonflies in Britain with Southern Hawker *Aeshna cyanea* known to favour and breed regularly at such sites. The study pond, approximately 5x4 metres, and with a maximum depth of 1 metre, was dug in June 2001, within one month of moving house, and is situated within one metre of a conservatory on the south facing side of the house (TL082357). The close proximity facilitates daily observations across the pond, from both inside and outside the house (Plates 1 & 2).

Marginal and submerged vegetation were planted in year one and have become well established. Marginal plants comprised Flowering Rush *Butomus umbellatus* (Plates 1 and 2, location A), Bogbean *Menyanthes trifoliata* (Plates 1 and 2, location B), Monkey Musk *Mimulus*, Purple Loosestrife *Lythrum salicaria*, Spike Rushes *Eleocharis* sp (Plate 1, location C), Water Forget-me-Not *Myosotis scorpioides*, Water Mint *Mentha aquatica*, Water Plantain *Alisma plantago-aquatica*, Yellow Flag Iris *Iris pseudochorus*. Submerged and floating plants included Duckweeds *Lemna* sp (not deliberately planted), Fringed Water Lily *Nymphoides peltata*, Broad leaved Pondweed *Potamogeton natans*, Hornwort *Ceratophyllum demersum* and Milfoil *Myriophyllum*. There was no deliberate introduction of *A. cyanea* larvae and all plant samples were checked for larvae before planting. The plants were obtained from the authors previous garden pond and stored in buckets of water for one to two months whilst the new pond



Plate 1. Plan view of garden pond, looking north towards author's house (11 June 2010). A, Flowering Rush; B, Bogbean; C, Spike Rushes; D, a mixture of Spike Rushes, Bogbean and Water Mint.

was dug. Female *A. cyanea* would not typically oviposit directly in these plant species; therefore it is unlikely that any eggs would be present. A small tree stump, along with several logs, were placed in the water at the pond margins to attract females of *A. cyanea* to oviposit. Pieces of wood introduced to the pond came from terrestrial habitats and could not have contained dragonfly eggs.

During the study period the maximum number of mature adults seen at the pond at any one time was two males and one female. The quantitative assessment of dragonfly populations presents many challenges, with counts and/or estimates of adult numbers representing a significant compromise. The sampling of larvae also presents difficulties for population studies. Small early instar larvae prove especially difficult to find.

Methods

Regular larval sampling was avoided during this study as it was deemed likely to cause significant disturbance to the habitat which would potentially impact on subsequent emergence patterns. Of the available methods for assessing the population of *Aeshna cyanea* at the pond the daily collection of exuviae was selected as the least invasive and representing the best method for assessing



Plate 2. View of pond looking south (09 June 2010). A, Flowering Rush; B, Bogbean. The tree stump (E) on the left was used frequently by ovipositing females.

dragonfly emergence numbers. “It is impossible to exaggerate the value of exuviae collection for population studies” (Corbet, 1999).

Following casual observations, in the early years after the pond was dug, systematic observations of the pond from mid-April onwards commenced in 2006. Large Red Damselfly *Pyrhosoma nymphula* was the first odonate species to emerge followed by Azure Damselfly *Coenagrion puella*. The earliest *A. cyanea* recorded emerging from the pond was on 31 May. Daily searches were made around the pond from the first emergence through to the end of October when emergent plants had died back.

In addition to searches, the surrounding emergent vegetation was also scanned with close focussing binoculars from inside the conservatory. To ensure a comprehensive daily count, family members were enlisted to record any signs of activity, including dragonfly emergence and signs of predation. The collection and removal of all exuviae, with a note on their location, ensured that they were not counted twice. The sex of each exuvia was determined by the presence or absence of the female’s precursor to an ovipositor. Two flood lights illuminated the pond, on demand, during hours of darkness, thus facilitating the observation of larvae leaving the water in late evening in readiness for emergence.

General maintenance of the pond was kept to a minimum during the summer period, limited to light clearance of algae and duckweed from the water surface. All removed plant material was placed on the bank of the pond and searched for larvae. It was left for several days to allow any missed larvae to crawl back into the pond.

During 2004 and 2005 only ad hoc recording of exuviae was made. A total count of exuviae was made in 2006 but no daily count details were recorded. Exhaustive daily exuviae counts were started in 2007 and continued each year through to 2011. For these years the cumulative percentile notation, EM_{50} , was determined. This is the time expressed as days elapsed when 50% of the total exuviae over the season have been collected since emergence began. It provides a comparable measure of spring and summer species (Corbet, 1999). For the 2011 emergence period each exuvia was sexed and its total length (front of head to tip of epiproct) measured and the EM_{50} determined for each sex separately. It was not possible to measure all exuviae due to damage or distortion during drying or curvature of the body. The location and orientation of emerging adults and exuviae was recorded throughout the study period.

Results

Female *Aeshna cyanea* started showing interest soon after the pond had been filled with water. The first female was observed ovipositing on 26 July 2001 into a piece of wood placed by the pond margin and this behaviour was observed repeatedly throughout August that year. One female also attempted laying on the bare leg of the author whilst sitting next to the pond. During the summer of 2002, females were observed ovipositing on 12 occasions between 25 July and 2 October.

Of the various pieces of wood that were placed around the pond one particular tree stump with a hole proved to be highly attractive to females (Plate 2 Location E). The hole was used frequently for oviposition during the study (Plate 3). A small sample of moss was collected from this on 11 September 2006 and revealed many eggs to be present (illustrated in Cham, 2007). The eggs were kept in a small water-filled dish on a north facing window sill inside the house where they started to hatch in December the same year.

Emergence

No emergence was observed at the pond during 2002, the year after pond construction, but during light pond cleaning and removal of debris in August a number of *A. cyanea* larvae were encountered. The range of sizes and length



Plate 3. Female *A. cyanea* ovipositing into the tree stump by the pond (E in Plate 2). The moss filled hole was used on numerous occasions.

of wing buds suggested that emergence would be likely to occur in the following year. Indeed, in 2003 the first exuviae were found on 25 June and continued to be found through to 26 July, thus confirming a two-year life cycle. This represented a relatively short period in the first year of emergence.

There was no evidence of larvae moving away from water and all emergence was recorded over water in each year of the study. Emergence was predominately on the south margin of the pond (i.e. north facing) (Plates 1 & 2, Locations A & B) which was illuminated by the late afternoon and evening sun. A smaller number emerged on the west and north margins (Plate 1, Locations C & D) which were illuminated with early and midday sun. No emergence was recorded on the east pond margin. This orientation may be influenced by plant composition as well as illumination levels. The predominant plants used for emergence were Flowering Rush and Bogbean, which grow predominantly in the south part of the pond. Water forget-me-not and Spike Rush were also used at each location. Emergence ranged in height from 5 - 35 cm above the water level, depending on the species of plant and the weather conditions. Following warm days, emergence tended to be higher up on Flowering Rush (Plate 4). Following or during periods of rain, emergence tended to be lower down in less exposed positions. The undersides of the large broad leaves of Bogbean were favoured.



Plate 4. Five *A. cyanea* emerging in close proximity on Flowering Rush (taken at 15.23 on 11 June 2010). A marker is placed just above each individual.

Emergence spanned a period of three months with the earliest on 31 May (2007, 2008) and the latest on 31 August (2011). The data over the five year period 2007-2011 indicated a bimodal emergence pattern. The first, larger peak of emergence represents larvae that enter the winter period well advanced. The second, lower peak of emergence represents individuals that catch up during the spring period. Indeed, at the end of October 2011 larvae were found with wing buds covering four segments (assumed emergence in the first wave of 2012), with wing buds covering two to three abdominal segments (assumed emergence in the second wave of 2012) and with no wing buds (assumed emergence in 2013).

Total annual numbers of emerging *A.cyanea*, as revealed by exuviae counts, steadily increased from the first emergences in 2003 up to a peak in 2007. Numbers declined in 2008 and 2009 but increased again in the following two years (Fig. 1).

Cumulative emergence curves showed significant differences in annual patterns (Fig. 2). During 2007 and 2008 the cumulative emergence curve showed a steady emergence over the season. The cumulative emergence for 2009 was lower than in any other year where daily counts were made. Note that this year

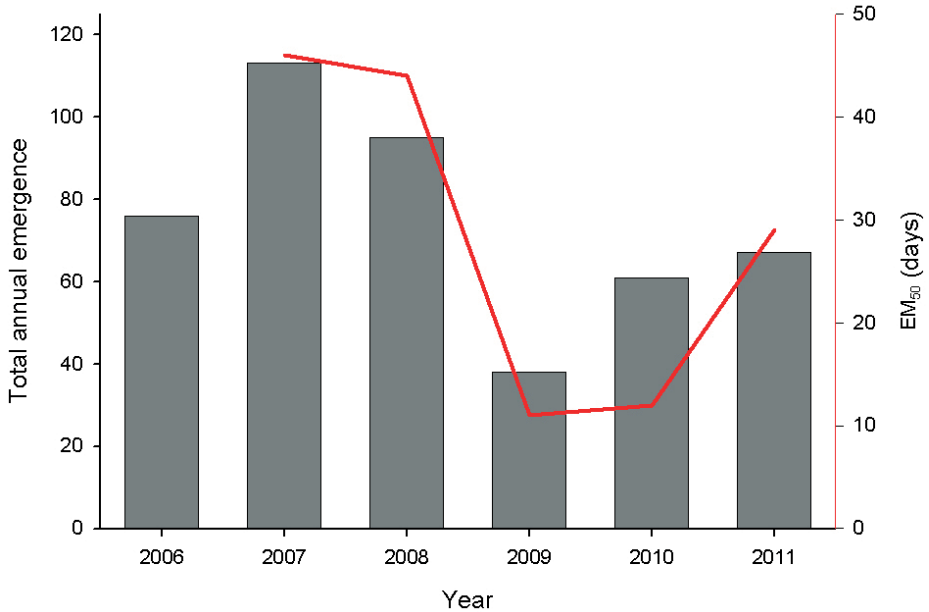


Figure 1. Total annual emergence of *A. cyanea* from 2006 – 2011 (vertical bars) and the EM₅₀ from 2007 – 2011 (red line and right hand scale).

also witnessed the highest levels of bird predation. In 2009 and 2010 emergence took place over a relatively short period in the early part of the season, with an early EM₅₀ in the first half of June. In 2011 the last exuviae was found on 31 August, which was three days after a final instar larva had been found when clearing some algae from the pond.

During warm days and nights over the study period adults emerged during the night and were ready to take their maiden flight early in the morning. Although it was not possible to always determine the exact time that emergence commenced it was observed at almost any time of day. This variation of times is best explained by variation in weather conditions impacting on the start and duration of emergence.

The 2011 emergence period started two weeks later than in preceding years, with individuals emerging in less favourable conditions when it was cold and wet (see below). This resulted in individuals staying at the emergence perch for many hours. The ability to take the maiden flight depends on air temperature.

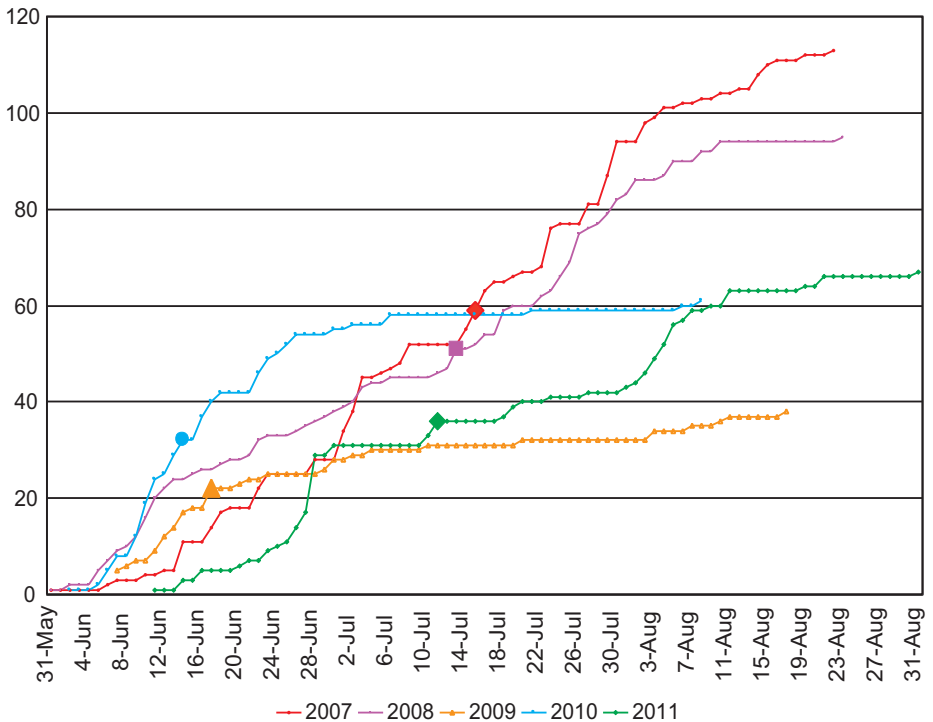


Figure 2. Cumulative emergence curves from daily exuviae counts EM_{50} shown by large data points.

By 28 June 2011, twenty nine individuals had emerged at erratic intervals over the two weeks. On the evening of Saturday 25 June it was warm and still and two individuals had started to emerge around 18.00 hours. It was assumed that they would remain overnight and take the maiden flight the following morning. However, that evening, just as it was getting dark, one individual took to the air at 21.35 and flew off to one side of the house, thus confirming that *A.cyanea* can take its maiden flight in twilight in the UK. The second individual had already gone but it could not be determined for sure that it took flight.

Mature adults were recorded at the pond throughout the summer flight period. The date of the first mature adult recorded each year at the pond varied from 16 – 76 days after the first emergence was recorded (Table 1). It should be noted that it was not possible to determine if adult sightings are of returning adults or wandering individuals from elsewhere. Observations of adults are dependent on observer availability and are biased towards times when they are present,

Table 1. The times of first emergence, first mature adult recorded at the pond and the first ovipositing female.

Year	First emergence	First mature adult at pond	First ovipositing female	No. of days between first emergence and first mature adult
2001	No emergence	26 July	26 July	NA
2002	No emergence	25 July	25 July	NA
2003	21 June	15 July	2 August	25
2004	16 June	10 August	10 August	56
2005	21 June	18 July	18 July	28
2006	14 June	16 July	30 July	32
2007	31 May	17 July	7 August	47
2008	31 May	3 August	10 August	65
2009	5 June	20 August	20 August	76
2010	2 June	2 July	2 July	30
2011	11 June	17 July	17 July	16

such as weekends.

Effect of the weather

Weather conditions have a significant effect on emergence. A warm, sunny period was often the trigger for emergence, especially if followed by a wet, cooler period. Under optimum conditions larvae were leaving the water in the evening and starting to emerge at 23.00-24.00 hrs ready to take their maiden flight before daylight the following morning. This gives the individuals their best chance of completing ecdysis during hours of darkness. When the weather was less favourable, due to rain or cold nights, emergence started during the early hours of the following morning. During the summer of 2007 there was heavy rain during June and July and intermittently in August. In periods of persistent rain no emergence was observed but emergence was observed during light rain.

On 11 June 2008 a larva was observed to leave the water and climb up an emergent stem of Flowering Rush. Emergence did not commence immediately due to rain. It was still in the same place later in the day and also overnight. It finally emerged the following day in the late afternoon. On 5 August 2008 three individuals were emerging from 07.00 onwards following a previous day and preceding night of very heavy rain.

Table 2. Details of emergences between 1-19 June, 2010. f, female; m, male.

Date	No. & sex	Notes on emergence
1 June	0	Cool, wet weather, no emergence
2 June	1m	Warm day triggered 1st emergence of the year in evening
3 June	0	No emergence
4 June	0	No emergence
5 June	1m	One emerged following relatively warm day.
6 June	3m	All three larvae seen leaving water previous evening to emerge overnight
7 June	2m 1f	All three emerged overnight
8 June	0	Heavy rain, no emergence
9 June	1m 3f	Emergence started early morning, maiden flight of one at 07.45
10 June	4m 3f	Warmer. Emergence of seven during night
11 June	4m 1f	All emerged from midday onwards following rain during the night and a dull cloudy morning.
12 June	1m	Emerged overnight
13 June	3m 1f	Emerged overnight
14 June	2m 1f	Emerged early morning during daylight after evening of torrential rain.
15 June	0	No emergence, quite cold day
16 June	2m 3f	One emerged very late in afternoon. Three did not take maiden flight that day despite warm windy weather. Cold night may have delayed emergence
17 June	3f	Cold night. Nothing emerging by 7.00am. One emerging at 7.45; two later in afternoon
18 June	2f	Emerged overnight
19 June	0	No emergence

In 2010 emergence started on 2 June, a few days later than in previous years due to cool damp weather. A warm sunny spell triggered the first emergence. Over the following seventeen days the pattern of emergence was affected by periods of heavy rain and cold nights (Table 2).

The emergence of 11 June 2010 is worthy of note. Rain the preceding night followed by a cloudy wet morning resulted in no emergence at night or early morning. From midday the sun appeared and five individuals started to emerge (Plate 4) on the south margin of the pond. These emergents were in close proximity to each other in a clump of Flowering Rush. Their close proximity and high visibility placed them at high risk of predation. The first maiden flights occurred at 17.00. These observations suggest that they had delayed

Table 3. Sex ratio of emerging adults by year.

Year	n	% Males
2007	113	50.4
2008	91	49.5
2009	38	52.6
2010	60	53.3
2011	67	44.8
Overall	369	49.9

emergence due to the poor weather of the previous night and were compelled to emerge at the earliest opportunity.

On 17 July 2011 a female was observed flying around the garden feeding off bushes. The weather was light rain with sunny spells. She oviposited in logs around the pond and also on a moss covered rock by the pond. Egg laying continued for approx 10 minutes into moss in the rain.

Sex ratio and size of exuviae

Sexing of exuviae from 2007 onwards revealed minor variations in the ratio of males and females each year but over the study period a mean ratio of 1:1 was recorded (Table 3) and in no year did the ratio differ significantly from 1:1 (Chi-square test, $p > 0.25$).

Exuviae in 2011 ranged in length from 41-49 mm (mean 43.9 mm, $n=55$) with extremes found throughout the emergence period. The length of males ranged from 41-46 mm (mean 43.4 mm, $n=25$) and females from 42-49 mm (mean 44.3 mm, $n=30$). Although females were 1 mm longer on average than males and tended to emerge later it could not be confirmed that emergence was related to size.

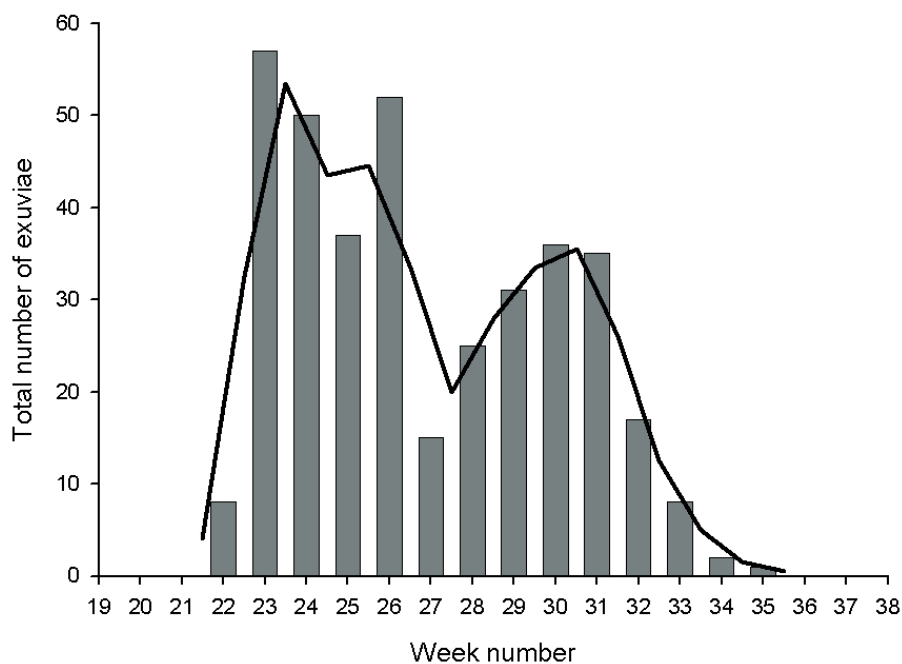
The EM_{50} for each of the five years of daily exuviae counts ranged from 11 to 46 days (mean 28.6 days). In 2009 and 2010 the EM_{50} was markedly earlier than in other years (Fig. 2) with a low number of individuals emerging later in the season, i.e. during the second peak of emergence (Fig. 3). The EM_{50} was directly proportional to the numbers emerging, i.e. a larger emergence resulted in a longer EM_{50} (Fig. 1).

The EM_{50} by sex in 2010 and 2011 showed marked differences with males appearing to emerge earlier than females each year as they have a shorter

Table 4. Length and date of the EM₅₀ for females and males in 2010 and 2011.

	EM ₅₀ in days	
	2010	2011
Females	15	42
Males	9	17
Combined	12	29

	Date of EM ₅₀	
	2010	2011
Females	17 June	23 July
Males	11 June	28 June
Difference (days)	6	25

**Figure 3.** Total emergence each week from consolidated daily exuviae counts from 2007-2011. The trend line shows the two-week rolling average.

EM₅₀. In 2010 the EM₅₀ for males was 6 days earlier than that for females; in 2011 it was 25 days earlier (Table 4).

Mortality

Over the period of this study failure to moult was only recorded twice, when emerging adults failed to extract from the larval skin. The causes for this are not known. Failure to expand and harden wings was observed on three separate occasions and was associated with periods of rain and high winds. Windy wet weather damaged two emergent individuals during June 2011, one of which failed to develop the wings and abdomen fully. On 4 August 2011, after heavy rain the preceding night, three emerging adults and their associated exuviae were found hanging from the leaves of Bogbean. They were unaffected by the rain and possibly the large leaves of this plant afforded shelter from rain to enable them to emerge successfully.

Predation by wasps. Wasps were frequently observed flying within 300mm of the water's surface and they would manoeuvre amongst the stems of Flowering Rush in search of potential prey. On 30 June 2007 a single *A. cyanea* larva



Plate 5. Common Wasp in flight carrying butchered parts from a recently emerged adult. The pieces were carried away by the wasp before returning to continue the process.

was seen leaving the water to climb a stem of Flowering Rush to emerge. It had emerged and separated from the exuvia when a Common Wasp *Vespula vulgaris* attacked it. It fell to the water surface following repeated attacks from the wasp. The wasp then started butchering and eating the eyes and head whilst the helpless dragonfly struggled. The head was severed and carried away in pieces. The wasp repeatedly returned to further butcher the now dead dragonfly. The thorax was chopped up into small pieces. Digital photos show the wasp in flight with joints of dragonfly meat nearly the same mass as itself (Plate 5). The wasp would leave the water and settle in nearby vegetation before flying off, presumably to the nest. On one occasion it landed on the upright stem of Purple Loosestrife allowing closer inspection. The wasp appeared to be masticating its dragonfly food to make it more manageable to carry off. The wasp returned until the dragonfly corpse was water-logged and attracting the attention of Smooth Newts *Lissotriton vulgaris* and the two Minnows *Phoxinus phoxinus* that inhabited the pond at the time. The remaining corpse was taken by the newts.

One wasp attacked another individual but this time the author intervened and prevented the attack from being successful. Two other emerged individuals were removed from their emergence supports and placed in bushes further away from the pond to complete the hardening of their wings. These individuals successfully took their maiden flights.

Predation by frogs and newts. Frogs *Rana temporaria* also represented a significant threat to emerging adults. They were observed regularly sitting in the pond close to emergence sites. Any movement attracted their attention. On one occasion a *A. cyanea* emerged close to where two frogs regularly sheltered. The exuvia was found later in the water with no sign of the adult body. On 8 August 2008 a frog was observed taking a newly emerged adult at the point of its maiden flight; the wing whirring associated with pre-flight attracted its attention.

Newts have been observed to sever the abdomens of female *Pyrhosoma nymphula* and *Coenagrion puella* when ovipositing in tandem into floating pond plants at the pond. On one occasion a recently emerged *A. cyanea* was found with segments 5-10 of its abdomen bitten off. It was found floating on water after several hours clinging to a stem of Spike Rush. This may have been a result of newt attack after it had become dislodged and fallen into the water.

Predation by birds. Blackbirds *Turdus merula* and House Sparrows *Passer domesticus* regularly breed in the surrounding area. House Sparrows which breed in nearby trees and buildings were the main predator species at the pond

followed by Blackbirds.

Dragonflies on their maiden flight are very noticeable to watchful birds and easily taken. During a maiden flight (15 June 2008) one individual narrowly missed being caught by a Blackbird. The dragonfly detected the impending attack by the bird and banked away to fly clear. On another occasion, in 2009, a Blackbird found a crippled individual and took it off in the direction of its nest to feed its chicks. It was observed returning to the same place searching for more.

A. cyanea typically emerges on emergent vegetation over water. At the pond they select patches of Flowering Rush that appears denser and taller than other vegetation. Bogbean leaves are also used to a lesser extent. In years of high bird predation the emergent vegetation starts to get knocked over making subsequent emerging dragonflies more visible. In late summer when water levels start to drop the emergent vegetation is more accessible to foraging birds.

Predation was especially high during 2009. Daily counts revealed various parts of exuviae, especially the distal section of the abdomen, in vegetation around the pond. This indicated bird rather than frog predation. Indeed, House Sparrow predation did have an impact on emergence numbers and it is thus highly likely that the numbers of exuviae counted were underestimates. The Sparrows were often active in the early morning before the observers were awake, so going unnoticed. This is a time when emergence for this species would typically take place. On 15 June 2009 a female House Sparrow was observed taking a newly emerged *A. cyanea*. The bird hovered, like a Kestrel *Falco tinnunculus*, over the pond approx 30cm above the water's surface. It then dashed in to pluck the dragonfly from its emergence support and fly off with it. This was subsequently observed on a number of occasions during the year. This individual had developed a search image for the emerging dragonflies and was using a strategy to exploit the food source. This behaviour was not observed in any other year.

During June 2010 the vegetation was especially lush and no predation was observed during the peak period of emergence. This suggests that the birds had not seen any emerging dragonflies and had not learnt of their presence.

Discussion

Corbet (1999) concluded that "The total numbers emerging from a habitat in a season can be determined by regular, exhaustive collections of exuviae throughout the emergence season". This study based on daily exuviae counts has revealed differences in patterns of emergence in each year. There are a number of considerations when collecting exuviae for population counts. One

has to ensure that no exuviae remain from the previous season. At the garden pond site the die-back of vegetation over the winter period would have removed any such exuviae. Corbett (1999) pointed out that exuviae can disappear from emergence supports before being counted, including as a result of wind or rain (Corbet & Hoess 1998). Dislodged exuviae were found on a few occasions during the study but it is unlikely that any were missed through being blown away from the immediate proximity of the pond, although strong wind can increase mortality by dislodging the emerging adult and causing irreparable damage to wings.

In the tropics, adult dragonflies emerge at night to fly before sunrise (Corbet 1962; Winstanley *et al.* 1981). This is thought to be the typical pattern for the larger Hawker dragonflies in the UK (Brooks 2004; Smallshire & Swash, 2010) also, as long as weather conditions are favourable, and this study has demonstrated that it occurs in *Aeshna cyanea*. It was thus surprising to observe daytime emergences of *A. cyanea* since, for a large species, such daytime emergence makes emerging adults more susceptible to predation. However, this occurred as a result of inclement weather conditions, either heavy rain or low temperature during the preceding night. During light rain, emergence of *A. cyanea* was observed and this has also been reported for *Leucorrhinia dubia* (Beynon, 1995).

The author recalls being surprised at the lack of emergence on days with seemingly ideal weather conditions in the middle of the emergence period. However it was noted that these coincided with the dip in the bimodal emergence. The first wave of emergence is individuals that have overwintered in a more advanced state of development, whereas the second wave results from individuals developing in the spring as prey becomes more plentiful. During February and March each year up to 30 pairs of Common Frog spawn at the pond and the resulting tadpoles provide a ready source of food in the spring months for dragonfly larvae large enough to take prey of this size.

Corbett (1999) gives EM_{50} values of 3 days for the Emperor Dragonfly *Anax imperator*, which is a spring species, and 25 days for *A. cyanea*, which is a summer species). The present results for *A. cyanea* confirm this, with a mean EM_{50} over the period 2007-2011 of 28.4 days.

Mortality

Corbet (1999) stated three causes of mortality during emergence: i) failure to moult, ii) failure to expand and harden wings and iii) predation. Over the period of the current study failure to moult was only observed twice and there were only three cases when emerging adults failed to expand and harden their

wings. The predation threat to emerging *A. cyanea* at the pond was from Wasps (*Vespa* and *Vespula* spp), Common Frogs, Smooth Newts, House Sparrows and Blackbirds. Corbet (1999) reported that Blackbirds are the major avian predator of emerging adults. Although Corbet (1999) stated that ants and spiders are known predators of emerging dragonflies, this was not observed, despite species of both being present.

Predation at emergence time can occur while i) larvae are travelling to the emergence site, ii) at the emergence site during or after ecdysis and iii) during the maiden flight. Larvae of *A. cyanea* typically emerge directly over water on suitable emergent vegetation (Wildermuth, 1991; present study). It is possible that predation occurs during travel to the emergence site. Newts would be the most likely predator at this time and final instar larvae would represent a large prey item. Newts have been observed to predate damselflies when ovipositing yet are more likely to be opportunistic scavengers of larger dragonflies, feeding on corpses rather than catching living adults (pers. obs.). Pre-emergent larvae were observed in close proximity to their emergence site on a number of occasions but no predation was observed at this stage. Once the larvae leave the water to emerge there is potential for them to attract the attention of predators and large dragonflies such as *A. cyanea* emerging during daylight hours face a range of predators. During the day they were noticeable to the human eye from some distance and thus probably also susceptible to daytime predation. Predators, especially avian predators, are opportunistic and if they encounter emerging dragonflies they will attempt to exploit this food source.

Predation by wasps. The observed predation by wasps may have been due to the close proximity to the pond of a wooden garden fence that attracts wasps looking for a source of wood for making their nests. Wasps require water to enable them to produce paper and using the garden pond as a water source brings them in close contact with emerging dragonflies. It is not possible to predict if predation would be reduced or eliminated if the fence was not present.

Predation by birds. Birds use garden ponds for drinking and bathing and this potentially brings them into contact with dragonflies, especially at times of low water levels when they are emerging during daylight hours. Periods of cold and wet weather which inhibit the drying process result in emerged dragonflies hanging out for longer during daylight hours. Jerking actions at various stages of emergence attract the attention of birds when they are bathing or drinking at the pond.

House Sparrows predated newly emerged adults, notably in 2009, which was the year when the highest levels of predation were observed. They presumably developed a search image which they used to continue exploiting their prey.

When this occurs the population is at risk from sustained predation. This may account for the low numbers recorded emerging during 2009. This cohort would have been from eggs laid in 2007, which saw the highest numbers of adults successfully emerge. Blackbirds were seen to take newly emerged adults in 2008 and 2009. They were regular visitors to the pond for bathing. They were also seen taking frog tadpoles and on one occasion a male caught a female Smooth Newt, flying to the nearest fence to kill it by hitting it repeatedly onto the hard surface before flying off. On 15th June 2008 an emerging *A. cyanea* was observed to take its maiden flight away and over the nearby fence. A male Blackbird saw it and flew up to try to catch it. The dragonfly veered away at the last second and successfully avoided capture.

Conclusions

This study has shown 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 start of the adult flight period is significantly misrepresented when based on records of mature adults alone. Adults of *A. cyanea* quickly disperse from the breeding site, rarely returning to water for several weeks after emergence. Observations of adults at the pond are also highly biased by the availability and presence of an observer at the time when an adult is present. Many sightings inevitably go unrecorded. Adult *A. cyanea* are frequently observed feeding in sheltered woodland rides away from water during the maturation period, with relatively few records for this species immediately after emergence.

It has been shown that the exhaustive collection of exuviae is the most effective method for assessing absolute population numbers. This is not without potential shortcomings; it is very labour intensive and would be more difficult at study sites of greater size and complexity.

At the pond more than 80% of emergence occurred at the south margin, where the vegetation was densest. This was the part of the pond illuminated by the late afternoon and evening sun. It is interesting to note that the opposite end of the pond was utilised by frogs for spawning, a species known to select the area of a pond with the warmest water temperature. This is suggestive that air temperature is more important to emerging dragonflies than water temperature.

Under warm, dry weather conditions emergence typically commences during late evening under darkness. The maiden flight is usually early the following morning. This study showed that the maiden flight can also take place during the hours of darkness. This is potentially a mechanism for adults to move away from the emergence site and find more protected sites for maturation

before predators are likely to be active. Inclement weather has a significant impact, resulting in emergence during daylight hours. This can expose adults to heightened risk of predation.

Predation at the pond was affected by a number of factors. The type and density of emergent vegetation around the pond affects the concealment of emerging dragonflies. Dense vegetation, especially Bogbean and Flowering Rush, makes them less visible to birds and frogs. This was especially the case in 2010 when up to five individuals emerged successfully in dense vegetation during daylight hours. Bushes and trees growing close to the pond, 'the hinterland', attract birds and this influences the potential for birds to visit the pond. In 2008 and 2009 predation by Blackbirds and House Sparrows had an impact on the numbers of adult *A. cyanea* emerging and surviving. In years with high levels of bird predation the numbers of exuviae being counted will be reduced, leading to an underestimate of the population emerging. During periods of drought and low water levels the water contracts away from the emergent plants that offer emergence sites. This can result in birds coming to bathe more frequently and therefore being in closer contact with dragonflies at emergence sites.

As the season progressed wasps regularly visited the pond and represented a threat to newly emerged dragonflies as they flew in amongst Bogbean and Flowering Rush. Dragonflies emerging during the hours of daylight are especially vulnerable from this threat. Whilst European Hornets *Vespa crabro* are large enough to catch active adult dragonflies as large as Southern Hawkers (Cham, 2004) it was surprising to observe smaller species also attacking non-motile adults at emergence. Small wasp species such as *Vespula germanica* and *Vespula vulgaris* have been reported to take smaller dragonfly species such as *Sympetrum sanguineum* and will also take large dragonfly prey before they take their maiden flight (Paine 1992, Taylor 1994). On 29 June 2011 the author also observed *V. vulgaris* predating emerging *Anax imperator* at a pond near Toddington, Bedfordshire.

It is a commonly held view that dragonfly species fall into either Spring or Summer species (Corbet, 1999). However, this classification may not be so clear cut. This study has shown a bimodal emergence pattern in *A. cyanea* related to the development of larvae. In years of high emergence a clear bimodal pattern is observed. In years where lower total numbers are observed the second wave of emergence is significantly reduced.

The close proximity of a garden pond to the author's house has afforded observations over an extended period that would prove more challenging at many other sites. It has revealed the multivariate factors that affect the survivorship of adults emerging each year.

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The terrestrial mite *Leptus killingtoni* Turk (Acari: Erythraeidae) as a parasite of the Small Red Damselfly *Ceriagrion tenellum* and other odonates.

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Introduction

The vast majority of mites found on dragonflies and damselflies are parasitic aquatic larval mites belonging to the genus *Arrenurus* (Baker *et al.* 2007, 2008). However, in an investigation in 1943, reported by Killington & Bathe (1946), a terrestrial larval mite was found on several odonates in Dorset. Specimens were sent to F. A. Turk who described it as a new species, *Leptus killingtoni* (Turk, 1945) and it has since been re-described (Southcott, 1992).

The genus *Leptus* is cosmopolitan and known largely from the six-legged larval stage as orange or red coloured parasites of arachnids and insects (Baker & Selden, 1997). The nymphs and adults, which are eight-legged, are free-living predators. Haitlinger (1987) has described several larval species of *Leptus* from Poland.

Killington & Bathe (1946) worked on an area of heathland on the Hampshire-Dorset boundary, and in the valleys, where two small streams run, they found *Leptus killingtoni*. The authors listed eight hosts - *Orthetrum coerulescens* (Keeled Skimmer), *Pyrrhosoma nymphula* (Large Red Damselfly), *Coenagrion puella* (Azure Damselfly), *Ceriagrion tenellum* (= *Palaeobasis tenella*) (Small Red Damselfly), *Lestes sponsa* (Common Emerald Damselfly), *Enallagma cyathigerum* (Common Blue Damselfly), *Cordulegaster boltonii* (Golden-ringed Dragonfly) and *Anax imperator* (Emperor Dragonfly). New hosts for this mite were reported recently (Lorenzo-Carballa *et al.*, 2011) from the Azores - *Ischnura hastata* (Citrine Forktail), *I. pumilio* (Scarce Blue-tailed Damselfly) and *Sympetrum fonscolombii* (Red-veined Darter).

In a long term on-going study of *Coenagrion mercuriale* (Southern Damselfly) and other damselflies in East Devon, one of the authors (L.K.) has recently found *L. killingtoni* on a number of odonates (Plate 1).

Material and Methods

Odonata from three commons on the East Devon Pebblebed Heaths were checked for mites. The East Devon Pebblebed Heaths (SSSI, SAC, SPA) are the largest block of lowland heath in Devon and associated with various mire communities. The main site investigated was Colaton Raleigh Common near Exmouth, which is owned and managed by Clinton Devon Estates. This site consists of a small area of shallow pools and runnels within tussocks of Black Bog Rush *Schoenus nigricans* and Purple Moor Grass *Molinia caerulea* and is at the base of a south-facing slope running down to a small stream with taller trees on the south side. Field work was also carried out at Meg Range Valley, which is part of Colaton Raleigh Common but lies to the north-east of the main site, at Venn Ottery Common (owned and managed by Devon Wildlife Trust) and at Bickton Common (Clinton Devon Estates). Both casual and more detailed observations were made using close-focus binoculars while the dragonflies and damselflies were at rest, although the underneath of the thorax could not be seen in many cases.

Several mites were placed individually in small containers as living specimens or preserved on site in 70% ethanol. The mites were then sent promptly to one of the authors (R.A.B.) for identification. Temporary mounts were made on slides using 50% lactic acid, which serves as both a clearing and mounting agent, and the identification was carried out using Turk's (1945) original description and Southcott (1992).

Results

In the present survey, these orange coloured mites were observed on the head, thorax, abdomen and legs (Plate 1). Based on size and especially on colour, the following hosts were recorded as infested - *C. tenellum*, *P. nymphula*, *C. mercuriale*, *O. coerulescens* and *C. boltonii*. *C. mercuriale* is a new host record. It should be noted that, although field observations were made on all the species, mites from some species were not collected.

The results for *C. tenellum* are – examined 123, infested 39, prevalence (percentage of individuals parasitized) 32%. Of the 56 mites observed, 23 (41%) were found on the legs and smaller numbers on other parts of the body; i.e. 2 (4%) on the head, 13 (23%) on the thorax, 10 (18%) on the abdomen and 6 (11%) on or near the eyes (Table 1). In the case of two mites, the site of attachment was not recorded. The majority of the odonates had only one mite per host.



Plate1. Small Red damselfly showing *Leptus killingtoni* at the tips of the legs. Photograph by Ian Ward.

Discussion

L. killingtoni appears to have a wide host range within the Odonata and other insect groups and no doubt other host species will be found in the future. At Colaton Raleigh, mites were also found on pond skaters but although these have not been examined, they are almost certainly the larvae of freshwater mites and not members of the genus *Leptus*.

According to Killington & Bathe (1946) the prevalence varied depending on the

Table 1. Distribution of *Leptus killingtoni* on the Small Red Damselfly *Ceriatrion tenellum* in Devon in 2011. CRC, Colaton Raleigh Common; MRV, Meg Range Valley.

Date of record	Site	No. of Odonates	No. + sex of Odonate infected	No. of mites	Site of attachment					Mating Odonates with mites	
					Head	Thorax	Abdomen	Leg	Near Eye		Other
3 July	CRC	14	1 male	1						Site unknown	1
			1 female	1						Site unknown	1
20 July	CRC	10	3 males	3		2					
			3 females	3		1	1			1	
25 July	CRC	28	6 males	10	1	3		6			
			6 females	11		3		6	2		5
26 July	CRC	28	7 males	12			6	4	2		3
			2 females	2		1	1			2	
26 July	MRV	8	1 male	2				2			
			1 female	1			1				1
3 August	CRC	26	3 males	3			1	1	1		
			2 females	4		3	1				1
17 August	CRC	8	2 males	2	1	1					
19 August	CRC	1	1 male	1				1			
Total		123	39	56	2	13	10	23	6	2	

species of odonate, 27% for *P. nymphula*, 8.3% for *C. tenellum* and 9.8% for *E. cyathigerum*, with an overall prevalence for all species of 16%. The intensity was from 0 to 8 parasites per host, with 76% carrying only one mite per host. Lorenzo-Carballa *et al.* (2011) give 0-41% prevalence on *I. hastata* and 0-35% on *I. pumilio* for the island of Pico, Azores and indicate that this figure was highly variable among different ponds. In a study by Townsend *et al.* (2006) on *Leptus* mites parasitizing the harvestman *Leiobunum formosum*, the authors found significant annual variation in prevalence, ranging from 0.5% to 20.3% and a mean intensity which varied from 1.0 to 1.3, with a maximum intensity of 3 mites per host. The results of the present study are therefore comparable with the results of other workers. However, it is possible that the prevalence figure of 32% may be too high since some of the infested odonates may have been observed and counted on more than one occasion.

The attachment sites given by Lorenzo-Carballa (2011) for *L. killingtoni*, were mainly on the abdomen (63%), with others on the legs (18.5 %) and thorax (18.5 %). Killington & Bathe (1946) give figures of 47% on the legs, 31% on the thorax, 21% on the abdomen, 1.2% on the head and 1.2% between thorax and abdomen. In the present study, the authors found that the majority of mites (41%) were on the legs of *C. tenellum* but not necessarily attached, with smaller numbers on other parts of the body. This is a similar figure to that given by Killington & Bathe (1946). The mite probably attaches to different sites on the host after making initial contact via the legs.

L. killingtoni has been found loosely attached, as Lorenzo-Carballa (2011) and our observations confirm, but Killington & Bathe (1946) indicated that their attachment can be very firm at times. This is important in establishing the true relationship between the mite and the odonate. Although it is not yet possible to say with certainty that *L. killingtoni* is parasitic, the evidence from other workers indicates that this is highly likely. Abro (1988), for example, stated that the *Leptus* species found on harvestmen was an ectoparasite and fed on the haemolymph of its host.

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Pseudopupils in Odonata

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Summary

Preliminary studies have shown that pseudopupils are not always present in the eyes of immature dragonflies. Thus pseudopupils were absent in the eyes of a teneral Common Hawker *Aeshna juncea* and in the eyes of immature Black Darter *Sympetrum danae* and Golden-ringed Dragonfly *Cordulegaster boltonii*. In immature Common Hawker there is some indication of their development and they are present, along with accessory pseudopupils, in the eyes of mature Southern Hawker *Aeshna cyanea*, Black Darter and Golden-ringed Dragonfly. In contrast, pseudopupils were present in the eyes of newly emerged Emerald Damselfly *Lestes sponsa*. The possible significance of these findings is discussed, including consideration that the presence or absence of pseudopupils may offer external criteria for determining the physiological age of dragonflies during maturation.

Introduction

To hunt other flying insects, dragonflies rely on superb flight skills and excellent vision. Their compound eyes each consist of several thousand elements known as facets or ommatidia. Each of these facets combines a surface lens with an internal crystalline, cone-shaped lens connected to the rhabdom. The rhabdom is a long cell which functions as the photoreceptor surface and light detector and it contains high concentrations of light-sensitive pigments called rhodopsins. Each ommatidium is innervated by one nerve fibre (Fig. 1) and thus provides the brain with one picture element (Land & Nilsson, 2002). From this mosaic of independent picture elements the brain forms an image.

In addition to ommatidia, there are three simple eyes - ocelli, occurring as small convex swellings located at the vertex and having only a single corneal surface lens. It is believed that the ocelli contribute a number of simple optical strategies to the vision of Odonata (Berry *et al.*, 2008).

Leidig (1855) observed a dark spot on the eye of the horseshoe crab *Limulus*, which differed in position when the eye was viewed from different angles. He termed this spot the pseudopupil, because of its apparent resemblance to the pupil of vertebrate eyes. Exner (1891) classified a number of different

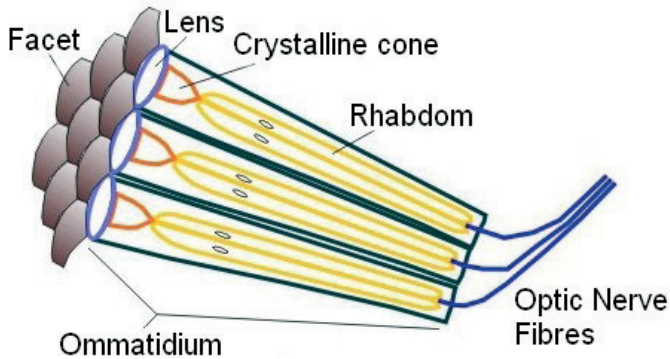


Figure 1. View of three ommatidia to show their structure (From Collicutt, 2006).

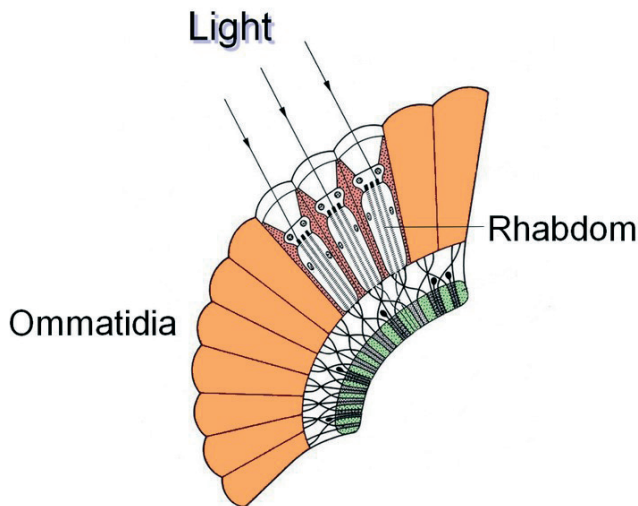


Figure 2. Details of how light from an object only activates the rhabdoms of those ommatidia that face the object. (After Katz & Minke, 2009).

pseudopupil types, including the wandering dark spot which he termed the principal pseudopupil, and the crown of dark spots or patches surrounding the principal pseudopupil, which can be observed in the eyes of butterflies and dragonflies, and which he called accessory pseudopupils.

The optical phenomenon of the pseudopupil occurs because the ommatidia which are in line with the direction of incoming light absorb rather than reflect that light (Fig. 2), thus resulting in the observed dark spot (Plate 1). The pseudopupil, together with the accessory pseudopupils, indicates the field of view being observed and from which visual information is being obtained. The pseudopupil can also be regarded as being the magnified image of the rhabdom and its associated visual pigments (Land, 1997). In very dark eyes, the pseudopupil is often not apparent.

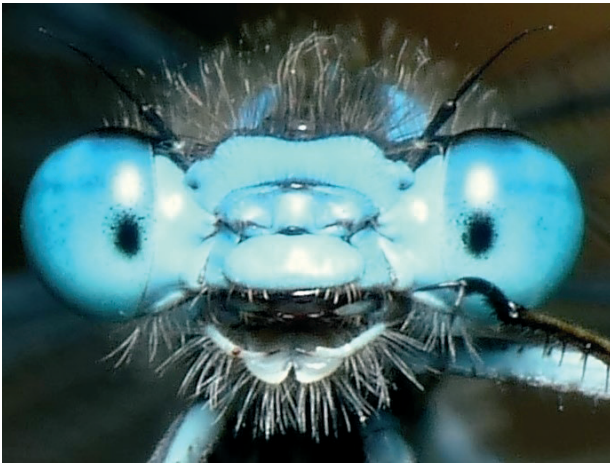


Plate 1. Front view of head with compound eyes of a mature Common Blue Damselfly *Enallagma cyathigerum* to show the pseudopupils (large dark spots), each surrounded by accessory pseudopupils (smaller black spots).

Material and Methods

I have been studying my local Odonata at Timble Ings, Fewston, North Yorkshire since 2008 and, whilst I had become aware of the 'patterning' on the eyes of some species, particularly Common Hawker *Aeshna juncea* and Southern Hawker *Aeshna cyanea*, it was not until I began macro-photography in 2011 that I was able to see more detail and made some interesting observations on pseudopupils. In addition to the Aeshnidae, observations were also made on Black Darter, *Sympetrum danae*, Golden-ringed Dragonfly *Cordulegaster boltonii*, and Emerald Damselfly *Lestes sponsa*.

Photographs were usually taken in the early morning, or in damp weather,

when the species had not commenced flight. Teneral and immature Common Hawker were carefully removed from their position in pond-side vegetation, a photographic record obtained, and then replaced. Other species were photographed in situ.

Recordings were made with a Panasonic Lumix FZ28 super zoom digital camera, with a DMW-LA3E lens adaptor and Raynox DCR-250 or DCR-150 Super Macro/Close-Up lens attached. A purpose made diffuser, placed over the built-in flash, was used to light the subject. The light areas in the photographs are the reflections of the flash.

Results

Dragonflies (Anisoptera)

In the teneral Common Hawker *Aeshna juncea* the pseudopupil is absent, with just an indistinct darkish area - the margin between the ventral ommatidia and those of the dorsal fovea - visible when an eye is viewed from the side (Plate 2A); when viewed from the front or above there is no sign of a pseudopupil whatsoever (Plate 3A, B). The pseudopupil becomes rather more distinct in the immature adult Common Hawker but is not fully developed (Plate 2B). Furthermore, it is absent from the eyes of immature Black Darter *Sympetrum danae* (Plate 4A) and was not observed in the light brown ommatidia of immature Golden-ringed Dragonfly *Cordulegaster boltonii*. Well developed pseudopupils and accessory pseudopupils were seen in mature Southern Hawker (Plate 2C), mature Black Darter (Plate 4B) and mature Golden-ringed Dragonfly (Plate 5). In this last species the accessory pseudopupils were configured in rows rather than clustered around the pseudopupil itself.

Damselflies (Zygoptera)

The Emerald Damselfly *Lestes sponsa* was the only damselfly where I was able to obtain images of all three stages of maturity and there was clear evidence of a pseudopupil at each stage, although slightly indistinct in the teneral and immature specimens (Plate 6).

Discussion

There have been many investigations of pseudopupils, which are often used as an experimental tool in research on insect vision (Stavenga, 1979; Land, 1997), in which references were made to the pale eyes of immature dragonflies but with no mention of the lack of pseudopupils. A photo on the website of



A

B

C

Plate 2. Compound eyes viewed from the side of (A) teneral Common Hawker *Aeshna juncea* showing a slightly darkened area but no clear pseudopupil, (B) immature Common Hawker with a developing pseudopupil and (C) mature Southern Hawker *Aeshna cyanea* with a distinct pseudopupil and accessory pseudopupils.



A

B

Plate 3. Compound eyes of a teneral Common Hawker *Aeshna juncea* from (A) front and (B) above. Note the absence of a pseudopupil.



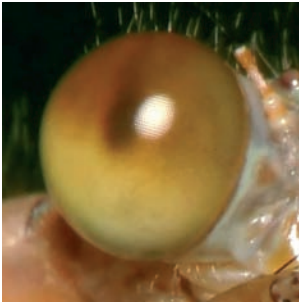
A

B

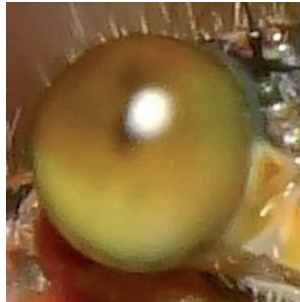
Plate 4. Compound eyes of (A) immature Black Darter *Sympetrum danae* lacking a pseudopupil and (B) mature Black Darter showing a clear pseudopupil and accessory pseudopupils.



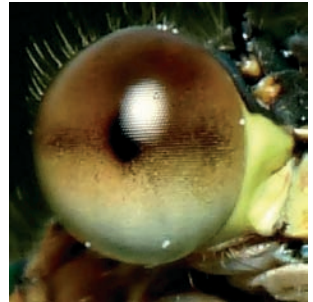
Plate 5. Compound eyes of mature Golden-ringed Dragonfly *Cordulegaster boltonii* showing a pseudopupil and accessory pseudopupils configured in rows rather than clustered around the pseudopupil.



A



B



C

Plate 6. Compound eyes of Emerald Damselfly *Lestes sponsa* to show the pseudopupil. (A) newly emerged, (B) immature and (C) mature. Note that the pseudopupil becomes increasingly well defined with maturity.

the Yorkshire Branch of the British Dragonfly Society shows an immature Migrant Hawker, *Aeshna mixta*, with pale eyes and no pseudopupils (Tillotson, 2011) and an illustration by Brooks & Lewington (1997) of the same species shows similar features. In addition, there are also many other online photos of emerging, e.g. American Emerald *Cordulia shurtleffii* (Cordulidae) (Johnson, 2011), and immature dragonflies showing pale eyes lacking pseudopupils. I have also received photographs from Hall, M.A. (pers comm.) of two immature species of dragonflies - Common Baskettail *Tetragoneuria cynosura* (Cordulidae) and Western Pondhawk *Erythemis collocata* (Libellulidae), both of which show no evidence of pseudopupils. Paulson (pers. comm.) has, on my behalf, examined samples of his large collection of North American dragonfly and damselfly photos, including several of emerging libellulids, which also appear to show no indication of pseudopupils. His photos of emerging Tawny Sanddragon *Progomphus alachuensis* and Least Club-tail *Stylogomphus*

albistylus dragonflies (Gomphidae) did however show a hint of pseudopupils. Interestingly, the only photos of emerging UK dragonflies that I have seen which show some evidence of pseudopupils were also of a Club-tailed dragonfly, the Common Club-tail *Gomphus vulgatissimus* (Darlington, 2011; Phillips, 2011a). However, pseudopupils are present in the final larval instar of at least some dragonflies eg. larva of Southern Hawker *Aeshna cyanea* (Corbet & Brooks, 2008; Phillips, 2011b).

Online photos of emerging damselflies, for example Common Blue *Enallagma cyathigerum*, Blue-tailed *Ischnura elegans*, Azure *Coenagrion puella*, Red-eyed *Erythromma najas* and White-legged *Platycnemis pennipes*, all show pseudopupils similar to those I have recorded for Emerald Damselfly *Lestes sponsa*. In addition, photos of emerging *Enallagma* sp. and Least Spreadwing (Paulson, pers. comm.) provide further evidence of distinct pseudopupils in the ommatidia of emerging damselflies. Online photos show pseudopupils are also present in damselfly larvae (Phillips, 2011b; 2011c).

The above give rise to a number of questions. For example, what significance can be attached to the lack of pseudopupils in many newly emerged and early immature dragonflies and, in contrast, why might damselflies and club-tails exhibit well developed ommatidia showing pseudopupils at emergence? In relation to my observations, Paulson (pers. comm.) has confirmed that lack of pseudopupils, which he has also now observed in his images of species in several families, seems to be characteristic of teneral and at least young immature anisopterans. He suggests that the ommatidia may be changing as the dragonfly matures, perhaps in the transparency of the outer cuticle or the cells themselves. Lew (1933) reported that the compound eye of dragonfly larvae is largely or wholly replaced at metamorphosis by the compound eye of the adult and Sherk (1978) concluded that the trend amongst advanced families of Odonata is to replace the larval ommatidia with an entirely new set of ommatidia. The period during metamorphosis at which the replacement of the ommatidia occurs may vary from family to family and even within families. This may account for the observations that pseudopupils are present in some tenerals, e.g. Gomphidae, presumably being carried over from the larval ommatidia. The Gomphidae are a very primitive family of dragonflies (Tillyard, 1917) and this carry over of pseudopupils from the larval ommatidia to those of the newly emerged dragonfly may relate to their phylogenetic development. Some members of the Gomphidae emerge on a flat horizontal surface (Corbet & Brooks, 2008), including pond-side stones (Paulson, pers. comm.), and have also been observed emerging on walls (Darlington, 2011; Phillips, 2011a). It may be that this type of emergence on a horizontal or vertical plane surface requires the best possible vision at the outset, hence the presence of pseudopupils in teneral club-tails. In this context, what might also be of significance is that, like

damselflies, the eyes of Gomphidae are relatively small and widely separated. Eye size affects ommatidial size and inter-ommatidial angle (Barlow, 1952). The smaller the inter-ommatidial angle the greater the distance at which objects - prey, predators or foliage - can be resolved (Land, 1997). This may be another factor contributing to what appears to be a fully developed visual system at emergence in gomphid anisopterans and in zygopterans. The presence or absence of pseudopupils at emergence may also be related to the development of visual pigments during the transition from larval to teneral and then immature ommatidia. However, regardless of the absence of pseudopupils and what that might imply, the ommatidia in dragonflies at emergence must be developed sufficiently to provide a visual system that allows for prey detection.

Schroder *et al.* (2009), in their studies on visual target detection in the damselfly *Megalagrion xanthomelas*, have commented that insects face several difficulties in visual performance related to their small size and the simplicity of the visual components comprising their compound eyes, including the lack of focusing mechanisms and relatively limited light capture. They concluded from their studies that, in this species, there was a high competence in visual target acquisition and that future research should examine prey pursuit trajectories in relation to the fine-scale distribution of visual units within the compound eye. The demands for visual target recognition, including fully developed visual units, may therefore be one reason why damselflies possess pseudopupils at the larval stage and at emergence, this possibly relating to their need to forage in vegetation which may consist of a somewhat dark, complex habitat.

More detailed studies are now required to determine the significance of the apparent lack of pseudopupils in some teneral dragonflies and their development during maturation. Corbet & Brooks (2008) have stated that more work is needed to establish reliable, and preferably external, criteria for determining the physiological age of dragonflies during maturity. Paulson (pers. comm.) has suggested that the presence or absence of pseudopupils might offer such criteria.

Acknowledgements

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Figure 2 from his illustration of ommatidia, and the staff of the British Library, Boston Spa, for their kind assistance.

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The occurrence of the Broad-bodied Chaser *Libellula depressa* L. at a nature reserve in Hampshire over a period of 25 years and a description of pruinescence in females

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Summary

The main flight period of the Broad-bodied Chaser *Libellula depressa* is reported for the 26 year period 1985-2011 at a site in Southern England and it is noted that it has not changed over this period. The occurrence and development of pruinosity in some females at this site is described and discussed.

Introduction

The main flight season of the Broad-bodied Chaser *Libellula depressa* in the UK starts in early to mid-May and lasts until late July or early August (Brooks & Lewington, 1997; Smallshire & Swash, 2010). The earliest date noted by Lucas (1900) was 28 April (by C.A. Briggs, Surrey) and the latest was 14 August (by W.J. Ashdown, Richmond Park, 14 August 1897).

The abdomen of the female is yellowish brown with yellow dorso-lateral margins on abdominal segments 4-7 (Askew, 1988; Brooks & Lewington, 1997), although pictures in Dijkstra & Lewington (2006) show the yellow markings also on segment 8 and, in an old specimen, on segment 9 as well (see also Longfield, 1949). There is also a pair of light coloured stripes on the dorsal surface of the thorax (Plate 1).

The male looks similar to the female when it first emerges, although its abdomen is noticeably narrower (Plate 2A). However, after several days, the male develops pruinosity over its abdomen (Lucas, 1900) (Plate 2B). This phenomenon is not common in the female. Indeed, Selys & Hagen (1850) noted that blue forms of the female are very rare. Lucas (1900) noted that the female "occasionally develops the blue colouration on the abdomen, causing her at first sight to resemble the male in general appearance" but goes on to note "No doubt the bloom only appears on very old specimens, and is therefore rather a sign of age than of



Plate 1. Recently emerged female *Libellula depressa* without any signs of pruinescence on the body.



A



B

Plate 2. Male *Libellula depressa*. (A) Recently emerged male without any pruinescence, (B) Male with well developed pruinescence.

variation.” He only recorded one such individual (in the New Forest on 2 August). Some recent field guides also mention this form, indicating that old females do sometimes become pruinose (Askew, 1988) and that old females may develop limited pruinosity (Smallshire & Swash, 2010) but it is not mentioned in others.

Study Site

The study site is a small nature reserve (The Secret Garden Nature Reserve) that lies next to the river Hamble in Hampshire (British National Grid Reference SZ4818). It started when, prior to 1985, I dug two ponds in my garden; these form

the centre of the present reserve. In 1987 I realized a long-standing ambition by buying farmland surrounding the garden to extend the reserve to about eight and a half acres. The reserve is situated on a south-facing slope with natural spring water running through quite shallow loam on a clay and gravel base. Several ponds were constructed, followed by a small lake in 1995. Also some three thousand trees were planted to form hedgerows and thickets. Twenty-eight species of dragonfly have been recorded on the reserve, 18 of which breed there; also 29 species of butterflies (21 of which are recorded regularly), eight species of reptiles and amphibians and numerous bird species, including five warblers and a breeding pair of barn owls. There are also harvest mice, water shrews and, as far as we know, it is the only place in the UK to have two species of glowworm. I have kept a detailed nature diary for more than 25 years about all that I have seen on the reserve, including the first and last sighting of species each year.

Observations

Date of first occurrence

From my records it takes in the region of five to seven days from emergence to the first appearance of a patrolling adult on the ponds. I have recorded the first date of the occurrence of adult Broad-bodied Chaser *Libellula depressa* at the study site each year since 1985. This date has ranged from 25 April (2011) to 27 May (1996) (Table 1). There is considerable variation from year to year and, although the only three dates in April all occurred in the last five years, a 3-year rolling average of the data does not reveal any clear trend.

For most years I have also made a note of the last recorded adult. This mostly occurred between late July and late August, with the latest date 3 September (in 2000). One exception was in 1997 when the last siting was unusually early (7 July).

Female pruinosity

In the female Broad-bodied Chaser the yellow dorso-lateral margins are very clear on abdominal segments 4-7 but can also be seen on segments 3 and 8 (Plate 1). I first noted the blue form of the female on 5 July 1989 and have recorded at least one such female in six of the 23 years from 1989 to 2011 (Table 2). These sitings were mostly in July. However, there were a couple of exceptions. Thus, in 2003 a blue form was seen in early June, although in that year the flight season did start fairly early (4 May), and in 1995 one was observed towards the end of August. However, they were probably all old females, those occurring in June and July having emerged early in the flight season, and I

Table 1. First and last dates recorded of Broad-bodied Chaser patrolling at water

Year	First recorded	Sex	Last recorded
1985	25May	♀♂	-
1987	19May	♀	-
1988	15May	♀	2 August
1989	17May	♂	13 August
1990	3May	♂	27 July
1991	21May	♀♂	25 August
1992	13May	NR	23 July
1993	10May	♀	31 August
1994	18May	NR	-
1995	5May	NR	28 August
1996	27May	♀	4 August
1997	2May	♀	7 July
1998	12May	♂	-
1999	2May	NR	-
2000	13May	♀	3 September
2001	20May	♂	-
2002	12May	♀	14 August
2003	4May	♀	3 August
2004	10May	♀	25 July
2005	9May	♂	21 August
2006	4May	♂	23 July
2007	26April	♀	-
2008	11May	♂	-
2009	29April	♀	-
2010	23May	♀♂	-
2011	25April	♀	26 July

NR, sex not recorded; - information unavailable.



A



B



C



D



E



F

Plate 3. Female *Libellula depressa* showing increasing degrees of pruinescence from (A) to (F).

Table 2. Dates when the blue form of female Broad-bodied Chaser was recorded

Year	Dates recorded
1989	3, 5 July
1990	8, 13, 26 July
1995	27, 28 August
1996	17 July
2003	17, 23 June
2009	12 July

have usually observed them resting or ovipositing alone. The colour of these specimens was darker and the pale thoracic stripes had generally become less obvious.

Varying degrees of pruinosity have been observed. The indications are that, as the abdomen becomes darker, pairs of small blue patches appear on the dorsal surface of abdominal segments 5-7, the lateral yellow markings still being apparent (Plate 3A, B). These patches become larger, leaving a narrow dark stripe in the dorsal mid-line and almost obliterate the yellow patches, which also become obliterated on the other abdominal segments as the abdomen darkens (Plate 3C, D). The blue then starts to spread onto abdominal segments 8 and 9, leaving a dark patch dorsally on segment 9 (Plate 3E). Further extension of the blue on to the dorsal surface of segment 3 may then occur (Plate 3F). By this stage there is little left of the lateral yellow markings.

Discussion

In general, the data collected on the reserve over the last 25 years indicate very little change in the advancement of spring or a change in climate. Although the first recorded date for the Broad-bodied Chaser *Libellula depressa* was in April in 2007, 2009 and 2011, rather than in May, there is no indication that climate change has had any effect since there is considerable variation in date and there is no obvious trend between 1985 and 2011. Indeed C.A. Briggs recorded a first date of 28 April in the 19th Century (Lucas, 1900)

There is a marked lack of information on the occurrence and development of pruinosity in the female Broad-bodied Chaser, with some recent field guides even failing to mention it. The development of this pruinosity described here is based on the observation of a number of individuals with varying degrees of blue on the abdomen. To confirm the sequence of events a study of marked individuals is necessary. The only clear records of where female pruinosity

occurs are in the New Forest, Hampshire (Lucas, 1900) and in Surrey (this paper), both in the south of England. It would be interesting to know where else it has been seen and, in particular, whether it occurs further north.

Acknowledgement

I wish to thank my wife Alison for her support over the last six years; without whom my data would still be on the shelf collecting dust.

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The Norfolk Hawker *Aeshna isosceles* (Müller): a step further from the brink?

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Summary

The change in the range of the Norfolk Hawker *Aeshna isosceles* between 1970 and 2009 was investigated using historic records from the Dragonfly Recording Network and an increase in range was confirmed. It is apparent that this range increase has been sustained by an increase in the number of breeding populations of *A. isosceles* and was in a generally southerly direction, although some westerly and northerly expansion has also occurred. This contrasts with the general northern range shift of most other British Odonata. The increase in the range and population numbers are considered most likely to be due to a combination of habitat restoration and improvement initiatives and water quality improvements, even though increases in recorder effort may have had an effect. Aspects of the habitat requirements of *A. isosceles* (Müller) were investigated using historic aquatic vegetation and salinity data collated with records of its distribution. It is shown to utilise a wider variety of vegetation communities and to be more tolerant of salinity than was previously thought.

Introduction

The Norfolk Hawker *Aeshna isosceles* (Müller) has 'Endangered' status in the UK (Daguet *et al.*, 2008) and is protected by inclusion in Schedule 5 (Amended) of the Wildlife and Countryside Act 1981 (Merritt *et al.*, 1996). The UK distribution of *A. isosceles* is largely restricted to the Norfolk and Suffolk Broads area and the coastal belts of these two counties (Hammond, 1977; Shirt, 1987; Miller, 1995; Merritt *et al.*, 1996; Brooks & Lewington, 1999; Southwood *et al.*, 2005; Moore, 2008).

Much of the ecological knowledge about *A. isosceles* in the UK derives from the study of Leyshon & Moore (1993) at Castle Marshes in Suffolk, which showed that populations of *A. isosceles* in the UK are strongly associated with

the aquatic plant Water Soldier *Stratiotes aloides* L. (Shirt, 1987; Miller, 1995; Brooks, 2000; Southwood *et al.*, 2005). However, the work by Leyshon & Moore (1993) does not explore in depth the dragonfly's habitat requirements, response to salinity, or the role of the wider aquatic plant community.

The purpose of this investigation was to quantify the changes in the distribution of *A. isosceles* and assess their possible causes; also to determine the salinity tolerance of this species and its association with the wider aquatic vegetation community.

Methods

The change in the distribution of *Aeshna isosceles* was determined using the Dragonfly Recording Network (DRN) records for the species, provided by the British Dragonfly Society (pers. comm.). The records of *A. isosceles* were plotted on separate maps for the time periods 1970-1979, 1980-1989, 1990-1999 and 2000-2009 using the ArcGIS Explorer (Build 1700) Geographic Information System (GIS) software package produced by Esri®. The range of *A. isosceles* was quantified using a tool within the GIS software package for each time period and the percentage difference from the previous time period was determined. Any change in the number of records of *A. isosceles* was investigated by determining the percentage difference from the previous time period. The extent of the change in the number of distinct locations supporting breeding populations of *A. isosceles* was investigated by tabulating records of larvae and oviposition (both record types taken as *indication* of breeding) and records of exuviae (taken as *evidence* of breeding). Where records of indication and evidence of breeding existed for the same location in the same year, only the evidence records were tabulated and displayed.

Datasets of plant community types and salinity measurements, provided by Natural England and the Environment Agency, Halcrow Ltd. (pers. comm.), were utilised to determine the reported association of *A. isosceles* with specific aquatic vegetation and the salinity tolerance of the species.

The association of *A. isosceles* with particular aquatic vegetation communities (as defined by Doarks & Leach, 1990) was investigated using the 1997 ditch survey dataset provided by Natural England (pers. comm.), which gave information on 2,711 sites. To determine any relationship it was assumed that data in this dataset were characteristic of the sites for the previous four years (1994-1997) and hence the records of *A. isosceles* (adults, larvae and exuviae) for the corresponding time period were examined in relation to the locations studied in that survey. Where records of *A. isosceles* were not specifically in the same location as a ditch survey vegetation record, the nearest vegetation

record within a limit of 500 metres was accepted as characteristic of the location where the dragonfly was recorded. Records were disregarded where the nearest vegetation record was greater than 500 metres from the dragonfly record. The vegetation records collated with the records of *A. isosceles* were utilised to determine the aquatic vegetation group community preference of the species.

In order to investigate the field salinity tolerance of *A. isosceles*, records of larvae and exuviae were considered in relation to salinity measurements. Where a salinity datum was absent from a record of *A. isosceles*, the nearest measurement within a limit of 500 metres was assumed to be characteristic of the location where the record was made. Records were again disregarded where the nearest salinity datum was greater than 500 metres from the dragonfly record. Data in four-year time periods were considered within each decade for the 1990s and 2000s because the selected periods contained the majority of the salinity data.

Results

Distribution changes

There is a clear increase in the range of *A. isosceles* between each of the time periods from 1970-79 to 2000-09 with the greatest increase occurring between the 1990-99 and the 2000-09 time periods (Fig. 1), which coincides with the greatest increase in the number of records of the species (Table 1). The greatest directional distance increase in range has been in a southerly direction (Fig. 2), although there has been some extension towards both the west and the north.

Table 1. The number of records (adult, larvae and exuviae) and estimated area occupied by *Aeshna isosceles* for each decade from 1970 to 2009.

Time Period	Area occupied by records (km ²)	Area increase on previous time period (%)	Number of records	Records increase on previous time period (%)
1970-79	59.7	-	38	-
1980-89	156.6	162.3	90	136.8
1990-99	260.9	66.6	105	16.7
2000-09	754.6	189.2	728	593.3

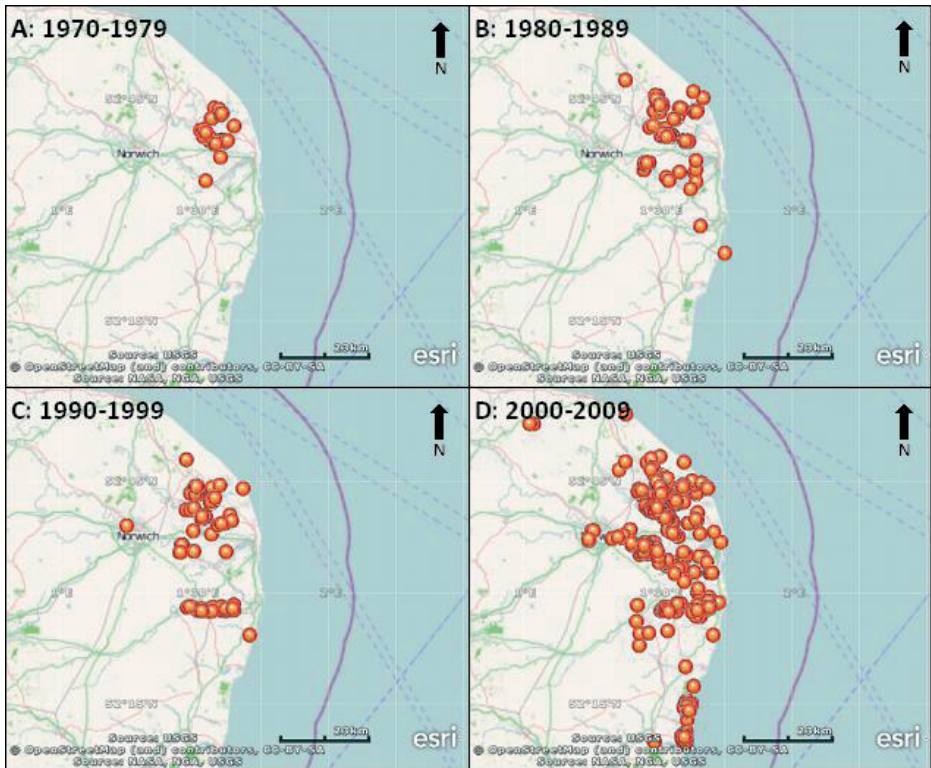


Figure 1. Records (adult, larvae and exuviae) of *Aeshna isosceles* for the time periods 1970-1979 (A), 1980-1989 (B), 1990-1999 (C) and 2000-2009 (D). The figure contains Ordnance Survey data © Crown copyright and database 2010, and was produced using data provided by the British Dragonfly Society, ArcGIS Explorer software and OpenStreetMap [Map data © OpenStreetMap contributors, CC-BY-SA].

Anecdotal evidence indicates that large populations of *A. isosceles* were present in the Norfolk Broads at the start of the 20th century (Heath, 1999; Southwood *et al.*, 2005). Although information on breeding populations of *A. isosceles* in the 1900s is sparse, there were a small number of such populations recorded in the early 1980s as was demonstrated by surveys undertaken at that time (Heath, 1999) (Fig. 3). Since then the general trend has been of increasing numbers of distinct locations where *A. isosceles* is breeding (Fig. 3).

Habitat

Over the time period that relates to the ditch survey of 1997, i.e. 1994-1997, there were only 30 records of *A. isosceles*, the majority (77%) of which were patrolling adults. It is likely that some of these had migrated to a different vegetation

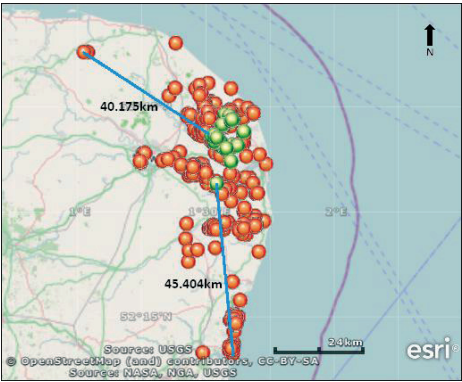


Figure 2. Records (adult, larvae and exuviae) of *Aeshna isosceles* for the time period 1970-1979 (green dots) superimposed over the records for the time period 2000-2009 (red dots), with the distance between the extreme records of each time period measured (blue lines). The figure contains Ordnance Survey data © Crown copyright and database 2010, and was produced using data provided by British Dragonfly Society, ArcGIS Explorer software and OpenStreetMap [Map data © OpenStreetMap contributors, CC-BY-SA].

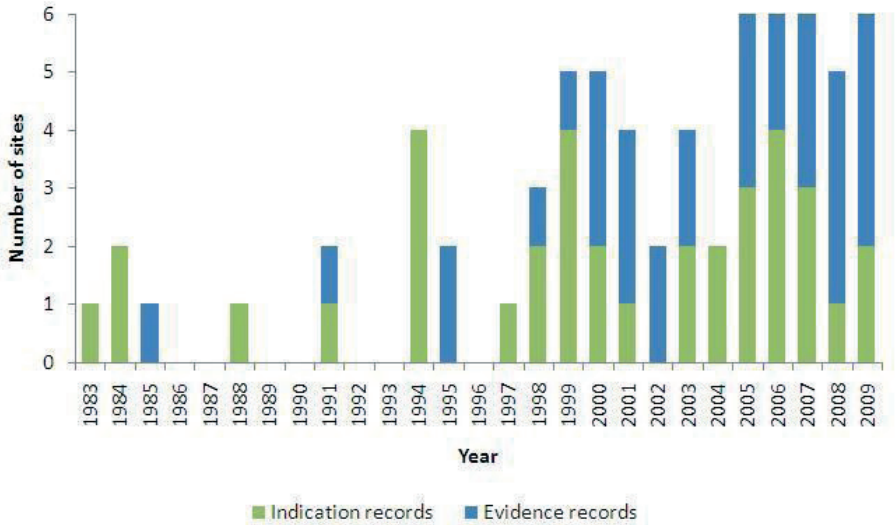


Figure 3. The number of distinct sites with records of larvae and/or oviposition (indication records – green) and records of exuviae (evidence records - blue) of *Aeshna isosceles* for the time period 1983-2009.

site from that where they had emerged. Nevertheless, it is clear from both the overall records and those of patrolling adults alone that *A. isosceles* is strongly associated with the *Potamogeton natans*-*Hottonia palustris*-*Myriophyllum* (A2), *Potamogeton natans* (A3a) and *Stratiotes aloides*-*Hydrocharis morsus-ranae* (A3b) plant communities (as defined by Doarks & Leach, 1990) (Table 2), rather than with the *Ceratophyllum demersum* (A4), *Lemna minor*-*Lemna trisulca*-Filamentous algae (A5b) and filamentous algae-*Enteromorpha* (A7a) communities (Fig. 4). Thus, chi-squared tests (using Yates correction) give significant differences of $P < 0.001$ ($\chi^2 = 12.03$) for the overall distribution and $P < 0.01$ ($\chi^2 = 10.23$) for patrolling adults alone. This, in spite of the fact that there were considerably more sites for the A4, A5b and A7a plant communities (1,627) than for the A2, A3a and A3b plant communities (646) in the area analysed. Oviposition behaviour (an indication of breeding) was only observed at A2, A3a and A3b plant community sites. However, what was particularly interesting was that exuviae (evidence of breeding) were only found at A5b and A7a plant community sites during this period; a clear indication that breeding populations of *A. isosceles* are not confined to areas dominated by *S. aloides*.

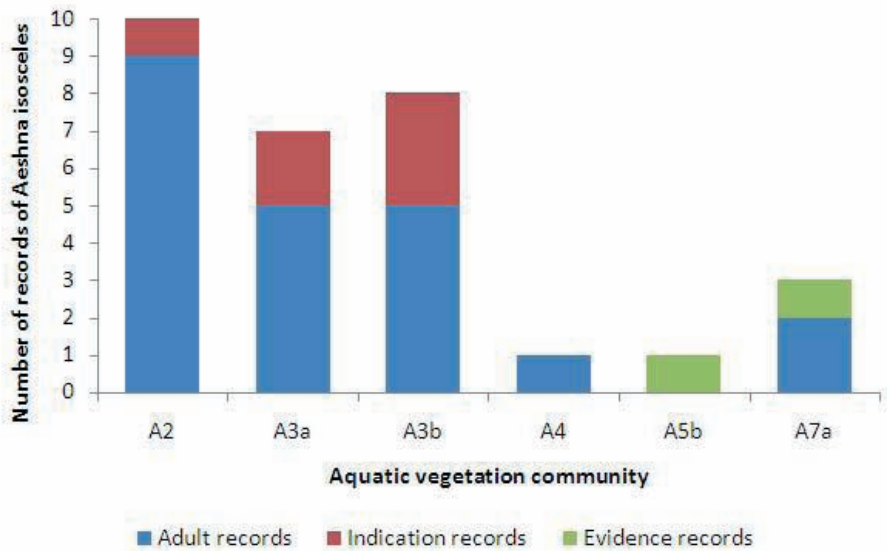


Figure 4. Number of records of adults (blue), exuviae (evidence records - green), oviposition (indication records - red) of *Aeshna isosceles* from 1994 to 1998, collated with the aquatic flora communities described in Doarks & Leach (1990). Aquatic flora data provided by Natural England; records of *A. isosceles* provided by the British Dragonfly Society. No larvae were recorded during this time period.

Table 2. Aquatic vegetation communities (as defined in Doarks & Leach, 1990) that were collated with records of *Aeshna isosceles*.

Community	Binomial Names	Common names
A2	<i>Potamogeton natans</i> - <i>Hottonia palustris</i> - <i>Myriophyllum</i>	Broad leaved pondweed-Water Violet-Water Milfoil
A3a	<i>Potamogeton natans</i>	Broad leaved Pondweed
A3b	<i>Stratiotes aloides</i> - <i>Hydrocharis morsus-ranae</i>	Water Soldier-Frogbit
A4	<i>Ceratophyllum demersum</i>	Rigid Hornwort
A5b	<i>Lemna minor</i> - <i>Lemna trisulca</i> -Filamentous algae	Common Duckweed-Ivy leaved Duckweed-Filamentous algae
A7a	Filamentous algae- <i>Enteromorpha</i>	Filamentous algae-Gutweed

In an analysis to determine the field salinity tolerance of *A. isosceles* it has been shown that breeding populations occur within the salinity range 0.38-0.96gL⁻¹ (Table 3). This analysis was undertaken using only larval and exuviae records of the species, thereby giving an accurate picture of the species' ability to tolerate different levels of salinity.

Discussion

Distribution changes

The conclusions drawn in recent years about increases in the population numbers (Kalkman, 2009) and range of *A. isosceles* (Heath 1999; Hickling *et al.*, 2005; Southwood *et al.*, 2005; Daguet *et al.*, 2008) are supported by the results of this study (Figs 1, 2, 3; Table 2). Furthermore, the general trend of increasing numbers of distinct breeding locations (Fig. 3) indicates that the expansion in the range of *A. isosceles* is not merely due to sightings of migrant individuals but results from colonisation of new breeding sites. The general southerly direction

Table 3. The estimated field salinity tolerance of *Aeshna isosceles* determined using historical data. Records of larvae and exuviae of *A. isosceles* were provided by the British Dragonfly Society; salinity data by the Environment Agency, Halcrow Ltd. and Natural England.

Time period	Salinity (gL ⁻¹)	
	Minimum	Maximum
1994-1997	0.52	0.96
2004-2007	0.38	0.72

of the range expansion of *A. isosceles* (Figs 1, 2) is in contrast to the general northern shift in the range margins of British Odonata reported by Hickling *et al.* (2005), Brooks *et al.* (2007) and Mill *et al.* (2010). Given this contrast, the directionality of the range increase of *A. isosceles* appears to be largely driven by habitat availability rather than climate change. Furthermore, it must be noted that the potential for northern range expansion in response to, for example, climate change, is reduced since *A. isosceles* is geographically limited by the Norfolk coastline and the spring wind direction originates predominantly from the northeast.

It is notable that the largest increases in the range of *A. isosceles* co-occur with the largest increases in the number of records (Table 2). Whilst this may be a result of increased recorder effort, as postulated by Daguet *et al.* (2008), the increases in records may equally result from real increases in the population numbers of *A. isosceles*. Indeed it is suggested that the increases in the population numbers and range may result from habitat restoration and improvement initiatives (Heath, 1999; Hickling *et al.*, 2005), such as that reported in Southwood *et al.* (2005) and/or improvements in water quality.

Between the late 1950s and 1977 the majority of the Norfolk Broads suffered from severe eutrophication due to increased nutrient enrichment from agricultural run-off (Lau & Lane, 2002) and phosphate-rich sewage inputs from sewage treatment plants (Perrow *et al.*, 1997). The deterioration in water quality was cited as one reason for the decline of *A. isosceles* in the region between 1950 and 1975 (Moore, 1976; Southwood *et al.*, 2005). Installations of nutrient reduction works at sewage treatment plants, isolation of individual Broads, removal of nutrients held in sediment through suction dredging and bio-manipulation have all been employed since 1977 to alleviate the water quality issue (Perrow *et al.*, 1997; Lau & Lane, 2002). Water quality improvements and clear water conditions were subsequently achieved in many of the Norfolk Broads (Perrow *et al.*, 1997). The increases in population numbers and distribution of *A. isosceles* (Figs 1, 2, 3; Table 2) clearly coincides with, and thus may also be a result of, the water

quality improvement initiatives undertaken in the Norfolk Broads.

Habitat

The results of the vegetation analysis (Fig. 4) indicates that *A. isosceles* utilises a number of different plant communities and is not restricted to habitats in which *S. aloides* is a dominant member (the A3b community), as was once believed (Shirt, 1987; Miller, 1995; Brooks, 2000; Southwood *et al.*, 2005). Although, whilst *S. aloides* is a dominant member of the A3b plant community, it may also appear as a minor member of the A2 and A3a communities with which *A. isosceles* was also found to be significantly associated. The conclusion that *A. isosceles* is not restricted to habitats with an abundance of *S. aloides* is supported by reports of the dragonfly successfully breeding at locations devoid of *S. aloides* (British Dragonfly Society, 2010), as well as sightings of *A. isosceles* using plant species other than *S. aloides* as oviposition sites (Heath, 1999; Bingham, 2006; Cham, 2007). It has also been recognised that in continental Europe *A. isosceles* reproduces in habitats without the presence of specific plants (Corbet and Brooks, 2008; Leyshon and Moore, 1993; Miller, 1995), though the species appears to favour habitats with *S. aloides* across the northern limit of its European range (Dijkstra, 2006; Kalkman, 2009).

Communities characterised by *Ceratophyllum demersum* (A4 community) and *Lemna minor*-*Lemna trisulca*-filamentous algae (A5b community) are typical of eutrophic water conditions, whilst the filamentous algae-*Enteromorpha* (A7a) community is typically found in the salinity range $2.7\text{--}13.3\text{gL}^{-1}$ (Doarks & Leach, 1990). In contrast, the A2, A3a and A3b communities, in which *A. isosceles* is most frequently recorded in the U.K., are characteristic of mesotrophic and meso-eutrophic water conditions where salinity is less than 1.33gL^{-1} (Doarks & Leach, 1990). This implies an upper salinity limit of 1.33gL^{-1} for habitats in which *A. isosceles* can be recorded and, indeed, this species is widely considered to be intolerant of brackish water conditions and restricted only to freshwater conditions (Leyshon, 1992; Brooks & Lewington, 1999; British Dragonfly Society, 2010), although Jović (2008) recorded it from brackish swamps in the background of a beach near the Bojana river in Montenegro. The Water Framework Directive, which is the most important piece of European legislation concerning the aquatic environment (Chave, 2001; Mostert, 2003; Allan *et al.*, 2006), defines freshwater as that with a salinity below 0.5gL^{-1} (European Commission, 2000). It is evident from the present study that *A. isosceles* tolerates and may successfully breed in salinities up to 0.96gL^{-1} (Table 3). Whilst this value is below the value of 2.65gL^{-1} used by Palmer *et al.* (2010) to distinguish freshwater ditches ($<2.65\text{gL}^{-1}$) from brackish ditches ($>2.65\text{gL}^{-1}$), the range is clearly within the salinity levels defined as oligohaline ($0.5\text{--}<5.0\text{gL}^{-1}$) in the Water Framework Directive (European Commission, 2000). Thus, *A. isosceles*

is not restricted to fully freshwater conditions and may be capable of breeding in low oligohaline conditions. It is acknowledged, however, that the previous classification of *A. isosceles* as restricted to freshwater sites arises from variation in the use of definitions of freshwater conditions. Use of the required definitions of water conditions described in the Water Framework Directive clarifies this particular issue. Given the implications of these conclusions, it is clear that there is still much to learn about the ecology of *A. isosceles*.

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