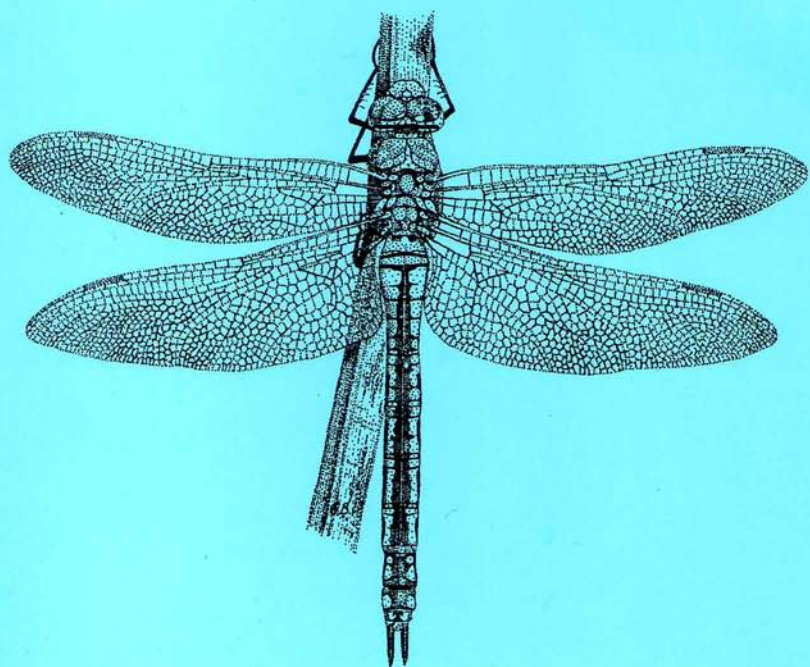




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Front cover illustration: Female Emperor Dragonfly *Anax imperator* at Church Wootton, Kent, 28 May 1989, by Gill Brook.

The territorial behaviour of the Keeled Skimmer *Orthetrum coerulescens* (Fabricius) at Holt Lowes, Norfolk

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Summary

A population of the dragonfly *Orthetrum coerulescens* (Fabricius) was observed at four wetland zones at Holt Lowes, Norfolk between 26 May and 18 September 2003. Territories occurred in discrete areas throughout the wetland zones of the site. The territories of 40 marked males were described and measured. Males averaged 59.6 ± 14.4 flights per hour and the mean number of matings was 1.1 ± 1.1 per hour with the males which held larger territories achieving more matings. It is suggested that this may be due to the arrangement and density of territories rather than size *per se*. The mean territory size was $5.75 \pm 10.16\text{m}^2$ with, on average, almost 50 per cent of the territory over water. The mean height of the vegetation within each territory was 356mm (range 50 – 600mm). Males spent on average 5.9 ± 2.0 min h^{-1} in flight, or about 10 per cent of their time. Habitat quality is discussed in relation to competition and territory fidelity. A case is argued for the site north of the Northern Mire being the area of highest habitat quality; it was occupied first, it was nearest to the approaching females and there was some evidence that competition was highest in this zone. It was also where the males showed the greatest territory fidelity. The relationship between territory holders and wandering males is discussed.

Introduction

The males of many species of dragonfly show territorial behaviour. Territoriality can be described as a form of space-related dominance, the primary function of which is to provide the territory holder with a supply of one or more essential resources (Kaufmann, 1983). In evolutionary terms, territoriality will be selected for when it increases the genetic fitness of an individual. In other words, the increased access to resources from maintaining a territory must outweigh the costs in time, energy and injury of defending it. In Odonata, the resource defended is usually, but not invariably, associated with reproduction (Corbet, 1999).

Different species adopt different patterns of territoriality and Parr (1983b) has defined territoriality in libellulids as full-time or part-time according to how much time males

spend each day at water, and described full-time territoriality in the libellulids *Orthetrum albistylum* Sélys and *O. julia* Kirby (Parr, 1980). Parr (1983b) suggested that the pattern in a given species or individual is determined by the interaction of spatial, temporal and biological factors. Individual males may demonstrate a strong attachment to a particular site (localisation). In *O. julia* the degree of localisation in individual males varies and there is a strong relationship between localisation and the ability of males to hold territories within the main breeding area (Parr, 1983b). Some species of territorial dragonfly display alternative reproductive tactics in certain conditions. Thus, by acting as non-territorial 'sneakers', matings can be gained, e.g. *O. julia* (Parr, 1980), *O. coerulescens* (Parr, 1983a) and *Calopteryx maculata* (Palisot de Beauvois) (Forsyth & Montgomerie, 1987).

The current study focuses on what determines the location, size, shape and density of territories of the Keeled Skimmer *Orthetrum coerulescens* at Holt Lowes, Norfolk – a very different habitat to where the species has been studied before.

Material and Methods

For a description of the history of the Keeled Skimmer, *Orthetrum coerulescens*, at Holt Lowes and a description of the site see White (2006). Four wetland zones were identified: 'Northern Mire', 'Mixed Mire', 'Glaven Valley' and 'Ponds Area'. The two mires each contain a small tributary stream of the River Glaven. Individual males were given a unique mark on their wings (White, 2006).

Detailed assessments of territories and behavioural observations were made from 16 June to 18 July 2003 but casual observations were made beyond then until 18 September. Data were only collected when weather conditions were suitable for the insects to be territorially active, i.e. in full sunshine, with an air temperature at ground level above 23°C and a wind speed of less than 4 (Beaufort scale). Times of day were recorded as British Summer Time (BST).

The territories of 40 different marked males were described in terms of their location and various physical and chemical parameters. The choice of the territories was governed by where the marked males took up residence. However, sufficient males were marked to allow a spread of territories in different locations within the site. For each territory holder behavioural data were collected for a period of at least one hour. Furthermore, the locations of the 40 territories were revisited to observe the territory fidelity of their owners and to note any movement of marked males over time. In addition, 39 episodes of mating behaviour by individuals (both marked and unmarked) were observed, timed and recorded. A 'Dictaphone' was used to record data whilst observations were made and a stopwatch was used to count and time events. The parameters recorded were:

- the total number of flights
- the number containing an aggressive encounter

- the number with one or more conspecific encounters
- the number with one or more interspecific encounters
- the number of conspecific and interspecific males encountered per hour
- the time spent in flight
- the time in flight with an aggressive encounter
- the number of matings
- the length of all flights
- the length of flights with an aggressive encounter
- the longest female guarding flight
- the longest flight excluding female guarding flights.

Also the number of other dragonfly species present was recorded.

After observing marked males for at least one hour and determining the distances flown, the area actively defended and the relationships to individuals holding adjoining territories, their core area of territory and the area of it over water were estimated using a tape measure. A portable, digital meter was used to measure pH. Three readings were made in each territory, mixing the water vigorously before inserting the probe. Three measurements were also made in each territory to determine water and sediment depth, the latter by pushing a metal ruler firmly into the sediment until resistance was encountered.

A plant species was considered to be the dominant vegetation type if it was estimated to cover 30 per cent or more of the territory. If a second species also covered a significant proportion of the territory, this was described as the co-dominant species. The minimum, maximum and predominant height of vegetation in the territory were recorded. The water area within the territory covered by vegetation was estimated. If more than 75% of the water surface was visible when viewed from directly above, the territory was assigned a vegetation-density score of 1. If less than 25% was visible, then a value of 3 was given. Territories with areas of visible open water in-between these figures were assigned a score of 2.

The following behavioural activities associated with oviposition were recorded:

- Whether the male was considered to be holding territory at the time of mating.
- Length of time the pair were flying or perched in tandem prior to copulation.
- Length of time in copulation.
- Presence or not of a post-copulatory resting period
- Length of any post-copulatory rest period.
- Presence of any activity by the male which could be interpreted as active encouragement to the female to begin oviposition
- Length of oviposition episode.
- Number of bouts of oviposition in one episode.
- Mean length of bouts of oviposition in one episode.

- Whether an oviposition episode concluded at the females behest or whether the episode finished prematurely due to disturbance from another male

In each case the location was also noted. Not every activity was recorded during each mating episode.

Results

Marked male *O. coerulescens* were observed for a total of 51.5 hours and none were seen to lose their territory to another in an aggressive encounter. Males were seen to leave their perch to chase off a conspecific male or a male of another dragonfly species, in pursuit of a female, to catch prey and to investigate another insect that entered its territory. On occasions, a male would pursue an intruding male for several metres (the furthest chase observed was estimated to be greater than 20m from the main perch). It was common for males on pursuit flights to cross the territories of other males and multiple encounters would then occur.

Territory-holding males spent on average 5.9min h⁻¹ in flight, or about 10% of their time. The mean flight duration for all flights was 5.9s and 7.3s for flights containing an aggressive encounter. The number of flights per hour containing an aggressive encounter was 36.0, which is 61% of all flights. The mean number of conspecifics encountered per hour was 59.1 and the mean number of non-conspecifics encountered was 11.5. Full details of these and the other recorded activities are given in Table 1.

Table 1. Behavioural activities for territory holding marked male *Orthetrum coerulescens* between 16 June and 18 September 2003 (n = 40).

Behavioural activities	Min	Max	Mean	S.D.
Flights (h ⁻¹)	41.3	103.0	59.6	± 14.4
Flights with an aggressive encounter (h ⁻¹)	11.1	86.0	40.9	± 15.1
Flights with one or more conspecific encounters (h ⁻¹)	11.1	79.0	36.0	± 12.8
Flights with one or more non-conspecific encounters (h ⁻¹)	0	60.7	7.5	± 14.2
Conspecific males encountered (h ⁻¹)	11.1	158.0	59.1	± 31.2
Non-conspecific males encountered (h ⁻¹)	0	108.6	11.5	± 24.9
Other dragonfly species present	0	8	2.1	± 1.7
Matings (h ⁻¹)	0	6.4	1.1	± 1.1
Time in flight – all flights (min h ⁻¹)	2.9	11.1	5.9	± 2.5
Time in flight – aggressive flights (min h ⁻¹)	2.0	10.3	4.9	± 2.5
Mean flight length – all flights (s)	3.6	12.7	5.9	± 2.0
Mean flight length – aggressive flights (s)	3.6	14.4	7.3	± 2.5
Minimum flight length (s)	1	2	1.2	± 0.4
Max flight length – excluding guarding (s)	9	47	22.2	± 10.7
Mean length of female guarding flight (s)	0	63	21.0	± 18.2

Females only visited the wetland areas to mate and appeared to approach the territories stealthily; frequently their arrival went unnoticed. The male would make a sudden dart and seize the female as she approached his territory. The sound of the clash of wings between the male and female as they adopted the tandem position was often the first indication of their presence. On numerous occasions a male was seen to enter an adjoining territory to obtain a female which the territory holder had not seen.

More than one male that was observed to defend a territory and achieve matings had not attained its full 'reproductive' coloration, retaining some yellow on its abdomen. These males were able to chase off mature males and copulate successfully with females, resulting in apparently normal oviposition.

The average territory size of the 40 males was 5.75m^2 , 2.78m^2 (40%) of which was over water. The vegetation in the territories was less than 0.5m high but was variable in its coverage. The water depth in the territories did not exceed 0.2m during the study and the pH varied from neutral to slightly acidic in different territories (Table 2).

Table 2. Territory parameters for territories held by marked male *Orthetrum coerulescens* between 16 June and 18 September 2003. n = 40.

Territory Attributes	Min	Max	Mean	S.D.
Territory size (m^2)	1.10	60.00	5.75	± 10.16
Open water (m^2)	0.30	16.00	2.78	± 3.26
Minimum vegetation height (mm)	0	400	104.50	± 117.89
Maximum vegetation height (mm)	50	1300	480.00	± 220.08
Predominant vegetation height (mm)	50	600	355.75	± 148.29
Vegetation density (Score 1 – 3)	1	3	1.70	± 0.76
Average water depth (mm)	5	183	28.06	± 31.64
Average sediment depth (mm)	12	379	112.24	± 88.48
Average pH value	5.81	6.93	6.56	± 0.30

The effect of time of day on territorial behaviour and the number of matings. Males commonly started adopting their territorial positions before 0900h. The majority appeared to 'roost' away from their territories but there were invariably a few males flying around water at around 0800 BST if the day was sunny. Mating was seen before 1000h on each day of study, the earliest occurring at 0827h on 25 June. The mean number of matings per hour achieved by marked males was $1.11 \pm 1.13 \text{ h}^{-1}$ and there was no significant difference in the number of matings observed before or after 1230h (before 1230h: $1.07 \pm 1.17 \text{ h}^{-1}$, n = 34; and after 1230h: $1.23 \pm 1.24 \text{ h}^{-1}$, n = 42).

The effect of territory size on the number of matings. There was a correlation between the size of a territory and the number of matings per hour, with males holding larger territories achieving more matings ($r = 0.690$, $p < 0.001$, $n = 40$).

Comparison of territorial behavioural activities in different areas. There were no significant differences in the observed behavioural activities in the different wetland areas. However, the total number of non-conspecifics encountered was higher at still water (20.60 ± 30.90 ; $n = 21$) than at flowing water territories (1.41 ± 1.61 ; $n = 19$) ($t = 2.75$; $df = 20$; $p = 0.012$) and the number of flights (h^{-1}) containing one or more aggressive encounters with non-conspecific males was also higher at still water (13.12 ± 17.95) than at flowing water territories (1.22 ± 1.40) ($t = 3.03$; $df = 20$; $p = 0.007$).

Territory fidelity. Some of the marked males showed great loyalty to the same territory. For example, insect no. 7 remained at the same territory at pond 14 for 21 days (16 June – 7 July), whilst insect no. 5 maintained an adjoining territory for at least 13 days. Both had full blue abdomens when they were marked. At least 14 of the marked males returned to the same territory for more than one day. Other males were seen to defend more than one territory. Insect no. 22, again showing a blue abdomen when marked, was seen to be defending different territories about 5m apart on consecutive days (14 & 15 July) in the Glaven Valley. Insect 17 was watched holding three territories in a single day. It was first observed holding a territory on the stream of the Mixed Mire for 39min up to 1229h on 29 June, during which time it was seen to catch and copulate with a female (although no oviposition was witnessed). It suddenly left the territory and was not relocated until 1304h, about 25m downstream. It appeared to defend a territory at this new site, chasing off intruding males, for at least 22min but then disappeared again. It was seen again at 1501h about 3m upstream from its original position (another male was now occupying its initial territory) and remained in this location until the observer left the site at 1700h. It was not seen subsequently.

Behaviour associated with oviposition. The male and female flew in tandem and the copulation position was usually adopted whilst in flight or shortly after the pair landed. For 15 timed occasions the mean length of time in tandem was 11.5s (range: 2 – 78s). Whilst copulation was occurring, the pair usually perched low down on vegetation ($< 200\text{mm}$) and often on the ground. The mean time spent in copulation was 83s (range: 12 – 261s, $n = 39$). After the pair separated, they both remained on the ground or low in vegetation until oviposition began. The mean length of this ‘post-copulatory rest period’ was 36s (range: 0 – 135s, $n = 39$).

After mating, the female laid her eggs either by hovering over the water and dipping the tip of her abdomen under the water or, more commonly, by perching on vegetation at the side of the water body and inserting her eggs under the surface. An ‘oviposition episode’ involved a number of bouts of egg-laying interspersed with short rests. The mean

number of bouts of egg-laying in a single oviposition episode was 2.6 (Range 1 – 6, $n = 37$). The mean total time spent egg-laying in a single oviposition episode was 62s (range: 0 – 215, $n = 37$) with the mean length of each bout of egg-laying being 21s (range: 0 – 48s).

The number of bouts of egg-laying in each episode of oviposition was different in different locations (ANOVA test: $F = 3.301$; $p = 0.031$; $df = 3$). Post hoc tests (Tukey HSD) showed that there were significantly more bouts of egg-laying per episode in the Ponds Area (mean number of bouts = 4.00 ± 1.41 , $n = 4$) than in the Northern Mire (1.92 ± 0.95 , $n = 13$). Also the length of the post-copulatory rest period was significantly shorter in the Northern Mire (23.9 ± 20.5 s, $n = 13$) than in the other areas (Mixed Mire: 37.1 ± 40.49 s, $n = 17$; Glaven Valley: 28.4 ± 8.56 s, $n = 5$; Ponds Area: 94.8 ± 36.75 s, $n = 4$) (ANOVA test: $F = 5.66$; $p = 0.003$; $df = 3$).

The male would fly over the female whilst she was ovipositing in a 'guarding flight', frequently hovering within a few centimetres of her. Usually he would perch whilst she was resting between bouts of egg-laying, only flying during these periods if another male approached his territory. The male did not try to re-mate with the female during these rest periods. Four times, a male was observed to 'nudge' or land on a resting female. On three of these occasions, the female immediately resumed egg-laying. In the other case, the female remained perched for several minutes and then flew off.

On at least five occasions a male guarding a female was seen to leave her unattended if a second female entered his territory. The male would approach and try to mate with the new female. In one case, a second male was seen to seize the original ovipositing female and fly off with her whilst the territory holder was occupied with a second female. Guarding of two adjacent egg-laying females was observed twice. An unusual situation was observed in the Glaven Valley on 10 July, when a male holding an isolated territory was seen to mate with four females in 22min. During this episode, three females were ovipositing concurrently.

The oviposition episode was concluded when the female left the territory or if she was disturbed. In the former, the female would suddenly 'tower' or fly sharply upwards to a height of 15m or more before leaving the area. The male would follow her for a short way before returning to his perch. Oviposition episodes would also be concluded if the female was seized by another male. Of 39 recorded episodes, 17 (44%) ended when the female was disturbed. The percentages of oviposition episodes that were concluded by disturbance varied in the different zones. Thus, in the Northern Mire 69% of episodes were disturbed ($n = 13$), whilst in Ponds Area none were disturbed ($n = 4$) (Table 3).

On a very few occasions a male holding territory made dipping movements with his abdomen, similar to those made by the female during oviposition, into (and just above) open water in his territory.

Table 3. The number of matings of *Orthetrum coerulescens* that were concluded in each of the wetland zones between 16 June and 18 September 2003.

	Disturbed	Undisturbed	Disturbed (%)
Northern Mire	9	4	69
Mixed Mire	7	10	41
Glaven Valley	1	4	20
Ponds Area	0	4	0

Observations on defence flights in relation to the status of the intruding conspecific male. Once territories had been established, the male holding territory would react differently depending on the status of the intruding male. If the intruder were holding the neighbouring territory, the males would approach each other at the common boundary and then turn away, often returning immediately to their original perches. However, if the intruder was a wandering male, perhaps a young adult looking to establish a territory, the territorial male would make a more determined attack and the chase could be prolonged.

Sometimes, early in the day, it was apparent that some 'filling-in' of territories was occurring, with a male trying to establish a territory between two existing ones. The intensity of confrontations with the adjoining territory holders would become noticeably lower as the morning progressed. This sometimes resulted in a small reduction in the size of the territories of the original territory holders and sometimes in a slight shifting of the boundaries or a change in their choice of regular perch.

Non-territory holding males at the breeding sites. The presence of non-territorial males or 'wanderers' at the breeding sites was observed frequently. Identifying individuals when only a small percentage of the population was marked was difficult but, in a situation when an area containing a number of territories had been watched for a lengthy period, it was possible to identify individuals by their favoured perches. Thus the presence of a 'new' individual was detectable by locating the usual males at their regular perches and by their behaviour when a male of different status approached.

None of the 40 marked males behaved as a wanderer. Thus it was not possible to determine if repeated sightings of wanderers were one individual making several visits or several different individuals. In an attempt to study this behaviour, a male showing 'wandering tendencies' was caught and marked on the Mixed Mire on 9 July, but when it was relocated the next day it was seen to be holding territory some 35m from where it had been caught.

Some attempt was made to age insects that appeared to be behaving as wanderers. Of the

few for which this was possible, four appeared to be mature adults which had obtained matings (tell-tale scratches on the top of the abdomen made by the legs of the females during copulation), two were clearly 'young' adults that had yet to attain the complete blue coloration on their abdomens and one showed the blue pruinescence on the thorax that suggests an 'old' individual.

By far the majority of observed matings were achieved by males that were actively holding territory. However, there were a number of occasions where it is believed that a non-territorial male achieved a mating. On at least four occasions (one in the 'mire-pools' region of the Northern Mire and three in the stream section of the Mixed Mire), an individual that had not been observed holding a territory caught and mated with a female. In each case, the wanderer (in tandem with his female) was harried by territory-holding males from territory to territory. For two of the wanderers and their mates, a quiet spot was found where they were undisturbed for long enough for her to lay eggs.

The effects of inclement weather on territory occupation and size.

Throughout the period 30 June–5 July the weather was overcast with extended periods of heavy rain and dragonflies were not active. I believe that this inclement weather reduced the size of the population of *O. coerulescens*. Only four of the 44 males (9%) that were marked prior to 30 June were relocated after this week. Two of these were on the Northern Mire, one of which was marked on 16 June and which was observed holding the same territory before and after the bad weather (and up to 7 July at least). The mark on the second individual was too faded for it to be positively identified. The two other survivors were at the Mixed Mire; both were marked on 29 June and one of them was seen holding territory on that date. After the storms, it was seen to be holding a different territory, some 10m north, which it continued to hold for at least the next three days.

The distribution of territories was mapped for a 35m section of the stream in the Mixed Mire before (29 June) and after (7 July) the week of bad weather. The number of territories fell from 15 (mean size $2.9\text{m}^2 \pm 0.91$) to 12 (mean size $3.1\text{m}^2 \pm 0.90$) but the difference in territory size was not significant ($t = 0.63$, $df = 25$, $p = 0.52$).

Changes in the distribution of territories during the season as a result of reduced rainfall. A number of temporary pools and areas of waterlogged mire vegetation dried out as the season progressed, and the water level dropped in some of the ponds. For example, on 10 July, a large area of waterlogged mire in the Ponds Area (in a section where scrub had recently been cleared to the north of the stream) contained 14 territories. This area rapidly dried out and by 15 July there was no remaining open water and no evidence of territorial males. About the same time, a male was seen for the first time in the season to be holding a territory at each of Ponds 2, 3 and 4 (some 30m from the area of flooded mire), perhaps indicating movement of individuals. A similar situation occurred in the Glaven Valley with the apparent movement of individuals from

a drying area to Pond 12. On 9 August, as the site became drier still, two males were seen holding territories at puddles on a ride in the conifer woods of the adjoining country park.

Discussion

It seems likely that the regular pattern of territories observed in the mire-pools in the Northern Mire was created by the uniformity of the habitat and the high density of males. A recent study by Switzer and Fason (2003) considered the use of space in territorial Amberwing dragonflies (*Perithemis* spp.). They noted that, as territories were arranged linearly around the edge of a pond, each resident male had two neighbours, one of which was often closer to the main perch than the other. Resident males experienced more intrusions by neighbouring males and fewer visits by females on the side of their closest neighbour. Resident males therefore perched in their territory on the side of their further neighbour, which over time produced a very regular distribution of territories. In the Northern Mire Pools such a process of adjustment of space in a uniform habitat could have produced the regular distribution of territories observed. This is further supported by the work of Morrell & Kokko (2003) who suggest a division of space through a process of 'nagging' rather than by decisive fights. In the current study, no marked male was observed to lose a territorial dispute and be forced off his territory. Corbet (1999) discussed the success rate of resident males of various species in territorial disputes; in most species studied the resident male won in excess of 97.5% of such encounters (range 71 – 100%).

Habitat quality. The current study suggests that males holding larger territories achieved more matings. This may be related to the arrangement and density of territories rather than to their size. Where territories are densely packed, as in the Northern Mire, each male is likely to have other males around him. Hence the likelihood of a female reaching a territory in the middle of the breeding zone without encountering another male is low and thus mating opportunities for males in the centre would be expected to be fewer than for those nearer the periphery. Consequently males may be expected to favour territories at the edge of the colony, or where there are fewer neighbours. The Northern Mire is almost completely ringed by trees with only a small area to the northwest of the mire open to the heath, which is where most females were located when away from the area of territories. The area nearest to the gap in the trees around a pond that retains water all year (White, 2006 – Pond 14) is where females first arrived and this area consistently had the highest density of males at Holt Lowes. However, no significant difference was recorded in the number of matings achieved in different regions of the Northern Mire.

Studies by Switzer (2002a) showed that amberwing dragonflies occupied high quality habitats first. In the current study, it would thus be expected that a preference for higher quality territories at the edge of the clearing would lead to these being occupied earliest

and this was indeed the case, with the first territories of the year being established at the above pond 14 and its surrounds. Switzer (2002a) also demonstrated that the higher quality sites were also more likely to be occupied by males showing high territory fidelity. Whilst the limited number of marked males meant that this could not be tested, it is noted that the two individuals that showed the highest territory fidelity (21 and 13 days) occupied adjacent territories at the northern edge of the pond.

In the current study, levels of territory occupancy varied greatly from 30 min to 21 days and at least 31% of the marked males that relocated were seen to be occupying the same territory on two or more consecutive days. This is at variance with the study of *O. coerulescens* by Parr (1983a) who observed that males did not return to the same territory "with much consistency". Work by Wolf *et al.* (1997) attempted to test the hypothesis that male *Leucorrhinia intacta* move from low to high quality sites by manipulating oviposition substrate and the number of perches but found the time an individual spent in a territory was not affected by these parameters. Switzer (2000b) investigated a number of factors that might have affected territory tenure in *Perithemis tenera* and found it was not related to site quality, age, wing length or the amount of time a male fought in a day. Tenure duration was longer for males that arrived earlier in the day and for males that had successfully caught and copulated with females, suggesting that it is mating success that causes them to stay longer.

Habitat selection theory predicts that there are likely to be more aggressive encounters at higher quality territories (Switzer, 2002a) but this was not shown by the data for the Northern Mire. However, no distinction was made between a contact with a male holding an adjoining territory where the 'fight' would be low key and fights that escalated. While it is not possible to show an effect of increased aggressive flights the data does show increased competition by the number of oviposition episodes that were concluded by disturbance. In the Northern Mire, 9 of the 13 recorded oviposition episodes (69%) were concluded by disturbance and all but one of these was at the above pond. This probably reflects the higher density of males since, when one intruder distracted a guarding male, another could enter his territory and capture the ovipositing female. The data also show that there were significantly more non-conspecific species at standing water and this too would increase the level of disturbance.

The length of the post-copulatory rest period was also shorter in the Northern Mire than in the other zones. Rehfeldt (1989) suggested that it may serve as a tactic to evade male disturbance or provide time to assess predator pressure at the oviposition site. Miller & Miller (1989) suggested it may allow females to judge the male's guarding capacity or to 'handle sperm' – either mobilising it for fertilisation or selecting it according to the quality of their mates. It is tempting to speculate that the shorter rest period observed in the Northern Mire may be connected with increased competition from the higher density of males.

'Water-dipping'. The purpose of this behaviour is uncertain and similar observations have been made for several species (Corbet, 1999). Suggestions include cleaning or cooling the abdomen, testing the suitability of the substrate for oviposition or courtship and (Parr, 1983a) thermal regulation. An odd aspect of the behaviour is that on one occasion the dips were made above the level of the water. It is probably connected in some way with testing the quality of the territory.

Alternative reproductive strategies. Non-territorial males (wanderers) of all age classes were observed at the territories and some undoubtedly achieved successful matings, but it was impossible to assess how frequent an occurrence this was. Territories are energetically expensive to defend but provide the holder with a higher chance of mating. Perhaps non-territorial behaviour may result in fewer mating opportunities but at a lower energy cost per mating. Alternative reproductive strategies have been recognised in Odonata (e.g. in *Nannophya pygmaea*, Tsubaki & Ono, 1986; in *Leucorrhinia intacta*, Wolf & Waltz, 1993, and in *C. splendens xanthostoma*, Plaistow & Siva Jothy, 1996). In *Calopteryx haemorrhoidalis* non-territory holding males were observed to achieve matings but had a much lower mating success than territorial males (Cordoba-Aguilar, 2000). A detailed study of *C. maculata* (Forsyth & Montgomerie, 1987) found that 78% of 600 males defended territories and 14% of those territorial males also acted as wanderers on some days. In *C. maculata* wanderers tended to be previously successful territorial males and the authors suggested they adopted this tactic when intense competition forced older males to abandon territories, allowing them to prolong their reproductive careers. In the study of *Nannophya pygmaea* by Tsubaki & Ono (1986), 23% of resident males that lost territories in disputes became wanderers.

In the current study, it does appear as if an alternative reproductive strategy exists. The presence of young males as wanderers means that it cannot be solely to prolong the reproductive life of older males and, as no males were seen to lose territorial fights, it is perhaps unlikely that the wanderers were ousted territory holders. Furthermore, one male was seen to behave as a wanderer and then became a territory holder, suggesting that males swap between strategies. A more detailed survey of wandering males is obviously required to elucidate their role in the reproductive biology of this species.

Acknowledgements

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Balkan Emerald *Somatochlora meridionalis* (Neilson, 1935) – A remarkable extension of the distribution range in Turkey

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Summary

Whilst working on a United Nations (Development Project) biodiversity study at Gökova in southwest Turkey in 2003 (Hope, 2004), I caught a metallic green dragonfly at a stream in the Çetibeli Forest. Although initially assumed to be a Brilliant Emerald *Somatochlora metallica*, the specimen was sent to Dr R. R. Askew for positive identification. He informed me that it was in fact a Balkan Emerald *Somatochlora meridionalis* and, according to him, not recorded in Asian Turkey. Later correspondence with odonatologists from the Natural History Museum (European Invertebrate Survey, Nederland) in Leiden, The Netherlands, confirmed that it was scarce to fairly common in Thrace (European Turkey) and had been recorded in the adjacent Asian Turkey just over the Bosphorus. My discovery put it some 900km to the south of any previous records, a remarkable extension of its distribution range.

Introduction

Somatochlora meridionalis replaces *S. metallica* in southeast Europe (Dijkstra, 2006). *S. meridionalis* is almost identical to *S. metallica* and can only be identified positively in the hand. The main difference is the presence in the former of one, sometimes two, yellow spots on the thorax sides just below the first wing pair. In the male of *S. meridionalis* the upper appendages are longer and thicker than in *S. metallica*. Unlike *S. metallica*, which can be found in various habitats such as ponds, oxbows, rocky lake shores, moorland lakes, canals and sluggish rivers (Dijkstra, 2006; Kalkman, 2006), *S. meridionalis* can only be found at running water such as lowland streams and rivers which are usually heavily shaded (Marinov, 2001). It can be found on the wing from June to August.

The history of *Somatochlora meridionalis* in Turkey

Most, including all of the early, records of this species refer to *Somatochlora metallica* (Morton, 1915, 1922; Kempny, 1908; Hacet and Actağ, 1997, 2004), and Dumont (1977) and Demirsoy (1982) listed it as a subspecies of *S. metallica*. Schneider (1986) showed that a specimen from the Belgrade Forest (Istanbul), identified by Morton (1922) as *S. metallica* was *S. meridionalis*; also a specimen from the Asian side of the

Bosphorus, near Istanbul (collector unknown) has been identified as *S. meridionalis*. Indeed, possibly all specimens from Turkey belong to *S. meridionalis*. Furthermore, the nearest locality where *S. metallica* has been found is in the mountains of southwest Bulgaria (Kalkman *et al.*, 2004). Kalkman *et al.* (2003) mention only one record of the species from the Belgrade Forest, Istanbul dated 2.6.1919 (Morton, 1922), which is in the collection of the British Museum (Natural History).

The site at Çetibeli, southwest Turkey

The location is a small forest of *Liquidambar orientalis* which is under special protection by the Forestry Department. It is situated about 15km from Gökova along the Marmaris road (Fig. 1). A small stream runs through the forest. Normally its depth is about 20cm but where the bed has been scoured away on bends, it is a maximum of 70cm deep. In winter, during times of heavy rain, the stream floods the forest floor up to a depth of one metre. The stream bed is mainly made up of gravel but on the deeper bends it is sandy. Trees and shrubs grow close to the bank, which has a luxuriant growth of moss and liverworts. At the time of my research, the stream ceased to flow by mid-July and the only remaining water was to be found at bends where it was normally much deeper.

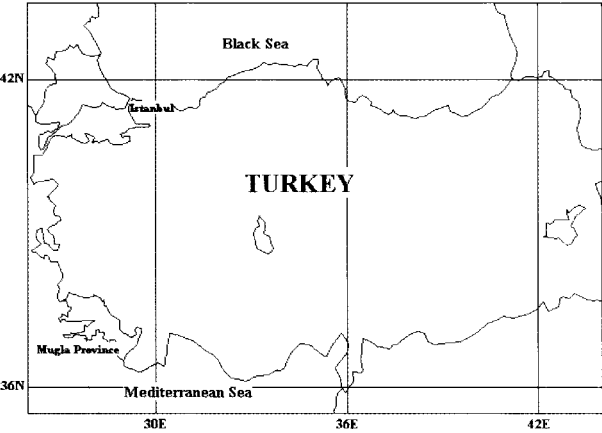
Observations

In June, 2003, whilst working in the Çetibeli Forest, I saw four metallic green dragonflies which were flying about a metre above the water at one of the larger bends of the stream (UTM UPS Grid Reference 35S 06154096). They made constant stops and hovered for several seconds before darting off to confront a rival. Apart from the iridescent green colour I noticed that one had a long vulvar scale which hung perpendicular to the abdomen (a prominent vulvar scale occurs in both *S. metallica* and *S. meridionalis*). This turned out to be a female which I was able to catch for closer examination. Unfortunately it died after a few minutes in the retaining envelope. The specimen was sent to Dr R. R. Askew for positive identification and he informed me that it was *S. meridionalis* and unknown in Asian Turkey beyond the Bosphorus. The specimen is now in the Odonata collection of the National Museum of Scotland in Edinburgh.

Conclusions

I have made several return visits to the site since the record was made but have not seen any further evidence of *S. meridionalis*. I do not think that it would be possible for any larvae to have survived due to the fact that the stream completely dried up in mid July and remained so until mid October when the winter rains began. Since 2003, the weather pattern in southwest Turkey appears to have changed considerably with there being far less rain in winter. The stream bed is now dry by the end of May, which is when the species should be present, therefore making it unlikely that it will appear again under the

a)



b)

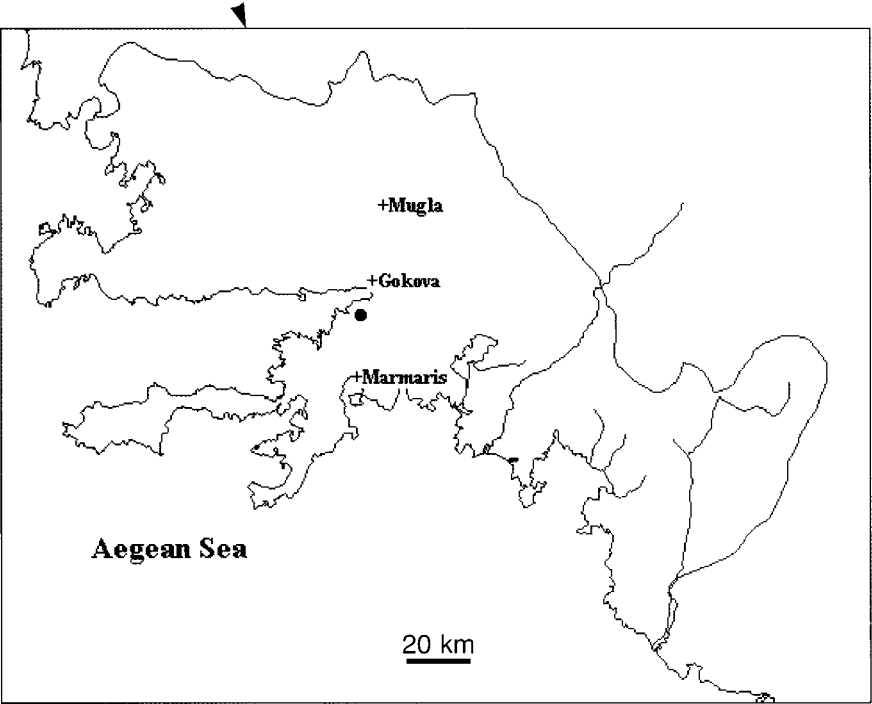


Figure 1. (a) Map of Turkey showing the location of Muğla Province. (b) Details of Muğla Province showing the location of *Somatochlora meridionalis*. ●, adults.



Plate 1. *Somatochlora meridionalis*. Photograph courtesy of J-P. Boudot.

present conditions. I have recorded a total of 13 species at the site but on my last visit, in June of this year (2007), I recorded only four species. There was only a trickle of water for a distance of 100m.

Acknowledgements

I would like to thank Dick Askew who identified the specimen and Vincent Kalkman and Gert Jan Van Pelt who published the record in *Brachytron* 10 (2006); also Jean-Pierre Boudot who kindly allowed me to use his photograph of *Somatochlora meridionalis*.

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Calopteryx splendens (Harris, 1780) – a note on the publication date of the description of the Banded Demoiselle

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Summary

The correct citation of the scientific name of the Banded Demoiselle is *Calopteryx splendens* (Harris, 1780). The description was published in the first edition of Moses Harris' *An exposition of English Insects*, which was issued in three or four parts in 1776–1780. In odonatological literature the date 1782, which refers to the publication of the second edition of the book, has been traditionally, but incorrectly, used for this species. The first available synonymic name of *C. splendens* is *Libellula ludovicea* Fourcroy, 1785.

Introduction

Moses Harris (1731–1785) was the first author to use Linnaean binomial names in describing dragonfly species from England. His book *An exposition of English Insects* (Harris, 1776–[1780]) included 16 species (14 of which were named) of dragonflies, illustrated on 7 plates; see also Lucas (1900a). Harris introduced eight new species-group names, all in the genus *Libellula*: *anguis* Harris, 1780 [= *Aeshna cyanea* (Müller, 1764)], *aspis* Harris, 1780 [= *Brachytron pratense* (Müller, 1764)], *coluberculus* Harris, 1780 [possibly *Aeshna mixta* Latreille, 1805], *fugax* Harris, [1780] [= *Libellula fulva* Müller, 1764], *maculata* Harris, [1780] [= *Libellula quadrimaculata* Linnaeus, 1758], *minius* Harris, 1780 [= *Pyrrosoma nymphula* (Sulzer, 1776)], *splendens* Harris, 1780 [*Calopteryx splendens*] and *splendeo* Harris, 1780 [= *Calopteryx virgo* (Linnaeus, 1758)]. He also provided an especially fine and accurate illustration showing the female of the Golden-ringed dragonfly, but unfortunately he misinterpreted the Linnaean name '*Libellula forcipata* L.', the present *Onychogomphus forcipatus* (Linnaeus), applying it to the wrong species, so that *L. forcipata* sensu Harris, 1780 (nec. Linnaeus, 1758) [= *Cordulegaster boltonii* (Donovan, 1807)].

History of the name *splendens*

Harris' coloured plate 'Tab. XXX' illustrates two distinct species, which in the adjoining descriptive text (p. 99) were named as *Libellula splendens* (Figs 1–3) and *L. splendeo* (Figs 4–6). In the text of Figs 1–3, Harris erroneously not only reversed the sexes, but

also combined two distinct species. Fig. 1, which shows an unmistakable male *splendens*, was described as a female *splendens*. A photograph of this figure is presented here (Plate 1). 'Another female *splendens*' (Fig. 2) is in fact a male of *C. virgo*. Fig. 3 purported to show a male *splendens*, but it is a female *splendens*. Fig. 4 (of *splendeo*) appears to be a teneral, brownish-winged male of *C. virgo* while Fig. 5 ('male' of *splendeo*) with brownish wings appears to be a female *virgo*, although the descriptive text fits a female *splendens* better. Fig. 6 depicts a *Calopteryx* larva. Complete texts of Harris' descriptions of *splendens* and *splendeo* are presented in Lucas (1900b, pp. 221–222).

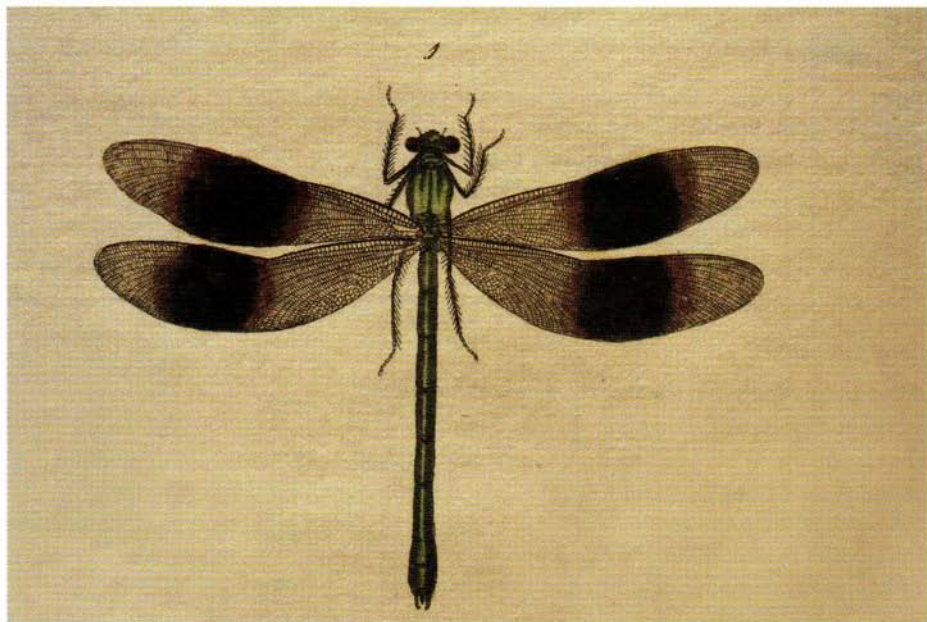


Plate 1. An extract of the coloured plate (Tab. XXX) showing a male of *Libellula splendens*. Photographed by the author from a copy of Harris (1776–[1780]) available at the Entomology Library of the Natural History Museum, London. Copyright: Natural History Museum, London.

The nomenclature and taxonomy of the European *Calopteryx* taxa were confused for a number of years. It is beyond the scope of this note to attempt to present a review here. For those interested in this subject, the thesis by Hagen (1840) provides a good reference to citations and nomenclature in the historical publications. The specific epithet *splendens* became established for the Banded Demoiselle only in the latter half of the 19th century, following the correct use in Selys Longchamps & Hagen's (1850) *Revue*, the standard work on European dragonflies for many years. In two earlier major publications on the European dragonflies, in Selys Longchamps (1840) and Charpentier (1840), this species was known as *C. ludoviciana* and *C. parthenias*, respectively. Confusingly, Selys

had first interpreted Harris' names wrongly, and in his 1840 monograph Selys considered *splendens* as synonym of *C. virgo* and *splendeo* as synonym of *ludoviciana*. Then, in his welcome revision of the British dragonflies (Selys Longchamps, 1846), two species were listed in the genus *Calopteryx*: *virgo* L. and *splendeo* Harris, the latter still being an incorrect name.

Surprisingly, the first available synonymic name of *C. splendens*, i.e. *Libellula ludovicea* Fourcroy, 1785 remained unnoticed in dragonfly catalogues and revisions since 1840 until the present. This name is also absent from all catalogues of the world odonate fauna (see Hämäläinen, 2008).

Publication date of the name *splendens*

The year 1782 has traditionally been linked to this species in the odonatological literature. This date is presented in all published catalogues of the world Odonata, starting from that of Kirby (1890), and is used in nearly all books and other publications of dragonflies. The few exceptions include Hammond (1977), where the name was given as '*Agriön splendens* (Harris, 1776)'. However, in the revised edition of Hammond's book (Hammond, 1983) it was changed to '*Calopteryx splendens* (Harris, 1782)'. Also, in the recent book by Grand & Boudot (2006), the year 1776 is used for *C. splendens*. However, both 1782 and 1776 are erroneous with respect to the name of *C. splendens*. According to data presented by Arthur A. Lisney (Lisney, 1960) in *A Bibliography of British Lepidoptera 1608–1799* (pp. 170–175) and by Neal L. Evenhuis (Evenhuis, 1997) in *Litteratura taxonomica dipterorum (1758–1930)* (pp. 341–343) the first edition of Moses Harris' book was published and distributed in parts between 1776–about 1780. The book is divided into five decads, each with 10 plates and corresponding text. The first decad was published separately in 1776. The second decad (with two plates of aeshnid dragonflies without scientific names) was published apparently in 1778. The third decad (including the description of *C. splendens*) contains four dated plates, two for 'Dec. 1779' and two for '1780'. Lisney concluded that decads 3–5 were issued together, probably in 1780, but Evenhuis claims that decads 3–4 were issued together, earlier than the fifth decad. However, whichever is the case, we have good reason to conclude that 1780 is the correct date of the description of *C. splendens*. In any case, the second issue of the first edition of the complete book was already published in 1781, and the second (most widely known) edition, with a slightly different title, in 1782 (Harris, 1782).

Taxonomists of other insect groups, including Syrphidae and various other families in Diptera and Hymenoptera, in which Harris also described new species, seem to have already followed Lisney's and Evenhuis' conclusions much earlier. In catalogues of these groups, Harris' species bear the dates 1776, 1778 and 1780. A Google search on the internet showed that '(Harris, 1782)' has remained in use only in the case of *C. splendens* and in those synonymous odonate names which he introduced.

In the nomenclatorial formal list of British dragonflies, Cowley (1935) presented the date of the name *Agrion splendens* in square brackets, '[1782]', indicating that the date was uncertain. Also Longfield (1960) wrote that Harris' book was "published in 1782, or possibly earlier". However, these remarks have not resulted in any change in the general citation practice. Now, almost 50 years after Lisney's conclusions, it may finally be a proper time to start writing correctly *Calopteryx splendens* (Harris, 1780). It is noteworthy that this most striking of insects is among the very few Odonata species originally described from England, and that by one of her most distinguished early entomologists.

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Underwater tandem formation in Common Blue Damselfly *Enallagma cyathigerum* and the need for contact guarding

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Summary

Observations on a large population of Common blue Damselflies *Enallagma cyathigerum* show competition for females between males to be very high at high population densities. This results in a number of aggressive tactics used by males to try to win over females by displacing the tandem male.

Introduction

Underwater oviposition only occurs in dragonflies that lay their eggs endophytically, i.e. within plant material (Corbet, 1999). It is found in a wide range of genera, including *Enallagma*, where it has been described in several of the 100 or so species in this genus. In *Enallagma cyathigerum* the female has been observed to descend as far as 1 metre below the surface (Macan, 1964) and she may remain submerged for up to an hour (Doerksen, 1980; Miller, 1990); *E. hageni* has been observed to oviposit in this way up to four times a day (Fincke, 1986). During submergence the forewings stay dry as they are shielded by the closed hindwings (Miller, 1995). While under water the female makes rocking movements and Miller (1994) suggested that these disturb the boundary layer around the animal and hence increase the uptake of oxygen from the water.

Newly flooded gravel pits with a sparse surround of marginal aquatic plants attract early coloniser species of dragonfly. The first species to be attracted to such open sites include *E. cyathigerum*. Large numbers of males of this species can be observed at such sites swarming over the water's surface. The males are attracted to areas where submerged plants come close to the surface. When such areas are limited, high densities of males can arise, resulting in competition and inter-male aggression. The swarming behaviour results from the release of females to submerge and oviposit in underwater plant stems.

Observation site

At Broom Gravel Pits in Bedfordshire the extraction of gravel has been carried out for over a decade. In recent years some parts of the area have been allowed to flood, forming large water-filled lakes. During July 2007 many thousands of *E. cyathigerum* were present, with swarms of males hovering over underwater plants in clear water close to the

bank. This provided an opportunity to study their behaviour above and below the water in close detail. A handheld Canon EOS 1D Mk2 digital camera was used with a 300mm lens with image stabilisation to record the activity within 1m of the water's edge. A $1/2000$ th second shutter speed was used to freeze movement so that behaviour could subsequently be analysed on the computer.

Observations

At low population densities there is little aggression towards flying tandem pairs as they arrive at the breeding pools looking for a suitable oviposition site. As a pair approaches the water's surface the female lowers her legs ready to grasp the underwater stems. On touchdown the female immediately climbs down into the water and the male releases her. The released female climbs down the stem ovipositing as the male hovers over the release point (Plate 1). The female remains below water for 15–30 minutes. The male will remain non-contact guarding for as long as possible and will leave if the female does not resurface in a short time or if it meets repeated aggression from other males. The female resurfaces to be retrieved by either the tandem or another male (Miller, 1990).

In high density populations tandem pairs are harassed as soon as they fly over the water's surface in search of oviposition sites. They are intercepted and attacked whilst flying into the ovipositing site (Plate 2). If the harassment is within an 'acceptable' level they will attempt to land. At this point the tandem pair will usually come under attack from rival males, frequently resulting in the pair flying off again.

When they finally find an oviposition site where they can settle, the female will attempt to go underwater held in tandem by the male. The male will normally release the female to go underwater, but if the pair is attacked by one or more rival males the male will remain in tandem contact guarding the female. Observations, revealed by examining photographs, show that males will also attempt to displace the tandem male by biting (Plate 3). This is used by the aggressor and is aimed at the lower half of the tandem male's abdomen. Male to male biting has also been reported in similar circumstances in *Calopteryx splendens* (Ruppell & Hilfert-Ruppell 2007).

The tandem male will partially submerge with the female. Rival males attempt to displace the male by getting between the male and female. As they submerge the hydrophobic properties of the body cuticle and the wings cause the meniscus of the water surface to form a hollow depression (Plate 4). This assists a rival male by enabling it to follow the pair as they submerge. The timing of release by the tandem male appears to be critical at this stage. If the female is released too early it gives an opportunity for a rival male to go underwater and form tandem with the female.

Underwater tandem formation is more prevalent and can involve more aggression than previously realised (Cham, 2002). Rival males can be very persistent, continuing attempts to displace the male below the water's surface. During high densities, several



Plate 1. At low population density a male hovers over the water as the released female submerges to oviposit.



Plate 2. At high population densities tandem pairs are attacked as they arrive at the water to oviposit. Rival males attempt to grasp the female with their legs.



Plate 3. As a tandem pair attempt to land, a rival male bites the male's abdomen.



Plate 4. As a tandem pair submerges a 'hollow' funnel is formed in the water's surface, allowing a rival male to follow.



Plate 5. Two rival males submerge in an attempt to break the tandem pair.



Plate 6. Submerging tandems attract attention of other males, resulting in three rival males submerging whilst others hover overhead.

males each try to displace the tandem male (Plate 5). Observations have shown up to three rival males descending below water in an attempt to gain the female (Plate 6). On occasions this is successful and one of the rival males triumphs.

Males can be so highly driven to mate they will sometimes form tandem with other males already in tandem, thus resulting in a threesome. The stimulus from blue coloration may also explain why males investigate blue objects and why they have been observed to land repeatedly on the upper abdomen of ovipositing female *Anax imperator*.

When the female rises to the water's surface after ovipositing the competition and aggression between males can be equally as intense as when they submerge. This results in a 'scrum' of males attempting to form tandem with the female on the water's surface (Plate 7). The successful male grasps the female and is attacked with male to male biting by the aggressors (Plate 8). Retrieval is most often successful and the female lifted from the water's surface, allowing the tandem to take off and fly to the bankside vegetation where copulation commences.

Discussion

It has been suggested that the benefit of underwater oviposition is to decrease the eggs to the possibility of being exposed to desiccation as a result of falling water levels (Fincke, 1986). This is unlikely to explain underwater oviposition in *E. cyathigerum*. The large open waters where they breed rarely if ever dry out. Neither would this apply to other British species such as *Erythromma najas* that oviposit underwater in well-established pools.

In many species of odonate that show mate guarding the guarding male waits at the surface. However, in *Enallagma civile* the male has been observed to partly submerge (Bick & Bick, 1963) and, in *Enallagma vansomerini*, to submerge completely (Martens & Grabow, 1994).

When a female *E. cyathigerum* returns to the surface she requires the assistance of the male for takeoff and Miller (1990) observed that 27% were abandoned and, presumably, drowned. In *E. hageni* it has been observed that lone males as well as guarding males may help a female take off from the surface (Fincke, 1986). Indeed, in this species, lone males appeared to be more vigilant and rescued floating females more often than did the guarding males; this potentially resulting in remating, although the longer a female remained under water, and hence presumably the fewer mature eggs that remained unlaidd, the less likely she was to remate (Fincke, 1986).

Males of *E. cyathigerum* will typically retrieve females as they rise to the water's surface after ovipositing (Miller 1990). Males hover over the release site in an attempt to retrieve the female. It may prove difficult for the male to predict the exact position that the female will rise. Rival males will swarm over likely areas thus reducing the probability for the original male to retrieve the same female.



Plate 7. A resurfacing female immediately attracts the attention of males attempting to retrieve her, leading to a 'scrum' of males.



Plate 8. As a male retrieves a female the resulting tandem is attacked by four rival males. This aggression involves males biting each other and one grasping the female.

Swarming is a successful strategy for males of *E. cyathigerum*, giving them a chance of encountering an 'available' female as they arrive in tandem to oviposit and also when they float to the surface afterwards. Rival males also have a higher probability of winning a female at the time of release from tandem just prior to ovipositing.

Underwater oviposition may be a mechanism for the female to avoid unwanted male attention and to increase the chances of laying more eggs from a recent mating. It is also in the male's interest to contact guard her to ensure the eggs that are oviposited are fertilised by him. At high population densities the demand for females is high, resulting in aggression between males. Underwater oviposition therefore further improves the probability of the male that is guarding the female until she is underwater having the eggs laid that he has fertilised. However, rival males are able to exploit this if they submerge at the point at which the tandem goes underwater. Thus, at high population densities, the probability of acquiring a female increases if the aggressor submerges with the tandem pair. It is possible that tandem males need to release females shortly after submergence due to oxygen depletion. Therefore the rival males that submerge have an opportunity to form a tandem underwater and retrieve the female, followed by rising to the surface with her.

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The Vagrant Emperor *Anax ephippiger* (Burmeister, 1839): proof of breeding in Turkey

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Summary

I have lived in southwest Turkey for the last 13 years working as a field research biologist, mainly in the field of ornithology. The last five years have been devoted to researching the dragonflies of the eastern half of Muğla province. On 17 November 2004 at 1830h I was about to return home after having checked some small ponds situated 50m from the Mediterranean Sea at Çalış (near Fethiye) when I saw a pair of dragonflies in tandem settle at the base of a stem of *Typha angustifolia*. They turned out to be *Anax ephippiger*. The following year 200 exuviae collected from the location were sent to the Natural History Museum (European Invertebrate Survey, Nederland) in



Plate 1. *Anax ephippiger*. Photograph by the author.

Leiden, Holland, where they were identified by A. Kop. He informed me that five of the exuviae were *A. ephippiger* and that this was the first proof of breeding for this species in Turkey.

Introduction

Anax ephippiger (*Hemianax ephippiger* until recently) is a strongly migratory species and mostly occurs in Africa, the Middle East and southwest Asia as far east as Pakistan (Askew, 1988) where it wanders, following the rains, in order to breed. It can be found at various times around the Mediterranean but is uncommon and scattered in occurrence. However, it probably breeds annually in the Mediterranean basin, including Turkey (Dijkstra, 2006). It has on occasions been found in central and north-western Europe, including several records from Britain, with one from the Shetlands (Brooks, 1997) and there are even a few records from Iceland (Norling, 1967; Mikkola, 1968; Tuxen, 1976), where it is the only recorded species of odonate.

In north-western Europe individuals tend to be found during late summer and autumn, which coincides with its main emergence period in West Africa (Brooks, 1997).

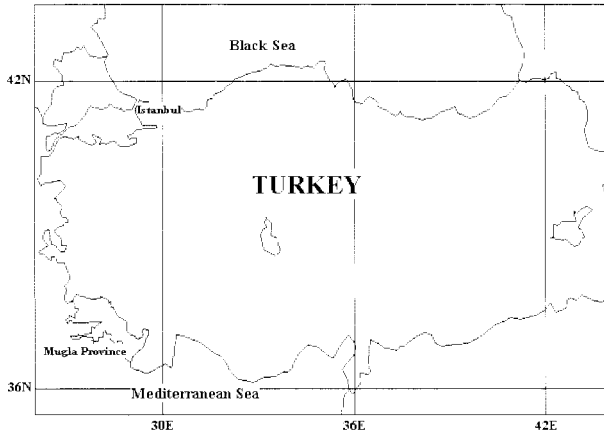
The history of *Anax ephippiger* in Turkey

Anax ephippiger is seen in the north of Turkey from July to September but in the Mediterranean basin it is possible to see it at any time of year. Even with limited records, a histogram of the flight period suggests that the species is present in two generations. This coincides well with the conclusions drawn by Peters & Günther (2000) that the species invades Turkey during the spring and develops a second summer generation here. My observations appear to confirm this conclusion (Hope, 2004, 2007). Kalkman (2006) states that the abundance of *A. ephippiger* in Turkey varies greatly from year to year and he also suggests that spring migrants probably reproduce successfully in Turkey. It is most common along the Mediterranean where larvae might endure the winter. Van Pelt (2004) mentions just one record of *A. ephippiger*. A single female (part of) was found dead at Trabzon – date unknown. Kalkman *et al.* (2004) list 11 records of *A. ephippiger*, mainly from along the Mediterranean coast but some from central and northern Turkey.

The site at Çaliş (Fethiye)

Just to the north of Çaliş (Fethiye) (Fig. 1) was quite a large wetland with a small lake surrounded by *Phragmites australis* (UTM UPS Grid Reference 35S 06894061). Several small ponds had been created by building contractors who illegally removed tons of sand by mechanical digger in 2000. The holes, which were approximately 30m × 20m and 1.5m deep, contained water to a depth of 50–100cm, depending upon water table levels. The following year *Typha angustifolia* had invaded the ponds and by 2004 the growth was prolific.

a)



b)

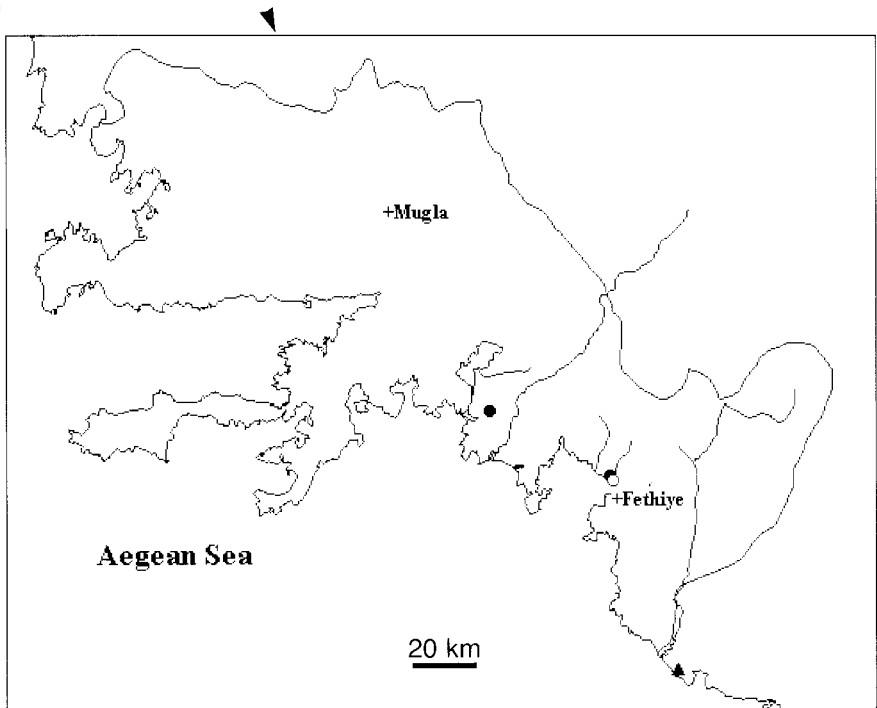


Figure 1. (a) Map of Turkey showing the location of Muğla Province. (b) Details of Muğla Province showing the locations of *Anax ephippiger*. ○, exuviae; ●, adults; ▲, adult recorded outside Muğla Province (at Patara).

Observations

On the 17 November 2004 at 1830h I saw a pair of dragonflies in tandem settle at the base of a reed. I noticed a blue saddle but it was not the vivid blue of *Anax parthenope* which also breed at this site, nor did it wrap around the abdomen, which was a sandy brown colour with a black dorsal band. The eyes and thorax were brown which became yellowish-green on the lower half. The abdomen of the female was a similar sandy brown colour but without a visible blue collar. They remained in tandem whilst the female oviposited into the reed, just below the surface. After a few minutes they moved to another reed and repeated the process. I had not seen this species before but it was obvious that it was an *Anax*. On arriving home I checked Askew (1988), which confirmed my identification. The following year (2005), I collected about 200 exuviae from the same location and these were sent to the Natural History Museum (European Invertebrate Survey, Nederland) in Leiden, Holland, where they were identified by A. Kop. He reported that five of the exuviae were *Anax ephippiger* and that this was the first proof of breeding of the species in Turkey. The site (where 21 dragonfly species have been recorded) despite being a grade one protected nature site, was filled in during 2006 and now has over 300 apartments even though Turkish law forbids the filling in of wetland.

In 2007, I recorded the species on two occasions, the first being on 27 March (UTM UPS Grid Reference 35S 06884062), not far from my original sighting. Two males were flying over grassland some 300m from the nearest water. I caught one and photographed it for record purposes. The second sighting was of a single female at Patara, some 80km away, on 24 May (UTM UPS Grid Reference 35S 07084016). I have recently been given a record of a female, photographed by Alan Fenn on 29 March 2007, at Oğular, 65km north-west of Fethiye (UTM UPS Grid Reference 35S 06524076).

Discussion

A number of dragonfly species are being recorded beyond their previously recorded breeding range, including, for example, the Red-veined Darter *Sympetrum fonscolombii* (Hursthouse, 2007; Parr, 2007) and the Small Red-eyed Damselfly *Erythromma viridulum* (Parr, 2007) in Britain. *Anax ephippiger* also appears to be expanding its breeding range. Thus it is well documented that there has been an increase in records in Bulgaria since 1990 (Marinov, 2001; Taylor, 2006) and proof of breeding in that country was obtained when an exuvia was found in 2004 (Taylor, 2006). During the period I have recorded it in Turkey (March, May and November), there are few other odonatologists there to observe it, i.e. it appears outside the normal 'holiday' period and so there is less chance of it being recorded.

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Comments on The Odonata Red List for Great Britain

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Summary

The background to the recent Odonata Red List (Daguet, *et al.*, 2008) is presented. Four British species are evaluated as 'Endangered', two as 'Vulnerable' and six as 'Near Threatened'. Of the remainder, 27 are of 'Least Concern', two recently established species have not been evaluated and there is insufficient data available for one. Red List status is not applicable for the 11 species that are occasional migrants. This list is compared with the previous one (Shirt, 1987).

Introduction

Recent years have seen great changes in the number and range of dragonflies in Great Britain (Hickling *et al.*, 2005; Brooks *et al.*, 2007). Increases in temperature, improvements in water quality and sensitive site management have all played their part in extending the geographical distribution of many species. However, other species are now becoming threatened by sea level rise, diffuse pollution and a reduction in their habitats. It was felt that 20 years after the previous red data book on insects had been published (Shirt, 1987) there was a requirement to revise the list for Odonata. The Joint Nature Conservation Committee (JNCC) commissioned the British Dragonfly Society (BDS) to undertake this revision and the full version of the final document (Daguet *et al.*, 2008) can be viewed on the BDS website or obtained on request from the BDS Dragonfly Conservation Group. This article summarises some of the key points of the analysis and shows the outcomes in terms of species assessment and each species' current Red List category (Tables 1–4).

Background to the Odonata Red List

The newly revised Odonata Red List and its associated report were produced as part of the JNCC Species Status Assessment project that aims to assign conservation status to the British flora and fauna using internationally approved IUCN Red Data Book criteria and categories (JNCC, 2006). The report assessed British Odonata using Version 3.1 of the IUCN Red List categories and criteria (IUCN, 2001). These categories and criteria have undergone extensive revision over the past 20 years, so the new Red List differs substantially from the previous version.

For the current review, an analysis was made of records held within the BDS Dragonfly Recording Network database and then expert opinion from members of the Dragonfly Conservation Group used to verify the conclusions reached and also to cover existing gaps in the data. The previous assessment (Shirt, 1987) listed four species as Endangered (three of which were regarded as extinct in Britain), two as Vulnerable and three as Rare. The present assessment lists three species as Regionally Extinct (RE), four as Endangered (EN), two as Vulnerable (VU) and six as Near Threatened (NT). There are no British species that currently qualify for the Critically Endangered category.

The remaining British resident species, including regular migrants that have bred sporadically over many years, such as Yellow-winged Darter *Sympetrum flaveolum* and Red-veined Darter *S. fonscolombii*, are listed in the not-threatened category of Least Concern (LC).

Vagrant species such as Southern Emerald Damselfly *Lestes barbarus* and Southern Migrant Hawker *Aeshna affinis* are classed as Non Applicable (NA), so do not qualify for evaluation against IUCN criteria. Similarly, species such as Small Red-eyed Damselfly *Erythromma viridulum* and Lesser Emperor *Anax parthenope* do not qualify for evaluation because they are recent colonists (NE – not evaluated). One other species not evaluated is Highland Darter *Sympetrum nigrescens*, because there is currently insufficient data to make direct or indirect assessment of its risk of extinction.

Methods and Analysis

The review of the Odonata Red List used records from the Dragonfly Recording Network spanning a twenty year period from 1986 to 2005. Over 320,000 records contributed to the analysis, representing 68% of the entire data set held at that time. Records from 2006 were not included, because they were incomplete at the time of the analysis.

The data were split into two ten-year periods, enabling a comparison of the first ten year period, 1986–1995, with the second, 1996–2005. The number of records in each time period was approximately equal. It should be noted that the data were not collected specifically for the purpose of this review and thus do not provide a complete picture. It was for this reason that the analysis was subsequently subjected to expert opinion.

The analysis was approached in two different ways. The first estimated the 'Area of Occupancy' for each species at the tetrad level (2km × 2km) as recommended by the IUCN guidelines (IUCN, 2005). Area of occupancy is defined as the area within the 'Extent of Occurrence' which is occupied by a taxon, excluding cases of vagrancy. This analysis necessitated the omission of a small number of hectad (10km × 10km) records in each time period. Once the analysis had been made for each ten-year period, the Area of Occupancy for the second time period was compared to that for the first to determine any trends.

The second analysis was an estimation of the 'Extent of Occurrence'. This is defined as the area contained within the shortest continuous imaginary boundary which can be drawn to encompass all the known, inferred or projected sites of present occurrence of a taxon, excluding cases of vagrancy. It is achieved by fitting an alpha shape to each species distribution and then adding up the areas of the resulting polygons. Again a calculation for each species was obtained for each time period and then values compared to estimate trends.

Criteria for including species in the review

A total of 56 species are included in the final report, 39 of which match the requirements for inclusion in the 'Breeding Species' group. The definition of breeding used was that agreed by the Dragonfly Conservation Group (Taylor, 2004). A further three species that were known to have bred in Britain previously, but were not recorded during the 20 year span of this analysis, are included as Regionally Extinct.

There is taxonomic uncertainty over one British species, Highland Darter *Sympetrum nigrescens*, and this has led to inconsistent recording, although the species has been noted as breeding in the past. The uncertainty centres on whether this is a species separate from the Common Darter *S. striolatum* or a melanic form of the latter. Recent work indicates that *S. nigrescens* is a junior synonym of *S. striolatum* (Pilgrim & von Dohlen, 2007), although this study did not include any Scottish specimens of the former. In recent years records for *S. nigrescens* in Scotland have been clumped with those for *S. striolatum*. On this basis, *S. nigrescens* is included in the list, but noted as Data Deficient (DD).

Included in the report, but excluded from the analysis, are those species deemed to be either 'Recent Colonists' or 'Vagrants'. Thirteen of the 56 species in the report fall into one or other of these two groups.

IUCN Red List Criteria

The IUCN criteria (IUCN, 2001) have been designed to apply to a wide range of organisms on a global scale, so not all are applicable to Odonata. The threat categories applied to British Odonata in this review cover three main areas; reduction in population size, extent of geographical range and small population size coupled with decline. The criteria are similar for each threat category, but differ in the qualifying levels. For example, a species observed or estimated to have suffered at least a 50% decline over ten years, but where the cause is unknown, would be assessed as Endangered, whereas a decline of at least 30% under the same conditions would only qualify the species for the Vulnerable category.

Similarly, an extent of occurrence estimated to be less than 5,000km² or an area of occupancy estimated to be less than 500km², linked to declining or fluctuating populations, would qualify the species as Endangered. However, an extent of occurrence

estimated to be less than 20,000km² or an area of occupancy estimated to be less than 2,000km², also linked to declining or fluctuating populations, would lead to no more than an assessment as Vulnerable.

Although the threat category of Small Population Size and Decline was considered in this analysis, no British species currently qualifies as Critically Endangered, Endangered or Vulnerable in this category. In order to qualify as Vulnerable, the lowest of these three assessments, the population would have to number fewer than 10,000 mature individuals. This figure would then need to be linked to either continuing decline of at least 10% within ten years or three generations, or to continuing decline linked to a single population or small subpopulation size or extreme fluctuations in the number of mature individuals.

The non-threat category of Near Threatened is used for a species when the best available evidence indicates it does not qualify for any of the threat categories, but is close to qualifying or likely to qualify for a threat category in the near future (IUCN, 2005). Species that have been evaluated against the IUCN criteria, but which have failed to qualify in any of the threat categories or as Near Threatened, are placed in the category of Least Concern. Twenty-seven of the 56 species included in the report fall into this group.

Threatened species

Six British species have been evaluated as threatened in this review. Four species qualify as Endangered (EN) and two as Vulnerable (VU) (Table 1).

The four Endangered species are Southern Damselfly *Coenagrion mercuriale*, Northern Damselfly *C. hastulatum*, Norfolk Hawker *Aeshna isosceles* and White-faced Darter *Leucorrhinia dubia*.

Coenagrion mercuriale was previously assessed as Category 3 – Rare (Shirt, 1987).

Although the present analysis appears to show an increase in this species' distribution, it was felt by the Dragonfly Conservation Group, which includes members of the Southern Damselfly Biodiversity Action Plan Steering Group, that this apparent increase was in fact due to increased recorder effort and greater surveillance. The species has in fact disappeared from at least five sites in Britain since 1985 (Purse, 2001).

Aeshna isosceles was previously listed as Category 1 – Endangered and continues with that assessment under the revised criteria. The current analysis also appears to show an increase in this species' distribution, but again it is believed that greater recorder effort is mainly responsible for this apparent increase. This species is considered highly threatened and at serious risk of extinction in Britain due to sea level rise, saline intrusion into freshwater habitats and proposed policies for coastal management and re-alignment (Defra, 2005, 2006).

Table 1. Summary of Odonata Red List (Daguet *et al.*, 2008) showing species in the categories RE, Recently Extinct; EN, Endangered; VU, Vulnerable; NT, Near Threatened; DD, Data Deficient; Endangered +, Extinct in the U.K.

Species	IUCN Category	Previous status in Shirt, 1987
<i>Coenagrion scitulum</i>	RE	Category 1 – Endangered +
<i>Coenagrion armatum</i>	RE	Category 1 – Endangered +
<i>Oxygastra curtisii</i>	RE	Category 1 – Endangered +
<i>Coenagrion mercuriale</i>	EN	Category 3 – Rare
<i>Coenagrion hastulatum</i>	EN	Category 2 – Vulnerable
<i>Aeshna isosceles</i>	EN	Category 1 – Endangered
<i>Leucorrhinia dubia</i>	EN	not listed
<i>Aeshna caerulea</i>	VU	not listed
<i>Somatochlora metallica</i>	VU	not listed
<i>Istes dryas</i>	NT	Category 2 – Vulnerable
<i>Ischnura pumilio</i>	NT	not listed
<i>Coenagrion pulchellum</i>	NT	not listed
<i>Somatochlora arctica</i>	NT	Category 3 – Rare
<i>Libellula fulva</i>	NT	Category 3 – Rare
<i>Gomphus vulgatissimus</i>	NT	not listed
<i>Sympetrum nigrescens</i>	DD	not listed

Shirt (1987) assessed *Coenagrion hastulatum* as Category 2 – Vulnerable. This species continues to undergo observed decline and is only found in four British locations, all of which are in Scotland. *Leucorrhinia dubia* was not previously listed, but is now considered threatened due to its declining range and retreat northwards in Britain. It has disappeared from Surrey, its most southern location and also from parts of Cheshire in recent years.

Two species, Azure Hawker *Aeshna caerulea* and Brilliant Emerald *Somatochlora metallica*, have been evaluated as Vulnerable using the revised IUCN criteria, although neither was listed previously.

Aeshna caerulea only occurs in seven British locations, all in Scotland, and is undergoing inferred decline. As with all Scottish specialist species there has been inconsistent recording in the past, an issue that needs to be addressed before the next review of the Red List takes place. *Somatochlora metallica* occurs in just two geographical areas, one in Scotland and one in south-east England. It is undergoing inferred decline, but again there is inconsistent recording at its Scottish locations.

A further six species are considered to be Near Threatened (Table 1); Scarce Emerald Damselfly *Istes dryas*, Scarce Blue-tailed Damselfly *Ischnura pumilio*, Variable Damselfly *Coenagrion pulchellum*, Northern Emerald *Somatochlora arctica*, Scarce Chaser *Libellula fulva* and Common Club-tail *Gomphus vulgatissimus*. For each of these there is either an

observed decline at least at some sites, a small geographical range or a risk of loss to its habitat. In some cases the current status of the species is uncertain, so the precautionary principle has been applied.

As mentioned above, for one species, *Sympetrum nigrescens* there is insufficient data to make an assessment and hence it is recorded as Data Deficient (Table 1).

Twenty-seven species show no indication of decline under the criteria listed and hence are considered as of Least Concern (Table 2). Eleven species are vagrants, only being recorded occasionally in Britain, and hence the criteria are Not Applicable. The two species that have recently colonised England, *Erythromma viridulum* and *Anax parthenope* have not been present long enough for the criteria to be applied and hence were Not Evaluated (Table 4).

Table 2. Summary of Odonata Red List (Daguet *et al.*, 2008) showing species in the category LC, Least Concern. None of these species were listed by Shirt (1981).

<i>Calopteryx virgo</i>	<i>Ceriatagrion tenellum</i>	<i>Libellula depressa</i>
<i>Calopteryx splendens</i>	<i>Brachytron pratense</i>	<i>Libellula quadrimaculata</i>
<i>Istes sponso</i>	<i>Aeshna juncea</i>	<i>Orthetrum cancellatum</i>
<i>Platynemis pennipes</i>	<i>Aeshna grandis</i>	<i>Orthetrum coerulescens</i>
<i>Pyrhosoma nymphula</i>	<i>Aeshna cyanea</i>	<i>Sympetrum striolatum</i>
<i>Ischnura elegans</i>	<i>Aeshna mixta</i>	<i>Sympetrum fonscolombii</i>
<i>Enallagma cyathigerum</i>	<i>Anax imperator</i>	<i>Sympetrum flaveolum</i>
<i>Coenagrion puella</i>	<i>Cordulegaster boltonii</i>	<i>Sympetrum danae</i>
<i>Erythromma najas</i>	<i>Cordulia aenea</i>	<i>Sympetrum sanguineum</i>

Table 3. Summary of Odonata Red List (Daguet *et al.*, 2008) showing species in the category NA, Not Applicable. These are all occasional migrants and none were listed by Shirt (1981).

<i>Istes barbarus</i>	<i>Crocothemis erythraea</i>
<i>Istes viridis</i>	<i>Sympetrum vulgatum</i>
<i>Gomphus flavipes</i>	<i>Sympetrum pedemontanum</i>
<i>Aeshna affinis</i>	<i>Pantala flavescens</i>
<i>Anax junius</i>	<i>Pachydiplax longipennis</i>
<i>Hemianax ephippiger</i>	

Table 4. Summary of Odonata Red List (Daguet *et al.*, 2008) showing species in the category NE, Not Evaluated. These are fairly recent colonists in England and hence cannot yet be assessed according to the criteria. Neither was listed by Shirt (1981).

<i>Erythromma viridulum</i>	<i>Anax parthenope</i>
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Conclusions

The review of the Odonata Red List used the best available information in the Dragonfly Recording Network database combined with expert opinion from the Dragonfly Conservation Group. Although a sound evaluation of the status of our British Odonata could be made on this basis, the process highlighted gaps in our current data which will need to be addressed before a further review can take place. It is hoped that the Dragonflies in Focus project, started by the BDS in 2007, will help to tackle this problem. As recording for the new national atlas project takes place between 2008 and 2012, special emphasis should be placed on the twelve threatened (Endangered and Vulnerable) or Near Threatened species. This will involve increased recorder effort throughout Britain, but in particular extra effort will be important in previously under-recorded areas such as Scotland. Also in Scotland, further recording will be needed to establish a more precise picture of the distribution of *Sympetrum nigrescens*. It is to be hoped that further DNA analysis will soon determine the exact genetic status of this taxon.

Acknowledgements

I would like to thank the entire Dragonfly Conservation Group for the vast amount of time and effort spent considering species for this current review. I would also like to thank the countless number of recorders who have provided records to the Dragonfly Recording Network since its inception or to the Biological Records Centre at Monks Wood before that. However, my greatest appreciation goes to my co-editors of the Odonata Red List, Caroline Daguet and Graham French, without whose efforts the project would never have been completed.

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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.

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Words that are to appear in italics (e.g. names of genera and species, though not of families) should be underlined if an italic font is not available.

Use of these terms is acceptable: 'exuvia' for cast skin (plural: 'exuviae'); 'larva' (instead of 'naup' or 'nymph') for a larva; to designate the first larval instar.

Dates in the text should be expressed in the form: 24 July 2004.

References cited in the text should be in the form '(Longfield, 1949)' or '... as noted by Longfield (1949)'. All references cited in the text (and only these) should be listed alphabetically at the end of the article in this form:

Hammond, C. O. 1983. *The dragonflies of Great Britain and Ireland*. 2nd edition (revised by R. Merritt). Harley Books, Aldechester. 116 pp.

Longfield, C. 1949. The dragonflies of the London area. *The London Naturalist* **28**: 90–98.

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Tables should be presented on separate, unnumbered pages.

Legends for figures should be presented together in sequence on a single, unnumbered page.

Figures should be prepared in black ink, and scaled to allow a reduction of 1.5 to 3 times.

The legend for each table and illustration should allow its contents to be understood fully without reference to the text. The approximate position of each table and figure should be indicated in the text.

SCIENTIFIC AND ENGLISH NAMES OF BRITISH ODONATA

ZYGOPTERA	DAMSELFLIES		
<i>Cabepteryx splendens</i>	Banded Demoiselle	<i>Aeshna mixta</i>	Migrant Hawker
<i>Cabepteryx zingis</i>	Beautiful Demoiselle	<i>Anax (Hemianax) ephippiger</i>	Vagrant Emperor
<i>Chalcolestes viridis</i>	Willow Emerald Damselfly	<i>Anax imperator</i>	Emperor Dragonfly
<i>Lestes dryas</i>	Scarce Emerald Damselfly	<i>Anax junius</i>	Green Darner
<i>Lestes sponsa</i>	Emerald Damselfly	<i>Anax parthenope</i>	Lesser Emperor
<i>Coenagrion tenellum</i>	Small Red Damselfly	<i>Brachytron pratense</i>	Hairy Dragonfly
<i>Coenagrion armatum</i>	Norfolk Damselfly	<i>Gomphus vulgatissimus</i>	Common Club-tail
<i>Coenagrion hastulatum</i>	Northern Damselfly	<i>Cordulegaster boltonii</i>	Golden-ringed Dragonfly
<i>Coenagrion lunulatum</i>	Irish Damselfly	<i>Cordulia aenea</i>	Downy Emerald
<i>Coenagrion mercatoriale</i>	Southern Damselfly	<i>Oxygastra curtisii</i>	Orange-spotted Emerald
<i>Coenagrion puella</i>	Azure Damselfly	<i>Somatochlora arctica</i>	Northern Emerald
<i>Coenagrion pulchellum</i>	Variable Damselfly	<i>Somatochlora metallica</i>	Brilliant Emerald
<i>Coenagrion scitulum</i>	Dainty Damselfly	<i>Crocothemis erythraea</i>	Scarlet Darter
<i>Enallagma cyathigerum</i>	Common Blue Damselfly	<i>Leucorrhinia dubia</i>	White-faced Darter
<i>Erythronma najas</i>	Red-eyed Damselfly	<i>Libellula depressa</i>	Broad-bodied Chaser
<i>Erythronma viridulum</i>	Small Red-eyed Damselfly	<i>Libellula fulva</i>	Scarce Chaser
<i>Ischnura elegans</i>	Blue-tailed Damselfly	<i>Libellula quadrimaculata</i>	Four-spotted Chaser
<i>Ischnura pumilio</i>	Scarce Blue-tailed Damselfly	<i>Orthetrum cancellatum</i>	Black-tailed Skimmer
<i>Porrhomma nymphula</i>	Large Red Damselfly	<i>Orthetrum coerulescens</i>	Keeled Skimmer
<i>Platynemus pennipes</i>	White-legged Damselfly	<i>Pantala flavescens</i>	Wandering Glider
		<i>Sympetrum danai</i>	Black Darter
		<i>Sympetrum flavesculum</i>	Yellow-winged Darter
		<i>Sympetrum fonscolombii</i>	Red-veined Darter
		<i>Sympetrum nigrescens</i>	Highland Darter
		<i>Sympetrum pedemontanum</i>	Banded Darter
		<i>Sympetrum sanguineum</i>	Ruddy Darter
		<i>Sympetrum striolatum</i>	Common Darter
		<i>Sympetrum vulgatum</i>	Vagrant Darter
ANISOPTERA	DRAGONFLIES		
<i>Aeshna caerulea</i>	Azure Hawker		
<i>Aeshna cyanea</i>	Southern Hawker		
<i>Aeshna grandis</i>	Brown Hawker		
<i>Aeshna juncea</i>	Norfolk Hawker		
<i>Aeshna mixta</i>	Common Hawker		

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