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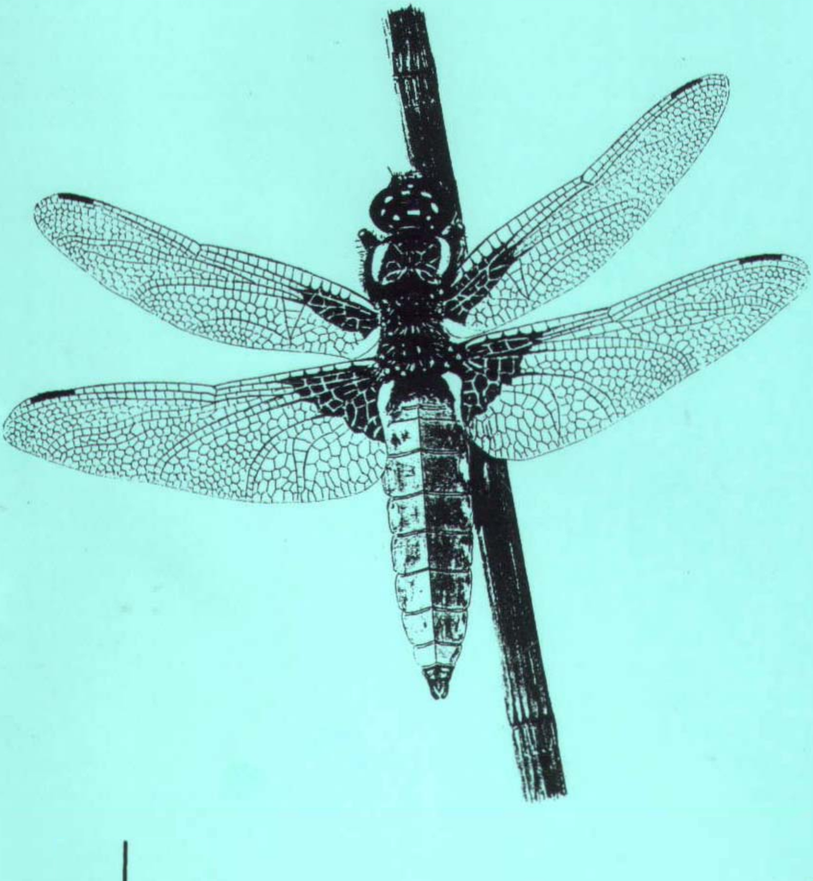

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member of the Societas Internationalis Odonatologica

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Front cover illustration of male *Libellula depressa* by Roderick Dunn

Dragonfly movement and migration in Britain and Ireland

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The movement and migration of dragonflies has long been recognized as of interest, in part because of how it influences the distribution and status of species at both a local and international level. In addition, the recently recognized prospect of global climate change in the short- to medium-term future means that the mobility of dragonflies, and their ability to colonize new habitats, takes on a special significance. It is clearly of importance to have a good general understanding of the nature of dragonfly movement and migration, and in recent years there has been renewed interest in this area (e.g. Parr & Eversham, 1991).

Many adult Odonata remain in the general vicinity of where they emerged, and dispersal of individuals is considered to be a relatively random and local affair. Some species which inhabit transitory habitats have, however, a more pronounced dispersal strategy (e.g. *Ischnura pumilio* (Charpentier) (Cham, 1993)). The life cycles of a number of other species (notably those breeding in temporary pools and other unpredictable water bodies) result in individuals undertaking long-distance movements or migrations, either on a regular basis or in response to particular environmental factors. It is these longer-range movements that will be primarily considered here.

In the British Isles dragonfly movements are most obvious with the occasional arrival to our shores of species not normally present, but there are also influxes of species where there are resident populations. Substantial movements, entirely within our own Isles, can also occur with a number of British species. Unlike the migrations of birds, and even the movements of certain Lepidoptera, the details of and reasons for these long-distance movements are, however, generally poorly understood. There have been a number of pioneering studies by individuals in the past (see Dumont & Hinnekint, 1973, and references therein), but much remains to be discovered. Clearly the situation is complex. For example, while movements of many species primarily involve immature insects, the genus *Sympetrum* is noted for showing marked movements of fully adult insects - indeed individuals may even be seen migrating while coupled (Dumont & Hinnekint, 1973). With the present rapidly growing number of active dragonfly enthusiasts, there is a clear opportunity to help clarify some of the outstanding uncertainties about dragonfly movements and migration. This paper sets out to summarize our present knowledge and presents a few 'speculations' in an attempt to facilitate this process.

One problem with migrant recording is in deciding exactly which individual insects are 'migrants'. Species which do not normally breed in Britain seldom present problems in this respect, but where the species involved has a resident population, individuals must be carefully assessed. In years gone by, records from manned offshore light-vessels provided useful information on movements of such species but, as yet, recording from the modern oil and gas platforms is not well structured. The occurrence of extra-limital forms and direct observations of individuals, or of groups of individuals, coming in off the sea or all travelling in the same direction provides evidence of migration. The sighting of a species outside its known breeding range, or its preferred habitat, is also a good clue. It is becoming clear that many bird observatories, established at key localities for watching avian migration, are also excellent sites for observing dragonfly movements (e.g. Odin, 1993). Large concentrations of dragonflies sometimes also indicate migrant origin, though the possibility of a mass emergence must not be overlooked. It should also be noted that not all, even very substantial, migration need necessarily involve an obvious concentration of individuals. Instances of individuals attracted to light, or otherwise observed flying at night, might similarly suggest migration, since this may continue overnight provided that the ambient temperature remains sufficiently high. Individuals of both *Sympetrum sanguineum* (Müller) and *S. flaveolum* (L.) were, for instance, caught in coastal moth traps during the start of the big *Sympetrum* influx of 1995 (M. C. Marsh, pers. comm.; Paine, 1995; Silsby, 1995). It should be remembered, of course, that non-migrating individuals of some species (e.g. several from the genus *Aeshna*) can also fly well into the evening during suitable warm weather.

Although most recorded vagrancy relates to anisopterans (see details below), the possibility that certain damselflies also reach the British Isles seems worthy of consideration. Small size and delicate build are certainly not a barrier – the avian world providing clear precedents, with some of the smallest species, such as various hummingbirds, wren and goldcrest, having strong migrant populations. In the Arabian region, *Ischnura evansi* Morton is known to accompany the larger dragonflies on their long distance movements during March and April (Walker & Pittaway, 1987). Closer to home, various species from the genus *Lestes* are seemingly good candidates for a partial migratory lifestyle. In mainland Britain, there is a single record of *Lestes viridis* (Vander Linden) from Shenley, Herts., on 11 August 1899 (Corbet *et al.*, 1960), and in the Channel Isles *L. barbarus* (F.) was recorded only twice between 1941 and 1951 (Silsby & Silsby, 1988). Although these records could refer to breeding populations now extinct, vagrancy is also possible. Longfield (in Corbet *et al.*, 1960), in describing the world-wide distribution of *L. sponsa* (Hansemann), thought it 'probably a partial migrant', and the species has been recorded from light traps (Paine, 1992). Less directly, there has also been speculation that the Essex (if not the Norfolk) population of *L. dryas* Kirby, rediscovered after the species' low-point in the 1970s, might in part have had immigrant origins (e.g. Gibbons, 1986). Some *Coenagrion* species may perhaps also be more mobile than they are currently thought to be. Although *C. scitulum* (Rambur) has been reported from Jersey, records are only sporadic, e.g. three were found in 1941, but there have been few or none since (Silsby & Silsby, 1988). This was a year of known migrant dragonfly activity in NW Europe (see below). It is also interesting to note that the now extinct mainland British populations of both *C. scitulum* and *C. armatum* (Charpentier) were known, even at their peak, from only tiny areas near the East Anglian coast. It seems at least possible that the breeding population of *C. scitulum*, and maybe even of *C. armatum*, was initially derived from immigrants from the Continent. If this is so, then one day the species may re-establish itself (themselves), provided that climatic conditions are favourable and that the continental populations do not decline too severely.

Known migrant species

Leaving aside some of the more speculative aspects touched on above, the status of migrant species in Britain and Ireland is summarized below. The list excludes those species known to have occurred in Britain solely as a result of accidental importation, several of which are detailed by Brooks (1988).

Aeshna mixta Latreille
In the nineteenth century, the status of this species was essentially that of a scarce immigrant to this country, but in recent times it has become so well established as a resident breeder that a full understanding of recent immigration has become difficult. Earlier this century there were numerous records of small arrivals of migrants, and even as early as the late 1890s there may have been temporary breeding footholds in areas such as Essex (Mendel, 1992). A substantial incoming movement was noted on 23/24 August 1935 by manned light-vessels off the East Coast (Dannreuther, 1935), and that year saw inland records over much of what is now the established range. Coastal arrivals of large numbers of males in Kent and Norfolk were also noted between 1 August and 3 August 1949 (Longfield, 1950). Numbers noted from a vessel off Clacton, Essex, in early November 1953 (Longfield, 1954) perhaps provide evidence of a return migration. As the breeding population continues to expand, consolidation and range extension by local dispersal seems to have become important, but no doubt substantial arrivals to our shore also continue to occur. At Landguard Bird Observatory, on the Suffolk coast, up to 100 individuals per day may have occurred on some days in recent years (Odin, 1993), though how many of these were of relatively local origin is not known (none breed in the immediate vicinity).

Aeshna affinis Vander Linden
This species shares many features of form and biology with *A. mixta*, but on average is a little more southerly in distribution (Aguilar *et al.*, 1986; Askew, 1988), which presumably accounts for it being a less common migrant to our shores than *A. mixta*. Single males have been recorded from Romney Marsh, Kent, on 5 August 1952 (Longfield, 1954) and from north Bristol, Avon, on 14 August 1992 (Holmes, 1993). Given the general similarity between *A. affinis* and *A. mixta*, it is however quite possible that it is under-recorded.

Aeshna cyanea (Müller)
A known migrant (Corbet *et al.*, 1960), but with the strong resident population in Britain very little information is available on the current (or, indeed, past) migratory status. At Landguard Bird Observatory, on the Suffolk coast, it has been recorded about once every two years in recent times (Odin, 1993), though these are probably mostly (all?) of local origin.

Aeshna grandis (L.)
As with *A. cyanea*, a known migrant (Corbet *et al.*, 1960), but there is very little information available on the precise migratory status in Britain. It has been recorded on occasion from offshore light-vessels (e.g. Dannreuther, 1937a), but whether this represents immigration, emigration or just 'wandering' is not always clear.

Anaciaeschna isosceles (Müller)
A worn specimen at Landguard Bird Observatory, Suffolk, on 1 August 1991 (Mendel, 1992) is well away from the British stronghold of this species, and as the prevailing air stream was from the N. African/Iberian region at this time (Mendel, 1992), an immigrant is possibly involved. The species is known to be capable of long movements, especially in the Mediterranean region (Aguilar *et al.*, 1986).

Anax imperator Leach
This is a species whose potential immigratory nature (Williams, 1965) is often overlooked, though the genus includes several powerful migrants and wanderers. The North American *A. junius* (Drury) is, for example, one of the better characterized temperate-zone dragonfly migrants (e.g. Johnson, 1969; Trottier, 1971). Virtually nothing is known about the current immigratory status of *A. imperator* in Britain. At Landguard Bird Observatory the species is not recorded annually, but in some years 3-4 transient visitors may be noted, mainly in late July and early August (Odin, 1993).

Hemianax ephippiger (Burmeister)
This species is an essentially subtropical long-range migrant showing some cyclicity of appearance in Europe (cf. Askew, 1988), which has been linked to rainfalls in the Sahel region of Africa (Dumont & Desmet, 1990). It is able to penetrate far to the north, being the only dragonfly recorded from Iceland, from where there are several records including no fewer than three in 1971 (Askew, 1988). Silsby (1993) has recently written about this species. In Britain and Ireland the first record was in 1903, then after another in 1913 it remained absent for many years. The period 1968-71 saw three more British records, after which it was again absent for a period. After 1983 the species has become almost annual, with three recorded autumnal sightings in the peak year, 1988, at least one of which was also associated with an influx of the locust *Schistocerca gregaria* (Forskål) (Paine, 1989). Records in Britain are widespread, as might be expected from a strong migrant. Whilst they show a southerly trend, no clear easterly or westerly bias is apparent, possibly because several different arrival routes could be involved. Reports cover an extended time period reaching even into winter, with an indication of two peaks during mid-summer and late autumn (Fig. 1). This is later than that for many migrants occurring in southern Europe, which are often reported in spring (Aguilar *et al.*, 1986; Maibach *et al.*, 1989; Dumont & Desmet, 1990). The autumn/winter peak in occurrences coincides with the main emergence period in west Africa (Dumont & Desmet, 1990), and may represent direct and rapid immigration from this area under the influence of favourable meteorological conditions. It should also be borne in mind that rather than being of central or west African origin, as has been proposed for many European immigrants (Dumont & Desmet, 1990), certain British individuals could rather be east African or Middle Eastern in origin. Mikkola (1968) has, for example, proposed that an immigrant found in Iceland in October 1964 came from the direction of the east Mediterranean. The nature of the summer peak in occurrences seen in Britain is currently unknown. The phenomenon may, in fact, be of recent origin; the first summer record for Britain was of a female at Portland Bill, Dorset, on as recent a date as 11 August 1983 (Silsby, 1993). Possibly this

movement may represent a later, more leisurely stage of the spring migrations into Europe which have been considered to be the basis of most of the southern European records (Dumont & Desmet, 1990). Occasional breeding in Mediterranean Europe has been observed (Askew, 1988; Maibach *et al.*, 1989) and, in at least one year, emergences have also been noted (in mid-August) in Switzerland (Maibach *et al.*, 1989) following an initial primary invasion in spring. Whether the newly emerged adults from this European breeding move on to make a significant contribution to the overall pattern of migration is not yet known.

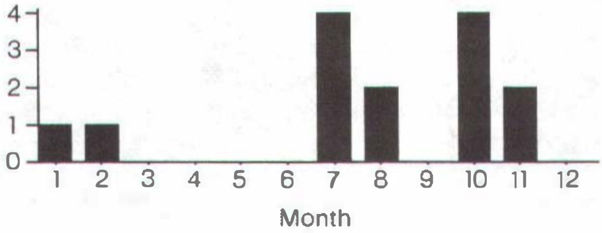

Figure 1. The number of records of *Hemianax ephippiger* for each month of the year

Gomphus flavipes (Charpentier)

A male from near Hastings, Sussex, on 5 August 1818 is the only record for the British Isles (Corbet *et al.*, 1960). The species seems to be declining in Europe (Askew, 1988), so the chance of further records seems small at present.

Libellula quadrimaculata L.

A well-known migrant; a movement observed during May 1862 in Germany was estimated to involve over 2000 million individuals, and another enormous migration, reaching as far as Britain, occurred in June 1900 (Corbet et *al.*, 1960). On the Continent, there is a suggestion of a 10-year cycle in migratory abundance (Dumont & Hinnekint, 1973). One hypothesis is that this results from cycles in the abundance of an internal parasite which can modify the dragonfly's behaviour (Dumont & Hinnekint, 1973), though other explanations are possible. As a widespread resident in Britain and Ireland, immigration is often difficult to detect unless large numbers suddenly arrive (generally at coastal localities), though in the past records from offshore lightships also provided evidence of immigration, e.g. on 1 July 1935 (Dannreuther, 1935) and 29 June 1940 (Dannreuther, 1941) to mention but two instances in the literature. With the loss of these manned light-vessels, and a paucity of reports (though not necessarily of occurrence!) of obvious movements in recent years, little information is available on the current immigratory status. Unusual numbers were noticed on Lundy Island in 1964 (French, 1964), but the large movements in Holland and Belgium in early June 1971 (Dumont & Hinnekint, 1973) were not apparently noticed in this country. At Landguard Bird Observatory, on the Suffolk coast, the species has been recorded in recent times only about once or twice annually, mostly in the second half of May (Odin, 1993).

Figure 2. The geographical distribution of records for the immigrant species plotted on a pre-1974 county basis. Figures relate to the number of independent records rather than to the absolute number of individuals. For clarity subdivision to vice-county level has been avoided with the one exception of Yorkshire where a separation into the coastal eastern region (VCs 61,62) and inland western region (VCs 63-65) helps in interpretation of the data.

Libellula depressa L.

Being a locally common resident species little definitive information is available, though the species is a known immigrant (Corbet *et al.*, 1960; Askew, 1988). *L. depressa* was unusually common in Suffolk in 1917, 1941 and 1990 (Mendel, 1992), which may relate to immigration; the species was also unusually common in the Bournemouth area in 1941 (Fraser, 1941), and that year saw a well-documented arrival of *Sympetrum fonscolombei* and some other migratory species.

Crocothemis erythraea (Brullé)

The species is a well-known migrant, able to penetrate far into northern Europe if conditions are right (Gibbons, 1986). Since it breeds in scattered localities quite nearby on the Continent, and more widely as close as central France (Askew, 1988), the occasional appearance of *C. erythraea* in the British Isles would not be unexpected, though the vaguely *Sympetrum*-like coloration of both sexes means that it could perhaps be overlooked at a casual glance. The first definite record was of a male at North Predannack Downs, the Lizard, Cornwall, on 7 August 1995 (Silsby, 1995), during the big *Sympetrum* invasion year. In the Mediterranean region the species is known to have two generations a year (Askew, 1988), resulting in a prolonged flight period. This, at present, makes it difficult to predict the most likely time of year for any future individuals to be seen.

Sympetrum striolatum (Charpentier)

As the commonest breeding darter in Britain, migration of this species can be easily overlooked, and our knowledge of the movements of this well-known migrant is incomplete. It has sometimes been recorded flying in from the sea under conditions suggesting immigration (e.g. Gorleston 29 July 1933 - Dannreuther, 1933), though individuals noted arriving in Glamorgan on 2 July 1949, from across the Bristol Channel (Longfield, 1950), could have had a more local origin. The species has also been recorded on several occasions from offshore light-vessels. One or two were noticed travelling west (i.e. incoming) on 2 and 3 September 1937 by the Outer Dowsing Light Vessel off Spurn Point (Dannreuther,1937b). Simultaneously, one or two were also recorded from the Happisborough Vessel off the Norfolk coast on 3 September 1937 (Dannreuther, 1937b). This points to a thin, but rather widespread, influx during early September of that year - one which probably involved a substantial number of individuals, but which would have been very difficult to detect from land-based observations only. More dramatic evidence of migration is provided by the report of what must have totalled thousands travelling west throughout the day at Ramsgate, Kent, on 6 September 1935 (Dannreuther, 1936). The most dramatic evidence for immigration to our shores was, however, the mass invasions of southern Ireland, and in particular County Cork, noted between mid-August and early/mid-September 1947 (Longfield, 1948; Corbet *et al.*, 1960). Individuals captured were of a smallish, dark form suggesting an origin in southwest Europe (Longfield, 1948), which would be compatible with meteorological data (Johnson, 1969). In more recent times such massive concentrated invasions have not been noted, and understanding of the current migratory status is poor, though occasionally individuals have been encountered amongst gatherings of other immigrant *Sympetrum*

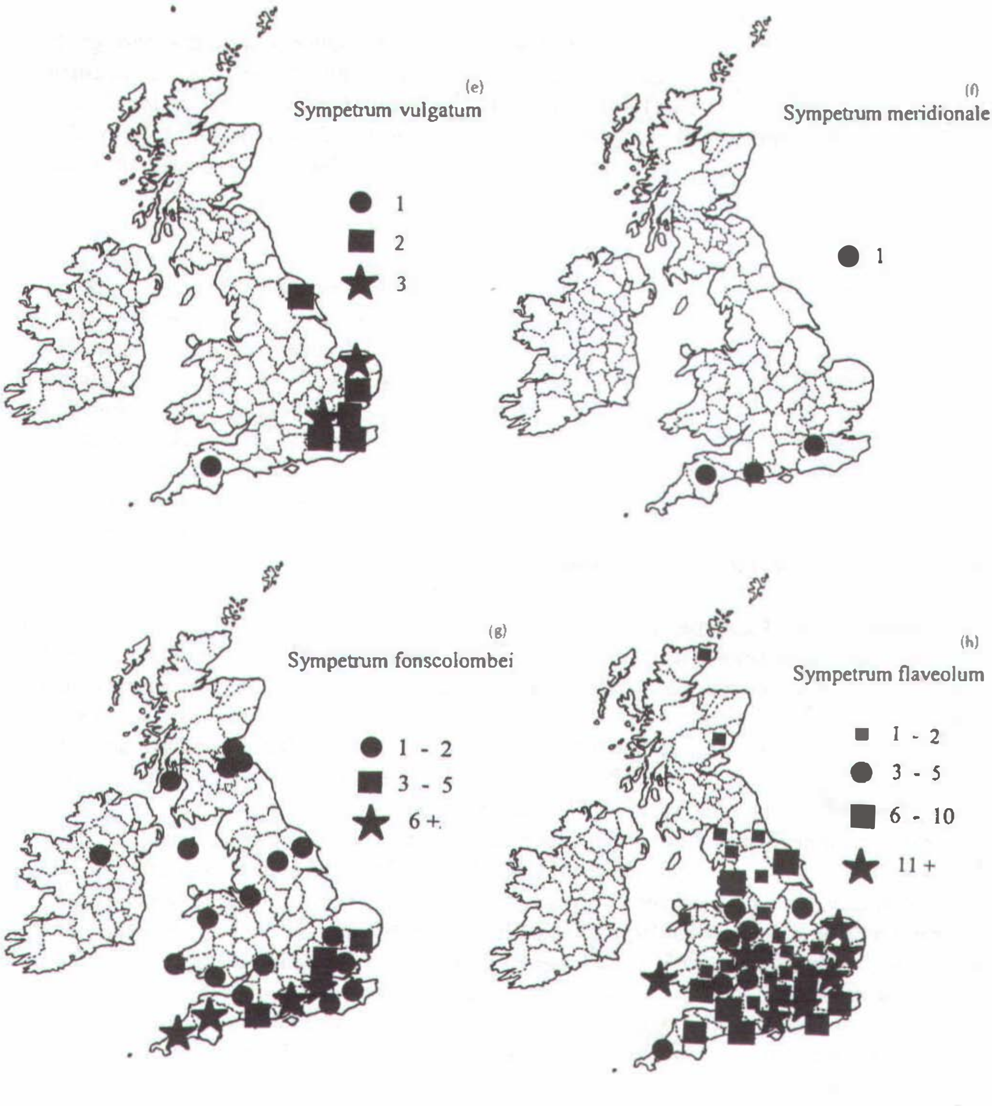

Figure 2 (contd). Maps for *S. fonscolombei* and *S. flaveolum* are approximate only, since not all sightings of these commoner 'rarities' are likely to have been published or otherwise documented in accessible form. Possibly not all records from the 1995 *Sympetrum* invasion are included. Despite these limitations, the maps do convey a good picture of the general features of the immigration of these two species.

species (e.g. Silsby, 1995). Observations at Landguard Bird Observatory show *S. striolatum* to be a quite common visitor to this coastal site in recent years, with a peak of abundance in September and early October (Odin, 1993). Numbers fluctuate from year to year, though maximum counts rarely reach double figures per day (Odin, 1993). Similar phenomena have been noted elsewhere on the Suffolk coast (Parr, unpublished). The exact significance of these observations is not fully clear since *S. striolatum* shows a substantial local dispersal, but there may be some relevance to migratory movements. It would be informative to be able to compare counts throughout late summer and autumn from a variety of inland and coastal sites, including those on the west coast.

It is of some interest that *S. striolatum* has been noted on several occasions in autumn migrating though passes in the high Pyrenees, in company with other known migrant insects and passerine birds. The most notable instance was of large numbers going WSW on 13 October 1950, as noted by Lack & Lack (1951), but Johnson (1969) details other records. This seems to suggest that *S. striolatum* shows a return migration from northern Europe towards Mediterranean regions in autumn, just as is typical of many bird migrants. The whole question of return migration in insects is a very understudied subject, and would repay much greater investigation.

S. vulgatum (L.)

Until the big *Sympetrum* invasion year of 1995, this species had been reported only about ten times from the British Isles (e.g. Hammond, 1983), with a few other sightings from the Channel Isles (Silsby & Silsby, 1988). The major influx of *S. flaveolum* and other migrant *Sympetrum* species in 1995 however produced additional reports from Norfolk (3 sites, at least 15 individuals), Suffolk (2 sites), Kent and the London area (Silsby, 1995 and in litt.). Overall, records show a pronounced (south) easterly bias (Fig. 2e), and span the period 15 June to 1 October. Despite the upsurge in interest in dragonflies in the last few decades, until the 1995 influx almost half of the records came from a short period around the turn of the last century. Given the general unfamiliarity with identifying this species in the field, it is however quite possible that this critical species is being overlooked. Certainly in 1995 it was the presence of *S. flaveolum* which first attracted observers' attentions, and the single male noted from the London area in 1946 was found in the company of many *S. fonscolombei* (Hammond, 1983). Not just other *Sympetrum* spp. seen in the company of the more readily identifiable immigrant species, but also any early-flying *Sympetrum* spp. and any coastal individuals may well repay closer attention.

S. meridionale (Sélys)

Although movements of large numbers of individuals have been noted further south in Europe (e.g. in Johnson, 1969), this species is apparently one of the rarest *Sympetrum* immigrants to British shores. A female was taken in Surrey in 1847, and a male recorded from Dawlish, Devon, in 1901 (Corbet *et al.*, 1960). There are also undated old specimens of a male from Swanage, Dorset, and of a female labelled, rather unhelpfully, 'South of England' (Gardner, 1956b). In addition, the species has been reported once from Jersey in the mid-part of the present century (Silsby & Silsby, 1988). Despite the increased interest in dragon-

Figure 2 (contd).

flies in the last few decades there are no recent records, though as with many of the *Sympetrum* species the possibility exists that it has been overlooked. There is but one old (nineteenth-century) record for Holland (Askew, 1988).

S. fonscolombei (Sélys)
This species has for a long time been well known as an erratic immigrant to our shores, sometimes absent for up to a decade but then occurring in significant numbers. Particularly good years included 1911, 1941 and 1946 (Longfield, 1949a). At a few sites, temporary breeding populations have become established following the larger arrivals, but these have persisted only a few years at most (Longfield, 1949a, b; cf. Moore, 1956). Records received since the inauguration of the British Dragonfly Society show that the present day situation remains little changed, or indeed the species may now be noted more often, having become nearly annual in recent years. The increase in recorders is one factor which must, however, be taken into account when assessing the frequency of reports. The year 1992 was another relatively good year, with reports from many sites, and with over a dozen individuals being seen. Recent records span the time period May to September, this closely following the pattern of older records. Longfield (1949a) suggested that occasional September and October records may relate to home-bred individuals; the species is known to be capable of two generations in a year, and mid-September emergences from an initial invasion in early August have been documented in Switzerland (Askew, 1988). The distribution of reports is somewhat different from that of many other immigrant species to Britain; in addition to a bias towards the south (and to some degree the east), there is also a strong westerly element (Fig. 2g). This, by analogy with the better studied avian migration (e.g. Hollom, 1980), suggests that the Iberian Peninsula (and/or Atlantic islands) may be a more important site of origin for these immigrants than for those of many other species.

S. flaveolum (L.)
This species has long been recognized as a fairly regular immigrant, occurring between July and September. There are also very occasional records of 'ship-assisted' importation (e.g. Paine, 1990). Particularly favourable immigration years include 1837, 1871, 1889, 1900, 1906, 1926, several years during the 1940s - most notably 1945 (Longfield, 1949a), 1953 (Longfield, 1954), 1955 (Gardner, 1956a) and, more recently, 1995 (Silsby, 1995 and in preparation). Records in this country have a general southerly and easterly bias (Fig. 2h), though odd individuals have occurred more widely, and there was also a significant westerly component to part of the 1995 invasion. There is some evidence that small local resident breeding populations may have become established following bigger invasions in the past (e.g. Ellis, 1948; Longfield, 1949a, b; Davies, 1991), but these all died out within 2 or 3 years. In the first half of this century isolated records occurred every few years even outside the peak periods. Until the big invasion year of 1995, however, recent reports of *S. flaveolum* were relatively few, with just a handful of isolated records received since the inauguration of the British Dragonfly Society. While some sightings of what used to be a not-unusual immigrant might not have been reported, the frequency of arrivals to our shore by this species does show signs of declining. This is perhaps a result of population declines in the

parts of the breeding range from which our immigrants originate. It is hoped that the large-scale arrivals of 1995 may signal a reversal of this trend.

As an example of what is likely to become increasingly more possible as interest in dragonflies continues to grow, and with it the number of active observers, the origin of many of the 1995 immigrants to Britain has been determined in outline. The main areas involved appear to be southern Scandinavia and perhaps northern Germany. Firstly, the early days of August also saw the start of a very large-scale invasion of the butterfly *Nymphalis antiopa* (L.) (Camberwell Beauty) to the east coast. This species is generally thought to be a migrant from Scandinavia (Ford, 1957). Immigrant moths of north European origin, e.g. *Drepana curvatula* (Borkhausen) (Dusky Hook-tip; tenth British record) and several *Eurois occulta* (L.) (Great Brocade) were also recorded from Norfolk during early August (Hipperson, 1995), at the same time as dragonflies were arriving in this area. More directly, young adult *S. flaveolum* were traced by general observations and by marking from southern Scandinavia, via Schleswig-Holstein, to the Amsterdam area (in Silsby, 1995). On 31 July 1995 hundreds were seen leaving the shores of Holland, on south-easterly winds. On 1 August 1995 the first arrivals on the east coast of Britain were noted, and numbers built up rapidly at a number of key coastal sites, e.g. Great Yarmouth, Norfolk (Silsby, 1995). Concentrations at the coast lasted for a few days, the individuals then apparently moving further inland in search of breeding-sites (Silsby, 1995). Interestingly, numbers of individuals were also noted at several sites to the west of the country quite early during the influx, some as early as 2 August 1995. These might represent individuals which did not stop on first reaching the British coastline, but it seems more likely that many were individuals of perhaps a more southerly origin which arrived via another route to that described above. No *S. vulgatum*, which accompanied *S. flaveolum* in the east of the country, were noted in the west. Rather, the two new species recorded from Britain in 1995, i.e. *Crocothemis erythraea* and *Sympetrum pedemontanum* (Allioni), were possibly part of the westerly influx. *S. pedemontanum* was not noticed until a few days after the main *Sympetrum* invasion and the exact date of arrival is unknown.

Sympetrum sanguineum (Müller)

As a breeding species in Britain, numbers have fluctuated somewhat this century, perhaps as a response to changes in the extent to which the population is reinforced by immigration (Hammond, 1983; Mendel, 1992). Its resident status has made it difficult to get a full picture of the extent of immigratory movements, though there are numerous records of odd individuals from unexpected localities which are presumed migrants, and the species has been noted from UV light traps on several occasions (e.g. Paine, 1992, 1995). Occasionally individuals have been noted in company with immigrant *S. fonscolombei*, e.g. at Goonhilly Downs on 20 June 1992 (Paine, 1993), or with *S. flaveolum*, e.g. at Covehithe, Suffolk, on 18 September 1926 (Mendel, 1992). These may well represent cases of co-migration. More clear is the mixed immigration of *S. flaveolum*, *S. sanguineum*, *S. vulgatum*, *S. danae* and *S. striolatum* seen on the East Anglian coast during the first few days of August 1995 (Silsby, 1995).

Sympetrum danae (Sulzer)

Contrary to one or two ideas that have crept into some recent British literature (e.g. Benstead, 1994), this species has well-known migratory tendencies. Hundreds were seen on 6 September and 11 September 1954 flying northwest over Tory Island, County Donegal, Ireland (Corbet *et al.*, 1960), these perhaps having originated from further south in Ireland. There are also several records throughout mainland Britain and Ireland and their offshore islands of individuals seen well away from known breeding localities (e.g. Corbet *et al.*, 1960; Milford & Irwin, 1990; Mendel, 1992), and in Norfolk, Suffolk and Kent the species was seen in the company of *S. flaveolum* and *S. vulgatum* during the big invasion of early August 1995 (A. G. Irwin, pers. comm.; Silsby, 1995 and in litt.).

Sympetrum pedemontanum (Allioni)

A male was seen, and photographed, on 16-17 August 1995 on the southern flanks of the Brecon Beacons, north of Ebbw Vale (Silsby, 1995), during the big *Sympetrum* invasion year. This species was considered by Aguilar *et al.* (1986) to be rather sedentary, but this is clearly not completely true.

Leucorrhinia dubia (Vander Linden)

Numbers were reported flying in off the sea at Scarborough, Yorkshire, in 1900 (Longfield, 1949a), and there are unprecedented sight records from Walberswick NNR, Suffolk, on 24 May, 10 June (2♂♂, 1♀?) and 11 June 1992 (Mendel, 1992). These records would seem to indicate that the species is an occasional immigrant to the east coast, but a full picture of migration in *Leucorrhinia* is still forthcoming (see also *L. pectoralis* (Charpentier) below; indeed since none of the reported individuals of *L. dubia* could be examined in close detail, it is possible that other *Leucorrhinia* species such as *L. rubicunda* (L.) are additionally, or even solely, involved here.)

Leucorrhinia pectoralis (Charpentier)

There is a specimen from Sheerness, Kent, in either 1859 (Askew, 1988) or 1860 (Davies, 1991). On the Continent, both *L. pectoralis* and *L. rubicunda* have been noted as showing migratory features under some circumstances (Fraenkel, 1932).

Pantala flavescens (F.)

This renowned migrant, sometimes known as 'The Globe Skimmer', does not occur in Europe as frequently as in other continents (Aguilar *et al.*, 1986), and has been recorded in Britain on only a few occasions. The first record was from the Norfolk Broads in 1823 (Corbet *et al.*, 1960), and Davies (1991) mentions, with few details, a specimen from Kent in 1989. In between, there are two records which definitely relate to 'ship-assisted' individuals; one from Bolton in 1952 (Ford, 1954) and the other from a ship off Devonport in 1955 (Corbet *et al.*, 1960).

Future additions to the list

It is highly unlikely that all the species that will be noted as immigrants to Britain in the coming years are included in the above list, and indeed some other species may have already occurred but have been overlooked. Challenging to identify is *Sympetrum depressiusculum* (Sélys), which although apparently more sedentary than some *Sympetrum* species (Aguilar et *al.*, 1986; Askew, 1988), would seem perhaps as likely an immigrant as *S. pedemontanum*, which has already occurred. *Anax parthenope* (Sélys) is another likely candidate (here requiring care in separation from *Hemianax ephippiger*); it has been recorded once from Holland (Askew, 1988). More speculatively, it should also not be forgotten that, in addition to numerous bird species, various insects of North American origin have been recorded from Britain. These include the lepidopterans *Danaus plexippus* (L.) (Monarch, or Milkweed butterfly), *Cynthia virginiensis* (Drury) (American Painted Lady), *Autographa biloba* (Stephens) and *Utetheisa bella* (L.) (Bretherton, 1983), *Sphinx drupiferarum* Smith (Wild Cherry Sphinx) (Skinner, 1984) and *Agrius cingulatus* (F.) (Sweetpotato Hornworm or Pink-spotted Hawkmoth) (Pittaway, 1993). It may therefore be possible that certain of the more mobile North American Odonata, e.g. *Anax junius*, *Libellula pulchella* Drury or *Tramea lacerata* (Hagen) (Williams, 1965), could also occur sporadically this side of the Atlantic.

In addition to these species it seems probable that, as our knowledge increases, other species with current resident populations in Britain will be found to be reinforced by migration under suitable conditions (e.g. possibly *Aeshna juncea* (L.)). This should help our understanding of the conservation needs of these species. The possible occurrence of immigration amongst the Zygoptera is another area where close observation in the coming years should prove decisive.

Conclusions

In recent years, *Hemianax ephippiger* and *Sympetrum fonscolombei* are two well-recognized extralimital migrant species which have been recorded fairly regularly, and there are also records of *Aeshna affinis*, which has only recently been recognized as a visitor to the British Isles. In addition, two new species were added to the British list in 1995; namely *S. pedemontanum* and *Crocothemis erythraea*. *S. flaveolum* continues to occur, although with the exception of the big invasion of 1995 perhaps at a lower frequency than during some parts of this century. *S. vulgatum* was also recorded in 1995, after a fifty-year absence. Despite the increased level of observation in the last two decades, a number of species recorded as vagrants in the past have not however recurred, possibly because population levels on the Continent have declined. Notable amongst these is *S. meridionale*, but as with other migrant *Sympetrum* species, problems of identification mean it could, however, have been overlooked.

In contrast to the information which is now emerging on those immigrants not normally breeding in Britain, the amount of information relating to migration in species which also show a current breeding population is still very little. Because of their resident status, it could be argued that it is these species which are really most important to us, and it is hoped that much more information on their movements will become available as a result of the current growth in the study of dragonflies. The occurrence, or otherwise, of return migrations might also become apparent for some migrant species.

In addition to understanding the occurrence and nature of migration, there is still much to be learnt about the geographical origins of the species involved. Bretherton (1983), in his analysis of lepidopteran migration, identified five broad areas of origin for immigrants to Britain: (i) Spain and the Atlantic Islands, (ii) areas around and to the south of the central and eastern Mediterranean, (iii) northern and central Europe, perhaps even occasionally from far into Russia, (iv) the near Continent, and rarely (v) North America. He (Bretherton, 1983) believed the greatest number of species, and probably also of individuals, to come from category (i), the southwest Palaearctic region. With the current exception of category (v), North America, there is evidence that dragonfly immigration into Britain and Ireland has broadly similar geographical origins, as reflected in the patterns of distribution of British records for the various immigrant species, the known European and world distributions of these species, and the few examples of influxes whose origins could be traced by meteorological data or more direct observations. The present lack of detailed quantitative knowledge about immigrant dragonflies, particularly those species which also have British resident populations, means that it is, however, difficult to assess which areas are most important as sources of migrants. The strong southwesterly element of lepidopteran immigration is present, but perhaps not quite so obvious, in the case of dragonflies. Most records of migrants, numerically, are currently in the extreme southeast corner of Britain, near the continental mainland. However, it seems probable that this, at least in part, is the result of observer bias (e.g. there has always been a concentration of recorders in this region), and as more data is gathered substantial insights into the true nature of the biology of dragonfly migration should be obtained.

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Colour polymorphism in odonates: females that mimic males?

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Summary

Female colour polymorphism is a widespread characteristic of many Odonata. Fifty-four per cent of the genera of European zygopterans have at least one polychromatic species, although this phenomenon is unequally distributed among families. In this paper we review the adaptive explanations that have been proposed to explain the maintenance of female polychromatism in damselflies, and the field and laboratory experiments that have been done to test these hypotheses. The available data suggest that this polymorphism is maintained by density-dependent factors in *Ischnura* species, but the maintenance of colour morphs in other genera remains poorly understood.

Introduction

In many species of Odonata, a marked polymorphism in coloration exists, restricted to the female sex. One of the female phenotypes is coloured like the conspecific male, whereas one or more additional colour morphs are very different from the male coloration. In the scientific literature male-like females have been named homeochromes, andromorphs, and *androchromotypics, in contrast to heterochromes, heteromorphs and gynochromotypics. Given that this polymorphism is based on colour and not on morphology (Hilton, 1987), we will call these females androchromes (literally, with male colour), and use gynochromes (i.e. with female colour) for those with a different coloration. This polymorphism is very common in Zygoptera. Fifty-four per cent of the genera of European zygopterans have at least one polychromatic species, although this phenomenon is unequally distributed among families (Table 1). Most European Coenagrionidae are polychromatic (65 per cent of species), particularly those of the genera *Ischnura*, *Enallagma*, *Ceriagrion* and *Pyrrhosoma* (see illustrations in Sandhall (1987) and Askew (1988)), while Lestidae are all monochromatic (although Andersson (1994: 317) indicates the opposite). In the three species so far studied, this polymorphism is controlled by a single autosomic gene (not linked to the sex chromosomes), but with expression restricted to the female sex (Johnson, 1964; Johnson,

Table 1. The incidence of female polychromatism in European damselflies.

		Monochromatic species whose female is:		Polymorphic
		androchrome	gynochrome	species
Calopterygidae	*Calopteryx*	-	3	1[a]
Euphaeidae	*Epallage*	1	-	-
Lestidae	*Lestes*	6	-	-
	Sympecma	2	-	-
Platycnemididae	*Platycnemis*	2	1	-
Coenagrionidae	*Pyrrhosoma*	-	-	1
	Erythromma	1[b]	1	-
	Coenagrion	4	2	5
	Cercion	-	1	-
	Enallagma	-	-	2
	Ischnura	-	-	7
	Nehalennia	-	-	1[c]
	Ceriagrion	-	-	1
	totals	16 (38%)	8 (19%)	18 (43%)

[a] *Calopteryx splendens* is polychromatic in some populations, see De Marchi (1990).

[b] In *Erythromma viridulum* two colour phenotypes exist, but we do not know if they are age-related or genetic.

[c] From the descriptions in Askew (1988) and the pictures in Sandhall (1987) we suspect that *Nehalennia speciosa* is polymorphic.

1966; Cordero, 1990a). In some species, the great resemblance that exists between the males and the androchrome females could deceive the most expert odonatologist in a quick examination! In *Ischnura graellsii* (Rambur), a small species extremely common in wide zones of Spain, most of the mature females (about 70 per cent) have brown coloration (gynochrome *infuscans*). The androchrome female represents between 6 and 30 per cent in several populations and its mature coloration is blue as in the males. This species also has gynochrome females of the *aurantiaca* phenotype (normally 4-10 per cent) whose coloration is orange or reddish in the juvenile phases and brown in maturity. In addition, males and the three female morphs each go through several phases of coloration during their life (Cordero, 1990a). This produces an enormous variability of coloration between the adults.

The question is, why do these different female morphs exist? The answer seems to depend on the reproductive behaviour of each species. Three main hypotheses have been proposed to explain this female polymorphism. The first of these is due to Johnson (1975), and we can term it the hypothesis of reproductive isolation. According to this author, the polymorphism is maintained because androchrome females rarely mate with males of another species (they have great reproductive isolation) while gynochromes are commonly involved in matings with heterospecific males. Obviously, this explanation assumes that polymorphic species coexist and cross-mate frequently. This advantage to the androchromes would be counterbalanced by a differential predation pressure: the androchrome females would be more attractive to predators, and this would reduce their longevity.

Robertson (1985) proposed a second explanation. In some species of *Ischnura*, mating is of very long duration (sometimes 6–7 hours). If a single sexual intercourse were enough to enable a female to fertilize all the eggs that she would lay throughout life, the androchrome coloration would be advantageous for 'deceiving' males and so avoiding unnecessary matings (these females could dedicate more time to feeding and oviposition). Males should be unable to distinguish between androchromes and other males. This is the hypothesis of intraspecific mimetism. As a balancing mechanism, Robertson proposed a more intense predation on the androchrome females, due to their more conspicuous coloration.

More recently, Hinnekint (1987) proposed a new explanation, based on density-dependence. For this author, the density of the population is the mechanism that maintains the polymorphism. At high densities (when the sex ratio is more biased toward males), the androchrome morph would have an advantage through not being disturbed by the males, but it would suffer a balancing disadvantage of reduced mating success at low male densities, and some would not be able to mate at all. The situation would be inverse for the gynochrome females. The existence of pluriannual cycles in the density of the population would permit the different morphs to achieve an evolutionary equilibrium (Hinnekint & Dumont, 1989). According to this hypothesis, the survival of the different morphs would be the same, independent of their coloration.

Interspecific matings are very rare in most species: in one population of *Ischnura graellsii* only one has been observed among 297 examined couples, and none among 435 in a second population (Cordero, 1992), and for this reason the first hypothesis is not applicable to most populations. We will therefore concentrate on the remaining two hypotheses: male mimetism and density-dependence.

Are androchromes male mimics?

If males can distinguish between androchrome females and other males, then both hypotheses are no longer applicable.

The assumption that males are unable to distinguish between androchrome females and other males has been tested by several authors using lures. Live or dead animals are presented to field males and the reponse recorded. The proportion of males trying to grasp in tandem the different models gives a measure of the sexual interest in that morph. Males of most species are rather indiscriminate in their mating attempts, but male models are not so attractive as female models. If we compare the response to the androchrome and gynochrome phenotype with that to the male model, then we can test the ability of males to identify androchromes as females. This has been done for several species (see Table 2 for references). In all *Ischnura* species so far studied, androchromes were less attractive to males than gynochromes, even in *I. denticollis* (Burmeister) where androchromes were about 50 per cent of the population (Córdoba Aguilar, 1992), and in *I. elegans* (Vander Linden), where androchromes comprised 55 per cent (Cordero *et al.*, unpublished). Mate-searching males of *Ischnura* are able to distinguish between androchromes and other males (Cordero, 1989). Fincke (1994a) indicates that among coenagrionids the proportion of the total sexual response to females that was directed towards androchromes was positively correlated with the frequency of androchromes in the population, suggesting that the commonest female morph is the most attractive to males. From Table 2 we conclude the opposite: there is not a significant correlation between the percentage of positive responses from males and the frequency of each colour morph in the population (live models: r=0.22, N=15, p=0.425 [excluding *Calopteryx*: r=0.26, N=13, P=0.390]; dead models: r=0.12, N=12, p=0.717). On the other hand, in *Ischnura graellsii*, *I. elegans* and *Ceriagrion tenellum* (Villers), there are two gynochrome female morphs, one of which is very rare but is as attractive to males as the commonest morph. Furthermore, there is a clear difference in male response to live and dead models in *I. elegans* and *C. tenellum*, which indicates that for a perfect imitation, androchromes should not only have male colours but also behave as males. Given this fact, to test the idea that males simply recognize as female the commonest morph in the population, we cannot put together in one comparison (as did Fincke (1994a)) the response

Table 2. Summary of tests of male response to different mature female morphs in polychromatic damselflies, when males are presented with one model per trial. Per cent of male sexual response per model (tandem, tandem attempt or attempted take-over of females already in tandem), excluding males that did not respond to the model (perched or flew away). The asterisk (*) indicates experiments where models were dead. Andro: androchrome, Gyno 1: type 1 gynochrome (most common), Gyno 2: type 2 gynochrome.

	% positive response to				Population frequency			
	Andro	Gyno 1	Gyno 2	male	Andro	Gyno 1	Gyno 2	source
Coenagrionidae								
*Argia vivida**	54	56	-	-	66^{a}	34	-	Conrad & Pritchard (1989)
Ceriagrion tenellum	63	82	83	45	12	62	26	Andrés (unpubl.)
*Cerigrion tenellum**	88	88	96	90	12	62	26	Andrés (unpubl.)
*Enallagma ebrium**	96	100	-	-	07	93	-	Forbes (1994)
Enallagma hageni	40	73	-	05	26	74	-	Fincke (1994)
Ischnura denticollis	49	86	-	00	51^{b}	49	-	Córdoba Aguilar (1992)
Ischnura elegans	33	60	63	37	55	27	18	Cordero *et al.* (unpubl.)
*Ischnura elegans**	83	90	93	83	55	27	18	Cordero *et al.* (unpubl.)
Ischnura graellsii	33	100	78	26	14	76	11	Cordero (1989, 1990a)
*Ischnura ramburi**	55	75	-	55	31	69	-	Robertson (1985)
Calopterygidae								
Calopteryx splendens	85	80	-	-	10	90	-	De Marchi (1990)

[a] largest sample in Conrad & Pritchard (1989)

[b] in litt. 10.2.93

Data for *Argia apicalis* by Bick & Bick (1965) and for *Enallagma boreale* by Forbes (1991) are not included because the experimental procedure was a simultaneous presentation of two female morphs.

of males to live and dead models. The correct way to test that hypothesis is to compare the degree of sexual response in populations of the same species that differ in the relative frequency of female morphs.

Is one mating enough from the female perspective?

Male odonates do not give nutrients to females during copulation. In fact, the only male contribution to reproduction is sperm. Therefore, if *copula* duration is very long, females could be selected to minimize the number of copulations. In *Ischnura graellsii*, the amount of sperm that females receive during copulation is enough to fertilize all the eggs produced during two weeks after mating (Cordero, 1990b). Given that the female lifespan is about one week, this amount of sperm is enough for lifetime egg production. The same is true for *I. verticalis* (Say) (Fincke, 1987).

Is predation phenotype-dependent?

Robertson's hypothesis assumes that male coloration is more conspicuous and therefore attracts predators. This should determine a shorter androchrome (and male) lifespan. Table 3 presents the results of measuring lifespan by means of mark-recapture methods under field conditions. Only in two cases (*I. damula* Calvert, and the 1981 data set for *Enallagma hageni* Walsh) was androchrome survival less than that of gynochromes. We conclude that survivorship is similar in all female colour morphs, probably because mortality factors are independent of female coloration. The only visual predators that regularly feed on damselflies are asilids and frogs, but asilids are not common, and we do not know if they select prey by colour, whereas frogs are very common but unselective: they attack any moving object (see Michiels & Dhondt (1990) and Rehfeldt (1992) for a description of frog predation on ovipositing dragonflies).

Is female mating rate density-dependent?

If copulation depends on the number of male-female encounters, it is easy to see that the more males there are at the mating rendezvous, the greater will be the probability that females will mate. In the low density population of *I. graellsii* studied by Cordero (1992), female mating rate was positively correlated with male numbers, but this did not occur in the high density population (Cordero *et al.*, unpublished). In one population of *I. elegans* there was a positive correlation between female mating rate and male density for androchromes but not for gynochromes (Cordero *et al.*, unpublished). In contrast, neither in *Enallagma hageni* nor in *E. boreale* Sélys, was the daily mating efficiency of females correlated with the density of males (Fincke, 1994a). Therefore, only in some populations is female mating rate density-dependent.

Table 3. Mean lifespan (±SE [N]) of female morphs in polychromatic damselflies. Part of the differences in longevity between species is due to the exclusion of unrecaptured individuals in some species.

	Andro	Gyno 1	Gyno 2	P	Source
Ceriagrion tenellum	2.6±0.2 (31)	2.8±0.1 (149)	2.9±0.1 (56)	0.148[a]	Andrés (unpubl.)
Coenagrion puella	3.4±0.8 (20)	3.1±0.4 (150)	-	0.815[c]	Thompson (1989)
	4.0±0.9 (31)	4.2±0.5 (178)	-	0.898[c]	Thompson (1989)
	7.9±1.6 (11)	5.4±0.3 (163)	-	0.064[c]	Thompson (1989)
Enallagma boreale	3.6±0.5 (53)	3.3±0.4 (66)	-	>0.05[c]	Fincke (1994a)
Enallagma hageni	2.2±0.3 (96)	2.2±0.2 (274)	-	>0.05[c]	Fincke (1994a)
	1.7±0.2 (51)	2.5±0.3 (115)	-	<0.05[c]	Fincke (1994a)
	7.3±1.1 (37)	8.0±1.1 (66)	-	>0.05[c]	Fincke (1994a)
Ischnura damula	3.8	10.0	-	[b]	Johnson (1975)
Ischnura elegans[d]	3.0±0.2 (319)	2.9±0.3 (168)	2.6±0.2 (158)	0.752[a]	Cordero *et al.* (unpubl.)
Ischnura graellsii	8.5±0.9 (34)	6.8±0.3 (153)	6.8±0.9 (16)	0.229[a]	Cordero (1992)
	7.2±1.5 (17)	8.2±0.5 (113)	7.4±1.0 (25)	0.506[a]	Cordero (1992)

[a] Kruskal - Wallis test.

[b] Data are expected lifespan, from estimates of daily survival rate.

[c] t-test.

[d] tenerals excluded due to the impossibility of distinguishing between androchromes and *infuscans* in this colour phase.

Table 4. Mating failure of females in polychromatic damselflies. The table shows the percentage of females that were never seen to mate. Probability after a χ^2 test.

	Sample	Andro	Gyno 1	Gyno 2	P	Source
Ceriagrion tenellum	all females	7.7	9.3	8.5	0.849	Andrés (unpubl.)
Enallagma cyathigerum	all females	30.8	18.8	-	0.379[a]	Garrison (1978)
Enallagma hageni	seen once	56.8	48.1	-	0.385	Fincke (1994a)
	seen> once	50.0	13.8	-	0.007	Fincke (1994a)
Ischnura elegans	young	58.9	20.8	74.8	<0.001	Cordero *et al.* (unpubl.)
	mature	25.7	6.6	11.1	0.003	Cordero *et al.* (unpubl.)
Ischnura graellsii	high density	32.1	41.6	47.4	0.298	Cordero *et al.* (unpubl.)
	low density	77.7	38.0	56.3	0.003	Cordero *et al.* (unpubl.)

[a] from Table 4 in Garrison (1978)

Are there differences in mating success between female morphs?

This is the main question relating to the maintenance of colour polymorphism. What is really important is not the number of matings females obtain, but the proportion of females that never mate. Several estimates of this mating failure are presented in Table 4. In one population of *Ischnura graellsii*, and another of *I. elegans*, the proportion of androchrome females that were never seen to mate was significantly higher than for gynochromes. The same was true for *Enallagma hageni* (Fincke, 1994a), but not for *E. cyathigerum* (Charpentier) (Garrison, 1978), or *Ceriagrion tenellum* (Andrés, unpublished). In *E. hageni*, the differences were probably due to the shorter lifespan of androchromes in the group of recaptured females, and not to their colour, but in *Ischnura* the failure of androchromes seems real, because they did not have a shorter lifespan (Cordero et *al*., unpublished). In *Coenagrion puella* (L.) the lifetime number of clutches was similar for andro- and gynochromes (Thompson, 1989).

Body size

Body size is a phenotypic variable that has an important influence on female fecundity. In most animals, larger females produce more eggs (Labarbera, 1989) and this is also true for damselflies (Gribbin & Thompson, 1990; Cordero, 1991). Table 5 presents body size comparisons between female phenotypes in the species that have been studied to date. In most species, all phenotypes have similar body size, but in one population of *I. graellsii* and another of *I. elegans*, androchromes were larger than gynochromes. However, longevity is a complicating factor in the size/fecundity relationship (Leather, 1988). Longevity, and the factors affecting it, seems to be the single most important influence on damselfly fecundity: 70 per cent of variance in female reproductive success in *Coenagrion puella* was due to differences in survival (Banks & Thompson, 1987).

Table 5. Body size comparisons (mean ±SE (N) in mm) of female morphs in polychromatic damselflies. When several values are presented for one species, averages refer to different samples, either from different populations or from different sets from the same population. P after a t-test.

	Andro	Gyno 1	Gyno 2	P (andro-gyno)	Source
Ceriagrion tenellum [a]	32.67±0.13 (53)	32.56±0.15 (242)	32.77±0.09 (85)	0.856	Andrés (unpubl.)
Coenagrion puella [b]	22.73±0.12 (20)	22.74±0.05 (150)	-	0.931	Thompson (1989)
	22.58±0.09 (31)	22.73±005 (178)	-	0.215	Thompson (1989)
	22.27±0.25 (11)	21.98±0.05 (163)	-	0.142	Thompson (1989)
Enallagma boreale [b]	19.96±0.2 (25)	19.53±0.2 (19)	-	>0.05	Fincke (1994a)
	12.4±0.08 (31)	12.5±0.12 (23)	-	0.70	Forbes (1994a)
Enallagma hageni [b]	18.26±0.1 (77)	18.21±0.04 (228)	-	>0.05	Fincke (1994a)
Ischnura elegans [a]	29.96±0.13 (270)	29.57±0.17 (120)	29.67±0.19 (146)	0.007	Cordero et *al.* (unpubl.)
Ischnura graellsii [a]	27.84±0.11 (84)	27.47±0.05 (452)	27.50±0.17 (62)	0.007	Cordero (1992)
	28.33±0.11 (98)	28.23±0.07 (297)	28.02±0.15 (55)	0.304	Cordero (1992)
	28.73±0.22 (21)	28.53±0.10 (79)	28.99±0.14 (20)	0.607	Cordero (1992)

[a] body length

[b] wing length

Conrad & Pritchard (1989) compared wing length between 11 androchromes and 11 gynochromes of *Argia vivida*, and they did not find significant differences, but averages were not presented.

Discussion

The results of investigations carried out in several natural populations suggest that the density-dependent hypothesis is the most likely explanation for the maintenance of female colour polymorphism in *Ischnura graellsii* and *I. elegans*. We therefore conclude that, at least in these species, the male coloration of androchromes confers some advantages under conditions of high male density. If this explanation is correct, then we should find a higher proportion of androchrome females in populations of high density than in populations of low density. The comparison of the frequencies of the different types of females in five natural populations of *I. graellsii*, supports this interpretation (Cordero, 1990a): the androchrome females represented only seven per cent in a population of low density and 18-30 per cent at high density. A similar result has been found in *Nehalennia irene* Hagen, where frequency of androchromes in several natural populations was positively correlated with an index of male density (Forbes *et al.*, 1995).

Recently Fincke (1994a) has analysed the maintenance of female polymorphism in *Enallagma hageni* and *E. boreale*, and arrived at the conclusion that there are no fitness differences between the two types of females of these species. This means that it has not been possible to reject the null hypothesis (i.e. that this colour polymorphism is maintained by chance) and the fact that a female has blue or brown coloration does not matter. The problem with this interpretation is that the available hypotheses are not valid for *Enallagma*, and Fincke tested them without testing their assumptions. In fact, androchrome *Enallagma* are not a perfect mimic of conspecific males and so cannot avoid male interest: males of *Enallagma* do distinguish between androchromes and other males (Fincke, 1994a; Forbes & Teather, 1994). Also, and more important, due to underwater oviposition in this genus, additional matings are advantageous for all female morphs, because females benefit from male help in escaping from the surface film (Fincke, 1986; Miller, 1990). Therefore, avoiding additional matings (as androchrome *Ischnura* females seem to do) does not confer any benefit on androchrome *Enallagma* females.

Robinson & Allgeyer (in press) reviewed the life-histories of seventeen *Ischnura* species from North America, Europe and Asia and found that these species can be grouped into three categories: small monandrous species, large polyandrous species without tandem guarding and polyandrous species with tandem oviposition. Of these seventeen species, all but four are polychromatic, and all four monochromatic species belong to the monandrous group. This fact suggests a relationship between the degree of polygamy and female polychromatism. They propose that the evolution of female monandry neutralized the selective advantage of colour patterns and for this reason fixation has occurred in this group (two of the monochromatic species have only androchrome females and the remaining two species only gynochrome females). The existence of polychromatic females in all polyandrous species supports the view that this polychromatism is not neutral, because if female morphs were maintained only by random factors, at least in some populations fixation should have occurred (Golding, 1992). In our experience all populations of *I. graellsii* and *I. elegans* are polychromàtic, although some populations of *I. pumilio* (Charpentier) (the only European *Ischnura* whose androchromes are not a perfect mimic of males) have only gynochrome females (e.g. in Britain, Corbet et *al.* (1960: 23)).

Two facts remain unexplained: the larger body size of androchromes in some populations and the existence of more than one gynochrome morph in many species. Cordero (1992) proposed that the individuals bearing the androchrome allele could be more aggressive during their larval stages, defending the best feeding sites and therefore achieving greater size. It is also possible that such a small body size difference as was detected among female morphs in *I. graellsii* and *I. elegans* does not have any important evolutionary effect. A study of more populations is required.

New explanations are needed for the existence of two (or even three) different gynochrome females in some species. We propose the following ideas: differential survivorship or competitive abilities during the larval or immature stages, differential habitat selection either by larvae or adults, differential dispersal tendencies (one morph could be better at finding new habitats), differential fecundity, and, of course, the neutral hypothesis.

Polymorphism of coloration has been a classic example of the action of natural selection; the case of industrial melanism in the Peppered Moth (*Biston betularia*) has been widely used as an example in biology text books. This emphasis on characters with great visual impact could lead to an erroneous interpretation and produce the generalization that all polymorphisms of coloration are maintained by the action of natural selection (Oxford, 1993). Several cases exist where colour polymorphism seems to be maintained by factors that have nothing to do with natural selection, such as random changes in the frequencies of the genes controlling the character in question, migration from populations with different gene frequencies, and so on. Even in *Ischnura graellsii*, the species that has been studied most intensively from the point of view of its polymorphic coloration, the situation is not fully clear, and perhaps, after all, random factors are the most important in the maintenance of the polymorphism, as Fincke (1994b) suggests. Certainly, this interesting topic will continue to inspire new studies until it is possible to determine the advantages and disadvantages of each coloration with greater precision. This intriguing phenomenon will be clarified only after the study of a greater number of species - we suggest *Pyrrhosoma nymphula* (Sulzer) as a good candidate.

Acknowledgements

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Mortality of emerging *Pyrrhosoma nymphula* (Sulzer) at a garden pond

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Observations in 1995

A surprisingly high 83 per cent non-predatory mortality of emerging *Pyrrhosoma nymphula* (Sulzer) (Large Red Damselfly) was recorded between 5 and 8 May 1995 at a garden pond in Fisherbridge, Weymouth, Dorset. The weather was very sunny and dry with occasional light breezes.

The pond is in a sunny situation in a private garden. It was constructed of brick about eight years ago, measures 2.8 x 1.9m with a depth of 0.4m, and is overfull of vegetation, mainly water weed (*Elodea*), water-lilies and four clumps of Yellow Flag (*Iris pseudacorus*). Goldfish and frogs breed in the pond which also supports a population of *P. nymphula*. In 1995, no other species of damselfly was present.

Over the four days of observation, 23 larvae of *P. nymphula* crawled up the central ribs of *Iris* leaves to heights of between 50 and 150mm above the water. During various stages of emergence, 19 of these fell off, of which 18 drowned and one died on a lily leaf. The *Iris* leaves were too wide for the legs of the centrally-positioned larvae to clasp both edges, so that larvae and emerging damselflies were totally reliant on their tarsal claws for gripping the shiny surfaces of the leaves. Although a few were blown off, most simply fell whilst extricating bodies and wings from the exuviae. Two of the four larvae which successfully developed into adults were in the centres of *Iris* leaves; one of these was helped by being in some spiderweb threads, and the other two were on small *Iris* leaves that were narrow enough for the larvae to obtain a grasp around the edges. Some of the fallen damselflies on the water surface had fully extricated themselves but died afterwards. It was surprising that the one on a dry lily leaf ceased trying to emerge and died despite being put on its feet; perhaps an upright support is necessary.

Climatic and other factors, such as undernourishment, may have been partly responsible, but it is believed that the selection of a too-wide emergence site was the principal reason for the emergence failure. No other type of marginal vegetation was available, but it is difficult to understand why the larvae positioned themselves so badly on the *Iris* leaves when, by climbing higher, they could have reached the tapering apices of the leaves.

In the BDS handbook *Dig a Pond for Dragonflies*, *Iris pseudacorus* is recommended as a marginal plant. The observations described above indicate that it should not be the only marginal plant in small garden ponds. During the four days a maximum of eight adult *P. nymphula* were observed at any one time, and many instances of oviposition behaviour were noted. The species seems to cope with the mortality rate and *Iris*.

In an attempt to avoid a recurrence of this high 1995 mortality rate, several narrow-leaved marginals were planted in the pond and the fish are now fed. Also, sixteen green garden sticks, of about 5mm diameter, were pushed into the roots of all the pond plants at various angles from vertical to about 30° to the water surface.

Observations in 1996

Between mid-April and mid-June 1996, the garden pond was inspected on most days but numbers emerging were not similar to those of 1995. The maximum number of emergences recorded over a comparable 4-day period, between 25 and 28 May, was five: three *P. nymphula* and two unexpected *Ischnura elegans* (Vander Linden) (Blue-tailed Damselfly). No non-predatory mortalities were observed. Over the 8-week period, a total of 14 empty exuviae were recorded: seven of these were on the *Iris pseudacorus*, six on the inclined garden sticks and one in the pond water. Only one partially-emerged *P. nymphula* was found dead in the water. The first four weeks of this period were cold, with an excessive amount of wind and rain, and the first emergence of *P. nymphula* did not occur until 25 May. On many occasions during early May, larvae were seen at the water surface starting to climb up the leaves or sticks but returning to the water as if anticipating the ensuing bad weather.

Discussion

The numbers and mortality rate for 1996 cannot be properly compared to those of 1995 because of the differences in the weather, observation times, emergence options and the extra species present. On only one occasion was a mating couple of *P. nymphula* seen to oviposit in the pond. In 1996 the larvae appeared to be larger and the *Iris* leaves narrower, possibly negating the need for the garden sticks. However the sticks and *Iris* leaves were both well used. Interestingly, no emerging damselfly was found on the new narrow-leaved marginal plants.

Notes and observations

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My thanks as usual to those who have contributed. Reports of local societies are a rich source of interesting but little publicized information. I include here a few notes that I have come across. Could I please have all contributions for the next issue by 10 January 1997.

Mixed pairing

On 21 June 1995 a male Blue-tailed Damselfly (*Ischnura elegans*) and female Red-eyed Damselfly (*Erythromma najas*) were found in tandem at Bunkers Hill, Norfolk. (A)

Dragonfly as prey and predator

On 8 August 1995 at Lound Waterworks, Suffolk, a live female Ruddy Darter (*Sympetrum sanguineum*) was found spread-eagled in a spider's web. It was photographed and then released. (A)

At Upton Fen, Norfolk, on 14 June 1996 a female Hairy Dragonfly (*Brachytron pratense*) snatched a large orb spider from its web in dyke-edge reeds, but the weight proved too much and she rapidly lost height and landed in the dyke, from which she was recovered and placed on pathside vegetation to dry and warm up. (E)

Dragonflies at light and after dark

A light is usually left on all night at the rear of a house in Hopton, Norfolk, and on two occasions in recent years a Brown Hawker (*Aeshna grandis*) has been found at rest beside the light which also attracts many moths. (A)

A dragonfly found in a moth trap at Portland Bill Observatory on 11 August 1983 was photographed and identified as a female Vagrant Emperor (*Hemianax ephippiger*). (B)

On the evening of 12 July 1995, at the Nene Washes reserve, a Brown Hawker (*Aeshna grandis*) was hawking along a field margin until at least 2210h, by which time it was so dark that its presence could be confirmed only by the sound of its wings. (D)

At 0530h on 18 July 1995 in Peterborough, Cambridgeshire, after a warm and humid night and immediately after a heavy downpour, a Brown Hawker (*Aeshna grandis*) was seen hawking along the side of factory buildings. (D)

Migration

On 22 August 1985, eighteen Brown Hawkers (*Aeshna grandis*) were found resting on low-growing shrubs along Corton Cliffs, Suffolk. As the observer prepared to photograph them they all rose up as one and flew off. (A)

Behaviour

At Caster Haylands NNR, Cambridgeshire, on 26 July 1995, a male Emperor (*Anax imperator*) was defending its territory when it attacked a Southern Hawker (*Aeshna cyanea*), holding it in the tandem position. After a few seconds they crashed down into long grass at the pond edge where they remained for about two minutes, the *Anax* retaining its hold on the *Aeshna*. They then separated and flew up, the *Aeshna* flying away seemingly unharmed. (D)

On 31 May 1995, at Aldeby Pits, Suffolk, about 50 teneral male and female Scarce Chaser (*Libellula fulva*) were seen. A newly-emerged female was seen to have a malformed hind-wing which resulted in her flying around in circles. (A)

Miscellaneous

On 18 June 1996 exuviae of an Emperor (*Anax imperator*) was found on the trunk of a Lombardy Poplar in the grounds of the Natural History Museum, London. It was on the north-facing side about 7 feet up; the tree itself is about 100 feet from the nearest pond. To get to the tree the larva had crossed a grassy meadow and passed several small trees, a fence, and large amounts of emergent vegetation surrounding the pond. (C)

On 9 June 1996 a tandem pair of Red-eyed Damselfly (*Erythromma najas*) were watched entering the water at Drake's Marsh, Norfolk, and ovipositing in a stem of Broad-leaved Pondweed (*Potamogeton natans*), remaining submerged for 27 minutes. On re-emerging they immediately separated and flew off. (E)

During various visits to Lound Waterworks, Suffolk in 1995, many trees were found to bear the spent exuviae of Common Darter (*Sympetrum striolatum*). Some were about 15 metres from the waters' edge and a further 140cm up the tree trunks, amounting to a considerable distance negotiated over dry land. (A)

Sources

(A) *Local dragonflies*, Tony Brown, Great Yarmouth Naturalists' Society, 1995.
(B) *The dragonflies of Portland Bill*, Portland Bird Observatory Report 1995.
(C) Stephen Brooks, Natural History Museum, Cromwell Road, London SW7 5BD.
(D) Andrew Frost, 28 Pheasant Way, Yaxley, Peterborough, Cambridgeshire PE7 3HN.
(E) Phil Heath, 73 Cozens Road, Norwich, Norfolk NR1 1JP.

Postcript

Dragonfly movement and migration by A. J. Parr

Since this article was prepared for publication, some significant observations have been made, and the author has requested the insertion of the following note added in proof.

Late records for 1995 include more *Sympetrum vulgatum* on the east coast, and the first record of *S. flaveolum* from Ireland. The sighting in Gloucestershire of *Anax parthenope* in June 1994 was reported to me in 1996 by John Phillips.

(An account of the circumstances relating to this latter exciting addition to the list of British species will be published in a forthcoming isssue of this journal – Eds).

INSTRUCTIONS TO AUTHORS

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.

Manuscripts should be typewritten using black ribbon, double-spaced, on one side of the page only and with margins at least 25 mm at the left, top and bottom; text pages should be numbered. Footnotes should be avoided.

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

Use of these terms is acceptable: 'exuviae' for cast skin or skins (singular and plural); '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 1994.

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, Colchester. 116 pp.

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

Titles of journals should be written out in full.

Tables should be typed, each on a separate, unnumbered page.

Legends for illustrations should be typed together in sequence on a single unnumbered page.

Illustrations (figures) should be prepared in black ink, and scaled to allow a reduction of 1.5 to 3 times. Lettering should be neat and uniform.

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	ANISOPTERA	DRAGONFLIES
Calopteryx virgo	Beautiful Demoiselle	*Aeshna caerulea*	Azure Hawker
Calopteryx splendens	Banded Demoiselle	*Aeshna juncea*	Common Hawker
Lestes sponsa	Emerald Damselfly	*Aeshna mixta*	Migrant Hawker
Lestes dryas	Scarce Emerald Damselfly	*Aeshna cyanea*	Southern Hawker
Platycnemis pennipes	White-legged Damselfly	*Aeshna grandis*	Brown Hawker
Pyrrhosoma nymphula	Large Red Damselfly	*Anaciaeschna isosceles*	Norfolk Hawker
Erythromma najas	Red-eyed Damselfly	*Anax imperator*	Emperor Dragonfly
Coenagrion mercuriale	Southern Damselfly	*Hemianax ephippiger*	Vagrant Emperor Dragonfly
Coenagrion scitulum	Dainty Damselfly	*Brachytron pratense*	Hairy Dragonfly
Coenagrion hastulatum	Northern Damselfly	*Gomphus vulgatissimus*	Club-tailed Dragonfly
Coenagrion lunulatum	Irish Damselfly	*Cordulegaster boltonii*	Golden-ringed Dragonfly
Coenagrion armatum	Norfolk Damselfly	*Cordulia aenea*	Downy Emerald
Coenagrion puella	Azure Damselfly	*Somatochlora metallica*	Brilliant Emerald
Coenagrion pulchellum	Variable Damselfly	*Somatochlora arctica*	Northern Emerald
Enallagma cyathigerum	Common Blue Damselfly	*Oxygastra curtisii*	Orange-spotted Emerald
Ischnura pumilio	Scarce Blue-tailed Damselfly	*Libellula quadrimaculata*	Four-spotted Chaser
Ischnura elegans	Blue-tailed Damselfly	*Libellula fulva*	Scarce Chaser
Ceriagrion tenellum	Small Red Damselfly	*Libellula depressa*	Broad-bodied Chaser
		Orthetrum cancellatum	Black-tailed Skimmer
		Orthetrum coerulescens	Keeled Skimmer
		Sympetrum striolatum	Common Darter
		Sympetrum nigrescens	Highland Darter
		Sympetrum fonscolombei	Red-veined Darter
		Sympetrum flaveolum	Yellow-winged Darter
		Sympetrum sanguineum	Ruddy Darter
		Sympetrum danae	Black Darter
		Leucorrhinia dubia	White-faced Darter

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