

***Dolomedes plantarius* (Clerck, 1757) (Araneae: Pisauridae): a reassessment of its ecology and distribution in Europe, with comments on its history at Redgrave and Lopham Fen, England**

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Summary

The frequent claims that the population of *Dolomedes plantarius* is declining in numbers in Europe due to loss of habitat is not supported by evidence. For many years, information on this species was unreliable due to taxonomic confusion with *D. fimbriatus* and because adults of both species are identical and cannot be separated in the field unless collected for examination. Greater interest in *D. plantarius* in recent years has revealed new records from many European countries, though data are still inadequate for a reliable assessment of its distribution and status. Available information on its behaviour, habitat and ecology in Europe is summarized. The conservation problems of *D. plantarius* at Redgrave and Lopham Fen, England, are discussed in relation to its status elsewhere.

Introduction

For many years, *Dolomedes plantarius* (Clerck, 1757) has been an enigmatic species because of confusion with its close relative *D. fimbriatus* (Clerck, 1757), and the lack of information on the habitat and distribution of both species. The genus *Dolomedes* was created by Latreille in 1804. During the following years, numerous authors confused its taxonomy by describing different colour forms as new species. Bonnet (1930, 1956) recognized that probably only *D. plantarius* and *D. fimbriatus* were known in Europe but also included the doubtful *D. pratensis* Risso, 1826, which was not accepted by Platnick (1989). *D. italicus* Thorell, 1875 was shown to be a synonym of *D. fimbriatus* by Renner (1987).

In the early years of the 1900s there was also widespread confusion about the distribution of *D. plantarius* and *D. fimbriatus* because the former was recorded as a variety or subspecies of the latter (e.g. Braendegaard 1932, cited in Gajdoš *et al.* 2000). The distinguished Finnish arachnologist P. Palmgren (1939) also held this view, and wrote that the ‘variety’ *plantarius* was about a quarter as frequent as the more common *fimbriatus*. Bonnet (1956) admitted that, of the numerous publications he listed referring to *D. fimbriatus*, many might include *D. plantarius*. The very detailed study by Bonnet (1930) was made during the 1920s and, although he clearly described the morphological differences between *D. plantarius* and *D. fimbriatus*, he seemed to assume that both had the same ecology, behaviour and lifestyle. His material for captive breeding of *D. plantarius* came from the Canal du Midi in Toulouse, where he lived, but *D. fimbriatus* was obtained from ditches around the Lac de Lourdes, 150 km further west. He collected 754 adults of *D. plantarius* and reared 177 from egg stage to adult, but only 47 *D. fimbriatus*, and it is not clear from his account

whether he made similar breeding experiments with the latter.

Bonnet (1930) described an attempt to get the two species to interbreed using a *D. plantarius* male with a *D. fimbriatus* female, and vice-versa, but both were unsuccessful as the spiders avoided each other. This is surprising as the two species are so closely related.

Plant names mentioned in the text follow Stace (1997).

The status of *D. plantarius* in Europe

D. plantarius has been described by Kennett (1985) and several other authors as a ‘rare, declining species which has lost much of its European range’, but this assumes that its actual distribution was known long ago. There is no evidence to support this. Numerous new localities have been reported in recent years. Prior to 1956 (Duffey 1958) it was not known in Britain, but three populations are now recorded: Pevensey Levels and Redgrave and Lopham Fen in England, and Crymlyn Bog in South Wales. Others have been rediscovered in Denmark, Belgium, France, Germany, Austria, the Netherlands, Switzerland, Sweden, Lithuania, Poland, Estonia and the Czech Republic (Steinberger 1986; Renner 1987; Vilbaste 1987; Terhivuo 1993; Iorio & Villepoux 2002; van Helsdingen 2006). A good example of the discovery of new sites was given to me by Dr P. van Helsdingen of the Netherlands. In 1990 (pers. comm.) he wrote ‘I had always assumed that *D. plantarius* had disappeared from our country’. In the following years he conducted extensive field work on the peatland fens in the central region of the Netherlands and was able to record 17 sites (van Helsdingen 2006). It was so abundant at some sites that he found 50 immature specimens in 3 m². The present greater interest in this species will no doubt reveal more new sites in the future. For example, in France, where members of the Association Française d’Arachnologie have recorded new sites in 2011, there are extensive areas of lakes which arachnologists have not yet searched. In the Sologne area south of Orléans there are over 2000 étangs 5–55 ha in area (Hesse 1979). An ‘étang’ is defined by Mulhauser & Monnier (1995) as a shallow lake in which aquatic vegetation may grow anywhere. Similar areas occur in La Brenne (Indre), where 1200 étangs are recorded (Trotignon & Williams 1994) and in Les Dombes (Ain). In addition, France has about one million ponds of 0.5 ha and 600,000 of up to 1 km² (Boissinot & Vaudelet 2011), some of which are probably included in the regions already mentioned. Most of the above are man-made for fish farming, to attract game, or for agricultural purposes. See Appendix 1 for further comment on the assessment of habitat loss.

It is possible that new collectors who are not familiar with the history of these two species may misidentify specimens by not taking enough care to examine adult genitalia under a microscope, or by assuming that immature *Dolomedes* are *plantarius* because the specimens are all brown, without pale lateral stripes. Until recently, this was regarded as a reliable identification, but it is now known that *D. fimbriatus* also has an all-brown colour form. In 1992, Dr P. Merrett (pers. comm.) was travelling in the Haute Savoie, France, with J. and F. Murphy and stopped by a marshy area

to collect spiders. They came across a few immature *Dolomedes* which were all brown without stripes, and assumed they were *plantarius*. They collected a few specimens and took them home to rear to the adult stage, and were very surprised to find that they were *D. fimbriatus*. Later, I found two adult female *D. fimbriatus* which were without pale lateral stripes on a garden pond in the Corrèze, France, where we lived for five years. So far, no records of all-brown *D. fimbriatus* have been reported from other European countries, although the late D. Clark (pers. comm.) reported that the abdominal lateral stripes were sometimes missing on British *D. fimbriatus*, but were always present on the cephalothorax.

Bonnet (1930) did not comment on the colour forms of *D. fimbriatus*, but described in detail the variations of *D. plantarius*. The stripes may be thick or thin, white, yellow or very faint, broken or interrupted, present on the abdomen but not on the cephalothorax, or *vice versa*. Bonnet did not comment on the proportion of his *D. plantarius* which were all brown. Estimates of this colour form have been made in Britain, but they are very variable, possibly because the counts include mainly the immature stages whose developing stripes may be faint or difficult to see by field survey. Jones (1992) estimated 28% for the large Pevensy population. At Redgrave and Lopham Fen Kennett (1985) recorded 2.4% from 1231 specimens and quoted 6.5% from D. Orr (pers. comm.). My own estimate from 127 specimens was 11.8%, and A. Thornhill (pers. comm.) thought it was between 10% and 20%. Future surveys should include separate estimates for adult specimens.

Ecological characteristics of the two *Dolomedes* species

Dispersal behaviour

This aspect of *D. plantarius* ecology has not yet been investigated systematically, but Dr Helen Smith (www.Dolomedes.org.uk) agreed that there is no evidence of ballooning in nature, but has seen what appears to be the beginning of tiptoe behaviour by juvenile *D. plantarius* and provided an illustration. It is not the typical ballooning behaviour, as the abdomen is not directed upwards and there are no floating strands of silk from the spinners. *D. fimbriatus* would appear to be a better candidate as it is often recorded away from water by sweeping in meadows, hedgerows, and tree foliage, but aerial dispersal has not yet been reported. The distances travelled from marsh or water, as I measured in France, were relatively short – 100–200 m – which is not typical of true aeronauts.

The strict attachment to water surfaces by *D. plantarius*, and especially large, still water, whether in the form of lakes, rivers, and canals as described in Germany (Harms, Dunlop & Schütt 2009), or interconnected waterways as at Pevensy Levels (Jones 1992), may indicate that *D. plantarius* has developed a dispersal technique by water, as suggested by Carico (1973) for an American *Dolomedes* sp.

In North America, there are nine species of *Dolomedes* (Carico 1973), but the two European species *D. plantarius* and *D. fimbriatus* do not occur. The most widespread and common species is *D. triton*, which has habitat similarities

to *D. plantarius*. Carico (1973) described its habitat as “amongst emergent vegetation in ponds, lakes and slow-moving streams which are characterized by relatively quiet water”. He discussed aerial dispersal and said he has not observed it, and added “whether ballooning is a generic characteristic of *Dolomedes* is unknown”. Frost (2005) described ballooning behaviour by *D. triton* in the laboratory. The juveniles were placed on a constructed platform next to an adjustable wind source and temperature. She reported that “more spiderlings ballooned at the highest temperatures, 30–32°C” but there were “far fewer successful ballooning attempts at the next lowest temperature, a mere 3–5°C cooler”. Ballooning behaviour peaked five days after hatch and occurred at the lowest wind speed tested, 0.1–1 ms⁻¹. This account is very incomplete, and one wonders why such high temperatures were necessary (30°C or more) before ballooning became active. In nature, convection currents generated by temperature determine ballooning (Duffey 1956, 1963; van Wingerden 1980), unlike the laboratory tests described in which wind speed and temperature appear to have operated independently.

The laboratory work on *D. triton* suggests that the juveniles start ballooning 3–5 days after hatching. Bonnet (1930) described *D. plantarius* in France as remaining in a tight bunch for 3–4 days before moving down towards the water, and no ballooning was seen. However, E. Jones (pers. comm.) had a strange and unexplained experience with *D. plantarius*. He described a hatch of this species introduced (under licence) to his garden pond. The young remained in a tight bunch for 25 days before dispersing. I had a similar experience (unpublished) in 1960 with a female and egg-sac introduced to a garden pond (before legal protection). The young formed a tight bunch in the nursery web. Immediately afterwards I was away for nearly one month and, on my return, the tight bunch was still there unchanged. I gently touched it and the young dispersed quite slowly into the vegetation close to the water surface. It is possible that the absence of a fully formed nursery web, which could not be transported to the garden ponds, inhibited dispersal activity because there was no web framework for the juveniles to climb onto as they do in nature.

In New Zealand, *D. minor* is of special interest because it is entirely terrestrial and has no attachment to water. It is widely distributed wherever there is cover for its nursery web, which is a conspicuous creamy-white colour. I have seen numerous webs by roadsides, in gardens, and in open areas with tall plants and bushes. It would seem a good candidate for active dispersal behaviour but the most distinguished New Zealand arachnologists (Forster & Forster 1999) stated that aerial dispersal is very rare in New Zealand, having only seen it once in 30 years, for the mynogenine group of linyphiid spiders. New Zealand is narrow and ocean-bound, over 1600 km from the nearest land. The Forsters commented that selection pressures would favour those native species which do not participate in mass ballooning. Nevertheless, the New Zealand arachnologist Dr Mike Fitzgerald told me that he has seen aerial dispersal several times by second instar *D. minor*, which frequently breeds in his garden.

We do not yet know enough about the ecology and behaviour of *D. plantarius* to speculate on the selection pressures

which have determined its method of dispersal. Ballooning by small linyphiids is typically regarded as long-distance travel because they have been collected in nets on the masts of ships far out to sea (Hardy & Milne 1937), in nets towed by aircraft (Freeman 1946), and by swifts *Apus apus* (Owen & Le Gros 1954).

For the immature stages of larger spiders, shorter distance travel would be safer and may provide a better chance of finding a new habitat location. I have noticed that immature *Xysticus* ballooning in Britain, and especially in France, were often appreciably larger than the typical linyphiids. Could the extra weight result in short-distance ballooning? The dispersal behaviour of spiders of different sizes would make a rewarding study for a student looking for a research project.

Water quality

The importance of a habitat with clean permanent water has been stressed by Bonnet (1930), Jones (1992), van Helsdingen (1993), Duffey (1995), Smith (2000), and Harms, Dunlop & Schütt (2009). Bonnet (1949, 1952) described his own experience of this problem. From 1923 to 1928 his supply of *D. plantarius* came from the Canal du Midi. After 1930, he was busy with the *Bibliographia Araneorum* (Bonnet 1956) and did not visit the Canal again until the late 1940s. He wrote that, in the 1920s, the canal was little disturbed because canal boats were few and drawn slowly by horses. The water was clear and clean, and the marginal vegetation undisturbed. In the late 1940s, barges were more frequent and driven by engines, so were faster, and the propeller blades churned up the muddy bottoms. Fuel oil contaminated the water, which was continually disturbed and discoloured. He made a thorough search of his former collecting area where *D. plantarius* had been so abundant, but failed to find any evidence of the spider. In 1952, he explored the ditches by the Lac des Lourdes, where he had formerly collected *D. fimbriatus* (Bonnet 1952). The ditches were dry and invaded by bramble *Rubus* sp., and no *Dolomedes* were found. Harms, Dunlop & Schütt (2009) emphasized the importance of permanent water because waterways which dry out seasonally seldom support populations of *D. plantarius*. On my first visit in 1990 to the Grangettes nature reserve in Switzerland, where the River Rhone empties into Lac Léman, I found an extensive marsh with water about 25 cm deep and an abundance of a tussocky *Carex* sp. *D. plantarius* was everywhere. On a second visit a year or two later, the marsh had no standing water and not a single *D. plantarius* was seen. The spider returned later on as conditions improved again (Neet & Delarze 1992).

Studies by Růžicka (1998) and Holec (2000) of the spiders on and around the numerous large fish ponds in the Czech Republic have demonstrated an interesting separation by habitat of *D. plantarius* and *D. fimbriatus*. The former species was taken only on the water surface among aquatic plants and in the marginal vegetation, while the latter was largely confined to the terrestrial, humid vegetation of grasses and sedges around the lakes, and extending into *Quercus* sp., *Pinus sylvestris* and *Alnus glutinosus* woodland. However, at three locations, both *D. plantarius* and

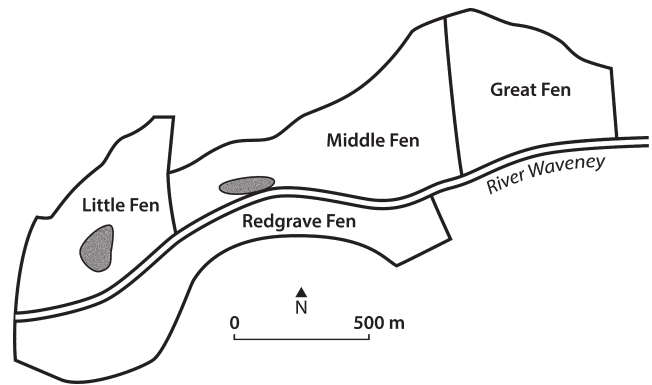


Fig. 1: Redgrave and Lopham Fen, England; distribution of *D. plantarius* in the 1990s. Modified from a map compiled by Dr Helen Smith for the Suffolk Wildlife Trust.

D. fimbriatus were taken in the transition zone of marginal vegetation and in floating pitfall traps. I do not know of a similar example in Europe of these two species living close together, though it has sometimes been suspected. Proof of both species having overlapping distributions depends on the reliable identification of both sexes of each species.

M. Holec (pers. comm.) told me that management of the fish ponds sometimes requires drainage in the winter months, but never in the summer. If *D. plantarius* hibernates in the vegetation, this may not affect the population. One December in the late 1970s, I searched the damp litter layer of marsh vegetation about 2 m from a small pond in Redgrave and Lopham Fen and came across one half-grown *D. plantarius* which was very lethargic and could be handled without it attempting to escape.

The influence of pH

Numerous authors have described the typical habitat of *D. plantarius* as mesotrophic–eutrophic, and *D. fimbriatus* as oligotrophic (Renner, 1987; Duffey 1995; Holec 2000; van Helsdingen 2006; Harms, Dunlop & Schütt 2009; J. Buchar, pers. comm.). This generalization is supported by much field observation, but probably is less true for *D. fimbriatus*, which may be found in bogs with a low pH, even at an altitude of over 1000 m in Switzerland (C. Neet, pers. comm.), but is also widely distributed in more eutrophic wet lowland grasslands and marshes. The extensive distribution of this species in much of Europe suggests that it is less sensitive to pH values, although clear evidence has not yet been established.

On the other hand, the far fewer records of *D. plantarius* are mostly associated with mesotrophic–eutrophic conditions. pH values have seldom been measured, but there are some data for Pevensy Levels. Between 1987 and 1991 the pH of the water channels was measured on 52 occasions (Emery 1991). The range varied from 6.8 to 8.4, with a mean of 7.6, confirming the eutrophic environment. This status may have been influenced by the management of the cattle-grazed pastures on either side of the waterways.

pH values were also obtained in July and August 1991 from Redgrave and Lopham Fen (P. Dolman, unpublished report commissioned for Natural England). On 29 pools in Middle Fen (Fig. 1) values ranged from 2.3 to 6.8, with a

mean of 5.4. Similar values were obtained from 28 pools in Little Fen: 2.4–7.0, with a mean of 5.5. It is difficult to assess with confidence whether low pH values affect *D. plantarius* as the total population at Redgrave and Lopham is very small and many pools do not appear to be occupied. However, the 7 pools with pH values between 2.3 and 4.6 in Middle Fen recorded only one *D. plantarius* and Dolman commented that, as the water level falls in the ponds, the acidity increases. Harms, Dunlop & Schütt (2009) have suggested that vegetation structure is probably more important than pH value but, of course, it may influence the aquatic plant life, such as the presence or absence of the water soldier *Stratiotes aloides*, which is an important habitat component.

The vegetation of the D. plantarius habitat

The vegetation which appears to be of special importance in the habitat of *D. plantarius* can be divided into two parts: the plants in the marginal zone by the water edge, and the aquatics which are floating or rooted in the lake bottom with leaves and stems emerging from the surface.

The most frequently mentioned marginal plants are *Carex* spp. In Belgium, *Carex acutiformis* is dominant, but numerous other species also occur: *Carex elata*, *Carex paniculata*, *Juncus* spp., *Typha angustifolia*, *T. latifolia* and *Calamagrostis canescens* (the late J.-P. Maelfait & A. Verlinden, pers. comm.). Large *Carex* tussocks are reported in Denmark (S. Toft, pers. comm.), and in Switzerland I found numerous *Carex* tussocks extending into the open water. Some of the thousands of fish ponds in the Czech Republic also have flooded stands of sedge tussocks *Carex gracilis*, *C. elata*, *Ledum palustre*, and the grass *Molinia caerulea* (M. Holec, pers. comm.). On the other hand, *D. plantarius* was taken in two localities in Germany in a bed of *Phalaris arundinacea* (Renner 1987), and reed beds (*Phragmites australis*) are frequently reported, especially in southern Europe. This may be a common plant in the marginal vegetation of Czech Republic fish ponds (M. Holec, pers. comm.). A similar situation has been reported in France (O. Villepoux, pers. comm.), and in Swedish lakes (T. Kronstedt, pers. comm.). At Redgrave and Lopham Fen, reed may have a deterrent effect by shading ponds so that they are avoided by *D. plantarius*. Perhaps the greater warmth, stronger light, and larger, more open water surfaces further south in Europe reduce this problem. If suitable aquatic plants are missing or scarce, the marginal vegetation is selected for building nursery webs. The stiffer structure of the sedge species provides the best support, particularly *Carex* spp., *Cladium mariscus*, *Juncus* spp., and *Schoenus nigricans*. Nevertheless, the first *D. plantarius* taken in England in 1956 (Duffey 1958) had built its nursery web in low reed stems by a pool. Nursery webs may also be built in the softer structure of grass tussocks, as I found in the vast marsh area of La Grande Brière in France.

The presence of floating leaves and emergent stems of aquatic plants enables *D. plantarius* to hunt over a wider area, gives access to numerous escape routes if danger threatens, as well as safe places to build nursery webs. The aquatic plant *Stratiotes aloides*, native in the UK, seems to

be particularly successful in providing these conditions. In the Netherlands, abundant populations are reported (van Helsdingen 2006), and also in the extensive network of channels in the Pevensey Levels (Jones 1992). *Stratiotes aloides* is an aquatic floating plant with an underwater base which can be used as a hiding place, and stiff erect leaves above the water surface suitable for supporting nursery webs. Some flooded peat excavations in the Netherlands may be completely covered by this plant. No other plant seems to be as successful, although the stems of *Juncus* spp. may occasionally be frequent in standing water in some areas. In the absence of erect stems, the floating leaves of *Potamogeton* spp., water lilies *Nuphar lutea* and *Nymphaea candida*, bladderwort *Utricularia australis*, frogbit *Hydrocharis morsus-ranae*, and water milfoil *Myriophyllum verticillatum* provide hunting sites, some cover, and escape routes into the water, but most nursery webs would have to be built in the marginal vegetation, which may be a less safe environment.

Predation

When alarmed, *D. plantarius* runs down an emerging plant stem into the water where it remains for 5–10 min, according to Bonnet (1930). If the disturbance is very short and not repeated, it may return to the surface after a few minutes. When the water is clear it is possible to see the spider in the water. On the few occasions I have been able to do this, the spider appeared to have descended to a depth of approximately 15 cm. On one occasion when I approached a pool in Redgrave and Lopham Fen, a spider which was not a *Dolomedes* ran down a stem into the water. I had a similar experience later on, and this time I waited for the spider to return to the surface, where I caught it in a net. It was a subadult female *Pisaura mirabilis*.

D. fimbriatus also avoids danger by hiding in the water, but often occurs in moist habitats where there is too little water to submerge. In my garden in France, their behaviour was slightly different because there were no emergent aquatic plants. Well-grown and adult *D. fimbriatus* were usually seen on the water surface beneath overhanging grass stems. When a grass stem was long enough to rest on the water, the spider attached itself by the fourth pair of legs. If alarmed, it immediately reversed its position by hanging in the water under the same leaf. The movement was so fast, the spider just seemed to disappear, but its claws could be seen either side of the leaf. Bonnet (1930) referred to the importance of leaves reaching the water surface to provide support for the fourth pair of legs as the spider waited for prey. He wrote that the water surface acted in the same way as a silk web because when an insect landed on it, the spider reacted to the faint vibrations and could detect in which direction to strike.

The well-developed escape behaviour of the two *Dolomedes* is probably directed against birds, which are known to take them. Small mammals such as shrews feed readily on spiders, so that the water shrew *Neomys fodiens*, which is adapted to all kinds of aquatic environments (Mitchell-Jones *et al.* 1999), may be a potential predator. Large numbers of common frog *Rana temporaria* have been seen in lake

marshes occupied by *D. fimbriatus*, but the spiders were absent from areas where the frogs were most numerous.

In my garden in the Corrèze I had two ponds with the same vegetation, but very few emergent plants, a very small one of 3–4 m² with no fish, and a larger one of over 80 m² with more than 100 carp 20–30 cm in length. *D. fimbriatus* was found in both ponds, but was only numerous and present throughout the summer in the smaller one. During five years, one or two immature *D. fimbriatus* were recorded in the larger pond in the spring, but disappeared after a few days, and I never saw an adult. The carp regularly fed along the marginal vegetation where the *D. fimbriatus* were usually seen, as did occasional ducks, and I assume this is the reason why the spider did not establish a population in the larger pond. Carico (1973) reported that the American species *D. triton* is preyed on by the little blue heron *Egretta caerulea*, one of which had 32 spiders in its stomach.

Warmth and light

D. plantarius is a lowland species in Europe and, in contrast to *D. fimbriatus*, is not recorded at high altitudes. There are several localities in southern Sweden where it is well established, and it is no longer on the national Red List. The need for warmth and light has been frequently recorded, particularly in Britain, where it has been studied in detail (H. Smith, unpublished report for Natural England). Warm, sunny days are chosen for surveys as the spider is more easily found because it prefers situations exposed to the sun. Fewer specimens are recorded on cool, cloudy days. Thornhill (1985) noted that a pond with low bushes growing near the margins at Redgrave and Lopham Fen never recorded *D. plantarius* but, after the bushes were removed, the spider was able to colonize. When a shadow fell over an adult spider it moved to one side to regain the sunshine. The same avoidance of ponds where the growth of reed *Phragmites australis* is too dense has been reported by Thornhill (pers. comm.) and Smith (unpublished reports). In Denmark, Gajdoš *et al.* (2000) found that the locality of an old population of *D. plantarius* had been abandoned, probably because too many trees had been allowed to grow close to the lake, causing shade. Van Helsdingen (1993) confirmed the preference for open, sunny habitats in the Netherlands, and wrote (van Helsdingen 2006) that *D. plantarius* prefers the north side of flooded peat excavations because it faces the sun.

The population of *D. plantarius* in England

There are three populations of *D. plantarius* in Britain. The most recent is in part of the Crymlyn Bog, South Wales. The locality is a short stretch of an abandoned canal which I have not seen. In England, Pevensy Levels has an extensive population scattered over 3500 ha living in 110 km of water channels which run through cattle-grazed meadows. Redgrave and Lopham Fen, 125 ha, is much smaller, and only a small part of the area appears to be inhabited by *D. plantarius* (Fig. 1).

This fen is situated on the Norfolk/Suffolk border, and includes the sources of the River Little Ouse flowing west

and the River Waveney flowing east. The landscape history of the area from 500,000 BP has been studied by West (2007, 2009). His work showed how geology can give a time dimension to natural history and explain the origin of this fen and several others nearby. About 10,000 BP, glaciations blocked the Little Ouse valley, causing a large lake to form, and also created numerous valley fens arising from chalk aquifers as artesian springs and seepages. Today, areas of peatland which are now drained and cultivated still show that, in the past, fen conditions were widespread. More than seven fens, including Redgrave and Lopham, are known. If *D. plantarius* was present at that time, it is likely that suitable habitat conditions were available over a wide area.

The social history of the area from the beginning of human settlement has not been researched, but at some early stage the local people began to exploit the peat deposits for fuel. Instead of cutting peat in long trenches, which is the usual method, they preferred to dig small pits (3–4 m²) which, when exhausted, filled with water. As the surface water on the fen disappeared, or was drained into the rivers, the water-filled pits became the only habitat enabling *D. plantarius* to survive. An aerial photograph of a small part of the ancient fen before the recent man-made changes, and before it became a National Nature Reserve (Duffey 1961), shows the numerous peat pits as small depressions.

In June 1958, D. J. Clark of the Natural History Museum, London, and G. H. Locket, joint author of *British Spiders* (Locket & Millidge 1953), accompanied me to try to survey the distribution of *D. plantarius* in Little Fen (Duffey 1960). The overgrown vegetation and absence of footpaths made walking very difficult, so only about six pits were examined. We collected 11 adult males (mean length 12 mm) and eight females (mean length 15.6 mm). The length values are at the lower end of the size range (11–17 mm for males and 13–23 mm for females) quoted by Bonnet (1930). Nevertheless, the numbers taken from only a few pits suggested that the population was well-established.

In 1960, a borehole for the domestic water supply was installed next to Redgrave Fen. Initially, the abstraction rate was low but by 1973 it had increased to 20 million gallons per month (Heathcote 1975), frequently causing a rapid fall in the water table. Although a system of irrigation for some of the pools was introduced in the 1970s, it did not make up for the water loss. The borehole was finally removed in July 1999, after which it was expected that the restoration of the natural water table would stimulate an increase in the spider population. The numbers recorded after 1999 were similar to the earlier totals in Table 1 (H. Smith, pers. comm.), so no increase was reported.

The abundance and success of the Pevensy population contrast with the low numbers at Redgrave and Lopham. Smith (unpublished report for Natural England) suggested that the reason may be the lower genetic diversity. She interested relevant experts to check the genetic diversity of the two populations. Vugdelic *et al.* (2004) found a lower

	1991	1992	1993	1994	1995	1996	1997	1998	1999
Total	177	50	35	63	143	61	81	193	114
Adult ♀♀	20	13	0	9	7	11	22	4	11

Table 1: Total *D. plantarius* recorded in Little and Middle Fen by Duffey for the years 1991 and 1992, and Smith (2000) for 1993–1999.

level of haplotype diversity in the Redgrave and Lopham *D. plantarius*, while Ya-Jie *et al.* (2004) commented that “each of the two British raft spider populations still maintain quite high genetic and allelic diversities”.

In retrospect, there appears to be more evidence that the reason for the poor population of *D. plantarius* at Redgrave and Lopham Fen is habitat-based, rather than a loss of genetic diversity, for the following reasons.

The *D. plantarius* population at Redgrave and Lopham Fen has been living in abandoned peat pits for at least 100 years. Initially, conditions were probably good, as the fen was very open and the water-filled pits at their most numerous. After 1960, as the water table was lowered, some pits lost so much water that conditions deteriorated. The 1991–1999 population counts (Table 1) show considerable variation from year to year. Although variation in numbers from season to season is a normal feature of animal populations, there was no evidence, in this case, of a declining trend. The persistent low numbers would seem to indicate that environmental factors were preventing expansion of the population.

The total water surface available to *D. plantarius* at Redgrave and Lopham is very small compared with Pevensy and elsewhere in Europe. Water quality varies according to the location of the peat holes, as many are not occupied by the spider. This contrasts with much larger water surfaces where *D. plantarius* populations seem to be more stable and successful. Heathcote (1975) pointed out that undulations in the sand substrate beneath the peat at Redgrave and Lopham Fen diverts basic water to certain areas so that acidic islands are created elsewhere, identified by *Calluna*, *Erica tetralix*, *Drosera* and *Molinia*.

In 2010, Natural England liberated 2800 captive-bred young *D. plantarius* to a new site further down the Waveney Valley, in what appeared to be a suitable habitat (H. Smith, pers. comm.). In the following year, some immature *D. plantarius* were seen, but no adults. A second introduction was made in 2011. Dr Smith (pers. comm.) told me that, in her experience, most *D. plantarius* take two years to mature. This contrasts with Bonnet (1930), who found that his captive-bred spiders only lived for 14–16 months. There is also some evidence that *D. plantarius* from the Canal du Midi were somewhat larger than those at Redgrave and Lopham (Duffey 1960). This suggests that there may be a size and life-span difference between the Bonnet *D. plantarius* and those in Britain. Jones (1992) also commented that some of the Pevensy population appeared to have a 2-year life cycle. This may be caused by latitudinal and climatic differences between France and England if the former breed earlier in the year than the majority of the latter.

The sensitivity to habitat change by *D. plantarius* is demonstrated by the history of the population in Bonnet’s Canal du Midi, where deterioration in water quality and increase in disturbance resulted in extinction. At Pevensy, the numbers of this spider may vary considerably from place to place, depending on the width and condition of the marginal habitat, and the presence, or absence, of a favourable aquatic flora (Jones 1992). The aquatic flora of the Redgrave and Lopham Fen pools is generally poor. *Stratiotes aloides*, the ideal component of the aquatic habitat,

is not present. An introduction of this plant was attempted (Smith, www.Dolomedes.org.uk), but was not successful. Stace (1997) commented that this plant is normally associated with base-rich water. At Pevensy, where it grows well, the mean pH is 7.6, while at Little Fen it was 5.7, and at Middle Fen 5.6.

The flora of the Fen has changed since the 1970s, perhaps due to the period of low water table and more recent stripping of vegetation to expose bare peat and creating shallow lagoons. Heathcote (1975) recorded *Schoenus nigricans*, *Carex panicea* and *Carex lepidocarpa* as dominants and I remember *Drosera* and *Sphagnum* spp. in the late 1950s. It is not known whether this plant diversity loss has influenced *D. plantarius*.

The present management policy of excavating larger, deeper pools at Redgrave and Lopham Fen, and liberating captive-bred spiders in them, should boost the population temporarily, but a habitat change is probably needed for a permanent improvement. However, some new pools do not seem to attract resident *D. plantarius* (Smith, unpublished report for Natural England). A study of these pools is needed to see whether they have differences compared with occupied pools.

An alternative management policy would be to create a Pevensy-type waterway in the form of a canal or, better still, two canals in different areas, 3–4 m wide and as long as possible, and deep enough to retain clean permanent water. If an area can be found where the pH is about 7.0, the canal may be suitable for another attempt to introduce *Stratiotes aloides*. If not, other, more tolerant, plants are available to establish the important aquatic flora. This system would create an open habitat, with more light and greater exposure to the sun, compared with the existing pit pools. The canals do not have to be straight. The vegetation along the canal margins should preferably consist of sedges, particularly the local *Schoenus nigricans* and *Cladium mariscus*. Planting may be necessary. Were this suggestion to be adopted, it would be interesting to see how long it would take the resident population to colonize the canal(s) rather than making an introduction.

Conclusions

1. Information on the distribution, habitat and ecology of *D. plantarius* in Europe is still inadequate. More survey is needed in most European countries to find populations which have been overlooked and to establish the current status of the species.

2. No precise information is yet available on the means of dispersal used by both species. Evidence for aerial dispersal in nature has yet to be established. *D. plantarius* is widely distributed in Europe north of the Mediterranean, extending into Russia and beyond, but not yet recorded in Spain. How has it achieved this extensive range?

3. The behaviour of *D. plantarius* in relation to some aspects of habitat change, water quality, disturbance, and vegetation structure is not always predictable and needs further study. It would be an excellent subject for experimental research to provide more accurate information.

4. The most extensive and successful populations seem to be on large water surfaces, whether lakes, étangs, or canal networks. The small peat-pit ponds at Redgrave and Lopham Fen are poor-quality habitats in contrast to larger, and more open, flooded peat cuttings as in the Netherlands.

5. There is some evidence, from data at Redgrave and Lopham Fen and Pevensy Levels, that the breeding cycle of *D. plantarius* sometimes extends to two years in the northern part of Europe. Body measurements of adult males and females in Britain (Duffey 1960) are somewhat smaller than those quoted by Bonnet (1930) for France. These differences may be due to climatic influences which result in earlier breeding in southern Europe than in England.

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Appendix 1. Evidence for the loss of *D. plantarius* habitat in Europe

The evidence that “*Dolomedes plantarius* is a rare, declining species which has lost much of its European range” has been made many times in reports, articles and elsewhere but no supporting evidence is provided. It also assumes, incorrectly, that its range in the past was known. Nevertheless, it is a rare species, though widely distributed from France to Siberia.

A species may be rare for many reasons, one of which is because it is associated with a specialized habitat. The consensus of views on the *D. plantarius* habitat, as far as it is known in Europe, can be described as permanent, open, clean water where there is no flow or very little; the locality is not shaded; emergent aquatic vegetation is present or, if not, the marginal vegetation is appropriate to provide food and a habitat for nursery webs. It is these characteristics which one must look for in the evidence for wetland decline.

The published statistics of habitat loss for wildlife in general are so great it is not surprising that people think it applies to all species. Smout (2009) recorded for Britain a loss of 95% of lowland herb-rich grassland, 80% of chalk/limestone grassland, 50% of semi-natural woodland, 50% of lowland marshes and fens, and 60% of lowland bogs and heaths. Baldock (1984) discussed the drainage of wetlands in the UK, Ireland, Netherlands, and France, and Hughes (1995) the current status of wetlands all over Europe. These authors found that a definition of what is meant by the terms ‘marine wetland’, ‘coastal wetland’ and ‘inland wetland’ is, almost without exception, absent, and different authors use them to mean different things. Many authors consider that ‘wetlands’ must be vegetated so that open-water areas are excluded. Others do not include man-made water bodies such as fish ponds and reservoirs.

The Ramsar Convention has designated 469 wetland sites in 25 European countries and is concerned with wetland resources, not losses, although the threats are recognized (Nivet & Frazier 2004). Stevenson & Frazier (1999) discussed wetland loss in Europe and summarized their conclusion as follows: “No attempt was made to make a detailed summary at a European level of wetland loss based on the information from the country chapters. It was noted that a wide diversity of methodologies are used to measure wetland loss and the lack of co-ordination between studies in different countries, or for different wetland types, prohibits any overview at regional level. In short data are missing for a large number of countries.”

Baldock (1984) considered wetland drainage in Europe and wrote that: “the primary reason is to improve agricultural potential”. Concerning France he wrote: “the most recent susceptible wetlands are wet pastures, flood meadows, grazing marsh, certain areas of bog and wet marsh where afforestation is feasible, coastal marsh, the valleys and estuaries of major rivers where flood control schemes are most often located and smaller rivers where little management has taken place”.

It is impossible, with this generalized evidence, to identify *D. plantarius* habitats because open, still water is never mentioned as a wetland category. It is up to the arachnologists in Europe to collect information about the localities where *D. plantarius* has been recorded, particularly those which have been lost or are threatened. Alain Pasquet of the Association Française d'Arachnologie has emphasized the importance for all arachnologists to follow an agreed format to describe the important features of each new habitat location. It is only in this way that we can build up the essential data for an accurate assessment of the ecology, status and distribution of *D. plantarius*.