Historical distributions in Britain of two species of large house spiders, *Tegenaria saeva* and *T. gigantea* (Araneae, Agelenidae), and their evolutionary implications

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Summary

Current relative distributions and evolutionary interactions of two species of large house spiders, *Tegenaria saeva* and *T. gigantea*, vary geographically in Britain. To understand fully their underlying causes requires knowledge of species ranges in the past. Here, information from five sources: (a) historical distribution maps based on county and vice county lists; (b) a re-examination of museum and other collections; (c) catalogues of museum specimens recently re-examined by experts; (d) scrutiny of the literature; (e) a request published in a Wildlife Trust magazine, is used to determine historical distribution patterns. It is shown that the northern limits of both species have generally increased through time and that this phenomenon is not a result of variable recorder effort. In the south of England, the species boundary in Dorset has apparently been stable for at least a century. The ecological and evolutionary implications of these results are discussed.

Introduction

Two species of large house spiders, *Tegenaria saeva* Blackwall, 1844 and *T. gigantea* Chamberlin & Ivie, 1935, commonly occur in buildings and in more natural, outdoor habitats throughout Britain (Harvey *et al.*, 2002). In southern and central England and Wales the species show clear, broadly allopatric, distributions with *T. gigantea* occupying the east and Midlands of England, and *T. saeva* the west of England and Wales (Merrett, 1980; Oxford & Chesney, 1994; Harvey *et al.*, 2002; Croucher *et al.*, 2007). By contrast in northern England, approximately north of an east-west line drawn along the North Wales coast, the species are broadly sympatric (Oxford & Chesney, 1994; Harvey *et al.*, 2002; Croucher *et al.*, 2007).

These distributions have implications for the ecological and evolutionary interplay between the species. On the south coast of England, where the species' distributions overlap in a fairly narrow zone in the county of Dorset, detailed molecular and morphological studies have shown that low levels of hybridisation and introgression are occurring (Croucher, 1998; Croucher *et al.*, 2004, 2007). In the north, levels of hybridisation and introgression are much higher (Oxford & Smith, 1987; Oxford & Plowman, 1991; Croucher, 1998) and the integrity of the species may be breaking down, a process that is likely to accelerate as the two taxa become genetically, and morphologically, more similar (Croucher *et al.*, 2007).

In order to understand fully the dynamics of species' range changes, and their consequential importance for interspecific interactions, an historical perspective is essential. Here I assemble data from a variety of sources on the past distributions of these taxa in order to (a) assess the stability of the species ranges in the south, (b) place in a more detailed temporal context the relatively recent expansion of both species into the north of England (Oxford & Smith, 1987; Parker, 1984), and (c) consider possible reasons for the rather sudden colonisation of Yorkshire and other northern counties.

Methods

Information was obtained from five sources: (a) distribution maps based on county and vice county lists; (b) a re-examination of museum and other collections; (c) catalogues of museum specimens recently re-examined by experts; (d) scrutiny of the literature; (e) a request published in the Yorkshire Wildlife Trust (YWT) magazine. *Tegenaria* specimens were re-examined from Doncaster Museum, Manchester Museum, the Natural History Museum (NHM, London), the Hope Entomological Collection (University of Oxford), and A. E. Binding (Lincolnshire Wildlife Trust). Catalogues of recently re-examined material were available from the museums at Liverpool and Rotherham. Most of the relevant literature and some of the distribution maps were published before the recognition of *T. saeva* and *T. gigantea* as separate species in 1975 (see Locket, 1975 and Oxford & Smith, 1987 for history of the nomenclature), when they were referred to collectively as "*T. atrica*" or "*T. saeva*". To provide some control for sampling effort the distribution of *Tegenaria domestica* (Clerck, 1757) has also been examined. Ordnance Survey grid references are provided for specific locations, but these will necessarily be approximate.

Results

Figures 1 and 2 are based on the county lists of species published by Bristowe (1939), the county maps in Locket *et al.* (1974), the location maps in Merrett (1980), and county distributions derived from the finer-scale mapping of the British Arachnological Society's Spider Recording Scheme (SRS) (Harvey *et al.* (2002) and an up-date produced in 2006 available on the NBN Gateway (www.nbn.org.uk)). For consistency the pre-1974 county names and boundaries are used throughout this paper in both figures and text. The distribution of *T. domestica* (Fig. 1) shows that there was sufficient recorder effort before 1939 for Bristowe to document the species in all 39 English counties, in 12 out of 13 counties in Wales and in 21 out of 33 in Scotland. Subsequent records in Locket *et al.* (1974) and by the SRS added one and five extra Scottish counties, respectively. Given this comparative background, the joint distributions of *T. saeva* and *T. gigantea* (as "*T. atrica*") are distinctly southern in Bristowe's (1939) list and tend to creep northwards in later surveys (Fig. 2).

Scrutiny of papers relating to spiders in the north of England from the mid-1800s through to the 1930s suggests that *T. domestica* (variously called *T. civilis* or *T. derhamii* — see Locket & Millidge, 1953) was common and widespread in that period. For example, Hardy

Fig. 1: Pre-1974 county map showing the distributions of *Tegenaria domestica* at three time periods (see text for more details).

(1858: 94) mentioned *T. domestica* as "our common domestic spider" in Berwickshire, Pickard-Cambridge (1895) recorded it at several sites in Cumberland, Hull (1896: 69) described this species as "the common house spider, to be seen in the unswept angles of buildings everywhere" in Northumberland and Durham, and Jackson (1906: 357) regarded *T. domestica* as "one of the two common house spiders" (the other was *Amaurobius similis* (Blackwall)) in the Tyne Valley, Northumberland. Likewise, Harrison (1909: 227) wrote "the common house spider of the district" in his report on the spiders of Middlesbrough, and Pickard-Cambridge (1907) recorded *T. domestica* from across Yorkshire, as did Falconer (1922).

Records of "*T. atrica*" are, however, not totally lacking from the north of England during this period. Hull (1896) catalogued an adult male from Jesmond (Northumberland, NZ2566) found in 1887 and an immature female from Winlaton (Durham, NZ1762). Jackson (1906: 402), referring to these specimens, wrote "This is a common spider in the south of England. It has occurred as far north as Glasgow, but I believe it has been introduced into these latitudes by man, and that recently". This was certainly the case in Southport ". . . where the spider radiates from the Botanic gardens, in which place alone it is abundant". Bagnell & Turner (1913), in a preliminary list of the spiders from the Derwent valley (Durham), mentioned a specimen from Winlaton in the Newcastle Museum (probably the same one described by Hull) and two immature individuals taken from Axwell Park greenhouses (NZ1962) in 1910. Axwell Park is about 1.5 km east of the centre of Winlaton. The 14 years or more between Hull's Winlaton specimen and those from Axwell Park suggests that a viable population may have been established in this area around the turn of the twentieth century. In a footnote, Falconer (1921: 314) reported two specimens of "*T. atrica*" from Yorkshire; a female from a public house in Barnsley (undated), and an adult female which ". . . travelled unharmed in the crack of a poplar tree from Montgomeryshire to a Huddersfield timber yard" in November 1911 (Falconer, 1913: 136). These early Yorkshire records were apparently overlooked by Bristowe (1939) and Locket *et al.* (1974) when compiling their distribution data (see Fig. 2). On the whole, the literature strongly suggests that in Yorkshire and the counties to the north by far the most common domestic *Tegenaria* species (before the 1930s at least) was *T. domestica* and that "*T. atrica*" was, with the one or two exceptions mentioned above, present only as occasional imports. The county records of Bristowe (1939) for Northumberland and Durham (Fig. 2) were probably based on the single Jesmond specimen and the three from Winlaton and Axwell Park, respectively. It is not unlikely that a similar situation pertained to the two

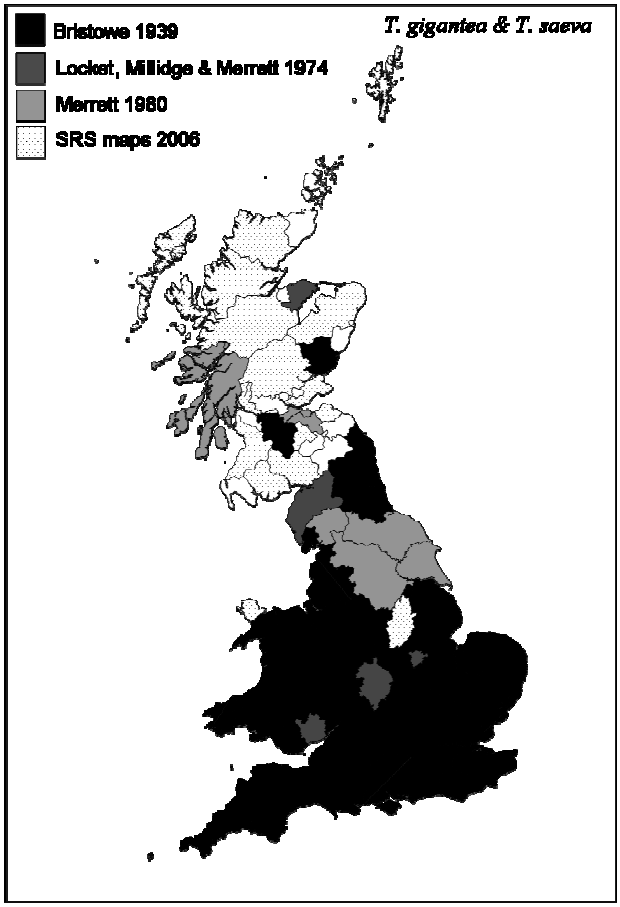

Fig. 2: Pre-1974 county map showing the combined distributions of *Tegenaria gigantea* and *T. saeva* at four time periods (see text for more details).

Scottish counties reported by Bristowe (1939) to contain "*T. atrica*".

The range expansion of *T. saeva* and *T. gigantea* into Yorkshire and Cumbria (the whole of the pre-1974 counties of Westmorland and Cumberland plus small areas of Yorkshire and Lancashire) was considered by Parker (1984) and Oxford & Smith (1987). Apart from the two specimens of "*T. atrica*" mentioned by Falconer (1921) the oldest modern records for Yorkshire found so far are a *T. gigantea* from Doncaster (1966, SE5702) and a *T. saeva* from Barlby, Doncaster (1969, SE5701) (Doncaster Museum collection). The species apparently colonised Cumbria at about the same time (Parker, 1984). The timing of the invasion of Yorkshire by these species, as suggested by museum material, is supported by anecdotal evidence from long-term residents in the county. A request for information in the YWT's magazine yielded a number of responses linking the discovery of large house spiders for the first time and datable events, e.g. house alterations or the number of years after moving house. The earliest record was from Bramham near Tadcaster in 1964 (SE4242), although the respondent thought the spider might have been imported in peat. Other correspondents, some familiar with large house spiders further south, noted them from the early 1970s onwards after they, the householders, had been in their Yorkshire homes for several years.

Tegenaria saeva and/or *T. gigantea* were reported at somewhat earlier dates in counties adjacent to Yorkshire. Thus *T. gigantea* was collected from widespread sites in Lincolnshire from 1948 onwards (A. E. Binding collection) and "*T. atrica*" was noted by Bristowe (1939), although earlier lists for the county (Smith, 1901a, b) failed to mention "*T. atrica*" or, indeed, *T. domestica*. Further west, "*T. atrica*" was recorded by Falconer (1930) as being present in both Cheshire and Lancashire, and *T. saeva* was collected in the 1950s at a number of locations in Cheshire (Liverpool Museum catalogue; D. W. Mackie collection, Manchester Museum) and in Bolton, Greater Manchester (Liverpool Museum catalogue). Thus if the range expansion of *T. saeva* and *T. gigantea* into Yorkshire and Cumbria occurred naturally, populations were present in adjacent counties to act as potential sources.

Searches for historical material from the current areas of parapatry in southern England revealed a small number of useful specimens. In particular, individuals collected in Dorset between 1887 and 1917 by O. Pickard-Cambridge (Hope Entomological Collection, University of Oxford) allow a comparison with current species distributions in the county. Unfortunately in some cases spiders from more than one locality seem to have been pooled, and the names of collection localities may have been used rather loosely, practices not uncommon at the time (P. Merrett, pers. comm.). Nonetheless, spiders can be assigned to six locations close to the current boundary between the two species. Four reliable locations (Dorchester, SY6990; Sherborne, ST6316; Warmwell, SY7687; Winfrith, SY8186) contained only *T. saeva*. Samples from one critical location, Bloxworth (SY8894), were apparently combined with those from Portland (SY6972) and contained both *T. saeva* and *T. gigantea*. However, as Portland is further west (i.e. in the present *T. saeva*-only region) than two of the other *T. saeva* sites, Warmwell and Winfrith, it is unlikely that the *T. gigantea* specimens originated there. The Bloxworth collections may therefore have comprised just *T. gigantea* or both species. In addition, the H. W. Freston Collection (Manchester Museum) contained three specimens from Holdenhurst, Dorset (SZ1395) collected in 1900 (all *T. gigantea*), and Merrett (1980) illustrated a *T. saeva* palp from Swanage, Dorset (SZ0378) dated 1896. Figure 3 plots the current, GIS-derived distributions of *T. saeva* and *T. gigantea* (Croucher *et al.*, 2007) with the *c.* 1900 records superimposed. As far as the evidence goes, and with the caveat regarding the sorting of the Bloxworth/Portland samples, the local distributions of species a century ago seem to match the present-day pattern extremely well.

Specimens in the H. W. Freston Collection for areas other than the parapatric zone in Dorset are as follows: *T. saeva* — Plymouth, Devon (1900, SX4756, $n=1$) and Towyn, Merionethshire (1905, SH9779, $n=1$): *T. gigantea* — Chalford, Gloucestershire (1890 and 1900, SO8902, $n=3$), Ettington, Warwickshire (1899, SP2648, $n=2$) and Epping Forest, Essex (undated, TQ4198, $n=1$). Material in the NHM includes *T. gigantea* from Shepperton (on Thames), Surrey (1896, TQ0767, $n=9$), Worcester, Worcestershire (1897, *c.* SO8555, $n=1$) and (apparently) the Natural History Museum, London (1897, TQ2679, $n=1$). All these species locations are entirely consistent with present-day distributions.

Unlike the situation in northern England at this time, "*T. atrica*" was not uncommon in the south. Thus, for Dorset, Pickard-Cambridge (1896: 57) wrote "Adults of both sexes . . . under heathy ledges in gravel pits, Bloxworth Heath; also rather abundantly in similar situations by the roadside near Cold-harbour, Wareham", and in *The spiders of Dorset*, Pickard-Cambridge (1879: 63) noted, "Found abundantly in cellars, dark unused rooms, and cupboards at Weymouth, as well as beneath large pieces of detached rock near Pennsylvania castle, Portland" but added "It appears to be a rather local spider, but is found in various other parts of England, though not abundantly".

Discussion

Reconstructing past distributions of spiders is often problematic because of both temporal and spatial variation in recorder effort. Mapping the historical ranges of *Tegenaria saeva* and *T. gigantea* has two advantages in this respect. First, they are large spiders closely associated with human habitation. If present in an area, and especially if they have newly arrived, it is unlikely they will be missed. Secondly, as a control for recording activity, there is the extremely widespread *T. domestica*, which occurs in almost the same domestic settings as the two target species. This species is smaller and less

obvious than *T. saeva* and *T. gigantea*, so if it is recorded the larger species should, if present, surely be noticed too.

The past distribution of *T. domestica* (Fig. 1) indicates that the species was recorded in virtually all counties by the time Bristowe (1939) published his list. Only the most northern Scottish mainland counties had to wait for later surveys. As an aside, anecdotal evidence suggests that *T. domestica* is now possibly less common than it was in the past and the larger *Tegenaria* species more common, perhaps hinting at an ecological interaction between them (P. Merrett, pers. comm.). The distribution of *T. domestica* in Fig. 1 provides some assurance that the general expansion northwards of *T. saeva* and *T. gigantea* (Fig. 2) is a real phenomenon. Indeed, this expansion of range is probably more spectacular than Fig. 2 suggests. As discussed above, Northumberland and Durham were recorded as having "*T. atrica*" by Bristowe (1939) on the basis of possibly only one and three specimens, respectively (although the latter may have represented an established local population). Thus "presence" in the northern counties (Bristowe, 1939) may have been the result of odd individuals transported by humans outside their normal range(s), as was certainly the case for one of the early Yorkshire specimens reported by Falconer (1913, 1921). Of course, it is not known whether some of the southern counties were also scored as positive for these species on the basis of one or two individuals.

The older literature fully supports the idea that the northern counties of England did not have widespread populations of *T. saeva* and *T. gigantea* in that *T. domestica* was widely recorded by a number of active arachnologists, but the larger species were not. Museum specimens, corroborated by anecdotal evidence, suggest that *T. saeva* and *T. gigantea* expanded their ranges into Yorkshire around the early 1960s (not the 1970s as suggested by Smith (1985) and Croucher *et al.* (2007)). These large species are highly likely to have been noticed when seen in a house for the first time and would stand a good chance of coming to the attention of a local museum as possible "exotics". If this is the case it raises the questions of how and why did the species' ranges expand so rapidly. *Tegenaria gigantea* was certainly widespread in Lincolnshire in the mid-1940s and *T. saeva* was recorded in Cheshire at about the same time. Yorkshire could therefore have been colonised naturally (i.e. without human assistance) by *T. gigantea* from the south and *T. saeva* from the west. This would be expected to generate a pattern of distribution with *T. gigantea* in the east of Yorkshire and *T. saeva* in the west. It is certainly the case that there is a preponderance of *T. gigantea* in the east of the county (Oxford & Smith, 1987; Croucher *et al.*, 2007), consistent with unaided colonisation, but both species can be found almost anywhere, suggesting that human-mediated transport has also been important. The very high frequency of *T. saeva* in York and surrounding areas (Oxford & Smith, 1987; Croucher *et al.*, 2007), and the occurrence of villages close to York containing only one or other species (Oxford & Smith, 1987), are difficult to explain other than by human inoculation.

Why did this invasion happen in the 1960s? People have moved large house spiders around throughout recent history, e.g. Jackson (1906) and Falconer (1913) quoted earlier, and an explanation is required for why such migrants were suddenly able to found large populations over such a wide area. One factor might have been increased propagule pressure, a key determinant of whether invasive organisms successfully establish or not

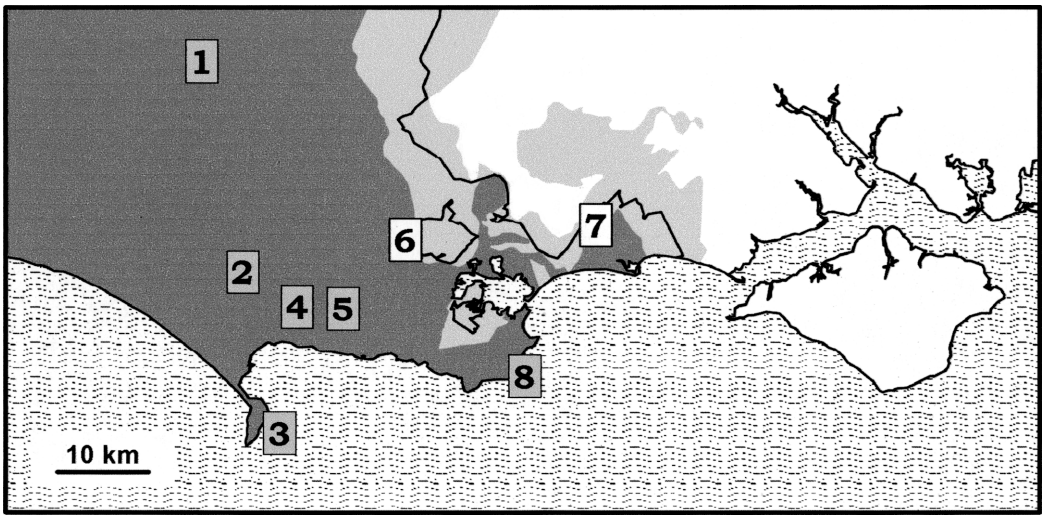

Fig. 3: Map of central southern England showing GIS-derived distributions of *Tegenaria saeva* and *T. gigantea*. Areas with >78% *T. saeva* shown in dark grey; those with <22% white, those with frequencies between 78% and 22% light grey. Black lines within light grey regions are where *T. saeva* and *T. gigantea* are predicted to be equally common, i.e. 50% *T. saeva* (see Croucher *et al.*, 2007 for more details of GIS technique). Locations collected around 1900 shown as numbers (*T. saeva*, light grey background; *T. gigantea*, white background). Sites and numbers of specimens (*n*): 1, Sherborne (*n*=1); 2, Dorchester (*n*=3); 3, Portland (*n*=?); 4, Warmwell (*n*=2); 5, Winfrith (*n*=2); 6, Bloxworth (*n*=?); 7, Holdenhurst (*n*=3); 8, Swanage (*n*=1). As discussed in the text, the tentative assignment of specimens to Portland and Bloxworth (overall *n*=18) is based on the composition of intervening sites; Bloxworth might have contained both species. All specimens are from O. Pickard-Cambridge Collection (University of Oxford) except those from Holdenhurst (H. W. Freston Collection, Manchester Museum) and Swanage (Merrett, 1980). Approximate map references for these specimens are given in the text. The figure is based on fig. 4B of Croucher *et al.* (2007), and is used here with the permission of the publishers.

(e.g. Williamson, 1996; Lockwood *et al*., 2005, 2007). Propagule pressure comprises two elements, the number of separate colonisation events (called, rather confusingly, "propagule number") and the number of individuals involved in each colonisation event ("propagule size") (Lockwood *et al*., 2005, 2007). The rate at which spiders were introduced into Yorkshire, for example, might have increased in the middle of the last century as a result of enhanced human mobility (increasing propagule number). Alternatively, or additionally, population densities in adjacent counties may have been building up and spiders were therefore more likely to be subjected to local transport, potentially affecting both components of propagule pressure. The probability of imported spiders surviving and establishing viable populations may also have been enhanced during this period as a result of increased use of central heating and/or global climate change. All of these factors could have acted in concert. There is, of course, the unlikely possibility that these large *Tegenaria* species had been gradually moving northwards over a longer period of time than supposed and, despite the arguments made above, were just not noticed in Yorkshire (and Cumbria) until the mid-1960s. Irrespective of these uncertainties, it is indisputable that *T. saeva* and *T. gigantea* have colonised the north more recently than areas further south. Both species were distributed across the whole of Yorkshire by the mid-1980s (Oxford & Smith, 1987). If they arrived only twenty years previously this represents an explosive spread, whatever the underlying mechanism(s).

The distributions of *T. saeva* and *T. gigantea* in central and southern England and Wales are even more intriguing. There are no known ecological differences between the species that would suggest an environmental (climatic) explanation for their largely allopatric, east-west distributions or why the boundaries between them are located where they are. Indeed, the broadly sympatric ranges of the species in the north of England and Scotland suggest that environmental factors may not differentiate between them, at least at large geographical scales. However, the possibility that climate plays some part in determining species distributions warrants closer investigation. In a study of two species of gorse, *Ulex minor* and *U. gallii*, which show similar allopatric distributions to the two *Tegenaria* species across England and Wales, Bullock *et al*. (2000) concluded that interspecific competition, possibly mediated by climatic factors, is responsible for their largely allopatric ranges. The same might be the case in *Tegenaria*. The limited evidence from spiders collected in Dorset around 1900 suggests that the boundary there has been geographically stable for at least a century despite the considerable human (and therefore *Tegenaria*) movement across the region, which should act to increase overlap in species distributions. Spiders collected elsewhere in England and Wales in the same era are also entirely consistent with the distributions found today.

For *T. saeva* and *T. gigantea* there really is a north-south divide in terms of the nature and stability of their distributions and the consequences of this for the interactions between the two species. In the south the highly stable distribution seems extremely resistant to the unwitting interchange by humans of species across the narrow zone of overlap. In this parapatric region hybridisation, and the subsequent introgression of genes, is detectable but low. There is, however, evidence of the inevitable long-distance movements of individuals across the boundary in the form of mitochondrial sequences in *T. saeva* that are characteristic of *T. gigantea* (Croucher *et al*., 2004). In contrast, in the relatively newly colonised areas of northern England, although species distributions are locally patchy they are broadly sympatric. It is possible that in these newly interacting northern populations, any barriers to gene flow present at the species boundary in the south have broken down, or have never established, and that this is the explanation for levels of hybridisation in excess of those expected even after allowing for the increased opportunity for interspecific interactions created by greater sympatry (Croucher *et al*., 2007).

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