A roll of the dice: the unnatural history of large house spiders (*Tegenaria*: Agelenidae) in the British Isles

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Introduction

It is often the case that we know much less about the biology of common and widespread species than rarer ones. Grants are more readily available for research on the ecological requirements of rare species of conservation concern, in order to save dwindling populations. It might also be assumed that for common species, being common, we know all there is to know already. This is seldom true. Here I discuss research conducted at the University of York over the past 35 years on a very frequently encountered guild of large house spider species, the *Tegenaria atrica* group[1] (Plate 1a, centre pages). These spiders are the scourge of all arachnophobes; yet dig deeper and the subjects of their fear reveal intriguing patterns of distribution and recent range expansions. They are also providing insights into aspects of interspecific interactions, which could determine the species' evolutionary futures.

Background

My interest in this particular group of spiders was kindled around 1980 when I was helping Clifford Smith map species distributions for his *Atlas of Yorkshire Spiders* (Smith, 1982). Merrett (1980) had just published a paper which sought to clarify the distinguishing features of species within the *Tegenaria atrica* group[1]: *T. saeva* Blackwall, 1844, *T. gigantea* Chamberlin & Ivie, 1935 (= *duellica* Simon, 1875) and *T. atrica* C.L.Koch, 1843 itself, and plotted their distributions. From the relatively few records then available, it appeared that *T. saeva* was found predominantly in the West Country and Wales with *T. gigantea* occupying the eastern and central parts of England. *Tegenaria atrica* records were rare and well scattered, apparently the result of infrequent, accidental importation of individuals from continental Europe or the Republic of Ireland, where it is common. Given these tentative distributions, the discovery of several *T. saeva* in my garage in York was unexpected. This prompted Clifford and me to organise a survey of large house spiders across Yorkshire, but concentrating on York and its environs. We were aided in our task by ample newspaper and television coverage – large, hairy spiders always go down well with the media. To our surprise, *T. saeva* turned out to be the commoner of the two species in York. We also found that some of the surrounding villages apparently contained only *T. saeva* or only *T. gigantea*, although most samples contained both species (Oxford & Smith, 1987). It seemed highly unlikely that villages just a few miles apart offered domestic habitats distinct enough to favour one species or the other. Most probably, a species' presence or absence was merely a result of random colonisation events. This was the first inkling that chance – a roll of the dice – plays a major role in determining the distributions of these two species.

[1] The nomenclature used here is that in the latest checklist of British spiders (Merrett, Russell-Smith & Harvey, 2014).

Mapping the distributions of *Tegenaria saeva* and *T. gigantea*

The discovery of *T. saeva* apparently 'in the wrong place' prompted a more thorough investigation of distributions of the three *Tegenaria atrica* group species in Britain. The Yorkshire survey entailed householders bringing live spiders to various depositories spread around York and further afield in the county. A reliance on the cooperation of the general public posed a serious logistical problem for mapping spiders more widely. As a result, a graduate student, Peter Croucher, and I developed a 'fishing' technique to enable us to catch large house spiders from habitats other than domestic premises (Oxford & Croucher, 1997). This entailed simply putting a fisherman's maggot onto a web and waiting for the incumbent to appear from its often impenetrable retreat. The spider is swept from the web with a hand and enticed into a specimen tube. Later, technology largely replaced the maggot in the form of a sonic toothbrush (Oxford, 2013), the vibrations of which mimic the beating wings of a medium-sized fly. These techniques revolutionised the mapping of *Tegenaria* distributions and enabled us to collect specimens from tree crevices, stone walls and the exterior of buildings. Intensive work along the south coast and in Yorkshire (Croucher, 1998), extensive collections from elsewhere (GSO and others), and appeals to the general public *via* natural history societies and the media have enabled us to generate a comprehensive picture of species distributions.

The distributions of *T. saeva* and *T. gigantea* are shown in Plate 1b (centre pages), updated to 31st December, 2015. The vast majority of the records shown have been verified by GSO or Peter Croucher. For reasons discussed below, species diagnosis, especially from some parts of the country, can be tricky; misidentified records are not uncommon. For this reason, maps available from the National Biodiversity Network, or even the Spider Recording Scheme, websites appear to be less clear-cut than that shown in Plate 1b. As far as possible we identify spiders in batches, without regard to which part of the country individuals come from, so that our identification of difficult specimens is not biased by knowledge of geography.

South of an east–west line drawn along the North Wales coast the distributions of *T. saeva* and *T. gigantea* suggested by Merrett (1980) are fully supported. The species are almost entirely allopatric across most of England and Wales, separated by geography such that they never interact. They meet and overlap in a relatively narrow band which runs from central Dorset northwards, approximately following the Welsh border (Plate 1b). This pattern is illustrated most clearly in the inset to Plate 1b, where species distributions are interpolated across the majority of England and Wales (Croucher *et al.* 2007). Data from further north were not, at the time, sufficient to apply this technique. In the zone where the species co-occur, some specimens show intermediate morphological characteristics of the female epigyne or the male palp, the only external features that allow species identification. These individuals seemed to be the products of interspecific hybridisation (Oxford & Plowman 1991), a conclusion later confirmed by studies of molecular markers (Croucher, 1998; Croucher *et al.* 2004).

North of the line drawn along the North Wales coast the clear, east–west distinction breaks down and both species can be found almost anywhere (Plate 1b). The situation Clifford and I found in Yorkshire is a reflection of this geographical homogenisation. A consequence of the enhanced contact between the two species is an increase in the rate and degree of hybridisation. In Yorkshire, for example, morphometric studies have shown that what appear to be 'good' *T. saeva* and 'good' *T. gigantea* are, in fact, more similar to one another than are specimens taken from within deeply allopatric locations further south (Croucher, 1998; Croucher *et al.*, 2007). This is

evidence for extensive past, and current, gene flow and introgression, the incorporation of genes from one species into the other. The consequences of this are discussed later.

What determines species distributions?

Consider first the distributions of species south of the line drawn along the North Wales coast. It has been shown that the geographical position of the contact zone, at least in central Dorset, appears to have been stable for at least a century (Oxford, 2009), and possibly for much longer. In the British Isles, major climatic gradients tend to vary in an approximately southeast to northwest direction, with the former experiencing a more continental climate, and the latter a more oceanic one (e.g. Chandler & Gregory, 1976). Mean altitude, by chance, also increases towards the north and west, steepening the wetness gradient through orographic precipitation (Atkinson & Smithson, 1976). It is therefore inevitable that east–west distributions of species in Britain will be highly correlated with a number of climatic variables, but the question is, are they causative?

Climate models

For *T. saeva* and *T. gigantea* this question was investigated by Anderson *et al*. (2009) who built predictive general linear models (GLMs) of distributions using, as a training set, empirical spider data and a whole suite of climatic and other variables within an east–west band drawn across Wales and central England. As expected, presence and absence of species were strongly associated with a number of climatic factors. When this model was used to predict distributions of species south of the Severn estuary, an extremely good fit to the observed pattern was obtained. However, when the model was applied to northern England, the fit of observed and predicted was no better than random. The conclusion was that if climate determined species distributions in the south, it appeared not to do so in the north. Alternatively, climate might indeed be important but species in the north may not yet have reached a stable distribution with respect to these factors (see below). There is another consideration that seems to argue against a climatic influence. Large house spiders are not only associated with human habitations, but also live outside in more natural habitats. If climate variables are important, one would expect that at least within the zone of overlap there would be a difference in the identities of species taken from the benign environment of buildings and those collected in the wild. Such a pattern has not been detected (Oxford & Smith, 1987; Croucher, 1998).

Human introductions

How else might the east–west distributions of *Tegenaria* species across England and Wales be explained? Unlike many spiders these species do not disperse long distances on gossamer (Bell *et al*., 2005) and so their large-scale dispersal is probably a result of hitch-hiking with humans. Towards the end of the last glacial period, some 10,000 years ago, the climate of Britain would not have been suitable for these species and they must have been introduced subsequently. In continental Europe, both species have predominantly Atlantic ranges (Portugal, Spain and France) (Maurer, 1992; Van Helsdingen, 2016), although little is known about their fine-scale distributions. Human movements from Europe to the British Isles have traditionally followed two routes: from the Low Countries into eastern England and from western France and the Iberian peninsula into western England, Wales and Ireland (Oppenheimer, 2006; Leslie *et al*., 2015). Indeed, the distributions of *T. saeva* and *T. gigantea* in Plate 1b correspond approximately to those of the Britons and the Saxons, respectively (see Figure 3c in Leslie *et al*., 2015). The details are, of course, unknown but the potential for separate colonisations of the two large house spider species is well established. It has been suggested that the species slowly spread across southern and central England and Wales, building up large populations until they met in the present zone of overlap

(Oxford, 2011). The stabilisation of this pattern may depend on subtle interactions between the species such that when one is well established, invasion of the other is prevented. Indirect evidence for such interspecific interactions is discussed later. It is also the case that individuals of one species transported into the land of the other may either die without reproducing or hybridise with the local species and, after subsequent backcrosses, characteristics of the displaced become swamped by those of the resident — they 'hybridise away' (Croucher *et al*., 2004; Oxford, 2011). If these present-day patterns really are a result of inoculation by humans then they present another example of how chance influences species distributions; another roll of the dice.

The situation in the north

Documentary evidence, museum material and personal recollections all suggest that prior to the mid-1960s, with just a few exceptions, large house spiders were not found in Yorkshire, Lancashire and counties further north (Oxford & Smith, 1987; Oxford, 2009, 2011). It seems that both *T. saeva* and *T. gigantea* rapidly expanded northwards at this time, presumably from neighbouring counties to the south. The reason(s) for these increases in range are unknown (Oxford, 2009) but are again probably mediated by human transportation. It was argued above that climate is probably not responsible for determining the position of the contact zone in England and Wales because distributions in houses and from the wider countryside correspond. Using the same argument, distributional changes in northern England and Scotland are probably not a response to recent climate change.

The broad-scale mixing of the species had important implications for their interactions, leading to hybridisation and introgression. As mentioned earlier, the relatively recent presence of the two species in Yorkshire and beyond may be a reason for a lack of associations with climatic variables if, indeed, these are influential in determining species distributions. It is highly likely that the local presence or absence of the two species across northern England and Scotland can be explained by chance colonisation events.

Hybridisation and its consequences

As mentioned, across most of England and Wales, *T. saeva* and *T. gigantea* are allopatric. The relatively narrow band of overlap from Dorset northwards along the Welsh border, and the much broader zone across the whole of northern England and Scotland, provide the opportunity for interspecific matings. The presence of individuals with intermediate genital structures in these areas suggests that this does happen (Oxford, 2011). Croucher *et al.* (2007) analysed the proportions of spiders with intermediate morphologies in the area around York and in a comparable area centred on the overlap zone in Dorset. Two different analyses, which took into account the intimacy of species contact in the two areas, strongly suggested that there are relatively fewer hybrids found on the south coast, and more in Yorkshire, than would be expected on the assumption that the propensity to hybridise, given the opportunity, is the same in the two areas. Thus in Yorkshire, hybridisation is rampant compared to that in the overlap zone further south. This begs the questions of how often interspecific matings take place and what are their results?

Interspecific matings

During his investigation of interactions between *T. saeva* and *T. gigantea*, Croucher (1998) set up a number of both intra- and interspecific single-pair crosses in the laboratory, using material from deeply allopatric zones on the south coast and from the zone of overlap in Dorset. More recently, in 2008, I have done the same with spiders collected from west Wales and central eastern

England. The success rate of all 120 crosses is shown in Figure 1 (data from Oxford & Croucher, 2014).

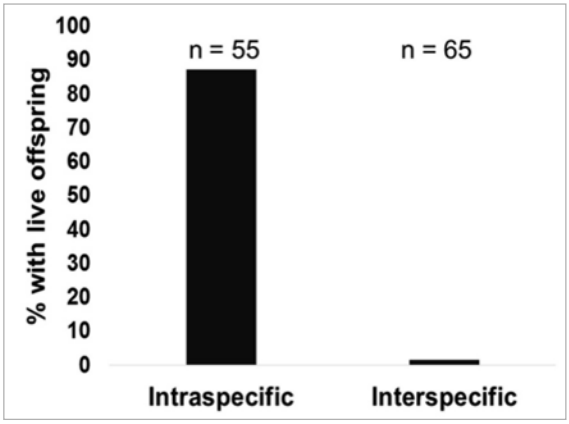

Figure 1. Success rate of intra- and interspecific crosses between *Tegenaria saeva* and *T. gigantea* under laboratory conditions. n = number of crosses.

Forty eight out of the 55 intraspecific matings produced viable offspring, whereas just two out of 65 interspecific matings were successful. One has to bear in mind that in these laboratory matings there was no possibility of (a) competition between males, and (b), sperm competition within multiply-mated females, and so the estimate of hybridisation success is likely to be higher here than that in the wild. Croucher's studies stopped at producing F_1 offspring but my crosses were specifically designed to examine the morphology of known F_1, F_2 and reciprocal back-cross progeny, in order to examine the genetics of diagnostic morphological features and to calibrate intermediate phenotypes found in the wild. Interspecific hybrids, once produced, mate with each other and backcross to both parent species with a success rate indistinguishable from that found within species. The factor impeding hybridisation is clearly acting during the initial courtship between males and females of different species.

The willingness of a male to court and mate was no different when partners were of the same or of different species, implying that the web-borne pheromones that indicate a virgin female are conserved across the species. Female co-operation was also the same, irrespective of the species of male courting. The critical feature turned out to be the length of time for which a male was able to insert his palp into the female epigyne. In interspecific matings, at least some insertions lasted for more than about 40 seconds whereas in the unsuccessful interspecific crosses insertions were on the whole considerably shorter than this. The two successful interspecific crosses had some insertions above the 40 second threshold (Figure 2 shows the data from the later set of crosses only, for the full dataset see Oxford & Croucher, 2014).

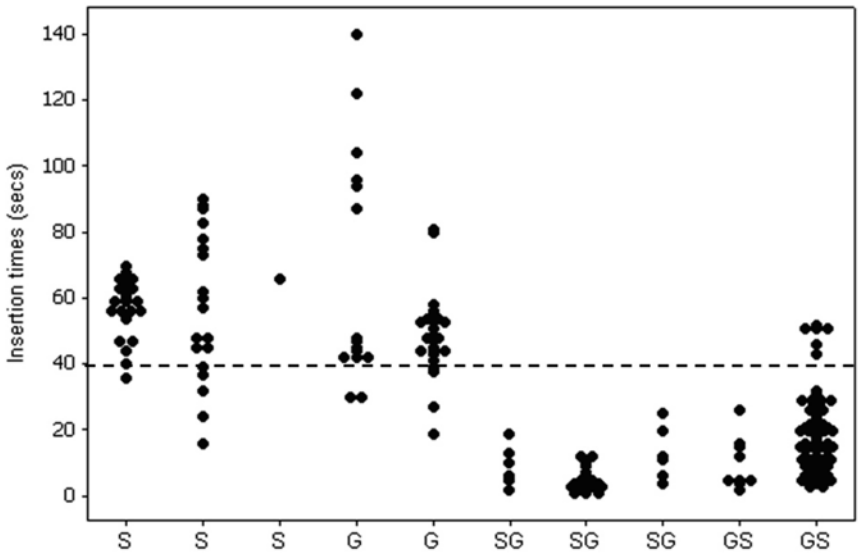

Figure 2. Measurements of male palp insertion durations for intraspecific (S = *T. saeva*; G = *T. gigantea*) and interspecific (SG and GS, female denoted first) crosses. Data shown are from the 2008 collections (see Oxford & Croucher, 2014 for details and the full dataset). The line at 40 seconds suggests a minimum insertion duration required for successful insemination; of the interspecific crosses shown, only the last produced live offspring.

In summary, the barrier to hybridisation between *T. saeva* and *T. gigantea* appears to be almost entirely mechanical; the male palp simply slips out of the female epigyne if it is the wrong species. Very occasionally, the palp insertion lasts long enough for sperm to be transferred and from that point on it seems to be as successful in fertilising eggs as sperm from the female's own species. Once produced, F_1 hybrids can cross between themselves and with both parent species with ease, presumably because their intermediate genital morphology is more compatible with that of their mating partners than was the case with the initial interspecific crosses. We have found no indications that F_1, F_2 and back-cross progeny are less fit than the offspring of intraspecific crosses, at least under laboratory conditions. A positive feedback is therefore set up which favours ever-increasing introgression between the two species.

The case of *Tegenaria atrica*

What of the third member of the *Tegenaria atrica* group, *T. atrica* itself? As mentioned, this species in Britain was generally regarded as an occasional vagrant that failed to establish breeding populations. In 1995 David Smith, a British Arachnological Society member from Burnopfield, Co. Durham, began keeping a record of the spiders found in his house and garden and, to his surprise, discovered a very high proportion of *T. atrica* amongst the large house spiders present. This was apparently the first self-sustaining population of the species in Britain (Smith & Oxford, 2009). We speculated that he might have brought a gravid female back from his continental holidays and, being a newish house, the species may have established in the absence of *T. saeva* and *T. gigantea*. However, he extended the search to his immediate neighbourhood and discovered that *T. atrica* was present throughout. Over

the next few years (2011 – 2013), we expanded the survey to cover the whole of the Newcastle upon Tyne area. We undertook our own fieldwork, examined museum specimens and, *via* the media, encouraged the public to collect and submit spiders found in their own homes. The results were most unexpected (Oxford & Smith, 2014); *T. atrica* was found to be established over a huge area of northern Co. Durham, Tyne & Wear and south-eastern Northumberland (Figures 3 & 4).

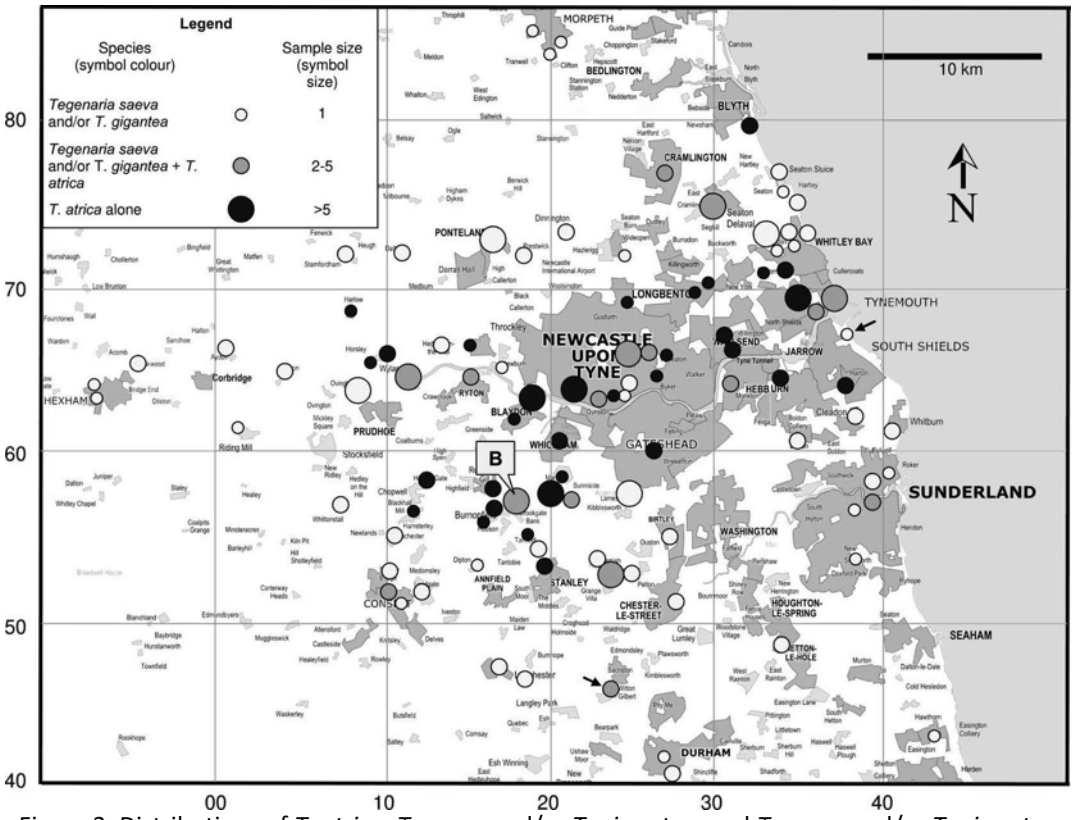

Figure 3. Distributions of *T. atrica*, *T. saeva* and/or *T. gigantea*, and *T. saeva* and/or *T. gigantea* + *T. atrica* in the area around Newcastle-upon-Tyne. Species combinations are indicated by symbol shade and an indication of sample size by symbol size. The original *T. atrica* population from Burnopfield, County Durham reported by Smith & Oxford (2009) is indicated as **B**. Marginal numbers are hectad grid squares within 100 km square NZ of the National Grid.

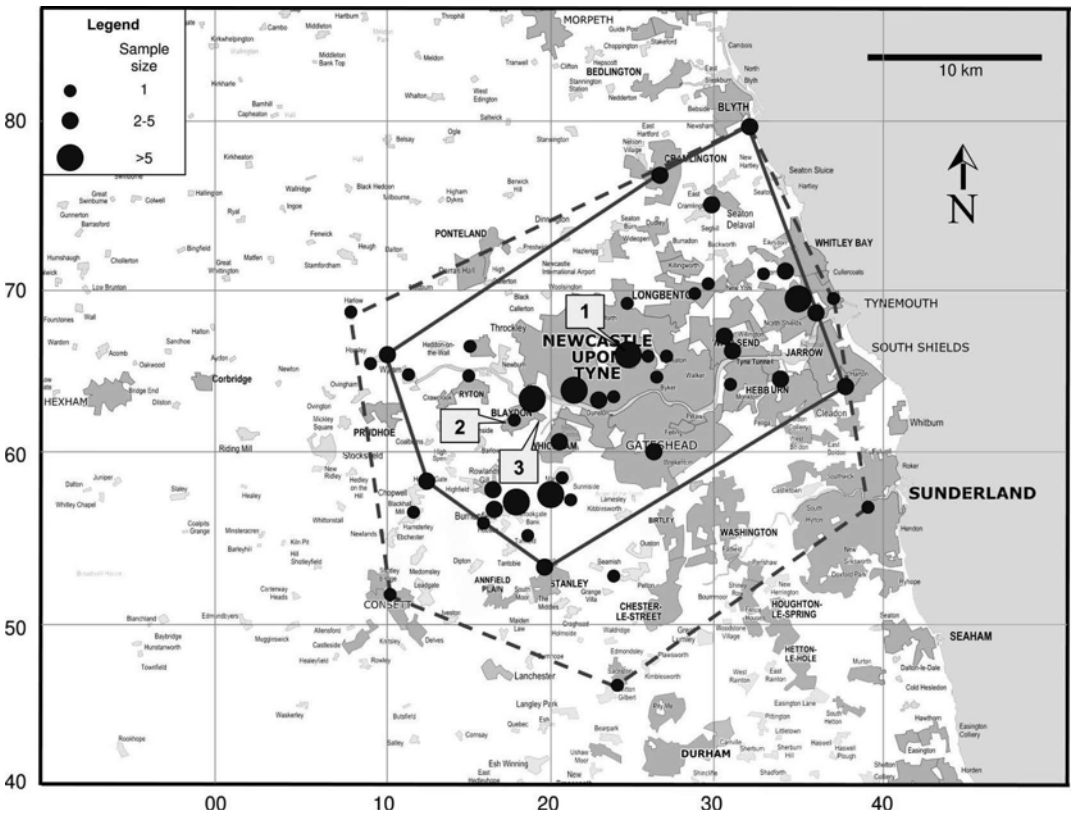

Figure 4. Distributions of *T. atrica* in the area around Newcastle-upon-Tyne. Sample size is indicated by symbol size. The dashed-line polygon joins locations with at least one *T. atrica* record, whereas the solid-line polygon joins locations with two or more *T. atrica* records (see text). Number labels refer to historical records of the *Tegenaria atrica* group: 1 and 2, Hull (1896); 2 and 3, Bagnell & Turner (1913), 1, Parker (1959) – see text. Marginal numbers are hectad grid squares within 100 km square NZ of the National Grid. Map © Crown Copyright/database right 2014. An Ordnance Survey/EDINA supplied service. Reproduced, with permission, from Oxford & Smith (2014).

A convex polygon drawn round the outermost locations suggests that the species is present over some 710 km^2 (Figure 4). However, many of these peripheral sites were represented by single specimens, which may or may not represent viable local populations. If one argues that two specimens are more likely to indicate an established population, the convex polygon linking such locations indicates that viable spider populations may extend over an area of some 400 km^2 (Figure 4). These area estimates are necessarily crude and depend, amongst other things, on multiple specimens being taken from any one location. Although this was the aspiration for the surveys we ourselves conducted, it wasn't always possible. Nevertheless, it is clear that a very large population of *T. atrica* exists in an extensive area in and around the city of Newcastle upon Tyne.

It is worth speculating about the origin of this population and how *T. atrica* interacts with the other two species. As already discussed, before the rapid spread of *T. saeva* and *T. gigantea* in the middle of the 20th century, there were few records of large house spiders in the north, but they were not totally absent. In the present context, Hull (1896) recorded a mature male *Tegenaria atrica*[2] from Jesmond, Newcastle upon Tyne, in 1887 (label 1 in Figure 4) and an immature specimen from Winlaton (undated) (2 in Figure 4). Bagnell & Turner (1913) referred to an immature specimen from Winlaton (probably the same as noted by Hull), and two immature spiders taken from Axwell Park in 1910 (3 in Figure 4). Whether some or all of these specimens represent established populations or merely separate, isolated importations of a *T. atrica* group species is not known, but the geographically adjacent Winlaton and Axwell specimens could well indicate establishment (Oxford 2009). Certainly a female, present-day *T. atrica* was reported from a school in Jesmond in 1949 (label 1 in Figure 4, Parker, 1959; see also Oxford & Smith, 2014). It seems likely therefore that *T. atrica* may have been established in this region at least by the end of the 19th century.

The original introduction of *T. atrica* must have been a chance event, with the inoculum coming most likely from the Republic of Ireland or continental Europe. Newcastle upon Tyne has a long history of importing timber from the Baltic ports, particularly in the mid- to late-1800s (Milne 2006: 144), and this could have provided a possible colonisation route (Oxford & Smith, 2014). That *T. atrica* survived and flourished was possibly contingent on the fact that no other large house spider species were present in the area at the time. Once established, the *T. atrica* population could act as a source for additional chance colonisation events further afield. One possible example of this might be the 1996 discovery by Ian Dawson of a mature male *T. atrica* in a holiday cottage at Low Newton-by-the-Sea, some 59 km north of Newcastle upon Tyne (Oxford & Smith, 2014).

It seems highly likely that a large population of *T. atrica* was well-established in the Newcastle upon Tyne area by the mid-20th century, when the other two species of the *T. atrica* group expanded their ranges northwards. Deducing ecological processes from current patterns of species distributions is not always easy (Warren *et al*., 2014). However, the distributions of *T. atrica* and combined *T. saeva*/*T. gigantea* (Figure 3) seem to suggest that the latter may have been repelled by the presence of an incumbent species, and spread around the *T. atrica* core during their northward expansion. In other words, there seems to be a degree of interspecific competition between *T. atrica* and *T. saeva*/*T. gigantea* although the mechanism(s) underlying possible competitive interactions are unclear.

Although we know more about the Newcastle upon Tyne population of *T. atrica* than any other, the species may also have established in other parts of Britain. For example, several specimens have been received from the Dundee/Perth area of Scotland (Oxford & Smith, 2014). Jackson (1906) reported a population of large house spider at Southport, Lancashire ''. . . where the spider radiates from the Botanic gardens, in which place alone it is abundant''. Bristowe (1939: 47) and Compton (1950: 54-55) refer to this Southport species as *T. larva* (the present-day *T. atrica*). The Botanic gardens have now gone and it is unknown whether a population of *T. atrica* still persists in

[2] Note that at the time *T. atrica* referred to *T. saeva* or *T. gigantea*, not then recognized as separate species; *T. larva* was the name then used for what is now *T. atrica* (Oxford & Smith, 2014). Hull's mature male, supposedly lodged in the collection of the Great North Museum: Hancock, could not be located for positive identification.

that location. The past initiation of viable *T. atrica* populations in the Newcastle upon Tyne and Southport areas is intriguing given the apparent failure to establish of more recent imports (Spider Recording Scheme, 2016). One obvious factor is that, at the time these *T. atrica* populations were founded, *T. saeva* and *T. gigantea* were absent. This again might suggest interspecific interactions such that the species first established is able to resist new arrivals – so called priority effects (Oxford & Smith, 2014). A similar process might also occur at the borders of the *T. saeva* and *T. gigantea* distributions in Wales and central and southern England. Finally, it is worth remembering that the Newcastle upon Tyne population of *T. atrica* was only recognized as being of interest because, by chance, the area was colonised by a species that was otherwise rare in Britain – yet another 'roll of the dice'.

Conclusions

I hope this brief overview has shown that large house spiders in the *Tegenaria atrica* group are not without both ecological and evolutionary interest. As mentioned throughout, chance seems to have played a significant part in determining species distributions at a number of scales. The major east–west split of *T. saeva* and *T. gigantea* across Wales and most of England (Plate 1, centre pages) was most probably a result of chance, human–mediated imports of the two species after the last glaciation. The rapid expansion of both species northwards, starting about half a century ago, essentially obliterated this east–west divide in northern England and Scotland (Plate 1) and provided further, local, examples of founder effects – villages with just one or the other species (Oxford & Smith, 1987). The early species inoculums in northern England and Scotland were also chance events, both in their locations and the species concerned.

In the present case, ecological interactions can only be inferred from species distribution patterns. As pointed out, this can be a problematic task but the patterns seem to be relatively clear and there is also temporal information to aid their interpretation. The population of *T. atrica* around Newcastle upon Tyne was established long before *T. saeva* and *T. gigantea* pushed northwards and seemed able, to some extent, to repel ingression by the new arrivals (Figure 3). Only future monitoring will reveal whether this apparent priority advantage shown by *T. atrica* is ephemeral or not. The reverse situation, where *T. atrica* is prevented from establishing by the presence of the other species, is suggested by the fact that at least two *T. atrica* populations were founded in the north of England (Newcastle upon Tyne and Southport) in the absence of *T. saeva* or *T. gigantea*, whereas contemporary and continuing imports of *T. atrica* further south apparently fail to survive. These situations, if interpreted correctly, are interesting in that competition between spider species has only rarely been detected in the wild (Wise, 1993).

One consequence of the northern expansion and concomitant homogenisation of *T. saeva* and *T. gigantea* distributions was that the opportunity for sexual interactions between species was enhanced. Although the mechanical barriers preventing interspecific hybridisation are effective, they are occasionally breached (Oxford & Croucher, 2014). The F_1 offspring are perfectly viable and fertile and can readily backcross to both parents and cross within themselves. This process will produce a positive feedback with introgression gathering pace as greater numbers of individuals have more compatible genitalia. The result is that both species in Yorkshire, at least, have to some extent converged in morphology such that they are more similar to one another than they are in the allopatric zones further south (Croucher *et al*., 2007). If this process of 'ever closer union' continues it seems likely that these two species will, in the north, collapse into a single entity with genital characteristics intermediate between those of the two parent species. A growing number of examples of this phenomenon have come to light over the last decade or so

(Bettles *et al*., 2005; Taylor *et al*., 2005; Seehausen *et al*., 2008; Webb *et al*., 2011; Ruskey & Taylor, 2016). Hybridisation is a well-recognized mechanism which can lead to the blurring of species boundaries and, potentially, to a loss of biodiversity. Future sampling coupled with analysis of both morphometric and molecular markers will provide information on the trajectory and rate of change of species-merger in northern England.

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Plate 1a. A female Large House Spider *Tegenaria saeva* in a familiar setting.

Geoff Oxford

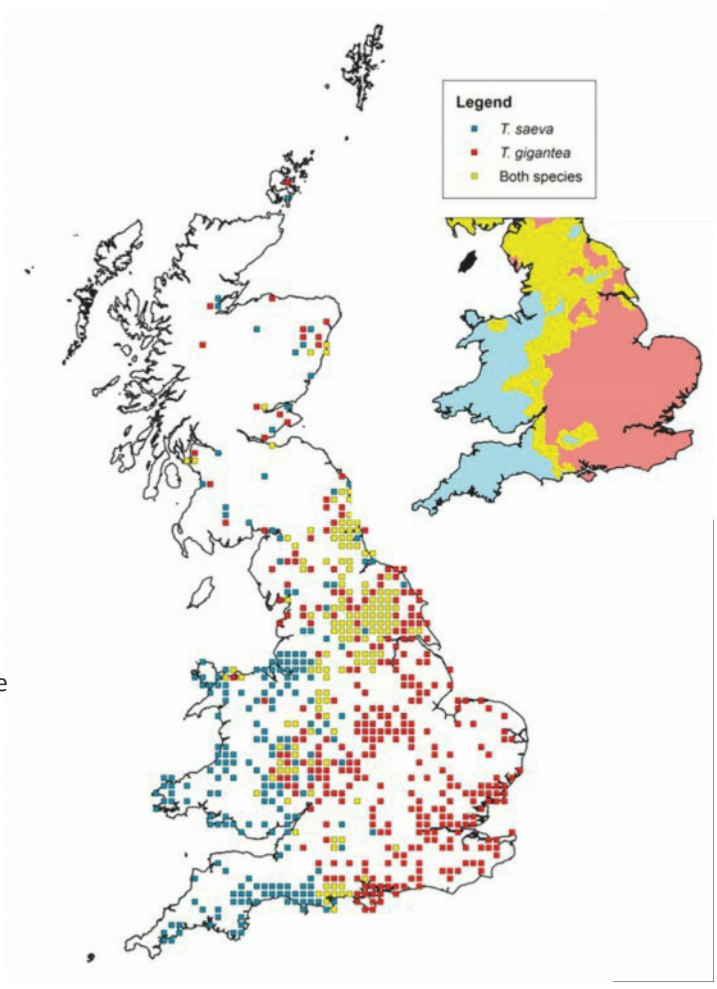

Plate 1b. Hectad distributions of *Tegenaria saeva* (blue) and *T. gigantea* (red) in Britain. Hectads in which both species have been recorded are shown in yellow. The main map includes all data verified by Geoff Oxford or Peter Croucher up to and including 2015. The inset shows an interpolated map generated with data collected up to 2003. For further information on interpolation methods see Croucher *et al.* (2004).