The distribution of *Tegenaria gigantea* Chamberlin & Ivie, 1935 and *T. saeva* Blackwall, 1844 (Araneae, Agelenidae) in Yorkshire

G. S. Oxford
Department of Biology,
University of York,
York, YO1 5DD

and

C. J. Smith
7 Malton Way,
York, YO3 6SG

Summary

Surveys have been made of the distribution of *Tegenaria saeva* and *T. gigantea* in Yorkshire. *T. saeva* is the commoner species in York but occurs at lower frequencies elsewhere. Species proportions also differ on a much more local scale. About 6% of spiders were intermediate between *T. saeva* and *T. gigantea*, both in palp morphology and in relative palp dimensions; these were considered hybrids. There may be absolute differences in palp size relative to carapace length between *T. gigantea* from York and from the south of England.

Introduction

It was only in 1975 that *Tegenaria propinqua* Locket and *T. saeva* Blackwall, 1844 were recognised as separate species in this country (Locket, 1975). Previously, both species had been classified within *T. saeva*. *T. propinqua* was later shown to be synonymous with *T. gigantea* Chamberlin & Ivie, 1935 (Crawford & Locket, 1976). There has been a recent claim that *T. gigantea* is itself synonymous with *T. duellica* Simon, 1875 (Brignoli, 1978), but this identity has not been endorsed in the latest checklist of British spiders (Merrett, Locket & Millidge, 1985).

Because of the confusion of *T. saeva* and *T. gigantea,* our present knowledge of their geographical distributions in the British Isles is scanty. In a paper setting out the major distinguishing features of the three British species in the *Tegenaria atrica* group, Merrett (1980) suggested, on the basis of the material then available, that *T. saeva* is essentially a western species whereas *T. gigantea* is found throughout central and eastern regions of the United Kingdom, although their distributions overlap to some extent. The situation for *T. atrica* C. L. Koch, 1843 is better known: it occurs commonly in southern Ireland but very rarely, probably as a result of accidental introductions, in other parts of the British Isles (Merrett, 1980).

The present study arose from an attempt to map more fully the distribution of all species of spiders in Yorkshire (Smith, 1982). In 1984 a number of *T. saeva* were collected in York; only two previous records of this species were known from the county (Smith, 1985). A small survey was undertaken in autumn, 1984 to investigate the local distribution of this species and of *T. gigantea.* A second, larger survey followed in autumn, 1985 and the combined results from both surveys form the basis of this paper.

Methods

Spiders were collected from throughout Yorkshire, but the vast majority were from York and district and from the larger conurbations to the south and west. Individuals were identified using the characters described by Merrett (1980). In a few cases, species identification was not clear and these individuals were

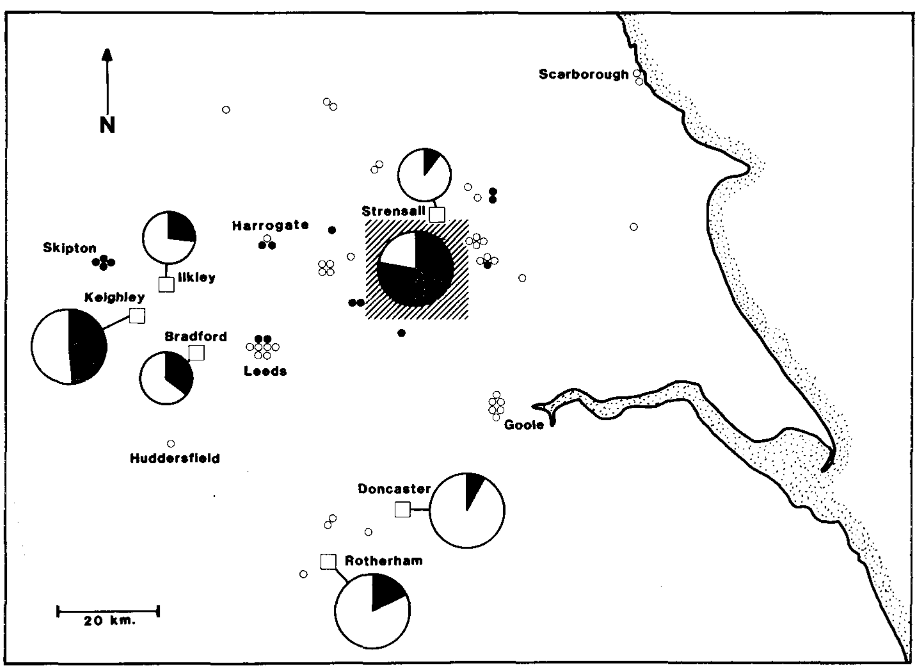

Fig. 1: Distribution of *T. saeva* (black dots and segments) and *T. gigantea* (white dots and segments) in Yorkshire. Where sample sizes are less than ten, individual spiders are shown as dots. For larger samples, relative frequencies are shown as pie diagrams. Sample sizes for these are as follows: Bradford, 17; Doncaster, 51; Ilkley, 15; Keighley, 27; Rotherham, 34; Strensall, 10; York and district (hatched square), 489. Unidentified spiders are not included. More detailed distributions within the York square are shown in Fig. 2

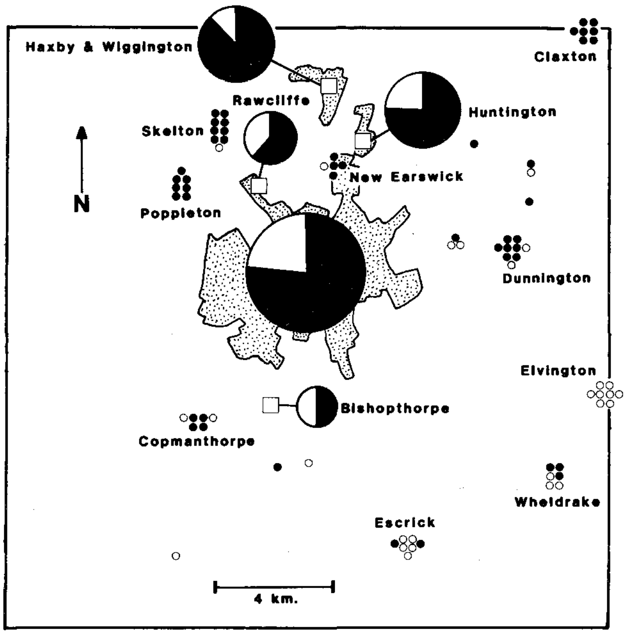

Fig. 2: Distribution of *T. saeva* and *T. gigantea* in the York area. Symbols as in Fig. 1. Sample sizes: Bishopthorpe, 16; Haxby & Wiggington, 60; Huntington, 49; Rawcliffe & Clifton, 36; York city, 241. Unidentified spiders are not included. Major built-up areas are shown stippled.

independently assessed by both of us. A small number were sent to Dr Peter Merrett for verification. As an aid to species identification we measured the carapace length and tegulum + conductor length of males (Merrett, 1980). All such measurements quoted in this paper were made by one person (G. S. Oxford). The date and place of capture for each spider were recorded wherever possible.

Results

In total 729 spiders were examined, of which 295 (40.5%) were *T. gigantea*, 391 (53.6%) were *T. saeva* and 43 (5.9%) were unidentified, having features of both species. In addition, one male *T. atrica* was taken at a garden centre near Poppleton, York (Smith, 1985). Most individuals were males (87.1% of *T. gigantea*, 87.7% of *T. saeva* and 100% of the unidentified group), which is to be expected given the time of year at which the surveys were conducted.

Geographically, there are considerable differences in the proportions of the two species on both a countywide and a local scale (Figs. 1 & 2). The frequency of *T. saeva* is very high in York city, its major suburbs and adjacent villages but falls off rapidly in all directions with distance from York. This species is also found in much lower frequencies in the conurbations of south Yorkshire. In the west of the county, frequencies of *T. saeva* are moderate (*c.* 25%) in the built-up areas of Leeds, Bradford and Ilkley but rise to *c.* 50% or more even further west in Keighley and Skipton (Fig. 1).

Even within York and its suburbs (Fig. 2) the relative frequencies of the species differ significantly (comparison of Haxby & Wiggington, Huntington, Rawcliffe & Clifton, University of York campus and the rest of York city; $\chi^2_{(4)} = 25.2$, $p < 0.001$). The highest frequency of *T. saeva* was found in Haxby & Wiggington (88%, $n = 60$) and the lowest on the University of York campus (39%, $n = 18$).

A plot of the dates of capture of *T. gigantea* and *T. saeva* is given in Fig. 3. For males of the two species it is clear that the distributions of capture dates are virtually identical. If time is measured as number of days after 20 August, the mean day of capture for *T. gigantea* is 37.9 and that of *T. saeva* is 38.7 ($d = 0.94$,

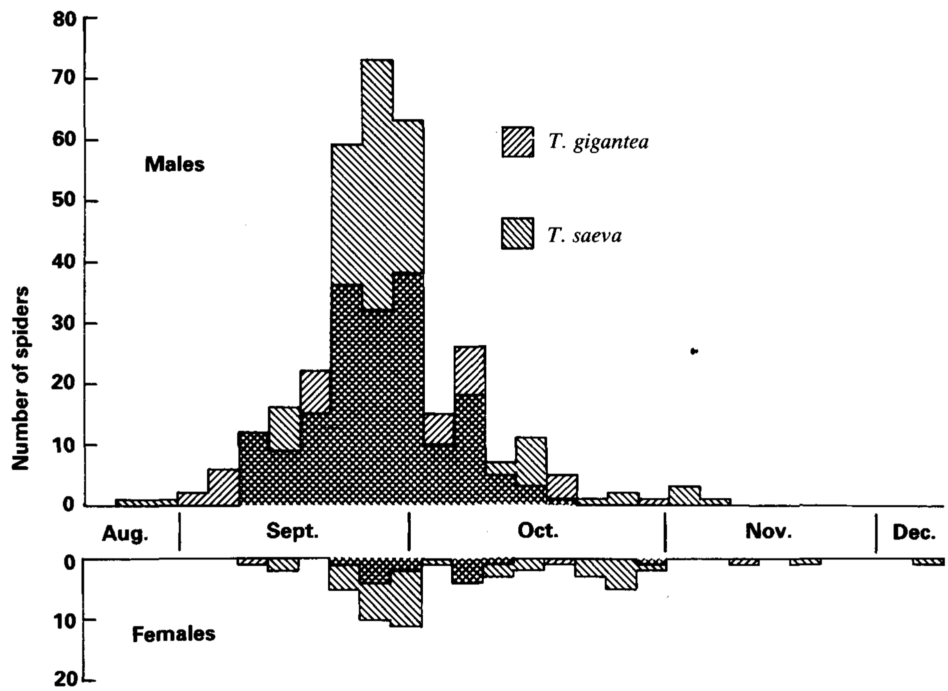

Fig. 3: Distribution of capture dates for males (above) and females (below) of *T. saeva* and *T. gigantea*. Time is plotted in four-day units, starting from 20 August.

n.s.). The same seems to be true for females although the data here are much sparser. As the season progresses, the sex ratio, initially so biased in favour of males, approaches unity.

It is also possible to seek differences between the species with regard to place of capture. This information was available for 149 *T. saeva* and 55 *T. gigantea*. The vast majority (85%) were caught inside houses, the remainder coming from garages, sheds and gardens. There were no differences in the proportions of each species found in houses or found elsewhere ($\chi^2_{(1)} = 1.1$, n.s.).

Merrett (1980) showed that, for males, a plot of tegulum + conductor length against carapace length clearly separated all three of the *Tegenaria* species he studied. As a check on identification the same measurements were made on our material. Plots for a random subset of spiders from York and district are shown in Fig. 4, and the regression equations given in Table 1. The data set is much larger than that used by Merrett (1980) and the variation in the data greater (Table 2). Despite the poorer resolution of the species in Fig. 4, compared with Merrett's plot, an analysis of covariance shows that regression lines fitted to the data for each species do not differ in slope ($F_{(1,254)} = 0.30$) but are highly significantly different in elevation ($F_{(1,255)} = 527$, $p << 0.001$). Also shown in Fig. 4 are measurements made on 24 individuals which could not be assigned to one species or the other on the basis of palp morphology. These specimens were designated as "unidentified" before palp measurements were made. A regression line fitted to these data does not differ in slope, but does differ in elevation ($p < 0.001$ in both cases), from those of the two identified groups (Table 1). Thus, not only are the unidentified

Source	Species	Sample size	Equation
Merrett (1980)	*T. gigantea*	39	y = 0.715 + 0.074x
York + district	*T. gigantea*	90	y = 0.765 + 0.071x
Rest of Yorkshire	*T. gigantea*	102	y = 0.750 + 0.073x
Merrett (1980)	*T. saeva*	57	y = 0.900 + 0.071x
York + district	*T. saeva*	168	y = 0.882 + 0.074x
Rest of Yorkshire	*T. saeva*	25	y = 0.858 + 0.081x
Merrett (1980)	*T. atrica*	12	y = 0.632 + 0.067x
York + district	Unidentified	24	y = 0.835 + 0.072x

Table 1: Regression equations derived from tegulum + conductor length (y) vs. carapace length (x) plots. In all cases p for the regression coefficient is < 0.001.

individuals intermediate in palp morphology, they are also intermediate in tegulum + conductor length for any given carapace length. Similar analyses were carried out on spiders from elsewhere in Yorkshire, as well as on data extracted from fig. 26 of Merrett (1980). Regression lines fitted to each data set are plotted in Fig. 5 and their equations set out in Table 1.

Discussion

It is clear from our surveys that *T. saeva* is not restricted to the western parts of Britain, as suggested by Merrett's data (Merrett, 1980). In Yorkshire, *T. saeva* is widely, but patchily, distributed. It is by far the commoner of the two species in York and the immediately surrounding areas, but also reaches moderate to high frequencies in the west of the county, as might have been expected from Merrett's map.

A lack of museum specimens collected before the mid-1960's, together with anecdotal evidence, suggests that the larger *Tegenaria* species may have only recently become at all common in Yorkshire (Smith, 1985), and apparently elsewhere in the north (Parker, 1984). If this is the case, we have a fascinating situation in which two closely related species are expanding their

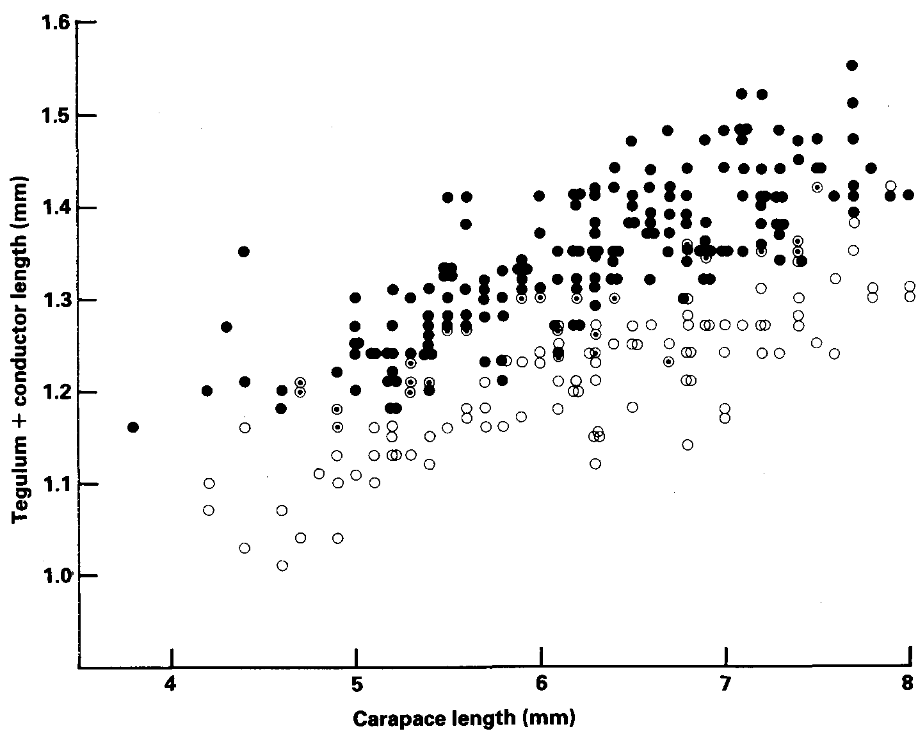

Fig. 4: Plot of tegulum + conductor length against carapace length for a subsample of male spiders from York and district. Closed circles = *T. saeva*; open circles = *T. gigantea*; open circles with dots = unidentified individuals (see text); closed triangle = *T. atrica*.

ranges together, both, presumably, in response to changes in the same environmental factor(s). The nature of this environmental change is unknown; it is tempting to suggest a link with the increased number of houses which are now centrally heated. This may not be the only reason, however, since a number of other spiders which are not synanthropic have also increased their ranges over the last few decades (Smith, 1981).

If the two *Tegenaria* species are still spreading, then they may not have reached an equilibrium with regard to their geographical distributions. If this is the case, their patchy occurrence in Yorkshire might reflect chance colonisation rather than a real difference in distribution resulting from interactions between the species and their environment. Since movement from place to place for synanthropic species will depend largely on the movements of man, a random element will always be a feature of their fine distributions. It is possible, for example, that the species composition of villages like Elvington and Claxton (Fig. 2) results from chance colonisation. Certainly, it is difficult to imagine significant environmental differences between the two places. Only a repeat survey some years hence will throw light on the permanence of the species' distributions described here.

No evidence has been found for a difference in the phenology of the species over the autumn months, or for a difference in their place of capture. The distributions of capture dates for the two species are virtually identical (Fig. 3). Autumn was chosen for the surveys because it is at this time of year that males wander in search of females and, as a result, are readily noticed. The sex ratio bias was therefore expected. In early September, the numbers of males caught increased rapidly, partly as a result of a change in their

	T.s.(M)	*T.s.*(Y)	*T.s.*(RY)	*T.g.*(M)	*T.g.*(Y)
T.s.(Y)	**0.0004**				
T.s.(RY)	**0.006**	0.434			
T.g.(M)	0.436	—	—		
T.g.(Y)	—	**0.028**	—	**0.05**	
T.g.(RY)	—	—	0.199	**0.016**	0.24

Table 2: Comparison of residual mean squares from regression for different data sets. Figures in the body of the table are probabilities, derived from *F* tests, that the residual mean squares from regression are the same for the data sets compared. *T.s.* = *Tegenaria saeva; T.g.* = *T. gigantea;* (M) = Merrett's data; (Y) = York and district; (RY) = Data from the rest of Yorkshire. Significant figures are shown in bold.

behaviour and partly because of an enhanced probability of capture as the surveys gathered momentum. The decline in numbers of males during October, however, probably reflects a real fall-off in their activity, for the following reason. Females are much more sedentary than males and have to be searched for, so the roughly constant rate at which females were caught throughout this month suggests continued interest in the survey. Despite this, there was a steady decline in the number of males captured.

Although the species identification characters noted by Merrett (1980) work well for the vast majority of individuals, about 6% of those examined in the present survey could not be assigned to a species. They had palpal features intermediate between those of definite *T. gigantea* and definite *T. saeva*. Subsequently, plots of tegulum + conductor length against carapace length for these individuals also suggested intermediacy (Fig. 4). It is tempting to regard these animals as interspecific hybrids, a possibility hinted at by Locket (1975) and Merrett (1980) and for which there is

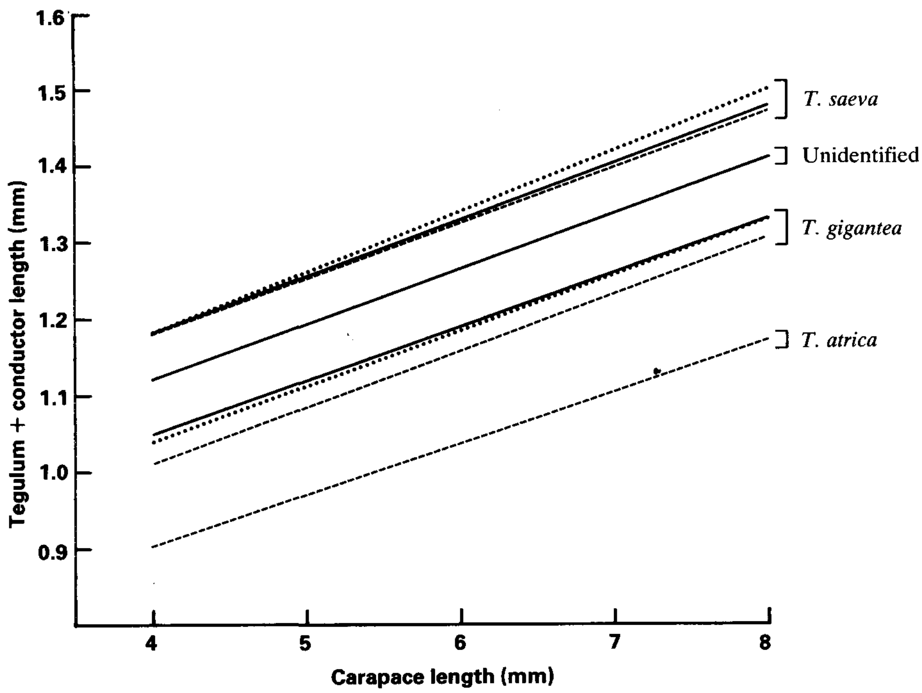

Fig. 5: Plot of regression lines of tegulum + conductor length against carapace length for all data sets. Individual data points are not shown. Solid lines = samples from York and district (see Fig. 4); dotted lines = samples from the rest of Yorkshire; dashed lines = data from Merrett (1980). Sample sizes are as follows: *T. saeva* — York, 168; Rest of Yorkshire, 25; Merrett, 57: *T. gigantea* — York, 90; Rest of Yorkshire, 102; Merrett, 39: *T. atrica* — Merrett, 12: Unidentified — York, 24.

experimental evidence (J. E. Dalingwater, pers. comm.). Of the 46 unidentified individuals, all but one were found in locations in which both *T. gigantea* and *T. saeva* were also taken, thus strengthening the hybridisation hypothesis. The one exception came from Stamford Bridge together with three other spiders, all *T. gigantea*. However, because of the small sample size, the presence of *T. saeva* in this village cannot be excluded.

No female was unassigned to one species or the other yet, given our sample sizes, about five would have been expected. This deficiency is statistically significant ($\chi^2_{(1)} = 6.1$, $0.05 > p > 0.01$). Perhaps the nature of the characters used to separate females of the two species make hybrids difficult to recognise.

These unidentified specimens were picked out because they had intermediate palp characters, but even in spiders classified as *saeva* or *gigantea* there is variation in the size and shape of the distal conductor tip, in the depth of the mid point of the conductor + tegulum, etc., as was pointed out by Merrett (1980). Indeed, there may even be a continuous gradation of characters from 'pure' *saeva* through to 'pure' *gigantea,* although only a detailed numerical analysis would throw light on this possibility.

The slopes of tegulum + conductor versus carapace length plots for all data sets, our own and those of Merrett (1980), are not significantly different ($F_{(7,501)} = 0.21$; pooled slope = 0.073). This means that for *T. saeva, T. gigantea* and *T. atrica,* the incremental change in palp length per unit change in carapace length is identical. There are, however, highly significant differences in the elevation of the regression lines (Fig. 5, Table 1), not only for different species but for different data sets within a species. The elevation of regression lines for *T. saeva* from the York area, from the rest of Yorkshire and from Merrett (1980) are not significantly different ($F_{(2,246)} = 1.51$). In contrast, for *T. gigantea* the elevation for the York area data is significantly higher than that for Merrett's data ($F_{(1,126)} = 17.9$, $p < 0.001$). There seem three possible reasons for this difference. First, our measurements on the palp of *T. gigantea* may have been, for some reason, biased upwards compared with those of Merrett. Second, hybridisation could be responsible. If some hybridisation is occurring in York, and hybrids are backcrossing to the parental species, one would expect a greater impact on *T. gigantea* than on *T. saeva,* because of the numerical inferiority of the former, i.e., one might predict that *T. gigantea* would be closer to *T. saeva,* in the elevation of its regression line, in York material. Third, the relationship between palp and carapace measurements in York and in the south of England, where most of Merrett's material came from (P. Merrett, pers. comm.), may be different for other, unknown reasons.

The first alternative seems unlikely because our data on *T. saeva* give results consonant with Merrett's, and there is no apparent reason why *T. gigantea* should be any more difficult to position and measure. However, until the same person measures specimens from both the north and the south, this possibility cannot be totally ruled out. The second alternative can be tested by looking at the regression line elevation for *T. gigantea* from the rest of Yorkshire, where this species, here in the majority, should be *least* affected by hybridisation. If the elevation of this line is no different from Merrett's, then this alternative would gain some support. On the other hand, if the elevation is no different from that found in York, then the relationship between palp and carapace lengths in the north and the south differ for reasons other than hybridisation. As can be seen from Fig. 5, the elevations of the two Yorkshire data sets agree ($F_{(1,189)} = 0.005$, n.s.; Table 1), so it appears that northern and southern populations of *T. gigantea* really do differ in this respect. For any carapace measurement, the tegulum + conductor of northern spiders is, on average, about 0.042 mm longer than that of spiders from the south. It is intriguing that *T. saeva* shows no comparable pattern.

It would certainly be of great interest to investigate the fine distributions of *T. gigantea* and *T. saeva* in other areas of Britain, in particular in regions where both species have been present for a long time or where the species are just appearing. The relationship between carapace length and tegulum + conductor length in other, relatively circumscribed, populations also warrants further attention.

Acknowledgements

We acknowledge with sincere thanks the help of local newspapers and radio, and BBC Television, in publicising our appeal for specimens. The museums in Bradford, Doncaster, Goole, Ilkley, Keighley, Leeds, Rotherham and York supported our survey and acted as collecting stations; we thank the curators for making this possible. Dr Peter Merrett kindly checked our identification of certain specimens. Finally, we record our gratitude to all those people who took the trouble to collect spiders for us; without their support this survey would not have been possible.

References

BRIGNOLI, P. M. 1978: Quelques notes sur les Agelenidae, Hahniidae, Oxyopidae et Pisauridae de France et d'Espagne. *Revue suisse Zool.* **85**: 265-294.

CRAWFORD, R. & LOCKET, G. H. 1976: The occurrence of *Tegenaria gigantea* Chamberlin & Ivie (1935) in North America and Western Europe. *Bull.Br.arachnol.Soc.* **3**: 199.

LOCKET, G. H. 1975: The identity of Blackwall's *Tegenaria saeva* (Araneae, Agelenidae). *Bull.Br.arachnol.Soc.* **3**: 85-90.

MERRETT, P. 1980: Notes on the variation, identification and distribution of British species of the *Tegenaria atrica* group (Araneae, Agelenidae). *Bull.Br.arachnol.Soc.* **5**: 1-8.

MERRETT, P., LOCKET, G. H. & MILLIDGE, A. F. 1985: A check list of British spiders. *Bull.Br.arachnol.Soc.* **6**: 381-403.

PARKER, J. R. 1984: Synanthropic spiders and other things — Part 2. *Newsl.Br.arachnol.Soc.* **39**: 1-2.

SMITH, C. J. 1981: Spiders in Yorkshire. *Naturalist, Hull* **106**: 45-52.

SMITH, C. J. 1982: An atlas of Yorkshire spiders. 1-134. Privately printed.

SMITH, C. J. 1985: The distribution of the larger *Tegenaria* spider species (Agelenidae) in the York area. *Newsl.Br.arachnol. Soc.* **42**: 5-6.