The biology of *Tuberta maerens* (Araneae, Agelenidae)

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Summary

The small agelenid *Tuberta maerens* (O. P.-Cambridge) is remarkable for its long lifespan (up to four years in captivity), small number of moults after leaving the egg sac (three) and small clutch size (three). It appears to be local because it is highly specialised to certain substrates and (warm) microclimatic regimes, particularly on tree trunks, and is slow to disperse. Psocoptera are probably important in the diet, and an ichneumonid wasp, *Gnypetomorpha* sp., is a significant egg parasitoid in at least one site.

Introduction

Tuberta maerens (O. P.-Cambridge) (Agelenidae) was until recently considered a very rare spider (Roberts, 1985): by 1985, only 11 adult specimens were known from Britain, and few from elsewhere in Europe. In 1980–1981, a few specimens were taken by pooter from the trunks of oak trees in Britain (D. Steel, pers. comm.), and this led to the discovery of the general habitat of this spider in 1986, as described below; many more specimens were subsequently found. The species is listed as "Rare" in the *British Red Data Book* (Merrett & Hambler, 1991) because the number of sites known is still small.

In this paper the life history and general biology are described, whilst details of microhabitat within woodland are presented elsewhere (Evans & Hambler, 1995).

The fundamental details required to understand the ecological strategy of a species of spider are suggested by Duffey (1978). Such data are available for few species, and even fewer threatened species (Bratton, 1991). This paper adopts Duffey's general framework, after describing the nature and placement of the web.

Web type

The web of the species had apparently not been seen in the wild until 1986, although it had been observed in captivity (F. Murphy, pers. comm.). It is a very small, fragile, funnel web of colourless silk, tapering only slightly and rapidly becoming a tube. The outer area of the funnel is ill-defined, often between 2–6 mm across — although the spider can sense prey at greater distances. When viewed directly along the axis of the funnel, there is a characteristic circular aperture, from 0.75–2.5 mm in diameter (varying with maturity of the spider). Occasionally there are two apertures, and rarely three, sometimes adjacent and sometimes at opposite ends of the tube. The funnel leads into a tubular silk retreat of roughly the same diameter as the aperture, then merges with the walls of the substrate.

The apertures of webs face out of crevices, usually on the bark of a tree trunk. The aperture may point upwards, downwards, or horizontally, depending on the opportunities the particular crevice presents for the construction of the retreat. Often, the aperture is at the apex of a crevice in the bark.

Taxonomic relations

T. maerens is close to *Cryphoeca* and *Mastigusa*; the habitat and form of the web most closely resemble *Cryphoeca*.

Geographical distribution

The species is reported from Austria, England, France, Germany, Hungary, Italy and the Balkans (Bonnet, 1959; Bristowe, 1939).

In England, the species is known from the following sites, with the Watsonian vice-county and the dates of records:

Brasenose Wood, Oxfordshire, 1985–1994 (D. Steel, pers. comm.; pers. obs.).
Wytham Woods, Berkshire, 1953, 1987–1993 (Locket *et al.*, 1974; pers. obs.).
Bagley Woods, Berkshire, pre-1939 (Bristowe, 1939).
Little Wittenham Wood, Berkshire, 1986 (pers. obs.).
Savernake Forest, Wiltshire, 1986–1987 (pers. obs.).
Chobham Common, Surrey, 1981 (F. & J. Murphy, pers. comm.).
Bloxworth, Dorset, 1862, 1879, 1883 (O. P.-Cambridge, 1863; 1881; 1885).
Horton Common, Dorset, 1980 (Merrett, 1980).

Habitat preferences

Range of variation in habitat

The species occurs in relatively open and sunny wooded areas, and occasionally on heathland. It has been recorded most often and abundantly from the trunks of oak (*Quercus robur*) (e.g. Brasenose, Wytham, Little Wittenham, Savernake).

However, a few specimens have also been found on the trunks of Scots pine (*Pinus sylvestris*), both on a dead trunk (at Chobham Common), and on live mature trees (at Savernake). A few have been found on the bark of mature birch (*Betula* sp.), beech (*Fagus sylvatica*), and (with eggs) on yew (*Taxus baccata*) in Brasenose Wood. A female was found on iron railings near woodland (O. P.-Cambridge, 1881: 571); an immature female (the type specimen) among low plants in a wood near Bloxworth (O. P.-Cambridge, 1863), another immature female among moss in the same wood (O. P.-Cambridge, 1885), and an adult male in a pitfall trap on dry heathland at Horton Common, again near woodland (Merrett, 1980).

In continental Europe, the habitats are less well known, but include crevices in the bark of elm trees (*Ulmus* sp.) in parkland in Germany (Bertkau, 1884). Bertkau observed that whilst the species appears rare, knowing where it lives reveals it to be more common.

Main, secondary and subsidiary habitats

The main habitat is the trunk of trees which have sufficient and suitable texture on the bark for the anchorage of the capture web and concealment of the retreat. It has so far been found on trees in the range 30–90 cm diameter at breast height (d.b.h.). The species occurs from ground level up to a height of at least 7 m, and occurs also on felled trunks and cut tree sections. It also occurs on major branches with suitable bark.

Apparently minor habitats include crevices beneath loosely fitting bark on dead trunks (F. Murphy, pers. comm.; pers. obs.). The records from railings and heathland may be of dispersing individuals, although it would not be surprising if some populations occur in crevices in soils, walls, etc. with physical and micro-climatic similarities to bark.

Habitat characteristics

The habitats from which the species is known are primarily relatively open woodland, or parts of woodland where the bark of trees is relatively dry and warm. This was anticipated by Bristowe (1939) from the southerly distribution, and is explored in more detail elsewhere (Evans & Hambler, 1995). Suitable conditions occur on scattered trees in some woodlands (Savernake Forest), in small groups of trees in others (Little Wittenham), and quite widely in a few woodlands (Brasenose Wood). The latter site is coppice with standards, and has been so for hundreds of years excepting a recent interruption in the cycle for about 40 years (D. Steel, pers. comm.).

The sites are also generally ancient woodland (i.e. sites which have been wooded for at least 400 years). Abutting on Brasenose Woods there is secondary woodland some 200 years old, in which a few specimens have been found although few trees are old enough to have suitable bark. An area of secondary woodland a few hundred metres from Brasenose Wood also has an apparently small population. The species appears rare in parkland with apparently suitable trees adjacent to Brasenose Wood, suggesting that a woodland understorey, or closely spaced trees, are as important as the bark itself.

Life history

Development and age at maturity

Two specimens were reared from eggs, in tubes containing paper or small fragments of wood as support for the webs, at about 20°C in a north-facing window. Nymphs (Foelix, 1982) emerge from the egg sac, leaving in the sac the remains of earlier stages but no nymphal cuticles. On hatching from the egg sac, nymphs are some 0.78–0.91 mm long when live (mean 0.85, $n=4$) and 0.90–1.15 mm long (mean 1.04, $n=6$) when preserved. Carapace length for recently emerged nymphs when live was 0.43–0.45 mm (mean 0.44 mm, $n=3$). Nymphs are initially orange in colour, but darken before the first moult. A male and a female were reared, each taking only three moults to reach adulthood after emergence from the egg sac. The male was evidently sub-adult, with large palps, after the second nymphal moult. Details of the size of the moulted nymphal cuticles are given in Table 1. It is remarkable that at emergence from the egg sac the first nymphal instar is already about one-half the size of the adult. The male became adult after 16 months, and the female after 20 months, although this may reflect differences in success of feeding these captive individuals.

Instar after emergence	Total length	Carapace length	Sternum length	Femur I length	Tibia I length	Chelicera length
1 (male)		0.55	0.35	0.40	0.35	—
1 (female)	—	—	0.33	—	0.21	0.21
2 (male)		0.65	0.40	0.50	0.35	0.25
2 (female)	—	—	0.33	—	0.33	0.21
3 (male)		0.69	0.42	0.60	0.54	0.30
3 (female)	—	—	0.46	0.46	0.54	0.29
Adult ♂	1.85	0.85	0.50	0.65	0.55	0.33
Adult ♀	2.18	0.88	0.52	0.65	0.56	0.31

Table 1: Approximate dimensions (mm) of *T. maerens* raised in captivity (one of each sex). Instar 1 is the first nymphal instar which emerges from the egg sac. The adult female was not measured, and its estimated dimensions are derived from 5 wild females. Measurements for juveniles are taken from moulted cuticles. Measurements for adults are from preserved specimens.

Longevity

A captive-reared male survived in total 17 months after emergence, maturing on 9 April 1989 and dying on 22 May 1989. A reared female survived 32 months, maturing on 26 August 1989, and dying in August 1990. A female taken as an adult from the wild survived 20 months in captivity.

It is possible that females may live over two years as adults and four years in total.

In the wild, males appear to be active for only part of the year, and have shorter lifespans overall than females. Live male specimens lived at most 6 weeks in captivity, although they occasionally built weak webs and fed in these or in empty webs they encountered.

Number of eggs and egg sacs

T. maerens lays a remarkably small number of eggs: a sample of 50 egg sacs from Brasenose Wood, 1987–1993, recorded 2.74 ± 0.08 (S.E.) eggs per sac (judged by remains in the sac). Clutches of one and four eggs were rare. Eggs are pale yellow-brown, average diameter 0.72 mm ($n=7$, from five clutches), and are not quite circular, with diameters ranging from 0.70–0.77 mm depending on orientation.

The egg sac is a weakly bi-convex lenticular structure of white silk, circular in horizontal section and oval in transverse section. One face is fixed to the substrate, and the outer face is usually camouflaged with lichen and detritus. The sac is 2.49 ± 0.04 mm in diameter ($n=70$).

Sacs are usually in or beside webs, within a crevice, but are occasionally on the exposed surface of the bark (not obviously associated with webs, and so well camouflaged as to be virtually invisible).

Two spiders in Brasenose Wood were observed to take 3–4 h from the point of laying to leaving the sac. Three spiders were observed laying on a bright but shady day at 11°C and 75–85% RH on 21 October 1987. Laying was divided into phases as follows, with the duration of each noted: (1) production of the plate on which the eggs are laid: duration probably over 1 h; (2) egg laying and compression of the eggs into the plate: 4 min; (3) production of the covering plate by repeated trips between the edge of the sac and the centre, whilst waggling the body and depositing multiple strands of silk (eggs barely visible after 5 min): 1–1.5 h; (4) collecting (in the chelicerae) lichen and other material from the bark, from up to 2 cm away, and, whilst apparently chewing it between the chelicerae, embedding this material in the developing outer silk plate, with occasional lifting of the sheet: 2.5–3 h. The females then retreated into crevices 2–10 cm from the sac.

The number of sacs laid by a female in a lifetime is unclear. In some crevices, a few cocoons can be found glued together with slight overlap: these may be from one or more females. However, egg sacs appear very rare, relative to female abundance, throughout the year, and it seems likely that females lay very few sacs in their lifespan.

In comparison, *Mastigusa macrophthalma* (Kulczynski) lays 3–5 eggs, 0.8 mm in diameter, in a "lenticular" sac some 4 mm in diameter, sometimes in groups of up to five; it uses bluish silk, unlike *T. maerens*, but does "decorate" webs with detritus (Crocker, 1973). *Cryphoeca silvicola* (C. L. Koch) makes small, white, "plano-convex" egg sacs (Nielsen, 1932). The described shape of these sacs appears similar to *T. maerens*.

Breeding season and duration

Adult males have been found in Britain between July and October. However, at Brasenose Wood, they are rare after August. In contrast, females can be found throughout the year, although they are easier to find, and probably more plentiful, from May to October. Immatures of all sizes (except possibly the smallest) are present throughout the year.

In Brasenose Wood egg sacs with undeveloped eggs have so far been found between October and March; this suggests eggs can be produced after most males are dead. Egg sacs containing developed eggs or nymphs have been found from December to March, and a sac containing nymphs on 8 August. Although the duration of the laying period is unclear, it appears prolonged.

Eggs which were laid on 11 October, and egg sacs collected on 6 and 25 March, all hatched after about ten weeks in captivity at 20°C. The young spiders leave the sac through a small hole they cut in the upper surface, near the edge.

Very small nymphs may be found in the old webs of their mother — although different generations have not been observed co-existing.

Dispersal

Dispersal is probably achieved by walking and by descent on silk threads (as when individuals are disturbed or extracted from crevices). The adult female found on railings in April (O. P.-Cambridge, 1881) may have been dispersing; adult females occasionally run on trunks by day (pers. obs.). Males are most active on the tree trunks by day during the late spring and early summer, presumably looking for mates (Bertkau, 1884).

However, dispersal powers appear limited: secondary woodland only 500 m from Brasenose Wood has apparently suitable trees but few *T. maerens*. Moreover, patterns of abundance within the coppice cycle suggest that the species does not colonise rapidly (Evans & Hambler, 1995). Poor dispersal may also limit the suitability of parkland and other habitats with widely spaced trees.

If dispersal was common, the species would be expected to be encountered more often in arachnological surveys, yet it has not been taken by sweeping or beating, and only once by pitfall trapping in Britain.

Prey preferences

In captivity, the species thrives best on Psocoptera, and the young find juvenile Psocoptera particularly manageable; however, a juvenile in a web pounced on a psocopteran twice its own length, and fed on it for 3.3 h within the retreat, turning it occasionally. Whitefly (Homoptera, Aleyrodidae), very small Diptera (usually smaller than *Drosophila*) and Collembola are taken.

In the wild, food preferences are difficult to observe: the spiders eject chewed food remains from the entrance of the web. It seems likely that Psocoptera and possibly Collembola are the main prey in the wild, since they are present in abundance and in a range of sizes on the trees where the spider is found. The remains of aphids (Homoptera) and Collembola were found in some webs, although these may have originated from other species which had used the same crevices.

In captivity these spiders drink readily if water is supplied occasionally: spiders run out several cm from the web to find droplets if water is sprayed at the webs, and a drinking bout may last over two minutes from a single drop.

Mortality

An adult female was found on 31 August 1988, in Brasenose Wood, in an unusual position: exposed on the trunk of an oak, at a height of about 1.5 m. This individual had three finger-like fungal fruiting bodies protruding horizontally from the abdomen. These were

grey/white in colour, approximately 0.3 mm long and under 0.1 mm in diameter.

Egg sacs were sometimes seen on tree trunks with the outer plate absent: this may reflect predation by birds. Egg sacs were sometimes found in crevices with large tears in the outer plate, which may be due to invertebrate predators.

In Brasenose Wood, between 0–3 m up the oak trunks, some 16% of egg sacs ($n=100$) were parasitised by one of Britain's smallest ichneumonid wasps, *Gnypetomorpha* sp., which grows within the egg sac. This proportion was much higher (28%) in a sample taken on 6 March 1994 from 4–7 m up a recently felled oak tree, when 85 sacs were collected in the following numbers: unparasitised, unhatched 12; unparasitised, hatched 45; parasitised, parasite unhatched, 3; parasitised, parasite hatched 21; unhatched or dead, other causes, 4.

This wasp was first reared from an egg sac collected on 1 November 1987, and hatched in April 1988. A male wasp hatched on 2 April from an egg sac collected on 6 March, and a sac collected in September also had a parasite emerge; since temperature and lighting were artificial, the phenology of the wasp is still unclear, but it seems likely to become adult at least in spring or summer.

This species of *Gnypetomorpha* appears new to science (M. R. Shaw, pers. comm.); specimens are in the National Museums of Scotland. Its brown, lozenge-shaped pupal cocoon fits snugly across the diameter of the egg sac, and it may have co-evolved with *T. maerens*.

Associated spider species

No systematic records have been made in the different sites, but those species which are commonest on the same tree trunks within Brasenose Wood are those most often found with *T. maerens* elsewhere in Britain. Most of the species below can also be found within Wytham, Savernake, and Little Wittenham Woods.

Species which have been found (pers. obs.) on the trunks of more than 50% of the trees with *T. maerens* within Brasenose Wood were: *Amaurobius fenestralis* (Stroem), *Clubiona brevipes* Blackwall, *Theridion mystaceum* L. Koch, *Milleriana inerrans* (O. P.-Cambridge), *Meioneta innotabilis* (O. P.-Cambridge) and *Drapetisca socialis* (Sundevall).

Species found on the trunks of 5–50% of trees with *T. maerens* in Brasenose Wood were: *Lathys humilis* (Blackwall), *Harpactea hombergi* (Scopoli), *Anyphaena accentuata* (Walckenaer), *Philodromus praedatus* O. P.-Cambridge, *Anelosimus vittatus* (C. L. Koch), *Zygiella stroemi* (Thorell), *Nuctenea umbratica* (Clerck) and *Lepthyphantes obscurus* (Blackwall).

In Germany, Bertkau (1884) found the species on elm trunks with numerous *Dipoena torva* (Thorell).

In contrast, it is notable that I have never been able to find *Cryphoeca silvicola* or *Segestria senoculata* (L.) on the same tree as *T. maerens*. The former (with very similar but slightly larger webs) appears to replace *T. maerens* in identical locations in all sites examined north of Oxford. The latter may replace *T. maerens* on very large trees, and in more open habitats.

Conclusion

T. maerens does not fit neatly into the r-K ecological continuum: it is a small organism, producing relatively large young. Its specialisms seem likely to render it susceptible to habitat change, and its presence may indicate long continuity of certain woodland micro-habitats at a site.

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