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The 'Noble false widow' spider *Steatoda nobilis* is an emerging public health and ecological threat.

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ABSTRACT

Steatoda nobilis, the 'Noble false widow' spider, has undergone massive population growth in southern Britain and Ireland, at least since 1990. It is greatly under-recorded in Britain and possibly globally. Now often the dominant spider on and in buildings in the region, the species occurs on many items which increase a risk of bites to people - including household furniture, railings, handles, lighting and street furniture. There is a lack of awareness amongst the public, medics and arachnologists as to the likely bite rate and severity with this spider, and there is under-recording of bites. There is thus a possibility of bites being left without adequate rapid treatment and monitoring - with a low but non-trivial risk of necrosis or sepsis. A plausible incident of anaphylactic shock is identified, requiring professional confirmation and case study. Further study of bite significance is urgently required but a typically precautionary approach should be adopted in the interim. A lag of over a century between introduction and the species rapidly becoming common in Britain indicates the risk of complacency over invasive species. Local eradication will be very difficult, so education is required on identification and response to possible bites. The species may become a widespread public health concern and a global conservation problem - particularly on islands with endemic invertebrates. Arachnologists typically have a conflict of interest which may result in understatement of risks. Research priorities include: assays for venom cytotoxicity and microbial carriage; improved immunological and clinical surveillance for possible spider bites; and monitoring of the global distribution and ecological impacts. This paper aims to facilitate and stimulate inter-disciplinary knowledge exchange and gathering, to enable more appropriate and proportionate responses to bites, infestations and invasions.
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Keywords: anaphylaxis • bite • education • microbiome • necrotic arachnidism • public health • ulcer• urban • venom

Introduction and aims

Steatoda nobilis (Thorell, 1875), often called 'the noble false widow spider', is widely regarded as the most dangerous spider breeding in Britain. Its recorded global range is expanding (Vetter & Rust 2015; Faúndez & Téllez 2016; Dunbar *et al.* 2018a, b; Bauer *et al.* 2019). It would therefore be expected that the species' distribution and abundance were well studied, and indeed, given its potential conservation relevance, there is a need for fuller investigation of its distribution (Dugon *et al*. 2017). However, I report here a very substantial increase in abundance, and associated under-recording, of *S. nobilis* in England, which indicate a very much greater likelihood of bites to people than is widely appreciated. The societal consequences have become non-trivial, with the recent closure of several schools (Murphy 2018) and fumigation of a block of flats in London. This is despite the widely reported observation that there have been no confirmed deaths or necrosis caused by *S. nobilis* (but see Dunbar *et al*. 2019) and that many bites ascribed to spiders globally, even by medics, are erroneous or unverified (Stuber & Nentwig 2016).

Whilst it is very likely that most people will not suffer serious consequences from a bite by *S. nobilis*, it is important to review how prevalent and medically significant this spider species is in the light of new information which might help a very small minority of patients with a much more severe reaction - as with the very closely related brown widow spiders *(Latrodectus geometricu*s C. L. Koch, 1841) which have previously been considered of minor significance (Goddard *et al*. 2008; Arnold & Ryan 2009). Globally there are tens of species of 'false widow' spiders (genus *Steatoda*) and *S. nobilis* is the one most commonly referred to as "the false widow" in Britain (where six *Steatoda* species are recorded). *S. nobilis* bites to humans have now been confirmed from Britain (Warrell *et al*. 1991), Chile (Faúndez & Téllez 2016) and Ireland (Dunbar e*t al*. 2017).

Awareness of the ecological context of infestations and of the improbability of eradication once established outdoors may permit more considered societal responses. Assessing the risk to public health and conservation requires use and expert screening of both the specialist literature and of numerous blogs, newspapers and other, often unreliable sources. Informal sources require the usual degree of scientific caution, especially for so emotive a topic which is often dramatised - but to ignore or as has often happened simply discount these observations risks missing accurate records and insights worthy of further investigation and could delay better understanding. Many media reports are quoted here as illustrative of errors, rather than as factual records. Media outreach by scientists working on *S. nobilis* has presented discoveries before formal publication, enabling links between disciplines to be proposed here. There may be a role for 'citizen science' in monitoring this distinctive spider and its effects, and this requires expert survey design and validation of reports (Henderson & Southwood 2016).

This paper is an attempt to highlight knowledge gaps and to improve surveillance and reporting of both the health impacts and the ecology of the species, in order to develop more appropriate responses to individual bites and to infestations. The intent is to facilitate inter-disciplinary debate, hasten correction of errors, and discourage potentially dangerous comments by spider enthusiasts. It draws on arachnological experience to assess media reports which appear hitherto to have been dismissed or overlooked by many commentators and researchers.

In particular, there is a need to improve communication between arachnologists clinicians, and public health authorities, in order to gauge more accurately the risks from this species and the types of precautionary policy, contingency planning and materials that might be appropriate in a range of locations. I present biological observations including novel video evidence that demonstrate some public statements about this species by experts on invertebrates are highly misleading. I also explicitly speculate and present testable hypotheses and predictions - which researchers with appropriate resources and skills might follow up.

I consider first the evidence of very rapid *S. nobilis* population expansion in urban environments in Britain, leading to greatly increased likelihood of bites to people in the last few decades. I then consider the incidence and possible effects of bites (aiming to precipitate discussion). I stress how a proportionate societal response is required and might be achieved. I then consider the ecology and behaviour of *S. nobilis*, including thermal tolerances and evolutionary origins relevant to increasing globalisation of health and conservation risks. I conclude with a summary of proposed research priorities, many of which will require inter-disciplinary teams.

Life-cycle

Aspects of the life-cycle of *S. nobilis* are described by Snazell & Jones (1993), Vetter & Rust (2012), Dugon *et al.* (2017) and B.A.S. (undated) and are supplemented here by personal observation. It is likely there is substantial variation between individuals and populations, so values given here are provisional. Females lay up to c. 200 eggs in each bluish-white egg sac, and may produce a few egg sacs in a year and several in a lifetime. Eggs hatch after an average of 18 days at $20_{o}C$. Spiderlings remain in the web at variable density for a variable period, likely with parental guarding and possibly other parental care known in the Family Theridiidae (Foelix 1982). Cannibalism amongst juveniles occurs in captive populations. Females take up to two years to become adult and may survive to a third year (B.A.S. undated) although there are media reports some may live up to 7 years. Adults of both sexes can be found year round in Britain (B.A.S. 2019a).

The web has similarities to both 'scaffold' and 'sheet' webs built by other spider species (Foelix 1982). Webs often appear as an undulating sheet or 'hammock' with depressions at the points the sheet is anchored to the surface beneath. There is an irregular tangle of silk below, and particularly above the sheet, which serves both to catch prey and anchor the web. The silk is sticky and strong. It has a tubular retreat (at various angles to the web dependent on suitable structures and crevices). The retreat is typically in a tubular crevice, but occasionally in the angle between two surfaces - particularly for juveniles. Older individuals which have laid eggs often have a gourd-shaped retreat and a few strong threads forming an anchor and scaffold - sometimes without much of an associated sheet. The species can survive in buildings for several months on little food and no water even as a juvenile, making dispersal by humans easier. Adult male specimens found indoors often look emaciated, possibly from desiccation, and some build simple webs in captivity.

Until familiar with the species' web, it could easily be mistaken for a member of the family Linyphiidae, or a *Tegenaria* (Agelenidae) or another of the Theridiidae including *Steatoda grossa* (C.L. Koch, 1838). Its retreat could be mistaken for *Zygiella* species (Araneidae) and *Tegenaria* species. If resting on a wall, from a distance the male looks rather like a *Metellina* species (Tetragnathidae) or *Amaurobius* species (Amaurobiidae). The general body pattern could be confused with *Zygiella* at a distance. Two of the most similar species in northwest Europe are compared with two of the many body patterns of *S. nobilis* in Figure 1.

Changes in local abundance and distribution and substantial under-recording in Britain

A rise in abundance of *S. nobilis* has roughly coincided with increased media coverage of spider bites in Britain (Bauer *et al*. 2019). Here I demonstrate the abundance and distribution of *S. nobilis* in Britain has increased rapidly in recent decades, likely leading to an increased bite rate and thence media coverage. Time series maps or diagrams showing the spread of records in Britain are available from B.A.S. (2019a) and Bauer *et al*. (2019), and selected British locations are given in Figure 2.

The first British specimen of the species (collected before 1879) was found near Torquay, Devon, and early reports are discussed in Snazell & Jones (1993) and Bauer *et al*. (2019). *S. nobilis* was rarely recorded and probably genuinely rare in Britain up to the mid 1980s, when it was observed to be common in Portsmouth (Bingham *et al.* 1999). By 1998 it was "everywhere" in Swanage (Merrett, P., quoted Moore 2003). It apparently became very abundant in parts of Plymouth and Torquay after the early 1990s (Smithers 2016). After near stasis in its reported northern distribution between about 1984 and 2010 there has been a rapid increase in records and apparent northward expansion (B.A.S. 2019a, 2019 b, 2019c; Bauer *et al*. 2019), excluding some outliers in Scotland. There has also been a recent spread in Ireland (Dugon *et al*. 2017; Dunbar *et al.* 2018b) and possibly globally (Bauer *et al*. 2019). It is hard to separate genuine population change from changes in recording effort, especially given pulses of media interest which may be causal of recording effort or responsive (Bauer *et al*. 2019).

Under-recording of the current abundance and range is illustrated by personal observations in Britain. From 1983, thousands of hours were spent recording spiders, particularly throughout Oxfordshire and parts of West Yorkshire, without encountering *S. nobilis*. During two days in late August 2016 with temperatures around 30^{o}C and high humidity, large spiders were observed active or hanging in their webs along a sunny brick wall of flats in south Oxford. This conspicuous behaviour is very unusual amongst British spiders, and investigation revealed the species to be *S. nobilis* - including an adult female and a sub-adult male. During very frequent examination of this wall in the 1980s, *S. bipunctata* (Linnaeus, 1758) was present but *S. nobilis* was not detected.

Steatoda nobilis. Photo: Copyright Daniel Blyto
Note silver / yellow patch on back has dark centre.
Note spider body (abdomen) is shiny.

Steatoda nobilis. Photo: Stu's Images. Creative Commons
Note silver / white patch on back is very broken-up (and can be absent). Note spider body (abdomen) is shiny.

Zygiella species. Photo: Dariusz Kowalczyk
Creative Commons
Note silver patch on back is spotty but solid.
Note spider body (abdomen) is shiny.

Amaurobius species. Photo: David Featherston
Creative Commons
Note paler mark on back is not made up of spots.
Note spider body (abdomen) is hairy and matt, not shiny.

Figure 1 Two spider genera which include species superficially similar to some *Steatoda nobilis* phenotypes in Europe and North America. Relatively consistent distinguishing features are noted amongst these species only, and many other species share these features.

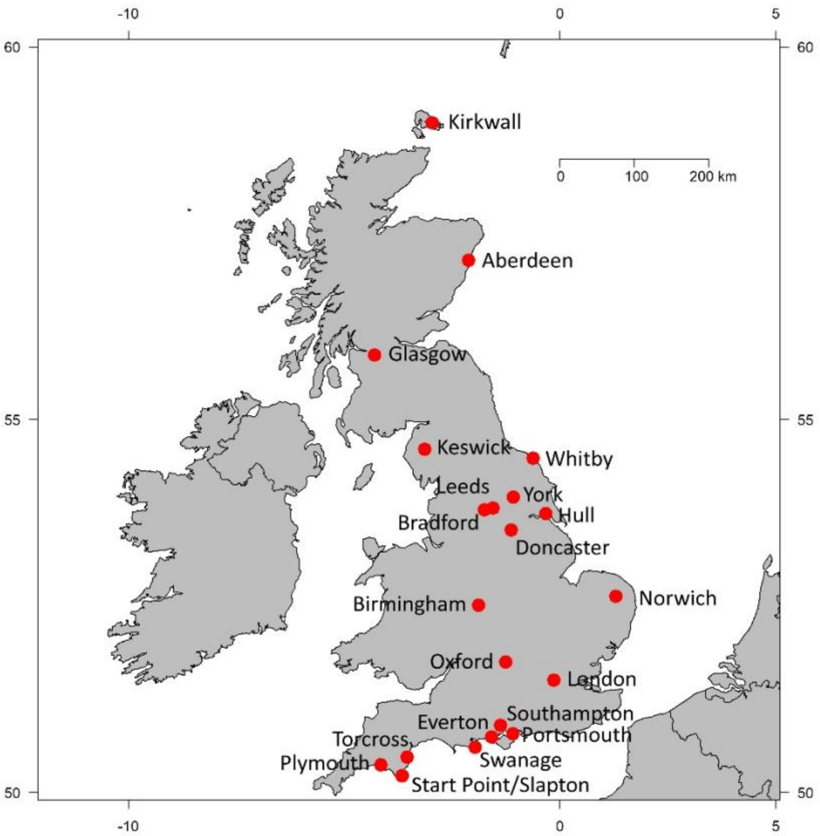


Figure 2 Map showing cities and town noted in the text. Wytham is c. 2 km west of Oxford; Start Bay and Slapton are immediately north of Start Point; Lymington is immediately east of Everton. All published records north of Doncaster are since 2012.

Recognising under-awareness of *S. nobilis*, during the first week of September 2016, many structures near roadsides on an east-west and a north-south route across Oxford (up to the ring road) were examined. *S. nobilis* was found to be very widespread and abundant. About three hours of inspection of structurally suitable rigid sites just outside Oxford (near Wytham village) revealed *S. nobilis* to be sparse, with these rural sites still dominated by the usual native species - although *S. nobilis* was quickly found on railings beside Port Meadow and a metal skip in Wytham Woods. Wytham Woods have a decades-long history of spider recording, including my personal observations spanning about 35 years, suggesting recent or incipient colonisation. In 2017 and 2019 I found the species to be common on buildings of the rural University Field Station near Wytham, where I had not encountered it during many visits in the 1980s and 1990s.

Similarly, the species has greatly increased in abundance in the Start Bay area of Devon, which is about 20 km from the first British record. In the mid 1990s the species was not found during annual visits and occasional examination of arachnids (personal observation). It had colonised Slapton village by 2013 (Oxford 2013). At the end of September 2016 I found the species to be very abundant on buildings I had previously examined, as well as common on buildings and some sturdy fences on the rural coast path from Start Point to Slapton. The species remained very abundant in October 2019.

The first published record from Oxford is 2014, and the second in 2016 (B.A.S. 2019a). It would be very remarkable if the spider became so dominant in Oxford in less than 6 years (*i.e.* between 2010 and 2016) so I argue that its increase in abundance is easily overlooked. The spider's increasing abundance was probably not apparent sooner because the web superficially looks like a number of other common species (Figure 3). Moreover, recording requires appropriate care in public and private urban areas - and often attracts security personnel - so may be neglected.

The species declines in abundance (density) from south to north in Britain, as reflected in the British Arachnological Society (B.A.S.) Spider Recording Scheme maps (B.A.S. 2019a). Despite much amateur and professional interest in the species, these maps are under-recording its distribution. Density is impossible to quantify due to access restrictions, and high heterogeneity of the built environment, but an abundance gradient is also very evident from my personal search effort in outdoors areas. Approximate times taken to find the species in a search are given in Table 1 for the few sites I have visited with this purpose - which may not be representative.

In Oxford at an unfamiliar location, I can generally find the species at any season within a few minutes. In Birmingham in 2017 and in Norwich in 2018, in targeted searches of a few hours, I found the species was abundant, but in both cities much more sparse than in Oxford in those years. In Bradford and Leeds I found it for the first time (in under one hour of targeted searching) in 2018, despite many years of casual personal observation and several hours of unsuccessful targeted searching in 2017. In Hull I found the spider within 15 minutes in August 2019. In Doncaster I found a single female in January 2019 (during about 2.5 hours of targeted searching). It was not mapped in these northern cities in the Spider Recording Scheme (B.A.S. 2019a) prior to my observations.

Table 1 Approximate search effort required for a professional arachnologist (the author) to find *S. nobilis* in selected British cities during 2016-2019. These are unreplicated observations and not designed to be systematic, but might permit detection of large changes in the future. See Figure 2 for map of locations.

City, town or village	Search effort (person-minutes) and season of observation	Number of visits (and years with targeted searches)	Subjective abundance and distribution
Slapton and Torcross	1 (autumn)	3 (2016-2018)	Abundant in villages
Everton and nearby villages	10 (any season)	c. 5 (2016-2019)	Abundant and widespread
London (central)	15 (summer, autumn)	c. 4 (2016-2019)	Abundant and widespread
Oxford	1 (any season)	Almost daily (2016-2019)	Extremely abundant and widespread
Norwich	30 (summer)	1 (in 2018)	Abundant and widespread
Birmingham	30 (summer)	1 (in 2017)	Abundant and widespread
Doncaster	30 (winter)	1 (in 2019)	Sparse, distribution not ascertained
Leeds	30 (any season)	c. 5 (2018, 2019)	Sparse but widespread
Bradford	30 (any season)	c. 10 (2018, 2019)	Sparse but widespread
Hull	15 (summer)	1 (2019)	Sparse but widespread
York	30 (spring)	1 (2019)	Sparse but widespread
Keswick	180 (spring)	3 (2017-2019)	Rare if present

In Bradford, Leeds and Hull it can be locally abundant (*e.g.* dominating a security fence) but in general is very sparse, with many suitable sites still dominated by the native species - particularly *Zygiella x-notata* (Clerck, 1757), members of the genera *Tegenaria*, *Amaurobius*, *Lepthyphantes*, *Linyphia*, *Neriene* and (in Bradford and York) *Tetrix denticulata* (Olivier 1789). In York, whilst I found the species as a first definite record for the city in under 0.5 hours, I found under 10 likely webs and only a few individuals in c. 6 hours of targeted searching; the species is sparse in the urban areas and native species (including *S. bipunctata*) are still dominant. Despite tens of hours of casual observation I have yet to record the species indoors in Leeds or Bradford in the types of sites it would occupy in Oxford, such as shopping centres and stations. I have not found the species during casual searching of a few hours on annual visits to the Keswick area of Cumbria around early May, suggesting it is rare (or less plausibly absent) there.

There are nine published British locations north of York, including the most northerly city of Aberdeen in 2013. Most are reports of single specimens and all are after 2012 (B.A.S. 2019a, as of 29 September 2019). Most of these are indoors, except for a male on a marine slipway at Whitby in September 2017 and an individual in a landfill site near Glasgow in 2013 (suggested to have been recently transported on equipment). Individuals and possible websites suggest breeding in a warehouse in Kirkwall (Orkney, Scotland) in 2017.

The species was "thought to be in London" by 2006 (Hine, S., quoted in Sapsted 2006). In London, I found the species easily (within minutes) near Hyde Park in the autumn of 2016, but found it sparse that year. In October 2018 I found it to be abundant in central London, including the area of Embankment / Blackfriars / Holborn / Oxford Street / Baker Street / Fleet Street / Regent Street / Portland Place / Regents Park / Marylebone. I am confident it is abundant throughout London.

Whilst I have found the species to be abundant in some villages and associated street furniture in Britain, my observations accord with those of Dugon *et al*. (2017) and Dunbar *et al*. (2018a) who find it rarer in more natural habitats in Ireland. However, the species is not exclusively synanthropic in Europe (Bauer *et al*. 2019). In both urban and rural areas, *S. nobilis* can be found on trees and bushes which have dense, rigid structures, particularly those in gardens, hedges and parkland. In highly rural settings I have found it in wetland nature reserves, cliff walks, tree trunks and woodland, despite few such records in Ireland (Dugon *et al*. 2017).

Webs are relatively robust, with strong silk, so can be found on bicycles (*e.g.* brake levers and callipers, baskets, gear-pulls and under saddles) despite the bikes being in regular use. They also occur on and in cars (for example round wing mirrors) and so doubtless in lorries, trains, ships and planes.

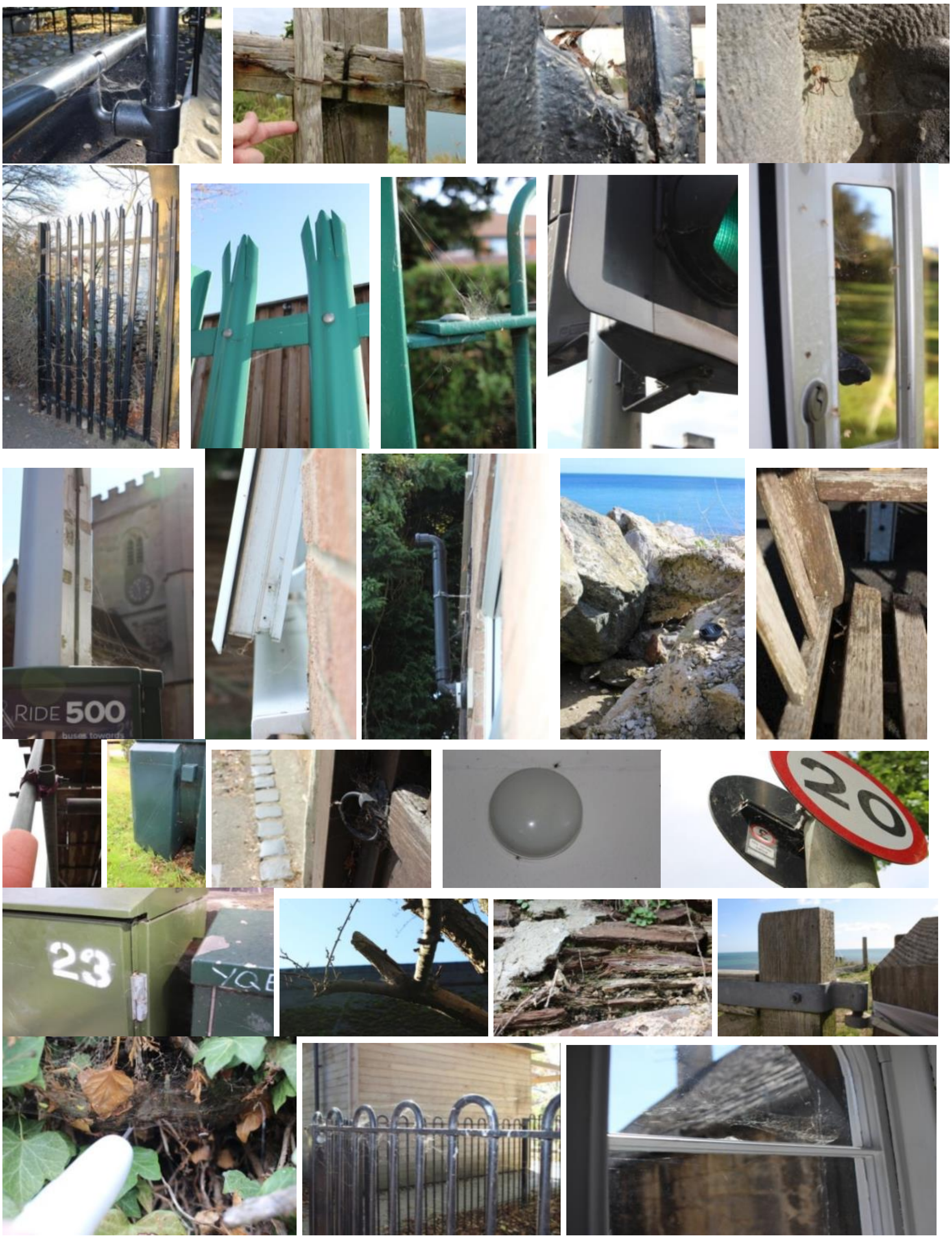
Some common websites in southern Britain (based on personal observation) are illustrated in Figure 3. These include: walls; drain pipes; guttering; road signs; lamp posts; traffic lights; street name signs; litter bins; salt bins; dustbins; porches; skips; park railings; metal, wood and plastic fencing (especially corrugated metal security fencing); junction boxes; window frames; lamp fittings; cistern overflow pipes; boiler flue vents; garage door frames; domestic and farm gates; ivy on walls / tree trunks. On street furniture they often occur near the clamps holding fixtures to poles. Indeed, almost any textured rigid structure with some crevices is suitable unless exposed to frequent disturbance or extremes of heat, dust *etc*.

S. nobilis can be very common indoors at various densities, for example in or round: ceiling light fittings; window frames; chairs; the corners of walls; in curtains; blinds; boxes; skylights; loft spaces and conservatories. The species occurs inside and outside blocks of flats and other tall buildings, from the ground to at least four floors up (and probably much higher, since the web can survive strong winds, although I have not yet searched tall buildings due to access restrictions).

Typical outdoor habitats (based on personal observation) in the northern cities of Leeds, Bradford, Doncaster and York are industrial areas and car parks *etc*. particularly with corrugated metal security fencing, and railings round urban greenspace. These are good places to start a search in a city. Unlike in southern Britain, sites such as drain pipes, traffic lights and road signs are occupied by few spiders of any species, presumably reflecting the south / north gradient in invertebrate richness and activity over this distance (personal observation).

Given the presence of the species in almost every suitable-looking crevice in some urban areas, I hypothesise that in many areas of southern Britain the abundance of this species is at carrying capacity, limited by suitable rigid structures for the combined overwintering retreat and web. This is in accord with the statement that "It is likely that the spider is present in urban and suburban southeast England in all suitable habitats" (B.A.S., quoted in Lazarus 2018), but I would expand this to include almost every suitable structure in some cities. In Oxford it became very common on a detached new building within two years (personal observation to 2018) as did *Z. x-notata*. The species is now the commonest spider on some structures, reaching high densities compared to many native species of urban environments.

I hypothesise that in the cities and towns of Britain south of Birmingham the species now occurs on almost all large buildings, most houses, many fences and railings, some benches and many other rigid structures, and that it will also be present in most villages in this region. I hypothesise that almost all 10 km map grid squares in England south of Birmingham will be found to host the species (although the current B.A.S. maps have many gaps).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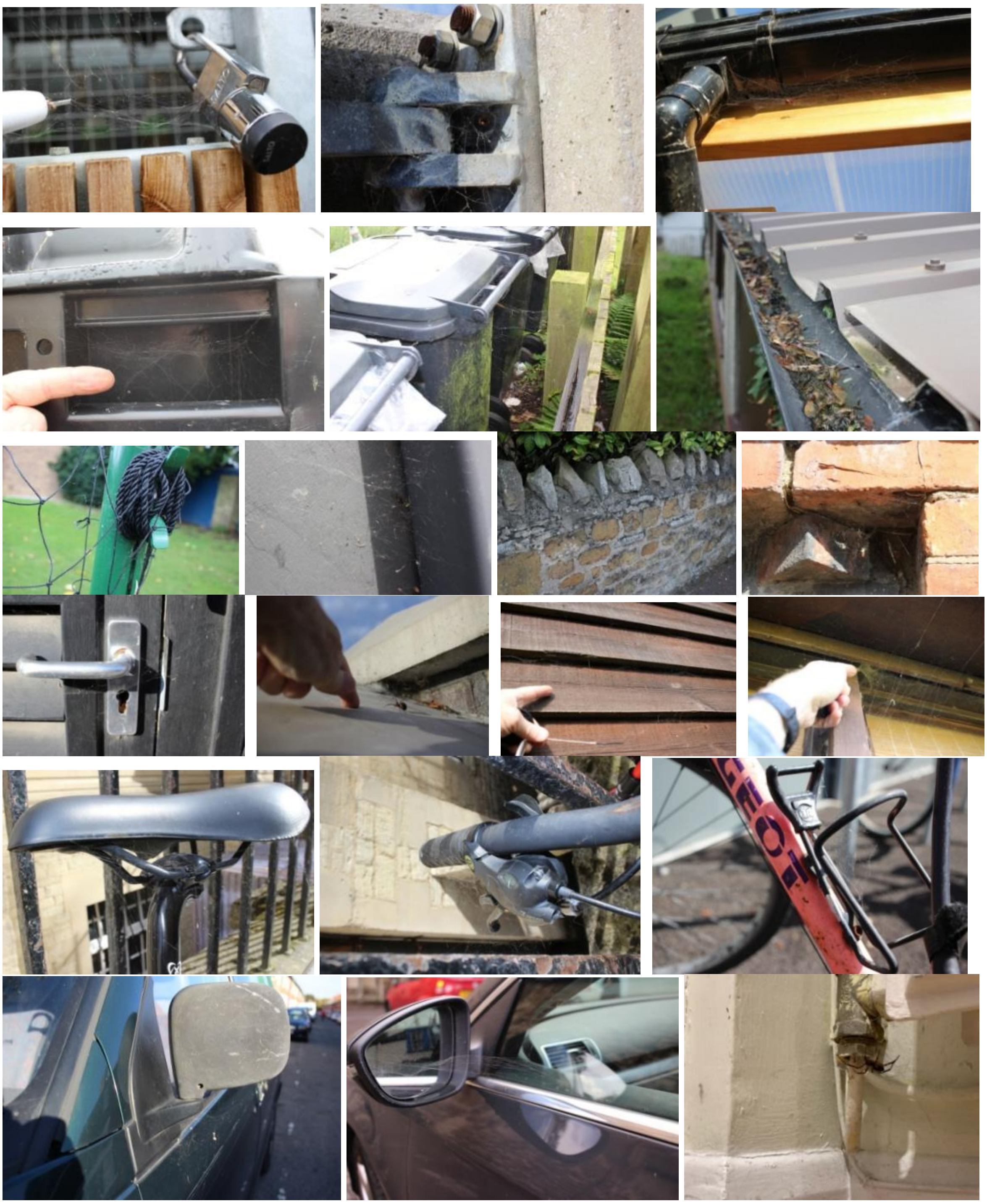

Figure 3 Examples of websites of *S. nobilis* in close proximity to people, in various parts of Britain. All photos 2018 or 2019 by Clive Hambler, except last one, 2019 Sophia Leroy-Puri. The vast majority of webs in these locations were from *S. nobilis.* If enlarged, spiders are visible in some photos.

Incidence of bites in Britain and elsewhere

Given the great local abundance and decades of close proximity to people in the houses and gardens of southern counties, it is very interesting and possibly reassuring that very few serious bites have been reported, at least until recent years (B.A.S. 2019b, 2019c). According to the Natural History Museum (N.H.M. 2012) there were under 30 cases of alleged *S. nobilis* bites brought to their attention in the preceding 16 years, and there have been very few verified cases since (Dunbar *et al.* 2017).

However, there may be a very substantial failure of communication between medics and arachnologists. A recent Freedom of Information request by the pest control company Fantastic Services reveals there have been over 2000 cases of spider bites or suspected spider bites reported by the National Health Service Trusts in the period 2014-2018 (Burrows 2019; Wathen 2019). The distribution of these cases is predominantly in the South East and South West of England, as with *S. nobilis* records, but includes a concentration in the Southport, Ormskirk and mid Cheshire area where there are also outlying records of *S. nobilis* (perhaps associated with the port city of Liverpool). Many of these may prove to be erroneous, but it raises the possibility of a surge in the bite rate corresponding to a surge in abundance and northern distribution. It would be valuable to have comparable data for earlier four-year periods.

Under-recording of bites is particularly likely if there is itching or pain but no hospitalization (for example due to swelling or ulceration) and most of the likely bites relayed by colleagues were not reported to medics. If, as with *Latrodectus*, pain often develops ten minutes to an hour after the bite (Maretić 1978b), then the involvement of a spider could be overlooked. However, it should be noted that an immediate prick or burning sensation was observed in all demonstrated cases of *S. nobilis* envenomation (Dunbar *et al.* 2017). I hypothesise that spider bites are greatly under-reported in the media or to medics compared to their actual frequency. After widespread media publicity in 2018 and the evidence in this paper, I predict the number of reported serious suspected bites will now increase substantially, as will the number verified with specific effects.

I suggest the abundance, habitats and behaviour of *S. nobilis* now make it one of the most likely species of spider to bite people in Britain. I therefore can no longer agree with B.A.S. (2019b) that "being bitten by a spider is very unlikely in this country in normal circumstances". I find it plausible that many people in southern Britain will be bitten by *S. nobilis* - and that most will not recognise this as a spider or false widow bite. Given its high densities in some homes, offices, workplaces and gardens, it could become one of the commonest sources of reported and of verified spider bites and their medical sequalae globally. Nevertheless, it is very important to remember that *verified* spider bites remain a rare phenomenon globally (Stuber & Nentwig 2016).

Possible bites reported in the British media

Several reports of possible bites are available which I suggest should not be overlooked if treated with appropriate skepticism. A formal search for cases is beyond my resources and expertise. As a provocation to professional medical research, my superficial online investigation of the popular media (using Google, Google Images and a range of search terms such as 'false widow' and 'bite') reveals there are now over 50 people in the British Isles who have reported spider bites since the year 2000 and had subsequent media attention. Many of these allege 'false widows' were involved. A formal inter-disciplinary review including arachnologists, public health specialists and medics would be necessary to locate, substantiate and quantify alleged spider bite records in Britain - which would require very considerable effort (probably taking months). It is not the intent of this paper to detail or quantify cases or risk, which should be done by medics and health professions. Rather, it is to illustrate the problems of such a study and encourage proper systematic research which may not have occurred in the absence of incentive and of recent arachnological, ecological, and toxicological evidence. Some bites by other identified *Steatoda* species or unspecified *Steatoda* or "false widow" species are discussed here since they help capture possible information on *S. nobilis* and indicate lines for future research.

Of the c. 50 alleged spider bite cases I found in the media, at least nine meet the criterion for a 'proven case' of spider bite proposed by Anderson (1997): a spider was found in immediate proximity to the bite. Many other cases meet Anderson's criterion for a 'probable case': spiders recorded promptly nearby or within the house. However, Anderson's criteria are arguably superseded by Stuber & Nentwig (2016) and many of the reports in Britain would not count as verified as spider bites, let alone as *S. nobilis* bites. Some examples of what I consider relatively likely cases of spider bites in Britain are illustrated in Table 2, with my assessment of the likely accuracy of the identification - and I suggest it is very risky to argue these are all misidentifications or misreporting. Whilst these include the nine arguably 'proven' cases of spider bite, I would not accept any of the cases in Table 2 as 'confirmed' or 'definite' or 'proven' *S. nobilis* bites, and it may be too late to confirm some of these should the effort be made. The many ambiguities and uncertainties give an indication of the challenge in confirming bites to medically satisfactory standards.

Several patients report a double puncture at the bite site (although absence of visible punctures does not disprove a bite). Proving the spider in question is a *Steatoda* species, or *S. nobilis*, and is the same individual that allegedly bit the patient is very much harder and there is ambiguity in many media reports. Bites were attributed to *Steatoda* species with varying confidence. In the vast majority of cases I have found in the media the species identification can be challenged. However, in my assessment after talking to several bite victims, many reported bites are the correct identification because *S. nobilis* is often relatively distinctive and now very abundant - and because there are very few other likely candidates for the injury in these cases. Amongst acquaintances, I know of two bites with photographs of the spider that non-specialists identified (and I have confirmed) as *S. nobilis* and *S. grossa* that have not received media attention.

In many reported alleged bites, especially in buildings, few other spider species are likely to be involved, nor are other invertebrates if there are double puncture holes in the skin. It is possible that Blandford fly (*Simulium posticatum*) bites and associated infections might be confused with *Steatoda* bites.

It is often reported that there are only about a dozen spiders in Britain that can draw blood, but in my experience the number is above this and likely well over 30 (including most large Araneidae and Agelenidae, and some *Dysdera*, *Segestria* and *Amaurobius* species). I have received bites from these species only when grasping the spider. Of these species, *Amaurobius* are very plausible for some alleged "false widow" (*Steatoda* species) bites (*e.g*. in trees, sheds and woodpiles) but this genus is far less common in houses in Britain (personal observation). In my experience, the British public are often familiar with the general appearance of *Tegenaria* 'house spider' species, which are very common in houses, so are unlikely to mistake its hairy abdomen for the shiny *Steatoda*. There are also occasionally imported species which can bite.

If it is established that other European spider species are involved in some of the ulcerations and other serious consequences in Table 2, the implications are even more profound, and much more general and restrictive advice would have to be given to the European public about the safety of handling any spiders - contrary to much existing advice.

Under-reporting of bites to humans, and of the spiders themselves, is likely to be a global phenomenon as illustrated in Chile where the spider was not known until recently and was not commonly observed (Faúndez & Téllez 2016).

Medical evidence and awareness of bites will likely rise through greater incidence and fuller investigation and reporting, especially following closure of several schools in Britain. The number of recent cases of *Steatoda* bites in Ireland (Dunbar *et al*. 2017) may reflect such media reports leading to presentation of spider specimens (Breitling, R. quoted Abbit & Rodger 2019) as well as rapid *Steatoda* invasion.

Whilst it is often said that the males of *S. nobilis* do not have notable bites (Maretić 1978a; ITV 2014) this is now known to be false (Faúndez & Téllez 2016); Dunbar e*t al*. 2017).

Defensive bites
Spider bites to humans are typically defensive and due to accidental compression. Contrary to some reports, in parts of Britain *S. nobilis* is now plausibly often encountered and might be easily compressed. Examples of sites of *S. nobilis* webs in close proximity to people (*ie* in a location less than 1m away from regular users) are illustrated in Figure 3.

Spiders that build in door and window frames, door handles, bin handles and under chairs and bench seats and in furniture are particularly easily encountered and compressed. The species builds webs in similar locations to *Latrodectus* species which can bite when handling an item causes them compression (Vetter *et al*. 2012).

Low metal school railings can have high abundances - especially in the loops at the top of fences, around bolts and at gateposts. Since the spider's retreat is not always in a crevice, but can be in a corner such as a junction of wooden or metal bars, it is becoming easier to touch or compress the spider by mistake as its population grows. In Oxford I have seen children leaning their hands on metal park railings in a play area on which *S. nobilis* is very common.

Table 2 Selected examples of popular media reports of alleged consequences of spider bites (from any species) in Britain and Ireland, illustrating challenges in confirming an *S. nobilis* bite. None are indisputably proven. * denotes report does not meet Anderson's (1997) criterion of a 'proven' case of spider bite. All patients known or very likely to be adults. Sources accessed 13 October 2019.

Alleged bite effect	**Alleged bite site on body**	**Place in Britain;** **activity and date;** **media source**	**Evidence of spider**	**Evidence it may be a 'false widow'** **(any *Steatoda* species)**	**Victim or media *imply* medical confirmation of a spider bite?**	**Data deficiencies**
Large blisters within minutes of being bitten; six days in hospital	Leg	Waterford, Ireland In sitting room 2019 https://www.thesun.ie/news/4341777/insect-spider-noble-false-widow-waterford-women/	Spider ran up the leg of jeans	Spider captured and photographed. Media report hospital staff identified the species as a false widow, from photo. Described as brown with white markings on its back and roughly the size of a two Euro coin Photo. confirmed as *S. nobilis* by C. Hambler Expert *reported* as believing false widow bite	Yes	Not clear if published photo. is the individual spider that bit the patient Direct report needed from quoted expert (J. Dunbar)
Awful pain; very sore next day; swelling within two days; reportedly requiring hospital visit and antibiotics	Foot	Waterford, Ireland In bed 2019 https://www.thesun.ie/news/4341777/insect-spider-noble-false-widow-waterford-women/	* Animal seen after waking with pain in foot	Pest controllers had previously tackled spiders in house "Thing" seen running down sheets immediately after bite Expert *reported* as believing false widow bite	No	No specimen or clear observation Direct report needed from quoted expert (J. Dunbar)

Ulceration; necrosis; induced coma; substantive debridement; at least eight operations	Upper arm	St Albans, Hertfordshire In living room 2017 http://www.bbc.co.uk/news/uk-england-beds-bucks-herts-40504978	Spider walked up arm and spontaneously bit	Patient thinks may have been' false widow' (*ie Steatoda* species)	Yes: reported diagnosis of necrotising fasciitis secondary to a spider bite	No specimen or photo Described large size of spider contradicts identification, but the origin of the description is unclear Possibly exotic species in bananas
Ulceration; necrosis	lower leg	Mansfield, Nottinghamshire Asleep in bed 2017 http://www.forces.net/news/toxic-spider-bite-leaves-soldier-unable-walk	Small brown spider seen, after woken with tingling sensation	Patient self diagnosis	Yes	No specimen Photo. of *Amaurobius* sp. in one report but not clear if this was the same individual Bite not witnessed
Ulceration; necrosis; cellulitis (recurrent over at least 8 months)	Top of foot	Rossendale Borough, Lancashire In hospital, foot on chair 2016 https://www.thesun.co.uk/news/3342794/mum-of-five-considering-amputating-her-zombie-foot-after-poisonous-spider-bites-her-while-in-hospital/	Woke and saw spider on top of foot Brushed off spider Felt bite like bee sting	Patient said it looked like a garden spider, with a pattern on it and with the two front legs longer than the others	Yes	No specimen or photo

Extensive necrosis; amputation risk; at least 3 weeks in hospital; months of problems walking	Thigh	Essex Decorating in a school https://www.dailymail.co.uk/news/article-2453833/Decorator-nearly-loses-leg-bite-UKs-poisonous-spider.html	Spider bit when brushed off leg Felt sharp pain on leg	Patient describes them as purplish brown, quite big with strange marking on their backs.	No	No specimen or photo
Dark itching skin; "reinfected" after 2 weeks	Arm	Leighton Buzzard, Bedfordshire In house putting on jumper Around 2007 http://naturenet.net/blogs/2007/05/02/the-truth-about-steatoda-nobilis-is-it-the-uks-most-dangerous-spider/	Spider found in sleeve after intense bite	Identified by patient	No	No specimen or photo Bite not witnessed
Anaphylactic shock	Hand	Bournemouth, Dorset Cleaning bathroom 2009 http://www.bournemouthecho.co.uk/news/4582887.Bite____nightmare_____close_encounter_with_a_false_widow_spider/	Picked up spider	Media photograph reportedly of spider that bit her: identified from this photo. as *S. nobilis* by C. Hambler (this author)	No	Direct medical diagnosis of anaphylaxis Ambiguity if the photo. is the same individual animal that bit
Burning pain; emergency hospital admission with suspected heart attack	Abdomen	Salisbury, Wiltshire Market stall moving boxes 2006 http://www.telegraph.co.uk/news/uknews/1534415/Watch-out-the-black-widows-sister-is-ready-to-bite-you.html	Spider seen on abdomen after burning pain on chest	Identified by patient using hospital computer	Yes: puncture wounds; doctor reportedly said no doubt about it being a spider bite	No specimen or photo Bite not witnessed

When woke c. 2 hours later: face puffy; conjunctivitis; blurred vision; weeping eyes	Abdomen near neck	Basildon, Essex In bed 2019 https://www.dailymail.co.uk/news/article-7455937/Mother-phobia-spiders-suffers-worst-nightmare-false-widow-bite.html and other reports	Woken by crawling sensation on arm, which reached face Spider seen, pinched and thrown off Possible bite marks	Told it was likely a false widow bite	Unclear	Bite not witnessed No diagnosis but anaphylaxis plausible No photo. or specimen of spider or the fragments of it Ambiguity if medics suggested false widow

(Table 2 continued above.)

Moreover, contrary to suggestions that the species rarely leaves its web, in Oxford I have found an adult female on a corridor wall without a web, a subadult female walking on a kitchen ceiling and abseiling from it, and several adult males and juveniles resting on indoor walls, particularly in spring and autumn. Females have been observed "dozens of times" walking on walls and the ground (anonymous reviewer, 2019). The species readily abseils to the ground if disturbed, and then often 'plays dead' and is hard to find. It could easily drop or retreat into furniture, clothing, bedding or stored items, in housing, garages, bin areas, polytunnels, sheds, greenhouses, woodpiles and the like - where the risk of a defensive bite increases.

The risk of contact is reinforced by my having found one juvenile walking on my sofa, one landing on my head in an office, one juvenile abseiling onto equipment in the same office, an adult female falling beside me as I opened a garage door and another falling beside me from a roller-blind. A colleague trod on a likely *S. nobilis* in his house which had built a web in the door frame. One likely encounter reported to me was from handling a tool box and another during tree surgery.

Dispersing animals, including males, could sometimes make their way into bedding and clothing - possibly as a refuge - and beds are the most common location for the verified bites in Britain and Ireland and Chile (Faúndez & Téllez 2016; Dunbar *et al*. 2017). An *S. nobilis* (possibly female or juvenile from the photograph) was reportedly found in a bed in Essex (Watham 2019). Moreover, I hypothesise the species might seek warm sites and is thus unfortunately attracted to beds. The frequency of bites in bed almost certainly reflects reporting bias. Compared to finding a spider which bit somebody in a garden, or even in clothing, it is relatively easy to find a squashed spider in bedding and send it to an expert. A possible lag between the bite and the pain (as above) would increase the proportion recorded from beds.

S. paykulliana is reported as "more aggressive than *Latrodectus*" and more willing to bite experimental animals when forced against them (Maretić *et al.* 1964; Maretić 1978a) - an unnatural and nowadays ethically unacceptable situation but possibly similar to some accidental human contact.

I think it plausible that *S. nobilis* may bite 'defensively' without compression: an invertebrate, probably a large juvenile or an adult of the species, fell onto a zoologist's hand in a lobby and bit her; such behaviour requires further investigation. A spider, probably *S. grossa* or *S. nobilis*, was disturbed by another zoologist when lifting items in Wytham Wood, Oxfordshire: it walked up her arm and bit her. When not in a web *S. nobilis* sometimes lunges and bites at an object if prodded (personal observation), which is probably a form of active defence. Some *Latrodectus* are reported to "attack" when disturbed (Eiden & Kaufman 2019) and it is possible some bites are to reduce damage to costly webs. Given its speed, *S. nobilis* is one of the British spiders I am most wary of capturing and handling.

Offensive bites and 'aggression''

I have found *S. nobilis* will approach and bite a finger that lightly touches the web in warm weather (videos 1 and 2: [Supplementary Material Online](https://osf.io/6j8c5/), https://osf.io/6j8c5/) and can be persistent in returning to bite it. Touching a web is suggested as a possible way to be bitten by B.A.S. 2019b.

Approaching a finger in a web is rare in my experience of British spider species, and casual observation suggests most species (including *S. nobilis*) are more prone to retreat rapidly. Despite such preparedness to attack, I predict bites from mistaking fingers *etc.* for prey will be found to occur very much less often than defensive bites.

Many *Latrodectus* bites occur when a hand touches the web (Australian Museum 2019), reportedly in defence (Victoria State Government, 2016) but offensive attacks would be worth investigating. I found *Latrodectus* (possibly *geometricus*) webs easy to touch accidentally under chair seats in Aldabra, Seychelles. *Latrodectus* bites to male human genitalia often occur in outdoor or portable toilets in Australia and North America (*e.g.* Bettini & Maroli 1978), presumably without compression.

S. nobilis may be relatively prepared to take on large prey items, and will attack a tuning fork, even as a small juvenile (video 3: Supplementary Material Online). It can catch and kill powerful moths such as the poplar hawk *Laothoe populi* which is much larger than the spider. The speed of attack on large objects touching the web is illustrated in videos 1-5, with wrapping behaviour suggesting hunting, not defence. *Latrodectus* can kill geckos a few centimetres long on Aldabra, Seychelles, leaving them suspended in the web under the seat of a chair (personal observation 1988); some kill frogs and might catch birds (Anderson 2011). *Steatoda* can kill lizards in Ireland (Dunbar *et al.* 2018a). Whilst *S. nobilis* often retreats when the object in a web is not vibrating, the lizards, snakes and geckos that *Steatoda* and / or *Latrodectus* kill must simply be rubbing on the web - as a finger might do by chance. Such reptiles (and frogs taken by *Latrodectus*, Anderson 2011) are often very fast, making a fast attack necessary. *S. nobilis* is also attracted to potential prey tugging to escape strands of the web, and not just by vibration (video 1: Supplementary Material Online), making bites on fingers more likely. It is parsimonious to assume that the common ancestor of *Steatoda* and *Latrodectus* within the subfamily Latrodectinae often killed vertebrate prey using webs.

As the videos illustrate, it is erroneous and potentially misleading to claim: "These spiders are in truth rather docile and slow moving and tend to live inside their rather dense square webs feeding off the insects that stray into their path. They will not go out of their way to bite" (Brown 2015). Similarly they have been reported as: "ponderous, very slow moving and not at all aggressive" (Falk, S., quoted BBC 2013); "ponderous, solitary and non-aggressive" (Buglife 2018); and "not an aggressive species" (CABI 2018). There are, very understandably, many such comments from arachnologists - who may consider terms such as 'aggressive' emotive or misleading relative to even faster species.

The term "aggressive" could indeed be considered very misleading and inappropriate for coerced defensive bites, but it is important to appreciate it is used subjectively, selectively and inconsistently by both arachnologists and the public. It is arguably less unreasonable to describe this spider as "aggressive" than it would be for most spiders. 'Aggression' has been used to describe spiders with vigorous attacks on prey (*e.g.* Oxford 2013) and is often used for *Latrodectus* species (Bertani *et al.* 2008). When attacking a tuning fork, sonic toothbrush or other large item, *S. nobilis* is relatively persistent and unafraid, even with a large moving prey item (videos 1, 3, 4 5: Supplementary Material Online). Many spiders retreat rapidly after first contact with such items (personal observation).

Effects of bite

There are as yet only a few medical cases which combine high probability of a bite, expert identification of *S. nobilis* and close observation of the consequences (Warrell *et al*. 1991; Faúndez & Téllez 2016; Stuber & Nentwig 2016; Dunbar *et al.* 2017). This is unsurprising given the improbability of a victim collecting the specimen and the appropriate reluctance of arachnologists to confirm identification without a specimen or photograph.

The severity of alleged or unverified spider bites in Britain varies, from a possible death through infection (in Aldershot), to an amputated leg (in Thorpe Astley) to a short term sting or itching.

It should be noted that *Steatoda* is very closely related to *Latrodectus*, the genus including black widow, redback and brown widow spiders and which is possibly paraphyletic (*e.g*. Garb *et al*. 2004). It is potentially informative to compare effects and possible effects of bites of the two genera, since their diets are similar and a common ancestor may have had many similar venom components. Whilst close relatedness of spider species does not guarantee similar effects of their venoms (Garb & Hayashi 2013), it makes them much more likely. *Steotoda* venom includes at least one specialised neurotoxic polypeptide, α-latrotoxin, that is shared with *Latrodectus* venom but there are molecular differences in the neurotoxin between these genera (Garb & Hayashi 2013).

Neurotoxicity and steatodism

The fast acting neurotoxic venom of *S. nobilis* can cause severe pain in humans and other symptoms of the medical syndrome 'steatodism', which overlaps with symptoms of latrodectism from some *Latrodectus* bites (Maretić *et al.* 1964; Warrell *et al*. 1991, Dunbar *et al*. 2017). So far, fewer than 10 cases of steatodism appear to have been confirmed and published in Great Britain and Ireland (Warrell *et al*. 1991; Dunbar *et al*. 2017). Bite effects of *S. nobilis* vary from case to case, and the full range of idiosyncrasies may not be known. It is worth being aware of rare and atypical severe effects of *Latrodectus* bites (Goddard *et al.* 2008).

Cytotoxicity, ulceration, necrotic arachnidism and putative bacterial carriage

Following the initial description of steatodism (Warrell *et al*. 1991), the medical and public health focus has been on neurotoxicity and pain. However, the venom of *Steatoda paykulliana* (Walckenaer, 1806) has long been known to be cytotoxic, causing topical ulceration and other necrosis in some lab mammals (Maretić 1978a). Furthermore, *S. grossa* was listed as having possibly cytotoxic properties by Horen (1963).

It is very notable that the experimental studies with *S. paykulliana* and *Latrodectus* reporting necrosis and cytotoxicity in mammals have not been widely discussed in relation to *S. nobilis*, even to dismiss them. This may be because of the accessibility of the literature, the ethics of the procedures, the variation of venom between species or individual spiders, the problem of translating such results to humans, or reluctance to cause alarm. It is to be hoped that tissue culture studies, immunological tools and improved reporting of human case studies could confirm the risks without requiring replication of the animal experimentation. Examples of areas deserving of such investigation include variation amongst venoms of individual spiders, cell lysis, immune response leading to controlled cell death (Dunbar *et al*. 2019) and synergies between venoms and symbionts.

The discovery that *S. nobilis* venom is strongly cytotoxic and "kills healthy cells at a massive rate" (Dugon, M., cited in Ahlstrom 2016) is consistent with several unconfirmed media reports of blistering and ulceration of bite sites. Publication and discussion of these very important data will be of great value. Casual online searching for images of alleged "false widow" bites reveals some 'bite' sites develop a small central black mark. A verified case study with "a minor, potentially necrotic wound" (Dunbar *et al*. 2017, 2019) is also consistent with the mammalian studies of *S. paykulliana*.

Local oedema (swelling) and necrosis at the bite site is reported in guinea pigs experimentally bitten by *S. paykulliana* (Maretić *et al.* 1964; Maretić 1978a). Notably, *S. paykulliana* bites were reported as mechanically stronger than *Latrodectus* and resultant "necroses were more pronounced" than in *Latrodectus* (Maretić *et al.* 1964). Internal damage in experimental animals includes ulceration of the stomach mucosa and necrosis of liver and heart tissue. The general effect was described as a less marked version of the stress response termed 'the general adaptation syndrome' which *Latrodectus* toxin can also trigger (Maretić & Lebez 1979). *Steatoda* (Dunbar *et al.* 2018a) and some *Latrodectus* (Shackleford *et al*. 2015; O'Shea & Kelly 2017) can feed on vertebrates including reptiles - raising the possibility of tissue damage by venom and / or digestive enzymes as in some *Latrodectus* (McCorkle 2002).

Latrodectus venom causes cytotoxic injury including necrosis involving blood vessels and epithelial cells in particular, and also involving nerve, liver, lungs, pericardium and lymphoid cells (Horen 1963; Maretić 1978a, b). *L. geometricus* venom can cause damage to adrenal glands of mice, causing acute adrenal insufficiency (Guerrero *et al*. 2010). Slight necrosis occasionally occurs in humans at the site of a *Latrodectus* bite (Maretić 1978b). At least one *Latrodectus* venom component (LV_1) is reported "highly toxic" to some cell cultures (KB line and Amnion I.S.S. line, but not monkey kidney primary cultures) and lethal if injected intravenously into mice (Vicari *et al*. 1965). Some *Latrodectus* venom includes proteinases and other potentially cyctotoxic components (Duan *et al.* 2008). *Latrodectus* antivenom is effective against *S. grossa* venom - although potentially very dangerous as a treatment through anyphylaxis related to injection of sera (Graudins *et al*. 2002; Isbister & Fan 2011; Murphy *et al*. 2011; Garb & Hayashi 2013).

A paradigm shift may have begun in understanding spider venom and necrosis, following review, discoveries and proposals by Dunbar *et al*. (2019); indirect effects of venom through person-specific immune responses may explain some inconsistencies between established venom activity and alleged or reported impacts.

Globally, confirmation of necrotic arachnidism is extremely rare (Vetter *et al*. 2015). There is likely over-diagnosis of spider bites in at least some countries, with many accounts of severe problems assessed to be anecdotal (*e.g.* Ahrens & Crocker 2011; Nentwig 2015). Indeed, it has been claimed that "[Arachnologists] are convinced that spider bites are rare and mostly harmless" (Stuber & Nentwig 2016).

However, much more research is needed on the possibility, risk and potential mechanism of necrosis and ulceration both from direct cytotoxicity and as a complication from compromised tissue in the bite area. It is very easy to see how ulceration might arise. *Steatoda* bites have been reported to cause blisters (*e.g*. Rutherford & Sutherland 1989; Jacobs 2015; T.E.R.R.A.I.N 2018) or minor skin lesions

(Dunbar *et al.* 2017; Gray 2018) but confirmation in most patients is difficult. Redness is common at the bite site (Isbister & Gray 2003) and itching lasting about two weeks has also been reported for a likely *S. nobilis* bite in Oxford (personal communication).

A risk of bacterial ulceration, introduced with the bite or by subsequent scratching or bursting of the blister, may prove to be the most common danger with *Steatoda* species (and is a common risk with many other minor injuries). If ulceration occurs from infection by bacteria such as *Staphylococcus aureus* (Fagan *et al*. 2003; Diaz 2004; Hine, S. quoted Peasgood 2014; but see Vetter *et al*. 2015) this is a very unpleasant and potentially dangerous problem. Without treatment there is a risk of cellulitis developing into gangrene, septicaemia, and even death - as may have happened with an elderly lady in Hampshire in 2014 (BBC 2016).

Some infections reported from unverified bites in Britain have established within a few days, and the patient's condition has deteriorated very rapidly. In at least some unconfirmed reports patients were at risk of amputations after bites (*e.g.* Marsh 2012). Informal online browsing of British media reports (as above) reveals several alleged bites requiring antibiotics of at least one type and several required hospitalisation - some as urgent cases. Notably, for about eight of the reports I found of ulcerating alleged bites a spider was observed in bedding or clothing - as with five recent confirmed cases of steatodism (Dunbar *et al*. 2017).

Whilst arachnologists are often very hesitant, medics in Britain may be increasingly prepared to attribute symptoms to spider bites, and I have found about 15 cases in the media in which medics are *reported* to concur a spider bite is a possible cause. For example, there is a reported diagnosis of necrotising fasciitis secondary to a spider bite (BBC 2017). An enlarged hand after leaning on a fence was reportedly attributed by a doctor to an unspecified "false widow" (Hughes 2016). Medics, however, may be misquoted and often lack specific training in recognising envenomation. I argue it is highly disrespectful of observers and the media to assume all such reports are false, and instead they should be investigated more carefully and urgently. It would be valuable if such historical and 'anecdotal' reports were compiled, compared, criticised and published by the medical profession, in collaboration with arachnologists who can advise on identification and spider behaviour. If even a very few such cases are confirmed, I suggest *S. nobilis* has the potential to become a globally widespread but infrequent cause of necrotising arachnidism.

It is noteworthy that some invertebrate prey remain alive for about 4 days whilst *S. grossa* feeds on them (Kenny 1998) which might give cytotoxins, including digestive enzymes (Foelix 1982; Preston-Mafham & Preston-Mafham 1996) and / or bacteria time to liquidise the prey to facilitate feeding. Dead prey in webs may be repeatedly visited over the course of hours with the spider feeding from different parts of the body (personal observation). I hypothesise that spiders might exploit bacteria, or bacteria might exploit spiders as vectors or weapons, with clones of those that degrade prey or cause ulcers in predators surviving in the spider. Some *Latrodectus* venom is also reportedly immunosuppressant (Ahrens & Crocker 2011).

After review of many studies Vetter *et al*. (2015) argue that current evidence does not support the suggestion that spiders vector bacteria, and note the risks of misinformation. This remains a highly controversial area requiring rigorous experimental studies of individual species and individual spiders, including *S. nobilis* and *Latrodectus* species, and highly specialist work to test for antibiotic resistance.

Some authors (Ahrens & Crocker 2011) have reported the microbiome on some *Latrodectus* fangs includes strains of medically significant bacterial species which are multiple antibiotic-resistant. The microbiome included bacteria requiring specific antibiotics not commonly used in skin infection (Ahrens & Crocker 2011); in theory this could cause necrosis, including the ulceration reportedly frequent after *Latrodectus* bites (Maretić 1978b; but see Vetter *et al.* 2015). Established antibacterial properties of venom (discussed by Vetter *et al*. 2015) could select for antibacterial resistance in the venom glands; if this is true in *Steatoda* it might explain some reports of patients requiring a second type of antibiotic in Britain after alleged spider bites.

With appropriate recognition of symptoms and treatment, serious bacterial complications from spider bites should continue to be very rare overall.

Anaphylaxis

It is widely claimed by naturalists that there is only a risk from a spider bite in Britain if one is 'allergic' to it. Indeed, immune hyperactivity can result from some spider bites (Maso *et al*. 1987; Victoria State Government 2016). One of the few patients reportedly bitten on a second occasion by *Latrodectus* developed anaphylaxis (Maretić 1978b).

At least two patients have been reported with anaphylactic shock allegedly from *Steatoda* species: an observed bite with an associated photograph which I identify as *S. nobilis* (in Bournemouth, 2009; see Magee 2009) and a possible case with a subsequent specimen of *S. grossa* (in Cumbria in 2009: Table 2). Another possible case in 2019 developed a swollen face and conjunctivitis. These cases merit urgent formal professional case review, if still possible. Such incidents should be routinely compiled and reviewed professionally. Some occupations may increase the risk of repeat bites, repeat bites are becoming more likely as spider density grows, and a possible example has been reported (Kitching 2019).

Medical significance and occupational risks

For proportionate response it is important to note that Dunbar *et al*. (2017) state "envenomations by *S. nobilis* should still be regarded as of moderate medical importance, requiring at most, monitoring and pain management strategies." Dunbar *et al*. (2017) argue that despite many media reports "extensive necrotic wounding (due to either envenomation or secondary infection) seems extremely unlikely to occur". *S. nobilis* is also assessed as of medical significance by Dunbar *et al*. (2018a) and "we do need to consider bites from False Widows as a potential health risk" (Dugon, M. cited in Anon 2017). Similarly, *S. grossa* is reportedly becoming a health concern in Australia (Gray 2018) and both species merit further study and global collation of reports (*e.g.* from Chile, Faúndez & Téllez 2016).

It is often argued that bees, wasps or nuts are more dangerous than false widows, and I do not attempt to rank risks here. Instead, the aim is to alert to unrecognised and potentially growing risks. The public in some regions have been warned or learned about risks from bees or nuts, and the possible need for *immediate* treatment, but have had much misinformation about spider bite frequency and effect.

However, I suggest the risks need to be reviewed urgently, given the bite rate is almost certainly increasing. I argue that on current evidence it is likely the bite of this spider can, in very rare cases, be very serious, and that this risk will be greatly increased if it is not recognised or acknowledged as a threat. I hypothesise *Steatoda* bites present a non-trivial risk of necrotic ulceration or anaphylaxis, with potentially fatal outcomes. Whilst the risk remains highly controversial (*e.g.* Stuber & Nentwig 2016), if confirmed to cause ulceration spider bites might require early aggressive treatment (*e.g*. Fagan *et al*. 2003; Vetter *et al*. 2015) but of course *with the usual considerations of the balance of risk from use of antibiotics based on clinical experience*. Even if the risk per bite is very low, the total number of bites I suggest are occurring may provide a very large catchment for rare reactions, particularly as repeat bites also become more likely.

Given the evidence of a strong web and a strong venom being evolved to kill large prey, I cannot agree with a B.A.S. statement (quoted in Lazarus 2018) that "The bite of the False Widow is of minor medical significance, comparable to common insect bites and stings". In my assessment, given the pathology of the unfortunate experimental mammals, it would be very remarkable if bites from this genus did *not* occasionally lead to severe ulceration or other complications in humans. There may be regional and seasonal variation in severity (Horen 1963; Dugon, M. cited in Buckler 2018). The B.A.S. (2019b) whilst suggesting the risk is low, gives important advice to seek immediate help in the case of ulceration.

The long-standing medical focus on the neurotoxins in bites of *Steatoda* and *Latrodectus*, and failure to recognise cytotoxicity, bacterial complications or risk of anaphylaxis, could lead to inadequate responses in human medicine (or veterinary medicine, *e.g.* Ahrens & Crocker 2011).

I argue that closer, appropriately weighted attention should be paid to the frequency and risk of bites using all information available - rather than be dismissive of the possibilities of bites and impacts simply because many media reports contain major errors or alarmism. Whilst there is resistance in this case, it is notable that the 'precautionary principle' is typically applied in medicine and public health, and I argue it is extremely unreasonable to wait until somebody dies before accepting this could happen. Evidence to help assess risk should be collected more routinely, including detailed examination of the wound. In future, molecular evidence such as immunology could be used to confirm bites. Spider identification is likely to become possible using DNA (Blagoev *et al*. 2016). DNA barcode sequence data (mitochondrial COI) are available for *S. nobilis* from the Barcode of Life Data System (Bauer *et al.* 2019). Specimens presented to medics should ideally be preserved in ethanol of at least 70% concentration, but even fragments of the spider in *e.g.* vodka can be valuable. With further evidence it will eventually become possible for people to respond in a highly proportionate way to the risk. Given public interest, very carefully designed citizen science studies may have a role, and some pest control specialists now have relatively good knowledge of this species.

I suggest bites from *S. nobilis* are now an occupational hazard for workers likely to have high exposure to the spider, such as some decorators, cleaners, removals firms, builders, scaffolders, plumbers, gardeners, tree surgeons, bin workers, mechanics and park attendants. Similarly, *Latrodectus* bites have an occupational character with the epidemiology of bites depending on the species and region (Maretić 1978b).

Putative risks to pets and livestock

Livestock and pets including cats, dogs, rabbits and guinea pigs may be at greater risk than appreciated and vets also need to become more alert to this spider (as with *Latrodectus*, Ahrens & Crocker 2011). The spider has been alleged in media reports to have killed a rabbit and bitten a cat. Under experimental conditions a female *S. paykulliana* can kill a large guinea pig and mice but no effects were detected on a cat (Maretić *et al.* 1964; Maretić 1978a). The identity and susceptibility of these strains of laboratory animals is not clear.

Societal response

Concern amongst parents of schoolchildren, authorities and the wider public are understandable, given the numerous very graphic images of alleged "false widow" bite impacts that are easily found with a web search. This could lead to over-reaction or futile, expensive responses if the detailed biology of the species is not considered.

Fumigation and biosecurity

Several buildings in Britain have now been closed for attempted eradication of *S. nobilis* using fumigation with insecticides, and with international media coverage (*e.g.* Lazarus 2018; BBC 2018; Drewett 2018; Hafner 2018; Coleman & O'Mahony 2019). Building closure can last weeks. However, given the predicted distribution of the species a consistent approach might involve repeated closure of most schools in southern Britain - which is patently unacceptable and unnecessary. Similarly, it will certainly not be practicable to repeatedly close the many hospitals, stations, universities, shopping centres, offices, flats, industrial sites *etc*. for weeks at a time, simply to temporarily reduce population sizes in and on such buildings in an urban matrix saturated with the species.

I concur with Bingham *et al*. (1999), Bauer *et al*. (2019) and Dunbar (2019) that attempts to eradicate or control the species at an urban site are likely to be of very temporary effectiveness: there are too many likely refuges, particularly for juveniles. This is the experience with spiders in Australia (Australian Museum 2018). To judge by colonisation of new buildings in Oxford, recolonisation after fumigation may begin almost immediately and be complete within very few years. Similarly, after a cold winter of 2017-2018 in Oxford, webs and large spiders became rare on park railings only for re-establishment during 2018. Dunbar (2019) reports recolonisation weeks after collecting individuals. The species is very mobile, both on its own and assisted by human transport, and will be common in the matrix round infested building in cities and some villages. In some areas it might be more realistic to use large vacuum cleaners, brooms *etc*. (with protective clothing against dislodged animals) to achieve temporary reduction. However, given the females and eggs may be deep in crevices, pesticide is much more likely to kill them than is regular, powerful vacuuming - which has been found insufficient to clear a kitchen in the Everton area of Britain (personal observation 2016-2019). Fumigation was reportedly unsuccessful in a flat in London where the building was infested (Drewett 2018). Destruction of the webs is likely to slow recolonisation.

I suggest eradication should be seriously considered as an option for colonies that are demonstrably isolated, indoors or outdoors, for example the first record in a region, after checking the scale of the invasion.

Pest control agencies are gaining valuable experience in *S. nobilis* control effectiveness, but might have a conflict of interest in assessment of risk. There is a trade-off between risks from control measures and from the spiders, with commentators sharply divided on the balance.

International experience will be valuable. Practical measures to prevent bites by *Latrodectus* species in urban areas include sealing off access routes into houses, destroying spiders and egg sacs and use of insecticides (Maretić 1978b). For both health and ecological purposes, preventing colonisation could be far more effective than eradication.

Biosecurity needs to be reviewed urgently to reduce the risks of spreading *Steatoda* species further globally. This will be very challenging, given the range of containers and structures in which *Steatoda* can occur. Invasion has presumably been so successful in part due to ability to survive months with few resources, and the strength of its web enabling it to persist on the outside of active vehicles (Figure 3). Lessons can be learned from how problems with *Latrodectus* are expanding in North America (Arnold & Ryan 2009).

Responsible reporting and commenting

It will be very difficult to get a balanced and proportionate debate and response for such a confused and emotive issue, especially with the many misleading popular reports.

Examination of reporting of "false widows" suggests that many people simply repeat information from a small number of sources, and that many of the experts and organisations quoted have little direct knowledge of the species. Misinformation has escalated rapidly in recent years (Crawford 2015). Online browsing reveals there are numerous examples of statements that are erroneous, misleading or subjective. Some of these are illustrated and corrected in Table 3.

Conversely, there is a lack of attention to detail and clear lack of expert input to some public information documents: for example, some of the local authority guidance to London schools in 2018 related to evacuation had a photograph of *Amaurobius* sp.! For the purposes of verification it is particularly important that media reports clarify if a photograph of a spider is definitely the actual individual animal seen (or alleged) to bite.

Responsible media coverage requires consultation of arachnologists with extensive direct experience of the species (or, with caveats, of *Latrodectus*) and information from medics having accurate records of the patient in question - subject to privacy restrictions. For perspective, more note should be taken from medics with experiences of verified bites from *S. nobilis* and related species internationally, including *Latrodectus*, and the generally good recovery from such bites (*e.g.* Vetter & Rust 2012). The context of low numbers of verified bite cases and the ubiquity of *S. nobilis* in some areas has been noted (B.A.S. 2019c) but perhaps needs to be repeatedly stressed to reduce extreme and possibly futile local action and alarm. The risks of unnecessary or inappropriate treatment and alarm, including further stoking arachnophobia and a backlash inflicted on benign species, would ideally be in all reports.

The British Arachnological Society group on spider envenomation has inter-disciplinary expertise and might benefit from hosting some joint meetings with responsible, influential journalists. A global repository of information on the species with some form of scientific accreditation of individual statements and observations by a large inter-disciplinary expert audience would be valuable to help lead journalists and the public to relatively reliable sources from a wider range of disciplines and perspectives.

Table 3 Examples of erroneous descriptions of false widows.

Misinformation or myth	**Correction or alternative opinion**
Ponderous / slow moving	Very fast, in or out of web, especially above 10$_{o}$C
Docile / not aggressive / retiring / elusive	Relatively "aggressive" towards prey and in defence, using term consistently with other spiders
Will not bite unless provoked / can be handled safely / will only bite humans as a defensive reaction	Several recorded spontaneous bites, in or out of web, in defensive and offense
Males don't bite	Several recorded bites by males, causing steatodism
Very unlikely to bite in normal circumstances	Easy to get bitten - perhaps likely in some regions
Never been associated with effects of medical concern	Often associated with very serious effects, sometimes by medics, but rarely confirmed incontestably
Does not have cell-killing venom	Has cytotoxic venom
Seldom leaves its web	Often leaves web (males, females and juveniles)
Ecologically harmless / beneficial	Displaces native species
Origin in Canary Isles / Madeira	Not certain: more likely from a continent
Not often seen in built up areas	Most often seen in built up areas
Prefers to be outside	Typically indoors in cold regions
Webs usually above 1.5 m off ground	Webs often touch ground
It would be unusual for the species to live in a cinema	Probably in most cinemas in Southern Britain, and many in northwest Europe
They will abandon your house if you keep getting rid of their homes	Will likely recolonise very quickly and repeatedly
Solitary	Often in pairs or small groups, possibly subsocial

Education and awareness and the potential value of media reports

Further contacts and bites are inevitable and it is possible some such bites will become infected, so I argue very pro-active education and close medical monitoring of suspected bites are increasingly important. Several British news reports of bites note that victims or observers were unaware of the potential risk - some complaining that medics should have been better informed. For example: "the doctors and nurses hadn't even heard of false widows" (Sarah, quoted Metro News Reporter 2013); "People tell you it’s such a silly phobia and they can’t hurt you, but now I know that they can" (Coombs, C., quoted Salkeld 2012); "It isn't big, you can see it is squashed. If it is a false widow spider that has done it the hospital should know this spider about in our country and if I've reacted like that others could do the same. If I've reacted this way how would a child react?" (Rogers, L. quoted MacDougall 2019). Medics may have been relying on perceived experts in spiders to assess the risk of spider bite as low. I meet many people who do not realise any spider in Britain can pierce skin, very many who do not appreciate a British spider might be dangerous and many biologists and medics who are unconvinced or unaware of the risks.

I argue that the British Arachnological Society guidance (B.A.S. 2019b, 2019c) on "false widow spiders" (all *Steatoda* species) needs substantive revision, both in terms of the likelihood of bites and the severity of effects. I disagree that "False widows are sedentary by nature, remaining in their webs". Nor do I agree that "the risk of being bitten by a false widow spider must surely be relatively small". I argue the statement that *S. paykulliana* "can deliver a painful bite but the venom is quite mild in its effect" should be revised in the light of the experimental studies on mammals (Maretić 1978a). I argue it important not to either overstate or neglect the risk a *Steatoda* bite poses, and that all bites by *Steatoda* species should be treated in a similar way until any species-specific variation is identified.

I suggest the most appropriate and effective societal response is to provide much greater education in natural history and invertebrate identification in Britain and in other invaded regions with little history of dangerous spiders, such as northwest Europe. That would help problematic species and likely places of contact be avoided and swift action be taken after exposure. Regions with long experience of dangerous spiders, particularly *Latrodectus* (black widows and red-backs) provide good models for education and prevention. In Australia, education about spiders includes 'look but don't touch' and advice on locations and activities which increase the risk of accidental contact (Victoria State Government 2016; Australian Museum 2018); advice on how to avoid bites through checking certain stored items is highly relevant.

Schools and parents may need precautions for "false widows" (all *Steatoda* species) similar to their approach to anaphylaxis from bees or foods. I believe this is the most urgent topic for proper review by health professionals.

Education is also an opportunity to reduce arachnophobic anxiety and indiscriminate backlash against benign species. This is in harmony with a rising interest in environmental education, outdoor classrooms, biophilia and rewilding. Funding aimed at bite prevention could have co-benefits if beneficial species are illustrated. Identification guides will be helpful, especially if photographic and including webs (*e.g.* Vetter & Rust 2012; Dugon *et al*. 2017; Bee *et al*. 2017; Pendleton & Pendleton 2018). Good diagrammatic identification charts, flow charts and dichotomous keys would be valuable to reduce anxiety and protect native species. Simple educational messages are possible: for example, in northern Europe if the spider is in a spiral orb web, or is hairy, not shiny, or is a pale colour it is likely to be a beneficial species. Keys need to allow for rarely imported dangerous species, and so illustrations might be clearest. Such materials would ideally be made freely available for download from a global repository on *Steatoda*, as mooted above.

Public education on scepticism and caution in interpreting information from all sources would be valuable for society - and perhaps the example of *S. nobilis* can be used as an opportunity to show how both media and scientific reports can be erroneous. Filtering material from many sources whilst capturing accurate information is one of the great challenges of the internet age. The public need to be alert to conflicts of interest amongst all parties.

Arachnophobia is probably an evolved response in humans to the very real health threat spiders pose over much of the planet. This behaviour has been temporarily of lower biological and cultural significance in northern Europe where there are few reinforcements of the fear. However, this is likely to change with an increasing number of introductions of dangerous species (breeding or not). *S. nobilis* is quite a large spider in northern Europe, and with various conspicuous behaviours has the potential to encounter or alarm people - as media reporting illustrates. Panic or severe pain could also cause risks through a startled reaction to a bite - for example on ladders or when handling power tools or driving. Conversely, many people in cultures familiar with dangerous spiders may habituate to them somewhat, know how to deal with them and have less acute anxiety - since the British media and public response appears, superficially at least, to be relatively alarmist (but see also Vetter & Rust 2012).

The arachnological conflict of interest

The reasonable reluctance of arachnologists and medics to stoke adverse publicity about spiders might become counter-productive or even negligent - as, of course, might alarmism. Confidence in arachnologists will decline if the problem is seen to have been understated whilst attempting to reassure the public, or if it is overstated. In my experience of scientific outreach on spider conservation, I find people are often relieved to hear arachnophobia is likely adaptive, not necessarily irrational, can often be desensitised - and are reassured that some scientists will at least listen to their experiences. Media alarmism should not prevent justifiable alarm being raised, particularly now it is evident the species is of more medical significance than the spiders the public and medics are used to in some regions (Dunbar 2019).

It is of course very important to avoid exaggeration of risk from the bites (Anderson 1997; Bingham *et al.* 1999; Vetter *et al.* 2015), from a public health, animal welfare and environmental perspective. Health and economic consequences will arise from inappropriate treatment or even worry and arachnophobic anxiety. However, some literature very evidently downplays the risk - in a common and understandable inclination of arachnologists and others to encourage appreciation of spiders. Arachnologists should be acutely aware of a very substantial conflict of interest between conservation and spreading concern about spiders. Greater awareness amongst medics of the possibility of complications from a spider bite might reduce the number of serious consequences, so it is important arachnologists are open-minded about what is reported or hypothesised to enable a reasoned balance of risks.

Species interactions and potential ecological impacts in Britain

Knowledge of co-occurring species can help identify and predict the ecological requirements and distribution of a focal species, as well as provide baselines for assessment of its ecological impacts. Species or genera I found in casual observation in close proximity to *S. nobilis* in Bradford (Bd), Birmingham (Bh), Doncaster (Do), Leeds (Le), central London (Lo), Lymington (Lm), Oxford (Ox), Norwich (Nr), Start Bay (SB) and York (Yo) at various times between 2016 and 2019 include: *Pholcus phalangioides* (Fuesslin, 1775) (Bd, Ox, SB); *Segestria senoculata* (Linnaeus, 1758) (Bh, Ox); *Segestria florentina* (Rossi, 1790) (Ox, SB); *Steatoda bipunctata* (Bd, Ox, SB, Yo); *Steatoda grossa* (Ox, Le, Lo); *Achaearanea lunata* (Clerck, 1757) (= *Parasteatoda lunata*) (Ox); *Achaearanea tepidariorum* (C.L.Koch, 1841) (= *P. tepidariorum*) (SB); *Theridion varians* Hahn, 1833 (Ox); *Theridion melanarum* Hahn, 1831 (Bd); *Theridion melanarum* or *T. mystaceum* L.Koch, 1870 (Le, Ox, SB, Yo); *Therdion blackwalli* O.P.-Cambridge, 1871 (Ox); *Lepthyphantes* sp. (Bd, Bh, Ox, SB); *Linyphia triangularis* (Clerck, 1757) (Ox); *Neriene montana* (Clerck, 1757) (Ox); *Neriene* sp. (Bd, Ox); *Metellina merianae* (Scopoli, 1763) (SB); *Metellina* sp. (Ox, SB); *Araneus diadematus* Clerck, 1757 (Bd, Bh, Do, Le, Lo, Ox, Nr, SB, Yo); *Larinioides cornutus* (Clerck, 1757) (Ox, SB, Yo); *Larinioides sclopetarius* (Clerck, 1757) (Ox); *Nuctenea umbratica* (Clerck, 1757) (Bd, Bh, Le, Ox, SB); *Zygiella x-notata* (Bd, Bh, Do, Le, Lm, Lo, Nr, Ox, SB); *Tegenaria* spp. (Bd, Bh, Do, Le, Lo, Ox, SB, Yo); *Tetrix denticulata* (Olivier, 1789) (Bd, Le, Yo); *Amaurobius fenestralis* (Stroem, 1768) (Ox, SB); *Amaurobius similis* (Blackwall, 1861) (SB); *Amaurobius ferox* (Walckenaer, 1830) (SB); *Amaurobius* sp. (Bd, Bh, Do, Le, Yo); *Salticus scenicus* (Clerck, 1757) (Ox); *Pseudeuophrys lanigera* (Simon, 1871) (Ox).

Some such species are likely to encounter each other frequently. Displacement by *S. nobilis* of native species with similar habitat has previously been suggested (*e.g.* Kulczycki *et al.* 2012; Smithers 2016; Dugon *et al*. 2017). In both Oxford and Start Bay it is apparent that in many of the sites the native species would likely occur (such as the corners of windows, beside pipework and on fences and railings; personal experience) they are now often replaced by *S. nobilis.* Based on casual personal observation of co-occurrence I hypothesise that *Zygiella x-notata* and *S. grossa* are two of the most resistant species to displacement in Britain; in Oxford it is only in shallow holes in crumbling limestone walls, and at ground level, that I can find *S. grossa* locally more abundant than *S. nobilis. Z. x-notata* often does not need a crevice for a retreat, and can build a retreat and egg sac in a right angle between surfaces, whilst this is uncommon for *S. nobilis* which typically have a concealed retreat in a crevice. The similarity in appearance of some *Zygiella* and *Amaurobius* species to *S. nobilis* raises the possibility of convergent evolution or co-evolution and mimicry over long timescales. Notably, at temperatures just above 0_{o}C when I find *S. nobilis* typically unresponsive, *Z. x-notata* is sometimes still active, building webs and attracted to a tuning fork. I hypothesise that in colder areas, including the north of Britain, *Z. x-notata* has a competitive advantage, and / or can kill *S. nobilis*, and is able to occupy more of the suitable sites for web-building.

S. nobilis has a wide diet in Ireland (Dugon *et al*. 2017, Dunbar *et al*. 2018a). I have found a similar range of prey in webs, including woodlice, earwigs, moths, flies and insects with defences such as wasps *Vespula* sp. and the invasive, noxious harlequin ladybird *Harmonia axyridis* (Pallas, 1773). In captivity, *S. nobilis* eats *Zygiella* and *Pholcus*, whilst a female *S. florentina* readily ate a female *S. nobilis.* In captivity, *S. grossa* eats smaller *S. nobilis* (and in the wild reportedly eats *Latrodectus*).

S. nobilis will be present in many protected areas, including, in the U.K., National Nature Reserves and Sites of Special Scientific Interest. For example, I have found them in Wytham Woods and Port Meadow (Oxford), Slapton Sands (Devon) and Lymington-Keyhaven Marshes (Hampshire). In such protected areas they are typically on artificial rigid structures such as walls, bridges and gates which support few rare native species, but also occurred at shingle level amongst rocky coastal defences and on a large tree trunk. Declines of the common and widespread synanthropic species such as *Amaurobius* spp. and *Tegenaria* spp. are of trivial conservation concern, with such urban species and their predators typically being of low 'species quality' (Hambler & Canney 2013). However, it is possible that uncommon European thermophilous species of cliffs and coasts will be impacted, as might local species such as *Larinioides sclopetarius*. Viviparous lizards are a protected species in Ireland (Dunbar *et al*. 2018a) but the contact rate is unlikely to be high.

Thermal tolerances

S. nobilis may have thermoregulatory behaviour which is unusual in Britain, including its positioning on the web. The species is tolerant of temperatures which are high by British standards. At temperatures above about 28°C, the species may come out onto its web even in daylight (personal observation). Such exposed behaviour has also been noted for some *Steatoda* on days over 30°C in Athens (Greg 2012). I hypothesise this may be associated with dangerously high temperatures of crevices in stone, brick and metal structures. It is also likely in some cases that the spider is basking. It is possible the spider moves out into the web to be in a better position to catch very active prey; however, a satiated juvenile found in this posture was unresponsive to a vibrating stimulus, suggesting basking was more likely in that case.

I have also observed such exposure of *S. nobilis* in Oxford on warm summer days amongst medium-sized juveniles that were not in direct sunlight, in adults in shade in a bin store with a warm roof, and in a warm conservatory. On 8 January 2019 in Oxford with air temperature about 5°C, two juveniles were seen out in the same web in a sunny warm microclimate - possibly basking. Other personal observations in Oxford of possible basking include an adult male in sunlight in a web on 1 April 2019 at about 4pm and about 13°C, and a juvenile on 11 April 2019 at about 4pm and about 11°C. My observations and other reports suggest the species is most abundant on sites exposed to sunlight, so this is likely to be a warmth-seeking ('thermophilous') species in cold regions. It can be abundant in dark indoor spaces if they are warm, such as lofts, but it is not commonly found in cool cupboards (personal observation).

The species rarely attacks a vibrating stimulus when temperatures are near 0°C. It can survive at least occasional freezing temperatures. For example, temperatures of around -8°C in Oxford in early 2016 did not prevent some adults and subadults surviving on exposed park railings, and then large populations occurring later in the year. Similarly, an adult found near Lymington on 8 April 2017 had survived temperatures around -6°C. Snazell & Jones (1993) observed survival outdoors in Portsmouth through a cold winter. However, after a night dropping to about -9°C on 12th December 2017 in Oxford, a large female was found on the ground - literally with its legs in the air; it recovered within an hour at room temperature. On 2 February 2019 an adult male was found dangling dead in a web in Oxford two days after temperatures had dropped to about -8°C, with possible ice damage having softened the abdomen (Figure 4).

Figure 4 Adult male *S. nobilis* possibly killed and internally liquefied by a frost. Outdoors drainpipe, Oxford, U.K., 2 February 2019. Photo: C. Hambler.

The species can survive for months, build a web and lay eggs in a domestic fridge (c. 9^{o}C, dark most of the time). In temperatures below about 5^{o}C, the species is difficult to attract onto the web using a tuning fork. I have found the species unresponsive on sunny, frosty mornings near 0^{o}C.

I argue *S. nobilis* is likely to have benefitted from the Central England warming of the late 1980s (Met Office 2019a), from urban heat islands (Goddard & Tett, 2019) and from increased numbers of heated buildings. I hypothesise milder winter Central England temperatures since c. 1980 (Met Office 2019b) may be more important than changes in mean temperature, given the species' frost-sensitivity and warmth-tolerance. Whilst Bauer *et al.* (2019) suggest the timing of northerly expansion in the U.K. does not coincide closely with regional warming, it is possible the pioneers into new areas will have benefitted - but that these were under-recorded. Observed warming in Europe over recent decades is projected to continue in some climate change modelling (Kovats *et al*. 2014) which might benefit the species in some areas although there is much uncertainty in climate change predictions at the regional scale (IPCC 2013).

Observations based on casual records are insufficient to identify the thermal requirements and other abiotic and biotic tolerances of the species, and explanation of its range will only be possible with more detailed autecology and laboratory study of its fundamental niche.

Global distribution, origin and invasiveness

The increasingly global reported distribution of this species (Vetter & Rust 2012; Dugon *et al*. 2017; CABI 2018) is intriguing, particularly the frequently repeated claim it is endemic to the Canary Islands or Madeira (*e.g.* Kulczycki *et al.* 2012). However, it is extremely unusual for an island endemic to invade and become abundant on continents, whilst the reverse is very common (Hambler & Canney 2013). The species is now known in North and South America, Iran, Morocco, as well as mainland Europe (reviewed by Bauer *et al*. 2019). Whilst it is possible it came into Britain from subtropical North Atlantic islands in the late 1800s, there is little evidence for this, nor for banana crates being the mechanism of import. I hypothesise it is an invasive species on the Atlantic islands, introduced by early travel along with very many other species (and conceivably via Britain). An exotic status has also been suggested by a naturalist reportedly familiar with these Atlantic islands (Machado, A., quoted in Jules 2009). However, given the occasional arrival of Saharan dust at various altitudes in the Canary Islands (P.F. Roche, personal communication), and in the Ecuadorian Andes (Boy & Wilcke 2008) a region where *S. nobilis* is recorded (Bauer *et al.* 2019), and in Britain, it is not impossible *S. nobilis* ballooned to such sites and is native to North Africa and to some downwind locations (including Britain).

Another possibility is that the species is intermittently native in northern Europe. It might have been abundant in the Holocene Thermal Maximum and Mediaeval Warm Period, when warmer than today, then survived indoors in urban areas or other refuges during the Little Ice Age until c. 1850 - but if so it is very surprising it was not discovered in the region sooner. It might have repeatedly colonised Britain. I find it more plausible it was introduced to Britain in the last 200 years, and it is possible that earlier introductions through international transport failed due to cold.

Behavioural observations including survival in very dry buildings (personal observation) and a southerly distribution in Britain imply the species evolved in a warm and fairly arid region where it can avoid temperatures much below about -5^{o}C. Snazell & Jones (1993) note tolerance of sub-zero temperatures is surprising for a species alleged endemic to the Canary Isles and Madeira, and I agree that sub-tropical spiders are unlikely to be cold-adapted. The temperature range in much of the alleged 'native range' is far narrower than its thermal tolerances. I therefore suggest a continental desert is a more likely origin, or alternatively a region with extensive arid, rocky, early-successional habitat. Rocky deserts, tropical mountains, cliffs and coastlines in North Africa, the Middle East and North and South America would be good places to examine, particularly in habitats that might pre-adapt species to urban environments. Genetic similarity to *S. maura* (Simon, 1909) implies its origin may be in the Old World (see Bauer *et al*. 2019).

It is possible the species has been overlooked in the native range because it is naturally at low density, regulated by parasites, parasitoids or predators from which it has been ecologically released in introductions. This might raise prospects for biological control, but given *Steatoda* and *Latrodectus* species naturally occur widely there might be a risk to non-target species. Some *Latrodectus* species have population irruptions leading to epidemics of bites, which might be mediated by natural enemies and / or weather (Maretić 1978b).

Based on recorded habitats, climate envelope modelling and recent changes in recorded distribution (Bauer *et al*. 2019) suggest that, globally, temperate and coastal areas are likely to be invaded. However climate envelope modelling has serious limitations (Hambler & Canney 2013), and particularly in the case of a species that can thrive indoors (insulated from the regional climate) and dispersed by people. I agree with Bauer *et al.* (2019) that these projections are likely to be conservative, perhaps the more so considering the data used to train the model are problematic due to under-recording of distribution and urban microclimates. Climate envelope modelling may be more valuable in predicting places where survival could be highest outdoors and thence flows between building interiors could be most rapid - particularly if combined with data on global trade flows.

If in northern areas the mortality of *S. nobilis* is higher for individuals outdoors and exposed to cold, movement between heated buildings will be slower - perhaps explaining why British cities such as Bradford, Doncaster, Leeds, and York do not yet have large populations recorded indoors. Native species may have greater frost hardiness. Natives might be better able to evade predation by *S. nobilis* in colder climates if they are more alert and / or faster. *S. nobilis* achieves larger size than many native spiders in Britain, disperses quickly and its web is very versatile. It is also possible that with more recent colonisation of more northerly British sites by *S. nobilis* and its currently lower density in the north, native species have not yet been excluded in many areas - but will be. Manipulation experiments are required to understand mechanisms for likely displacement in warmer regions.

I hypothesise the species could establish outdoors globally almost anywhere which is not often far below -5^{o}C, and even then it could colonise inside buildings, including those in both polar regions (such as research bases). I hypothesise that *S. nobilis* is hugely under-recorded globally at the present time, is increasing in range rapidly, and that it is already established in many cities of Europe (*e.g*. Bauer *et al.* 2019), coastal and inland.

With internationalisation of its distribution, I suggest *S. nobilis* has the potential to become a very serious conservation problem on oceanic islands, as with many invasive invertebrate species; islands are often easily invaded and older islands have endemic species that are relatively easily driven extinct by invasives (Hambler & Canney 2013). Australia and New Zealand may be particularly vulnerable to invasion (Bauer *et al*. 2019) as might be their endemic fauna. *S. grossa* is already a very widespread invasive in Australia.

After introduction, it took *S. nobilis* over 100 years to become a very abundant and socially problematic species in Britain (Bauer *et al.* 2019), despite good dispersal abilities. Even near the site of the first record, the species did not come to be abundant for over 100 years. Observed impacts in Ireland have also been delayed (Dugon, M. quoted in Bailie 2018). Such long lags between invasion and becoming a problem are known in other species (Hambler & Canney 2013) and should give pause to those who consider the global threat from invasive species is overstated.

Other behaviour

In Oxford I have observed walking dispersal behaviour indoors (isolated individuals resting or walking on walls, as above). These include adult males in February and October - suggesting some adult males may overwinter. Ballooning (as per Kulczycki *et al*. 2012) and human transport seem the most likely method for colonisation of many sites, helping explain its colonisation of street furniture *etc*. in rural areas; unlike Dugon *et al*. (2018) I think this is also a likely long-distance dispersal mechanism. Abseiling of juveniles is likely to result in local dispersal. The species sometimes abseils from threat, but may drop to the ground without a thread, and this can be fatal for gravid females. It is likely the species must often move to find new websites as it grows. Juveniles are often in small crevices or have limited attachment sites for web anchoring. A juvenile which had possibly outgrown its shallow retreat after a large meal and was seen 'basking' on 11 April 2019 was absent by 12 April, in an urban site very unlikely to have much predation (personal observation); its shallow silk retreat and website were occupied a few days later by a much smaller *S. nobilis*.

Sometimes one can find small juveniles using large webs, or a small and large individual responding simultaneously to stimulation of a web by a tuning fork, with the small spider often responding first but also retreating if touched by the larger one (Video 6, Supplementary Material Online). In Oxford on 24 February 2019 a vibrating stimulus in a web was approached by a juvenile c. 2 mm long. A second stimulus led to a juvenile c. 4 mm long approaching, and then an adult female. These three spiders had retreats at different locations. This female and web had been present at least since October 2018, and the retreat of the female included at least two hatched egg sacks. Similarly, two juveniles (c. 2 mm and c. 3 mm) observed sharing one web (Oxford, 10 January 2019) approached a vibrating stimulus (Figure 5). In Slapton on 5 October 2019 four juveniles of sizes c. 2-3 mm approached a vibrating stimulus in a web. A web with a tubular retreat used by an adult until November 2018 was in use by a mid-sized juvenile in mid December 2018; a small individual had been present in the same metal crevice as the adult using this web for some months, sometimes responding to stimulation of the web which brought out the adult, but not using the main web itself. The web and retreat persisted to early 2019, but were replaced by a *Zygiella* sp. by June 2019.

Figure 5 Two juvenile *S. nobilis* sharing a web by a drainpipe, Oxford, U.K., with both responding to a tuning fork. The breadth of each tuning fork limb is c. 5mm. Photo: C. Hambler.

I hypothesise webs may be inter-generational or taken over by younger spiders, and sometimes last years. This may occur in other *Steatoda* species: in central Oxford some large webs of *Steatoda* contained only small *S. grossa* unlikely to have built the web. Subsocial behaviour (as in some other spiders, Kim 2005), facultative sociality (Bertani *et al*. 2008), and possible matriphagy would be worth investigating, as would the fitness effects of web removal. It can be difficult to see where one web ends and another begins. The strength and longevity of the silk mean that an old web can be used as a scaffold for webs by other spider species. Adult males can often be found in the same retreat as adult females, perhaps mate-guarding.

Although widely described as 'sluggish' juvenile and adult *S. nobilis* can run very fast on the ground - at least at temperatures over about 10°C. Indeed, I find it a relatively difficult species to capture once extracted from its web. The species can be collected using flexible tweezers or a vacuum sampler (Dugon *et al*. 2017). I find it simplest to whisk it tangled in silk from the web with a tuning fork, or dislodge it with a stick, and then extremely carefully herd it into a specimen tube. The spider's speed, even when cool, can require fast obstruction of the retreat and then very great care in driving it into a container using a stick, tuning fork or similar; I would *not* recommend using fingers, even in gloves. Transferring the spider between tubes can be difficult, since it can climb fast, including up the walls of glass tubes. Having had several near-misses with dislodged spiders, and escapes in captivity, *I advise great caution if attempting capture*. I propose a safe-handling protocol be formally developed.

The species very readily approaches a vibrating stimulus, except when near freezing, or in rain or strong wind when the web is being disturbed, or sometimes when the web has many seeds of *e.g.* *Salix* spp. in it. An electric 'sonic' toothbrush (*e.g.* Philips 'Sonicare') or a tuning fork (frequency A440) can be used to draw it out onto the web, and the stimulus need not always touch the web to evoke attack. An attack on a tuning fork (and presumably prey) may start with either a bite or wrapping using the rear legs, and often involves multiple bites over some minutes. Heavy or repeated contact with the web often causes the spider to retreat rapidly or become unresponsive.

The spider is reportedly more active at night (Dugon *et al*. 2017). It is often conspicuous in low light or at night, waiting on the web surface and web building. It can be found easily using torchlight at night. Timing of emergence is likely predominantly triggered by light level, not a body clock: if the web is in an interior light fitting the spider may only come out when the light goes off - *e.g*. at dawn. It is very prepared to attack prey in bright daylight, and in winter is more likely to attack during warmer daylight hours (personal observation).

I have a few times observed a pungent smell when collecting or disturbing females with egg sacks. Observation is difficult, but I suspect this may be from a fluid I have once seen near the mouthparts, and I hypothesise *S. nobilis* has a volatile defensive chemical but this is rarely used. One possible victim of a bite noted a smell of burning hair when the spider was rolled onto, which faded fast. In Britain, predation occurs at some sites: webs and old egg sacs can disappear rapidly from crevices that have been occupied for years (personal observation). In some elevated locations, birds seem the most likely predator, and a Eurasian wren was seen repeatedly fluttering to feed on a fence with many *S. nobilis.*

Egg sacks, if partially unravelled, can unwrap explosively scattering tens of eggs - a possible defensive and dispersal mechanism. Large females taken into captivity at any time of the year often lay fertile eggs within a few days - possibly triggered by a rise in temperature.

Proposed research priorities

I summarise in Table 4 testable speculation and hypotheses, to reinforce uncertainties in the discussion above and as provocation to further debate and research.

Table 4 Hypotheses and predictions for bites by *Steatoda* species.

Prediction or proposal	Requirements and data deficiencies
The species is present indoors in almost all European cites, particularly in the northwest and south of Europe.	Targeted survey.
Present outdoors in all cities in Britain.	Targeted survey.
Present in most urban areas and 10 km map grid cells of Britain south of Birmingham.	Targeted survey.

The number of reported bites by *S. nobilis* will rise rapidly.	Compilation of reports into a central global database.
The number of confirmed bites by *S. nobilis* will rise rapidly.	Compilation of reports into a central global database. Improved surveillance. Immunological assay for antigens.
The number of confirmed serious bites by *S. nobilis* will rise rapidly.	Compilation of reports into a central global database. Information for practitioners for improved surveillance. Immunological assay.
Bites from spiders in webs will be much rarer than from spiders not in webs.	Awareness that spiders can bite without compression. Detailed reporting of circumstance of suspected and observed bites.
Bites whilst walking on skin are triggered by heat or chemical stimuli.	Experimental.
Bite risk and effects vary regionally.	Experimental.
Cytotoxic venom predisposes to ulceration.	Biomedical experimental, with specimens in many regions. Improved surveillance and reporting of possible cases.
Bacterial carriage occurs and predisposes to ulceration.	Biomedical experimental with specimens in many regions. Improved surveillance and reporting of possible cases.
Antibiotic resistant bacteria live in venom and /or mouthparts.	Biomedical investigation in laboratory with appropriate safety category (Containment Level).
Venom induces anaphylaxis.	Medical review of past possible cases. Review of photographic evidence of possible case. Systematic monitoring.
Distribution outdoors limited by temperatures below c. -10$_o$C.	Systematic recording with microclimate data. Lab studies of preferences
Abundance limited by structural features in exotic range above limiting temperature	Manipulation studies.
Once established in a region the species is unlikely to retreat, even under cooling scenarios.	Long term monitoring, including sites it is already known.
Steatoda and *Latrodectus* taxonomic distinctions artificial.	Taxonomic review with genetic / genomic evidence.
Spider can sense Infra-Red light and seeks warm locations (such as beds).	Lab studies. Field trials.
Millions of people in southern Britain will be bitten by *S. nobilis* at some time, many repeatedly.	Improved surveillance and reporting of possible cases. Education. Immunological markers.
Species is invasive or non endemic to the Atlantic islands.	Genetic studies.
Global origin in Northern African mountains, Middle East or other continental site with warm or hot arid or semi arid climate.	Targeted field searches. Genetic studies. Central database of global observations.
Can competitively displace native species, particularly in warmer regions.	Empirical evidence.
Moves out onto web to bask and to avoid extreme heat in crevices.	Behavioural observations. Lab studies of preferences.
Will cause global extinctions or declines of endemic and native invertebrates on oceanic islands.	Monitoring of native invertebrates where invasion is occurring.
Webs can be inter-generational.	Multi-year monitoring of webs and individual spiders. Genetic methods to identify spider individuals and relatedness.
Has a defensive, pungent secretion, used particularly in parental care.	Empirical studies.

I suggest further work is most urgently needed on:

1) The potential for anaphylaxis after *Steatoda* bites, with a professional review of informally reported cases.
2) The mammalian cytotoxicity of *Steatoda* venoms.
3) The risk and mechanism of ulceration and necrosis after *Steatoda* bites. This should include professional compilation and review of an international database of medical, citizen and media

reports in the light of recent confirmation of cytotoxicity in *Steatoda* venom. Possible symbiosis and synergisms with necrotising bacteria requires very urgent investigation in *Steatoda* collected from multiple regions.

4) The potential complications of *Steatoda* bites in pregnancy.
5) Novel *Steatoda* bite symptoms.
6) The global distribution of *S. nobilis* (particularly in cities and on tropical islands with endemic animals) and its likely region of origin.
7) Thermal requirements and their relevance to the distribution and invasiveness of *S. nobilis*.
8) Natural enemies in potential biological control of *S. nobilis*, considering risks to native species.
9) Orientation, thermotaxis and dispersal.
10) Potential behavioural triggers for bites, including movement, warmth and chemicals.
11) Review of which other species, such as *Amaurobius*, might be misidentified as *Steatoda* and be causing ulcerating bites in Europe.
12) Immunological assays for *Steatoda* bites.
13) Methods of raising public awareness of risks of spider bites, and of reducing encounter rates, without reinforcing arachnophobia. This should be based on best practice globally.
14) Horizon scanning and contingency planning for future invasions.

Such research will require inter-disciplinary collaboration including pathologists, immunologists, clinicians, ecologists, arachnologists, psychologists, physiologists, climatologists and epidemiologists. I hope this paper will enable comments from multiple specialists who might not have easy access to literature outside of their field. Opportunistic reporting has proved inadequate to clarify risks. Currently, the onus for improved reporting and verification of bites has often been placed onto the public - with some medics and arachnologists essentially requiring direct observation of the biting animal and presentation of the same spider to an arachnologist: I suggest this is unreasonable and potentially risky. Moreover, it will take many years to record and confirm a wide range of person-specific symptoms from the bite. There is a need for much more systematic inspection and formal recording of possible bites, for collection of spider specimens and for archiving of well-labeled photographs when possible. Given the many current difficulties of obtaining all the required evidence for confirmation of a *Steatoda* bite, immunological surveillance may prove the only realistic way to assess bite frequency and symptoms.

It is likely that much can be learned from the numerous studies of *Latrodectus* and latrodectism (Maretić 1978b) regarding the effects, action, treatment and avoidance of *Steatoda* bites.

Despite its prevalence and the public interest, *S. nobilis* illustrates we have much to learn about European spiders in terms of distribution, ecological and medical impacts. Moreover, *S. nobilis* has characteristics that might make it amongst the most widespread and ecologically significant of global invasive species.

Supplementary material

Materials available at OSF https://osf.io/6j8c5/

Videos by C. Hambler, using a Canon EOS 100D with 24 mm lens.

1) S. nobilis female attacking a finger. Oxford, U.K., 31 October 2018. Ambient temperature c. 10°C.

2) S. nobilis female biting a gloved finger. Oxford, U.K., 6 November 2018. Ambient temperature c. 12°C. The bite slightly penetrated the skin, causing mild tingling.

3) S. nobilis female attacking and wrapping a tuning fork. Oxford, U.K., 31 October 2018. Ambient temperature c. 10°C.

4) S nobilis juvenile (c. 3 mm body length) attacking a tuning fork. Oxford, U.K., 6 November 2018. Ambient temperature c. 12°C.

S. nobilis female attacking a tuning fork. Oxford, U.K., 31 October 2018. Ambient temperature c. 10°C.

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Conflict of interest disclosure

The author of this preprint declare that he has no financial conflict of interest with the content of this article. C. Hambler is one of the PCI Zool recommenders.

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