The false widow spider *Steatoda nobilis* is a notable invasive species.

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Abstract

Steatoda nobilis, a 'false widow' spider, has undergone massive population growth in southern Britain, at least since 1990, and is greatly under-recorded. 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, sepsis or anaphylactic shock. 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 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.

Introduction and aims

Steadoda nobilis (Thorell, 1875), often called a 'false widow' spider or 'the noble false widow', is widely regarded as the most dangerous spider breeding in Britain. Its recorded global range is expanding (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*, 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 false widow bite, it is important to review how significant a 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 geometricus*, C. L. Koch, 1841) which have previously been considered of minor significance (Goddard *et al.* 2008; Arnold & Ryan 2009).

Awareness of the ecological context of infestations and of the improbability of eradication may permit more considered societal responses. Assessing the risk to public health and conservation requires use of both the specialist literature and of numerous blogs, newspaper and other non-specialist and potentially 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. There may be a role for 'citizen science' in monitoring this distinctive spider and its effects.

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. I hope that publishing it initially as an open access preprint will enable fast inter-disciplinary review and correction of errors.

In particular, I perceive 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 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, 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 interdisciplinary teams.

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 false widows in Britain has increased rapidly in recent decades, likely leading to an increased bite rate and thence media coverage.

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, Devon, 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; 2019b; 2019c; Bauer *et al.* 2019), excluding some outliers in Scotland. There has also been a recent spread in Ireland (Dugon *et al.* 2017) 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. In the 1980s I spent thousands of hours 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°C and high humidity, I observed large spiders 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 my very frequent examination of this wall in the 1980s, *S. bipunctata* (Linnaeus, 1758) was present but *S. nobilis* was not detected. Recognising my under-awareness of *S. nobilis*, during the

first week of September 2016 I examined many structures near roadsides on an east-west and a north-south route across Oxford (up to the ring road). I found *S. nobilis* 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 20km from the first British record. In the mid 1990s I did not find the species during annual visits and occasional examination of arachnids. 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 abundant in September 2018.

The spider's increasing abundance was probably not apparent to me sooner because the web superficially looks like a number of other common species. Whilst the web has a typical scaffold structure, it also has a sheet or hammock beneath most of the scaffold. It has a tubular retreat (at various angles to the web dependent on suitable structures and crevices). 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. 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 suggest that its gradual increase in abundance is easily overlooked. Moreover, recording requires appropriate care in public and private urban areas, and can attract 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 very evident from my personal search effort in outdoors areas.

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. It is not yet (25 June 2019) mapped in these cities in the Spider Recording Scheme. In Doncaster I found a single female in January 2019 (during about 2.5 hours of targeted searching). In Bradford and Leeds 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 *Z. x-notata* (Clerck, 1757), members of the genera *Tegenaria*, *Amaurobius*, *Lepthyphantes*, *Linyphia*, *Nerienne*. 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.

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 and 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.* (2018) 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).

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192 Some common websites in southern Britain (based on personal observation) are illustrated in
193 Figure 1. These include: walls; drain pipes; guttering; road signs; lamp posts; traffic lights;
194 street name signs; litter bins; salt bins; dustbins; skips; park railings; metal, wood and plastic
195 fencing (especially corrugated metal security fencing); junction boxes; window frames; lamp
196 fittings; cistern overflow pipes; boiler flue vents; garage door frames.

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Figure 1: Examples of websites of *S. nobilis* in close proximity to people, in various parts of Britain. All photos 2018 or 2019, Clive Hambler, except last one, 2019 Sophia Leroy-Puri. The vast majority of webs in these locations were *S. nobilis*.

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. 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.*.

The species occurs inside and outside blocks of flats and other tall buildings, from the ground to at least four floors up (and I predict much higher). Webs are relatively robust, 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.

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 clarify 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). From the ease it is found in Oxford, Norwich and London and the south coast, and its mapped distribution, I predict 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. I predict it will also be present in most villages in this region. I predict almost all 10km 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.

The species is now the commonest spider on some structures, reaching high densities compared to many native species of urban environments.

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).

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256 However, there may be a very substantial failure of communication between medics and
257 arachnologists. A recent Freedom of Information request by the pest control company
258 Fantastic Services reveals there have been over 2000 cases of spider bites or suspected spider
259 bites reported by the National Health Service Trusts, particularly in the south of Britain, in
260 the period 2014-2018 (Burrows 2019; Wathen 2019). Many of these may prove to be
261 erroneous, but it raises the possibility of a surge in the bite rate corresponding to a surge in
262 abundance and northern distribution.

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264 Under-recording of bites is particularly likely if there is itching or pain but no hospitalization
265 (for example due to swelling or ulceration) and most of the likely bites I have heard of via
266 colleagues were not reported to medics. If, as with *Latrodectus*, pain often develops ten
267 minutes to an hour after the bite (Maretić 1978b), then the involvement of a spider could be
268 overlooked. I suggest that spider bites are greatly under-reported in the media or to medics
269 compared to their actual frequency.

270

271 I suggest the abundance, habitats and behaviour of *S. nobilis* now make it one of the most
272 likely species of spider to bite people in Britain. I therefore can no longer agree with B.A.S.
273 (2019b) that "being bitten by a spider is very unlikely in this country in normal
274 circumstances". I find it conceivable that millions and perhaps most people in southern
275 Britain will be bitten by *S. nobilis* - and that most will not realise it. Given its high densities
276 in some homes, offices, workplaces and gardens, it could become one of the commonest
277 sources of reported and of verified spider bites and their medical sequelae globally.
278 Nevertheless, it is very important to remember that *verified* spider bites remain a rare
279 phenomenon globally (Stuber & Nentwig 2016).

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281 ***Possible bites reported in the British media***

282 Several reports of possible bites are available which I suggest should not be overlooked if
283 treated with appropriate caution. A formal search for cases is beyond my resources and
284 expertise. As a provocation to professional medical research, my superficial online
285 investigation of the popular media (using Google, Google Images and a range of search terms
286 such as 'false widow' and 'bite') reveals there are now over 50 people in the British Isles who
287 have reported spider bites since the year 2000 and had subsequent media attention. A formal
288 inter-disciplinary review including arachnologists, public health specialists and medics would
289 be necessary to locate, substantiate and quantify alleged spider bite records in Britain - which
290 would require considerable effort (probably taking months). It is not the intent of this paper to
291 detail or quantify cases or risk, but to encourage proper systematic research which may not
292 have occurred in the absence of incentive and of recent arachnological, ecological, and
293 toxicological evidence.

294

295 Of the c. 50 alleged spider bite cases I found in the media, at least six meet the criterion for a
296 'proven case' proposed by Anderson (1997): a spider was found in immediate proximity to the
297 bite. Many other cases meet Anderson's criterion for a 'probable case': spiders recorded
298 promptly nearby or within the house. However, Anderson's criteria are arguably superseded
299 by Stuber & Nentwig (2016) and many of the reports in Britain would not count as verified.

300

301 Some examples of what I consider relatively likely cases of spider bites in Britain are
302 illustrated in Table 1, with my assessment of the likely accuracy of the identification - and I
303 suggest it is very risky to argue these are all misidentifications or misreporting.

304

305 **Table 1:** Selected examples of popular media reports of alleged serious consequences from
306 observed or extremely likely spider bites in Britain. The ambiguities and uncertainties
307 indicate the need for more systematic inspection and formal recording of possible bites, and
308 for collection of spider specimens when possible

Alleged bite effect	Alleged bite site on body	Place in Britain, activity and date	Evidence of spider	Evidence it may be false widow	Victim or media imply medical confirmation of a spider bite?
Ulceration; necrosis; induced coma; substantive debridement; at least eight operations	Upper arm	St Albans, Hertfordshire In living room 2017	Walked up arm and spontaneously bit	Patient thinks may have been false widow	Yes: reported diagnosis of necrotising fasciitis secondary to a spider bite
Ulceration; necrosis	lower leg	Mansfield, Nottinghamshire Asleep in bed2017	Small brown spider seen, after tingling sensation	Patient self diagnosis	Yes
Ulceration; necrosis; cellulitis (recurrent over at least 8 months)	Top of foot	Rossendale Borough, Lancashire In hospital, foot on chair 2016	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
Extensive necrosis; amputation risk; at least 3 weeks in hospital; months of problems walking	Thigh	Essex Decorating in a school 2013	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.	
Dark itching skin; "reinfecting" after 2 weeks	Arm	Leighton Buzzard, Bedfordshire In house putting on jumper c. 2007	Spider found in sleeve after intense bite	Identified by patient	
Anaphylactic shock	Hand	Bournemouth, Dorset Cleaning bathroom 2009	Picked up spider	Photograph reportedly of spider that bit her: identified as <i>S. nobilis</i> by C. Hamblen	
Burning pain; emergency hospital admission with suspected heart attack	Abdomen	Salisbury, Wiltshire Market stall moving boxes 2006	Spider seen on abdomen after burning pain on chest		Yes: puncture wounds; doctor reportedly said no doubt about it

Several patients report a double puncture at the bite site. Proving the spider in question is a *Steatoda* species, or *S. nobilis*, and is the same individual that allegedly bit the patient is much harder and there is ambiguity in many media reports. Bites were attributed to *Steatoda* species with varying confidence, but in my assessment many of these 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.

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 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 plausible for some alleged false widow 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. It is possible that Blandford fly (*Simulium posticum*) bites and associated infections might be confused with *Steatoda* bites.

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. 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 (Dunbar *et 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 1.

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.

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. 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 verified bites in Britain and Ireland (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 a museum. A possible lag between the bite and the pain (as above) would increase the proportion recorded from beds.

Steatoda 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 ethically disturbing 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. 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) 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 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). 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. Whilst *S. nobilis* often retreats when the object in a web is not vibrating, the lizards, snakes and geckos that *Steatoda* and *Latrodectus* kill must simply be rubbing on the web - as a finger might do by chance. Such reptiles 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), making bites on fingers more likely. It is likely the common ancestor of *Steatoda* and *Latrodectus* 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) 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). 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; Stuber & Nentwig 2016; Dunbar *et al.* 2017). This is unsurprising given the improbability of a victim collecting the specimen and the 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. *Steatoda* 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

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).

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. 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) is also consistent with the mammalian studies of *Steatoda 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).

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 (LV₁) 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 cytotoxic components (Duan *et al.* 2008). *Latrodectus* antivenom is effective against *Steatoda grossa* venom - although potentially very dangerous as a treatment through anaphylaxis related to injection of sera (Graudins *et al.* 2002; Isbister & Fan 2011; Murphy *et al.* 2011; Garb & Hayashi 2013).

Steatoda (Dunbar *et al.* 2018) 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* 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). *Steatoda* can kill lizards in Ireland (Dunbar *et al.* 2018). It is also 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 liquify 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).

Bacterial carriage?

Possible symbiosis with necrotising bacteria would be worth investigation in *Steatoda* and *Latrodectus*: spiders might exploit bacteria, or bacteria might exploit spiders as vectors or weapons, with clones of those that degrade prey surviving in the spider. However, Vetter *et al.* (2015) argue evidence does not support the suggestion that spiders vector bacteria.

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; in theory this could cause necrosis, including the ulceration reportedly frequent after *Latrodectus* bites (Maretić 1978b).

Ulceration and necrotic arachnidism

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, I argue 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 (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 bite (personal communication). Some *Latrodectus* venom is also reportedly immunosuppressant (Ahrens & Crocker 2011).

A risk of bacterial ulceration, introduced with the bite or from subsequent scratching or bursting of the blister, may prove to be the most common danger with *Steatoda* species. 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). The microbiome of some *Latrodectus* includes bacteria requiring specific antibiotics not commonly used in skin infection (Ahrens & Crocker 2011); if the same is true in *Steatoda* it might explain some reports of patients requiring a second type of antibiotic in Britain after alleged spider bites. 'Hospital superbugs' (such as MRSA) introduced in the bite area may become the highest risk from spider bites in Britain.

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 hospitalization - 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) and one very probable bite in Oxford (personal communication).

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 a false widow (Hughes 2016). 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 the biggest source of necrotising arachnidism worldwide.

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 modern tissue culture studies and improved reporting of human case studies could confirm the risks without requiring replication of the animal experimentation.

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). Such incidents should be routinely compiled and reviewed professionally. Some occupations may increase the risk of repeat bites.

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.* (2018) 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).

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 or putative bacterial carriage or risk of anaphylaxis, could lead to inadequate responses. Notably, it has been suggested medical and veterinary diagnosis and treatment standards for *Latrodectus* be reviewed in the light of microbiological evidence (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 and possibly, in future, molecular evidence such as immunology or spider identification using DNA. Specimens presented to medics should be preserved in ethanol of at least 70% concentration. 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 false widows are now an occupational hazard for workers likely to have high exposure to the spider, such as some decorators, cleaners, removals firms, builders, plumbers, tree surgeons, bin workers, mechanics and park attendants. Severe pain could also cause occupational risks through a startled reaction to a bite - for example on ladders or when

handling power tools. 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 false widows, using fumigation with insecticides, and with national media coverage (*e.g.* Lazarus 2018; BBC 2018; Drewett 2018). 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) and Bauer *et al.* (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. 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 New Forest area of Britain (personal observation 2016-2019). Fumigation was reportedly unsuccessful in a flat in London where the building was infested (Drewett 2018).

Pest control agencies are gaining valuable experience in false widow 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. 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. The spider has been described as: "ponderous, solitary and non-aggressive" (Buglife 2018) and: very elusive; timid; solitary; very slow moving; not often seen in built-up areas. There are comments to the effect that: media reports are scaremongering; the venom is not cytotoxic; the spider has never been associated with effects of medical concern; males do not bite; it would be unusual for the species to live in a cinema; it prefers to be outside; webs are usually above 1.5m off the ground; it is sedentary and remains in webs; they will abandon your house if you keep getting rid of their homes. Whilst some such comments pre-date recent discoveries, they illustrate over-confidence in biological understanding and failure to indicate uncertainties.

734

735 Conversely, there is a lack of attention to detail and clear lack of expert input to some public
736 information documents: for example, some of the local authority guidance to London schools
737 in 2018 related to evacuation had a photograph of *Amaurobius* sp.!

738

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

749

750 ***Education and awareness and the potential value of media reports***

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

765

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

774

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

785

786 Schools and parents may need precautions for false widows similar to their approach to
787 anaphylaxis from bees or foods. I suggest this is the most urgent topic for proper review by
788 health professionals.

789

790 Education is also an opportunity to reduce arachnophobic anxiety and indiscriminate
791 backlash against benign species. This is in harmony with a rising interest in environmental
792 education, outdoor classrooms, biophilia and rewilding. Funding aimed at bite prevention
793 could have co-benefits if beneficial species are illustrated. Identification guides will be
794 helpful, especially if photographic and including webs (*e.g.* Dugon *et al.* 2107; Bee *et al.*
795 2017; Pendleton & Pendleton 2018). Good diagrammatic identification charts, flow charts
796 and dichotomous keys would be valuable to reduce anxiety and protect native species. Simple
797 educational messages are possible: for example, in northern Europe if the spider is in a spiral
798 orb web, or is hairy, not shiny, or is a pale colour it is likely to be a beneficial species. Keys
799 need to allow for rarely imported dangerous species, and so illustrations might be clearest.

800

801 Arachnophobia is probably an evolved response in humans to the very real health threat
802 spiders pose over much of the planet. This behaviour has been temporarily of lower
803 biological and cultural significance in northern Europe where there are few reinforcements of
804 the fear. However, this is likely to change with an increasing number of introductions of
805 dangerous species (breeding or not). This is quite a large spider in northern Europe, and with
806 various conspicuous behaviours has the potential to encounter or alarm people - as media
807 reporting illustrates. Conversely, many people in cultures familiar with dangerous spiders
808 may habituate to them somewhat, know how to deal with them and have less acute anxiety -
809 since the British media and public response appears, superficially at least, to be relatively
810 alarmist.

811

812

813 ***The arachnological conflict of interest***

814 The reasonable reluctance of arachnologists and medics to stoke adverse publicity about
815 spiders might become counter-productive or even negligent - as, of course, might alarmism.
816 Confidence in arachnologists will decline if the problem is seen to have been understated
817 whilst attempting to reassure the public, or if it is overstated.

818

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

829

830 **Species interactions and potential ecological impacts in Britain**

831 Knowledge of co-occurring species can help identify and predict the ecological requirements
832 and distribution of a focal species, as well as provide baselines for assessment of its
833 ecological impacts. Species or genera I found in casual observation in close proximity to *S.*
834 *nobilis* in Bradford (Bd), Birmingham (Bh), Doncaster (Do), Leeds (Le), central London
835 (Lo), Lymington (Lm), Oxford (Ox), Norwich (Nr), Start Bay (SB) and York (Yo) at various
836 times between 2016 and 2019 include: *Pholcus phalangioides* (Fuesslin, 1775) (Bd, Ox);
837 *Segestria senoculata* (Linnaeus, 1758) (Bh, Ox); *Segestria florentina* (Rossi, 1790) (Ox, SB);
838 *Steatoda bipunctata* (Bd, Ox, SB, Yo); *Steatoda grossa* (Ox, Le, Lo); *Achaearanea lunata*
839 (Clerck, 1757) (= *Parasteatoda lunata*) (Ox); *Achaearanea tepidariorum* (C.L.Koch, 1841)
840 (= *P. tepidariorum*) (SB); *Theridion varians* Hahn, 1833 (Ox); *Theridion melanarum* Hahn,
841 1831 (Bd); *Theridion melanarum* or *T. mystaceum* L.Koch, 1870 (Le, Ox, SB, Yo); *Theridion*
842 *blackwalli* O.P.-Cambridge, 1871 (Ox); *Lepthyphantes* sp. (Bd, Bh, Ox, SB); *Linyphia*
843 *triangularis* (Clerck, 1757) (Ox); *Nerienne montana* (Clerck, 1757) (Ox); *Nerienne* sp. (Bd,
844 Ox); *Metellina merianae* (Scopoli, 1763) (SB); *Metellina* sp. (Ox, SB); *Araneus diadematus*
845 Clerck, 1757 (Bd, Bh, Do, Le, Lo, Ox, Nr, SB, Yo); *Larinioides cornutus* (Clerck, 1757) (Ox,
846 Yo); *Larinioides sclopetarius* (Clerck, 1757) (Ox); *Nuctenea umbratica* (Clerck, 1757) (Bd,
847 Bh, Le, Ox, SB); *Zygiella x-notata* (Bd, Bh, Do, Le, Lm, Lo, Nr, Ox, SB); *Tegenaria* spp.
848 (Bd, Bh, Do, Le, Lo, Ox, SB, Yo); *Tetrax denticulata* (Olivier, 1789) (Bd, Le, Yo);
849 *Amaurobius fenestralis* (Stroem, 1768) (Ox, SB); *Amaurobius similis* (Blackwall, 1861)
850 (SB); *Amaurobius ferox* (Walckenaer, 1830) (SB); *Amaurobius* sp. (Bd, Bh, Do, Le, Yo);
851 *Saliculus scenicus* (Clerck, 1757) (Ox); *Pseudeuophrys lanigera* (Simon, 1871) (Ox).

852

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 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 *S. grossa* appears more successful than *S. nobilis*. The similarity in appearance of some *Zygiella* and *Amaurobius* species to *S. nobilis* raises the possibility of convergent evolution or co-evolution and mimicry.

S. nobilis has a wide diet in Ireland (Dugon *et al.* 2017, Dunbar *et al.* 2018). 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.* 2018) 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 suggest 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 can survive at least occasional low 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 (Hampshire) 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 2).

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

In temperatures below about 5°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°C. Notably, at such temperatures, *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. 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 cities such as Bradford, Doncaster, Leeds, and York do not yet have large populations recorded indoors.

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 suggest 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, I suggest the pioneers into new areas will have benefitted - but that these were under-recorded.

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 (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 predict it will be found to be 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).

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

972

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

985

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

992

993 Based on recorded habitats, climate envelope modelling and recent changes in recorded
 994 distribution (Bauer *et al.* 2019) suggest that, globally, temperate and coastal areas are likely
 995 to be invaded. However climate envelope modelling has serious limitations (Hamblen &
 996 Canney 2013), and particularly in the case of a species that can thrive indoors, insulated from
 997 the regional climate, and dispersed by people. I agree with Bauer *et al.* (2019) that these
 998 projections are likely to be conservative, perhaps the more so considering the data used to
 999 train the model are problematic due to under-recording of distribution and urban
 1000 microclimates. I predict the species could establish outdoors globally almost anywhere which
 1001 is not often far below -5°C, and even then it could colonise inside buildings, including those
 1002 in both polar regions (such as research bases). I predict that evidence will accumulate that *S.*
 1003 *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. 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.

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 (Hamblen & Canney 2013) and I predict this will occur with *S. nobilis*. 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). 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 (Hamblen & 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 spider.

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). In Oxford on 24 February 2019 a vibrating stimulus in a web was approached by a juvenile c. 2mm long. A second stimulus led to a juvenile c. 4mm 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. 2mm and c. 3mm) observed sharing one web (Oxford, 10 January 2019) approached a vibrating stimulus (Figure 3). 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 3: 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 suggest 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 matrophagy would be worth investigating. 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 spiders.

The retreat may be in a corner, rather than a hole - 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. Adult males can often be found in the same retreat as adult females, perhaps mate-guarding. The species can survive in buildings for several months on little food and no water (personal observation), even as a juvenile, making dispersal by humans easier. Male specimens found indoors often look emaciated (personal observation), possibly from desiccation once unable to catch food in a web.

1074

1075 Although widely described as 'sluggish' juvenile and adult *S. nobilis* can run very fast on the
1076 ground - at least at temperatures over about 10°C. Indeed, I find it a relatively difficult
1077 species to capture once extracted from its web.

1078

1079 The species can be collected using flexible tweezers or a vacuum sampler (Dugon *et al.*
1080 2017). I find it simplest to whisk it tangled in silk from the web with a tuning fork, or
1081 dislodge it with a stick, and then extremely carefully herd it into a specimen tube. The
1082 spider's speed, even when cool, can require fast obstruction of the retreat and then very great
1083 care in driving it into a container using a stick, tuning fork or similar; I would *not* recommend
1084 using fingers, even in gloves. Transferring the spider between tubes can be difficult, since it
1085 can climb fast, including up the walls of glass tubes. Having had several near-misses with
1086 dislodged spiders, and escapes in captivity, *I advise great caution if attempting capture.* I
1087 suggest a safe-handling protocol be developed.

1088

1089 The species very readily approaches a vibrating stimulus, except when near freezing, or in
1090 rain or strong wind when the web is being disturbed, or sometimes when the web has many
1091 seeds of *e.g. Salix* spp. in it. An electric 'sonic' toothbrush (*e.g.* Philips 'Sonicare') or a tuning
1092 fork (frequency A440) can be used to draw it out onto the web, and the stimulus need not
1093 always touch the web to evoke attack. An attack on a tuning fork (and presumably prey) may
1094 start with either a bite or wrapping using the rear legs, and often involves multiple bites over
1095 some minutes. Heavy or repeated contact with the web often causes the spider to retreat
1096 rapidly or become unresponsive.

1097

1098 The spider is reportedly more active at night (Dugon *et al.* 2017). It is often conspicuous in
1099 low light or at night, waiting on the web surface and web building. It can be found easily
1100 using torchlight at night. Timing of emergence is likely predominantly triggered by light
1101 level, not a body clock: if the web is in an interior light fitting the spider may only come out
1102 when the light goes off - *e.g.* at dawn. It is very prepared to attack prey in bright daylight, and
1103 in winter is more likely to attack during warmer daylight hours (personal observation).

1104

1105 I have a few times observed a pungent smell when collecting or disturbing females with egg
1106 sacks. Observation is difficult, but I suspect this may be from a fluid I have once seen near
1107 the mouthparts, and I hypothesise *S. nobilis* has a volatile defensive chemical but this is
1108 rarely used. One possible victim of a bite noted a smell of burning hair, which faded fast,
1109 when the spider was rolled onto. In Britain, predation occurs at some sites: webs and old egg
1110 sacs can disappear rapidly from crevices that have occupied for years (personal observation).
1111 In some elevated locations, birds seem the most likely predator.

1112

1113 Egg sacks, if partially unravelled, can unwrap explosively scattering tens of eggs - a possible
1114 defensive and dispersal mechanism. Large females taken into captivity at any time of the year
1115 often lay fertile eggs within a few days - possibly triggered by a rise in temperature.

1116

1117 **Proposed research priorities**

1118 I suggest further work is urgently needed on:

1119 1) The mammalian cytotoxicity of *Steatoda* venoms.

1120 2) The risk of ulceration and necrosis after *Steatoda* bites, including assessment of *S. nobilis*
1121 as facilitators or vectors of MRSA and other bacteria in their microbime. This should include
1122 professional compilation and review of an international database of medical, citizen and
1123 media reports in the light of recent confirmation of cytotoxicity in *Steatoda* venom.

1124 3) The potential for anaphylaxis after *Steatoda* bites, with a review of informally reported
1125 cases.

1126 4) The potential complications of *Steatoda* bites in pregnancy.

1127 5) The global distribution of *S. nobilis*, particularly in cities and on tropical islands with
1128 endemic animals, and its likely region of origin.

1129 6) Thermal requirements and their relevance to the distribution and invasiveness of *S.*
1130 *nobilis*.

1131 7) Natural enemies and the potential for gene-drive in control of *S. nobilis*.

1132 8) Orientation, thermotaxis and dispersal: *e.g.* does the species seek warm sites such as beds?

1133 9) Methods of raising public awareness of risks of spider bites, and of reducing encounter
1134 rates, without reinforcing arachnophobia. This should be based on best practice globally.

1135 10) Horizon scanning and contingency planning for future invasions.

1136

1137 Such research will require inter-disciplinary collaboration including pathologists, clinicians,
1138 ecologists, arachnologists, psychologists, physiologists, climatologists and epidemiologists. I
1139 hope this preprint will enable comments from multiple specialists who might not have easy
1140 access to literature outside of their field. Opportunistic reporting has proved inadequate to
1141 clarify risks. Currently, the onus for improved reporting and verification of bites has often
1142 been placed onto the public - with some medics and arachnologists essentially requiring
1143 direct observation of the biting animal and presentation of the same spider to an
1144 arachnologist: I suggest this is unreasonable and potentially risky.

1145

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.

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Conflict of interest

I have no financial conflict of interest.

Supplementary Material Online

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

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.

1179 4) *S. nobilis* juvenile (c. 3mm body length) attacking a tuning fork. Oxford, U.K. 6 November
1180 2018. Ambient temperature c. 12°C.

1181

1182 *S. nobilis* female attacking a tuning fork. Oxford, U.K., 31 October 2018. Ambient
1183 temperature c. 10°C.

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