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The Speckled Bush-cricket – an unusual orthopteran

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Marion Hall worked for the Open University for over 30 years before retiring in 2014. She is now an Honorary Associate at the Open University. With interests in animal behaviour and evolution, she has been carrying out research on Speckled Bush-crickets for the last 25 years.

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Wandering through a meadow on a warm summer’s afternoon, most people will be aware of the rasping chirps of grasshoppers. If they visit the New Forest in late summer they may hear the gentle trilling of wood crickets emanating from under the fallen leaves. But the songs of bush-crickets – the third main group within the orthopteran insects – are often not quite so obvious. Many of them consist of short clicks or chirps and are high pitched and difficult to hear. The Speckled Bush-cricket, *Leptophyes punctatissima*, is particularly unusual for three reasons. Firstly, its song is ultrasonic – so high pitched that most people can’t hear anything. Secondly, the song is incredibly brief – a tiny click only a few milliseconds long. And third, it is the only bush-cricket in the British Isles where the female also sings – the male and female perform a duet that bring the pair together for mating.

We have been working on various aspects of the ecology, behaviour and acoustics of the Speckled Bush-cricket for several decades and reckon we have seen over 500 matings, both in the lab and in the field. So in this article we aim to give you a synthesis of our various observations on this fascinating insect.

Classification and species characteristics

The Speckled Bush-cricket is one of around 35 species of orthopteran insects in the British Isles, of which 30 are native and the rest naturalised (Sutton & Beckmann 2020). Of the 30 native species, 13 are grasshoppers, three are ground-hoppers, 10 are bush-crickets, three are crickets, and one is a mole-cricket. Two of the grasshoppers and one of the bush-crickets are only found in the Channel Islands.

![Figure 1. The Speckled Bush-cricket: (a) the male (b) the female. Marion Hall](image)

Compared with the other native species, the Speckled Bush-cricket is small to medium-sized. As is typical of orthopterans, females (Figure 1a) are bigger on average than males (Figure 1b) – mean body length, measured from the front of the head to the end of the abdomen, is 15.6mm for females and 13.5mm for males. It is flightless, though both male and female have a pair of tiny wings, used only to produce the mating song. The common name comes from the tiny dark spots all over the body. Otherwise, male and female are both basically green, with a brown stripe down the
back which is thicker and much more prominent in the male. They both have very long thread-like antennae, though these sometimes get broken off, plus a pair of pointed tactile appendages (ceri) sticking out from the end of the abdomen. For the male, these are important in mating behaviour. As is typical in tettigoniids, the female has a large egg-laying organ (ovipositor) which she uses to insert eggs into vegetation. In Speckled Bush-crickets this is characteristically shaped like a scimitar.

Distribution, habitat and food plants
The Speckled Bush-cricket is common throughout western Europe. In the British Isles its distribution is mainly in southern England, though there are a few populations as far north as south-west Scotland. It has protected status on the Isle of Man under Schedule 5 of the Wildlife and Countryside Act of 1990. In England over the last 30 years or so, the number of populations in the north has increased and the species has extended its range into the north-west. Assuming this is not just the result of better recording, it’s likely to be a response to climate change (Sutton et al. 2017).

The Speckled Bush-cricket is usually found very patchily distributed in mixed vegetation close to trees or tall shrubs in places that get plenty of sunshine. These are usually south or west facing in areas that are open on one side, such as hedgerow along a path (Figure 2), or the edge of a piece of woodland. Though we have also found them living in urban gardens and parks.

Figure 2 Typical habitat for Speckled Bush-crickets; a south-facing hedgerow next to a road, with a mixture of low-growing plants in front of trees and shrubs. Marion Hall

Speckled Bush-crickets show a lot of variation in their diet. With our colleague Patricia Ash, we have studied three different populations in detail: one at East Cliffs and Warren Country Park, an area of coast near Folkestone, one at Little Wittenham Wood in Oxfordshire, and one in an old apple orchard surrounded by fields, hedgerows and native trees in northern Germany near the small town of Nordkirchen. At The Warren, bush-crickets mostly feed on Wood Sage, *Teucrium scorodonia*, plus quite a lot on Bramble, *Rubus fruticosus*, and to some extent on Old Man’s Beard, *Clematis vitalba*. At Wittenham, there is no Wood Sage and the preferred food is Nettle, *Urtica dioica*, with Common Comfrey, *Symphytum officinale*, Common Cleavers, *Galium aparine*, and Hedge Woundwort, *Stachys sylvatica*, also eaten to a large extent. In Germany again the preferred food is Nettle. Even though Bramble is present at Wittenham, we have rarely seen any bush-crickets there on it, so the
differences in food preferences between populations can’t be explained by what plants are actually available.

If you are looking for Speckled Bush-crickets they can be difficult to find simply because you can search innumerable patches of vegetation that look perfect for them, without finding any at all. The easiest way to spot them is actually to look for the characteristic damage they leave after feeding on the leaves (Figure 3).

![Figure 3. Characteristic ‘tracery’ of leaf damage after Speckled Bush-crickets have been feeding. Marion Hall](image)

**Life cycle and movement patterns**

The first person in the UK to publish a detailed description of the life-cycle and behaviour of Speckled Bush-crickets based on observations in the field as well as in captivity was Duncan (1960). Speckled Bush-crickets lay their eggs in late summer and these then overwinter before hatching from around the middle of May the next year. Some eggs don’t hatch until they have been through two or even more winters, and according to Deura & Hartley (1982) two winters is likely to be the norm for this species in the cooler parts of its range, including the British Isles. The eggs hatch into nymphs (Figure 4), which are basically small immature versions of the adults but with only partially developed reproductive organs and sex characteristics (Benton 2012).

![Figure 4. Nymphs of the Speckled Bush-cricket: (a) 6th instar male nymph with a body length of about 10mm (b) 5th instar female nymph with a body length of about 11mm. The female’s ovipositor is clearly visible but isn’t fully formed. Marion Hall](image)

The nymphs go through six immature stages, or instars, moulting at the end of each to emerge as a slightly bigger, more developed version. Each instar takes 1-2 weeks, depending on the weather. After the sixth moult they emerge as adults. The first instar that emerges from the egg is tiny – about the size of an aphid. The female’s ovipositor starts to be visible by the third instar. The brown stripes
down the back of the male and female don’t appear until they emerge as adults. Once adult, they take about another 7-10 days to become sexually mature. So adults generally begin to appear in early to mid-July with mating starting to take place from around the third week of July. Mating tails off after the end of August and most adults are dead by the end of October. Though individuals have very occasionally been seen in the field as late as the end of November.

Nymphs are more likely to occur in low-growing vegetation but sexually-mature adults are often found high up in the trees. We have recorded a male singing at night 14m up in a fir tree. Because of this Duncan (1960) thought that movement was a one-way process, with immatures hatching out close to the ground and staying at a low level until they become sexually mature, at which point they move up into the trees, with the females only coming back down to lay their eggs. But in the population we studied in Germany, we actually tracked individually marked individuals in three dimensions (Hall 2010) and found the story is much more complicated than that. It’s true that nymphs don’t move much, so tend to stay close to where they hatch, which is often (though not always) fairly close to the ground. And adults of both sexes do move up into the trees. But they also move outwards from where they hatch, in all directions. And not only that, they keep on moving. Despite being flightless they can cover surprisingly long distances on foot. We tracked one male that covered over 50m along the ground in the space of a day and several other individuals who moved tens of metres away into a field, then came back a couple of days later, then moved away again to somewhere else. It’s more like they are moving around randomly in all directions. The spreading out over a large area that results seems to be counterproductive in terms of trying to find a mate. There has to be some movement away from the hatching area if the offspring of a single female are going to avoid inbreeding with each other but, in nature generally, to avoid inbreeding one sex usually moves away while the other stays where it is. But both male and female Speckled Bush-cricket move away and they move a lot. So far we haven’t managed to come up with any explanation for why they apparently make things so difficult for themselves!

Natural enemies
Like other orthopterans, Speckled Bush-cricket have a multitude of enemies (Benton 2012). They are preyed upon by bats and other small mammals, birds, lizards, wasps, robber flies and spiders, and are affected by various parasites, including the hairworm Spinochordodes tellinii. The microscopic larvae of this hairworm are eaten by the bush-cricket and develop inside them into worms that can be three to four times longer than the host. When adult, this parasite lives and breeds in water, and it can actually change the behaviour of its host to its own advantage (Thomas et al. 2002). Once it is fully grown, it can make the bush-cricket jump into any nearby water, where it is likely to drown. The hairworm then leaves its host to start the aquatic stage of its life-cycle.

Singing behaviour
The Speckled Bush-cricket is particularly interesting because it has a highly specialised acoustic communication system. Unlike the other bush-cricket species found in Britain, where the male produces a song and the female is silent, both male and female Speckled Bush-cricket produce sound as part of their courtship and mating behaviour (Robinson et al. 1986). The female sound barely justifies the description ‘song’ as it is a very short click and it is only produced in response to a male call. The tight coupling of male and female songs, called duetting, is found in related genera in continental Europe, for example Poecilimon (Heller & von Helversen 1986), but in Britain only in the Speckled Bush-cricket.

The predominant frequency in the songs of both sexes is 40 kHz, well beyond the upper limit of human hearing, which is generally defined as 20 kHz (Pumphrey 1950). Bat detectors, instruments that make ultrasonic bat sounds audible to humans, readily detect Speckled Bush-cricket songs too.

Males sing both during the day and at night, with three peaks of singing in the field occurring from midnight to 04.00, from 09.00 to 11.00 and from 14.00-19.00. The male song usually consists of a
chain of five to eight ultrasonic pulses although a smaller number is sometimes observed. Each of the pulses has a duration of around 1 millisecond (ms) and is produced by an impact between a hardened area of the right forewing – the plectrum – and one of a group of teeth on the underside of the left forewing. You can imagine this method of producing sound as similar to running your fingernail along the teeth of a comb, with each impact between fingernail and comb tooth producing a pulse of sound. The female song is produced in a different way from the male and is not as loud. The teeth are on the upper surface of the right wing and are rubbed by a hardened area of the left forewing. Clearly the sound-producing mechanisms of male and female have evolved independently.

The timing of the female’s reply to a male song is crucial, as the male only responds to the female if he receives her reply within a narrow time window of 20-55ms after his song starts. The window is so narrow that the time taken for sound to travel between male and female becomes significant. For example, if they are 3m apart, the song of the male takes about 9ms to reach the female and similarly her reply takes a further 9ms to reach him (Figure 5). We have never observed a male respond in the field at a distance greater than 9m from the female.

![Figure 5. A timing diagram of a single male call and the female reply, showing the travel time of the sound and the time window of the male, for a separation of 3m between male and female.](image)

David Robinson and Marion Hall

Receiving a response within the time window encourages the male to increase his rate of singing and he approaches the stationary female, finding her by orienting to her song (phonotaxis), with the pair continuing to duet throughout his approach (Zimmermann et al. 1989). Some other bush-crickets have a duetting mating system in which the male calls and the female replies, though which sex then approaches the other varies in different species (Robinson & Hall 2002). None of these species is found in Britain.

We are fascinated by the duetting of the Speckled Bush-cricket because some of the features of the system are counter-intuitive. For example, the male locates the female from her song, yet such a short sound just 1ms in duration does not appear to be a good beacon and both songs are so short that it’s unlikely much information is encoded in them. A female willing to mate raises her wings in response to male singing but, once she has done that, the female song is a reflex reaction to the male’s song, with no time for the brain to be involved. Any short click that contains ultrasound can elicit a reply from a female, even a click from your fingernails. So, it appears that in courtship and mating the sound frequency in the song is significant, but timing is everything.
As the male gets close to the female, his approach during the last few centimetres often becomes less direct. He seems to move more hesitantly, sweeping his antennae around as if trying to find her (Figure 6). We believe that when the pair are in close proximity, phonotaxis may be hampered, and the male may have to use cues other than the female’s song, such as her smell or vibrations from her movements.

Figure 6. Mating in Speckled Bush-crickets (a) the male is close to the female but is not moving straight towards her. Marion Hall

Mating behaviour
In the field we have seen mating take place in daylight at pretty much any time. We haven’t managed to observe any matings in the dark, but we have seen males performing phonotaxis then, so we assume mating also takes place at night.

Once the male has found the female after performing his phonotaxis, the pair explore each other with their antennae (Figure 7). This antennation behaviour is common in orthopteran mating and it may be important in sex recognition. This has been shown in decorated crickets, *Gryllodes sigillatus* for example (Ryan & Sakaluk 2009). Then the male positions himself in front of the female and backs towards her (Figure 8). He pushes his abdomen underneath her, arching his body, and the female starts to feel his back with her mouth and palps (two pairs of sensory appendages next to the mouth) (Figure 9). Gradually, she moves forward, working her way up the back of the male as she continues to mouth and palpate it (Figure 10).

Figure 7. Mating in speckled bushcrickets (b) the male antennates the female. Marion Hall

If nothing else during this stage, the female must be receiving chemical stimuli from the male. But it is also possible, as in some other orthopterans, that she is ingesting secretions produced by the male from glands situated on his back that specifically encourage the female to copulate (Gwynne 2001; Vahed 1998).
Figure 8. Mating in speckled bushcrickets (c) the male positions himself in front of the female and backs towards her. Marion Hall

Figure 9. Mating in speckled bushcrickets (d) the male pushes his abdomen underneath the female, arching his body, and the female begins to mouth and palpate his back. Marion Hall

Figure 10. Mating in speckled bushcrickets (e) the female moves forwards, up the back of the male, as she continues to mouth and palpate it. Marion Hall
When the female has moved forward enough so that she is fully mounted over the male, she stops mouthing and palpating his back and curves her abdomen downwards. The male explores the female’s genital area with the tip of his abdomen until he and the female lock genitals (Figure 11). This is achieved by means of the male’s cerci. These are bigger than the female’s, are curved inwards, and have a tooth at the end that hooks into a pit situated on the outer surface at the base of the female’s ovipositor (Vahed et al. 2014).

Figure 11. Mating in speckled bushcrickets (f) the pair lock genitals. Marion Hall

At any point up to the time when they lock genitals, either the female or the male may reject their potential partner, either by simply moving away or by kicking them with their hind legs to push them off. Females are much more likely to reject their partner than males are. In the 249 attempted matings we observed in the lab where we recorded whether or not rejections took place, mating took place successfully in 173 (69.5%), the female rejected the male in 57 (22.9%) and the male rejected the female in 19 (7.6%). This is despite the fact that the refractory period (the length of time after mating until the individual is willing to mate again) is shorter for females than it is for males: we have seen females mating again almost immediately after they have finished mating whereas males will not mate again for at least a day.

About 2 to 3 minutes after the pair have locked genitals, the male transfers his sperm in the form of a spermatophore (Figure 12). In most bush-crickets and some crickets, the spermatophore is relatively large and consists of a sperm sac, the ampulla, surrounded by a mass of edible, sperm-free material, the spermatophylax. These large spermatophores are attached externally to the female’s genital opening. In grasshoppers, on the other hand, the spermatophore is small, with no spermatophylax, and it is inserted directly into the female’s genital tract (Ingrisch & Rentz 2009).

Figure 12. Mating in Speckled Bush-crickets (g) the male transfers a spermatophore to the female. Marion Hall
The spermatophylax is normally eaten by the female and this ‘nuptial gift’ from the male can be very large in some species. For example, in *Uromenus stalii*, a bush-cricket found in mainland Europe, the spermatophore can be up to 40% of the male’s body weight (Gwynne 2001) but the Speckled Bush-cricket’s gift, as measured in our lab, is a much more modest 6.6%. The main function of the spermatophyllax is to protect the ampulla. While the female eats the spermatophylax, the sperm have time to transfer to her sperm-storage organ, the *spermatheca*, before she can get at the ampulla, which she then eats as well.

In many bush-cricket species, the spermatophore has little food value, but in others it provides important nutrients that contribute towards the female’s egg production or the survival of her offspring (Gwynne 2001). The male is therefore ‘investing’ in his own potential offspring by providing food to the female. In the Speckled Bush-cricket there is so far no evidence that the spermatophore has any such paternal investment function (Vahed 2003).

Soon after spermatophore transfer is complete, the female dismounts from the male by moving forward over him (Figure 13). The whole copulation process, from locking genitals to the point where the female dismounts only lasts around 3.5min on average. Once the pair have separated they usually wander away from each other (Figure 14), though the female tends to move farther than the male.

![Figure 13. Mating in Speckled Bush-crickets (h) the female dismounts. Marion Hall](image1)

![Figure 14. Mating in Speckled Bush-crickets (i) after the female dismounts, the male and female gradually move away from each other. Marion Hall](image2)

After the pair separate, the male normally grooms his genitals. Then about 5min after mating he *tremulates* for several minutes. In this behaviour, which usually takes place close to where mating happened, the male performs a series of rhythmic ‘push-ups’, raising his body and then flexing his legs repeatedly so his body moves up and down quickly several times without actually touching the surface he is standing on. He then pauses for at least a few seconds before performing another bout of push-ups. This tremulation behaviour is often performed in the complete absence of the female and has no effect that we have been able to observe on any other individuals who happen to be
nearby at the time. So it’s not clear why males do it. But in 68 matings by 17 males where we recorded whether the male tremulated or not, we saw the behaviour in 90% of cases and all the males tremulated for at least some of their matings. Tremulation was only observed in males after mating and was never observed in females. We believe it must serve some purpose, but we need to investigate it further to find out what that purpose is. Very similar behaviour has been described in various orthopteran insects but in other bush-crickets it usually takes place before mating and functions either to attract females or as part of courtship (Gwynne 2001). The only other bush-cricket we know of that tremulates after but not before mating is the long-tailed Speckled Bush-cricket, Leptophyes laticauda, a close relative of the Speckled Bush-cricket from mainland Europe (Vahed 1994). Post-mating tremulation is the norm, however, in some crickets (e.g. Brown 2016; Stritih & Cokl 2012).

Usually about 20 minutes after the female dismounts, she starts to eat the spermatophore. She bends her whole body downwards so that she can reach the spermatophore with her mouth parts, biting it and pulling strings of it away (Figure 15). Then she slowly consumes the lump she has pulled away before taking another bite (Figure 16). It can take her up to 2 hours to finish eating the spermatophore.

![Figure 15. Mating in Speckled Bush-crickets (j) the female bends to bite the spermatophore and pull away pieces. Marion Hall](image)

Even though they do not mate again until at least 24 hours after mating, males may start to sing again very quickly, sometimes within minutes. Males singing soon after mating reject any attempts by females to mate with them. It is unclear why males sing when they cannot mate, unless it has some function in male–male competition. However, though we have not studied this systematically, we have not observed nearby males being affected in any obvious way by the singing of another male: they do not appear to move away from him, for example. This is another example of Speckled Bush-cricket behaviour that needs further investigation.
Egg laying

Egg-laying usually takes place at night (Deura & Hartley 1990; Duncan 1960) so it is extremely difficult to observe systematically in the field. As a result it has only been studied in detail in the lab, though Deura & Hartley (1990) did look at egg-laying sites in an experiment set up under semi-natural conditions in the field. They found that females prefer to lay in bark, either in crevices or, if the bark is soft enough such as in Elder, Sambucus nigra, inserted into the bark itself. Some eggs were laid in dead Bramble stems.

According to Duncan (1960), when the female is ready to lay her eggs, she crawls over the bark, exploring it with her mouth and palps. Then she bends herself double so that the ovipositor is brought up close to her mouth and inserts its tip into the crack (Figure 17). The ovipositor is moved gently up and down for about 15 minutes.

![Figure 17. A female laying her eggs in a crack in the bark of an oak tree. Bill Welch](image)

Females may start to lay eggs (Figure 21) the first night after they mate (Vahed 1994), though we have found in our lab that there can be a delay of several days, and usually continues for the rest of the female’s life. Eggs are oval and flat, with an average length of 3.5mm. There is very little variation in egg size. We have recorded a huge variation in the total number of eggs a female lays, from as few as 10 to as many as 185. And this variation isn’t necessarily due to differences in lifespan because the rate of egg laying per day averaged over her whole lifetime also varies enormously, from as low as 0.15 eggs per day (i.e. roughly one every 7 days) to as many as 3 eggs per day. But the rate of laying is not uniform: a female may lay batches of eggs, sometimes as many as 10 at a time, stuck together with a kind of gum, and egg laying also tails off towards the end of her life.

Conclusion

The longer that we study this insect, the more questions emerge, prompting new observations and experiments. The Speckled Bush-cricket also acts as a model, allowing us to address broader questions about orthopteran behaviour in general, such as the role of sounds in mate choice, the factors that drive the evolution of different male and female sound production mechanisms, and the interactions between acoustically signalling orthopterans and their predators. It is an inhabitant of our woods and hedgerows that is rarely noticed but continues to fascinate.

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References


