NEWS AND VIEWS

PERSPECTIVE

The public world of insect vibrational communication

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Food webs involving plants, herbivorous insects and their predators account for 75% of terrestrial biodiversity (Price 2002). Within the abundant arthropod community on plants, myriad ecological and social interactions depend on the perception and production of plant-borne mechanical vibrations (Hill 2008). Study of ecological relationships has shown, for example, that termites monitor the vibrations produced by competing colonies in the same tree trunk (Evans *et al.* 2009), that stink bugs and spiders attend to the incidental vibrations produced by insects feeding or walking on plants (Pfannenstiel *et al.* 1995, Barth 1998) and that caterpillars can distinguish among the foraging-related vibrations produced by their invertebrate predators (Castellanos & Barbosa 2006). Study of social interactions has revealed that many insects and spiders have evolved the ability to generate intricate patterns of substrate vibration, allowing them to communicate with potential mates or members of their social group (Cokl & Virant-Doberlet 2003; Hill 2008). Surprisingly, research on the role of substrate vibrations in social and ecological interactions has for the most part proceeded independently, in spite of evidence from other communication modalities – acoustic, visual, chemical and electrical – that predators attend to the signals of their prey (Zuk & Kolluru 1998; Stoddard 1999). The study by Virant-Doberlet *et al.* (2011) in this issue of *Molecular Ecology* now helps bring these two areas of vibration research together, showing that the foraging behaviour of a spider is influenced by the vibrational mating signals of its leafhopper prey.

The study is an excellent example of how collaboration between behavioural and molecular ecologists can provide unparalleled insights into ecology and behaviour. To test the hypothesis that spiders can eavesdrop on the vibrational signals of their prey, the authors first surveyed trophic relationships among spiders and a common leafhopper species in South Wales (Fig. 1a). Predator–prey relationships of invertebrates are often exceedingly difficult to observe, but molecular diagnostic methods can bring them to light. The authors collected a range of spiders from the same habitat as the leafhoppers, and then tested the gut contents of the spiders with leafhopper-specific primers, targeting the mitochondrial COI gene. The authors determined that one species of spider was a frequent predator of the leafhopper (Fig. 1b). Tellingly, predation was much higher when sexually mature leafhoppers were present than when only nymphs – which are not known to signal – were present. The authors then conducted the critical test: during playback of the leafhoppers' vibrational mating
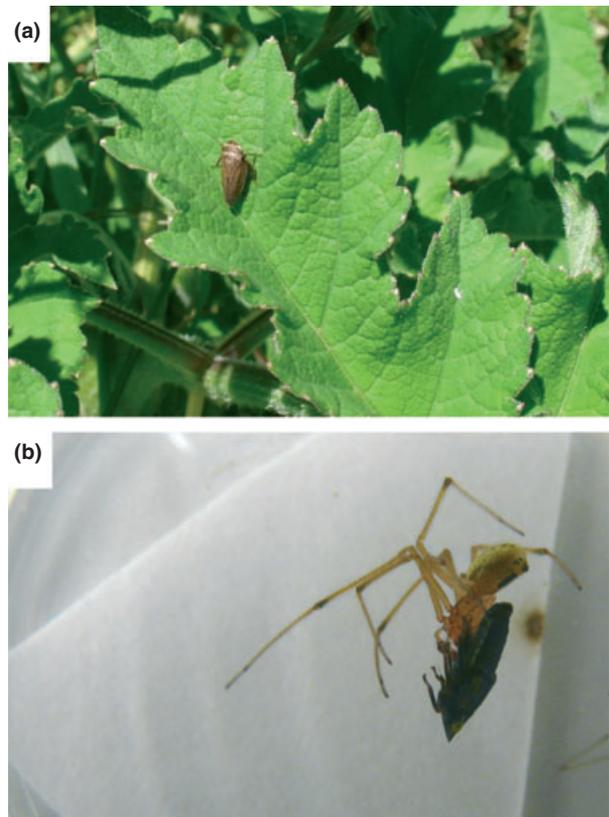

Fig. 1 (a) Adults of the cicadellid leafhopper *Aphrodes makarovi* communicate by means of plant-borne vibrational signals. (b) The therediid spider *Enoplognatha ovata* is a frequent predator of leafhoppers, and its foraging behaviour is influenced by detection of the signals of male *A. makarovi*. Image credits: (a) M. Virant Doberlet and (b) W.O.C. Symondson.

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signals, the spiders altered their foraging behaviour in response to the higher-amplitude signals of males, but not to the lower-amplitude signals of females or to vibrations produced by a walking leafhopper. Although the response variable was simply the spiders' residence time on the plant, where the lack of movement could also be interpreted as antipredator behaviour, some spiders approached the vibration source, clearly attempting to forage.

What implications does this study have for our understanding of vibrational communication, still the least understood of communication modalities? Plant-borne vibrations were once widely thought to provide a 'private' communication channel, allowing a male to signal to a female without interference from rivals, signals of other species or eavesdropping predators. However, this view is being abandoned, as research on vibrational communication has moved from the laboratory into the field. A researcher listening in on the vibrational 'soundscape' of a plant in nature may detect many signallers (Cocroft 2003), sometimes in choruses much like those of frogs or acoustic insects (Hunt & Morton 2001). Frequently, the singers share the plant with a range of vibration-sensitive predators. Accordingly, in a review of vibrational communication, Cocroft & Rodríguez (2005) predicted that predator use of prey vibrational signals was inevitable: 'A vast number of predators could exploit insect vibrational signals… it is clear that a signalling insect is never far from an enemy capable of eavesdropping on its signals'. With this prediction now met by the results of Virant-Doberlet *et al.*'s (2011) study, the 'private channel' notion can safely be put to rest.

In contrast to the black-and-white categorization of acoustic signals as 'public' and vibrational signals as 'private', a more realistic view will take into account the interaction between the two modalities. Given the existence of both acoustically and vibrationally orienting predators, species producing acoustic signals are vulnerable to both sets of predators (a singing cicada or frog produces not only an acoustic signal, but also an unavoidable vibrational signal in the surface it stands on [Stölting *et al.* 2002; Caldwell *et al.* 2010;]), while species using vibrational signals are vulnerable to just one. Even here one has to be careful; parasitoid wasps might be able to detect the vibrations of their leafmining hosts simply by flying over the leaf, using air currents set up by the leaf's vibrational motion (Casas & Magal 2006).

Virant-Doberlet *et al.* (2011) lay the groundwork for a productive line of research into how predation has influenced the evolution of vibrational signals and signalling behaviour. In the light of the diversity and density of spiders in many habitats – as Bristowe (1971) put it, 'Picture a small defenceless insect in an acre field surrounded by 2 000 000 pairs of spiders' jaws' – spiders are probably the most important of the vibration-guided predators of singing insects. Importantly, the molecular diagnostics of this study reveals that only a fraction of those two million pairs of chelicerae are a threat to a given species of singing insect. One especially likely group of predators is the sal-

ticids. Although jumping spiders are highly visual (Jackson & Pollard 1996), they use vibrational signals in their multimodal mating displays (Elias *et al.* 2003), and at least one species attends to the vibrational component of the courtship signals of its wolf spider prey (Roberts *et al.* 2007). Even more suggestive, Narhardiyati and Bailey (2005) describe unpublished observations of salticids approaching duetting pairs of leafhoppers, and orienting to vibration transducers that played back leafhopper songs.

An important question in the study of predator eavesdropping is how a particular signal in the environment becomes a foraging cue. In the case of vibrational communication, an ancient and widespread modality, the result of ongoing sexual selection in hundreds of thousands of arthropod species is a dazzling variety of signals (Cocroft & Rodríguez 2005). The sheer diversity of vibrational signals in the environment presents both an opportunity and a challenge for vibrationally orienting predators. For specialists, the signals that guide them to prey may be sufficiently predictable that natural selection can shape responses that do not depend on experience (e.g. Robert *et al.* 1992). But for more generalized predators, learning is likely to play a role. Predators learn to avoid prey with warning coloration, and indeed some warning signals appear to have evolved features that make them easily learned and remembered (Speed 2000). Although learning in predators that home in on prey mating signals has been little explored, frog-eating bats (Page & Ryan 2006) and parasitoid wasps (Huigens *et al.* 2009) can quickly learn to attend to the mating signals of their prey. The possibility of predator learning is recognized by Virant-Doberlet *et al.* (2011), who make the intriguing suggestion that the variation they observed in spider response to prey signals might be caused by differences in the signals the spiders learned in the field. Predators that exploit vibrational signals in prey capture could simply use particular amplitude and frequency ranges as a cue that potential prey are present, or they could learn to selectively attend to the signals of frequently encountered prey. For now, the mechanistic links between prey vibrational signals and predator responses remain speculative, but that will surely change over the next few years.

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