
Commentary

Textbook cricket goes to the field: the ecological scene of the neuroethological play

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Summary

Sensory ecology has recently emerged as a new focus in the study of how organisms acquire and respond to information from and about their environment. Many sensory scientists now routinely explore the physiological basis of sensing, such as vision, chemoreception or echolocation, in an ecological context. By contrast, research on one of the most performing sensors in the animal kingdom, the wind-sensitive escape system of crickets and cockroaches, has failed so far to encompass ecological and evolutionary considerations. We report survival and behavioural experiments in which wood crickets interacted freely with natural predators in the field. Our results illustrate how the lack of knowledge about the ecology of these insects may entail our understanding of the biological relevance of their wind

sensors. We found that predation pressure was most important on early stage crickets. Because laboratory studies have focused exclusively on adults' sensory systems, it is crucial that physical, physiological and neurobiological studies now turn to juveniles.

Another common assumption challenged by our results is the nature of the air flow to which crickets are sensitive. Our results identify wolf spiders as the major predatory risk for wood crickets. Air movement stimuli produced by hunting spiders are likely to be strikingly different from air flows produced by flying insects. Yet, our theoretical understanding of air motion sensing is currently drawn from oscillatory flows of flying predators only.

Key words: sensory ecology, mechanoreception, natural predators.

Introduction

Sensory organs are the interfaces between the central nervous system of organisms and the environment in which they live. Many crucial behavioural decisions of animals are based on information transmitted through the sensory system. The technical perfection of many sensors and their associated information-processing structures has long motivated neurobiologists, physiologists, biophysicists, and ethologists who have accumulated a broad knowledge of their functioning (e.g. Barlow and Mollon, 1982; Smith, 2000; Greenfield, 2002; and the many volumes in several compendiums such as the Autrum's *Handbook of Sensory Physiology*). More recently, sensory ecology has emerged as a new focus in the study of how organisms acquire and respond to information from and about their environment (Dusenbery, 1992; Barth and Schmid, 2001; Chittka and Thompson, 2001; Koehl, 2001; Collin and Marshall, 2003).

Visual and chemical ecology have developed so much over the last decade that they have both become independent lines of research, devoted to understand the ecological significance of sensory organs. Both fields have been promoted by well

known monographs (Lythgoe, 1979; Roitberg and Isman, 1992; Eisner and Meinwald, 1995; Archer et al., 1999) and the Society of Chemical Ecology publishes its own journal, with over a thousand pages a year. Similarly, research on other animal senses such as echolocation in bats and dolphins, electroreception in fish, and magnetic field reception in birds and rodents, has traditionally explored the physiological basis of sensing in an ecological context (Griffin, 1982; Fullard, 1987; Thomas et al., 2004; Arnegard and Carlson, 2005). A similar explosion of studies, best demonstrated by the several volumes published each year in the Fay and Popper's *Springer Handbook of Auditory Research*, has greatly increased our understanding of audition in vertebrates. This is also true for invertebrate audition based on pressure and pressure gradient reception (Ewing, 1989; Bailey, 1991; Gehardt and Huber, 2002; Drosopoulos and Claridge, 2005), with explicit attempts to relate hearing to ecological constraints (e.g. Römer and Bayley, 1986; Michelsen and Rohrseitz, 1997). Contrary to the notable exceptions of marine crustacean antennal mechanoreceptors (Fields and Weissburg, 2005) and spider trichobotria (Barth, 2001), mechanoreception based on particle

movement receptors has seldom been explored in relation to the environment. Yet this type of mechanoreception is one of the most widespread means of sensing in the animal world, particularly in invertebrates. The wind-sensitive filiform hairs of orthopteroids are among the most performing sensors in the animal kingdom (Shimozawa et al., 2003). In this system however, perhaps more so than in most sensory systems, the emphasis has been heavily placed on the physiological properties of neurons, with little consideration given to how the animals actually use the information gathered by their sensors.

An incredible amount of knowledge has accumulated on filiform hairs and their associated neural network because of the multitude of successful neurobiological, physiological, physical and modelling studies (Edwards and Palka, 1974; Kanou and Shimozawa, 1984; Shimozawa and Kanou, 1984; Miller et al., 1991; Humphrey et al., 1993; Landolfi and Miller, 1995; Humphrey et al., 2003; Shimozawa et al., 2003). This knowledge has been obtained from experiments conducted exclusively in the laboratory, often under severely constrained conditions. The neuroethology of the cricket escape has long since attained the status of a story that is complete enough to be reported in lay journals and textbooks (Camhi, 1984; Miller, 1989; Jacobs, 1995; Burrows, 1996; Gnatzy, 1996; Rieke et al., 1997; Young and Simmons, 1999; Dayan and Abbott, 2001). However, interpreting mechanosensory behaviour of crickets requires not only investigation of proximate factors of sensor functioning but also replacing the study of organisms in an ecological perspective (Chittka and Briscoe, 2001; Greene, 2005). The aim of this commentary is to put the cricket back on the ecological scene where its mechanoreceptors operate. We discuss how the lack of knowledge of the ecology of these insects in the field may entail our understanding of the biological relevance of their wind sensors, and how our results point towards the need to revisit some of the most basic assumptions.

Air sensing and ecological interactions

Wind sensing receptors are outstandingly used by crickets and cockroaches to detect the air currents generated by approaching predators, under both laboratory and natural conditions (Camhi et al., 1978; Gnatzy, 1996; Dangles et al., 2006; O.D., A. Olivier and J.C., unpublished data). One of the key steps in determining the ecological significance of cerci is therefore to document the array of predators that crickets are exposed to and their impact on survival. Most literature on orthopteroid mechanoreceptors concerns the cockroach *Periplaneta Americana* L. and the crickets *Acheta domestica* L. and *Gryllus bimaculatus* de Geer, but little is known about their natural history and interactions with predators in the field. The numerous lists of species found to attack crickets in the field can at best be used as hints, as they are qualitative, with one exception (Gabbutt, 1959). The seminal work of Camhi et al. (1978) argues that cockroaches are naturally predated upon by toads in tropical forests, but this claim is based on a short naturalistic note describing the occurrence of both species in the same habitat (Roth and Willis, 1960). The decade-long work of Gnatzy and collaborators (see Gnatzy, 1996 and

references therein) shows very convincingly that *Liris niger* Fabr. wasps are a real threat to crickets and that their nest is often filled with such prey. However, it is disturbing that W. Gnatzy has observed only a handful of several predation events in the field, despite several excursions in their habitat (W. Gnatzy, personal communication). Thus, the impact of this predatory wasp on its host is unknown, whether in terms of life table or of evolutionary pressures on crickets' escape system. The gap between the detailed neuroethological and neurobiological understanding and the sheer lack of knowledge about the simplest aspects of the predation on these crickets is surprisingly wide.

We have been working on the ethology of predation in the field with the most common cricket in Europe, the wood cricket *Nemobius sylvestris* Bosc. To assess the importance of known predators, i.e. wolf spiders, predatory wasps, birds, parasitoids (Fabre, 1925; Gabbutt, 1959; Bellmann and Luquet, 1995; Gnatzy, 1996; O.D., unpublished data) on wood cricket survival and behaviour, we experimentally submitted crickets to different types of predation: an 'air' treatment allowed for predation by aerial predators only (e.g. birds, parasitoids, predatory wasps), a 'spider' treatment allowed for predation by wolf spiders only, and a 'control' treatment allowed for no predation, thereby accounting for natural mortality (Fig. 1). We also included three different cricket instars to determine how sensitivity to predation varies with life stage. We ran this experiment using cages set in the field and using crickets found at the very same location. We filled five replicate cages each with 15 juvenile crickets of stage 2–3 and six adult crickets, and later in the season with 15 juveniles of stage 4–5. Each of the cages of the 'spider' treatment also contained five wolf spiders (*Pardosa* sp.), the most abundant predator in the litter. Data were collected once a week, survival data being directly obtained through the exhaustive count of remaining crickets. For behavioural data, the proportion of crickets seen at the surface of leaves over the total number of crickets still alive was computed to generate a measure of crickets' visibility (see more details in the legend of Fig. 1).

Effects of natural predators on cricket survival and behaviour

Predation pressures appeared important in juvenile stages, particularly the early ones (Fig. 2A–C). Juveniles of stage 2–3 were the most predated upon of all stages, mostly by wolf spiders and also by flying predators, probably Dipteran Tachinidae or wasps ($X^2_2=77.22$, $P<0.001$). The fact that spiders were enclosed with crickets suggests that predation in that treatment may have been forced unnaturally. However, natural densities of spiders, of which wolf spiders constitute the majority, have been reported to reach peaks of 50 individuals m^{-2} (Gabbutt, 1959), whereas the densities we used were equivalent to 20 spiders m^{-2} . Therefore, although the predation by spiders reported here may have been increased by enclosure effects, it is likely to be balanced in natural conditions by spider densities more than twice those we used. Spiders should thus be considered as a major predator of young stages of wood crickets.

Consistent with that assertion, juveniles of stage 2–3 altered their behaviour in the ‘spider’ treatment, compared to the ‘air’ or the ‘control’ treatment (Fig. 2D). In the presence of spiders, significantly fewer juveniles of stage 2–3 were visible at the surface of leaves compared to the other treatments (ANOVA $F_{2,9}=12.05$, $P<0.005$). The fact that spiders were typically on the surface of leaves suggests that vulnerable juvenile crickets

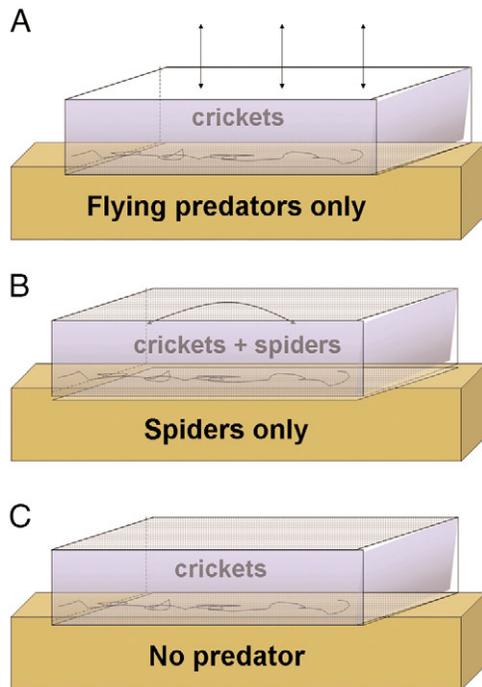


Fig. 1. Experimental design used to assess the importance of natural predators on cricket behaviour and survival. For each treatment, cages were built so as to allow for a single type of predation. (A) Cages for the ‘air’ treatment had an open top to allow flying predators to access the encaged crickets, and a plastic border at the top of the cages on which fluon was applied to prevent escapes or unwanted intrusions. (B,C) Cages for the ‘spider’ (B) and the ‘control’ (C) treatments were closed at the top with mosquito screen. All cages had a wooden frame of 0.5 m × 0.5 m × 0.25 m covered with clear plastic on the sides and a fabric bottom. In total, we used 225 juvenile crickets of stage 2–3, 225 juvenile crickets of stage 4–5 and 90 adults (45 males and 45 females), all caught from the local population. Behavioural and survival data were collected once a week from each cage. The experimenter first watched the inside of the cages from above for 1 min and counted the number of crickets from each age category that were visible at the surface of leaves, and then made an exhaustive count of the number of crickets still alive. The computed proportion of individuals visible at the surface of leaves was compared among treatments using ANOVA. To ensure that the effect seen on the proportions was not a byproduct of the total number of individuals still alive, proportions were weighted by numbers still alive before being compared among treatments. Given that total numbers still alive were not found to differ significantly among cages, the weight used was the mean number still alive for each cage over weeks. Survival data were directly obtained through the exhaustive count of crickets. Survival data were compared among treatments independently for juveniles of stage 2–3, juveniles of stage 4–5, and adults, using Tarone-Ware survival tests.

alter their vertical distribution in the litter as a predator-avoidance behaviour, supposedly to decrease the probability of encountering a spider. Although juvenile crickets of stage 2–3 appeared to be predated upon by flying predators as well, this predation was less than in the ‘spider’ treatment, and failed to increase their hiding tendency there. Our results thus suggest that juvenile stages adjust their behaviour to the actual level of risk, consistent with the threat-sensitive predator-avoidance hypothesis (Helfman, 1989; Engstrom-Ost and Lehtiniemi, 2004).

For juveniles of stage 4–5, no differential predation pressure could be detected among treatments in terms of survival ($X^2_1=0.24$, $P=0.63$, $\alpha^*=0.0167$). However, those juveniles were significantly less visible at the surface of leaves in the ‘spider’ than in the other two treatments ($F_{2,12}=17.28$, $P<0.001$), indicating that spiders probably remain potential predators for those stages. This result is consistent with our observations that spiders did attempt to capture juveniles of stage 4–5 on a regular basis and were occasionally successful. The discrepancy between survival and behavioural data here allows for several interpretations that, far from being mutually exclusive, rather reinforce each other. First, spiders probably reduced their attack rate on stages 4–5 compared to stages 2–3, because of the increased body size of the older crickets. Indeed, when offered juvenile crickets of various sizes, wolf spiders have a strong preference for prey half their size, and gradually reject prey as their size increases relatively to that of the spider (Nentwig, 1987). According to the relationship Nentwig found, prey the size of juveniles of stage 2–3 and 4–5 would have been accepted 79.1% and 41.8% of the time, respectively, supporting the hypothesis that predation attack rates must have been higher on stages 2–3 than on stages 4–5. Second, the cercal system of wood crickets increases in complexity as they get older (O.D., D. Pierre, J.-P. Christides, C. Magal and J.C., unpublished data). The sensory system of stages 4–5 may thus be more apt than that of stages 2–3 to detect repeated predation attempts from various directions. Third, juveniles of stage 4–5 have probably encountered spiders (and survived) in their earlier stages, so that experience may also increase crickets’ ability to detect and escape spiders. A combination of those factors could account for the maintained behavioural response of juveniles of stage 4–5 to the presence of spiders, despite the lack of any visible effect on their survival. Note that stages 4–5 appear threatened by spiders though not heavily predated upon, further indicating that the effect observed on stages 2–3 cannot be merely due to the enclosure of crickets with spiders.

A framework to study the sensory ecology of air motion sensors

In the light of our results, we propose a framework presenting the basic assumptions that should be revisited to replace the cricket’s escape sensing system in an ecological context (Fig. 3). To date most research on cricket mechanoreception has focused on the characteristics of the physical and physiological response of the sensor, and on the

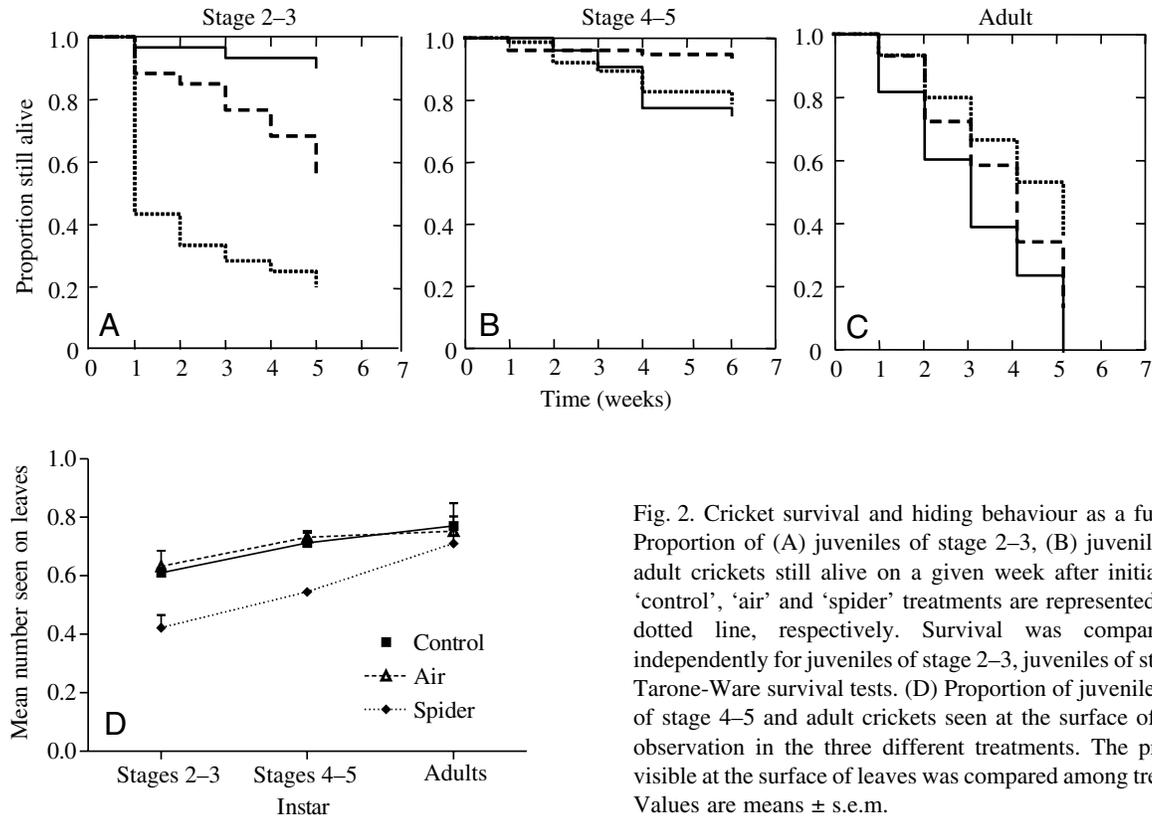


Fig. 2. Cricket survival and hiding behaviour as a function of predator type. Proportion of (A) juveniles of stage 2–3, (B) juveniles of stage 4–5 and (C) adult crickets still alive on a given week after initiation of treatments. The ‘control’, ‘air’ and ‘spider’ treatments are represented by the full, broken and dotted line, respectively. Survival was compared among treatments independently for juveniles of stage 2–3, juveniles of stage 4–5 and adults using Tarone-Ware survival tests. (D) Proportion of juveniles of stage 2–3, juveniles of stage 4–5 and adult crickets seen at the surface of leaves during 1 min of observation in the three different treatments. The proportion of individuals visible at the surface of leaves was compared among treatments using ANOVA. Values are means \pm s.e.m.

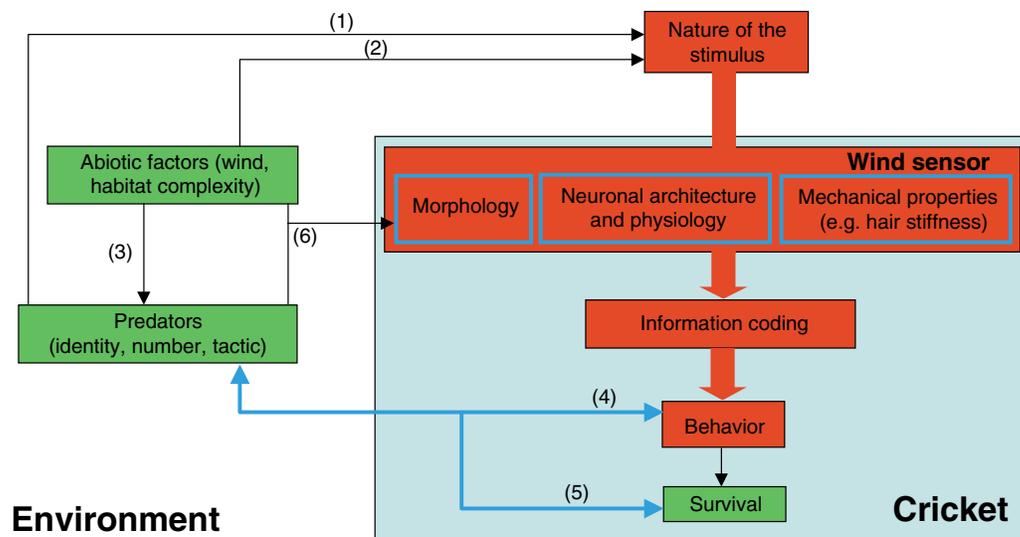


Fig. 3. Framework to study the ecological significance of crickets' escape system. (1) The identity of the predator greatly affects the nature of the stimulus perceived by the cricket. (2) The relative conspicuousness of a stimulus can be strongly affected by how well it transmits through the local environment. Although undocumented in crickets, signal perception has been related to habitat type in bats and fishes (Jones and Rydell, 1994; Domenici and Blake, 1997). Background noise (e.g. wind) may also impair crickets' ability to extract information from stimuli. (3) Hunting tactics of crickets' predators are likely to be influenced by the surrounding environment as shown for other predators. Bats for example, increase both the frequency and the bandwidth of their echo during target approach, thereby reducing the masking effect produced by the cluttering of nearby vegetation (Jones and Rydell, 1994). (4) Behaviour and therefore survival of crickets vary depending on the identity of predators (this study) and their attack tactic (Dangles et al., 2006). In return, cricket behaviour is likely to influence predator tactics. (5) Cricket cercus morphology is variable among populations from different environments (Dangles et al., 2005), suggesting an influence of predator and/or environmental characteristics on cercus morphology. Such a reaction norm is well documented in aquatic organisms that are capable of inducing defences (e.g. spines) in the presence of predators (see Schlichting and Pigliucci, 1998).

relation between physiology and behaviour (red pathway, Fig. 3). Although the transduction of the mechanical signal into a physiological signal is the first step to the cricket's behavioural response, physical and ecological constraints also influence the way in which organisms optimize their performance of stimulus acquisition and processing. The numerous connections between the neuroethological and ecological aspects vividly show that one cannot truly understand one without considering the other (see the extended legend of Fig. 3). Moreover, it appears obvious from our results that the stage of development of the cricket is an important control variable of this framework (blue lines). Predation pressure is most important on early stage juvenile crickets, and juveniles differ from adults on a behavioural level, adding to the already documented morphological and neural changes through stages (Kämper, 1994). Because most predation events occur during the juvenile stages, it is thus crucial that physical, physiological and neurobiological studies now turn to juveniles to understand the ecological significance and evolution of wind sensors.

Morphological, neurophysiological, behavioural and life history characteristics should be jointly investigated by ecologists and evolutionary biologists. Our results, the first to our knowledge to identify, in the field, the relative importance of different types of predators for any cricket species, point towards wolf spiders as the major predatory risk for wood crickets. Nothing is known about the air movement stimuli that predatory arthropods produce while hunting in the litter. However, we can safely assert that these air movements will be strikingly different from those produced by flying wasps. Since modelling efforts have, so far, invariably been targeted at oscillatory flows produced by flying insects (see Shimozawa et al., 2003), it thus appears necessary to identify the air flows generated by attacking spiders and to adapt the air flow model accordingly.

Given their evolutionary importance for survival, growth, and reproduction, sense organs must have undergone strong evolutionary pressures to allow organisms to extract and respond to ecologically relevant information. Except for fish and bees (Lythgoe and Partridge, 1989; Chittka and Menzel, 1992), the evolutionary link between environment and sensory systems is virtually unexplored (Endler and Basolo, 2001). Because there are physical and biological limits to what sensory systems can do in a particular environment, we expect sensory systems to evolve properties matching the environment in which they are used (Dusenbery, 1992). Any new environment could induce different natural selection on a sensory system (Endler and Basolo, 2001) and there is evidence that the structure and function of cricket air motion sensors vary among habitats (Dangles et al., 2005). Furthermore, the hundreds of cricket species occurring in very different habitats (ground, trees or caves) are valuable sources for the study of air sensing and how it operates under different selection pressures (Fig. 4). It appears obvious from our study that this question should be tackled through a combination of laboratory and field perspectives. Given the strong asymmetry of knowledge accumulated to date, it is now time to let the cricket out of its box.

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A Temperate forest ground



B Tropical cave walls



Fig. 4. Illustration of cricket–predator interactions in two contrasting habitats: (A) Temperate forest ground (France). The predation by wolf spiders (*Pardosa* sp.) on wood crickets (*Nemobius sylvestris*) takes place in the complex three-dimensional structure of the ground litter. The air flow produced by the spider is linear, coming from one direction. (B) Tropical cave wall (Gabon). Cave crickets (e.g. Phalangopsidae) are commonly preyed upon by whip spiders (*Amblypygi* sp.) in various tropical regions around the world (O.D., unpublished; Louis Deharveng, National Natural History Museum of Paris, personal communication). In contrast to A, this interaction occurs on a simple structure, the bare and flat walls of caves. The air flow produced by the two raptorial pedipalps of the whip spider comes from opposite directions. Cave pictures by Richard Oslisly/WCS Gabon.

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