

Variation in morphology and performance of predator-sensing system in wild cricket populations

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Summary

Even though variation in morphology is known to translate into variation in performance, studies looking at structural variability of a sensor to predict its consequences on the performance of animals are exceedingly rare. We investigated the morphological variability of air-flow-sensing receptors in wild populations of wood crickets (*Nemobius sylvestris*) sampled in a wide variety of habitats differing in latitude, litter structure, vegetation and predator communities. These hair receptors act as predator sensors. The observed levels of hair morphological variation were then incorporated into a biomechanical model of the hair canopy response to air flow to predict their influence on cricket predator perception. Cricket populations differ from each other, often strongly so, in the total number of hairs and in the number of hairs longer than 1 mm, which

are the hairs most sensitive for the perception of approaching predators. The hair canopy response, the output of the biomechanical model, sums up over the entire canopy the angles of deflection at which a neurophysiological response is triggered and represents the sensitivity of the cercal system. It is 35% higher in the most sensitive population, compared with the least sensitive population. These large differences in perception sensitivity for a given predator signal translate into larger distances at which predators could be perceived. Thus, differences in morphology at the sensor level seem to be translated both at the perception level and subsequently at the performance level of crickets.

Key words: air current detection, biomechanical model, mechanoreceptors, predator-prey interactions, sensory ecology.

Introduction

The interaction between the morphology of an organism and the biotic and abiotic environments can affect physiological and ecological performance (Wainwright and Reilly, 1994). Moreover, it has recently become apparent that morphological traits important to ecological interaction are likely to be plastic and sometimes inducible (Schlichting and Pigliucci, 1998; West-Eberhard, 2003). Although the evolutionary aspect of phenotypic plasticity has been well documented, we still know little about functional consequences of trait variability for species interactions in natural communities (Werner and Peacor, 2003).

Given the centrality of predation in the spectrum of ecological interactions, focusing on predator detection by animals offers an ideal opportunity for testing the functional relationships between morphology and performance. Adaptations of prey to deal with environmental variables and risks of predation are likely to occur at the detection stage as it confers substantial selective advantages on prey (Endler, 1991; Fox et al., 2001). Many arthropod species have evolved high performance detection systems consisting of mechanoreceptive cuticular hairs sensitive to the slightest air displacement, such as that generated by approaching predators. Patterns of air movement are, therefore, an important source of

information for crickets (Tobias and Murphey, 1979), cockroaches (Camhi et al., 1978), caterpillars (Tautz and Markl, 1978) and crayfish (Breithaupt et al., 1995). Among them, crickets have the best sensors (Barth, 2002) as they can detect air signals of $<0.03 \text{ mm s}^{-1}$ (Shimozawa et al., 2003). These hair receptors act as efficient predator sensors.

Cricket cerci are covered with hundreds of filiform hairs that excite giant interneurons and induce escape behaviour from predators (Edwards and Palka, 1974; Miller et al., 1991). A variation of hair length fractionates both the intensity and frequency range of an air stimulus (Shimozawa and Kanou, 1984) and, as a result, the morphology of the cercal sensory system is tightly linked to cricket perception. Based on a fluid-mechanical theory of air movement around hairs, an extensive development of cricket perception modelling has been performed in the last decades (Tautz, 1979; Shimozawa and Kanou, 1984; Humphrey et al., 1993; Shimozawa et al., 1998; Humphrey et al., 2003; Shimozawa et al., 2003). Recently, Magal et al. (C. Magal, O. Dangles, P. Caparroy and J. Casas, manuscript submitted for publication) have built a model that links the morphology and biomechanics of the entire cercal hair canopy and the response of crickets to approaching predators.

We investigated how morphological variability of cricket sensors translates into functional variability of predator–prey interactions. Although evolutionary biologists have long recognized plasticity of traits, sensory ecology theory has rarely incorporated trait variability into predictions of the response of organism to predators (see Barth and Schmid, 2001). Crickets experience a wide range of environments and predatory communities where they need to maximize the performance of their sensory system. We thus explored the natural range of variability for air sensors in wild populations of wood crickets (*Nemobius sylvestris*) sampled in a variety of habitats. We further assessed how these levels of variability influence air movement perception in crickets using a biomechanical model of cercal hair population coding.

Material and methods

Biology of the wood cricket

The wood cricket (*N. sylvestris* Bosc 1792) is the dominant cricket in Western Europe where it lives in a wide range of habitats, including forests, grasslands and moorlands (Bellman and Luquet, 1995). These small crickets (7–10 mm in body length) are common on deciduous forest floors, reaching locally and temporally high densities up to 400 individuals m⁻² (Gabbutt, 1959). The wood cricket life cycle consists of one generation each two years with diapause in both eggs and juveniles stage during winter (Gabbutt, 1959; Campan, 1965). These insects spend their day time foraging on the ground, actively moving in the three-dimensional medium of the substrate. As detritivores, they play a crucial role in nutrient cycling in soils and, with respect to their abundance, have a key role in the food web dynamics of these terrestrial systems (Ponsard and Arditi, 2000). Because of their small size and foraging habits, wood crickets are exposed to a wide array of wandering predators, including centipedes (Lithobiidae), beetles (Carabidae), ants (Formicidae) and spiders (e.g. Zoridae, Salticidae, Lycosidae; Gabbutt, 1959; Edgar, 1969; O.D., unpublished). As with many other cricket species (e.g. *Gryllus bimaculatus*, *G. campestris*, *G. integer*; see Fabre 1925; Cade 1984; Gnatzy 1996), they are also potentially predated by flying parasitoids.

Cricket sampling

In August 2002, we carried out cricket sampling from five geographically widespread locations in France. Study sites were selected to include latitudinal (from 49°01'50"N to 43°36'43"N), longitudinal (from 06°05'52"E to 01°12'30"W) and climatic gradients (Table 1). We maximised site heterogeneity also at the habitat scale by including different types of environments that wood crickets live in: oak forest, pine forest, grassland, open woodland and Mediterranean scrubland. At each site we surveyed predator communities by pitfall trapping (6 cm diameter, 24 h), quadrat sampling (50×50 cm, three replicates), and net collecting (30 min). Wandering and flying predators were both present at all sites but the dominant taxa varied among sites (Table 1). At each site, ten adult female crickets were hand-netted and stored in 70° ethanol. We studied the adult female phenotypes as they are easily identifiable in the field by their ovipositor, which are longer than the cerci. Only crickets with fully intact and normal cerci were used for measurements.

Cercal traits measurements

Adult wood crickets typically bear about 350 cercal filiform hairs divided into two cohorts (Edwards and Palka, 1974; C. Magal, O. Dangles, P. Caparroy and J. Casas, manuscript submitted for publication): short hairs (<500 µm) with a median length around 150 µm and long hairs (>500 µm) with a median length around 750 µm. It was impossible to measure all hairs for the 50 studied individuals. Exhaustive hair surveys over the cerci require acquisition and analysis of 40 SEM pictures per cerci, which needs around 60 man-hours of work per cerci. We therefore focused on long hairs because they were easily measured using a stereomicroscope but also because they are more sensitive than short hairs to low-velocity air currents and assure early detection of predators (Shimozawa and Kanou, 1984; Gnatzy and Kämper, 1990; C. Magal, O. Dangles, P. Caparroy and J. Casas, manuscript submitted for publication).

In the laboratory, the animals' right cercus was removed and mounted on a broken capillary electrode, which was mounted on a positioning stage allowing three axes of translation and one axis of rotation. The length of long hairs was measured

Table 1. *Environmental variables of the study sites of the five cricket populations*

Population	Pop. 1	Pop. 2	Pop. 3	Pop. 4	Pop. 5
Location	Metz	Tours	Saujon	Naucelle	Montpellier
Grid reference	49°01'50"N 06°05'52"E	47°17'06"N 00°47'13"E	45°38'38"N 01°12'30"W	44°10'56"N 02°22'47"E	43°36'43"N 03°52'38"E
Climate	Continental	Moderate oceanic	Oceanic	Mountainous	Mediterranean
Habitat	Grassland	Wood	Pineland	Open woodland	Scrubland
Ground structure	Short grasses	Moist litter (common oak)	Pine needles and sand	Tall grasses	Dry litter (green oak)
Dominant potential predators	Parasitic wasps, mantids, heteropterans	Parasitic wasps, spiders, centipedes	Parasitic wasps, ants	Parasitic wasps, spiders	Parasitic wasps, lizards

with a dissecting microscope (Leica, MZ 12.5; Bannockburn, IL, USA) and calibrated ocular micrometer. The positioning stage permitted accurate measurements as each hair could be placed in a plane perpendicular to the microscope. Repeated measurements of identified hairs ($N=30$) on the same animal revealed that the experimental measurement error associated with the use of the ocular protractor was low (<5%). Other morphological measurements including total body length, cercus length and cercus diameter at the base were performed for each cricket.

Statistical analysis

We performed a canonical discriminant analysis (CDA) to test multivariate differences among cricket populations and to identify which morphological variables were most useful for discriminating among populations (ter Braak, 1988). Discriminant analysis is related to multivariate analysis of variance and to multiple regression. It is particularly efficient to test multivariate differences among groups, but also to explore which variables are most useful for discriminating among groups. CDA finds linear combinations of discriminating variables that maximize the differences between groups and minimizes the differences within the groups. We considered six variables to describe the wind-sensitive cercal system of the crickets: (1) the total length of the cercus; (2) the length of the cercus relative to body length; (3) the total number of hairs; (4) the density of hairs (total number of hairs relative to the surface of the conic-shaped cercus); (5) the median length of the sampled hairs; and (6) the number of hairs longer than 1000 μm (very long hairs are likely to be the most efficient hairs for early detection of predators). The Wilk's lambda test was used to test whether the differences explained by the discriminant variables were significant. Only statistically significant discriminating variables were retained in the explanation of the results. We used the Mahalanobis distance (D^2) to discriminate between groups – a large value indicating good discrimination. It was converted to an F-statistic to test if the populations were significantly different from each other (Klecka, 1980).

Modelling the sensitivity response of crickets to air signals

The model we developed aims at reproducing the cercal population coding of oscillatory air flows by the hundreds of hairs on cerci. Its building blocks are the biomechanics of hair movement, the distribution of hair length in the canopy, the relationship between single hair movement and its neurophysiological activity and the overall canopy response (C. Magal, O. Dangles, P. Caparroy and J. Casas, manuscript submitted for publication). Details of parameter values and code implementation can be found in the above reference.

The mechanical behaviour of hair movement in an oscillating fluid has been modelled extensively in the past (Tautz, 1979) and our model is identical to those developed so far (see Humphrey et al., 2003; Shimozawa et al., 2003 for latest reviews). A filiform hair is defined as an inverted

pendulum with a rigid shaft supported by a spring at the base. The system can be described by four parameters: the moment of inertia that represents the mass distribution along the hair shaft; the spring stiffness, which provides the restoring torque towards the resting position; the torsional resistance within the hair base; and the coupling resistance between hair shaft and the air. For a rigid hair oscillating relative to a fixed axis of rotation, conservation of angular momentum $L(t)$ states that the rate of change of angular momentum is equal to the sum of torques acting on the hair:

$$\frac{dL(t)}{dt} = \frac{d^2\theta}{dt^2} = T_D(t) + T_{VM}(t) - T_R(t) - T_S(t)$$

where I is the inertia momentum of the hair relative to the axis of rotation and θ is the angular deflection of the hair with respect to its equilibrium orientation. The drag torque T_D arises due to frictional drag acting along the hair shaft. The torque T_{VM} is associated with the virtual mass of fluid, which at any instant must be also accelerated along with the hair. The damping torque T_R arises at the rotation point of the hair and results from frictions between the hair base and the surrounding cuticle. The restoring torque T_S is equivalent to spring stiffness, expressing the elasticity of the socket membrane and arises at the rotation point of the hair. The first two torques drive hair motion whereas the last two always oppose to hair deflection.

Long hairs have their peak response at low frequency, while shorter hairs display a flat response over most of the frequency range, with a peak response at high frequency. As a consequence, hair number and the variation of hair length are key features of the cercal system of crickets as they fractionate both the intensity and the frequency range of an air stimulus. The model uses several approximations and is precisely valid for a hair on a plate, with the fluid oscillating in the plane of the plate. These approximations have been tested and found appropriate for a hair on a cercus in a flow oscillating parallel to it. The maximal angular hair deflection during a single oscillation is used for modelling electrophysiological activity. We assumed here that the action potential frequency in the associated cercal afferent was directly proportional to the maximal angular deflection. Population coding was done in an additive way, borrowing the approach used for the vector coding in the cricket sensory system (Jacobs, 1995; Dayan and Abbott, 2001). The canopy response is therefore the sum, over each hair length, of the maximal hair deflection multiplied with the number of hairs of that length. Its units are radians. The cercal best frequency is the frequency at which the canopy response reaches its maximal value. The cercal best frequency shifts to lower frequencies and to higher response levels with increasing air velocity.

In the present study, we implemented the model with the hair length distributions measured for the five cricket populations. We thereby obtained the cercal canopy response as a function of signal frequency for each population for hairs longer than 500 μm . By selecting ecologically relevant acoustic signals,

such as those generated by running (~30 Hz) and flying (~170 Hz) predators (Gnatzy and Kämper, 1990), we evaluated the sensitivity response of crickets to natural predators.

Results

CDA ordination of populations

The first two discriminating variables of the CDA had the greatest discriminating power, 93.1% of the total variation (Table 2A). These first two variables were significant (Wilks's lambda test, $P < 0.001$) but the remaining were not. The ordination of individuals on the first two canonical axes shows that populations were mainly discriminated along the first axis and, to a lesser extent, by the second axis (Fig. 1). The number of hairs longer than 1000 μm was positively correlated with the first axis. Cercus length was positively correlated with the second axis and the total number of hairs negatively correlated with it. These three variables were the only significant canonical variables. The canonical correlations indicate that these correlations were highly significant (Table 2A). The ordination diagram (Fig. 1) separated out populations 1 and 4 from other populations at the negative and positive end of axis 2, respectively. In the middle of this axis, individuals from population 2 were intermixed with some of the population 3. Population 5 was positioned at the positive end of axis 1. All populations were significantly different from each other ($P < 0.05$) except population 2 and population 3 ($D^2 = 1.615$) (Table 2B).

Hair length distributions

Because hair number and hair size were both significant canonical variables, we built the hair length distribution diagram for each mean population (Fig. 2). Populations had

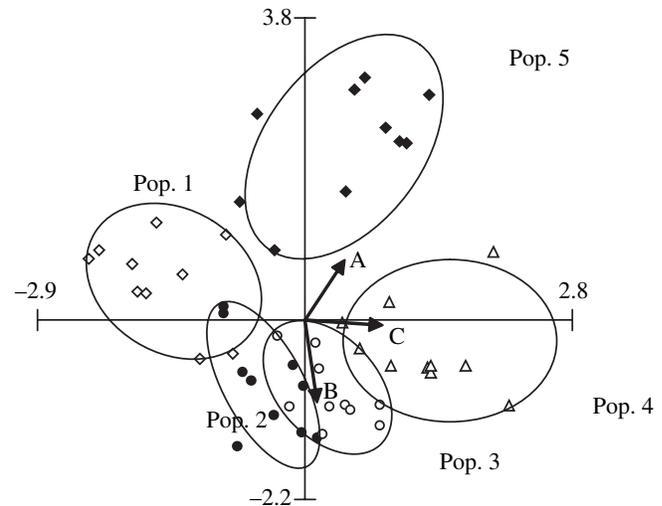


Fig. 1. Canonical discriminant ordination of the five cricket populations based on cercal variables. Arrows drawn from the centroid of the population dispersion indicate cercal variables that significantly contribute to the model (A, total length of the cercus; B, number of hairs; C, number of hairs longer than 1000 μm).

heterogeneous hair length distribution with a number of hairs ranging from 32 (Pop. 1) to 49 (Pop. 3) and a median hair length from 711 μm (Pop. 1) to 809 μm (Pop. 5). Hairs longer than 1000 μm were abundant in populations 4 and 5 but rare in population 1 (Fig. 2; grey bars).

Modelling of cricket perception

The integration of hair length distributions into the model revealed that the cercal canopy response to an oscillating signal of various frequencies varied among populations (Fig. 3A).

Table 2. Canonical discriminant analysis of the five cricket populations

Discriminating variables	Eigenvalue	Eigenvalue cumulative proportion	Canonical correlation	Wilk's lambda	Probability derived from Wilk's lambda
A					
1	2.872	0.522	0.861	0.057	<0.0001
2	2.252	0.931	0.832	0.063	<0.0001
3	0.361	0.997	0.213	0.89	0.1565
4	0.017	1.000	0.129	0.99	0.9563
B					
	Pop. 1	Pop. 2	Pop. 3	Pop. 4	Pop. 5
Pop. 1	—	3.887	9.591	17.800	12.629
Pop. 2	*	—	1.615	7.529	11.722
Pop. 3	‡	NS	—	4.736	11.679
Pop. 4	‡	‡	†	—	10.523
Pop. 5	‡	‡	‡	‡	—

NS, not significant; *significant at $P < 0.05$; †significant at $P < 0.01$; ‡significant at $P < 0.01$

A. Results for the four discriminating variables. The maximum number of discriminating variables is the number of groups minus one. The first two discriminating variables are treated as axes in Fig. 1.

B. Mahalanobis squared distances (D^2 , upper right portion) and level of significance of differences between populations (F values, lower left portion).

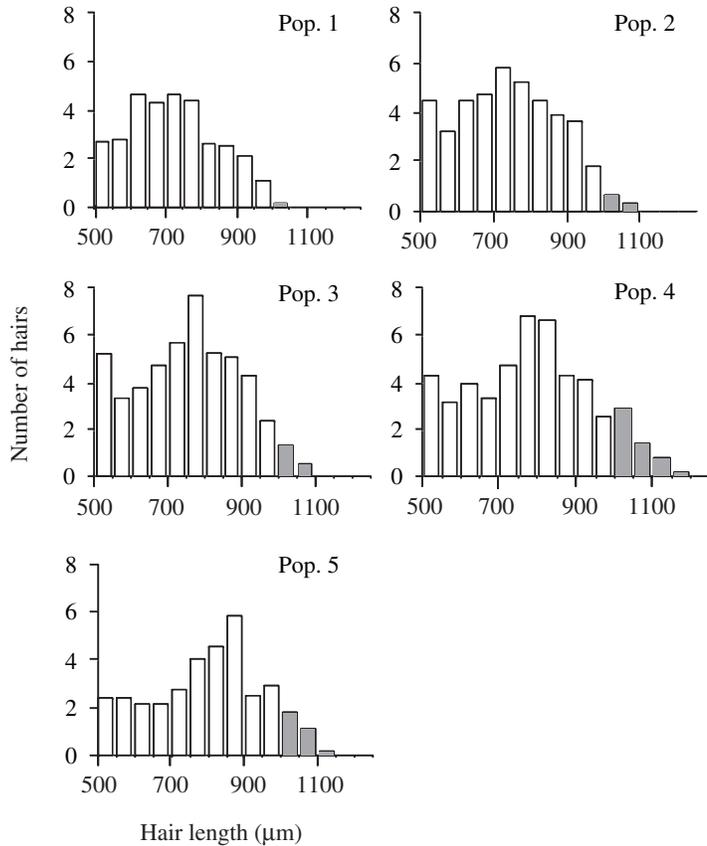


Fig. 2. Distribution of hair lengths of a mean cricket from the five populations. Grey bars indicate hair with a length longer than 1000 μm .

The response was higher for populations having more hairs (Pop. 3 and Pop. 4) than populations with fewer hairs (Pop. 1 and Pop. 5). However, the best detected frequency (maximum of the curve) was rather similar among populations, between 57.5 and 62.5 Hz. To better visualize among-population difference in the canopy response, we calculated the percent of variation in the canopy response of the five populations from a ‘reference’ population (determined as the mean of canopy responses of all populations, Fig. 3B). On average, the more sensitive populations (Pop. 3 and Pop. 4) had a canopy response $\sim 35\%$ higher than less sensitive ones (Pop. 1 and Pop. 5; Fig. 3B). These differences varied across signal frequencies: the decreasing pattern of Pop. 4 and Pop. 5 suggests that populations with the largest proportion of long hairs had an increased sensitivity at low frequencies; the opposite pattern was observed for other populations (Fig. 3B).

The measured hair length distribution heterogeneity had strong functional implications for the perception of natural predators among cricket populations (Fig. 4A,B). Whatever the type of predator signal considered (running, 30 Hz, or flying, 170 Hz; see Fig. 3A), cricket perception level increased with predator signal intensity. For any perception level, the more sensitive populations (Pop. 3 and Pop. 4) were able to detect air signal intensity $\sim 40\%$ lower than that detected by the less

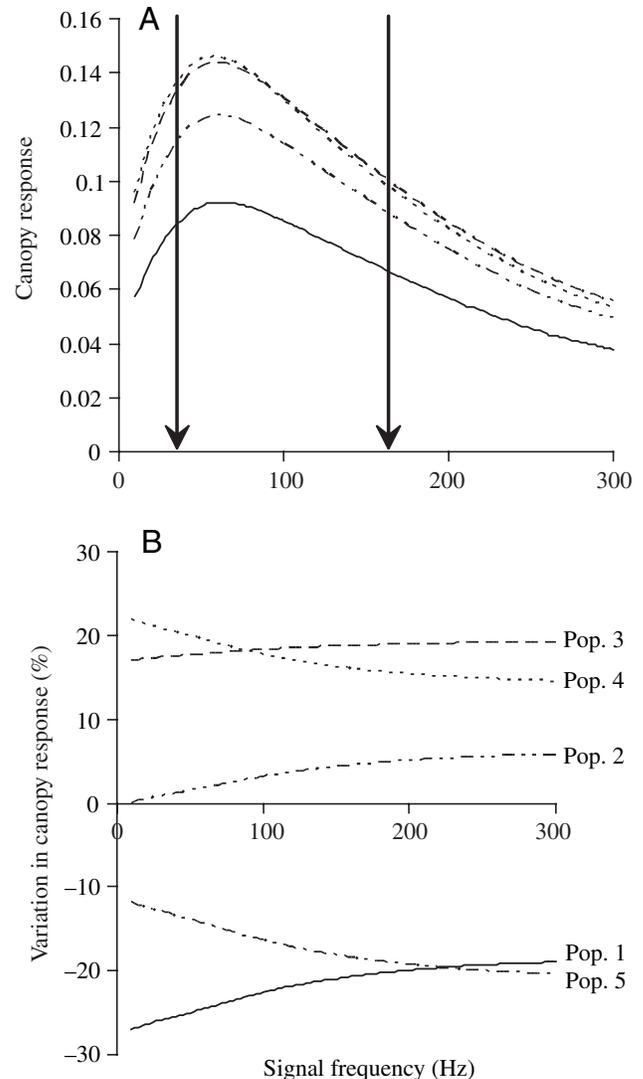


Fig. 3. Cercal canopy response as a function of signal frequency for the five cricket populations. (A) Total response, (B) proportion (%) of variation from a mean cercal canopy response. Legends of populations are given in (B). Peak air velocity is 0.3 mm s^{-1} . Arrows in (A) indicate signal frequencies emitted by running (30 Hz) and flying (170 Hz) natural predators of crickets.

sensitive population (Pop. 1). This pattern was consistent for both types of predator signals, although Pop. 5 had a better average perception level at low rather than high frequencies. In this case, the presence of very long hairs ($>1100 \mu\text{m}$) partly compensated for the low number of hairs.

Discussion

Sensor morphology

Although functional consequences of intraspecific morphological variation have been demonstrated for a variety of organisms (e.g. macroalgae, Hanisak et al., 1988; insects, Kölliker-Ott et al., 2003; fish, Brönmark and Miner, 1992;

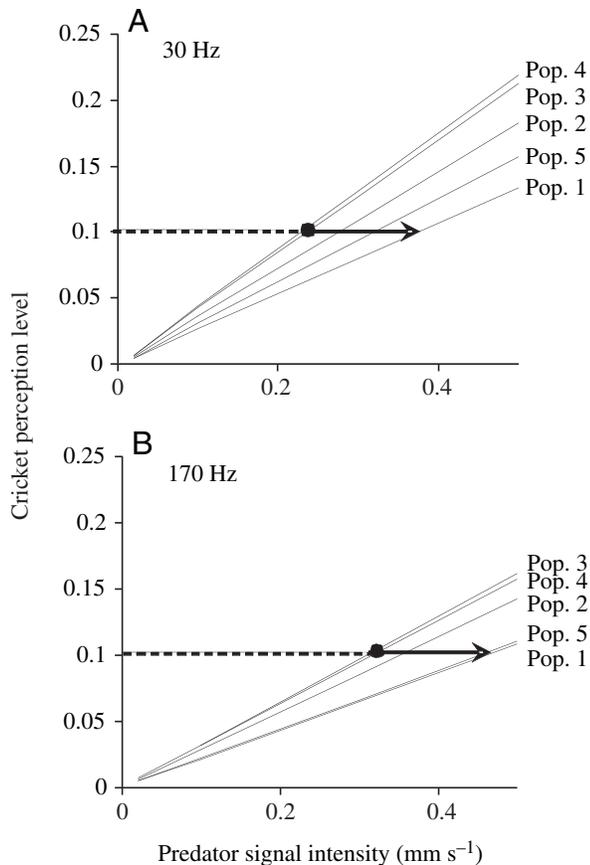


Fig. 4. Relationship between cricket perception level (cercal hair canopy response) and predator signal intensity (air particle velocity) for the five cricket populations. (A) Running predator ($f=30$ Hz), (B) flying predator ($f=170$ Hz). Arrows indicate, for a given perception level, the difference in air flow intensity detected between the more and the less sensitive population.

Svanbäck and Eklöv, 2003; lizards, Van Damme et al., 1998; Bats, Norberg, 1994), this aspect is generally disregarded by sensory ecologists. Many of them have treated variation as noise or as a result of methodological artefact and have not considered variation as an opportunity to study adaptation (see the warning issued by Chittka and Briscoe, 2001).

Morphological variation has been quantified in both invertebrates and vertebrates (Archer et al., 1987; Ayala et al., 1993; Shyue et al., 1995; Jokela et al., 2003; Spaethe and Chittka, 2003; Opstad et al., 2004) but most studies have been restricted to visual systems. This study confirms that morphological variation is also found in the air-flow sensory system of wild crickets. Variation is expressed both in terms of hair densities and hair length frequencies on the cerci, two characteristics that greatly influence cricket perception (Shimozawa and Kanou, 1984).

Sensor performance

We do not know to what extent the measured variation characterizes the full range of variability expressed in natural populations but this variation has strong functional

implications for the detection of predator signals. To our knowledge, none of the numerous models built to understand animal perception (Neumann, 2002; Ritz et al., 2000; Svendsen and Kiorboel, 2000; Erwin et al., 2001), has ever incorporated the potential structural variability of a sensor to predict consequences on the performance of animals. Notable exceptions are the recent studies performed by Spaethe et al. (2001) and Spaethe and Chittka (2003) who suggest that inter-individual variation in the morphology of the compound eye and the performance of the linked neural circuitry influences foraging efficiency of bumblebees under natural conditions. They found that the larger ommatidial diameter in larger bumble bees could make a sevenfold increase in sensitivity. Here the threshold sensitivity of the more sensitive cricket population was 35% lower than the less sensitive one and was independent on the size of the individuals. Although we disregarded short hairs (<500 μm) in this study, their contribution is not likely to change the measured variability because low-velocity air signals, such as those emitted by natural predators in the early approaching phase, are mainly perceived by hairs longer than 500 μm .

Ecology, evolution and fitness of crickets

Both morphological and performance variation in cricket sensors exist at individual and population levels. However, the latter largely overcame the former suggesting that our results can be analyzed in ecological and evolutionary terms. Cricket sensing variability might be a consequence of genetic differentiation resulting from selection, or may be due to the effect of different environments on the expression of phenotype. For example, the high degree of reproductive isolation among cricket populations (Fulton, 1952; Mousseau and Roff, 1989), the influence of the habitat structure on air signal transmission (e.g. Dusenbery, 1992; Bradbury and Vehrencamp, 1998) or the inducible response of insects to predatory pressure (e.g. Weisser et al., 1999) are potential hypotheses to explain measured morphological and performance variability.

To investigate the relationship between performance (e.g. escape success) and ecology (*sensu* Arnold, 1983), the morphological variation has to be in turn translated into fitness variation associated with predator escape. However, while crickets and cockroaches are reported to encode information on their fluid dynamical environment (Rinberg and Davidowitz, 2000), the information available for crickets during predator-prey interaction in the field remains unknown as only a couple of laboratory measurements of the predator signal have been conducted (Tautz and Markl, 1978; Gnatzy, 1996). Some of these experiments can, however, provide helpful data to discuss the fitness relevance of cricket sensor variability. For example, the negative relationship ($y=1/x^2$) between air amplitude displacement of the predator signal (y) and the distance to the predator (x) quantified by Tautz and Markl (1978) allowed us to calculate the signal intensity of predator (equal to $2\pi \times \text{signal frequency} \times y$). We thus estimate that crickets belonging to the more sensitive population (Pop.

3, at predator signal intensity=0.31 mm s⁻¹; see Fig. 4B) could perceive an approaching flying predator at a distance (x) 20% higher than the less sensitive ones (at predator signal intensity=0.47). This is valid up to a maximal distance of 70 cm (Tautz and Markl, 1978). Because long hairs are extremely useful to detect predators in the far field (low signal intensity), having more and longer hairs could confer substantial selective advantage on crickets.

In conclusion, the present study is a first bridge between the numerous classical neuroethological studies and the ecological and evolutionary understanding of the exceedingly well performing cricket air-flow sensor. We quantified for the first time the natural variability in sensor morphology of an insect prey which may translate into variability of predator detection. This study needs further work to interpret the potential adaptive significance of cercal trait patterns among cricket populations. First, studies on a larger set of populations should allow us to disentangle genetically and environmentally induced sources of variation. Second, we need to confirm that the variation in the phenotype increases fitness in the environment encountered. As proposed by Irschick (2003), measuring performance of animals in the field is a potential avenue for linking morphology and fitness of these organisms.

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