13 Communication by Substrate-Borne Vibrations in Cave Planthoppers

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INTRODUCTION

With an estimated number of about 50,000 described species worldwide, Auchenorrhyncha (Fulgoromorpha and Cicadomorpha) is the largest hemimetabolous insect taxon which includes exclusively phytophageous species. As such, most Auchenorrhyncha are associated with the green parts of plants in grasslands and forests (Hoch, 2002). Auchenorrhyncha appear to be unlikely candidates for a permanent life underground. Nevertheless, five (out of 18) families of the Fulgoromorpha (planthoppers), a total of more than 50 subterranean species are now known from different parts of the world (Table 13.1). So far no cave-adapted Cicadomorpha (leafhoppers) have been reported.

In the cave planthoppers, adaptation to similar environments has given rise to the evolution of strikingly similar external appearance in different parts of the world, constituting a prime example of convergent evolution. Like many other obligately cavernicolous arthropods, cave planthoppers are characterised by a set of morphological features which have been acquired during the course of adaptation to cave life. Most represent reductive evolutionary trends, *e.g.* reduction and loss of compound eyes and ocelli, tegmina, wings and body pigment (Figure 13.1 to Figure 13.4).

TABLE 13.1
Cavernicolous *Auchenorrhyncha*

Family	Geographical distribution	Reference
Hypochthonellidae	Zimbabwe	China and Fennah (1952)
Delphacidae	New Caledonia	Fennah (1980a)
Kinnaridae	Mexico	Fennah (1973b)
	Jamaica	Fennah (1980b)
Meenoplidae	Australia	Fennah (1973b), Hoch (1990, 1993)
	New Caledonia	Hoch (1996)
	Western Samoa	Hoch and Asche (1988)
	Canary Islands	Remane and Hoch (1988), Hoch and Asche (1993)
	Cape Verde Islands	Hoch *et al.* (1999)
Cixiidae	Madagascar	Synave, (1953)
	Canary Islands	Remane and Hoch (1988), Hoch and Asche (1993)
	Azores	Hoch (1991)
	Mexico	Fennah (1973b), Hoch (1988a)
	Hawaii	Fennah (1973a), Hoch and Howarth (1999)
	Galápagos	Hoch and Izquierdo (1996)
	Argentina	Remes Lenicov (1992)
	Australia	Hoch and Howarth (1989a, 1989b)
	New Zealand	Fennah (1975)
	Reunion Island	Hoch *et al.* (2003)
	[Baleares]	Racovitza (1907) (unconfirmed record)

Other morphological characters observed in cave-dwelling planthoppers, although less obvious, may be of more adaptive value in the underground environment, *e.g.* specialised spine configurations on the hind tibiae and tarsi, serving for enhanced walking on wet or rocky surfaces (Hoch, 2002).

Why did all these species abandon environments abundant in food and light for a life in the seemingly hostile underground where permanent darkness and other adverse conditions such as high relative humidity close to saturation (Howarth, 1983) and sometimes abnormally high carbon dioxide concentrations (Howarth and Stone, 1990) prevail? Which physiological and behavioural adaptations did their epigean ancestors possess which enabled them to survive and even complete their life cycle underground?

FIGURE 13.1 *Oliarus polyphemus*, adult female, body length *ca.* 4 mm, Hawaii Island. (From Hoch, H. and Howarth, F. G., 1993. With permission.)

FIGURE 13.2 *Solonaima baylissa*, adult female, body length *ca.* 4.5 mm, Australia. (From Hoch, H., 2002. With permission.)

FIGURE 13.3 *Solonaima pholetor*, adult female, body length *ca.* 8 mm, Australia. (From Hoch, H., 2000. With permission.)

The past 30 years have seen a paradigm shift in our understanding of the evolution of terrestrial troglobites, especially in the tropics. Discoveries of terrestrial troglobites (mainly arthropods) from young oceanic tropical islands have challenged the long held belief that obligate cavernicoles were necessarily relicts, driven to inhospitable environments by deteriorating ecological conditions on the surface, *e.g.* during glaciation. According to this relict hypothesis (Barr 1968), these troglophilic populations acquired cave adaptations subsequent to the extinction or extirpation of

FIGURE 13.4 *Tachycixius lavatubus*, adult male, Canary Islands, Tenerife. (From Hoch, H., 2002. With permission.)

closely related epigean populations. Following his discoveries of a highly diverse cavernicolous fauna in lava tubes on Hawaii, Howarth (1986) suggested an alternative hypothesis. Here, the exploitation of a novel food resource is assumed to be the driving force in cave colonisation and evolution of terrestrial troglobites (the adaptive shift hypothesis). Howarth (1986) argues that if there were enough food, suitable habitats to lay eggs, and most crucially, if they had the ability to locate a mate and reproduce underground obligately cavernicolous species may derive from accidental invasions into subterranean spaces. In the planthoppers, nymphal habitat points to conceivable preadaptation.

All cavernicolous Fulgoromorph species belong to taxa in which even immature stages of epigean species live close to the soil, *e.g.* under the dead bark of rotting logs, in leaf litter or moss or even within the soil, feeding on roots or perhaps on fungi (Remane and Hoch, 1988). From this level of ecological preadaptation, it appears to be a small evolutionary step also for adults to switch to a permanent life underground (Hoch, 2002; Howarth and Hoch, 2004). Here, we shall focus on the characteristics of the mating behaviour of planthoppers which facilitate mate location and recognition in a permanently dark environment.

INTRASPECIFIC COMMUNICATION IN SURFACE-DWELLING PLANTHOPPERS

Mobile, sexually reproducing organisms have developed specific behaviour patterns which serve to bring together conspecific males and females for mating. These patterns may consist of visual, chemical, tactile or acoustic signals, or a combination thereof. In the Auchenorrhyncha (leaf- and planthoppers), it has been shown that mate recognition is primarily based on substrate-borne vibration signals (Ossiannilsson, 1949; Ichikawa, 1976). Little is known about the visual signals that may play a role in courtship, but observations in some epigean species suggest that wing fluttering of the male, which often accompanies acoustic signalling (*e.g.* Strübing, 1960; Ichikawa, 1976; Booij, 1982b; Drosopoulos, 1985) may provide additional stimulus for the female. Hitherto, there has been no confirmed evidence of chemical communication signals by pheromones in the courtship and mating of Auchenorrhyncha.

INTRASPECIFIC COMMUNICATION IN CAVE-DWELLING PLANTHOPPERS

Research on the intraspecific communication in obligately cavernicolous planthoppers in the Cixiidae has been conducted in Hawaii Island (*Oliarus*), Queensland, Australia (*Solonaima*) and the Tenerife, Canary Islands (*Tachycixius*).

Recording Techniques

Recordings were made in the field and in the laboratory. We used the *magneto-dynamic* (MD) system developed by Strübing and Rollenhagen (1988), which is comfortably portable and allowed an experimental setup inside a cave (Figure 13.5). In Hawaii, field recordings were made in a lava tube of Kilauea volcano (Pahoa Cave) to test the efficiency of vibratory communication in the natural habitat of *Oliarus polyphemus*. Roots of the endemic host tree, *Metrosideros polymorpha* (Myrtaceae), form dense curtains inside the lava tube (Figure 13.6), and particularly early instar nymphs (I–IV) are found feeding on these roots, while older nymphs (V) and adults are often observed on the rock surfaces of the cave (Hoch and Howarth, 1993). Tested substrates were:

(a) Living roots of Metrosideros polymorpha
(b) Rock surface

FIGURE 13.5 Recording the communication signals of cave-dwelling planthoppers in Pahoa Cave, Hawaii Island. (M. Asche, original photograph. With permission.)

FIGURE 13.6 Interior of a Hawaiian lava tube with root curtains (*Metrosideros polymorpha*). (From Hoch, H., 2002. With permission.)

A modified loudspeaker (a pin attached to the membrane) guaranteed the transmission of purely vibratory signals. Signals were recorded by a tape recorder (Sony TCD 5M Professional), subsequently digitised (40,000 data points/sec) and measured with MacLab/4s (AD Instruments) using Chart v. 3.5.4/s.

The Specific Mate-Recognition System of Cavernicolous Planthoppers

Our experiments revealed that cave-dwelling planthoppers retain the intraspecific communication system of their epigean relatives through communication by substrate-borne vibratory signals (Hoch and Howarth, 1993). The field experiments showed that communication by substrate-borne vibrations is extraordinarily efficient in cave environments. Living root tissue is a very well-suited substrate for the transmission of low-frequency vibrations (waterpipe principle), as is living plant tissue in general (Michelsen *et al.*, 1982). Signals travelled along root curtains and could be detected at distances up to 2.50 m from the source of vibration. In contrast, rocky substrates proved to have very poor transmission capacities: even intense banging with a forceps was not detectable by the MD system at a short distance (less than 10 cm) from the source (Hoch and Howarth, 1993).

HAWAII: *O. POLYPHEMUS* FENNAH — SPECIES COMPLEX

In Hawaii, the colonisation of caves has occurred repeatedly within *Oliarus*:

On the island of Molokai (one adaptive shift)
On Maui (three adaptive shifts)
On Hawaii Island (at least three adaptive shifts) (Hoch and Howarth, 1999)

Morphologically nearly identical populations of one of the evolutionary lineages on Hawaii Island which have invaded caves, *O. polyphemus* (Figure 13.1), are found in numerous lava tubes of four of the major volcanoes, Hualalai, Mauna Kea, Mauna Loa and Kilauea, ranging in age from less than a hundred to several thousand years.

A comparative analysis of male and female courtship call patterns in 11 populations from lava tubes in the Hualalai, Mauna Loa and Kilauea volcanic systems revealed the following results (Hoch and Howarth, 1993; Wessel and Hoch, 1999).

Courtship Behaviour

In all *O. polyphemus* populations studied, the following courtship pattern was observed. In the majority of male–female interactions, the female emitted spontaneous calls, that is, the female performed the initial step of courtship behaviour. In cases where these initial calls remained unanswered, the female eventually stopped calling. In cases where a nearby male answered these calls, the female did not change location and continued to emit calls at regular intervals. The male then usually approached the calling female, while responding to the female calls at irregular intervals. In all observed cases, courtship lasted for *ca.* 1 h before copulation commenced, while copulations persisted from 36 to 57 min. While in copula, neither male nor female emitted calls. Remarkably, in none of the observed male–female interactions displaying the described courtship pattern was a song-active female found to reject a responding male or to show avoiding or rejection behaviour when the male attempted to mate (Hoch and Howarth, 1993). Drosopoulos (1985) reported that there is specificity in precopulatory behaviour even in closely related species of the planthopper genus *Muellerianella*.

Call Structure

The time vs. amplitude pattern of the courtship signals of *O. polyphemus* individuals consisted of more or less homogenous pulse trains (Figure 13.7). Both sexes displayed similar call structures.

Both observations are in strong contrast with observations in epigean planthoppers which usually display highly complex time–amplitude patterns, especially in the male call, while females appear to be less differentiated (*e.g.* Claridge, 1985b; de Vrijer, 1986).

Within each population variation of courtship calls among individuals was found to be greater than individual variation of calls, although overall variation was comparatively small (Figure 13.7).

Remarkably, variation between populations was higher than within single populations (Figure 13.8; see song examples of *O. polyphemus* populations from Kaumana Cave, Pahoa Cave and McKenzie Park Cave on CD). Consequently, Hoch and Howarth (1993) assumed that *O. polyphemus*, previously considered to be a single species widely distributed on the island of Hawaii, was rather a complex of reproductively isolated populations, *i.e.* separate species. In the meantime, we showed that *O. polyphemus* is indeed a species complex *in statu nascendi* (Wessel and Hoch, 1999). Evidence is accumulating (Wessel and Hoch, in preparation) in support of the model suggested by Hoch and Howarth (1993) and Hoch (1999) which links evolutionary divergence to the succession of vegetation in dynamic, that is, volcanically active environments.

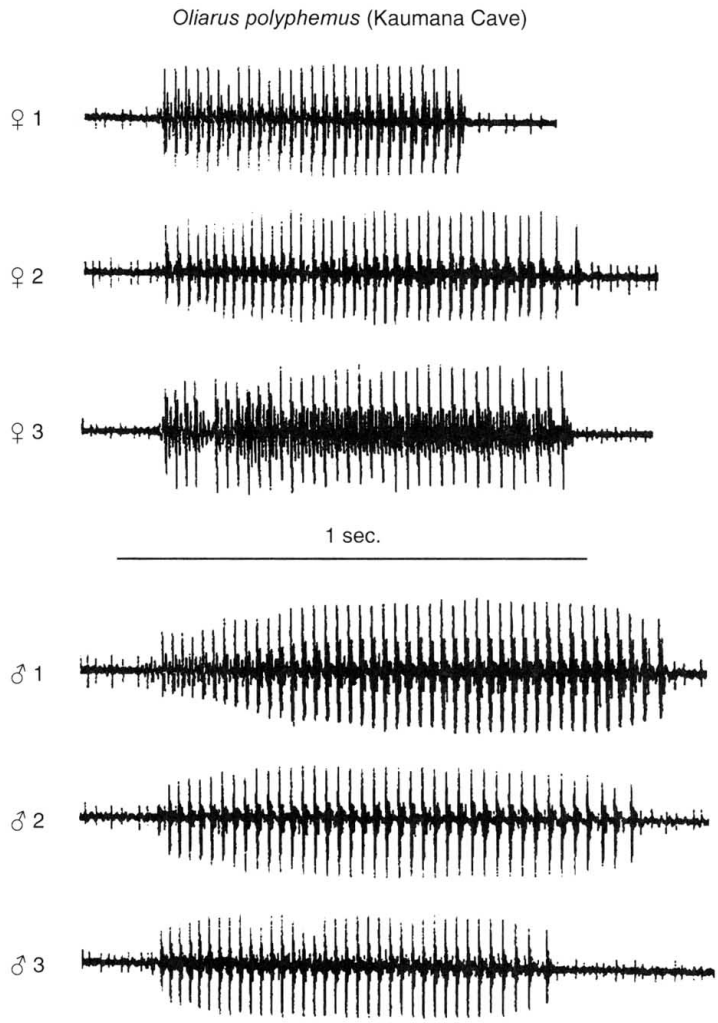

FIGURE 13.7 Variation of *Oliarus polyphemus* male and female calls from Kaumana Cave population, Hawaii Island. (From Hoch, H. and Howarth, 1993. With permission.)

AUSTRALIA: *SOLONAIMA* KIRKALDY— SPECIES

In Australia, the (monophyletic) genus *Solonaima* is represented with nine epigean and six cavernicolous species in Queensland and New South Wales (Hoch, 1988b; Hoch and Howarth, 1989b; Erbe and Hoch, 2004). Cave-dwelling *Solonaima* occur in several million-year-old limestone caves in the Chillagoe and Mitchell Palmer Karst as well as in young lava tubes in Undara. The cave-dwelling *Solonaima* display varying degrees of troglomorphy, with external morphologies ranging from a virtually epigean appearance with only slightly reduced compound eyes, yet fully developed wings and body pigmentation, to greatly modified taxa, blind, flight- and pigmentless. In *Solonaima*, the degree of troglomorphy is positively correlated with the physical features of their respective environments rather than with the age of the caves. *S. baylissa* (Figure 13.2), which is strongly troglomorphic, is restricted to the deep cave zone of lava tubes in the 190,000-year-old Undara lava flow, while the only slightly troglomorphic species, *S. sullivani,* is found in limestone cave at Mitchell Palmer,

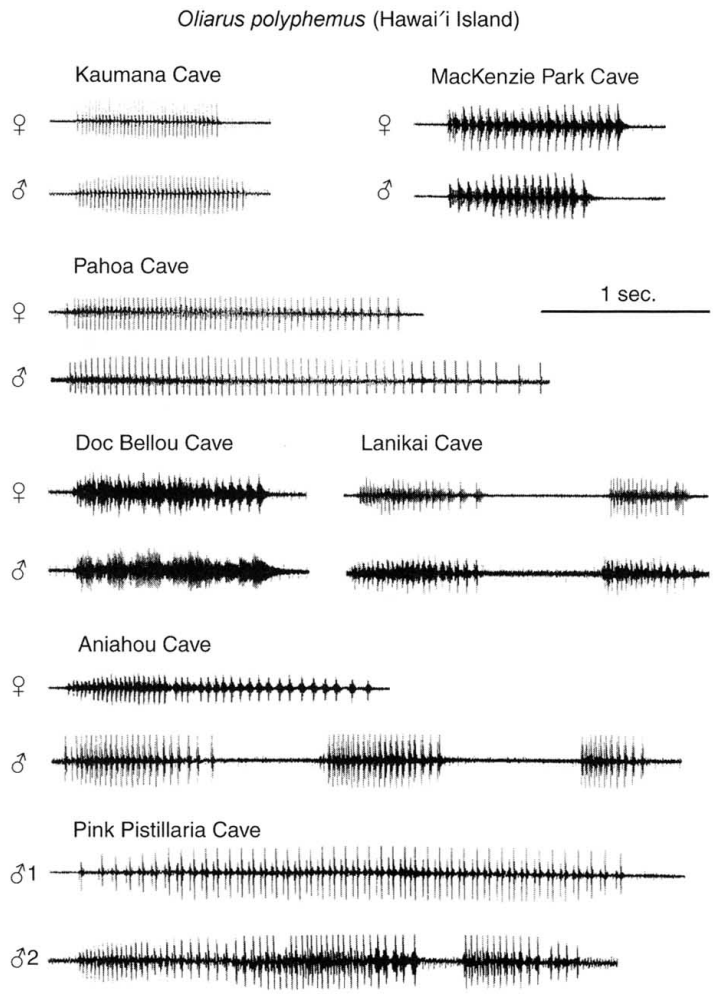

FIGURE 13.8 Female and male calls from *Oliarus polyphemus* populations from different lava tubes on Hawaii Island. (From Hoch, H. and Howarth, 1993. With permission.)

estimated to have been available for colonisation for at least 5 million years (Hoch and Howarth, 1989b).

Here, we compared the courtship behaviour of a facultatively cavernicolous species, *Solonaima pholetor* (Figure 13.3), which displays only slight modifications in external morphology, and the troglobitic, *S. baylissa*, which is highly troglomorphic.

Courtship Behaviour

From both cavernicolous *Solonaima* species, observations and recordings were obtained under field conditions. For each species, only a few male–female interactions were observed. Available information is too sparse to recognise a specific behaviour pattern.

Call Structure

In the facultative cave species, *S. pholetor*, an extremely simplified call structure was observed: calls of male and females consisted merely of single "clicks" (Figure 13.9 and song example on CD).

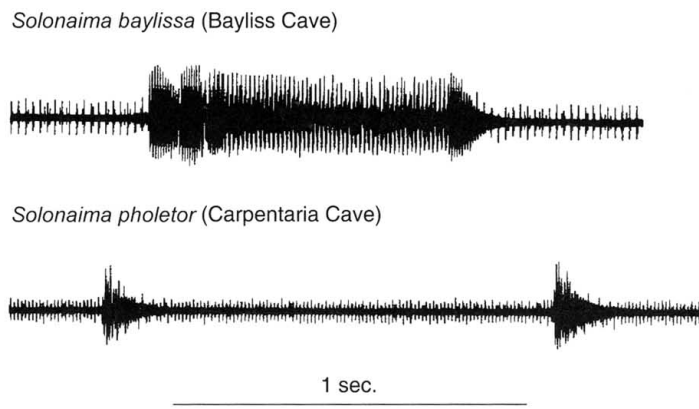

FIGURE 13.9 Structure of male courtship call of *Solonaima baylissa* (Queensland, Australia: Bayliss Cave) (above) and *Solonaima pholetor* (Queensland, Australia: Carpentaria Cave, Chillagoe) (below). (From Hoch, H., 2000. With permission.)

Amazingly, these signals obviously contain sufficient information to lead to successful courtship and copulation. In contrast, males of the obligate cave species studied, the pale, blind and flightless *S. baylissa*, display a much more differentiated calling signal, which consists of three distinguishable elements — two initial chirps, a longer trill and a final pulse resembling the sound of a fog-horn (Figure 13.9, and song example on CD) (Hoch, 2000).

Canary Islands: *Tachycixius lavatubus* Remane and Hoch

In the Canary Islands, several evolutionary lineages have colonised subterranean habitats on Tenerife, La Palma and El Hierro (Hoch and Asche, 1993). On the island of Tenerife, populations of *T. lavatubus* were found to occur in lava tubes in three disjunct areas, *e.g.* in the western part of the island, the north and the northeast (Hoch, 1994).

Recordings of courtship signals were obtained from *T. lavatubus* individuals from populations in the respective areas. Although very few male–female interactions were observed either in the field or the laboratory and recorded signals might not have been truly representative, a high degree of variation among the populations from different caves was observed (Hoch and Asche, unpublished). Unfortunately, recorded signals were erased from the tapes due to inadequate tape quality and/or storage, rendering preliminary results irreproducible. They are nevertheless mentioned here to point out the possible existence of another species complex comparable to that of *O. polyphemus* in Hawaii which now awaits further investigation.

EVOLUTIONARY INFERENCE AND POSSIBLE ADAPTIVE VALUE OF OBSERVED MODIFICATION OF BEHAVIOUR DURING CAVE ADAPTATION

Alteration of General Courtship Pattern during Cave Adaptation

Here, we refer to observations on the *O. polyphemus* species complex in Hawaii.

It is remarkable that, in nearly all cases observed, females initiated calling and remained the more song-active partner throughout the courtship phase. No female was ever observed to reject a responding male which had been successful in locating her (Hoch and Howarth, 1993). This behaviour is contrary to the courtship and mating behaviour observed in numerous epigean planthopper species (*e.g.* in the family Delphacidae, except for *Muellerianella brevipennis*

(Drosopoulos, 1985). There, males usually initiate calling, and in the genus *Javesella* males were observed to emit a few successive calls, then to stop calling for a variable amount of time, walk off the grass stem if there is no response by a female and, when placed back on the grass stem, produce a new series of calling signals. Under natural conditions, this strategy of acoustic exploration of environments with complex architecture (*e.g.* dense vegetation, grass tussocks, *etc.*) is apparently applied by males to locate receptive females (de Vrijer, 1986). Unfortunately, little is known about the courtship pattern in epigean *Oliarus* species which are closely related to the cavernicolous species. This limited knowledge makes it impossible to confirm that the switch from male to female initial calling occurs during cave adaptation. It is conceivable that the behaviour observed in *O. polyphemus* is a strategy to economise mate location under the specific conditions of the cave environment. The fact that song-active females readily accepted responding males for copulation indicates that song activity in females is usually directly correlated with receptiveness or, in the epigean delphacid *Muellerianella brevipennis*, to ensure pair forming (Drosopoulos, 1985). The female is actively advertising an opportunity for males in search of a mate. Consequently, males are made aware of receptive females only and, by this investment of less energy in exploring the environment acoustically in search for a receptive female, may instead be able to cover a wider area (Hoch, 2000). In the natural habitat, signals of a *Oliarus* female are perceptible by males within a radius of at least 2.5 m. The first male to reach the female will most likely perform a successful mating. The apparent low motility of the female during the courtship phase may facilitate the male's attempts to locate her. Both low song activity in the male and low motility of the female may also serve to minimise predation risk (Hoch and Howarth, 1993) by other troglobitic arthropods, *e.g.* spiders and crickets which also colonise the lava tubes (Howarth, 1981).

Reduction of Signal Complexity in Cave-Dwelling Planthoppers

An interesting phenomenon observed in the call structure of cavernicolous planthoppers is the reduction of complexity of single calls as compared with epigean taxa (see other contributions on Auchenorrhyncha in this volume), although substrate-borne vibratory signals are apparently the most important, if not the only, component, of the specific mate-recognition system of cave-dwelling planthoppers. Alternative hypotheses to rationalise this phenomenon have been discussed (Hoch, 2000). Preference was given to the ethological-release hypothesis which assumes that, when organisms are released from the competitive pressure of related species, selection on highly specific sounds may be less intense (Booij, 1982b). In Hawaii, the members of the *O. polyphemus* species complex occur largely in allopatry, and in any given cave there is only one cavernicolous planthopper species present (with one exception — see Hoch and Howarth, 1993). Consequently, competitive pressure by sympatric allies enhancing the maintenance of high signal complexity in order to minimise or avoid interspecific mating (which would probably yield less viable offspring) does not exist. Thus, maintaining a signal with minimal complexity may have been sufficient to serve the purpose of mate recognition and location under the specific conditions of the cave environment.

In *Solonaima* from Australia, the degree of reduction of signal complexity differs between the two cavernicolous species studied. The strongly troglomorphic, obligate cave species, *S. baylissa,* maintains a remarkably higher degree of call complexity than the less troglomorphic, facultative cave species, *S. pholetor*. In the cave where *S. pholetor* is found, it is the only cave-dwelling cixiid and perhaps the only insect using substrate-borne vibration as a means of intraspecific communication. The *S. baylissa* population studied, however, occurs in sympatry with another cavernicolous cixiid, *Undarana* species (Hoch and Howarth, 1989a). Although *Undarana* is not a close relative of *Solonaima*, maintaining signal complexity might be necessary to ensure specific

mate recognition in an environment where mate recognition is apparently totally dependent on acoustic clues (Hoch, 2000).

SUMMARISING REMARKS AND PERSPECTIVES

From the results of behavioural studies on cave-dwelling planthoppers from Hawaii, Australia and the Canary Islands we are tempted to conclude that the maintenance of the intraspecific communication system based on substrate-borne vibrations in taxa with subterranean immature stages was crucial for the major ecological shift from surface to subterranean habitats. Whether or not the alterations of courtship and mating behaviour specifically observed in cave-dwelling *Oliarus* from Hawaii (female vs. male calling activity) are directly linked to the process of cave adaptation, however, is yet unknown. Although studies on intraspecific communication in cave-dwelling planthoppers have contributed to our knowledge of the reproductive biology of these insects, many questions remain open. In-depth studies on intraspecific communication in other cave-dwelling Fulgoromorpha may hold surprises and give new insights into the evolution and adaptation of communication systems in the course of major ecological shifts.

Very little is known about sensory structures and their physiological properties either in cave-dwelling planthoppers or even in Auchenorrhyncha in general (Čokl and Doberlet, 2003). Another promising field for further research is the role of sexual selection and female choice in the process of species formation in cave planthoppers. The only information on their prospective mating partner available to cave planthoppers must be encoded in the vibratory signals (Hoch, 2000). Other influences on choice which are critical to ensure mating success in epigean species, such as optical cues, are absent in troglobitic taxa. Obligately cavernicolous planthoppers offer prime opportunities to study sexually selected traits in a communication system with a minimal set of signal types, as compared with epigean taxa. Suitable laboratory facilities which are mandatory for rearing cave planthoppers by simulating the natural conditions of the cave environment (provision of root supply, permanently high relative humidity and darkness) are now becoming available for these studies at the *Museum für Naturkunde*, Berlin.

Considering that much of the existing knowledge stems from very few cavernicolous taxa and given the small proportion of investigated karst and volcanic areas containing suitable habitat, especially in the tropics, we predict that exploration of the respective areas will bring to light many more exciting discoveries.

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