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Behavioural studies on neotropical grasshoppers: implications for taxonomy

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The value of behavioural data in taxonomy is discussed by means of examples from distinct subfamilies of neotropical grasshoppers. The comparison of time-structure of songs can be used for distinction of closely related species in Gomphocerinae, but not in Romaleinae. Courtship songs and rival songs could be used to detect phylogenetic relations within a subfamily. The possible taxonomic value of visual displays in non-stridulating subfamilies is discussed. Like morphological features, behavioural data show convergence and variation. The behavioural significance of a signal has to be known before it is interpreted taxonomically.

Behavioural data, especially on acoustic behaviour, have been of extreme value in orthopteran systematics ever since the pioneer studies of Faber (1953), Perdeck (1958), and Ragge (in the present volume) helped to discover and separate cryptic species (see review of Vickery 1985). When extending this application to other kinds of behaviour or to subfamilies of grasshoppers, some problems and questions of a more general nature arise: how can the ethologist help the taxonomist, and at which taxonomic level? And how, the other way round, can the taxonomist stimulate ethological research? What has to be taken into account when incorporating behavioural data into taxonomic work? What are the practical consequences of the necessary cooperation between ethologist and taxonomist? These questions are relevant for any taxonomic group. However, I think that they can be discussed more easily if I sketch some results of my work on neotropical grasshoppers which I have done in the last three years in Argentina and Ecuador. For a detailed account, see Riede (in preparation). Here, I can give only some examples relevant for the above questions.

The South American fauna consists of very different subfamilies of Old and New world origin distributed over diverse biotopes from deserts to rain forest-canopy, and therefore provides an

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excellent opportunity to investigate the impact of ecology on communication strategies. The profound study of Amedegnato (1977) revealed the phylogenetic relations of neotropical Acridoidea and thus made it possible to integrate my behavioural data into a modern systematic framework.

I soon realized that only a small fraction of ethograms could be registered during this study on a huge group where taxonomic revisions of many groups are still lacking. Though my data are based on only a few representatives of each subfamily and therefore are still preliminary, it was possible to relate a coarse classification of communication strategies with the phylogenetic tree designed by systematists.

It will sketch the mating behaviour of the following groups: first, the Gomphocerinae of South America which are invaders from the Old World and show elaborate acoustic communication; second, the Romaleinae which are endemic to South America and also show acoustic communication, but in a different behavioural context; and third, the Rhytidochrotinae, also purely South American, as an example for an optical display by 'knee-waving'.

Gomphocerine mating behaviour

There exist many studies on Gomphocerinae (Faber 1953, Jacobs 1950, Loher 1957, Helversen 1979 for European species, Otte 1970 for North American species). South American Gomphocerinae — recent immigrants from North American — fit well into the following general scheme:

- Sound production by a femuro–tegminial mechanism in both sexes by rubbing a row of femoral pegs against a tegminial vein.
- Species-specific songs with characteristic temporal pattern, but broadband frequencies.
- Complex acoustic interaction by various song types: ordinary song, rival song, and courtship song.
- The ordinary song of males attracts sexually receptive females by phonotaxis; they respond with their own songs.
- Female behaviour changes cyclically from a defensive state to passive copulatory readiness to active copulatory readiness signaled by a song (Loher & Huber 1966).
- Copulation lasts between 30 and 90 minutes.

Two closely related species of *Euplectrotettix* can be separated clearly by the time-structure of their song, while their morphological differentiation is extremely difficult. Future systematic work on South American Gomphocerinae should include, from its commencement, sound recordings, especially for morphologically homogeneous groups like *Euplectrotettix* or *Amblytropidia*.

Courtship and rival songs are completely different from the ordinary song both in structure and function. The courtship song is performed near the female; it is softer and generally emphasizes higher frequencies. In all the South American species studied so far it is produced by alternating leg movements. *Peruvia nigromarginata* adds optical signals produced by antennae and palps to its courtship song, similar to the European *Gomphocerus* or the North American *Syrbula* species.

Romaleine mating behaviour

Romaleinae are large, conspicuous grasshoppers. The subfamily consists of at least 55 genera mainly limited to South America. The following summary is based on observations of the genera *Elaeochlora* and *Coryacris*.

- Males approach females slowly and mount without preceding display.
- Males stridulate by rubbing front wings against hind wings, producing a non-structured, short sound pulse.

- Phonotaxis has not been observed.
- Males stridulate principally during mounting and copulation.
- Males approach copulating pairs, probably attracted by female pheromones. They try to replace the copulating male, thereby showing 'stridulatory duels'.
- Copulations last between 8 and 30 hours.

Visual displays

Many subfamilies of South American grasshoppers do not produce sound, for example the Leptysminae, Rhytidochrotinae, Proctolabinae, and Bactrophorinae (see Riede, in preparation). Some species exhibit characteristic, soundless movements of their hindlegs ('knee-waving') and/or their contrastingly tipped antennae. The male of *Galidacris* sp. (Rhytidochrotinae) approaches the female and exhibits a characteristic sequence of leg-movements and flip-backs of his antennae, marked with a yellow tip. The function of these movements is still obscure; the movement-pattern could serve as a species-isolating mechanism analogous to the calling songs in Gomphocerinae, but so far no such display could be observed in related species of the genus. The Rhytidochrotinae cannot be differentiated by genitalian morphology, and members of the genus *Galidacris* are candidates for the discovery of cryptic species by the analysis of displays. These resemble the visual displays observed in some Gomphocerinae; it has been shown that the courtship song of *G. rufus* modifies the locomotor activity of the female (Riede 1983). Therefore, the effect of the *Galidacris* display on female behaviour should be examined.

Most species of the subfamilies Proctolabinae and Bactrophorinae inhabit the canopy of the Amazonian rain forest. They are characterized by protuberant eyes and brightly coloured knees; knee-waving in males and females could be filmed in a variety of species, but its function is still unclear.

Convergences

The mating system of the Gomphocerinae is strikingly similar to that of the Corixidae (Hemiptera): males perform a species-specific calling, courtship, and rival song, females have a characteristic cycle of receptivity (Jansson 1973). As in Gomphocerinae, receptive females are rare, which leads to increased male-male competition (male-biased operational sex-ratio: Emlen 1976). This could have been the driving selection pressure to the convergent development of an acoustic communication system both in Gomphocerinae and Corixidae.

Waving of contrastingly tipped antennae and their rapid flip-back can be observed in several Gomphocerinae, in the *Galidacris* group (Rytidochrotinae), and in species with white-tipped antennae belonging to the subfamilies Leptysminae and Proctolabinae. These convergences clearly show that it can be dangerous to establish phylogenetic relations only on the basis of behavioural data. If one were to do so, Corixidae and Gomphocerinae would be related more closely than Gomphocerinae and Romaleinae. This absurd example shows that behavioural data always have to be interpreted on a solid systematic background. But how, then, can the study of behaviour help the systematist? Wherever optical, acoustical, or chemical signals are used for precopulatory isolation, their analysis and comparison can clarify problems of microevolution and speciation. However, the more closely related two sympatric species are, the more divergent may be their songs. This is of extreme value for the taxonomist for the separation of species, but in contrast to morphological features, similarity is no measure of relationship. Integrating song structure as an OTU into a study of numeric taxonomy would lead to chaos. Therefore the analysis of species-specific signals serves only for splitting and not for lumping.

The case is different with intraspecific communication behaviour, for example the rival or courtship song in Gomphocerinae, or sound production during male–male interaction in Romaleinae. These signals do not underlie the selection pressure of species recognition; they are produced after pair formation has taken place. The variation in temporal structure of courtship songs seems to be less than in ordinary song, at least in the South American species of Gomphocerinae (Riede, in preparation). However, only ordinary songs have so far been much considered for taxonomic analysis, and other song types like courtship and rival songs have been neglected.

These examples show that it is important to analyse the function of a behaviour before the taxonomist integrates it into the list of diagnostic features.

Conclusions and consequences

The above examples demonstrate that behavioural data have to be interpreted differently in various subfamilies.

In the Gomphocerinae, the discovery of cryptic species or separation of similar species is possible by analysing the ordinary song, i.e. separation on the microsystematic level. The analysis of rival or courtship song may reveal phylogenetic relations of higher systematic units.

In the Romaleinae studied up to now, songs cannot be used to separate species; they are too similar and are principally used in rival interactions. However, the behaviour of many species has not been studied; members of the genus *Xyleus* produce more complex, longer, and louder songs which may have a similar function to gomphocerine ordinary songs.

Visual displays are widely spread among various subfamilies; convergences as, for example, the rapid flip-back of the antennae in various subfamilies, demonstrate the dubious taxonomic value of these characters. The display of *Galidacris* could serve for species recognition, but an unambiguous demonstration of the function has to precede the application of this character in taxonomy.

Behavioural data can be very valuable for the taxonomist, but, like morphological features, can lead to misinterpretations: a systematic interpretation is only possible when the function of the respective trait is understood. Like any other morphological feature, behaviour is variable, so that series of records have to be compared. This means, for the ethologist, that he has to document his data in a museumlike fashion, with cross-reference to collected specimens. It means, for the taxonomist, that he has to consult the museums to integrate the data collected by the ethologist: tapes, films, and possibly field notes. They have to be accessible so that they can be analysed by different methods, and thus could be of great value in taxonomy.

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