

Experimental hybridization of *Sigara striata* and *S. dorsalis* (Heteroptera, Corixidae)

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Sigara striata (L.) and *S. dorsalis* (Leach) are morphologically very close. In both species mating behaviour involves exchange of acoustic signals, which enable the males to locate the females. The males produce two structurally different signals, a rubbing call and a broken call; receptive females respond more readily to the latter. The corresponding calls of the two species, though differing in many details, sound much alike.

In playback experiments between specimens of *S. striata* from Finland and *S. dorsalis* from Scotland, the species failed to discriminate between each other's calls, and interspecific matings occurred without much difficulty. In reciprocal crosses, however, only a few of the hybrid larvae survived long enough to emerge as adults. Backcrosses showed that the hybrid males were sterile or had very low fertility; the hybrid females had low fertility in backcrosses to *S. striata* males, but almost normal fertility in backcrosses to *S. dorsalis* males.

In mixed culture *S. striata* survived better than *S. dorsalis*. The progeny of this culture showed that under laboratory conditions hybridization occurred in spite of free mate selection. Thus, in areas of sympatric distribution isolation of the species must be ensured by other mechanisms besides behavioural differences.

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1. Introduction

Morphological similarity of species usually reflects their genetic closeness, but their hybridization affords even more conclusive proof. However, hybridization of species is commonly prevented by various isolating mechanisms, which may be classified as either premating or postmating (e.g. Mayr 1963). In natural conditions the premating mechanisms are usually effective enough to prevent interspecific matings and waste of gametes. In contrast, in the laboratory the conditions can often be changed in such a way that the premating mechanisms are foiled. In this way, experimental hybridization can be used for studying genetic closeness of populations, subspecies, or related species, i.e. the stage of speciation.

The corixids *Sigara striata* (L.) and *S. dorsalis* (Leach) are morphologically very much alike, — so much so that their status as distinct species

has been doubted (cf. Leston 1956). Also ecologically the two seem to favour very similar habitats, reed beds of lakes and other large and permanent waters (Macan 1954a, 1954b). In distribution *S. striata* seems to have a wide range throughout most of Europe into northern Africa in the south and into Siberia in the east, but *S. dorsalis* seems to be restricted to the British Isles and SW continental Europe, with occasional records from southern Scandinavia (Nieser 1978, Coulianos & Ossiannilsson 1976). Thus, with the exception of most of the British Isles (Lansbury & Leston 1966) the range of *S. dorsalis* seems to lie within the range of *S. striata*. However, as Nieser (1978) notes, difficulties in identification of the species may have caused errors in these records.

The present study on experimental crossbreeding of *S. striata* and *S. dorsalis* was prompted by the morphological similarity of the two, the aims of the investigation being to examine

possible differences in mating behaviour and determine firmness of reproductive isolation between the species.

2. Material and methods

Experimental animals were collected from the following localities:

S. striata: Finland, Hanko, Tvärminne Zoological Station, island of Långskär, 15.X.1973.

S. dorsalis: Scotland, Glasgow, some ponds NW of the town, 6.X.1973.

In the laboratory in Helsinki the animals were treated as described in Jansson (1978, 1979), and reciprocal crosses were arranged in January-February 1974. During March-July the fertility of hybrids was tested in back-crosses, and the original crosses were repeated. In addition, a mixed culture was arranged to test the ability of the species to maintain pure lines in each other's presence, i.e. under experimental sympatric conditions.

3. Results

A. Mating behaviour

The fore femoral stridulatory pegs of *S. striata* and *S. dorsalis* are very well developed in males, but relatively small in females. In both sexes

the pegs of *S. dorsalis* are somewhat thicker than those of *S. striata*, and in males in particular the pegs are more numerous in *S. dorsalis* (Fig. 1).

In both species the behavioural sequence of events leading to copulation involves exchange of stridulatory signals between the two sexes. In the laboratory no differences were detected in the sequences of mating behaviour of the species: males stridulated spontaneously when sexually mature and receptive females responded to the male calls by producing agreement signals, according to which the males approached the females. Occasionally a male mounted a female which did not produce the agreement signals (= unreceptive female), but such a visually induced approach usually went no further than an attempt at copulation.

Males of both species produced two kinds of signals, a rubbing sound that consisted of a simple succession of pulse-trains, and a broken call composed of pulse-train groups separated from each other by clear intervals. Both these calls were produced by movements of alternate fore leg femora over the maxillary plates (cf. Jansson 1972), and only in the broken calls was the alternation somewhat variable in that the last pulse-train of a group was often produced by movement of the same leg as the first pulse-

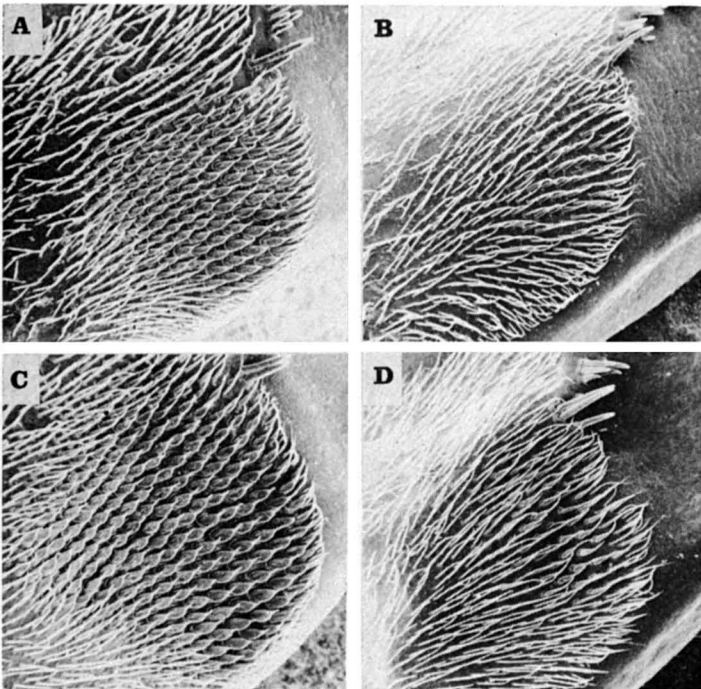


Fig. 1. Fore femoral stridulatory pegs of *S. striata* (A = ♂, B = ♀) and *S. dorsalis* (C = ♂, D = ♀) magnification $\times 130$. — Photographed in the SEM Laboratory, Faculty of Agriculture and Forestry, University of Helsinki.

train of the following group. Despite the overall similarity of the mechanism, the individual pulse-trains of the two call types were very different; in the rubbing call the pulse-trains were produced at a relatively slow rate and included some 9–13 pulses, but the louder broken calls had a much faster pulse-train rate (within the pulse-train groups) and only 2–3 pulses per pulse-train (Table 1). Thus, in the rubbing calls most of the stridulatory peg rows were used, but in the broken calls only a few of the peg rows were involved.

Males of *S. striata* usually produced the two types of call alternately, and in response to playback of various other signals they might give either call. *S. dorsalis* males, in contrast, produced the broken call much more commonly and the rubbing call was observed only occasionally. Females of both species produced the agreement signals almost exclusively in response to the male broken call. However, no further experiments were made to ascertain whether the two male calls had different functions, for instance in spacing behaviour of the males (cf. Jansson 1973).

The corresponding calls of the two species sounded in general very much alike, but audio-spectrographic analysis (Table 1, Figs. 2–4)

revealed many specific differences, the most important being as follows:

1) The male rubbing call of *S. striata* included on average some 60 pulse-trains but that of *S. dorsalis* only about 20; because of the faster pulse-train rate, however, the duration of the call in the former was only one and a half times that of the latter. In *S. striata* the consecutive pulse-trains partly overlapped in the beginning, but were well spaced in the rest of the call; in *S. dorsalis* the pulse-trains were well spaced throughout the call, except that sometimes the bugs coupled the movements of the two legs, thus also coupling the pulse-trains (Fig. 2). Individual pulse-trains of *S. striata* included fewer pulses than those of *S. dorsalis*, and the pulses of the latter were more evenly spaced. In both species, the amplitude of the sound gradually changed during the calls, but whereas the call of *S. striata* was faint in the beginning, loud in the middle, and again faint towards the end, the call of *S. dorsalis* ended abruptly at the height of the loud part. Further, *S. striata* males produced the rubbing call frequently, and independently of the broken call, but *S. dorsalis* males produced the rubbing call only occasionally and then it was usually either preceded or followed immediately by a broken call (Fig. 2).

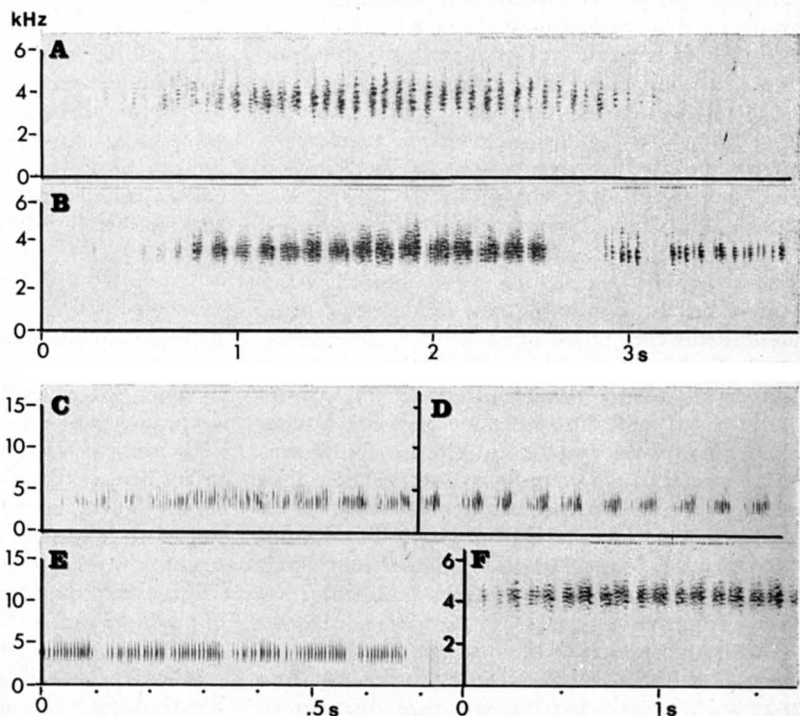


Fig. 2. Male rubbing calls. A = *S. striata*; B = *S. dorsalis* (a rubbing call immediately followed by a broken call); C–D = details of *S. striata* call above, from the beginning (pulse-trains overlapping) and from the middle (pulse-trains well-spaced); E = details of *S. dorsalis* call (the last 6 pulse-trains of B above); F = part of *S. dorsalis* call with coupled pulse-trains.

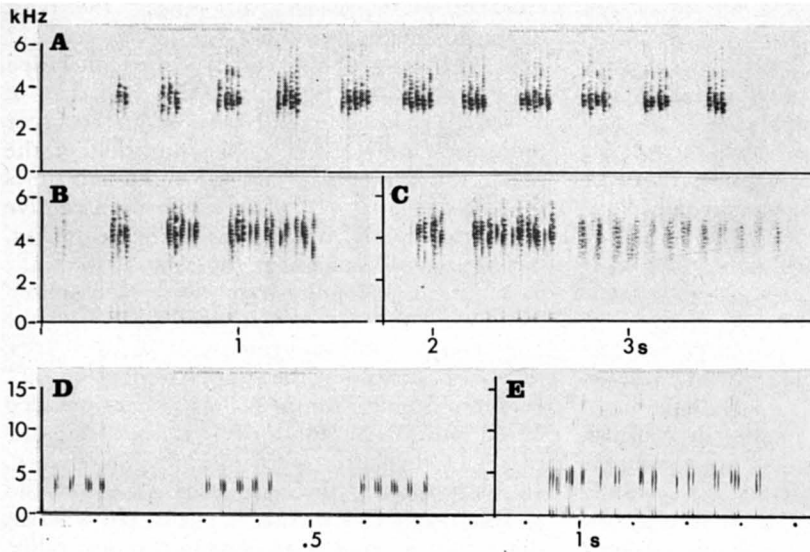


Fig. 3. Male broken calls. A = *S. striata*; B = *S. dorsalis*; C = *S. dorsalis*, a broken call followed by a short series of rubbing pulse-trains; D-E = details of *S. striata* and *S. dorsalis* calls, from A and B above.

2) The male broken call of *S. striata* was a sequence of about a dozen very regularly spaced pulse-train groups with 2–6 pulse trains per group (smallest number of pulse-trains in the first 1–2 groups and somewhat reduced number in the last group). In *S. dorsalis* the broken call included only 2–4 irregularly spaced pulse-train groups, sometimes followed by a few rubbing pulse-trains (Fig. 3), and while the average number of pulse-trains per group was about 5–6, their distribution was very uneven: the first groups usually included about 4 pulse-trains and the last one nearly 10. In duration the broken call of *S. dorsalis* was only about a quarter of the *S. striata* call.

3) The female agreement signal of *S. striata* was a regular sequence of evenly spaced pulse-trains. In the beginning the female call of *S. dorsalis* was very much like that of *S. striata* (Fig. 4), but after some 20–30 regularly produced pulse-trains there was another set of 20–30 pulse-trains with intermittent pauses (but as the pauses were very irregular the signal was still considered to be composed of a single pulse-train group). Because of its somewhat faster pulse-train rate the call of *S. striata* lasted only about half as long as that of *S. dorsalis*, although the number of pulse-trains per call was only one-third less.

In addition, in all signals the frequency of the sound of *S. striata* was somewhat lower than that of *S. dorsalis*, but this was probably due to

the slightly smaller size of the *S. dorsalis* specimens (cf. Jansson 1976).

Despite the specific differences in the calls, playback experiments showed that the species were unable to discriminate between each other's signals, and readily responded crosswise. Further, placing of receptive *S. dorsalis* females with *S. striata* males and vice versa immediately resulted in interspecific pairings. Only in the beginning of genital contact did there seem to be slight difficulties, the females making some attempts to resist the males by pushing and kicking with the hind legs. However, in most cases the females calmed down in a second or two, and allowed the males to complete copulation.

B. Experimental crosses

When interspecific matings were observed to occur without much difficulty, the pieces of rock and water-logged wood supplied for egg-laying were transferred daily to other vessels in the hope that larvae would develop. Simultaneously, pure cultures of both species were set up as controls.

In the beginning progenies of the control cultures as well as those of the reciprocal crosses proceeded well. However, while the control cultures produced some 30–40 new adults in less than two months, in the hybrid cultures the

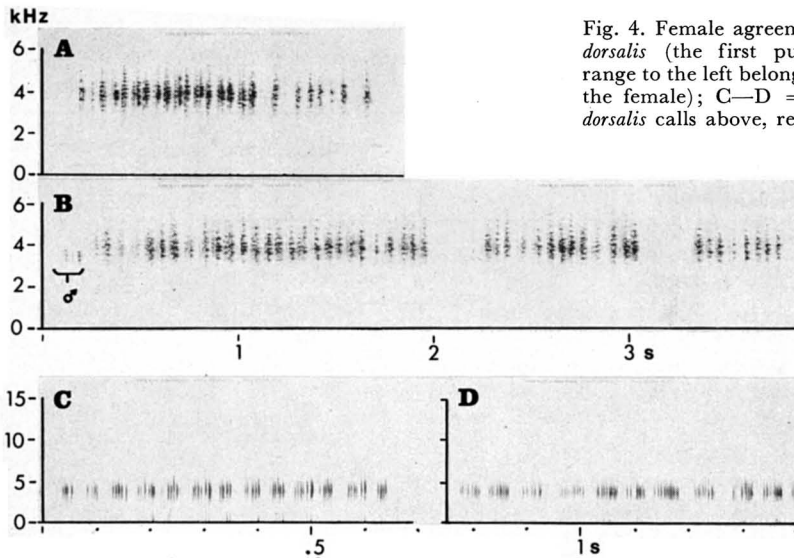


Fig. 4. Female agreement calls. A = *S. striata*; B = *S. dorsalis* (the first pulse-trains with lower frequency range to the left belong to the male call used to stimulate the female); C—D = details of the *S. striata* and *S. dorsalis* calls above, respectively.

numbers of larvae decreased gradually during development and the final scores were meagre (Table 2). In the combination of *dorsalis* ♂♂ × *striata* ♀♀, coinciding with the control cultures, altogether 14 specimens emerged as adults; however, three of these died within a day or two, and the final result was only 5♂♂ and 6♀♀. In the reverse combination, *striata* ♂♂ × *dorsalis* ♀♀, only six larvae reached the fifth instar, and at this stage their development seemed to stop: in cultures kept in controlled temperature cabinets at 20°C development of each larval instar takes on average about 1 week, but in this particular case the larvae remained at the fifth instar for nearly 3 weeks. Three of the larvae died during this period, and the final result was only three males (Table 2).

In repetition of the crosses the results were very meagre in both combinations (Table 2). Development of the fifth instar larvae of *striata* ♂♂ × *dorsalis* ♀♀ was again delayed, but hybrids of the reverse combination developed at the normal rate.

In the tests of hybrid fertility the *striata* × *dorsalis* males were kept alternately for periods of one week with females of both parental species, as only three hybrids were available; in this way they could be tested with both parental species. Matings were observed in both vessels, and the females laid eggs normally, but the eggs did not hatch. A similar result was obtained when the only hybrid male from the repetition of the

original test was backcrossed to *S. striata* females (Table 2).

Of the 5 hybrid males from the cross *dorsalis* × *striata*, three were placed with *S. striata* females and two with *S. dorsalis* females. In both these vessels the females laid eggs abundantly, and good numbers of first instar larvae appeared in the vessels to which the eggs were transferred. As in the original crosses, however, the numbers of larvae gradually decreased, and the final scores remained very meagre (Table 2). The only hybrid male obtained in the repetition of the original cross was not tested for further backcrosses.

In the *dorsalis* × *striata* hybrid females a clear difference appeared in the two combinations: in backcross to *S. dorsalis* males the hybrids produced nearly as many progeny as the control cultures, but in backcross to *S. striata* males the score was only three adults (Table 2). The two females obtained in repetition of the original cross were not tested for further backcrosses.

In the first attempt to cross *S. striata* males with *S. dorsalis* females, no females were obtained, but the repeated cross gave one female hybrid. This specimen was given a chance to mate with males of both parental species; it was placed in a vessel with five males of each species. In all other experiments the females began to lay eggs in less than 2 weeks, but in this particular case nearly 2 months elapsed before the female began to lay eggs. However,

Table 1. Numerical data on signals of *S. striata*, *S. dorsalis*, and some of the hybrid individuals. For most characteristics $\bar{x} \pm SD$ were calculated, but because signal duration and pulse-train rate are greatly affected by temperature, only approximate values for these characteristics were measured at 19–20°C.

Species	Type of signal	Signals analysed/ specimens in recordings	Dominant frequency area (kHz)	Pulse-train groups per signal	Pulse-trains per group	Pulses per pulse-train	Signal duration (sec at 19–20°C)	Pulse-train rate at 19–20°C
<i>S. striata</i>	♂ rubbing	50/5	2.5–4.0	1	60.08 ± 19.50	9.09 ± 1.99	3.8	15
<i>striata</i> ♂ × <i>dorsalis</i> ♀	»	3/1	3.5–5.0	1	52.33 ± 11.15	8.96 ± 1.79	3.0	17
<i>dorsalis</i> ♂ × <i>striata</i> ♀	»	6/2	4.0–5.5	1	34.00 ± 9.80	12.75 ± 2.81	3.0	12
<i>S. dorsalis</i>	»	34/5	4.0–5.0	1	23.09 ± 6.66	13.40 ± 3.08	2.5	10
<i>S. striata</i>	♂ broken	50/5	2.5–4.0	12.86 ± 2.33	4.02 ± 0.91	2.85 ± 1.10	3.5	32
<i>striata</i> ♂ × <i>dorsalis</i> ♀	»	30/3	2.7–4.5	8.60 ± 1.43	3.24 ± 0.90	2.38 ± 0.76	1.8	36
<i>dorsalis</i> ♂ × <i>striata</i> ♀	»	30/3	3.5–5.5	7.57 ± 0.90	3.98 ± 1.10	2.92 ± 0.85	1.8	36
<i>S. dorsalis</i>	»	50/5	3.5–5.0	3.32 ± 0.91	5.73 ± 3.79 ¹	2.48 ± 1.12	0.8	36
<i>S. striata</i>	♀ agreement	50/5	2.5–4.0	1	27.02 ± 7.85	5.50 ± 1.15	1.4	20
<i>dorsalis</i> ♂ × <i>striata</i> ♀	»	50/5	3.0–5.0	1	25.45 ± 7.57	8.43 ± 1.84	1.5	16
<i>S. dorsalis</i>	»	50/5	3.0–4.5	1 ²	44.74 ± 13.10	9.66 ± 1.66	3.0	16

¹ last group 9.26 ± 4.97, other groups only 4.22 ± 1.53.

² with numerous irregularities; see text and Fig. 4.

the final result was surprisingly good, — altogether 23 adult specimens as offspring. Although the paternity of the offspring is not certain, the males in this progeny were morphologically almost identical with *S. dorsalis*, which suggests that the hybrid female was successfully mated by *S. dorsalis* males (see below).

C. Hybrid characters

Females of *S. striata* and *S. dorsalis* are indistinguishable. In males the clearest distinguishing characters are the shapes of the parameres (Macan 1954a, 1956, Leston 1956) but, as Lansbury & Leston (1966) pointed out, sometimes even the males cannot be identified reliably. In the Finnish males of *S. striata* and Scottish males of *S. dorsalis* the parameres have distinct shapes, and a further difference was noticed in the median lobe of the 7th abdominal tergite: at the edge of the lobe *S. striata* males had a prominent tuft of hairs, but *S. dorsalis* males had at most a few short hairs (Fig. 5). In all these characters the hybrid males were clearly intermediate, but progenies of reciprocal crosses tended to show a closer resemblance to the parental female species (Fig. 5). In backcrosses the characters shifted towards the species used as the pure-line parent, even to the degree

that the backcross progenies could not be reliably distinguished from the pure lines.

An abnormal character appeared in only one of the hybrids, a female from the cross *dorsalis* × *striata*. This specimen had a completely yellow pronotum without any brown pigment. Other-

Table 2. Results of experimental crosses between *S. striata* and *S. dorsalis*. Symbols for genotypes: s = *striata*, d = *dorsalis*; in combinations the first letter refers to the parental male, the second to the female. Other explanations: e = eggs laid but no larvae observed, — = not tested further; numbers in parentheses indicate repetition of the tests.

Original crosses	Hybrids obtained (♂♂/♀♀)	Backcross combinations ♂♂ × ♀♀	Results of backcrosses (♂♂/♀♀)
♂♂ × ♀♀			
5ss × 5dd (1)	3/0	3sd { × 5ss × 5dd	e e
5ss × 5dd (2)	1/1	1sd × 5ss	e
		5ss } × 1sd 5dd }	11/12
5dd × 5ss (1)	5/6	3ds × 5ss	1/2
		2ds × 5dd	2/2
		5ss × 3ds	2/1
		5dd × 3ds	10/16
5dd × 5ss (2)	1/2	—	
Control cultures:			
5ss × 5ss	16/22		
5dd × 5dd	18/15		

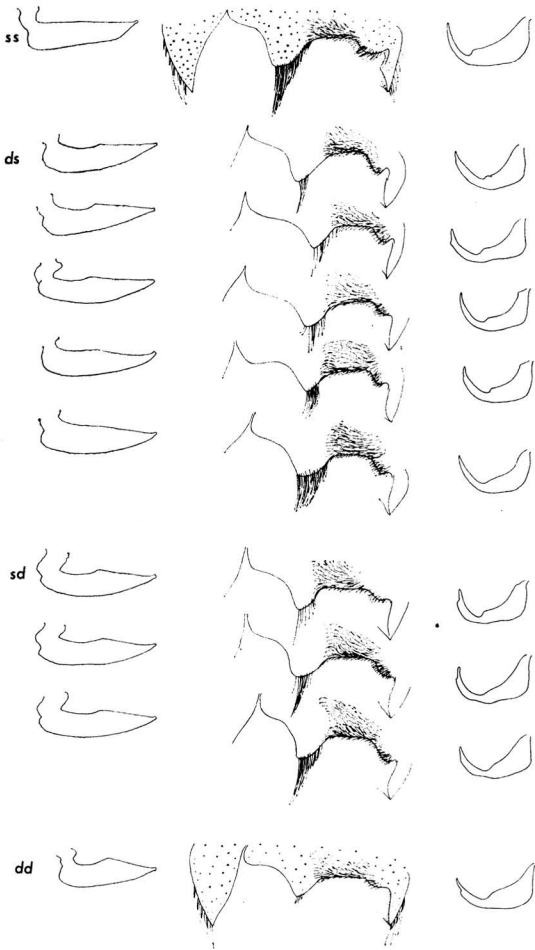


Fig. 5. From left to right: left paramere, median lobe of 7th abdominal tergite, and right paramere in males of *S. striata*, *S. dorsalis*, and the hybrids. In genotypes the first letter refers to the parental male, the second to the female.

wise this female seemed to be normal, and was used in one of the backcross experiments where she lived until the termination of the culture.

Like the morphological characters, the stridulatory signals of hybrid males were intermediate, but the two lines of the reciprocal crosses were somewhat different from each other. As already mentioned, *S. dorsalis* males produced the rubbing call much less frequently than the broken call. The same tendency was also evident in both hybrid lines; only one of the *striata* × *dorsalis* hybrids and two of the *dorsalis* × *striata* hybrids produced a few rubbing signals during the recordings (Table 1). In general, the rubbing calls of the *striata* × *dorsalis* individual seemed to be closer to the *S. striata* call, but on all three occasions when the individual produced a rubbing call it was immediately followed by a broken call (Fig. 6). The rubbing calls of the *dorsalis* × *striata* individuals, in contrast, were structurally closer to the *S. dorsalis* call, but the signals were produced independently of the broken calls. However, the number of rubbing calls obtained from the hybrids was altogether far too small for the results to be considered reliable.

The broken call was obtained from the hybrid males without difficulty. In all hybrids it resembled the call of *S. striata* in being composed of regularly repeated pulse-train groups with 2–5 pulse-trains per group (Fig. 6). However, the number of pulse-train groups per signal was always clearly less than in the *S. striata* call (Table 1), and at 20°C the pulse-train groups were produced at a somewhat faster rate in the hybrids.

In the only hybrid female obtained from the cross of *striata* × *dorsalis* sexual maturity was

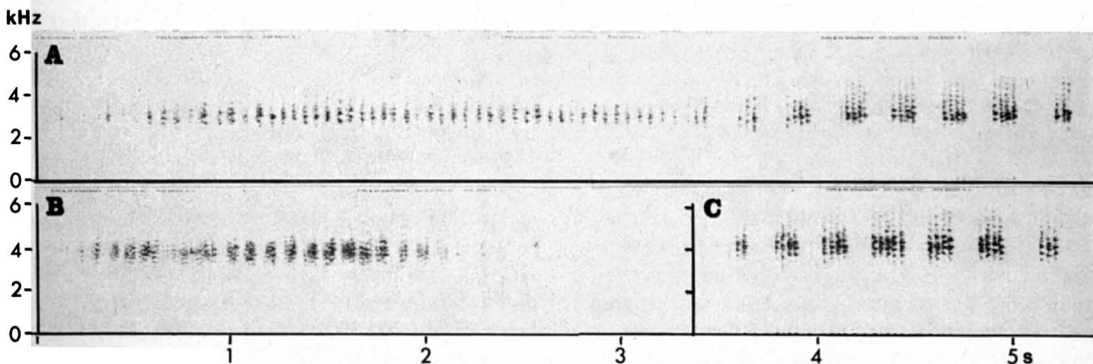


Fig. 6. Male calls of hybrids between *S. striata* and *S. dorsalis*. A = *striata* ♂ × *dorsalis* ♀, a rubbing call immediately followed by a broken call; B–C: *dorsalis* ♂ × *striata* ♀, separate rubbing and broken calls.

greatly delayed (see above), and no signals were obtained. Thus, female signals of hybrids could be studied only from the *dorsalis* × *striata* specimens. On the whole, these signals were closer to the *S. striata* female signal, having a generally regular structure, a small number of pulse-trains, and a relatively short duration; however, they closely resembled the *S. dorsalis* signal in pulse-train rate and number of pulses per pulse-train (Table 1).

D. Mixed culture

In a test for the ability of *S. striata* and *S. dorsalis* to breed in pure lines under artificial sympatric conditions a culture was set up with five males and five females of each species, thus, as compared with the other cultures, having double the density of adult specimens. At first this culture proceeded normally and the females began to lay eggs in about 2 weeks. However, during the next 2 weeks nearly all the *S. dorsalis* specimens died, and only two males and one female survived for the 6 weeks that the adult culture was kept going. Of the *S. striata* specimens only one male and two females died before the culture was terminated.

In the vessel in which the progeny of the mixed culture was reared, larval development proceeded well, and the final result was altogether 36 adults. According to morphological evidence the 19 males in the progeny could be identified as follows: 12 *S. striata*, 3 *S. dorsalis*, and 4 hybrids. The hybrids probably originated from a cross of *striata* ♂ × *dorsalis* ♀, because they were morphologically slightly closer to *S. dorsalis*.

4. Discussion

In mating behaviour of both *S. striata* and *S. dorsalis*, as in several other species of Corixidae, exchange of stridulatory signals was found to be an essential part of the sequence of events leading to copulation (cf. Jansson 1973, 1976). Of the two structurally different male calls the broken call was the one to which receptive females readily responded, but the rubbing call did not seem to be associated with mating behaviour. Thus, in contrast to some corixids in which structurally different male signals are used for calling and for courtship (Jansson 1976,

1979), in *S. striata* and *S. dorsalis* the broken call seems to serve both these functions. The rubbing call may have a role in territorial and rivalry behaviour of the males (cf. Leston & Pringle 1963, Jansson 1973), but this aspect was not studied in the present work.

Previously, females of *S. striata* have been claimed to respond to conspecific male calls by increased swimming, after which the males would find the females by visual cues (Schaller 1951, Finke 1968). In the light of present results, especially those on the stridulation of receptive females, it appears that both Schaller and Finke evidently had only unreceptive females. In *S. striata* and *S. dorsalis*, as in many other species of Corixidae, the response of unreceptive females, when in close proximity to stridulating males, is to swim away; however, in laboratory cultures the females are unable to get away, and the males easily find the females and make attempts at mounting, although these attempts seldom lead to actual mating (cf. Jansson 1973, 1979). Also, the faint sounds produced by rubbing of the hind legs against the abdomen, which, when produced by *S. striata* females, were suggested possibly to be the female response to male calls (Finke 1968), are clearly not true stridulation but only by-products of cleaning activity or the like (Jansson 1972, 1973).

Finke (1968) published both oscillograms and sonograms of parts of male signals of *S. striata*. In the sonograms the dominant frequency area was 3–5 kHz, as my recordings confirmed, but in addition Finke obtained harmonics at 6–10 and 9–15 kHz. By overloading the input voltage of the sonograph I could also create these harmonics. However, when working on sounds of *Cenocorixa* (Jansson 1973) I made tests for the existence of harmonics by rerecording signals with similar frequency patterns through a 2–4 kHz filter and analysing the rerecorded signals: there were no sounds above 5 kHz, and the harmonics were thus artefacts created by overloading the analyser.

Haskell (1961) published oscillograms of signals of *S. dorsalis*: a male call and a call of unknown origin. Structurally the former corresponds to the male broken calls that I recorded, and the latter to the male rubbing calls. Evidently in Haskell's cultures, as in my recordings, the males produced the rubbing call only occasionally, and thus the origin of the latter signal remained obscure.

von Mitis (1936), Haskell (1961), and Finke

(1968) all held the opinion that the males produce the rubbing calls by moving the fore leg femora alternately over the sharp edges of the head whereas during the broken calls the movements are simultaneous. At temperatures of about 20°C the leg movements during the broken call are too fast for the human eye to follow and seem to be simultaneous, but at 10°C or below the movements are easily seen to be alternate. Thus, despite the great difference between the pulse-trains of the rubbing and broken calls the mechanism is basically the same.

Experimental crosses between *S. striata* and *S. dorsalis* gave results very similar to those obtained in crosses between *Arctocoris carinata* (C. Sahlberg) and *A. germari* (Fieber) (Jansson 1979). The numbers of hybrids obtained were small, in backcrosses the hybrid males appeared to be sterile or have very low fertility, and the hybrid females had low fertility in backcrosses to one of the parental species, but nearly normal fertility in backcrosses to the other. Further, both in morphological characters and acoustical signals the hybrids were intermediate. However, while in the *Arctocoris* hybrids the closer resemblance to the parental female species was clearer in the acoustic signals (Jansson 1979), in the *Sigara* hybrids it appeared more clearly in the morphological characters.

Earlier playback experiments have shown that corixids in general recognize signals of the conspecific opposite sex (Jansson 1973, 1976) and, for instance, males of *A. germari* had to be tricked by playback of conspecific female signals before they mated with females of *A. carinata*

(Jansson 1979). In contrast, *S. striata* and *S. dorsalis* failed totally to discriminate between each other's signals, and slight difficulties at the time of genital contact were the only hindrance to crossing. This is rather surprising, as the species have been reported to be sympatric over wide areas (e.g. Nieser 1978), and they also seem to favour ecologically similar habitats (Macan 1954a, 1954b). However, the test animals for the present work were collected from areas of allopatric distribution, *S. striata* from Finland and *S. dorsalis* from Scotland, and in areas of sympatric distribution the behavioural and/or other isolating mechanisms may be stricter. The existence of other mechanisms besides behavioural isolation is further indicated by the failure of the species to breed in pure lines in the mixed culture, and the superiority of *S. striata* in that particular experiment. On the other hand, Lansbury & Leston (1966) reported that some specimens from SE England are very difficult to identify. It is not impossible that such difficult specimens are natural hybrids, for SE England is a marginal area for *S. striata*, and interspecific matings may occur because of a lowered response threshold when, in low population densities, the conspecific opposite sex is not found.

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