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Geographic variation in the stridulatory signals of Arctocorisa carinata (C. Sahlberg) (Heteroptera, Corixidae)

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Audiospectrographic analysis of male stridulatory signals of *A. carinata* from geographically more or less isolated populations in Iceland, the British Isles, northern Finland, central Sweden, the east and west coasts of Sweden, the south coast of Finland, and the Swiss Alps revealed a certain degree of population specificity. The differences lay mainly in the proportion and consistency of the loud pulse-trains; the loudest signals appeared in the populations living near the extreme limits of survival of the species, and apparently reflect adaptation to low population densities at the breeding season. Combinations of the signal characteristics grouped the populations into both ecological and geographical sets, thus indicating both environmental adaptation and kinship.

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1. Introduction

In Europe *Arctorisa carinata* (C. Sahlberg) occurs in several geographically isolated populations. Experimental crosses between some of these populations have indicated that, in general, the greater the distance between the populations, the lower the viability of the progeny, and in certain combinations the crosses were totally unsuccessful (Jansson 1978a). Yet, although individuals from different populations show no obvious morphological differences (Jansson 1978 b), morphometric analysis enabled most individuals to be placed in the correct population (Jansson & Pajunen 1978). Morphometry, when applied to general body measurements, arranged the populations in an ecological grouping, thus indicating environmental adaptation. But when applied to the male genital characteristics, morphometry gave a somewhat different grouping, reflecting the probable kinship of the populations.

The present paper concerns the stridulatory signals of *A. carinata*, their geographic variation and its adaptive significance. Both males and females of the species are able to stridulate (Jansson 1979), but as the female signals are very faint, only male signals are considered here.

2. Material and methods

Individuals of *A. carinata* were collected from Iceland, the British Isles, northern Finland, central Sweden, the Swedish east and west coasts, the Finnish south coast and the Swiss Alps. The exact collecting localities and dates were as described in Jansson (1978a). Live animals were transported to the laboratory in Helsinki, but because they were collected during several autumns, when they were not sexually mature and so would not stridulate (Jansson 1974a), they were placed in constant temperature cabinets at 5°C and a photoperiod of 8 h light and 16 h dark for overwintering. After 2—3 months the individuals were transferred to a temperature of 20°C and the photoperiod was reversed. With this treatment the males began to stridulate in a few hours, but recordings were not made until about a week later. Feeding and general treatment of the cultures were as described in Jansson (1978a).

From each population, 10 males were taken at random for individual recordings, and the first 10 signals from each individual were analysed. The recordings were made in a round plastic basin (diameter 50 cm) half filled with sand sloping from the edges and forming a depression in the middle. The depression was filled with water to a depth of about 10 cm in the middle (Jansson 1973).

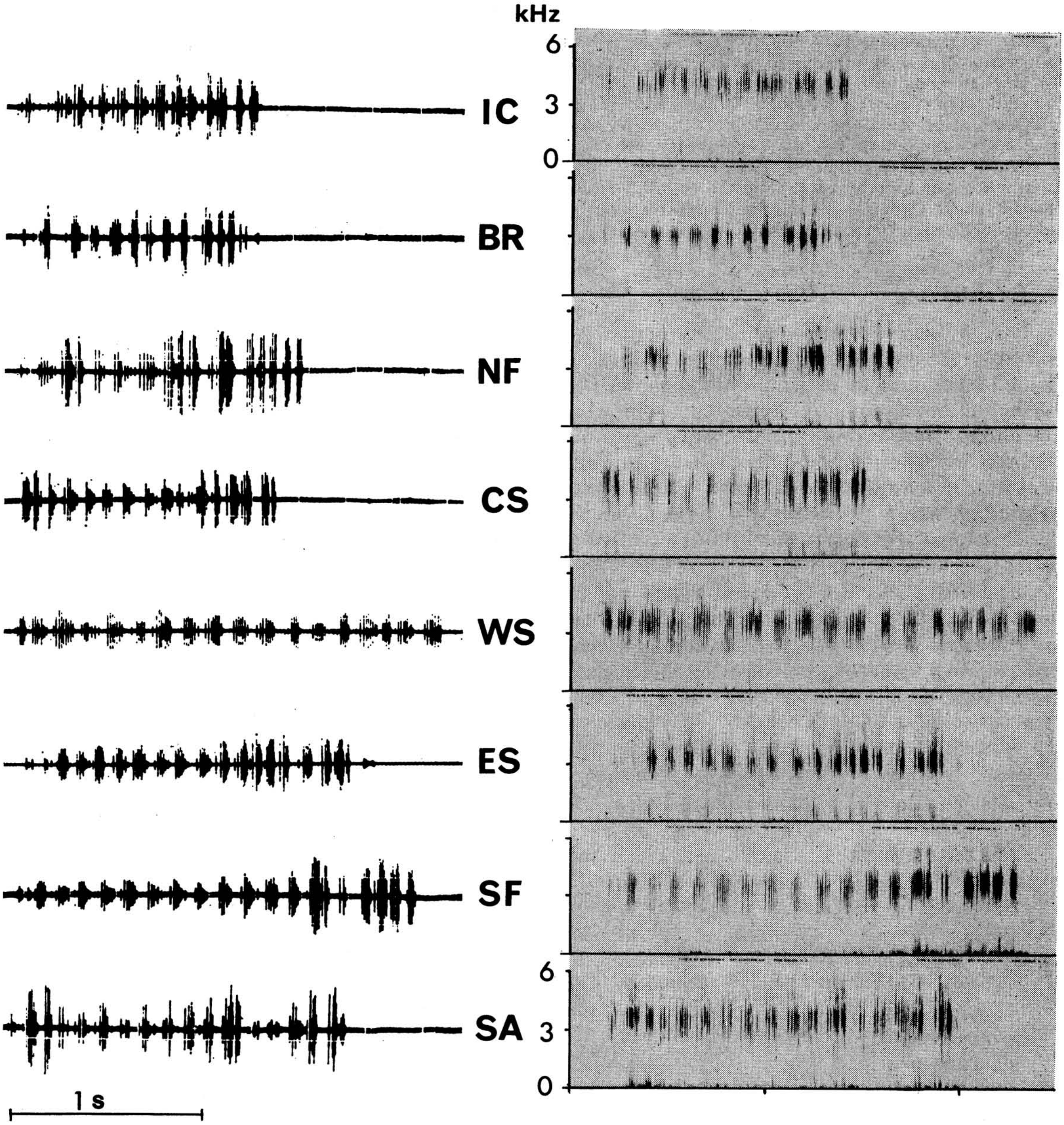

Fig. 1. Oscillograms (left) and sonagrams for typical signals of *A. carinata* from the various populations. Symbols for populations: IC = Icelandic, BR = British, NF = northern Finnish, CS = central Swedish, WS = western Swedish, ES = eastern Swedish, SF = southern Finnish, and SA = Swiss.

The recordings were made on a hydrophone type LC-10 (Celesco Ind., Costa Mesa, California) connected via an impedance matching device (Oy Yleiselektroniikka Ab, Helsinki, Finland) to a Uher 4000 Report-L tape recorder. The hydrophone was placed horizontally on the bottom of the basin, and a cage (diameter 5 cm) made of fibreglass screen was used to keep the bugs within a convenient recording distance. To avoid effects of changing temperature (Jansson 1974c), the recordings were all made at 20 ± 0.5 °C. The signals were analysed on a sonagraph type 675 Missilyzer (Kay Electric Co., Pine Brook, New Jersey).

Sexually active males of *A. carinata* produce acoustic signals both spontaneously and in response to visual or acoustic stimuli of other individuals (Jansson 1979). In all these situations the signals are structually alike, as with many corixids (Jansson 1973, 1976). Thus, playback of previously recorded signals could be used to stimulate the individuals. Playback was done through a small loudspeaker protected from wetting by a thin plastic bag and submerged outside the recording cage. The playback signals were simultaneously recorded to adjust loudness to levels as natural as possible.

3. Results

The *A. carinata* male signal is somewhat variable. Its dominant frequency area is about 3—4.5 kHz, and at its simplest the signal is a series of monotonously repeated, somewhat irregular pulse-trains (for terminology, see Jansson 1973), on average about 16 in number, and at temperatures of about 20 °C the whole signal lasts about 1.6 seconds. Variations on this basic pattern are due to some of the pulse-trains being produced faster and louder. These "fast" pulse-trains may be produced quite inconsistently at any time during the signal, but mostly there are 1—3 of them at the beginning, then several "slow" pulse-trains in the middle, and a series of fast pulse-trains at the end.

In comparing the populations the following signal characteristics were measured: Total number of pulse-trains per signal, numbers of slow and fast pulse-trains, duration of signals, average pulse-train rate, numbers of pulses in slow and fast pulse-trains, and rates of producing the pulses in slow and fast pulse-trains. Although the signals did not differ greatly from each other (Fig. 1), analysis of variance applied to the mean values calculated from the signals of each individual showed that the differences between populations were significant for each characteristic measured (Table 1).

In general, the stridulatory signals of male Corixids are species-specific, and this specificity depends chiefly on the temporal pattern of the pulse-trains, which is a combination of several characteristics. In signals that include both slow and fast pulse-trains, the particular temporal pattern mainly depends on the rates and groupings of the pulse-trains, the proportions of the different types of pulse-trains, the total number of pulse-trains, and the signal duration. Calculation of the relative deviations of the population means from the overall mean values of the characteristics measured from the *A.*

Table 1. Numerical data on male stridulatory signals in the various *A. carinata* populations ($\bar{x}$ above, SD below). All recordings at 20 ± 0.5 °C. Symbols for populations: IC = Icelandic, BR = British, NF = northern Finnish, CS = central Swedish, WS = western Swedish, ES = eastern Swedish, SF = southern Finnish, and SA = Swiss Alpine.

Characteristic	Populations									
	IC	BR	NF	CS	WS	ES	SF	SA	Overall mean	Anova F
Total number of pulse-trains/signal	11.78	13.73	16.63	16.39	18.23	19.49	18.61	16.33	16.40	12.33***
	2.82	2.81	2.18	2.14	3.21	3.54	3.77	4.14		
Number of slow pulse-trains/signal	10.41	9.69	9.12	10.80	16.01	12.43	12.69	12.21	11.67	8.90***
	1.27	1.60	1.31	1.38	3.06	3.04	3.40	2.27		
Number of fast pulse-trains/signal	1.17	4.00	7.31	5.53	2.10	6.99	5.81	4.07	4.62	36.28***
	0.78	1.17	0.88	1.31	1.00	1.48	1.02	1.41		
Signal duration (seconds)	1.20	1.20	1.58	1.54	1.94	1.90	1.96	1.71	1.63	11.32***
	0.20	0.20	0.17	0.13	0.31	0.25	0.53	0.32		
Pulse-train rate (pulse-trains/second)	9.92	11.57	10.63	10.81	9.45	10.30	9.79	9.64	10.26	6.54***
	0.66	1.08	0.91	1.04	0.84	0.61	0.99	0.78		
Number of pulses/slow pulse-train	5.38	5.32	6.33	6.09	7.35	7.26	6.87	6.05	6.33	11.76***
	1.37	1.60	1.47	1.42	1.78	1.49	1.73	1.55		
Number of pulses/fast pulse-train	6.44	6.10	6.38	6.43	8.09	7.68	6.96	6.36	6.81	13.07***
	1.26	1.19	1.32	1.24	1.59	1.50	1.55	1.46		
Slow pulse rate (pulses/second)	89.31	100.42	100.13	94.79	105.32	115.14	108.21	92.20	100.71	6.70***
	9.76	7.21	14.14	10.68	9.96	7.36	14.14	8.95		
Fast pulse rate (pulses/second)	135.91	162.03	150.34	147.46	150.05	155.39	151.35	146.30	149.91	3.55**
	18.18	8.95	12.26	8.08	13.42	6.93	15.89	12.70		

Table 2. Relative deviations (%) of population means from overall mean values in the various characteristics of *A. carinata* male signals. Symbols for populations as in Table 1.

Characteristic	Overall mean deviation	Populations IC	BR	NF	CS	WS	ES	SF	SA
Fast pulse-trains/signal	38.8	−74.7	−13.4	58.2	19.7	−54.5	51.3	25.8	−12.8
Signal duration	15.3	−26.4	−26.4	− 3.1	− 5.5	19.0	16.6	20.2	4.9
Slow pulse-trains/signal	14.4	−10.0	−16.7	−20.9	−10.1	37.2	6.6	8.9	5.0
Pulse-trains/signal (total)	11.2	−28.2	−16.3	1.4	− 0.1	11.2	18.8	13.5	− 0.4
Pulses/slow pulse-train	9.8	−15.0	−16.0	0.0	− 3.8	16.1	14.7	8.5	− 4.4
Pulses/fast pulse-train	8.5	− 5.4	−10.4	− 6.3	− 5.6	18.6	12.8	2.2	− 6.6
Slow pulses/second	6.6	−11.3	− 0.3	− 0.6	− 5.9	4.6	14.3	7.5	− 8.5
Pulse-trains/second	5.4	− 3.3	12.8	3.6	4.4	− 7.9	0.4	− 4.6	− 6.0
Fast pulses/second	3.3	− 9.3	8.1	0.3	− 1.6	0.1	3.7	1.0	− 2.4

carinata male signals revealed that the most deviating features were the numbers of fast and slow pulse-trains, the total number of pulse-trains, and the signal duration (Table 2), i.e. the same characteristics that contribute greatly to the specificity of the signals of corixids in general. When the numbers of slow and fast pulse-trains are expressed as proportions of these pulse-trains, the populations can be arranged in the following order:

	slow	:	fast
Icelandic	90	:	10
western Swedish	88	:	12
Swiss	75	:	25
British	71	:	29
southern Finnish	68	:	32
central Swedish	66	:	34
eastern Swedish	65	:	35
northern Finnish	56	:	44

These proportions, when combined with the total number of pulse-trains and the signal duration, led to a clear grouping of the populations (Fig. 2). The Icelandic population appeared at one extreme, with a very short signal and a small proportion of fast pulse-trains. The British population also had a short signal, but it differed clearly from the Icelandic population in the number of pulse-trains (i.e. the pulse-train rate was faster) and in the proportion of fast pulse-trains. The rock pool populations of southern Finland and eastern and western Sweden formed the group with the longest signals. However, the western Swedish population differed clearly from the other two in having a very low proportion of fast pulse-trains. The northern Finnish and central Swedish populations had a high proportion of fast pulse-trains, and the signal duration was near the overall average value; from these, the Swiss population differed mainly in having a slightly longer signal duration.

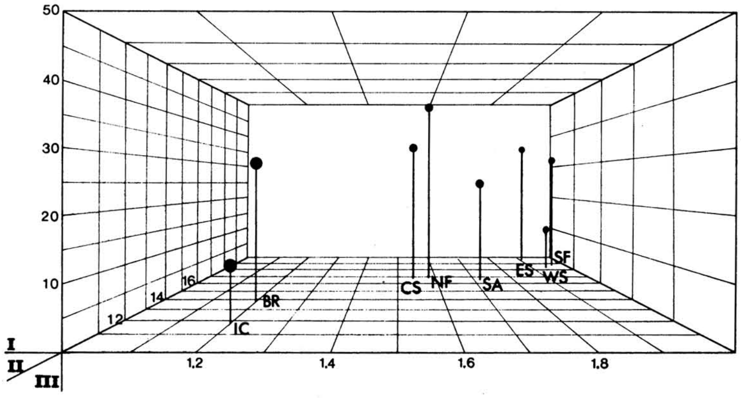

Fig. 2. The relations between signal duration (axis I), total number of pulse-trains per signal (II), and proportion of slow and fast pulse-trains per signal (III) in *A. carinata* male signals in the populations studied. Symbols for populations as in Fig. 1.

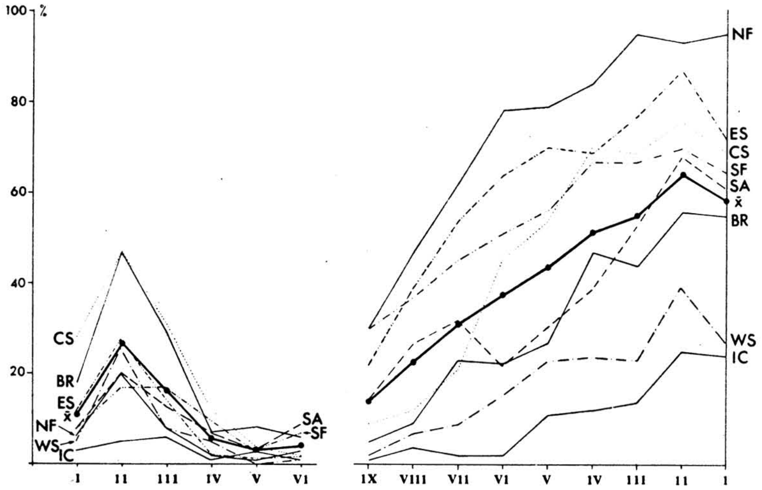

Fig. 3. Proportions of fast pulse-trains in the first six and the last nine pulse-trains of male signals of *A. carinata*. Symbols for populations as in Fig. 1.

Because the arrangement of the fast pulse-trains in the signals of *A. carinata* males is rather variable, the consistency of delivering these pulse-trains also affects the pattern of the signals. In Fig. 3, the proportions of fast pulse-trains at the beginning and end of the signals are expressed independently of the total number of the pulse-trains. In the beginning of the signals, although the frequency of producing the fast pulse-trains was clearly lowest in the Icelandic and somewhat higher than average in the British and central Swedish populations, the differences were in general very small. At the end of the signals, in contrast, the differences were very clear. The overall average number of fast pulse-trains increased steadily from the 9th pulse-train from the end to the next to last pulse-train, and fell slightly for the last pulse-train. The Icelandic and western Swedish populations had by far the lowest proportions of fast pulse-trains throughout the signals, and the British population was also somewhat below the average. The Swiss population followed the average curve almost exactly, deviating only for the 6th—4th pulse-trains from the end, for which it was lower than average. The eastern Swedish and southern Finnish populations had high proportions of fast pulse-trains throughout the last part of the signals, but by far the highest proportion appeared in the signals of the northern Finnish population. The central Swedish population had a general signal pattern very similar to that of the northern Finnish population, but at a somewhat lower level of fast pulse-trains throughout.

In the signals of various Corixids the fast pulse-trains, besides being louder than the slow ones, are usually produced at a faster rate as well (Jansson 1973, 1976). This also applies to *A. carinata* male signals in general. However, many of the signals recorded from the Icelandic and western Swedish individuals did not include any fast pulse-trains, and in the other populations the fast pulse-trains were often produced very irregularly. Thus, only the average pulse-train rates were calculated for each population, but the differences were relatively small (Tables 1 and 2).

While in most species of Corixidae the pulse-trains are usually well spaced, in *A. carinata* the spacing seems to vary from one population to another. In the signals of the British, and in particular the Icelandic individuals, the pulse-trains almost overlapped, but in the signals of the western Swedish individuals they were widely and regularly spaced (Fig. 1). In the other populations the slow pulse-trains were usually distinctly spaced, but the spacing of the fast pulse-trains was rather variable.

For detailed characteristics within the actual pulse-trains the deviations from the overall average values were relatively small (Table 2). When plotted against each other, the numbers of pulses per slow and per fast pulse-trains grouped the populations as follows: The Icelandic and British populations were close to each other, with small numbers of pulses; the Swiss, central Swedish, and northern Finnish populations formed a closely set arcto-alpine group near the overall mean values, and in

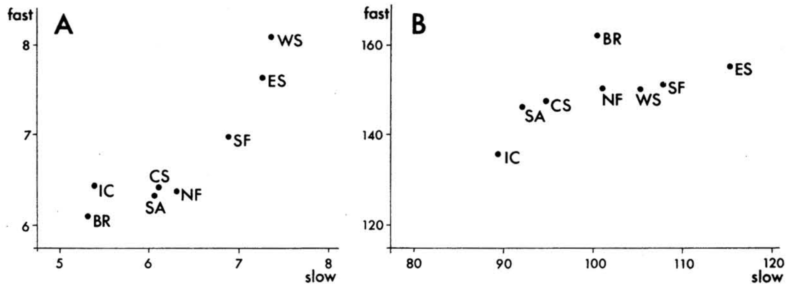

Fig. 4. Numbers per slow and per fast pulse-train (A) and rates of producing the slow and fast pulses within the pulse-trains (B) in the male signals of *A. carinata*. Symbols for populations as in Fig. 1.

the rock pool populations the numbers of pulses increased from east to west (Fig. 4A). In the rates of producing the pulses within the pulse-trains there were also some geographic patterns whereby the rock pool populations formed a group with the highest rates of slow pulses, and in the arcto-alpine group the rates decreased from north to south (Fig. 4B). The Icelandic and British populations became separated from the others, but also from each other.

4. Discussion

In the morphometric comparison of *A. carinata* populations (Jansson & Pajunen 1978) the general body measurements indicated the adaptation of the populations to their environments, while the genital characters indicated the kinship between them. Similarly, in the structure of the male stridulatory signals, certain characteristics may be considered to be more readily affected by the environment than the others.

In general, the stridulatory signals of male corixids function both in territorial behaviour between the males, and in attracting receptive conspecific females; in the latter case the signals also have an important function in premating isolation of sympatric species (Jansson 1973, 1976). In low population densities loud signals would obviously be of advantage in aiding the two sexes to find each other, and in the presence of other stridulating species clear and consistent signal structure would likewise be of importance.

In the laboratory, the male stridulation of *A. carinata* often appears as part of the territorial behaviour of males, while in mating behaviour acoustic signals do not always seem to be necessary (Jansson 1979). However, in laboratory cultures population density is not an applicable concept, since the density is usually far above the natural levels (Jansson 1978a). Thus, in a species with alternatives in the behavioural sequence of events leading to copulation, the importance or frequency of a particular sequence may be incorrectly stressed. Consequently, the role of stridulation in bringing the two sexes together in *A. carinata* may be much more important than was indicated by the laboratory experiments (Jansson 1979).

In the signals of *A. carinata* males the fast pulse-trains are always much louder than the slow ones. Thus, the number of fast pulse-trains per signal can be taken as a measure of the relative loudness of the signals and accordingly the signals of the northern Finnish population were the loudest (Table 1). In Lapland *A. carinata* lives at the extreme limit of its ability to survive, and during the long, cold winters the species frequently becomes extinct over wide areas. Under these circumstances a loud signal may well be an adaptation to low population densities in spring and early summer, i.e. during the breeding season.

In central Sweden *A. carinata* was collected from the same pond in 1973 and 1975, and both times the species was abundant. Although this collecting site evidently belongs to the same distributional range as the northern Finnish locality (Jansson 1978a), the central Swedish locality is quite different in nature. It is located in woodland, well below the tree line, and presumably serves as a permanent reservoir from which water bodies at higher altitudes are repopulated by dispersal. Possibly, the permanence of the habitat is reflected in the somewhat lower proportion of fast pulse-trains in the male signals.

In the rock pool populations the southern Finnish and eastern Swedish individuals had high proportions of fast pulse-trains per signal, while the western Swedish population was quite the opposite in this regard. Again this correlates with population densities in spring and early summer. In the Baltic archipelagoes there is a seasonal change of habitat whereby breeding occurs in small rock pools, but overwintering is successful only in ponds that are deep enough not to freeze through (Pajunen & Jansson 1969). During cold winters overwintering is thus successful in relatively few ponds, and in the following spring the population densities are at a very low level. On the west coast of Sweden, in contrast, the winters are mild (cf. Jansson 1974b), and *A. carinata* is able to overwinter in the small breeding pools; obviously the mild winters do not cause any drastic decreases in population level.

For the Icelandic, British and Swiss populations I have no information on population density in the spring. Museum records indicate that in Switzerland the species occurs at both relatively high and low altitudes, but in 1972, a cold summer, I found the species only at low altitudes. Thus, at high altitudes extinctions are presumably common, but in warm summers ponds are effectively restocked by dispersal from lower altitudes, the situation being similar to that in central Sweden.

In Britain, *A. carinata* occurs mainly in peat pools on hill tops in the Lake District and in Scotland. The habitats are permanent and the winters evidently are not severe enough to cause drastic decreases in population density. In Iceland, in contrast, the species occupies a variety of habitats, and in many of the large, deep ponds the species is obviously able to overwinter without difficulty. Further, the total absence of other species of Corixidae from Iceland (Fristrup 1945) would perhaps make a loud and distinct signal unnecessary.

The differences in signal structure show that the populations of *A. carinata* are evolving in different directions. Because of adaptation to different environmental pressures, the value of the signal characteristics in reflecting kinship between populations is somewhat difficult to assess. Moreover, the characteristics that varied most, i.e. the proportions of slow and fast pulse-trains, the total number of pulse-trains, and the signal duration, are strongly correlated and their effects are thus reinforced. Yet these characteristics grouped the populations into clusters very similar to those suggested by the detailed characteristics within the pulse-trains (cf. Figs 2 and 4), and in the latter environmental adaption is not obvious. For instance, the number of pulses per pulse-train, which actually expresses the number of fore femoral peg rows used to produce the sound (Jansson 1972), does not seem to have clear adaptive significance. Thus, the geographic variation of the male stridulatory signals of *A. carinata* may be considered to support earlier views on the kinship of the populations (Jansson 1978a, Jansson & Pajunen 1978), whereby:

— The Icelandic and British populations are relatively close to each other.

— The rock pool populations are a close set, in which the western Swedish population, for ecological reasons, differs slightly from the eastern Swedish and southern Finnish populations.

— The arcto-alpine group, consisting of the northern Finnish, central Swedish, and Swiss populations, show general similarities that must be the result of parallel development.

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References

Fristrup, B. 1945: Hemiptera 1. Heteroptera and Homoptera Auchenorrhyncha. – The Zoology of Iceland 3 (51):1– 21.

Jansson, A. 1972: Mechanisms of sound production and morphology of the stridulatory apparatus in the genus Cenocorixa (Hemiptera, Corixidae). – Ann. Zool. Fennici 9:120– 129.

– »– 1973: Stridulation and its significance in the genus Cenocorixa (Hemiptera, Corixidae). – Behaviour 46:1—36.

—»— 1974a: Annual periodicity of male stridulation in the genus Cenocorixa (Hemiptera, Corixidae).

— Freshwater Biol. 4:93—98.

—»— 1974b: Wintertime fluctuations in the epifauna of Cladophora rupestris in a rock pool on the Swedish west coast. — Ann. Zool. Fennici 11: 185—192.

—»— 1974c: Effects of temperature on stridulatory signals of Cenocorixa (Hemiptera, Corixidae). — Ann. Zool. Fennici 11:288—296.

—»— 1976: Audiospectrographic analysis of stridulatory signals of some North American Corixidae (Hemiptera). — Ann. Zool. Fennici 13:48—62.

—»— 1978a: Viability of progeny in experimental crosses between geographically isolated populations of Arctocorisa carinata (C. Sahlberg) (Heteroptera, Corixidae). — Ann. Zool. Fennici 15:77—83.

—»— 1978b: Characteristics of Arctocorisa carinata pyrenaica Poisson (Heteroptera, Corixidae) within the variation of the nominate form. — — Ann. Entomol Fennici 44:98—100.

—»— 1979: Reproductive isolation and experimental hybridization between Arctocorisa carinata and A. germari (Heteroptera, Corixidae). — Ann. Zool. Fennici 16 (in press).

Jansson, A. & Pajunen, V. I. 1978: Morphometric comparison of geographically isolated populations of Arctocorisa carinata (C. Sahlberg) (Heteroptera, Corixidae). — Ann. Zool. Fennici 15: 132—142.

Pajunen, V. I. & Jansson, A. 1969: Dispersal of the rock pool corixids Arctocorisa carinata (Sahlb.) and Callicorixa producta (Reut.) (Heteroptera, Corixidae). — Ann. Zool. Fennici 6:391—427.

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