GENETICS OF ETHOLOGICAL ISOLATING MECHANISMS IN THE SPECIES
COMPLEX JAERA ALBIFRONS (CRUSTACEA, ISOPODA).

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Introduction

The Jaera albifrons complex includes five related species found in cold and temperate coastal regions of the North Atlantic. The species are limited to the intertidal zone and live under stones or among algae.

Females of the five species are morphologically indistinguishable, while differences in the male pereiopods allow specific identification (Bocquet, 1953). In each species, the sexual variants (secondary sexual characters) are closely related to the stimulus-signals emitted by the male during the precopulation phase (Solignac, 1975).

Three species, Jaera (albifrons) albifrons, J. (a.) ischiosetosa and J. (a.) praehirsuta have a widespread distribution on both sides of the Atlantic. The two other species, J. (a.) posthirsuta and J. (a.) forsmani are limited to the east coast of North America and to western Europe respectively.

It is fairly easy to obtain interspecific hybrids in the laboratory when no choice of mate is allowed. The ten possible hybrid combinations and their reciprocals can all be obtained but with varying degrees of success. In nature, however, where mixed populations are not uncommon, the frequency of hybrids generally does not exceed 1%.

In the absence of temporal (Jones and Naylor, 1971),
mechanical and gametic isolation, the sexual barrier guarantees specific integrity in mixed populations. Hybrids of the first generation are usually perfectly viable, except in some crosses (and then only in one direction) where females (the heterogametic sex) are produced in reduced numbers. The $F_1$ hybrids produce numerous and apparently normal gametes, but offspring of hybrids crossed among themselves or with parents are significantly fewer in number (Solignac, 1976).

The present work is limited to a study of sexual isolation. Some aspects of the genetic determination and of the variation between pairs of species of this isolating mechanism are analysed. In the sexual behaviour of this isopod, two steps are likely to be important (Solignac, 1975):

1. Discrimination by males during pair formation:
   males take the initiative and the study was made by the male choice technique.

2. Female reactivity to heterospecific overtures:
   studies were made on isolated heterospecific couples.

Sexual Choice by Males

The male choice technique has been widely used for the study of the degree of isolation between species of Drosophila and of the incipient isolation between geographic strains (reviewed by Anderson and Ehrman, 1969). Results have generally been based upon the percentage of homogamic and heterogamic insemination. In Jaera albifrons, ethological isolation between species is very strong, both in nature and in the laboratory. As observation of heterospecific impregnation in Jaera would be relatively infrequent, this study was limited to pair formation. This is, of course, only one component of isolation, but the level of discrimination shown by males is important in avoiding the formation of heterospecific couples with consequent wastage of time by partners in a pairing without issue.

Analysis of sexual choice. Some preliminary experiments were performed before the technique was standardized in order to establish the optimal conditions for repeatability, and to establish the limits of reliability of the data. Two populations belonging to different species, ischiosetosa and albifrons, both originating from Kiel (Germany) were studied in some detail.
Equal numbers of females of the two species (20 of each) were introduced into a sea water tank. Females, being morphologically indistinguishable, were identified by genetic markers. A choice was then given to a sample (generally about 40) of the males of the first species; the test was considered as positive when a male mounted a female in the "head-to-tail" position characteristic of the initial precopulation phase in the *Jaera albifrons* complex. The two partners were then separated, the male was removed and the female put back in the tank. The nature of the female chosen was noted. After 20*, most of the males had made a choice and had been substituted by males of the second species which were tested in the same manner.

These experiments were repeated several times with the same animals, intervals of one week separating each test. Results were generally homogeneous and summed.

Following this protocol, a series of nine experiments was performed on these two populations using different generations, over a period of more than four years. The results are shown in Table 1. They are homogeneous for *albifrons* and slightly heterogeneous for *ischiosetosa*. Nevertheless, considering the diversity of tested animals, particularly in body size and in the genetic markers carried, the results may be taken as reasonably consistent. Another presentation is given in Figure 6: the variability observed for this pair of populations is small compared to those obtained by changing the nature of populations.

The data indicate two rather extreme cases: *albifrons* males appear to be indifferent in their choice of female, while *ischiosetosa* males choose their own females far more often than alien ones, showing only an average rate of error of twenty percent.

The nine experiments described above were performed with animals isolated from birth and replaced in individual dishes after each test. Other males extracted from mass cultures, and kept with their own females between tests were also studied. The ninth experiment in Table 1 was the control (isolated males) for this experiment. Males extracted from mass culture were less active than isolated males (Table 2). In both species, males from mass culture showed more pronounced homogamic tendencies than isolated males.

From these results, it can be concluded that the degree
TABLE 1

Choice by *ischiosetosa* and *albifrons* males between *ischiosetosa* ($\varphi$ I) and *albifrons* ($\varphi$ A) females and percentages of *albifrons* females chosen. Each experiment represents the sum of several tests.

<table>
<thead>
<tr>
<th>DATE</th>
<th>ISCHIOSETOSA MALES</th>
<th>ALBIFRONS MALES</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>$\varphi$I</td>
<td>$\varphi$A</td>
</tr>
<tr>
<td>IV 72</td>
<td>81</td>
<td>10</td>
</tr>
<tr>
<td>VIII 72</td>
<td>24</td>
<td>4</td>
</tr>
<tr>
<td>II 73</td>
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<td>11</td>
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<tr>
<td>V 73</td>
<td>150</td>
<td>34</td>
</tr>
<tr>
<td>V 74</td>
<td>133</td>
<td>27</td>
</tr>
<tr>
<td>X 75</td>
<td>71</td>
<td>17</td>
</tr>
<tr>
<td>II 76</td>
<td>196</td>
<td>39</td>
</tr>
<tr>
<td>IX 76</td>
<td>216</td>
<td>63</td>
</tr>
<tr>
<td>X 76</td>
<td>414</td>
<td>137</td>
</tr>
<tr>
<td>MEAN</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOTAL</td>
<td>1344</td>
<td>342</td>
</tr>
</tbody>
</table>

Homogeneity

$\chi^2_8 = 17.99 \quad \chi^2_8 = 14.98$

$0.01 < P < 0.05 \quad P > 0.05$
TABLE 2

Sexual activity of and discrimination by *ischiosetosa* and *albifrons* males. For both species, isolated and non-isolated males were tested.

<table>
<thead>
<tr>
<th></th>
<th>% of males having chosen:</th>
<th>ischiosetosa females chosen</th>
<th>albifrons females chosen</th>
<th>% ♀ A</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>20°  60°</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>albifrons</em> males</td>
<td>isolated</td>
<td>89</td>
<td>314</td>
<td>390</td>
</tr>
<tr>
<td></td>
<td>isolated from mass culture</td>
<td>42</td>
<td>63</td>
<td>202</td>
</tr>
<tr>
<td><em>ischiosetosa</em> males</td>
<td>isolated</td>
<td>92</td>
<td>414</td>
<td>137</td>
</tr>
<tr>
<td></td>
<td>isolated from mass culture</td>
<td>18</td>
<td>32</td>
<td>170</td>
</tr>
</tbody>
</table>
of sexual choice of males, for a given pair of populations, is reproducible in defined conditions and is hereditarily transmissible. Learning cannot be excluded, but the greater discrimination of males with previous contact with females is perhaps a secondary result of their lower sexual activity.

A modified technique was used in an attempt to search for variation in the sexual choice of males. Results from experiments of this sort could reveal behavioural heterogeneity of males, some of them with homogamic tendencies, others being indifferent or preferentially heterogamic.

Males of the two species, isolated from birth, were allowed five successive choices at intervals of one week. After five experiments, males were distributed in six classes based upon having chosen one kind of female (in this case ischiosetosa) 0 to 5 times. In Figure 1, the experimental distributions are compared to the theoretical binomial ones calculated with the same respective mean of choice. The experimental distributions for the two species, for the five successive tests are not significantly different from expected.

Although the technique is far from sensitive these results suggest the absence of any obvious intra-specific genetic variability for this behaviour. All males seem to have the same probability of error in making their choices.

Using this experimental procedure, strictly homogamic or heterogamic albifrons males were selected. After the four generations of selection so far completed no consistent results have been produced in promoting choice of their own or alien females. The number of generations of selection is low, but these early results are not in conflict with the inference drawn from the shape of the distributions in Figure 1.

Genetic determination of sexual choice. As the variation in sexual choice is weak in parents, the study of the genetic determinism of these choices must be approached by the shift of interspecific hybrids. Two independent experiments were performed.

In the first experiment, pure albifrons and ischiosetosa males and F₁ hybrid males were given a choice between hybrid and/or pure females (Table 3). The results were as follows:

ischiosetosa males always rejected albifrons females and apparently confused hybrid females with their own;
Figure 1. Experimental and theoretical binomial distribution in five successive mate choice experiments with albifrons and ischioseptosa males. The theoretical distribution is established using the value of $p$ obtained as a mean of the five experiments.
TABLE 3
Choices by *ischiosetosa*, *albifrons* and *F*₁ hybrid males between hybrid and/or purebred females.

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>A</th>
<th>IA</th>
<th>AI</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>( \sigma )</td>
<td></td>
<td>( \varphi )</td>
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<tr>
<td>( \Omega )</td>
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<td></td>
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</tr>
<tr>
<td>I</td>
<td>133 83</td>
<td>168 46</td>
<td>212 55</td>
<td>93 53</td>
</tr>
<tr>
<td>A</td>
<td>27 17</td>
<td>197 54</td>
<td>173 45</td>
<td>82 47</td>
</tr>
<tr>
<td>I</td>
<td>137 55</td>
<td>95 45</td>
<td>169 41</td>
<td>77 44</td>
</tr>
<tr>
<td>AI</td>
<td>114 45</td>
<td>118 55</td>
<td>244 59</td>
<td>98 56</td>
</tr>
<tr>
<td>AI+IA</td>
<td>78 89</td>
<td>74 45</td>
<td>167 54</td>
<td>81 58</td>
</tr>
<tr>
<td>A</td>
<td>10 11</td>
<td>89 55</td>
<td>144 46</td>
<td>59 42</td>
</tr>
<tr>
<td>( \Sigma )</td>
<td>46</td>
<td>30</td>
<td>32</td>
<td>32</td>
</tr>
<tr>
<td>3 Hyb.</td>
<td>45</td>
<td>33</td>
<td>38</td>
<td>38</td>
</tr>
</tbody>
</table>

* \( P < 0.05 \)

- *albifrons* males, as in the preceding experiments, showed a low discriminatory capacity.

- hybrid males obtained from the two reciprocal parental crosses showed the same behaviour with, generally, a slight preference for the hybrid females.

A second experiment was performed with pure males and various types of hybrid males, but with a choice only between parental female types. 18 kinds of males were tested:

- pure *albifrons* and *ischiosetosa* males;

- reciprocal hybrids of the first generation;

- second generation hybrids from crosses \( \varphi \) *AI* x \( \sigma \) *AI*;
- male products of the three first generations of recurrent or non-recurrent back crosses (BC).

The back cross males were obtained by crossing hybrid females A1 to the two types of pure males (BS1 I_ and BC1 A); female offspring of these two back crosses were then crossed either to ischiosetosa or to albifrons males, giving four kinds of BC2: II, IA, AI and AA, considering only the nature of males to which F1 and BC1 females were back crossed. Of the 8 kinds of the third back cross, only seven were tested, the number of IIA males being too small to test.

Males can be characterized by an average genetic constitution, in terms of the percentage of genes of one species they carry (in this case albifrons).

The correlation between the percentage of albifrons females chosen and the genetic constitution of the males was very strong ($r = +0.92$) (Fig.2). The experiment involved a total of 4,376 choices.

It can therefore be concluded that there is genetic determination of male sexual choice. A monofactorial determination cannot be totally excluded because each point corresponds to a mean based upon numerous males (45 as an average for each category). It seems, however, reasonable to attribute a polyfactorial basis to this character.

Variability in sexual choice of males. Male choice experiments were carried out with a number of populations belonging to the same species or to different species. Genetic markers were again used to recognise the two kinds of females. Intrapopulational references were also needed to test the effects of these markers.

Choice indices of males 1 and 2 were calculated. These two categories were males of different colour morphs within the same population or were individuals from different populations within the same species or were individuals of different species. Male 1 choices were classified as homogamic (or positively assortative) if females of type 1 were chosen, heterogamic (or negatively assortative) if females of type 2 were chosen. The choice index is the difference between the number of homogamic and heterogamic choices, divided by the sum of the two. The index ranges from -1 to +1, positive values denoting homogamy, negative values heterogamy, and a zero value, random choice. This simple index is derived from the isolation index of Stalker (1942) calculated on the
Figure 2. Choice between *ischiosetosa* and *albifrons* females shown by pure-bred males, F1 and F2 hybrid males and males produced by the three first back crosses. Open circles represent results obtained with the experiments reported in Table 3.
percentage of inseminated females. The reciprocal index is calculated in the same way for males of type 2.

The results are presented graphically (Fig. 3): the index of male 1 is plotted along the abscissa, male 2 being plotted on the ordinate. The two kinds of males are permutable and there is a symmetry along the NE-SW axis. The male with the highest index was always designated as male 2 (all points are on the same side of the axis of symmetry). The joint choice index (half of the sum of the two reciprocal indices) can be read on the NW-SE diagonals.

The distance of points from the axis of symmetry gives the attractiveness index of females (half of the difference between the two reciprocal indices, derived from Bateman's index, 1948). According to our convention, the index is positive for female 2, negative with the same absolute value for female 1. Absolute values are on the same scale as the joint isolation index.

The positions of points on the plan define immediately the quality of the choice.

(a) Intrapopulational choice: the two sexes were marked by genes of the natural polychromatism of these isopods. Variations affect the colour of the pigment, the pattern of chromatic cells distribution, the development of chromogranules and the degeneration of the pigmentation system (Bocquet, 1953; Cléret, 1970). Alleles controlling the phenotypes were maintained, not in separate stocks, but in a polymorphic state in mass culture. The so-called wild type phenotype (Cléret, 1970) nigrom granulatum uniforme is characterized by black chromatophores uniformly distributed.

The deviations are relatively moderate (Fig. 4) compared with random choice: most of the points occupy a very small area, near the origins. Nevertheless, the nonrandomness is statistically significant ($P < 0.05$) in 7 out of 28 chi-squares (calculated for males 1 and 2 in 14 experiments): in some instances selective choice exists. One kind of male (male 2 according to our convention) chose the category of female marked by the same allele as he possessed (female 2) (homogamy). The second kind of male also preferred the type 2 females (heterogamy). The choice shown by males was independent of the genes they carried, but one kind of female was more attractive to the two kinds of males.

In the genus Drosophila, experiments using mutant and wild-type stocks have demonstrated discrimination by females,
Figure 3. Graphic representation of male choice. Reciprocal indices of choice (i \( \delta_1 \) and i \( \delta_2 \)) are plotted along the coordinates. Joint isolation index and female attractiveness can be read along diagonals. Broken lines indicate limits of significance of \( \chi^2 \), compared with random choice, for an arbitrary number of 100 choices. The occurrence of points in various sectors indicates the quality of choices.
Figure 4. Distribution of points observed with individuals marked by genes for colour polymorphism within populations (circles: albifrons, stars: ischiosetosa, squares: praehirsuta).
and the absence of male discriminating ability (Bateman, 1948). In his review, Spiess (1970) concluded: "genotypes of males may be selectively different and females are the selective agents in the process". The conclusions in Jaera are different but the technique used does not show whether any dissimilarity exists in the courtship propensity of males.

Some other points of interest, still under investigation, appeared during this experiment.

The most notable is that selective choices (combining both significant or non-significant deviations) are in favour of wild type females in 9 cases out of 10 (four other experiments were performed with non-wild type animals). In the last one (prashirsuta of Woods Hole), Aurantiacum females were preferred. It is interesting to note that this phenotype has a high frequency in this strain.

Genes affecting the colour polymorphism of Jaera have pleiotropic effects on behaviour. Colour alleles do not appear to influence the extent of isolation (the average index of choice is -0.004) but may, in some cases, influence selective choice.

(b) Interpopulation choices: the results of these tests are illustrated in Figure 5, and are seen to be very different from the intrapopulation tests. Some pairs of populations show an absence of choice in a few cases, but frequently one type of male and often the two types show homogamic tendencies. Considering couple formation, the existence of an incipient isolation between geographic strains within a species can be concluded. The average index is +0.200. Further analysis of data indicates a lack of correlation between the geographical distance separating populations and the degree of isolation.

(c) Interspecific choices: the average value is just a little higher (+0.279) and the distribution of points in Figure 6 is very similar to that of Figure 5. For some pairs of populations, isolation is rather high: the number of heterospecific couples formed is reduced by the discriminatory faculties of males. In nature, isolation by male choice is probably higher since previous contacts render males more homogamic as we have seen.

Comparison of the three diagrams (Fig. 4, 5 and 6) allows further conclusions. Single genes influencing colour change the attractiveness of females, but do not generate isolation within populations. Incipient isolation between strains and
INTERPOPULATION

Figure 5. Distribution of points for mate choice between populations within species (same symbols as Fig. 4).
INTERSPECIFIC

Figure 6. Distribution of points for mate choice between different species. Each symbol corresponds to a given pair of species. The dotted polygon is the envelop of points obtained from data of Table 1 for *ischiosetosa* and *albifrons* populations from Kiel.
Figure 7. Crossing rate (CR) expressed as a cumulative percentage as a function of time (in weeks) in reciprocal crosses between *ischiosetosa* and *albifrons* (the first letter indicates the species of the female).
species (considering male choice) cannot result from the simple accumulation of such point mutations.

The homogamy observable in interspecific choices is close to that obtained between strains of the same species. These incipient isolations must be considered more as a by-product of the geographical divergence of populations rather than as a consequence of a previous differentiation preceding or accompanying speciation.

Crosses without Choice and Female Reactivity

Using the same two populations of *albifrons* and *ischiosetosa* from Kiel, hybridizations were performed with heterospecific isolated couples. The success of crosses was estimated by the appearance of hybrids. If couples are infertile it is judged that impregnation has not taken place. Offspring appear 2 to 5 weeks after insemination, depending on the time of copulation in the female sexual cycle.

**Analysis and repetitivity.** The curves of Figure 7 depict the cumulative percentage of fertile couples over time. This kind of presentation is preferred because once a female has been inseminated, even by a heterospecific male, she continues to produce broods. These data were corrected to take into account mortality (Solignac, 1976).

Hybridization progressed only slowly during the course of weeks and even months. Three independent experiments were performed, in each direction of crossing, with the same result. The two reciprocal crosses give approximately the same results, but this may not always be the case (see below). Reciprocal hybridization rates can be considered as characteristic of a given pair of populations.

The probability of finding new fertile couples among those which were previously unmated seems to be more or less constant over the weeks: the curve is damped as the number of virgin females diminishes. This suggests the involvement of a random process in the partial success of hybridization, rather than a high receptivity of certain females to heterospecific sexual overtures. This was also supported by complementary experiments. *Albifrons* females were crossed with wild-type *ischiosetosa* males. As soon as a female produced a brood, the male was changed for another *ischiosetosa* male bearing a dominant marker. First and second heterospecific fertilizations
Figure 8. Crossing rate (cumulative percentage) as a function of time (in weeks) in various kinds of intra- and interspecific crosses: upper curves: ischiosetosa females: A: virgin ischiosetosa females crossed to their own males  B: already inseminated ischiosetosa females crossed to their own males (second conspecific insemination) C: virgin ischiosetosa females mated to albifrons males; lower curves: albifrons females A: hybridization of virgin albifrons females with ischiosetosa males  B: second interspecific insemination of albifrons females by ischiosetosa males.
Figure 9. Hybridization rate of *ischiosetosa* and *albifrons* males with pure or hybrid females. Hybridization rate (percentage of successful crosses after 16 weeks, corrected for mortality) is expressed as a function of female genotype.
Figure 10. Frequency of precopula phase observed during weekly examination of crossings for both *ischiosetosa* and *albifrons* males as a function of the genotype of the females to which they were crossed.
kinds of pure females. In this case, the result of crossing is evidently due to female reactivity to male stimuli.

With *ischiosetosa* males, the distribution of points is not so clear, but a similar conclusion can reasonably be drawn.

This kind of comparison must be limited to one type of male with different types of females. Indeed, the length of precopulation is very variable between populations or from one species to another.

It seems logical to suppose that the success of these crosses, in the absence of choice, depends largely on female reactivity. Such a reaction is genetically determined but it is not possible to conclude much as to the nature of the genetical determinants. Indeed, most of the results can be explained by assuming the existence of two alleles, each of them characterizing one species. Nevertheless, as in the male choice experiments, the hypothesis of a polyfactorial basis of female reactivity is highly probable.

**Variations of hybridization rate.** When varying the pairs of species or even the populations within the species, considerable variation in results was obtained. Often, the final hybridization rate was between 30 and 50%. But female *posthirsuta* originating from Newport (United States), crossed with *albifrons* or *ischiosetosa* males as rapidly as they did with their own. On the contrary, *praehirsuta* males, from Roscoff (France) produce a hybridization rate always close to zero with *ischiosetosa* and *albifrons* females.

Some curves are given in Figure 11. It can be seen that the results obtained from the two reciprocal crosses are sometimes strikingly different. For the moment, no general rule can be drawn: the data are few due to the long time needed for such experiments.

**Conclusions**

An attempt will be made to correlate the results obtained by the two types of experiments. When choice of mate is available, the role of the two sexes is rather clear:

- due to male discrimination in certain pairs of populations, most couples are of the homogamic type;
Figure 11. Crossing rate (CR, cumulative percentage) in various pairs of species: A: ♀ posthirsuta (Newport) x ♂ ischiosetosa (Ringkøbing). B₁: ♀ praehirsuta (Roscoff) x ♂ ischiosetosa (Kiel); B₂: reciprocal cross. C₁: ♀ ischiosetosa (Kiel) x ♂ albifrons (Kiel); C: reciprocal cross.
- females are rapidly receptive to males of their own kind and show a low receptivity to alien males;

- fertilized females are less receptive than virgin ones, especially to heterospecific courtship.

When no mate-choice is allowed, the situation is not so clear and three kinds of rather conflicting conclusions can be drawn:

- in many experiments on hybridization, the rate of fertilization depends on the discriminating faculties of the male. The more discriminating the male during choice, the lower the success of hybridization with that male. Consequently, the role of the male seems important.

- nevertheless, the frequency of precopula in isolated heterospecific couples does not confirm the above conclusion. The attempts of males to copulate seem to be characteristic of the kind of male and independent of the genotype of the female. The reactivity of the female seems most important in crosses, depending on the female genotype.

- this last impression is also supported by inter-population crosses. Males are sometimes very discriminating in their choices, as much as in interspecific choices. Nevertheless, in the absence of choice they fertilize females from alien populations very rapidly.

Consequently, the hybridization rate seems to be the consequence of both frequency of attempts made by the male (male activity) and of female reactivity. Nevertheless, in the absence of choice, the female receptivity is probably the most important factor.

More difficult, but also more important is the problem in nature. The frequency of hybrids can be established in males without difficulty, F1 hybrids and often products of first back cross being morphologically identifiable. The hybrid rate is generally between 1% and 0.1%. The actual rate of hybridization in nature can also be established. Hybrids in *Jaera albifrons* develop quite well under laboratory conditions, as well in fact as the parental forms. Offspring raised in the laboratory from inseminated females collected in the field permit the estimation of the actual hybridization rate. The frequency of hybrids in the off-
spring of such females is never higher than the hybrid fre­
quency observed in natural conditions among samples of males
collected at the same time as the females. In other words,
the real frequency of hybridization is close to the observed
frequency of hybrids.

In the laboratory, in experimentally mixed populations,
species remain isolated with the same intensity as in nature
(Solignac, 1976). Experimental analysis seems therefore to
give an accurate picture of what occurs in nature. This is,
however, not a general conclusion valid for all organisms.
For instance, Drosophila pseudoobscura and D. persimilis, are
more isolated in the field than in the laboratory for reasons
which are not clear (see for example Dobzhansky, 1951).

Summary

The complex Jaera albifrons includes five related species
of the cold and temperate coasts of the North Atlantic. In
the laboratory, species can be hybridized if there is no
choice of mates, but in nature, they remain reproductively
isolated in the zones of contact or overlap. A genetic study
of ethological isolating mechanisms has been carried out.
In Jaera albifrons, couples are established following male
initiative. In male choice experiments, using males and fe-
males from the same population marked by different alleles of
loci controlling the natural colour polymorphisms, sexual
choice is either at random or is strictly selective i.e. one
kind of female is preferred by both types of males. On
the contrary, interspecific choice, and at a lower level inter-
population preferences within a species, are of the homogamic
type. The choice made by parental males and various kinds
of hybrid males (F1, F2 products of recurrent or non-recurrent
back crosses) show a genetic determination of sexual preferen-
ces, probably of a multifactorial nature.

Female refusal to alien male stimuli is the main bar to
hybridization. In the absence of mating choice, the success
of crosses between females or various degrees of hybritity and
parental males depends on the degree of genetic resemblance
between the two parents. Full success of the cross is assured
if the female possesses at least 50% of genes in common with
the male. Both under natural conditions and in laboratory
populations, the frequency of hybrids does not exceed 1%.
The frequency of hybrids, estimated from males, is a good in-
dex of the frequency of hybridization and hence the ethological
differences appear to be established as the main isolating
mechanism in nature.
REFERENCES


