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Sexual behaviour and evolution of sexual dimorphism in body size in *Jaera* (Isopoda Asellota)

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Individuals of the genus *Jaera* do not mate at random. In the species from the Mediterranean group, *J. italica* and *J. nordmanni*, large males and medium sized females are at an advantage and their sizes are positively assorted. These effects are attributable to sexual competition between males. In the Ponto-caspian species *J. istri*, no advantage of large males exists, but sexual selection could be the cause for a long passive phase prior to copulation and for normalizing selection upon female size at pairing. In the Atlantic species *J. albifrons*, no selection can be ascertained.

Differential mating success in males appears as one of the causes of the evolution of sexual dimorphism in body size, which makes males larger, of equal size, or smaller than females according to the species. The reason for this reversal in dimorphism seems to differ in the two sexes. Sexual selection provides an explanation for the evolution of male size, while the interspecific changes in female length are more likely due to ecological factors.

KEY WORDS: – sexual competition – sexual dimorphism – body size – Crustacea.

CONTENTS

INTRODUCTION

Reproduction plays a central role in the biology of populations and is subjected to many selective factors acting on animals at the level of sexual behaviour, breeding, parental care, or reproductive strategies. These constraints differ between the sexes and sometimes result in sexual dimorphism which permits their study. A convenient character for this purpose is body size, which

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can be measured whatever the species, and which has considerable influence on the mating success of males (Maynard Smith, 1978) and on ecophysiological adaptation.

The main selective factor classically recognized as acting upon sexual dimorphism is sexual selection, in which Darwin distinguished the intrasexual competition for mates of the opposite sex, and the choice of mates by members of the other sex. Since Darwin, many authors have attempted to explain the empirical rule that intrasexual selection generally occurs in males, while females are the main agent of epigamic selection. According to the theory of 'parental investment' (Trivers, 1972), where one sex invests more than the other in its progeny, it becomes a limiting resource for the other sex. This would result in differential sexual selection and explain most cases of sexual dimorphism.

As regards body size, sexual dimorphism may be related to a competitive advantage of large males, which has been demonstrated, e.g., in lizards (Trivers, 1976), toads (Wilbur, Rubinstein & Fairchild, 1978), primates (Clutton Brock & Harvey, 1977) and birds (Verner & Wilson, 1969). Sexual dimorphism in body size is frequently associated with conditions of increased competition between males, as in the case of polygynic mating systems (Clutton Brock & Harvey, 1978; Leutenegger, 1978).

Sexual selection is unlikely to be the sole factor acting upon a character such as body size. Alternative ecological arguments emphasize the importance of reducing niche overlap between the sexes (Selander, 1966), or of the bioenergetic requirements of reproduction in females (Ralls, 1976, 1977; Myers, 1978; Downhower, 1976).

The isopodan genus *Jaera* is suitable material for the study of the differential evolution of sexual dimorphism in body size, since the species differ in the degree and direction of sexual dimorphism. Depending on the species, females are smaller, of equal size, or larger than males. The mating success of individuals of different sizes is easy to record. Fertilization is internal and the sexes must meet for copulation. They have evolved a long phase of sexual behaviour during which the male remains paired to the female prior to insemination. It is therefore possible to test in each species whether or not mates of either sex are selected according to body length, and whether or not this selective pressure is in accordance with the kind of sexual dimorphism observed in that species.

MATERIALS AND METHODS

The genus *Jaera* is divided into three groups of species distributed in the Atlantic ocean, the Mediterranean sea, and Ponto-caspian basin. Species are very similar within each group, but the groups themselves differ in sexual dimorphism, behaviour, and the reproductive biology of females (Veuille, 1978, 1979). The representatives of each group utilized in this study are *Jaera albifrons* (Atlantic group) from Haiçabia (France), *J. istri* (Ponto-caspian group) from Kladovo (Yugoslavia), and *J. italica* from Siponto (Italy) and *J. nordmanni* from Calvi (Corsica), for the Mediterranean group.

All these species live in large crowded populations under pebbles, in the intertidal zone for Atlantic species, on the shore of rivers in Ponto-caspian ones, and in brackish water along the shore in Mediterranean species.

Laboratory populations

These were made from mass samples taken in the wild and transferred into laboratory. They were reared in water basins and fed with elm leaves and enteromorph algae under a photoperiod L/D = 16/8, which corresponds to the breeding season of northern species. The marine species *J. albifrons* and *J. nordmanni* were reared in natural sea-water; *J. istri*, from the Danub river, was reared in fresh-water, and *J. italica* was reared in $1.5^0/_{00}$ salinity brackish water. The medium was renewed every four weeks. The size range in adults is between two and six millimetres. Each strain was constituted from several basins which were blended at each renewal of the medium to homogenize the population. There were usually several hundred individuals per basin, and the total adult number was between 500 and 2000, depending on the species. Such experimental populations are stable over numerous generations.

Sexual selection

This was estimated by comparing the body length of individuals of the actual experimental population to the size of the animals found in precopula. Mates of each sex were removed from the strain each morning at 10.00 hrs, measured, and replaced so as not to change competitive conditions. The results of several days were pooled. A control sample of the remaining population was made and compared to experimental data.

Body length was measured between the front of the head and the caudal end of the pleotelson. Animals were measured alive in a drop of water, between a slide and a cover-glass.

Sexual behaviour of the species

Jaera albifrons is a member of the Atlantic '*Jaera albifrons*' superspecies (Bocquet, 1954), in which females are larger than males. During its display, as described by Solignac (1972, 1978), the male climbs on the back of the female and stays there, in an antiparallel orientation (his anterior turning toward her caudal end) for a time varying from some seconds to several hours (Fig. 1A). Attempts to copulate are made but insemination does not necessarily ensue and rejection is frequent. This phase of behaviour stops as soon as copulation has occured. Females are usually inseminated for the first time as juveniles and retain spermatozoa in their genital tracts over several sexual cycles. They can yield several broods and fertilize their eggs without any further insemination. They can store the sperm of several successive mates.

The reproductive biology of the three remaining species is quite different. Females do not store the sperm of their mates for more than one sexual cycle. Sexual cycles are made of two intermoults. Females mature their eggs during the first one, and lay them in the marsupium during the second intermoult (Veuille, 1978). The female is inseminated at the beginning of each cycle, during the 'parturial moulting'. Males and females pair during a phase which extends over three days. This period corresponds to the end of the 'D' stage of the female moulting cycle, during which she prepares moulting and releases the newborns of the preceding brood. At moulting, she is inseminated and separates from the male. Copulation always follows this phase, but an outsider male may have displaced the first one through competition.

Jaera istri is a member of the Ponto-caspian group of species, in which males and females are of nearly equal size. Mates usually do not move during precopula. The male remains on the back of the female in a parallel, antiparallel, or more frequently in a transverse orientation (Fig. 1B).

Jaera italica and *J. nordmanni* are representative of the Mediterranean species of *Jaera,* in which males are larger than females. The mating behaviour depends on the size of the animals. Large old males hold females upside down between their legs, their ventral parts facing each other, in a parallel orientation (Fig. 1C).

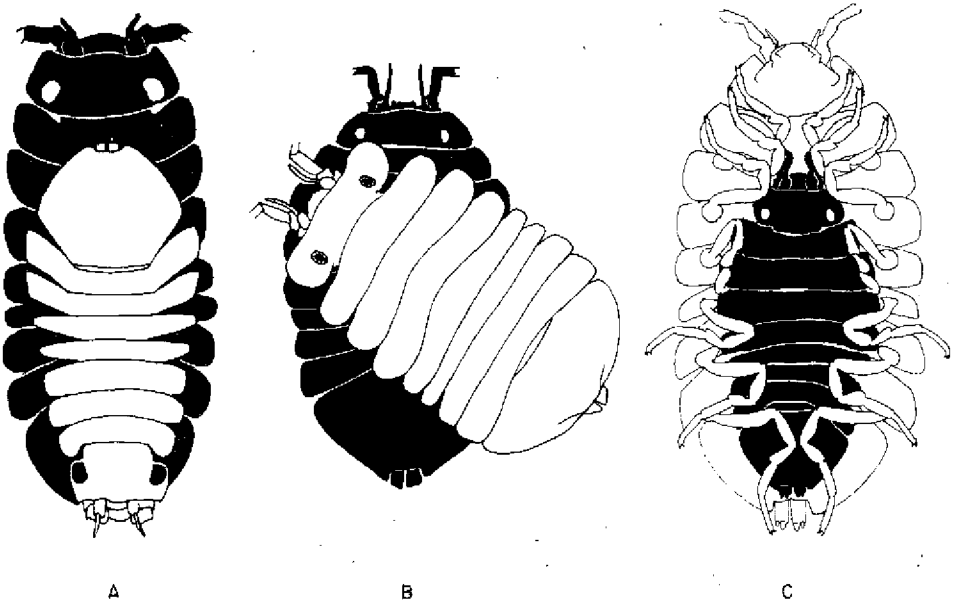

Figure 1. Relative positioning of male (white) and female (black) *Jaera* during precopulation. A. Dorsal and antiparallel precopulation of *Jaera albifrons.* B. Dorsal and transverse precopulation of *Jaeri istri.* C. Ventral and parallel 'typical' precopulation of large males *Jaera nordmanni.* (Animals are seen from below.)

These males possess 'sexual hooks' made from the modified fourth pairs of peraeopods, which they utilize to grasp the female tightly. Young males do not possess modified appendages, and are too small to perform the typical behaviour of large males, yet they are able to inseminate females. When encountering a receptive female, they utilize the 'albifrons-type' behaviour and achieve a dorsal precopula in an antiparallel orientation, from which they are usually dislodged in competitive conditions (a detailed description of this behavioural variability will be published elsewhere).

RESULTS

The length of sexually active and inactive animals is compared in Table 1. Figures 3 to 6 show simultaneously the length of the mates and the mean length of the pairs and the control, compared to the slope of theoretical monomorphy

Table 1. Comparison of the size of the animals in the whole population and in the pairs.

Species	Population	Number experiment/ control	Males				Females				Correlation ♂/♀
			mean		variance		mean		variance		
			population	pairs	population	pairs	population	pairs	population	pairs	
J. albifrons	Haiçabia	30/30	1.65 ±0.02	1.69 ±0.02	0.009	0.008	2.06 ±0.05	2.36* ±0.02	0.071	0.044	0.090
J. istri	Kladovo	103/110	1.97 ±0.03	1.96 ±0.03	0.079	0.078	1.96 ±0.03	2.02 ±0.02	0.061	0.025	0.090
J. italica	Siponto	99/100	2.32 ±0.04	2.92* ±0.03	0.155	0.097	2.13 ±0.03	2.19 ±0.02	0.063	0.029*	0.017
	Siponto†	83		2.98* ±0.03		0.061		2.17 ±0.02		0.022*	0.317*
J. nordmanni	Calvi	36/40	2.36 ±0.08	2.90* ±0.04	0.249	0.040	1.98 ±0.05	1.88 ±0.04	0.093	0.065	0.586*

* Highly significant deviation between pairs and control.

† Values for males in typical passive phase only (*J. italica,* see text).

(bisector of the coordinates), on which males and females would have the same body size.

In *J. albifrons,* the sexual dimorphism of mated animals far exceeds that of the overall population (Fig. 2). The tendency is the same, with females larger than males, but the means are different at a highly significant level (Table 1). This is entirely due to female mean length, since the male body size is the same in both groups.

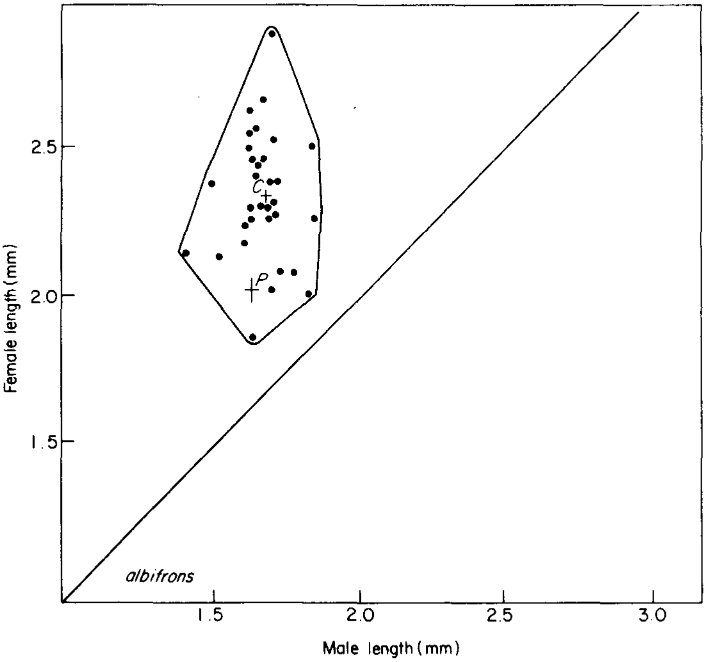

Figure 2. Body length of mated males and females in *J. albifrons* (●). Solid line, theoretical monomorphy; C, mean of mated animals (± S.E.); P, mean of the whole population (± S.E.).

The result yielded by *J. istri* is quite different (Fig. 3). No deviation in mean is found, either in males or in females, although a large sample of pairs was available. The mean sizes of sexually active or inactive animals are superimposed on the bisector. This result is congruent with the previous observation that *J. istri* is monomorphic for body size. Although there is no sexual selection on the mean size, the variance is significantly lower in mated females than in the control. This seems to indicate a case of normalizing selection, where females of intermediate size are more likely to be found in precopula, while large and small ones are at an equal disadvantage.

The results obtained in *J. italica* and *J. nordmanni* are the converse of those found in *J. albifrons* (Figs 4, 5). Here too, sexual dimorphism is enhanced in the pairs. The difference between the control and the pairs is highly significant. No difference is found between the mean values for female size (Table 1), and males are fully responsible for this deviation: a selective advantage of larger males exists at this stage of courting. As in *J. istri,* stabilizing selection upon female size is apparent through the reduced variance in mated females (this result is not

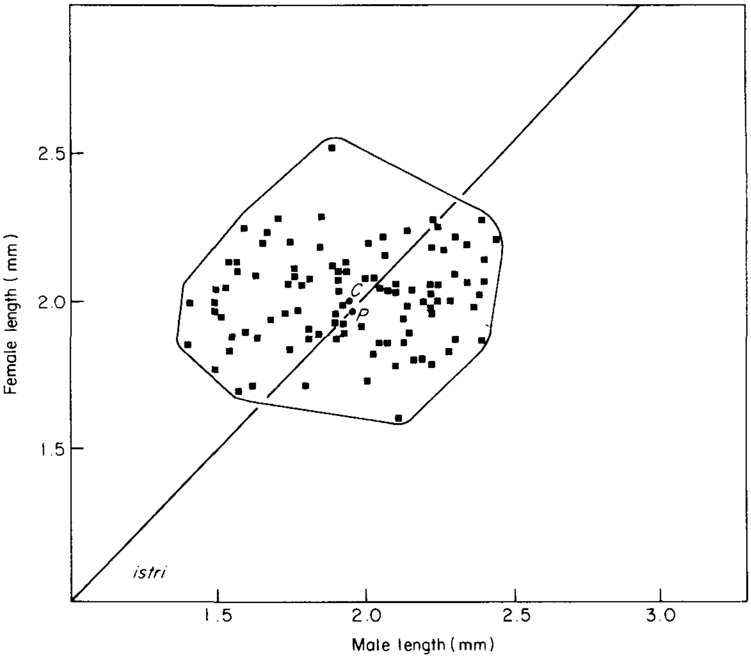

Figure 3. Body length of mated males and females in *J. istri* (■). Other legends as in Fig. 2.

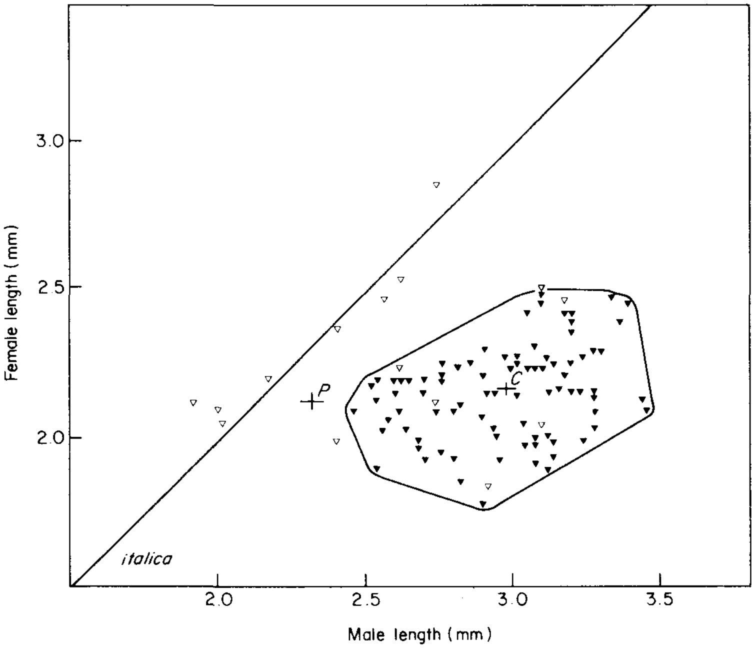

Figure 4. Body length of mated males and females in *J. italica*. ▲, males in typical position; △, males in 'albifrons-like' dorsal antiparallel position. Other legends as in Fig. 2.

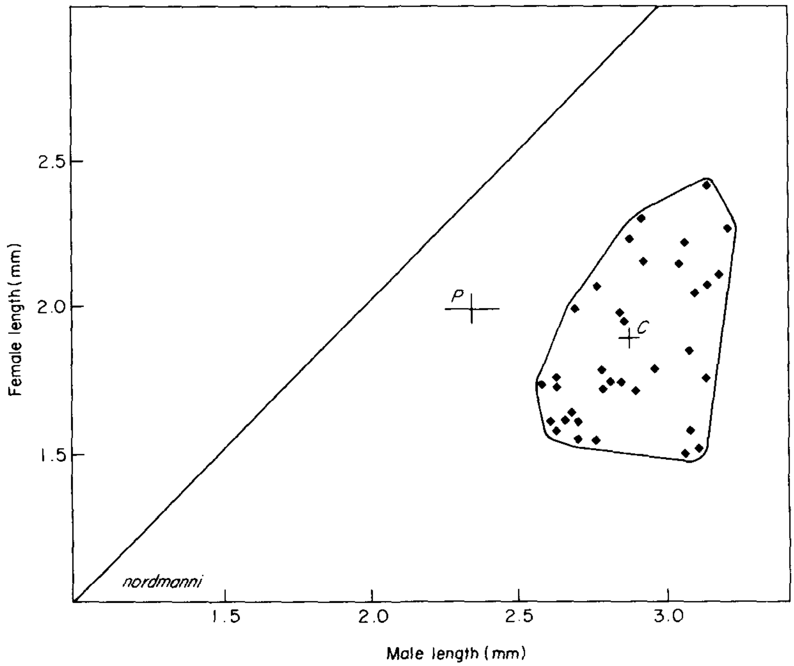

Figure 5. Body length of mated males and females *J. nordmanni* (◆). The animals where all in 'typical' position. Other legends as in Fig. 2.

significant in *J. nordmanni,* perhaps because of the reduced size of the sample). Another phenomenon appears from a consideration of the relationship between male and female size in the pairs. A highly significant correlation is found between the length of mates in *J. nordmanni,* and in *J. italica* individuals in typical precopula. Animals are selected not only for their own length, but for the length of their partner too. The positive value of the correlation means that larger females tend to be paired to the largest males. Sexual selection in the Mediterranean group involves simultaneously three components; there is an intrasexual advantage of large males, an intrasexual advantage of females of intermediate size, and an intersexual component determining positive assortment.

DISCUSSION

The purpose of this study was to check the hypothesis that sexual selection due to competition or partner discrimination could be the cause of the evolution of the sexual dimorphism in body size in *Jaera.* Given a species where females are a 'limiting resource' for reproduction and where the absolute size of males confers on them an advantage for access to mating, then, natural selection will favour an increase in the mean body size of that sex. The sexual dimorphism in body size will shift accordingly. In the peculiar case of *Jaera,* the larger size of one sex is attained through continuous growth during adult life. A wide phenotypical variation due to non-genetical factors will remain in that sex, in which larger animals will still be at an advantage. This advantage will have no selective outcome, but the condition will persist, and the sexual dimorphism at pairing will be more accentuated than the sexual dimorphism of the whole population.

The results fit this general statement. Nevertheless, what has been measured is not strictly speaking sexual selection, but selective pairing prior to copulation, and an agreement between the facts and the hypothesis may appear too slender to demonstrate an evolutionary process. Assortative pairing and sexual dimorphism are two independent observations, and it is necessary to specify rationally the causal relationship between both phenomena before drawing any conclusion. In this case, the problem is to know whether or not this phase of sexual behaviour provides a convincing mechanism for governing the evolution of the size in either sex.

This stage of mating is related to what Parker (1970, 1974) defines as the 'passive phase' of the male sexual behaviour of some species. It tends to exist in species where males are in competition for mating and where they can predict the receptivity of females to courting some time before they actually accept copulation. It becomes advantageous for males to recognize such females as soon as the cue indicating imminent receptivity is exhibited, and to monopolize them until insemination is made possible. This stage of the female sexual cycle will be critical for the mating success of males, and behaviour will evolve in the latter so as to stabilize their association with females. Despite this close association, males will remain sexually 'passive', since 'female-guarding' is principally directed toward other males.

All these conditions are met in *J. istri, J. italica* and *J. nordmanni.* In the three species, females copulate at a definite stage of their sexual cycle. Only a small fraction of them is likely to mate at the same time, and the male-male competition will be increased. They tend to associate closely to females preparing the moult at which copulation is possible, and this behaviour may be viewed as a true passive phase. The suitability of this stage of reproduction for the study of sexual selection does not only hold in the fact that pairs of mates are easily recorded. Since most of the competition between males concentrates on this phase, it is also a pertinent character for such a study.

The results obtained in the four species are summarized on Fig. 6 for checking these hypothesis.

The richest information comes from the two Mediterranean species *J. italica* and *J. nordmanni.* In this group, three kinds of deviation from panmixia have been distinguished.

The first effect is a shift in male mean length. It may be easily interpreted as a result of intrasexual competition between males. It is an 'all-or-none' mechanism of decision for sorting out which males will reproduce, where the largest are at an advantage.

The second effect is a decrease in the variance of female length. Its meaning is that intermediate females are more likely to be found in passive phase than their larger or smaller counterparts. The same phenomenon is recorded in the related isopod genus *Asellus* by Manning (1975) who interpret it as a result of male discrimination between females for choosing those which will maximize their probability of progeny. In *Jaera,* the brood size of females is correlated to size (Jones & Naylor, 1971). The larger the female, the greater her capacity to produce ovocytes, but also the greater her probability of death in the time lapse of two intermoults required for maturing the ovocytes and carrying the eggs in her marsupium. The 'optimal choice' for a male will then be to attempt copulation with a female of intermediate size. As long as males will get the same

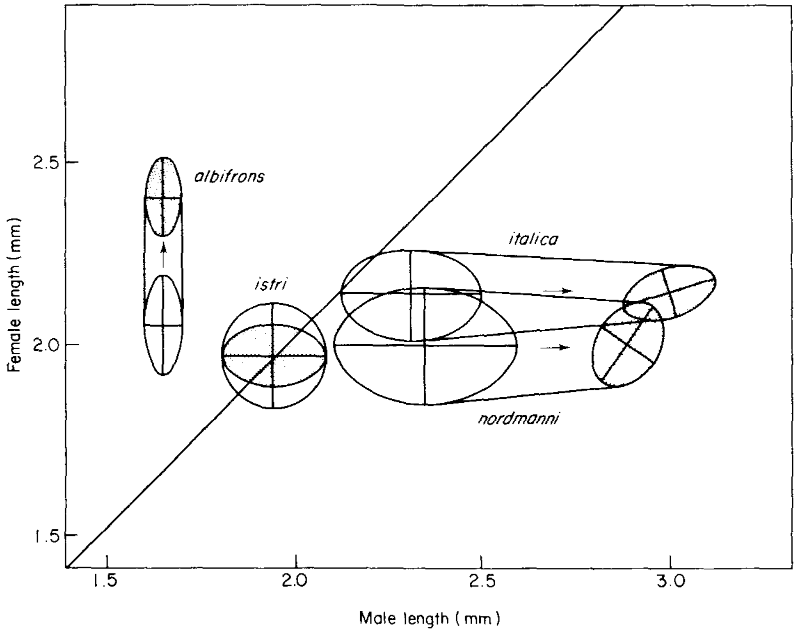

Figure 6. Deviation from panmixia at mating in *J. albifrons*, *J. istri*, *J. italica* and *J. nordmanni*. Dotted ellipse, distribution of pairs (normality is assumed); light ellipse, theoretical distribution of pairs in panmictic conditions; ellipses are constructed from the standard deviation and correlation of male and female lengths ($P = 0.67$).

'investment' from the insemination of large and small females, their lesser advantages will be balanced and male discrimination will have no effect on the mean size of females.

The third effect is the positive assortment of males and females. One can assume that the largest males tend to mate preferentially with the largest of the intermediate females, whose clutch size is the greatest, in which case the determinism of this phenomenon is simultaneously intrasexual and epigamic.

Although this distinction between the three phenomena does not necessarily appear as such in the wild, it is convenient to distinguish the effects of sexual selection upon the evolution of body size within each sex. As a result of this selection, the length of males will tend to increase, while the size of females will not change: this provides an argument for explaining the evolution of sexual dimorphism in body size as a consequence of the differential investment of each sex: in both Mediterranean species, males are larger than females.

The results yielded by *J. istri* are understandable in the light of what is observed in the preceding species. Here, the first and the third effect do not exist (the size of males has no effect on their mating success). Only the second effect persists (males tend to copulate with intermediate females). This absence of sexual selection provides an explanation for the monomorphic condition of this species, and may be regarded as a control of the former experiment.

It is difficult to extrapolate these explanations to *J. albifrons*. Large females are more frequently mounted by males, but since they are already inseminated, it is questionable whether or not this is a good strategy for maximizing the progeny of males: an alternative would be for mates to choose younger females, so as to insure the utilization of the sperm over several sexual cycles. Too little is known about the reproductive biology of this species to answer this question. Furthermore, although this stage of precopulation may be phylogenetically related to the passive phase of the other species, it is very different. Females do not copulate at a definite stage of their sexual cycle. When a male waits for a longer time on the back of a female, its probability of mating does not improve, as in the other species where this wait is necessary when the receptivity of the female is imminent. In *J. albifrons,* prolonged mountings are indicative of the active refusal of females (Solignac, 1978).

In no species of *Jaera* does the sexual behaviour of males seem to have any effect on the evolution of the size of females, despite the fact that larger females have greater clutch sizes. The evolution of the size of females is more conveniently explained in terms of reproductive strategies.

Females *J. albifrons* are not only bigger than the males from their own species. They are generally bigger than the females from the other species too (Veuille, 1979). Atlantic species live in a highly variable intertidal habitat, and their populations fluctuate seasonally. They reproduce at a given period of the year. In temperate latitudes, ovigerous females are found all year round, but they are scarce in winter and their peak of breeding occurs in spring and in summer (Jones & Naylor, 1971). In subarctic regions, as in Newfoundland (Steele & Steele, 1972), females are at a resting stage from September to March, and hatching is restricted to three months, from June to August. The first brood of each year is produced by large overwintering females, with a burst in population growth. The high fecundity required in these Atlantic species may be the cause for the rise in female size.

In conclusion, no symmetry is apparent in the evolution of the size of males and females *Jaera.* Sexual selection is an important factor determining male length, but one can doubt its influence on the evolution of the size of females. It is striking that workers who study the origin of sexual dimorphism in body size utilize selectionist or sociobiological arguments when dealing with male length, and ecological ones when they are chiefly concerned with the evolution of the female size. The observations made in *Jaera* seem to confirm the fact that the selective factors acting on each sex are quite different in nature.

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