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Premating behavior and male discrimination in *Jaera ischiosetosa* (Isopoda)

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Summary. Premating in females of *Jaera ischiosetosa* is statistically biased according to body size, to the size of males, to their physiological stage, and to their fertility irrespective of size. Most of these features are in agreement with the hypothesis of male discrimination between females.

Key words. Sexual selection; behavior; mate choice; body size; Isopods.

In developing the concepts of sexual selection and mate choice, Darwin[1] regarded females as the discriminating sex in most animal species. A genetic explanation for this rule, put forward by Bateman[2], states that females are in most cases the limiting factor for offspring production while males are in competition for access to mates, a view later generalized in Trivers' theory of 'parental investment'[3]. The adaptation of female discrimination between males for 'distinguishing the really fit from the pretended fit'[4] is thought to be widespread.

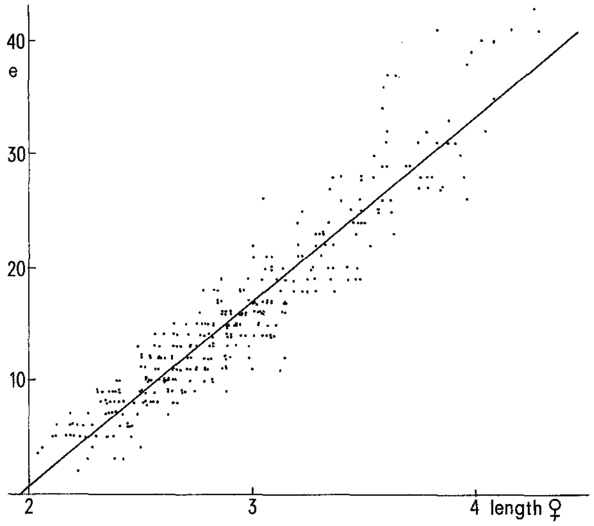
The picture of mate choice seems to be different in Isopod Crustaceans where premating behavior may discriminate between females. Although females make a large parental investment in incubating a few eggs in their ventral marsupium, large females are more likely to enter into precopula than smaller females[5–8]. Female size is positively correlated with fertility through the continuous growth of the adult stage, which suggest that the non-random distribution of precopulae results from a choice by males. The adaptive advantage for a male to choose a large mate is dubious, however, because copulation occurs one or two intermolts before the release of juveniles, depending on the species; due to aging, mortality during this period is correlated with size as well as fecundity. Furthermore, ecological studies carried out on the *Jaera albifrons* complex of species[9–12] have shown that the distribution of size fluctuates seasonally in natural populations, which are of a large number of small fast-reproducing females in spring and summer, and of a small number of large slow-reproducing females in autumn and winter. In studying mate choice in these species, these variations in reproductive strategies have to be taken into account. I report here seasonal variations of mate assortment in *Jaera* and a case of non-random mating which is not correlated with size.

Nine samples of *Jaera ischiosetosa*[13] were collected at intervals of 1½ to 3½ months from the large population of Le Gouinel (northwest of Plouescat, Britanny), and reared for a week under laboratory conditions[6]. The number of individuals in each sample, and the dates of collection, are shown in the table. Individuals were distributed into several buckets, with about 200 individuals in each. One bucket, the control, was kept separate while the others, the experiments, were used for recording mate choice. Mating pairs were collected every morning at 9.00 from the experiment buckets, while about a seventh of the control was sampled at random after agitating the bucket (pairs separated during this process, and therefore, no copulating pairs were recorded). The experiment and the control were therefore begun in identical conditions, and were later sampled at the same time. In both samples, the body length of individuals of the two sexes, the physiological stage of the females and the number of eggs in their marsupium (fresh eggs and rounded developing embryos corresponding to stages A and B of Stromberg)[14] were recorded. Measurements were made using a Profilprojector Carl Zeiss (magnification × 50, precision to the nearest 0.02 mm). Measured individuals were discarded; the resulting change in the composition of the experimental sample may be considered negligible in comparison to its size (table).

The reproductive cycle of females involves two intermolts: oocytes mature in the ovaries during an intermolt 'without oostegites', and embryos develop in the ventral marsupium during an intermolt 'with oostegites'. Fertilization and egg-laying occur at the molting between, and juveniles are released at the other molting. In *Jaera ischiosetosa*, the fecundation of the female may occur at any intermolt before egg-laying. Ecological data (Veuille, in preparation) indicate that there are between two and

Mean length of mating females as compared to the control (+ standard deviation and sample size), correlation in length between males and females, and fertility differential (F.D.) (number of ovigerous females more/less fertile than predicted from the fertility curve of each control) in nine successive samples of *Jaera ischiosetosa*. Body lengths are in mm. *, $p < 0.05$; **, $p < 0.01$.

Date	5.X.1979	5.XI.1979	20.II.1980	20.IV.1980	21.VI.1980	21.VIII.1980	5.XI.1980	8.I.1981	20.11.1981
N. sample	536	> 700	1885	2134	3494	1332	793	817	709
N. pairs	84	73	85	93	108	89	58	50	32
N. control	122	115	169	173	172	124	122	152	134
Length									
pairs	2.47 + 0.28	2.37 + 0.35*	2.71 + 0.52*	2.62 + 0.46*	2.40 + 0.38	2.34 + 0.32*	2.68 + 0.39	2.84 + 0.46	2.79 + 0.49
control	2.45 + 0.35	2.51 + 0.49	2.88 + 0.68	2.81 + 0.63	2.49 + 0.50	2.22 + 0.43	2.55 + 0.44	2.96 + 0.69	2.82 + 0.74
Corr. pairs	0.37**	0.50**	0.58**	0.62	0.52**	0.32**	0.34*	0.55**	0.79**
F.D.	4/6	18/10	12/7	19/4	17/11	15/8	16/3	8/3	2/5



Number of eggs and rounded embryos in the marsupium of female *Jaera ischiosetosa* (e) as a function of body length (L, mm.). Results from the nine samples are pooled.

three sexual cycles in the lifetime of a female (several months). Precopulae are easily recorded: the male, usually smaller than the female, climbs onto her back for a period of some minutes to several hours; copulation does not necessarily occur, and sperm displacement is possible[15].

Results are shown in the table. There was no definite tendency for large females to enter into precopula, as mating females were larger than the mean from November to April and smaller in August. There was a slight but significant correlation in body length between males and females. The mean length of mating males was 25% smaller than the mean length of mating females (male/female mean length = 0.74 + 0.02); these are the best relationships in size for males to hold on to the back of females, and for them to position the genitalia in front of each other[16].

The ratio of females with oostegites was smaller in the pairs than in the control (pooled results: 28.7% + 1.7 in the pairs versus 44.2% + 1.6 in the control). This was partly a bias due to the first mating of females occurring before any cycle of oogenesis. When considering the only females larger than 2.4 mm, which all have reached maturity in every sample, the proportions are still 36.1% + 2.3 versus 65.9% + 1.7 respectively.

The fertility of females of similar size in the two groups may be easily compared, as the number of eggs in the control (fig.) is linearly related to body size (slope: 16.33 eggs/mm; intercept = −31.91 mm; correlation: 0.94; N: 332). This linearity is a possible consequence of the ovaries being two slender rows of maturing oocytes in line, end to end with the axis of the body. When the values of the mating females are plotted on the fertility curve of the control, they appear significantly more fertile than the average, i.e. most of them range above the regression line (100/68 individuals above/below the regression line, vs. 157/175 in the control; P(X2) = 0.01). Comparisons with the fertility curves computed from each seasonal sample yield the same result (table; pooled result: 108/60).

Assuming that non-random pairing in *Jaera ischiosetosa* is an adaptive outcome of sexual selection, the modalities of competition peculiar to each sex need to be considered. Competition between females depends on their rate of survival, on their generation time and on their fertility throughout adult life, while competition between males depends on the broods they contribute to. The reproductive success of a male will therefore depend on (a) the size of its mates, (b) the time elapsing between copulation and the fertilization of the eggs (hence biasing mating records towards non-ovigerous females), and (c) the fertility of its mates as compared to the average fertility (biasing mating records towards the most fertile ovigerous females); the optimal mate size is likely to vary seasonally.

Students of behavioral evolution have paid much attention to competition between members of the sex investing less in its progeny, usually through genetic material only, despite the fact that genetic variation in fitness is assumed to be very low in a natural population[17,18]. On the other hand, a wide variation in fitness is expected in the sex investing more. This variation may be purely environmental; a correlation in fitness exists, however, between individuals sharing a part of their offspring. Behavior could therefore evolve in one sex as a response to a non-genetical variation in the fecundity of the other sex: the sex investing less would evolve discrimination between members of the sex investing more. This would explain the non-random distribution of precopulae in female *Jaera*.

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Defensive alkaloid in blood of Mexican bean beetle *(Epilachna varivestis)*[1]

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Summary. The blood of the Mexican bean beetle *(Epilachna varivestis)* contains a homotropane alkaloid, euphococcinine (**1**). The beetles 'reflex bleed' when disturbed, thereby deploying the alkaloid, which is provenly deterrent to spiders and ants. Newly emerged adults lack the alkaloid, but the compound builds up to deterrent levels in their blood within days. Eggs and larvae of *Epilachna* are devoid of the compound.

Key words. Coleoptera; chemical defense; feeding deterrent; alkaloid; homotropane.