Ann. Zool. Fennici 18: 179–190. 1981

Polymorphism and reproductive strategies of Enoplognatha ovata (Clerck) (Araneae, Theridiidae) in northern Europe

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Hippa, H. & Oksala, I. 1981: Polymorphism and reproductive strategies of Enoplognatha ovata (Clerck) (Araneae, Theridiidae) in northern Europe. — Ann. Zool. Fennici 18: 179—190.

This is a study of the population structures and dynamics of the polymorphic spider *Enoplognatha ovata*. It is based on samples of females with their progeny from populations in southwestern Finland.

The populations were found to be internally heterogeneous, consisting of at least two separate groups, both of which include all three traditional colour forms of the species. The groups differ from each other in the size of the females, in the number of eggs laid and in the rate of development of the offspring. The variation in these characters between the populations is largely due to the different proportions of the groups. A few other morphological characters, i.e. the number of black abdominal spots, the colour of the egg cocoon and the size of the eggs did not correlate with these groups, with the colour forms, with the size of the female or with the number of eggs laid.

The colour polymorphism and the distribution of the population into the groups mentioned obviously arise from the same genetic basis. Of the two genes *red I* and *red II* known to affect the colour polymorphism, the red producing dominant alleles also influence the smaller size of the female, lower number of eggs and, apparently only in the case of *red I*, retarded development of the offspring. The gene *red I* is responsible for the distribution of the populations into the two above-mentioned groups. The absence of the red pattern is proposed as arising from the absence of the required allele(s) and, in addition, from the presence of a factor inhibiting the penetrance of the colour.

A general hypothesis on the roles of genes *red I* and *red II* in the heterogeneity of the populations is presented and suggestions on the adaptive value of the different phases are briefly discussed.

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1. Introduction

Due to its striking colour polymorphism and to its abundance in many habitats in Europe and eastern North America, *Enoplognatha ovata* (Clerck) has induced a degree of research unusual to a species of spiders. The existing studies cover the frequencies of the different colour forms in many European populations (Gerhardt 1921, Nielsen 1932, Bristowe 1958, Oxford 1976, Hippa & Oksala 1979), ontogenic development (Seligy 1971, Hippa & Oksala 1979), biochemical aspects concerned with the colour phases (Seligy 1969) and the genetic basis of the colour polymorphism (Geyer 1967, Tweedie 1970, Oxford 1976, Hippa & Oksala 1979).

Hippa & Oksala (1979) found that the traditional colour forms — *lineata* without red pigment, *redimita* with red dorsolateral abdominal stripes, and *ovata* with the abdominal dorsum wholly red — were only artificially discriminated. At least in most of the populations studied, there was a continuous series between the narrow *redimita* type and the *ovata* type. The simple genetic basis of the polymorphism independently presented by Geyer (1967) and Tweedie (1970), based on a single pair of alleles with incomplete dominance, the *redimita* form being the hetero-

zygote, was also found to be wrong. Instead, a genetic basis of two different genes called *red I* and *red II* was proposed. Of these, the dominant allele of *red I* causes a narrow *redimita* pattern appearing at the third juvenile instar and the dominant allele of *red II* has the potential to produce a series of red patterns ranging from the *redimita* form to the distinct *ovata* form, both of which penetrate at the ecdysis to the adult instar. The effect of *red II* results in the true colour phases not being fully distinguishable by studying adult samples of the populations. The frequencies of the alleles proved to vary between populations. The red forms appeared to be more frequent in the northern European than in the central and southern European populations, and the dominant allele of *red II* was assumed to cause the total lethality of males in the north (Hippa & Oksala 1979).

Few attempts have been made to define the biological function of the colour polymorphism of *E. ovata*. Bristowe (1958) and Oxford (1976) noted the differences in the traditional colour form frequencies between populations even within the same small geographical area. Later, we (Hippa & Oksala 1979) referred to the higher frequency of the dominant allele of *red II* in open, sunny and dry habitats than in more shady and moist ones in Finland. In addition, the experimental rearings recorded more fundamental and interesting differences between the colour morphs, viz. the apparent differences in fecundity. In 1979 we concentrated on a study of the characters of the fecundity of *E. ovata* in natural populations in order to acquire more information concerning these fundamental questions necessary to an understanding of its biology. It soon became evident that the relationship between the colour morphs and the fecundity, in particular, was not as direct as might have been expected on the basis of our earlier studies, but was far more complicated and combined with many other hitherto unknown characteristics of the spider. Although many of the ideas which arose can only tentatively be shown and documented, the results are published below because they do introduce information of basic importance to the understanding of the strategy and tactics of the existence of *E. ovata*, and because they may open prospects for understanding other, similar cases elsewhere.

2. Materials and methods

In addition to earlier published data, the present study concentrates on populations in six different habitats in the city of Turku, Finland, all in the immediate neighbourhood of the University of Turku: two are on the University Hill (Yliopistonmäki), and four at the nearby, old barracks area (Turun kasarmi). These two main areas are separated by about 500 m of built-up area. Both areas are natural, park-like areas with a wild field layer, bushes and old deciduous trees and neither is in the immediate vicinity of busy streets or heavy traffic. The characters of the individual habitats and populations are as follows:

1. University Hill: a shallow depression with a dense stand of high nettles *(Urtica dioica)* covering an area of about 6 m^2, surrounded by dry, grassy meadow; a slight north-western exposition; no shade; open to winds from all directions; density of nests over 10/m^2; collected on August 20, 1979.

2. University Hill: an approximately 20×6 m strip supporting a mosaic of bramble bushes *(Rubus idaeus)*, nettles and grassy patches about 50 m downhill from area 1; northern exposition; effectively sheltered by deciduous trees and bushes; open to winds from the north especially; average density of nests under 0.5/m^2, but sporadically over 5/m^2; collected on August 22, 1979.

3. Barracks: a grassy depression of about 100 m^2 with scattered low nettles, avens *(Geum urbanum)* and artemisias *(Artemisia vulgaris)* as suitable for the spider; shaded partly by high deciduous trees allowing sunshine from late morning, but especially during late afternoon; well sheltered from winds from all directions; density of nests under 0.5/m^2; collected on August 25, 1979.

4. Barracks: a practically pure stand of high nettles on flat ground between a gentle slope in the west and a building in the southeast, about 100 m from the former; shaded by deciduous trees from late afternoon onwards; well sheltered from winds from all directions; density of nests over 10/m^2; collected on August 25, 1979.

5. Barracks: a plot of wildly growing meadow on flat ground, with abundant low nettles and avens as suitable plants for the spider, a few metres from the high wall of an abandoned factory in the north, about 100 m from areas 3 and 4; sheltered by old deciduous trees in the northwest, north and northeast, but open to the sun from early morning till late afternoon; well sheltered from winds, especially northerly and easterly; density of nests about 20/m^2; collected on August 25, 1979.

6. Barracks: principally similar to area 5, but slightly drier and with more scattered nettles and avens, about 40 m from area 5; collected on September 3, 1979.

There is obviously gene flow between these populations, but nothing is known about the amount, and this is also outside the scope of the present paper.

The observed nests of *E. ovata*, i.e. leaf rolls (see e.g. Nielsen 1932, Bristowe 1958, Oxford 1976) including a female with her egg cocoon(s) or newly hatched second instar juveniles, were collected from the described habitats. Each nest was placed into a separate glass tube and frozen. All females observed moving in the vegetation were also collected and frozen. Later, the nests were thawed, opened and the contents analysed. The red and white colour forms and the number of black abdominal spot pairs were recorded and the length of the sternum was measured from the air-dried specimens. The number and the colouration of the egg cocoons, the number and developmental stages of the progeny and the dry weight of the eggs were also carefully measured. Where necessary, the methods, including all statistical analyses, are described in greater detail under the sections concerned.

The following symbols are used for the statistical significance: ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$, °: $P < 0.10$, no symbol: $P > 0.10$.

To avoid any confusion with the respective genes or loci the dominant alleles of the genes *red I* and *red II* are called *R I* and *R II* and the respective recessive alleles *r I* and *r II*.

Although there is a continuous series between the two traditional red forms *redimita* and *ovata*, their discrimination is useful for some purposes because the *ovata* form is known to include at least the dominant allele *R II* (cf. Hippa & Oksala 1979). The *ovata* form always comprises only those specimens without any white or yellow dorsal median abdominal markings.

3. Results and discussions

3.1. Morphological and biometrical characters of populations

Red-white colour polymorphism

The frequencies of the forms of the red-white colour polymorphism in the populations were compared by 1) contrasting only the white and red coloured forms and by 2) contrasting the three traditional forms *lineata, redimita* and *ovata*. The *ovata* form is known to include the dominant red-producing allele of at least the gene *red II* (Hippa & Oksala 1979).

The proportions of the red forms varied in different populations from 67.79 % to 80.00 % (Table 1) and they do not differ significantly in this respect. Furthermore, when the red forms are further divided into *redimita* and *ovata* there is no heterogeneity in the total material, despite the variation in the frequency of the *ovata* form between 7.69 % and 28.30 % (Table 1).

Black abdominal spots

Another abdominal colour character known to vary is the number of the paired dorsolateral black spots (cf. Seligy 1971, Oxford 1976). In rare cases the rows of spots are unsymmetrical, the most anterior or most posterior spot being missing on one side. Such unpaired spots were recorded. The number of spot pairs in different individuals varied from 4 to 7 and the means for different populations were similar (Table 1). There was, moreover, no difference in the number of spots between the red and white forms, the means being 5.51±0.04 for the red and 5.51±0.07 for the white forms ($t = 0.02$, $n = 351$).

Colour of the egg cocoon

The colouration of the egg cocoon has been mentioned as ranging from white to blue (Wiehle 1937, Seligy 1971). A similar apparent variation was also observed in our material, but when the empty cocoons were contrasted against white paper in the same illumination all of them proved to be the same dark greyish blue colour. The impression of differences was caused by the thickness of the silk wall as well as the colouration, i.e. the developmental stage, of the contents of the cocoon.

Size of females

The length of the sternum was chosen as a measure of size. It remains rigid even in dry specimens, it is rather easily measured and is usually regarded as having no allometric tendencies. The

Table 1. Frequencies of the different colour forms and the average numbers of the black abdominal spots in different populations.

Population	*lineata*		*redimita*		*ovata*		*redimita* + *ovata*		Total	Black spots	
	n	%	*n*	%	*n*	%	*n*	%	*n*	Mean	*n*
1	12	22.64	26	49.06	15	28.30	41	77.36	53	5.51±0.09	53
2	13	25.00	35	67.31	4	7.69	39	75.00	52	5.64±0.07	52
3	10	20.00	30	60.00	10	20.00	40	80.00	50	5.44±0.07	50
4	30	29.13	58	56.31	15	14.56	73	70.87	103	5.53±0.06	103
5	17	26.56	41	64.06	6	9.38	47	73.44	64	5.44±0.08	64
6	48	32.21	83	55.70	18	12.08	101	67.79	149	5.48±0.12	29
Total	130	27.60	273	57.96	68	14.44	341	72.40	471	5.51±0.03	351

measuring was done on air-dried specimens to an accuracy of 0.02 mm.

The length of the sternum varied from 0.88 to 1.44 mm the mean for the whole material being 1.142+0.004 mm ($n = 457$). If the sternum length cubed is considered to describe the relative masses, the largest individuals are about 4.4 times larger than the smallest ones. The means of the sternum length varied noticeably in the different populations (Table 2). The variation seems to depend mostly on the proportions of the alleles of the genes *red I* and *red II* in the populations and is discussed in section 3.2. below.

The size distributions in the different populations and in the total material (Fig. 1) do not differ significantly from the normal distribution,

Table 2. The mean length (mm) of sternum in different populations.

Population	Length ± *SE*	*n*
1	1.106±0.012	51
2	1.167±0.011	48
3	1.152±0.012	45
4	1.164±0.008	103
5	1.189±0.011	63
6	1.109±0.007	149

despite the two maxima in the total material. The sizes of the two main colour types, red and white, in the populations are similar, except in population 5 (Table 3), in which the white females are significantly larger than the red ones. Whether or not this can be explained by chance remains unresolved here.

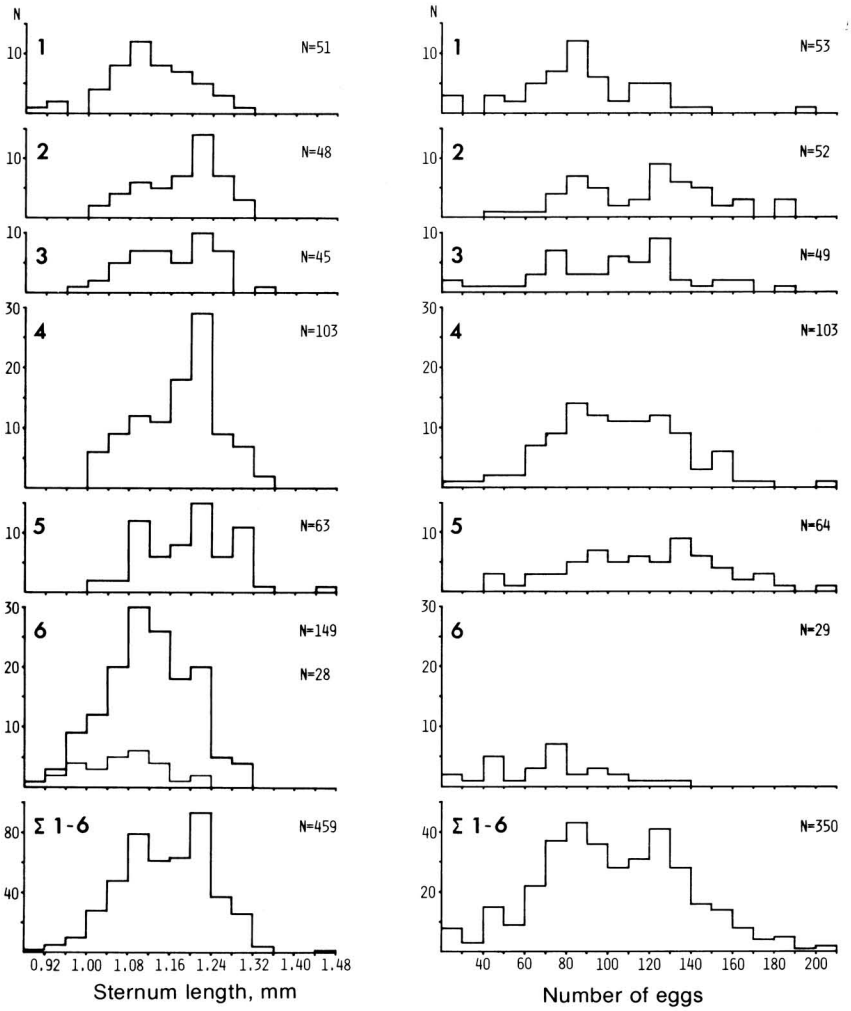

Fig. 1. Distributions of the female sternum length and the number of eggs per female in populations 1—6; in population 6 the lower diagram describes that part of the population still in their nests.

Table 3. Comparison of the female sizes (length of sternum in mm) between the two main colour forms in different populations.

Population	Colour form	Length ± *SE*	*n*	*t*
1	red	1.113±0.013	40	1.01
	white	1.084±0.028	11	
2	red	1.167±0.013	36	0.09
	white	1.165±0.022	12	
3	red	1.145±0.014	35	1.03
	white	1.174±0.022	10	
4	red	1.164±0.010	73	0.02
	white	1.164±0.013	30	
5	red	1.172±0.011	47	2.97**
	white	1.240±0.023	16	
6	red	1.105±0.013	101	0.35
	white	1.099±0.011	48	

Size of eggs

To measure the egg size, eggs and first instar juveniles were dried at +80 °C for a day and then were weighed in groups of 10—40 to accuracy of 0.001 mg. The first instar juveniles were considered to equal the weight of the eggs within the measuring accuracy: they do not feed or move and the egg shell is usually still attached to them. Egg samples were taken from the nests which had only eggs, first instar juveniles or both from the four suitable populations 1, 2, 4 and 6.

The mean dry weight of one egg was 0.0497± 0.0009 mg (n = 91) and the values of the individual populations do not differ significantly from this. In all cases the sizes of the eggs were independent of the size of the female and the number of eggs. Furthermore, from the point of view of the total material, there was no correlation between the size and the number of eggs (r=0.11) (Fig. 2), and none between the size of the eggs and the size of the female (r = 0.07). The egg sizes of the two main colour forms were also similar in all populations except population 2, in which the red females seemed to have slightly heavier eggs than the white ones (Table 4).

Number of eggs and egg cocoons

The eggs are laid as clusters and enclosed in a compact cocoon. Usually a female produces only one cocoon, but occasionally also a second. The second cocoon is produced much later than the first. It is attached to the wall of the latter and is easily recognized by its smaller size and the earlier developmental stage of the progeny.

Of the 351 nests studied, 21 (5.98 %) included two egg cocoons. Because, in the whole material, some of the females might not yet have produced the second cocoon the more probable frequency was calculated from the nests in which the juven-

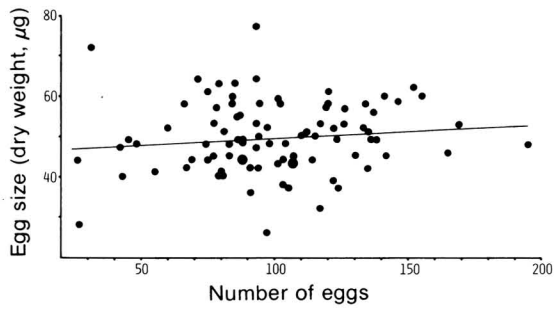

Fig. 2. Correlation of the egg size and the number of eggs produced by a female: y = 46.66 + 0.03x, r = 0.11.

Table 4. The mean dry weights (mg) of the eggs in different populations with comparisons between the main colour forms.

Population	Dry weight ± *SE*	*n*	Colour form	Dry weight ± *SE*	*n*	*t*
1	0.0471±0.0018	23	red	0.0483±0.0021	17	1.12
			white	0.0437±0.0034	6	
2	0.0504±0.0014	31	red	0.0518±0.0014	21	1.81°
			white	0.0473±0.0021	10	
4	0.0493±0.0019	29	red	0.0490±0.0025	19	0.23
			white	0.0499±0.0027	10	
6	0.0558±0.0038	8	red	0.0575±0.0045	6	0.78
			white	0.0505±0.0075	2	

iles of the first cocoon had already reached the second instar. The second cocoon had always been produced by that time in our laboratory rearings (Hippa & Oksala 1979). The material delimited in this way consisted of 191 nests, of which 12 (6.28 %) included two egg cocoons. There was no difference in their frequency between the colour forms or different populations. In our earlier laboratory experiments (Hippa & Oksala 1979) the presence of a second cocoon was significantly more frequent, occurring in 37.50 % of the nests ($n = 40$, $t = 5.59$***, $df = \infty$), and the colour forms differed slightly from each other.

The number of eggs in the second cocoon varied from 7 to 25, values similar to those of Seligy (1971), who observed from 6 to 25 eggs. The mean was 14.0±1.1 ($n = 21$) and was similar in all populations and colour forms. The mean number of eggs in the laboratory experiments (Hippa & Oksala 1979) was 14.4±1.9 ($n = 14$) and was also similar to the present field data ($t = 0.18$, $n = 35$). The mean published in that report is wrong because the number of cases *(n)* was given as 15 instead of the correct $n = 14$.

In further calculations the number of eggs in the second cocoon is added to that of the first one.

The total number of eggs laid by a female varied from 20 to 202, the mean being 102.8±1.9 ($n = 350$). Wiehle (1937) mentioned a variation from 150 to 180 and Seligy (1971) reported the mean as 100.6±19.6 *SD* (with unknown *n*), apparently from combined laboratory and field observations. In our material (Table 5), the relatively great differences between the populations seem to be primarily dependent on the genetic structure of the populations as well as the date of collection of the sample. These are discussed under sections 3.2 and 3.3.

The distribution of the number of eggs in the populations, in the different colour forms and in the sum total (Fig. 1) do not differ statistically from the normal distribution, except in population 1 which has a slight, positive skew ($G_1 = 0.597$, $t = 1.82$, $n = 53$, $df = \infty$) and a clear, positive kurtose ($G_2 = 1.764$, $t = 2.74$**, $n = 53$, $df = \infty$). The great variation in the egg numbers (standard deviations independent on the variation of the female size, $s_{y.x}$, varying from 23.7 to 30.2) together with more than one apparent maxima in the distributions (Fig. 1) may indicate that the populations are composed of at least two groups of animals differing in the egg production. This idea becomes more evident when the distributions of the egg numbers are dealt with in tributions ot the egg numbers are dealt with in correlation to the size distribution (see under 3.2.).

Table 5. The mean number of eggs per female in different populations.

Population	Number of eggs ± *SE*	*n*
1	87.4±4.3	53
2	117.0±4.7	52
3	101.8±5.1	49
4	103.9±3.1	103
5	116.9±4.5	64
6	71.9±5.3	29

Earlier, we (Hippa & Oksala 1979) noted that the females with the allele *R II* laid significantly more eggs than the white females under laboratory conditions, and that the difference was largely due to the more frequently occurring second egg cocoon in the former. The number of eggs in the females with the allele *R I* was also larger, but the difference was not statistically significant. This cannot be confirmed as such on the basis of the present field work. Within the field material the true phases cannot be distinguished, but in any case the number of eggs laid by all the red forms should surpass that of the white ones; however, no difference was observed. There is no serious reason to suspect that the results of the laboratory breeding experiments should fit the field observations, because they also differ in many other respects: the egg numbers are generally smaller in the laboratory than in the field and under laboratory conditions the second egg cocoon appeared frequently in all the colour forms, but was distinctly an exception under natural conditions (cf. Gerhardt 1921, Wiehle 1937, Seligy 1971). In any case, it is important that the differences in the potentials of fecundity in different colour forms can be directly observed under exceptional conditions.

3.2. Correlation between size of female and egg production — the internal heterogeneity of populations

The bivariate distributions of the size of the female and the number of eggs produced (Fig. 3, Table 6) in the individual populations, in the main colour forms and in the total from all populations seems to deviate from the bivariate normal distribution, which should include a clear maximum around the intersection of the means of the two variates. All the distributions in Fig. 3, estimated using the naked eye, are peculiar in

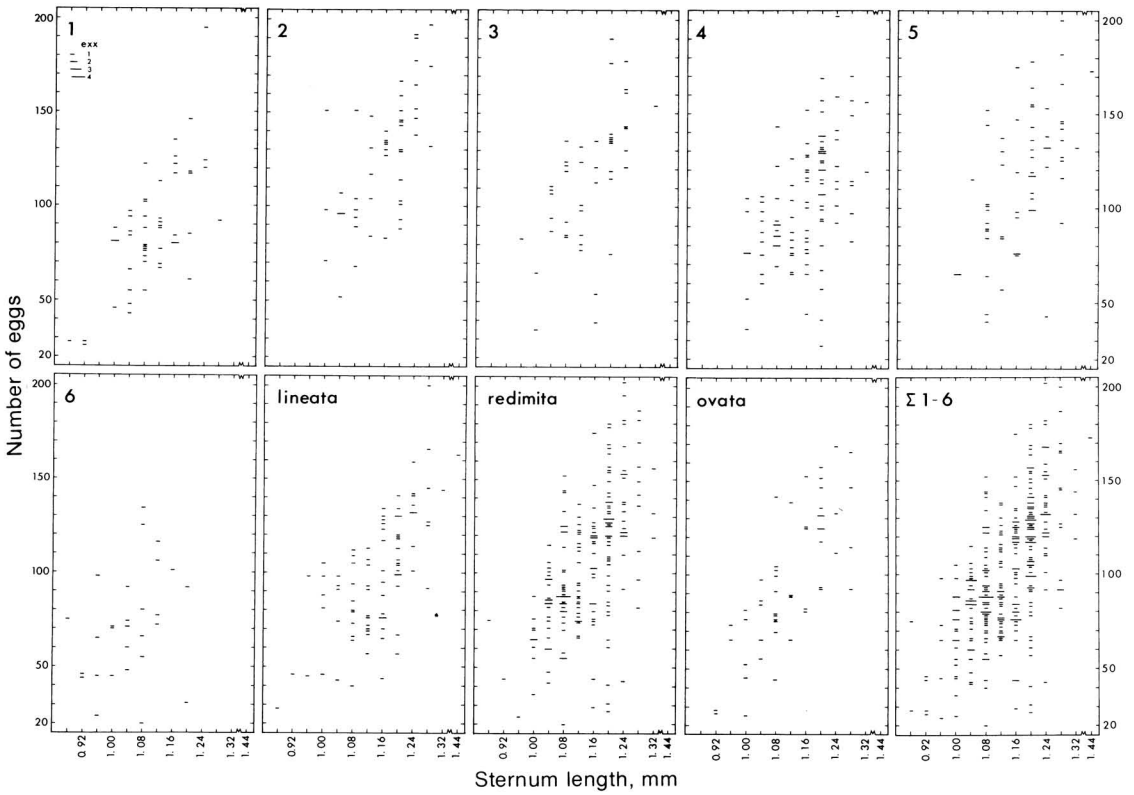

Fig. 3. Correlation between the size and fecundity (number of eggs) of the females in populations 1—6, in the colour forms *lineata, redimita* and *ovata* as sum totals from populations 1—6, and in the sum total.

having two more or less distinct maxima in the direction of the regression line and thus suggest that the populations are composed of more than one group.

The following method was used in order to test the normality of the observed distributions: Because the y-values corresponding to any given x-values are normally distributed in the bivariate normal distribution, the expected frequency of any class with given limits for both x and y ($x \pm n \cdot s_x$; x = mean, n = the coefficient of the standard deviation s_x and $y \pm n \cdot s_y$, respectively) can be calculated from the theoretical expected frequencies of the univariate normal distribution. Let the expected frequency in the univariate distribution for $x \pm n \cdot s_x$ be a (x = mean, n = coefficient of standard deviation s_x), then the expected frequency of a class with $x \pm n \cdot s_x$ as the limits for x and $y \pm n \cdot s_y$ as the limits for y is a^2 (different coefficients of the standard deviation for both variates can naturally also be used, but the calculations are simpler when using the same for both). Furthermore, within the present material it is evident that the number of eggs laid by a female depends to at least some extent on her size. That is why the standard deviation of the egg number, s_y, should possibly be replaced by the standard deviation of y independent on the standard de-

Table 6. The correlation of the size of the females and the number of eggs laid by them in different populations, different colour forms and the sum total.

Sample	r	Significance of r	n
Population 1	0.66	t = 6.17***	51
» 2	0.73	t = 7.16***	48
» 3	0.61	t = 5.07***	45
» 4	0.49	t = 5.71***	103
» 5	0.56	t = 5.27***	63
» 6	0.35	t = 1.90***	28
lineata	0.67	t = 8.30***	88
redimita	0.58	t = 10.03***	198
ovata	0.76	t = 8.25***	52
Total	0.63	t = 14.92***	338

viation, s_x, of the size; it would thus be $s_{y \cdot x}$ (the standard deviation of y in relation to the regression line). Using either of these as the standard deviation of y indicates that the distribution of the total material (1—6 in Fig. 3) differs significantly from the bivariate normal distribution: with s_y as the standard deviation of y, $\chi^2 = 19.46^{**}$, and, with $s_{y \cdot x}$, $\chi^2 = 20.44^{**}$ ($df = 5$, $n = 338$).

The other distributions in Fig. 3 are more difficult to test because the material is apparently too small to allow sufficiently precise comparisons in the area near the intersection of the means (expected frequencies under 5) and in the area between the suggested two maxima. However, as these distributions, when estimated with the naked eye, are similar to the sum total with regard to the two maxima, there is no reason to believe that their distributions are normal, either. Thus, the following conclusion derived from the analysis of the total material is regarded as applying to all of the populations and all the colour forms: the populations consist of two groups of animals (see the χ^2-values above, the distributions in Fig. 3, the great variation in the egg numbers referred to in section 3.1.), one of females of larger size, larger number of eggs and also faster developing offspring (section 3.3. below) and another with females of smaller size, smaller number of eggs and slower developing offspring. An important aspect resulting from this situation is that the calculated means and standard deviations for the sizes and numbers of eggs of the females, as well as the correlation between these variates, are much dependent on the proportions of the two groups in the populations (see the variation of the correlation coefficient in Table 6). In fact, the groups should be treated separately with their own means, standard deviations etc. for their different variates. However, our present knowledge is not sufficient to place all the individual observations in their proper groups.

3.3. Rate of development of the offspring

The field observation that the females which had already left their nests after the dispersal of their progeny seemed to be larger than those still in their nests in the same population promoted the analysis of the material in this respect, too. From the different populations, which, at the same time of the sampling, were in different developmental stages, two groups were separated for comparison (Table 7): A) the females which had only eggs or first instar juveniles or both, and B) the females with only second instar juveniles. In population 6, where a large proportion of the females had already left their nests the comparison of the sizes was made between the free running females (B) and those still in the nests (A). The result (Table 7) strongly supports the rather surprising idea that the females with their progeny at a later developmental stage were larger and had a higher fecundity than those with their progeny at an earlier developmental stage.

The result is of primary importance concerning the biological meaning of polymorphism in the species. In order to find out whether the differences were able to appear already in the rate of maturation, and hence able to affect the panmixy of the population, successive samples were collected during the maturation period of populations 5 and 6 in 1980. Comparison of the maturation of the two juvenile colour phases (total $n = 827$, number of successive samples $= 4$), caused by the gene *red I*, which also seems to be responsible for the division of the population into two groups (section 4), did not, however, reveal any difference regarding the time of maturation. Consequently, the above discussed difference appearing in the progeny must be due to the earlier egg-laying or the faster rate of development of the offspring, or to both of these in the larger females.

3.4. Productivity of females

In order to discover any possible differences in the productivity, a reproductive index, number of eggs per sternum length to the power three, was calculated for each female and the distribution of the indices was analysed. In all populations and in all colour forms the index appeared to be independent of the female size, but was positively correlated to the number of eggs due to the much greater variation in the latter. No sign of aggregation within populations could be traced. As an example of the method, the comparisons in the combined material of all the populations are presented in Fig. 4. Using a similar method, Campbell (1962) was able to show the existence of two reproductive types in the populations of the tortricid moth *Choristoneura fumiferana* (Clem.).

Although the material is too small for detailed analyses, the comparisons of the exact values of the reproductive index in different populations indicate interesting deviations. The highest index value was found in population 2, which, estimated

Table 7. Comparisons of the size (length of sternum in mm) and number of eggs between females with juveniles of earlier (A) and later (B) developmental stages in different populations.

Population	Length ± *SE*	*n*	*t*	Number of eggs ± *SE*	*n*	*t*
1 A	1.097±0.013	42	1.49	86.9±5.0	43	0.30
B	1.145±0.025	8		90.3±8.3	9	
2 A	1.151±0.012	32	1.21	110.2±5.1	37	2.19*
B	1.180±0.022	12		134.3±10.7	11	
3 A	1.156±0.025	16	0.17	96.2±10.0	18	0.86
B	1.152±0.015	21		106.7±7.4	22	
4 A	1.128±0.013	38	3.82***	96.4±4.3	38	1.94°
B	1.188±0.009	55		109.1±4.6	55	
5 A	1.142±0.018	12	2.27*	91.6±7.3	13	2.90**
B	1.201±0.013	46		122.6±5.3	46	
6 A	1.055±0.015	28	4.04***	61.3±7.4	12	2.18*
B	1.121±0.007	121		84.3±7.4	14	

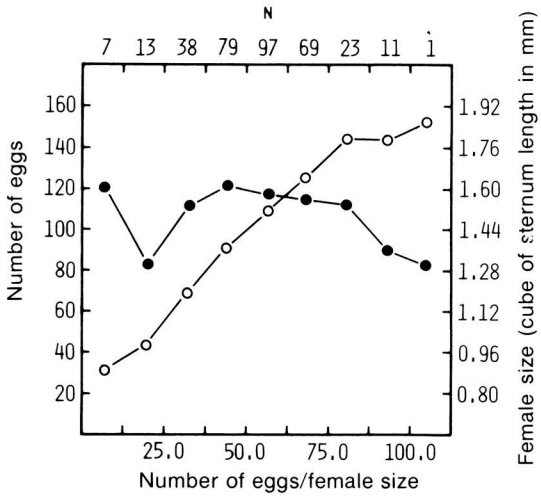

Fig. 4. Dependence of the fecundity (number of eggs) (open circles) and the size of the female (solid circles) on the reproductive index (number of eggs/female size), calculated from the summed data of populations 1—6. The material is divided into nine classes according to the index, N indicating the frequency in each class.

only according to our experience, seems to live in the most unsuitable habitat for the species when compared to the five others. The index in population 2 differs significantly from the lowest record found in population 1 ($t = 2.91^{**}$, $n = 99$). Less significant differences were found between populations 2 and 4 ($t = 2.15^{*}$, $n = 151$), between 1 and 5 ($t = 2.01^{*}$, $n = 114$) and between 2 and 6 ($t = 1.90°$, $n = 76$, $df = 40$). In consequence, these may reflect the adaptation of populations to different habitats.

4. Conclusions and a hypothesis derived from the internal heterogeneity of populations

The most important result of the present work is the internal division of the populations of *E. ovata* into the two groups best observed in the bivariate distribution of the animal size and fecundity (section 3.2.). Although these groups do not directly coincide with any of the colour forms, their common genetic basis is not eliminated. In a study of the female adult populations, the two genetically based, independent, red-patterned phases, caused by the genes *red I* and *red II*, cannot be differentiated (see above and Hippa & Oksala 1979). If either of the genes, *red I* or *red II*, is causative for the division of the population, the concept of the genetic basis of the colour form *lineata*, which also distributes into the two groups, must be modified. Although the form *lineata* has been considered to have the recessive alleles of both colour-producing genes, it must also be assumed to include a component with one or both of the respective dominant red-producing alleles, but the penetrance of the red colour is inhibited by a factor not influencing its other effects. The ommochrome pigment concerned appears red in the reduced form, but is colourless in the oxidized form (Seligy 1969). Only one enzyme would thus be enough to cause the absence of the red pattern.

Arguments have been put forward which consistently refer to the connections between the colour-producing genes and the upper and lower groups in the bivariate distribution of the size and fecundity, and by which the characters of the groups can be largely explained:

1. The proportions of the lower and upper groups can be calculated from the bivariate distribution in Fig. 3: Σ 1—6 if it is assumed that equal parts of both overlap each other. Starting from the intersection point of the means as the centre of one class, the material can be divided into classes by lines crossing the regression line perpendicularly at equal distances. When the division is made according to the perpendicular between the two maxima and through the centre of the minimum class, which in this case also goes through the intersection point of the means, 48 % will be included in the lower group and 52 % in the upper. In our earlier material (Hippa & Oksala 1979), collected from the same area as the present populations 1—6, 45 % of all the red-patterned adult females have the dominant allele *R I*. Although this is not proof, the coinciding proportions may refer to the common basis for both of the divisions and also to the correspondence of the lower group with the *R I* females.

2. In adult populations of *E. ovata*, the phenotype *ovata* is in an important position because it is known to have at least the dominant allele *R II*, whereas the animals with the *redimita* phenotype may have the dominant allele *R I* or *R II* or both (Hippa & Oksala 1979). Against this background the comparison of the size and fecundity between the two red phenotypes in the upper and lower groups of the bivariate distribution gives an interesting result. In the upper group the *redimita* and *ovata* females are similar in size (sternum 1.207±0.005 mm and 1.211±0.011 mm, respectively) and in fecundity (number of eggs 132.5±2.4 and 132.1±4.9, respectively), but in the lower group the *redimita* females are significantly larger than the *ovata* females (sternum 1.102±0.006 mm and 1.064±0.013 mm, respectively; $t = 2.84^{**}$, $df = 105$, $n_1 = 81$, $n_2 = 26$) and have a slightly larger number of eggs (78.3± 2.0 and 72.5±4.4, respectively). The result is consistent with the idea that *red I* divides the population, in which case the red females of the upper group would be homogenous in having *R II* as the only red-producing allele, whereas the lower group would be heterogenous because the red females could have either allele *R I* or *R I* and *R II*.

3. Although the dominant allele *R II* does not always produce the phenotype *ovata*, the frequency of that phenotype is evidently a valuable indicator of the frequency of the respective allele. Because, as a result of the analysis in point 2, it is apparent that *R II* is responsible for decreased size and fecundity, the higher the frequency of the *ovata* phenotype in the population, the smaller the mean size and fecundity should be. This was tested by the rank correlation (Kendall's tau) from populations 1—5 only, because, due to the late sampling date, the material of population 6 is composed almost totally of animals from the lower group of the bivariate distribution. The frequency of the phenotype *ovata* is fully negatively correlated to the mean number of eggs ($\tau = -1^{**}$) and significantly negatively correlated to the mean size of the females ($\tau = -0.8^{*}$) (for the data used, see Tables 1, 2 and 5). This result agrees well with the assumed role of the genes *red I* and *red II*.

4. The dominant allele *R I* is very rare in or totally absent from Germany (Hippa & Oksala 1979), which, according to our suggestion, would cause the populations there to be composed of only the upper group of the bivariate distribution. Wiehle's (1937) report on the variation in the number of eggs from 150 to 180 in Germany is in good accordance with our hypothesis.

5. The division of the populations into the two above-mentioned groups cannot be caused by the alleles of the gene *red II*, because the phenotype *ovata* occurs in both of the groups.

The discussion above can be summarized as the hypothesis in Fig. 5: the alleles of the gene *red I* determine the division of the population into two main groups which appear in the bivariate distribution of the size and fecundity, and which are further divided by the effect of the alleles of the gene *red II*, into four subgroups. It can be seen that, according to that hypothesis, the phenotype *ovata* occurs only in subgroups 1 and 3 and that one group of the sequence of the increasing size and fecundity is missing between them. This is made more apparent by the more distinct gap between the lower and upper groups in the size/ fecundity distribution in the *ovata* phenotype than in any other case (Fig. 3). The distribution of the phenotype *lineata* in all the subgroups is based on the inhibitor of the penetrance of the red colour suggested above.

Data have been accumulated suggesting that the visible colour polymorphism of *E. ovata* is not of primary importance to the spider, but rather a pleiotropic expression of the genes regulating the adaptation of populations to local environmental conditions and also to larger climatic regions through the size and fecundity of the animals.

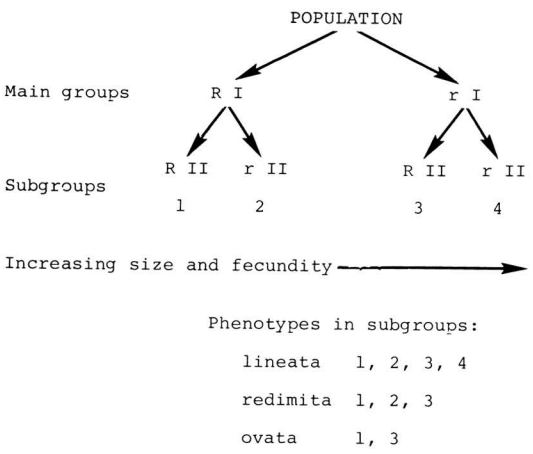

Fig. 5. Hypothetic division of the population of *E. ovata* into groups on the basis of differences in the genes *red I* and *red II*.

The abundancy of the dominant allele *R I* in northern Europe and its possible total absence from continental western Central Europe (Hippa & Oksala 1979) refer to its adaptive value in the northern environment, with an apparently more severe climate and fewer resources, and are reflected in the smaller size and lower fecundity. Similarly, the retarded rate of development of the offspring can be explained by the apparent better winter hardiness of the smaller juveniles.

The fact that the allele *R I* has not been distributed throughout all of the northern populations still requires explanation. If it is assumed that allele *r I* is kept within the population by higher fecundity, its frequencies in the populations could be expected to vary from year to year according to the climatic conditions. So far this has not been observed (cf. Hippa & Oksala 1979), but the fluctuations are not also necessarily very rapid.

The existence of the two independent systems, the genes *red I* and *red II*, with their reminiscent effects must have a special meaning. There is reason to believe that they are in a rather fixed state of equilibrium in the individual populations and that their combined effect would be of great value in adapting a population to its habitat. That the truth of the matter is something like this is also suggested by the facts known about the dominant allele *R II*. In the north, where its frequency is high, its possible homozygoty is eliminated by elimination of the *R II* males from the population (Hippa & Oksala 1979). Concerning the gene *red I*, the frequencies of the alleles are apparently balanced by the special advantages of both, as discussed above. With respect to the survival of the population, the retention of all the alleles through heterozygoty seems to be valuable. It is also easy to suggest that only the coincidence of the dominant alleles as such would have a special function in the adaptation of the population to different habitats. Because the frequencies of the alleles of *red I* are known to be rather stable over wide areas (Hippa & Oksala 1979), the adaptive characters of populations would largely be regulated by regulation of the frequency of the alleles of the gene *red II*.

Acknowledgements. We wish to thank Mr. Lasse Iso-Iivari, B. A., Turku, for computing part of our material and for much advice on statistics, and Prof. Yrjö Mäkinen, Turku, for valuable discussions concerning our trials to test the normality of the bivariate distribution. Our thanks are also due to Mr. Pekka Niemelä, Lic. Phil., Turku, for critical reading of the manuscript. The English text was kindly checked by Nigel Billany, B. Sc.

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Received 2. VI. 1981
Printed 19. XI. 1981