Heredity (1976), **36** (3), 369-381

THE COLOUR POLYMORPHISM IN *ENOPLOGNATHA OVATUM* (CLERCK) (ARANEAE: THERIDIIDAE)—TEMPORAL STABILITY AND SPATIAL VARIABILITY

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Received 28.xi.75

SUMMARY

Colonies of the visually polymorphic spider *Enoplognatha ovatum* have been studied in Nidderdale, Yorkshire, for up to six years. Morph frequencies are found to be stable within colonies between years but to vary between colonies only short distances apart. The stability of the polymorphism argues in favour of powerful selection acting on this character. The nature of the selective factors are unknown but they are not those which influence time of maturity of the spiders or the mature female population size, both of which have varied between years. A genetic basis proposed for the polymorphism is considered and rejected as being incompatible with stable morph frequencies.

1. INTRODUCTION

VISUAL polymorphisms are intriguing because they must exist for very g reasons. The argument, voiced by some in reference to enzyme polymorphisms, that the morphs may be selectively neutral and that the polymorphism is merely a stage in the replacement of one neutral allele by another (see Lewontin, 1974, for a review) can hardly apply to alleles which affect the appearance of an organism. These polymorphisms are almost certainly maintained by some form of balancing selection, although morph frequencies may be changed by stochastic processes if the population size is low and/or selective pressures are weak or by changes in the environment. There are many examples of polymorphisms which affect the colour or patterns of animals although with some notable exceptions (Ford, 1971) the selective agents are not known. One such striking colour and pattern polymorphism occurs in the spider *Enoplognatha* (*Theridion*) *ovatum* (Clerck).

This species has a wide geographical distribution, occurring throughout the British Isles (Locket and Millidge, 1974), in northern and southern Europe, south-west Asia and Japan (Bristowe, 1939), along the north-eastern and western coasts of the United States and on the south-eastern and western coasts of Canada (Levi, 1957). Typically the spider is found amongst low bushes, *e.g.* bramble (*Rubus* spp.), and in herbage such as nettle (*Urtica dioica* L.) and umbellifers where it spins a small, inconspicuous web (Bristowe, 1958).

Three basic colour morphs have been recognised (Locket and Millidge, 1953). The opisthosoma may be a creamy yellow (var. *lineatum*), creamy yellow with two dorsal carmine stripes fused anteriorly (var. *redimitum*) or creamy yellow with a solid shield of carmine on the dorsal surface (var.

ovatum) (fig. 1, A, B and C). For simplicity the morphs will be referred to as yellow, striped and red, respectively. The red and yellow colours are thought to be due to different redox states of the pigment xanthomatin (Seligy, 1969). Variation in the exact shade of the colours is considerable; the red pigment can vary from a distinct orange to a deep violet-red while

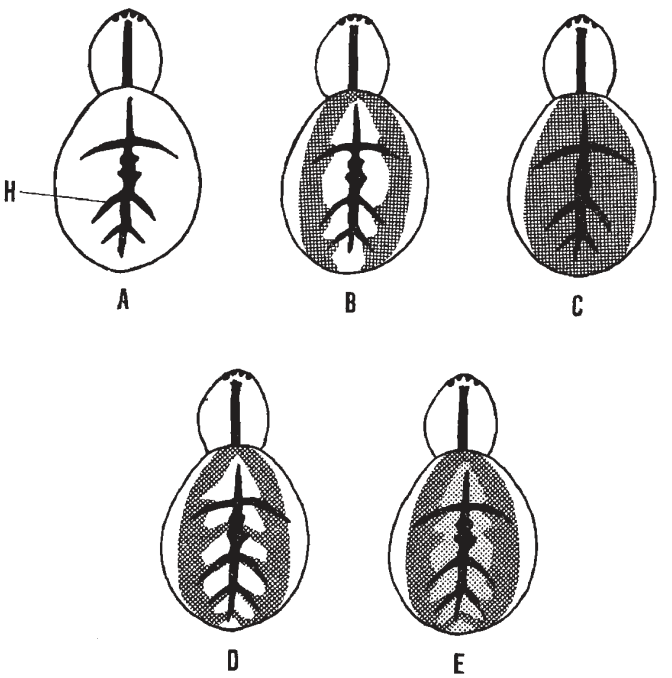

FIG. 1.—The three common colour morphs of *E. ovatum* with two intermediates from laboratory-reared material. A = yellow morph, B = striped morph, C = red morph, D and E = two intermediates between striped and red morphs. Heavy shading represents carmine, light shading represents pale pink, white represents yellow. H = heart.

the shade of yellow can vary from deep to very pale. Often yellow individuals have slightly darker yellow stripes in the positions of the carmine stripes of the striped morph. In the striped form the red pigment may have smooth outlines or it may project as a series of spikes into the central yellow shield. These projections may fuse in the mid-dorsal line to give chevrons pointing anteriorly—a condition common in laboratory-reared spiders (fig. 1, D). In some populations individuals may have additional black stripes which, in the striped morph, can obscure the red pigment except for a small triangle at the anterior end.

In addition to the colour variation, the opisthosoma can bear black spots which form two rows, originating near the spinnerets and passing over the dorsal surface following the outer edge of the red pigment in red and striped forms. The maximum number of spots per row is six although there are very often fewer, many individuals having none. Yet another variable character is the colour of the silk used in making the cocoon after egg laying. Some females produce white cocoons which remain white throughout while others

produce initially white cocoons which gradually turn a shade of grey or blue (Nielsen, 1932; Seligy, 1971). The underlying basis for this variation and the spotting is not known.

This paper is concerned with the temporal stability and spatial variability of the colour polymorphism in colonies of the spider situated near Pateley Bridge in Nidderdale, Yorkshire.

2. Inheritance of the colour morphs

At least two authors (Geyer, 1967; Tweedie, 1970) have presented data which they interpret as showing that the three colour morphs are produced by two alleles with no dominance; yellow and red morphs are regarded as homozygotes and the striped morph as the heterozygote. This conclusion is, in both cases, based on an analysis of the proportions of each morph given by Bristowe (1958, p. 217) from a countrywide survey. The analysis consists of showing that the proportions of the three morphs actually found fit the expected proportions if it is assumed that two alleles are involved and that the " population " is in Hardy-Weinberg equilibrium.

In neither paper was the homogeneity of the separate collections made by Bristowe questioned, a condition which must hold if calculations based on the grand total are to be valid. In fact, a breakdown of most of the collections (3804 out of 4228 individuals quoted by Bristowe (1958)) was given in an earlier paper (Bristowe, 1931). Comparisons of collections from each locality show them to be highly heterogeneous so that totalling across collections is not legitimate. The grand totals for each morph given by Bristowe (1958) happen, by chance, to fit the expected proportions derived from the Hardy-Weinberg law since the separate collections often deviate widely from the morph distributions expected on this basis. Clearly it is unwise to draw inferences about the genetic control of the colour polymorphism from data of this sort.

3. Sampling methods

All of the populations investigated in the present study were sampled in late July or early August when females had enclosed themselves and their cocoons within rolled leaves. Males, by this time of year, are nearly all dead and so counts are almost exclusively of gravid and nursing females. Rolled leaves were gently opened and the phenotype of the enclosed spider, the presence or absence of a cocoon and, if present, the colour of the cocoon were scored. Sampling started at one end of the vegetation patch and proceeded to the other. In this way, because of the stationary nature of the spiders, none was scored twice and few were missed. The total number counted therefore represents approximately the mature female population size within that particular stretch of vegetation.

The panmictic area for *Enoplognatha ovatum* is difficult to estimate as the young disperse on gossamer in their second instar and mature males can parachute for several hundred metres (Seligy, 1971). Seligy (*loc. cit.*) mentions dispersal radii of between 2·5 and 600 m for second instars but he does not discuss the method used to arrive at this estimate. In the present study a vegetation strip up to 40 m long was regarded as containing a panmictic population and in most cases an analysis of phenotype

frequencies along the length of the site does not counter this assumption. In successive years, exactly the same stretch of vegetation was searched for spiders.

All of the sampling sites are situated such that they receive light, wind, etc., only from certain directions. Site F is on a low roadside bank while the rest back on to dry stone walls flanking roads or tracks. Table 1 gives information on the altitude, aspect, length and vegetation of each sampling site and fig. 2 shows their relative positions.

TABLE 1

Descriptions of the Nidderdale sampling sites

Site	Altitude ft (m)	Aspect	Length (m)	Vegetation
A	860 (262)	E.S.E.	18·6	Bramble clump (*Rubus spp.*), bracken (*Pteridium aquilinum*) at north end.
B	902 (275)	S.S.E.	10·2	Bramble clump bordered on three sides by long grass.
C	905 (276)	S.E.	4·6	Bramble clump adjacent to site B.
D	785 (239)	S.S.E.	8·0	Open bramble clump bordered by long grass on three sides.
E	912 (278)	S.E.	9·3	Bramble clump bordered by long grass on three sides.
F	812 (247)	S.	*c.* 8·0	Scattered bramble interspersed with long grass on roadside bank.
G	875 (267)	S.S.E.	11·2	Bramble clump, rather open with interspersed long grass.
H	842 (257)	S.S.E.	9·3	Scattered raspberry (*Rubus idaeus*) and bramble in long grass.
I	881 (268)	S.S.W.	8·4	Bramble patch with scattered nettles (*Urtica dioica*) in long grass.
Ja	1027 (313)	E.S.E.	8·4	Hedge woundwort (*Stachys sylvatica*) in long grass. Some raspberry at north end.
Jb	1029 (314)	E.S.E.	13·0	Raspberry patch with some hedge woundwort and long grass.
K	980 (299)	E.S.E.	24·3	Dense willowherb clump (*Epilobium angustifolium*) with long grass.
L	848 (258)	E.	*c.* 20·0	Scattered bramble in long grass.
M	854 (260)	S.S.E.	6·5	Scattered raspberry in long grass.
N	1075 (328)	E.N.E.	39·1	Dense raspberry with a pure stand of bracken in the centre of the site.
O	886 (270)	S.S.W.	12·1	Open bramble with interspersed nettle and long grass.
Q	923 (281)	S.E.	10·2	Bramble clump bordered on two sides by long grass.
R	918 (280)	S.E.	15·8	Dense bramble clump bordered with long grass. Continuous with Q.

4. RESULTS

The numbers of spiders of each phenotype are given for the 18 sites in table 2. Figure 3 illustrates the proportions of each morph totalled over all years.

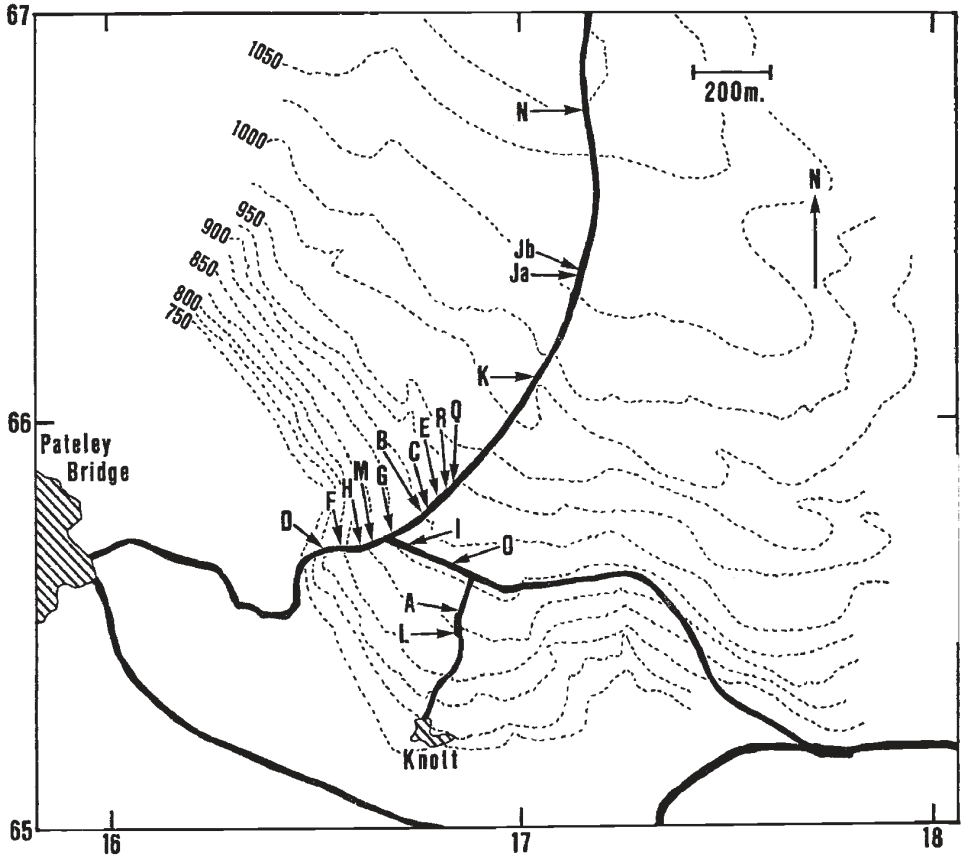

FIG. 2.—A map of the area of Nidderdale containing the sampling sites showing the exact positions of each sample in relation to roads (black) and inhabited areas (hatched). Contours are in feet and the marginal numbers are kilometre squares of the Ordnance Survey (Map ref. of south western corner is SE158650).

(i) *Internal homogeneity of the samples*

Samples were tested for internal homogeneity by dividing the total number of spiders from a colony into halves, quarters or eighths, depending on sample size. As density differences along the vegetation were, with one exception, small, the first quarter of the scores represents the spiders occupying the first quarter of the vegetation and so on. Numbers of spiders of each morph in each sub-section were tested against those in other sub-sections of the site with an $r \times c$ contingency χ^2. Where the total was not divisible by two, four or eight, odd spiders were omitted from between sub-sections. For example, if 85 spiders were sampled they could be divided into two halves each of 42 individuals. The remaining individual would be omitted by counting spiders 1 to 42 as being the first half and spiders 44 to 85 as being the second. Where numbers of striped and red morphs were small they were combined. The site which obviously varied in the density of individuals along its length was N which contained only yellow spiders (table 2).

TABLE 2

Numbers of the three phenotypes in each sample

		Yellow		Striped		Red		
Colony	Date	N	%	N	%	N	%	Total
A	27.7.70	137	87·8	18	11·5	1	0·6	156
A	27.7.71	100	84·0	19	16·0	0	0	119
A	23.7.72	48	88·9	6	11·1	0	0	54
A	11.7.73	86	87·8	12	12·2	0	0	98
A	14.8.74	258	83·2	52	16·8	0	0	310
A	28.7.75	81	82·7	17	17·3	0	0	98+†
B	27.7.70	290	74·3	42	10·3	58	14·9	390
B	27.7.71	476	76·4	46	7·4	101	16·2	623
B	23.7.72	72	75·0	14	14·6	10	10·4	96
B	11.7.73	80	80·8	8	8·1	11	11·1	99
B	14.8.74	324	75·2	40	9·3	67	15·5	431
B	28.7.75	75	76·5	9	9·2	14	14·3	98
C	11.7.73	11	84·6	0	0	2	15·4	13
D	11.7.73	56	84·8	10	15·2	0	0	66
D	22.8.74	59	76·6	18	23·4	0	0	77
E	14.8.74	106	74·6	13	9·2	23	16·2	142
E	29.7.75	17	85·0	0	0	3	15·0	20
F	22.8.74	16	94·1	1	5·9	0	0	17
G	22.8.74	100	86·9	11	9·6	4	3·5	115
G	29.7.75	95	89·6	8	7·5	3	2·8	106
H	22.8.74	22	71·0	9	29·0	0	0	31
H	29.7.75	29	64·4	15	33·3	1	2·2	45
I	22.8.74	42	72·4	16	27·6	0	0	58
I	27.7.75	52	71·2	21	28·8	0	0	73
Ja	22.8.74	60	65·2	32	34·8	0	0	92
Ja	28.7.75	52	58·4	37	41·6	0	0	89
Jb	22.8.74	288	67·3	140	32·7	0	0	428
Jb	28.7.75	215	71·2	87	28·8	0	0	302
K	29.7.75	137	86.2	15	9.4	7	4.4	159
L	29.7.75	114	78·6	31	21·4	0	0	145
M	29.7.75	15	78·9	4	21·1	0	0	19
N	29.7.75	50	100·0	0	0	0	0	50
O	29.7.75	149	87·1	21	12·3	1	0·6	171
Q	28.7.75	22	73.3	8	26·7	0	0	30
R	28.7.75	10	58·8	3	17·6	4	23·5	17

† Only part of the population was sampled—see text.

All except one colony in one year were shown to be homogeneous by this method. The aberrant sample was from site Jb in 1975 ($\chi^2_{(3)} = 11{\cdot}3162$, $0{\cdot}05 > P > 0{\cdot}01$).

(ii) *Temporal stability of morph frequencies*

Sites A, B, D, E, G, H, I, Ja and Jb have been sampled in at least two years. *Enoplognatha* is an annual with discrete generations so these samples represent two or more successive generations. Homogeneity between years was tested as before with an $r \times c$ contingency χ^2, red and striped morphs being combined when expected numbers were small. In all cases samples taken from the same site in different years were homogeneous.

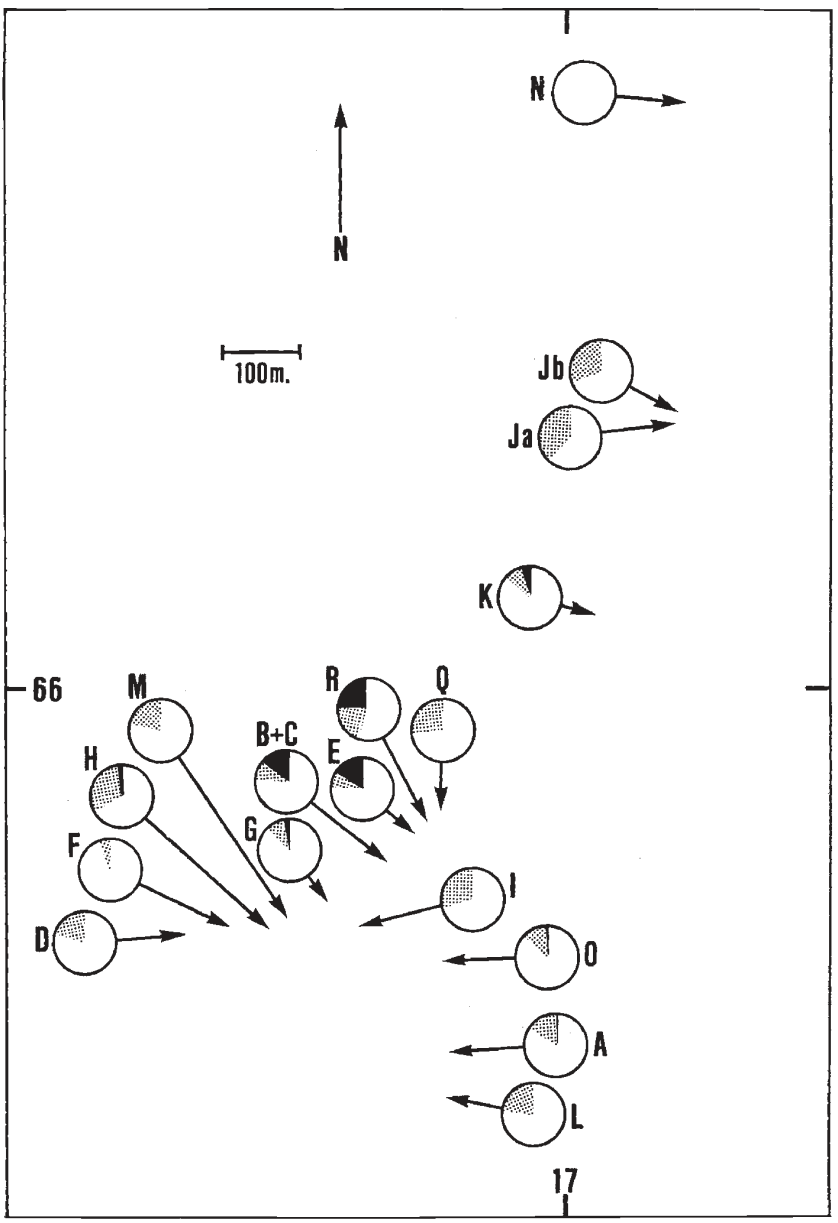

FIG. 3.—A map showing the frequencies of the three colour morphs in each colony summed over all years. White segments represent the frequency of the yellow morph, the dotted segments the frequency of the striped morph and the black segments the frequency of the red morph.

(iii) *Spatial variation in morph frequency*

The most obvious feature of fig. 3 is the region in the centre of the area with a relatively high frequency of red, a morph which is very rare or absent in the peripheral colonies. There seems to be regular variation in the frequency of this morph along a line running from south-west to north-east. In the extreme south-west red is absent. It increases in frequency as one passes north-westwards reaching a high at sites B, E and R only to decrease again to nothing at sites Ja, Jb and N. The increase in the proportion of the red morph seems to be at the expense of striped in some colonies but at the expense of yellow in others. Site Q contains no red spiders yet is contiguous with site R which has a relatively high frequency of this morph. Although numbers of individuals in these samples are small, Fisher's exact test for number of reds against number of yellow plus striped in the two collections indicates that the differences are significant ($P = 0{\cdot}0133$).

5. Discussion

Samples of *Enoplognatha* taken over six generations from sites A and B indicate that the colour polymorphism is stable rather than transitory. Data from other colonies sampled for shorter periods support this conclusion. In contrast to the stability of morph frequencies two other population parameters have varied widely—the population size of mature females and the proportion of females with cocoons at the time of sampling.

The mature female population size has varied by a factor of six at both sites A and B although the fluctuations are not significantly correlated in the two ($r = 0{\cdot}4684$, d.f. $= 3$, $P > 0{\cdot}05$). Unfortunately only five years' data can be used for this calculation since part of the population at site A was not counted in 1975 due to a fault in the recording equipment. The factors which determine population size are not known but they clearly do not differentiate between the three colour morphs as the proportions of these have remained stable throughout.

In the six years that the Nidderdale colonies A and B have been studied the proportion of females with cocoons at the time of sampling has varied markedly (table 3). Part of this variation is due to slightly different sampling dates but most must result from weather conditions advancing or retarding the onset of maturity in these spiders. This suggestion is strengthened by the fact that males have only been collected in years when the proportion of females with cocoons was very low (site A, 11·1 per cent males in 1972, 6·1 per cent in 1973; site B, 11·4 per cent males in 1972). Males die fairly soon after reaching maturity so the presence of males in these years points to the onset of maturity being retarded. In the years when samples were taken in late July (1970, 1971, 1972 and 1975) cocoons have been present in from 0 to 100 per cent of spider leaves. The proportions of females with cocoons in Colonies A and B are highly correlated ($r = 0{\cdot}9449$, d.f. $= 4$, $0{\cdot}01 > P > 0{\cdot}001$), showing that colonies with very different morph frequencies react in the same way to these conditions. Colonies sampled for shorter periods show the same trends (fig. 4). A direct demonstration that the weather conditions which influence cocoon production do not differentially affect the colour morphs is provided by a comparison of the proportion of cocoons from each morph within a colony. In only one case (Nidderdale E, 1975) was there a

significant difference between morphs (red versus yellow, $P = 0{\cdot}031$) although in some samples statistical tests were not possible.

It is obvious that, to some extent, the population sizes recorded could depend on the degree of maturity of individuals since only those advanced

TABLE 3

Cocoon production of the colour morphs

		Yellow		Striped		Red		Total	
Site	Date	%†	N‡	%	N	%	N	%	N
A	27.7.70	100·0	137	100·0	18	100·0	1	100·0	156
A	27.7.71	99·0	100	94·7	18	—	—	98·3	118
A	23.7.72	2·3	43	0	5	—	—	2·1	48
A	11.7.73	10·0	80	25·0	12	—	—	11·9	92
A	14.8.74	94·6	258	98·1	52	—	—	95·2	310
A	28.7.75	65·4	81	58·8	17	—	—	64·3	98
B	27.7.70	73·4	290	71·4	42	74·1	58	73·3	390
B	27.7.71	89·7	476	93·5	46	90·0	101	90·0	623
B	23.7.72	0	63	0	13	0	9	0	85
B	11.7.73	23·1	78	12·5	8	0	11	19·6	97
B	14.8.74	84·9	324	85·0	40	83·6	67	84·7	431
B	28.7.75	61·3	75	22·2	9	64·3	14	58·2	98
C	11.7.73	9·1	11	—	—	0	2	7·7	13
D	11.7.73	35·1	57	22·2	9	—	—	33·3	66
D	22.8.74	96·6	59	100·0	18	—	—	97·4	77
E	14.8.74	86·8	106	69·2	13	95·6	23	86·6	142
E	29.7.75	76·5	17	—	—	0	3	65·0	20
F	22.8.74	93·7	16	100·0	1	—	—	94·1	17
G	22.8.74	99·0	100	100·0	11	100·0	4	99·1	115
G	29.7.75	63·1	95	87·5	8	50·0	2	64·1	106
H	22.8.74	100·0	22	100·0	9	—	—	100·0	31
H	29.7.75	100·0	29	100·0	15	100·0	1	100·0	45
I	22.8.74	97·6	42	100·0	16	—	—	98·3	58
I	29.7.75	82·7	52	80·9	21	—	—	82·2	73
Ja	22.8.74	96·7	60	100·0	32	—	—	97·8	92
Ja	28.7.75	72·5	51	67·6	37	—	—	70·4	88
Jb	22.8.74	93·7	288	95·7	140	—	—	94·4	428
Jb	28.7.75	65·9	214	69·0	87	—	—	66·8	301
K	29.7.75	83·9	137	80·0	15	71·4	7	83·0	159
L	29.7.75	73·7	114	74·2	31	—	—	73·8	145
M	29.7.75	100·0	15	100·0	4	—	—	100·0	19
N	29.7.75	52·0	50	—	—	—	—	52·0	50
O	29.7.75	81·1	148	90·5	21	100·0	1	82·3	170
Q	28.7.75	86·4	22	62·5	8	—	—	80·0	30
R	28.7.75	70·0	10	66·7	3	50·0	4	64·7	17

† % of spider leaves with cocoons.

‡ Numbers of female spiders examined, where these totals do not agree with those in Table 2 some males were also found in the sample.

enough to roll leaves were counted (although odd spiders seen in the general vegetation were also scored). If stage of maturity was the only cause of fluctuations in total numbers from year to year there should be a strict positive relationship between the proportion of spiders with cocoons and the population size. At both sites A and B correlations between these two parameters are not significant ($r = 0{\cdot}615$, d.f. $= 3$ and $r = 0{\cdot}802$, d.f. $= 4$ respectively, proportions converted to angles), suggesting that factors in

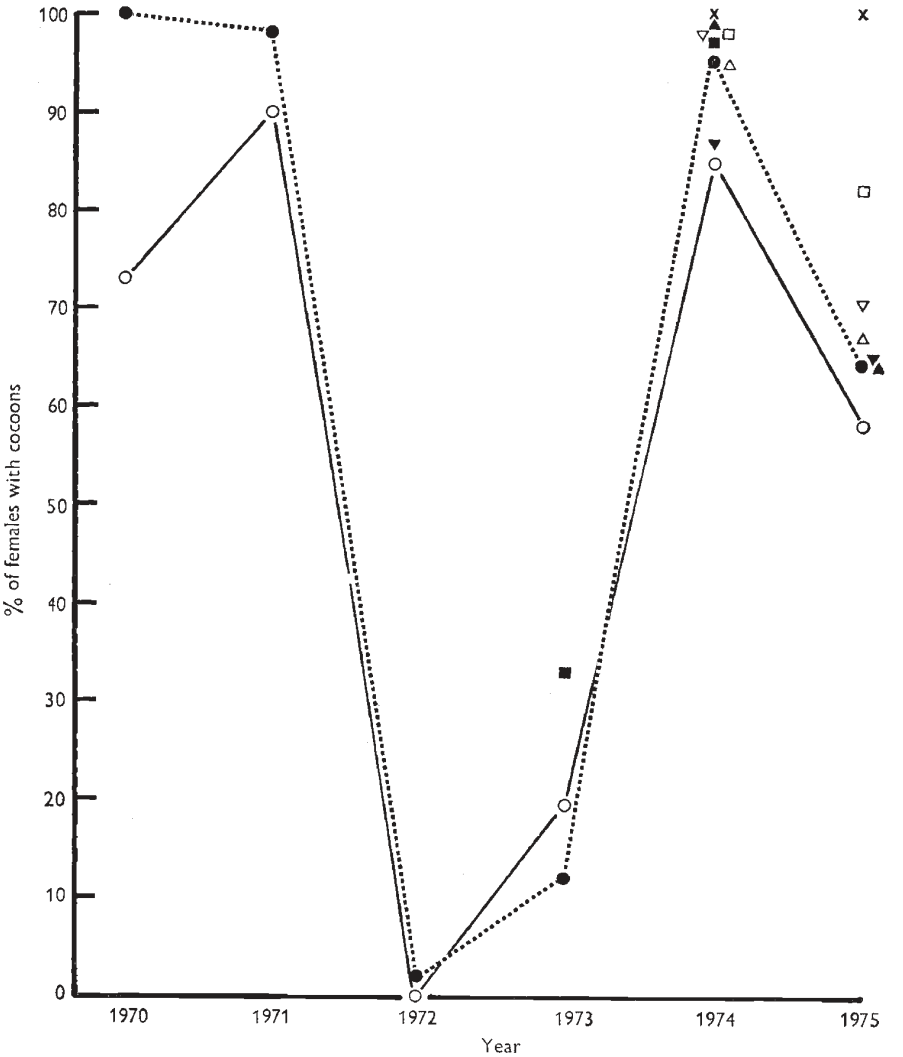

FIG. 4.—The relationship between the proportion of females with cocoons in each colony for each sampling year. Closed circles—A, open circles—B, closed squares—D, open squares—I, closed triangles—G, open triangles—Jb, closed inverted triangles—E, open inverted triangles—Ja, crosses—H. Only colonies sampled in at least two years are included.

addition to stage of maturity may be influencing estimates of the female population size.

Meteorological data are not available for this area of Nidderdale; the nearest weather stations are at Malham (map ref. SE893672, altitude 395 m), 27 km to the west, Leeming (map ref. SE305890, altitude 32 m), 27 km to the north-east and Ilkley (map ref. SE125478, altitude 83 m), 19 km to the south. Attempts to correlate the proportion of females with cocoons at sites A and B in any year with monthly mean maximum, mean minimum and mean daily temperatures, total rainfall, mean daily hours of sunshine and

number of days on which grass temperatures were below 0°C (Meteorological Office monthly weather reports (1970-1974) were unsuccessful. That very local effects can be important in this respect is shown by the spread of values between colonies for 1974 and 1975 (table 3, fig. 4).

The apparent uniformity of response of the colour morphs to environmental influences contrasts sharply with the dramatic changes in morph frequencies which occur over very short distances at Nidderdale. For example, the frequency of the red morph drops from 15·5 per cent at site B to 0 per cent at site I, a mere 70 m away. Even more remarkable is the significant difference in the frequency of the same morph between sites R and Q (23·5 per cent and 0 per cent respectively) which are in the same stretch of bramble and abut on to one another. Considering the potential for gene flow in these animals (see Sampling methods), such disparate morph frequencies argue in favour of powerful selection. Unfortunately further sampling sites, for example between K and J and J and N, are unlikely to be discovered since the roadside vegetation is unsuitable for *Enoplognatha* and the land east and west of the road is either pasture or, towards site N, moorland. Thus from a distributional point of view little new can emerge and a further understanding of the polymorphism must come from other sources.

The genetic basis of the colour polymorphism is not known but an analysis of the data from the Nidderdale sites can suggest what it is *not* likely to be. Initially, let us assume that the two allele, no dominance hypothesis suggested by Geyer (1967) and Tweedie (1970) is correct. On this assumption allele frequencies between years at sites A and B are homogeneous when tested by the chi-squared method of Workman and Niswander (1970) and so calculations can be made on the grand totals. From the observed numbers of each morph allele frequencies of Y, the "yellow" allele and R, the "red" allele, can be found and hence the expected numbers of each morph calculated according to Hardy-Weinberg proportions. Observed and expected numbers are not significantly different at site A ($\chi^2_{(1)} = 3{\cdot}464$, $P > 0{\cdot}05$) but at site B there is a massive deficit of putative heterozygotes (table 4).

Allele frequencies in this population appear to be at equilibrium so the

TABLE 4

Observed and expected numbers and relative fitnesses of the genotypes assuming a two allele, no dominance basis for the colour polymorphism

	Site B			
	Yellow	Striped	Red	Total
Observed numbers	1317	159	261	1737
Expected numbers	1122·7446	547·5024	66·753	1737
Relative fitnesses	0·300	0·074	1	—
Selective coefficients	0·700	0·926	0	—

f Y = 0·80397 f R = 0·19603

Comparison of observed and expected numbers $\chi^2_{(1)} = 874{\cdot}534$, $P \ll 0{\cdot}0001$

	Site Jb			
	Yellow	Striped	Red	Total
Observed numbers	503	227	0	730
Expected numbers	520·6433	119·7126	17·6441	730
Relative fitnesses	0·816	1	0	—
Selective coefficients	0·184	0	1	—

f Y = 0·84452 f R = 0·15548

Comparison of observed and expected numbers $\chi^2_{(1)} = 24{\cdot}737$, $P < 0{\cdot}0001$

quotient of observed numbers over expected numbers can be used to give a rough estimate of the relative fitnesses and the selective coefficients associated with each morph (Lewontin and Cockerham, 1959). In Colony B, if the red morph is assumed to have a relative fitness of 1 ($s = 0$) (table 4), then the yellow morph has a fitness of 0·3 ($s = 0{\cdot}7$) and the striped morph has a fitness of only 0·074 ($s = 0{\cdot}926$). That is to say, about 93 per cent of striped spiders produced each generation must die before the population is sampled the following year.

The assumptions implicit in these calculations are that morph frequencies are the same in both sexes and that mating is at random. Contrary to the opinion of Gerhardt (1921), who claimed that the red morph does not occur in males, the small samples of mature males obtained from Nidderdale and elsewhere show morph frequencies similar to those in females. There is no evidence for or against random mating. Strong positive assortative mating *could* explain the distribution of phenotypes at Site B but not, for example, at site Jb (table 4), where only complete *negative* assortative mating between striped and yellow morphs would produce a total lack of reds.

If the genetic hypothesis of Geyer and Tweedie *is* true then selection must be very powerful indeed. At site B selection would favour any mechanism which would reduce the frequency of red × yellow matings since only about seven per cent (relative to the other morphs) of the young from such a mating will reach maturity. Over the last six generations there is no indication that the proportion of the striped morph at site B is anything but stable (table 2). Clearly this stability is inconsistent with the prediction of strong disruptive selection. This suggests that the simple genetical model proposed for the polymorphism by Geyer (1967) and Tweedie (1970) is wrong, at least in these colonies.

Few results have been obtained from breeding experiments carried out so far. High juvenile mortality and cannibalism mean that very low numbers of spiders reach maturity. The few data that are available indicate again that the Geyer-Tweedie hypothesis is at least sometimes incorrect. Thus, two striped females collected from the wild with their cocoons (the males are therefore unknown) gave rise to all yellow offspring (deviation from a 1:1 ratio is measured by $P = 0{\cdot}0156$ in both cases). Also, a few red females produced young some of which were yellow. Neither of these results, especially the latter, is consistent with the two allele, no dominance model. Other females did produce the expected phenotypes but because of low numbers and the possibility that females may mate more than once (Bristowe, 1941) the ratios of the morphs are meaningless. That red females can give rise to yellow offspring suggests that either red or yellow must be dominant in some individuals.

Another complication raised by the breeding work is that individuals with colour patterns intermediate between striped and red (fig. 1, D and E) occur regularly in the laboratory but they are extremely rare in the wild. Of the 1737 spiders scored at site B, for example, only two have been in any sense intermediate between striped and red. This raises the question of possible environmental influences on the expression of alleles responsible for colour and pattern.

The visual polymorphism in *Enoplognatha ovatum* exemplifies the pitfalls encountered in deducing the genetics of morphs merely from an examination of their frequencies in a few populations sampled on a single occasion.

Samples from the same colonies taken in successive generations can at least indicate whether the polymorphism is stable or not and can, as in the present case, eliminate some modes of inheritance. The temporal stability of morph frequencies in the Nidderdale colonies when contrasted with the spatial variability between sites suggests that these frequencies are determined by very *stable* selective forces. The nature of the selective agent(s) is not yet known. There are no obvious relationships between morph frequencies and any of the variables listed in table 1 or any correlation between changes in morph frequencies and the factors (which are also unknown) which influence the onset of maturity and population size, both of which have varied considerably over the years. Clearly, elucidation of the ecological genetics of this polymorphism will depend heavily on the success of future breeding work coupled with transplant experiments between sites and a more thorough analysis of the microclimate associated with each sampling area.

Acknowledgments.—I would like to thank Professor Mark Williamson and Dr T. J. Crawford for their comments on drafts of the manuscript. Roma Oxford assisted in the scoring of spider populations between 1970 and 1973.

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