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Visible morph-frequency variation in allopatric and sympatric populations of two species of *Enoplognatha* (Araneae: Theridiidae)

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Samples were taken from single- and mixed-species populations of two spiders, *Enoplognatha ovata* and *E. latimana*, which share visible polymorphisms. The range of colour-morph frequencies was comparable between the species but *E. latimana* had a uniformly lower proportion of individuals with black spots. Spotted *E. ovata* females were more likely to have cocoons when collected than females without spots, although in spotted individuals there was no relationship between presence of cocoons and spot number. Colour-morph frequencies varied both within and between the seven study areas, sometimes over very short distances. A similar, though less marked, pattern was shown by the black spotting phenotype. This variation, on two geographical scales, was present in both species. No evidence was found for consistent shifts in morph frequencies between allopatric and sympatric populations, and morph frequencies were not correlated between species across sympatric populations. Thus, common selective agents acting on the polymorphisms could not be demonstrated, although species-specific factors cannot be eliminated. It is possible that stochastic processes influence local morph frequencies, as has been suggested for *E. ovata* elsewhere.

Keywords: colour polymorphism, *Enoplognatha*, selection, spider, sympatric populations.

Introduction

The role of genetic drift in determining allele frequencies in natural populations has always been a controversial issue, particularly when visible variation is involved. In at least some cases, claimed examples of drift acting on visible morphs have, on closer examination, been found to involve local selective forces (e.g. Cain & Sheppard, 1950). In other instances, however, it is highly likely that stochastic influences do have major effects on allele frequencies even though the morphs they control are visibly very distinct. One well studied example concerns the colour polymorphism in the spider *Enoplognatha ovata* (Clerck) (Oxford, 1983, 1989, and references therein). Three major morphs are recognized, *lineata* has a plain yellow/cream opisthosoma, *redimita* has superimposed on this a pair of dorsolateral carmine stripes, whereas *ovata* has a solid shield of carmine on the dorsal surface (Plate 1 in Oxford, 1983). The aim of much of this work has been to elucidate factors responsible for the maintenance of the visible polymorphism and for determining morph frequencies in natural populations. Although there are indications that selection is maintaining the polymorphism and influencing morph frequencies on a gross geographical scale (Oxford, 1985a), evidence for natural selection at a local level has been elusive, despite extensive observations and experiments (Oxford & Shaw, 1986; Reillo & Wise, 1988). This has led to the suggestion that stochastic processes play a major role in determining morph frequencies in local populations (Oxford, 1989; Oxford & Shaw, 1986; Reillo & Wise, 1988). Analyses of a further two polymorphisms, one regulating the colour locus, the other determining black spotting, re-inforce this interpretation (Oxford, 1985b, 1989). However, genetic drift is a default hypothesis and it is very difficult to eliminate entirely the influence of subtle and local selection on morph frequencies.

In their revision of the '*Enoplognatha ovata*' group, Hippa & Oksala (1982) described from continental material a sibling species, *E. latimana*, which possesses

polymorphisms apparently homologous to those studied in *E. ovata* (Hippa & Oksala, 1982; Oxford, 1991; Snazell, 1983). *E. latimana* has subsequently been found in a number of areas of Britain (Oxford, 1985a, 1991; Snazell, 1983). This situation opens up a further avenue through which to explore the possible action of weak natural selection in local populations. If visible morph frequencies in mixed species populations co-vary then, barring hybridization, natural selection alone must be responsible (Endler, 1986). However, the converse is not true; if species do not co-vary, selection acting in a species-specific manner cannot be dismissed. In the present paper, I examine morph frequencies in single- and mixed-species populations of *E. ovata* and *E. latimana* in an attempt to answer the following questions: (i) within a locality, do morph frequencies of a species differ between allopatric and sympatric populations? (ii) are morph frequencies correlated between species across sympatric populations?

Methods

Collections of mature females of both species were made in south-west Wales during early August 1990. From mid-July onwards, females establish themselves within rolled leaves where they produce and guard their egg cocoons. *E. latimana* matures slightly later than *E. ovata* (Oxford, 1991; Snazell, 1983) and the sampling was timed such that all females of both species should be within leaves, thus allowing an assessment of species composition within a site. Although virtually any broad-leaved plant can be used by the spiders, the vast majority of individuals were collected from bramble (*Rubus fruticosus* agg.). A small number of males was found associated with female-rolled leaves. Specimens were located by thoroughly searching an area for rolled leaves and then preserved in 70 per cent alcohol; *E. ovata* and *E. latimana* can only be distinguished reliably by means of microscopic examination. Since the red pigment of morphs *redimita* and *ovata* fades in alcohol, individuals were sorted for colour within 24 h of collection. Later, sex, species and spotting patterns were also scored. Samples had to be taken 'blind' without knowledge of species composition, but previous arachnological work helped to locate areas containing both species.

Results

In total, 33 samples were obtained from seven different geographical areas, Freshwater West (FW), Broad Haven (BH), Orielton (O), Freshwater East (FE), West Angle Bay (WAB), Sawdern Point (SPt) and Manorbier (MAN) (Fig. 1). *E. latimana* was found in all but one area, though not always in useful numbers (Table 1). Of the 1757 females collected, 1394 (79.3 per cent) were *E. ovata*, and although several sites were found to contain *E. ovata* alone, only one small sample (FW4, $N = 16$) comprised only *E. latimana*. Fourteen males were also taken, four *E. ovata* and ten *E. latimana*. Proportions of males in the two species differ significantly ($\chi^2_{(1)} = 21.53$, $P < 0.001$). Males were not considered further.

Ignoring very small samples, the frequency of the *lineata* colour morph in *E. ovata* varied from 28 per cent at FE2 to 95 per cent at O1b. The majority of the rest were *redimita* except in FE2 where *ovata* made up 44 ± 5 per cent (1 s.d.) of a large sample, the highest frequency of this morph recorded so far in Britain (Oxford, 1985a and unpublished). Indeed, the three FE sites nearby also had relatively high *ovata* frequencies of about 17 per cent. In *E. latimana* only the *lineata* and *redimita* morphs have been found to date (Oxford, 1991; Snazell, 1983). In the present samples, again ignoring those with small numbers, the frequency of *lineata* varied from 36 per cent at BH3 to 88 per cent at O2c.

Variation within species within areas

Within each of the seven areas, colour–morph, spotting and cocoon frequencies of each species were tested for heterogeneity between sites with a log likelihood ratio (G) test (Sokal & Rohlf, 1981), or, where small samples from only two sites were involved, Fisher's exact test. Sites contributing to this heterogeneity were identified with a simultaneous test procedure (Sokal & Rohlf, 1981: 728–730), again using G. Table 2 shows the results of these tests.

First consider the colour polymorphism. With the exception of Freshwater East samples, the majority of *E. ovata* were of the *lineata* or *redimita* colour morphs and so comparisons were made between proportions of *lineata* versus non-*lineata*. In all sites except for FW, SPt and MAN, significant differences were found, sometimes over very short distances. For example, O1b and O1c are contiguous yet differ significantly in the frequency of the *lineata* and *redimita* morphs (Table 2). At Freshwater East, FE2 and FE4 are homogeneous with respect to *lineata* versus other colour morphs, and are significantly different from the other homogeneous group, FE1 and FE5 (the exclusion of FE4 from the latter group is very marginal). If one considers the *ovata* morph versus the rest then FE1, FE4 and FE5 are homogeneous and differ significantly from FE2. The distance between FE1 and FE2 is only about 80 m. Fewer comparisons were possible between *E.*

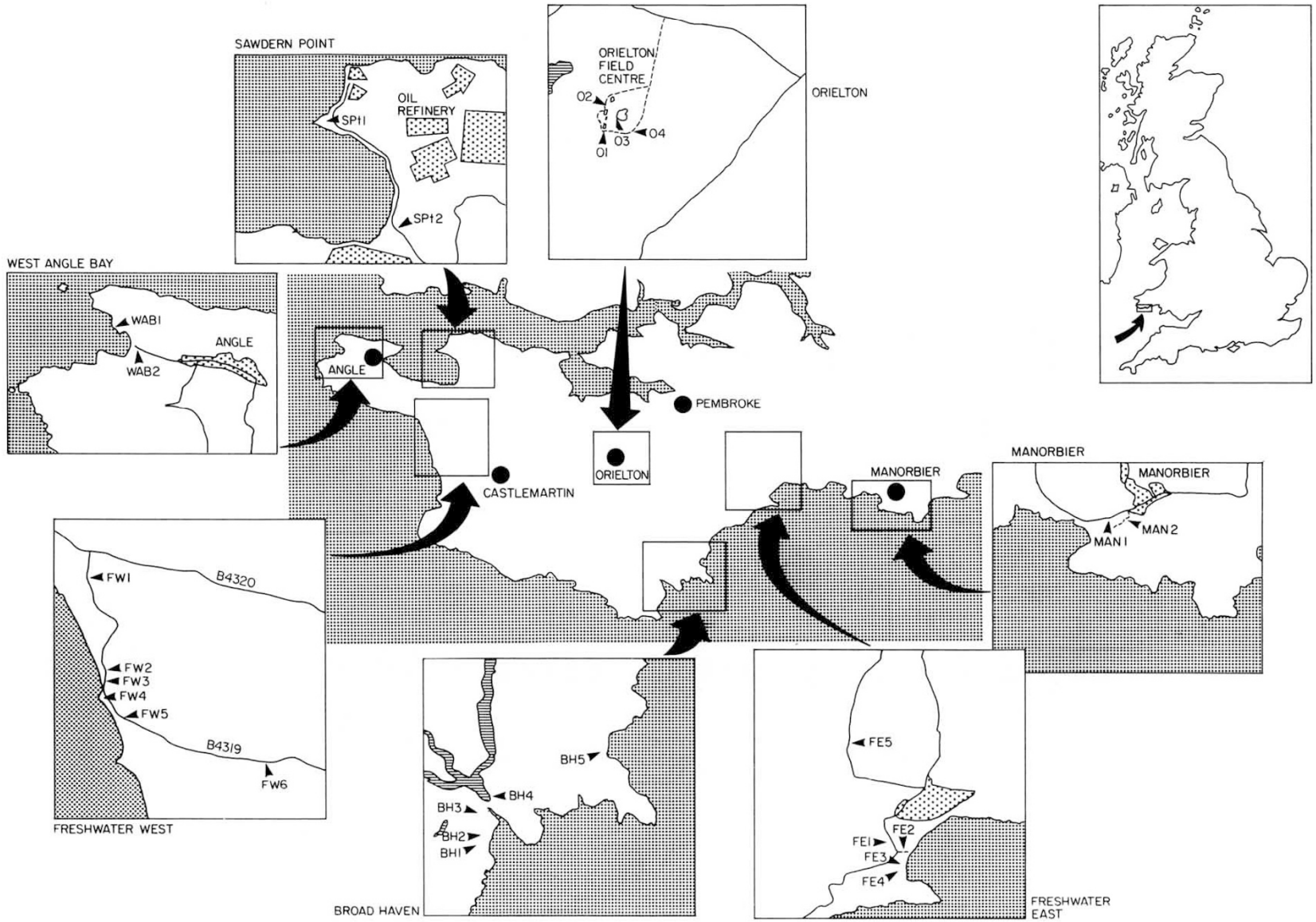

Fig. 1 Sampling sites for *E. ovata* and *E. latimana* on the Pembroke peninsula. The inset to the top right shown the position in the British Isles of the Pembroke peninsula (centre). The seven sampling areas and specific sites within them are detailed in peripheral insets and their relative locations indicated on the central map. Sea is represented by dense stippling, freshwater by horizontal lines and built-up areas by light stippling. Roads and tracks are shown as solid and pecked lines; road numbers are indicated where there are no other landmarks. All insets are 3 km from east to west with the exception of Orielton, which is 2 km, east to west. Map references for the south-west corners of the insets are as follows: Orielton, 11 950980; Sawdern Point, 12 840020; West Angle Bay, 12 880020; Freshwater West, 11 880980; Broad Haven, 11 970930; Freshwater East, 21 010970; Manorbier, 21 050960.

Table 1 Summary data from *E. ovata* and *E. latimana* populations. Sites distinguished only by a lower-case letter are contiguous. At Orielton site O2c, 22 individuals, specifically selected because they possessed cocoons, were omitted from the calculation of cocoon frequency. This was also the case for all individuals at site O2d

	Ovata				*Latimana*					*cf.spp*		
Site	N	%Y	%S	%C	N	%Y	%S	%C	%L	Col	Spot	Cocc
Freshwater West												
FW1	26	73.1	80.8	96.1	1	0	0	0	3.7	ns	ns	ns
FW2	77	61.0	70.1	84.4	—	—	—	—	0	—	—	—
FW3	8	100.0	50.0	100.0	65	60.0	0	21.5	89.0	*	***	***
FW4	—	—	—	—	16	75.0	18.7	43.7	100.0	—	—	—
FW5	7	42.9	71.4	85.7	29	44.8	6.9	37.9	80.5	ns	***	*
FW6a	48	72.9	85.4	89.6	3	100.0	33.3	33.3	5.9	ns	ns	*
FW6b	61	67.2	75.4	72.1	2	100.0	50.0	50.0	3.2	ns	ns	ns
Broad Haven												
BH1	74	63.5	75.7	85.1	7	71.4	28.6	57.1	8.6	ns	*	ns
BH2	71	38.0	73.2	69.0	—	—	—	—	0	—	—	—
BH3	44	65.9	54.5	81.8	33	36.4	12.1	39.4	42.9	*	***	***
BH4	12	66.7	58.3	100.0	2	50.0	0	100.0	14.3	ns	ns	ns
BH5	57	80.7	80.7	98.2	41	56.1	21.9	39.0	41.8	**	***	***
Freshwater East												
FE1	28	60.7	75.0	96.4	14	50.0	0	78.6	33.3	ns	***	ns
FE2	123	28.4	49.6	78.9	—	—	—	—	0	—	—	—
FE3	6	33.3	66.7	100.0	6	66.7	0	66.7	50.0	ns	ns	ns
FE4	45	35.6	55.5	100.0	7	57.1	0	71.4	13.5	ns	**	*
FE5	43	62.8	74.4	100.0	—	—	—	—	0	—	—	—
Orielton												
O1a	53	88.7	75.5	98.1	—	—	—	—	0	—	—	—
O1b	46	95.5	58.7	95.6	2	100.0	0	50.0	4.2	ns	ns	ns
O1c	28	67.8	75.0	96.4	—	—	—	—	0†	—	—	—
O2a	25	84.0	68.0	88.0	—	—	—	—	0	—	—	—
O2b	100	83.0	78.0	99.0	6	83.3	0	50.0	5.7	ns	***	***
O2c	131	84.6	71.7		61	88.5	9.8		31.8	ns	***	
	115			98.3	55			41.8				***
O2d	8	87.5	85.7	—	5	80.0	0	—	38.5	ns	**	—
O3	21	76.2	61.9	95.2	1	100.0	0	100.0	4.5	ns	ns	ns
O4	83	92.8	73.5	95.2	4	100.0	25.0	50.0	4.6	ns	ns	*
West Angle Bay, Sawdern Point and Manorbier												
WAB1a	11	90.9	72.7	63.6	—	—	—	—	0	—	—	—
WAB1b	19	73.7	63.1	47.4	—	—	—	—	0	—	—	—
WAB2	40	47.5	85.0	85.0	—	—	—	—	0	—	—	—
SPt1	20	75.0	90.0	50.0	7	42.8	0	71.4	25.9	ns	***	ns
SPt2	38	68.4	89.5	94.7	2	50.0	0	50.0	5.0	ns	*	ns
MAN1	14	78.6	71.0	100.0	45	56.0	13.3	46.7	76.3	ns	***	***
MAN2	22	95.4	91.0	100.0	4	0	50.0	75.0	15.4	***	ns	ns

N = sample size (females). %Y = per cent yellow (*lineata*) colour morph. %S = per cent black-spotted morph. %C = per cent with cocoons. %L = per cent *E. latimana* in sample. cf.spp = comparison of colour (Col), spotting (Spot) and cocoons (Cocc) between species.

ns = Non-significant. * = $0.01 > P > 0.05$. ** = $0.001 > P > 0.01$. *** = $P < 0.001$.

† = one male, but no female, *E. latimana*.

Table 2 Comparisons of character frequencies between *E. ovata* populations within areas; *lineata* for colour, presence for spotting and cocoons. Only areas/characters with significant heterogeneity are shown. For Freshwater East, the analysis was performed for both *lineata* (L) and *ovata* (O) colour morphs. Sites are arranged from left to right in order of increasing frequency of the character; those joined by a continuous line are not significantly different. Dotted lines indicate borderline cases (Freshwater East, *lineata*) or where tests could not be done

Freshwater West								
Cocoons:	FW6b	FW2	FW6a	FW1				
Broad Haven								
Colour:	BH2	BH1	BH3	BH4	BH5			
Spots:	BH3	BH4	BH2	BH1	BH5			
Cocoons:	BH2	BH3	BH1	BH5	BH4			
Orielton								
Colour:	O1c	O3	O2b	O2a	O2c	O1a	O4	O1b
Freshwater East								
Colour: (L)	FE2	FE4	FE1	FE5				
(O)	FE5	FE4	FE1	FE2				
Spots:	FE2	FE4	FE5	FE1				
Cocoons:	FE2	FE1	FE4	FE5				
West Angle Bay								
Colour:	WAB2	WAB1b	WAB1a					
Cocoons:	WAB1b	WAB1a	WAB2					
Sawdern Point								
Cocoons:	SPt1	SPt2						

latimana populations within areas and only one, between the two Manorbier sites, was significant ($P = 0.0003$, Fisher's exact test).

With regard to black spotting, heterogeneity was found between *E. ovata* populations in only two areas, Broad Haven and Freshwater East. At Broad Haven, the significantly dissimilar groupings are not those identified with respect to the colour polymorphism. At Freshwater East the groupings are the same as for *lineata* versus other colour morphs, mentioned above. For *E. latimana*, comparison between FW3, FW4 and FW5 yields a significant chi-squared value (since one observed value is zero, G cannot be calculated), although the expected numbers of spotted individuals are small and will artificially inflate the overall chi-squared value. If a comparison is made between sites with the highest (FW4) and lowest (FW3) frequency of the spotted morph, the difference is highly significant ($P = 0.006$, Fisher's exact test).

Finally, although the proportion of individuals with cocoons at the time of sampling is not a genetic trait, it can indicate environmental differences between sites which might have genetic implications. For *E. ovata*, heterogeneity between populations was found in five areas, Freshwater West, Broad Haven, Freshwater East, West Angle Bay and Sawdern Point. At West Angle Bay, the groups identified are the same as those for colour, while at Freshwater East, groups correspond to those recognized on the basis of frequency of the *ovata* colour morph. In other cases, groupings do not correspond. None of the small number of *E. latimana* comparisons within areas was significant.

Variation within species between areas

For *E. ovata*, one way analyses of variance on arcsine transformed data were used to investigate whether variation between areas in mean frequencies for the three measured characters was significant. Using all sites with sample sizes of 15 or more, F-values for colour (*lineata*), spotting and cocoons were all significant, although two were borderline ($P = 0.003$, $P = 0.04$ and $P = 0.05$, respectively).

As noted above, with the exception of Manorbier sites, *E. latimana* collections were homogeneous for colour–morph frequencies within areas, so numbers of

lineata and *redimita* were therefore summed. Comparisons between areas revealed highly significant differences ($\chi^2_{(4)} = 32.7$ if Manorbier was included, $\chi^2_{(3)} = 30.3$ if it was not; $P < 0.001$ in each case), ranging from 89 per cent *lineata* at Orielton to 49 per cent at Broad Haven. For spotting and for cocoons, comparisons between areas were also significant ($\chi^2_{(4)} = 11.5$, $0.01 < P < 0.05$, and $\chi^2_{(4)} = 20.2$, $P < 0.001$, respectively). Black-spotting frequency varied from zero at Freshwater East to 18 per cent at Broad Haven, while the frequency of spiders with cocoons ranged from 29 per cent at Freshwater West to 74 per cent at Freshwater East. Sawdern Point was excluded from all these analyses because of the small sample sizes.

Associations between characters within species

Associations were sought between pairwise combinations of colour (*lineata* vs. others), spotting and cocoons (presence/absence) within populations using 2×2 contingency tables. Significance was assessed with chi-squared when numbers were large and with Fisher's exact test when numbers were small, which they usually were. In 108 separate tests, involving both species, only one was formally significant. Trends among contingency tables were tested using Cochran's Y statistic (Everitt, 1977). Out of the six tests (three pairwise comparisons × two species) that for spotting vs. cocoons in *E. ovata* was highly significant ($Y = 3.54$, $P = 0.0004$, number of populations (n) = 24), suggesting that spiders with spots were more likely to have cocoons at the time of sampling. The corresponding comparison in *E. latimana* showed a trend in the same direction but was not significant ($Y = 1.52$, $P = 0.12$, $n = 7$). No trends were shown in either species for comparisons of colour and spotting. Colour vs. cocoons showed no trend for *E. ovata*, but for *E. latimana* it was just significant ($Y = 2.06$, $P = 0.04$, $n = 13$), suggesting that individuals of the *lineata* morph were more likely to have had cocoons when sampled. To explore further the relationship between spotting and cocoons in *E. ovata*, those spiders with spots were cross-classified according to whether they were with or without a cocoon and whether they fell above or below the median spot number for all spotted individuals within a sample. Even numbers of spiders falling in the median spot class were divided equally between the above and below categories; for odd numbers, one individual was omitted. Only 16 populations could be used and many of these had zeros or very small numbers in one or more cells of the contingency table. None of the tests was individually significant and there was no discernible trend among populations ($Y = -0.60$).

Associations between species within sites

Tests were also made to investigate whether there were significant differences between the two species when living sympatrically. The results of analysing frequencies of colour, spotting and cocoons in 2×2 contingency tables, using chi-squared or Fisher's exact tests, are indicated in Table 1. In many cases numbers of one of the species are small, and the power of the test will consequently be reduced. For colour, out of 22 comparisons two were formally significant at the 5 per cent level, one at the 1 per cent and one at the 0·1 per cent level. In all four cases *E. latimana* had a lower frequency of the *lineata* morph than *E. ovata*, although other populations do not support this trend. In five sites (BH3, BH5, O2c, FE1 and MAN1) numbers of both species were relatively large while in five others (FW3, FW5, BH1, FE4 and SPt1) one or other species was represented by only seven or eight individuals. Correlations of *lineata* morph frequencies (after arcsine transformation) in the two species in all ten sites, or in just those five with appreciable numbers, were not significant ($r = 0.291$ and $r = 0.752$, respectively).

For spotting, every one of the 22 samples containing both species showed *E. latimana* to have fewer spots, and this is formally significant in 13 comparisons, nine at the 0.1 per cent level. Correlations of arcsine-transformed frequencies of spotted individuals in the two species in all ten, or in the five larger, populations are not significant ($r = 0.167$ and $r = -0.020$, respectively).

A similar situation obtains when cocoons are considered. In all but three sites, *E. latimana* had a lower proportion of cocoons at the time of sampling; two of the exceptions were samples with only one or two *E. latimana* individuals, the third had seven (SPt1). Ten of the comparisons were significant, six at the 0.1 per cent level. Correlations of transformed cocoon frequencies between species were not significant ($r = -0.290$ and $r = 0.083$, for 10 and for five populations, respectively).

Discussion

The extensive heterogeneity in colour-morph frequency in *E. ovata*, identified both within and between the seven areas examined here, comes as no surprise. Microgeographical differentiation is one of four features common to most studies of colour variation in this species; the other three are: (i) the ubiquity of the polymorphism; (ii) the consistent rank order of colour morphs within populations i.e. *lineata* > *redimita* > *ovata*; and (iii) the temporal stability of morph frequencies within populations (Bristowe, 1931; Hippa

& Oksala, 1979; Oxford, 1985*a*, 1976; Oxford & Shaw, 1986; Reillo, 1989; Reillo & Wise, 1988; Wise & Reillo, 1985). Unfortunately, fewer comparisons were possible for *E. latimana* and sample sizes were generally lower, but this species too shows highly significant differences in colour-morph frequencies between areas and in some cases over shorter distances within areas (e.g. FW3, 4 and 5). The range of morph frequencies in medium to large samples is comparable in the two species.

A similar, but less marked, situation obtains with regard to black-spotting. In *E. ovata*, differences in morph frequencies between areas were at best only marginally significant and there was less evidence for heterogeneity within areas (Table 2). Only two other studies have investigated this trait in natural populations. At seven Norfolk sites, distributed within an area of *c.* 10 km^2, spotting frequencies were very similar to one another (range 92–100 per cent) (Oxford, 1991). In Nidderdale, Yorkshire, there were marked differences in spotting between sites, but possibly over a larger geographical scale than that shown by the colour morphs (Oxford, 1989). For spotting, patterns of variation in *E. latimana* again resemble those in *E. ovata* with indications of heterogeneity in spotting frequency within one area (Freshwater West) and significant differences between areas.

The geographical heterogeneity in both colour pattern and spotting makes it much harder to approach the first question posed in the introduction, i.e. within a locality, do morph frequencies within a species differ between allopatric and sympatric populations? The problem is exacerbated by the fact that the majority of populations sampled contain both species, although often with one at low frequency. Bearing in mind the very small number of comparisons available, inspection of Table 1 does not suggest consistent morph-frequency shifts between single- and mixed-species populations.

Comparisons of colour, spotting and cocoon frequencies between species within sympatric populations revealed some differences with respect to colour but highly significant differences for spotting and cocoons. Four out of 22 populations showed significant differences for colour, all in the direction of *E. ovata* having a higher frequency of the *lineata* morph. However, lack of a similar trend in other populations urges caution in interpreting this result. Colour-morph frequencies are not correlated between species, although the number of suitable sympatric populations is not large. For spotting, *E. latimana* had the lower frequency in all 22 comparisons. This observation is consistent with the tentative conclusion of Snazell (1983), based on material from Dorset, and with data from sympatric populations in Norfolk (Oxford, 1991). It appears that, in Britain at least, *E. latimana* generally has a lower frequency of spotting than *E. ovata*, although populations of the latter can vary widely in this respect (Oxford, 1989). Spotting frequencies for the two species in the present populations are not correlated.

The highly significant differences between numbers of *E. ovata* and *E. latimana* females with cocoons were expected. An earlier maturation of *E. ovata* was suggested by Hippa & Oksala (1982) and Snazell (1983), and confirmed and quantified by Oxford (1991). This difference in phenology is also indicated by the higher number of *E. latimana* males recorded, despite lower numbers of this species overall. Males die soon after mating. Within species, differences in cocoon frequency, both between populations and between areas, probably reflect aspects of the environment such as food availability, insolation etc. Surprisingly, therefore, cocoon frequencies in sympatric populations were not correlated between the species. This might reflect the small sample size, species-specific ecological factors, or both.

In *E. ovata*, there was a highly significant trend for females with cocoons to have black spots, although this was not statistically discernible within individual populations. A similar, but non-significant, trend was suggested by the much sparser *E. latimana* data. It is possible that the presence of spots advances reproductive maturity through the heat gathering properties of the black pigment, a phenomenon well studied in a variety of invertebrates (e.g. Digby, 1984). If this is the case, however, one might expect those females with fewer spots to be less well advanced, as judged by cocoon production, than those with more. There was no evidence of this in the present case. Whether the association between spotting and rate of maturation is detected in populations elsewhere remains to be seen.

In conclusion, the large amount of variability in morph frequencies exhibited by both *E. ovata* and *E. latimana* in the area studied makes comparisons between species difficult. For *E. ovata*, evidence for local selection acting on colour is lacking despite substantial efforts to detect it (Oxford & Shaw, 1986; Reillo & Wise, 1988, see also Oxford, 1989). These authors have suggested a major role for intermittent drift in determining colour-morph frequencies in local populations. By extension, the same process might also be important in *E. latimana*. A similar argument also applies to black spotting (Oxford, 1989). Very local, species-specific, selection cannot be eliminated for either species, but in other populations of *E. ovata* this seems unlikely (Oxford & Shaw, 1986; Reillo & Wise, 1988). There is no evidence in the present morph-

frequency data to suggest interactions between the species or systematic changes in sympatric populations which would have been indicative of a common selective agent, but obviously more data are required to check these tentative conclusions. To some extent, patterns of morph-frequency variation in the two *Enoplognatha* species resemble those found in the land snails *Cepaea nemoralis* and *C. hortensis*. In *Cepaea* the frequencies of identical visible morphs often differ within sympatric populations and in at least some cases this is a result of a species-specific response to the same visual selective force (e.g. Clarke, 1960, 1962).

Finally, the patterns of morph-frequency variation observed mean that possible gene exchange between species is not a contributory factor. In any case, a small-scale electrophoretic investigation in the Orielton populations revealed diagnostic markers for the species, and no evidence of hybridization (G. S. Oxford, unpublished).

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