Enoplognatha ovata and *E. latimana*: A comparison of their phenologies and genetics in Norfolk populations

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Summary

Data on the distribution, phenology and genetics of *Enoplognatha ovata* and *E. latimana* populations in Norfolk, UK are presented. The distribution of *E. latimana* here and at other British sites suggests an association with more open and drier habitats. *E. latimana* matures at a slightly later date than *E. ovata* but the reproductive maturity period within the latter species also varies between sites, probably as a result of aspects of the local environment. The sizes of adults and later instars of both species are similar. *E. latimana* is shown to possess the same polymorphisms affecting colour and black-spotting previously studied in *E. ovata*. Colour-morph frequencies are similar in the two species but *E. latimana* has significantly fewer individuals with black spots. The regulatory polymorphism affecting the timing of pigmentation in *E. ovata* also seems to be present in *E. latimana*.

Introduction

Enoplognatha ovata (Clerck) (Theridiidae) has a wide geographical distribution, occurring throughout the British Isles (Locket, Millidge & Merrett, 1974; Oxford, 1985a) and western continental Europe (Hippa & Oksala, 1979), and has been introduced into North America (Levi, 1957). In the vast majority of populations so far investigated the species exhibits a striking polymorphism for colour and pattern (Hippa & Oksala, 1979; Oxford, 1985a; Reillo & Wise, 1988a; Reillo, 1989). Three major morphs are recognised: in *lineata* the dorsal surface of the opisthosoma is plain yellow, *redimita* has in addition a pair of dorsolateral carmine stripes, while in *ovata* the whole of the dorsal surface is carmine (illustrated in fig. 1 of Oxford, 1983). This variation is genetically determined (Oxford, 1983; Reillo & Wise, 1988b). There is also genetic variation in the timing of red-pigment deposition during development in morphs *ovata* and *redimita* (Hippa & Oksala, 1979; Oxford, 1983), and in black spotting (Oxford, 1989).

In the early 1980s, Hippa & Oksala examined material from continental Europe and discovered within the *Enoplognatha ovata* group two new species, *E. penelope* Hippa & Oksala and *E. latimana* Hippa & Oksala (Hippa & Oksala, 1982). *Enoplognatha latimana* was subsequently found at a number of sites in mainland Britain (Snazell, 1983; Dobson, 1988; Merrett, 1989). In gross appearance the species are virtually identical but can be readily separated on the basis of their genitalia. It has yet to be established to what extent they differ in their ecology and their genetics. Hippa & Oksala (1982) noted that the phenologies of *E. latimana* and *E. ovata* in sympatric populations seem to be different, with *ovata* maturing earlier than *latimana*. Snazell's (1983) observations in Dorset also suggest that *E. ovata* has a slightly earlier breeding season.

E. ovata shows genetic variation for a number of characters, as described above. It is of interest, therefore, to discover whether *E. latimana* also shares these polymorphic systems and, if so, whether morph frequencies are similar in the two species. In *E. ovata*, the red pigment of *ovata* and *redimita* morphs is lost on preservation in alcohol. Since most of the specimens of *E. latimana* examined so far have been preserved, the presence of parallel colour morphs in most collections is indeterminate. However, Snazell (1983) and Hippa & Oksala (in Oxford, 1985a) reported colour morphs in *E. latimana* which are identical to *lineata* and *redimita* of *E. ovata*. Snazell (1983) and Hippa & Oksala (1982) also noted that a similar variation in black spotting on the opisthosoma is found in both species but suggested that in *E. latimana* the unspotted form might be the more common. There is no information on whether *E. latimana* exhibits the polymorphism regulating the timing of red-pigment deposition found in some populations of *E. ovata* (Oxford, 1983, 1985b).

The present paper considers the distribution and phenology of *E. ovata* and *E. latimana* in a small area of Norfolk, UK. In *E. latimana*, morph frequencies for colour and spotting are described for the first time and evidence is presented for a regulatory polymorphism acting on the colour locus.

Methods

The study sites lie approximately 11 km north-west of Thetford, Norfolk (Nat.grid: 52 815898) in the vicinity of Grimes Graves, an area of neolithic flint mining. The presence of *E. latimana* on Grimes Graves was established on 12 August 1989, and a number of individuals were subsequently collected and preserved on 2 September 1989. On 27 and 28 June 1990 samples were taken at two sites on Grimes Graves and at eight other sites to the north and west (Fig. 1). Data were also available from a sample of mature females taken at or near site GGC on 1 August 1980.

The Grimes Graves populations themselves (GG1, GG5) were in low-growing vegetation in circular pits, *c.* 8–10 m in diameter and *c.* 2 m deep, separated from one another to varying extents by close-cropped chalk grassland. Most spiders here were found associated with regrowth of buckthorn (*Rhamnus catharticus* L.) and hawthorn (*Crataegus monogyna* Jacq.), and with nettles (*Urtica dioica* L.). Collections in 1989 were made from pits GG1, GG5 and three in between. Pits GG1 and GG5 are about 100 m apart. At sites GGA and LH, spiders were found in stands of nettles and hedge woundwort (*Stachys sylvatica* L.) in dense shade from mature trees. GGB and GGC were similar but also contained bramble (*Rubus fruticosus* L. *sensu lato*). They were situated on the margin of a narrow track and were therefore slightly more open. GGD consisted of low-growing, open bramble in long grass on the corner of a track and a woodland ride. LRL was on an open road verge and had a tall and very mixed flora. LXR and GGE were also roadside verges but even more open and drier with shorter vegetation. In the field, and before any information had been extracted from the samples, the ten sites were subjectively ranked according to their degree of shading (Table 1).

At all sites the whole depth of vegetation was thoroughly searched and all specimens of *Enoplognatha*

captured. Rolled leaves were also investigated. Individuals from six sites (LRL, LXR, GGA, GGB, GGC and GGE) were immediately preserved in 70% alcohol using a different vial for each colour morph. The majority of spiders from GG1 and GG5 were measured in the field, and their spots and colour morph recorded, before being returned to their respective sites. Most of these individuals were immature and could not be identified, but a few from both populations were returned to the laboratory to be reared to maturity. All individuals from GGD were retained for rearing. Finally, animals from LH were collected and measured alive in the laboratory and then preserved to assess the degree of shrinkage in alcohol. Maximum carapace width was used as an indication of size (Seligy, 1971). Live individuals were restrained in a holding device (Oxford, 1981) and measured with a binocular microscope fitted with an eyepiece graticule; preserved animals were likewise measured submerged in 70% alcohol.

Animals retained for rearing in the laboratory were placed in individual glass vials containing damp tissue and stoppered with cotton wool. Vials were examined daily, except at weekends, and one or two fruit flies (*Drosophila melanogaster*) added every few days. The tissue was re-moistened when necessary.

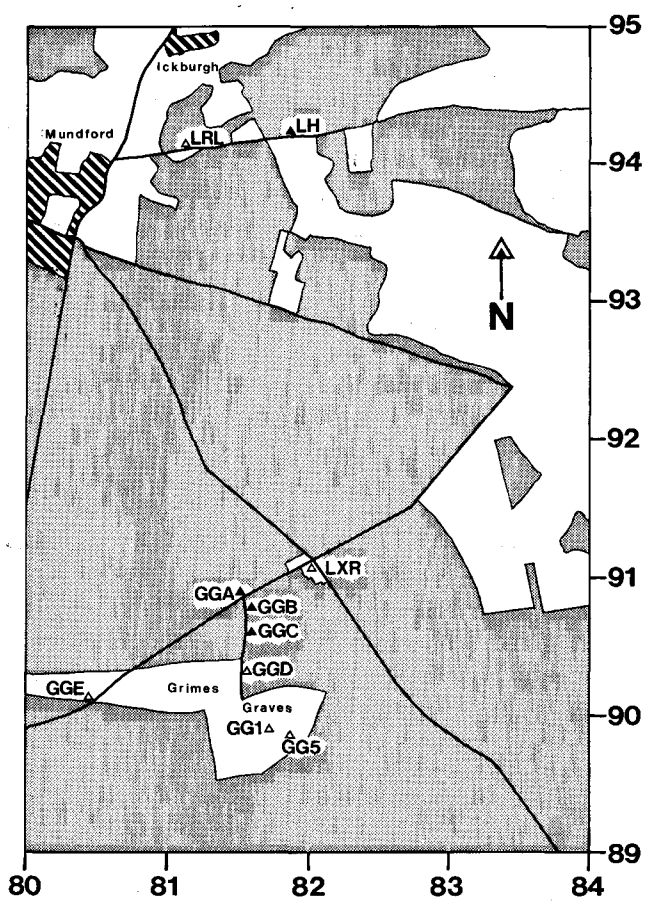

Fig. 1: Map of the Grimes Graves study area with sampling sites indicated by triangles: open symbols = both *E. ovata* and *E. latimana* populations, closed symbols = *E. ovata* populations alone. Lines denote roads or tracks, villages are shown hatched and stippled areas represent forest. Ordnance Survey 1 km co-ordinates are shown on the margins; the full map reference for the south-west corner is 52 8089.

Results

Basic data collected from each population are shown in Table 1. Except where noted, descriptions of results refer to the collections made in 1990. Of the eight sites chosen without prior knowledge of their species composition, four contained single species *ovata* populations and the other four contained populations of both *ovata* and *latimana* (Fig. 1). *Enoplognatha latimana* therefore seems to be fairly widely distributed in this area.

The degree of reproductive maturity at the time of sampling differed markedly between populations. For example, all females at LH (female sample size, $n=28$) but none at GG1 and GG5 ($n=29$ and 25, respectively) were mature. These differences in relative reproductive advancement between sites could be a result of differences induced by the local environment and/or differences resulting from the species composition. Evidence that *E. ovata* and *E. latimana* do differ in phenology, as suggested by other authors (Hippa & Oksala, 1982; Snazell, 1983), is discussed below. However, this cannot be the whole explanation. A simple index of the reproductive status of a population is given by the number of mature males divided by the total number of mature spiders. This proportion will be high initially, because males mature before females, but will drop subsequently to zero as males die after mating. Within *E. ovata*, the index varies from 0.065 in GGA to 0.545 in GGD (Table 2) and the differences in proportions of males and females between sites are highly significant ($\chi^2_{(5)}=23.2$, $p<0.001$). Expected values in the contingency table for site GGD are small and will disproportionately inflate the overall chi-squared value. If this site is ignored, however, significant heterogeneity remains ($\chi^2_{(4)}=11.9$, $0.05>p>0.01$). The very small numbers of mature *E. ovata* in GG1, GG5 and GGE preclude calculations for these samples. Mature females in GGA and LH were mostly swollen with eggs and one at GGA had produced a cocoon. Local environmental effects are probably responsible for the observed differences in reproductive timing within *E. ovata*.

There is, in addition, a clear indication that *E. latimana* matures more slowly than *E. ovata*. All 27 individuals from GGD were retained for examination and rearing. At the time of capture 11 animals were mature and all were *ovata*. Two of the remaining animals died and two more escaped, one before colour and spotting could be scored. Of the 12 which attained maturity in the laboratory all but three were *E. latimana*, a highly significant difference ($p=0.0003$, Fisher's exact test). If one considers the mean number of moults after capture to achieve maturity, female *latimana* took 2 ($n=2$), male *latimana* 1.3 ($n=7$), female *ovata* 0.4 ($n=8$) and male *ovata* 0 ($n=6$). This difference is also seen in the smaller, non-random selection of animals reared from sites GG1 and GG5. If the data from site GGD are representative, *E. latimana* is on average approximately 1.5 moults behind *E. ovata*, assuming the same number of moults to maturity in the two species.

The maximum carapace width of all individuals was measured, either fresh or after preservation. A comparison of measurements made on live individuals from LH with those on the same animals after preservation indicated a mean shrinkage in alcohol of one graticule unit

(0.04 mm). The shrinkage was independent of original carapace width. One unit was therefore added to the carapace measurements of preserved specimens before converting to millimetres.

Carapace widths of mature *E. ovata* females from sites in which sufficient numbers were found (viz. LXR, LRL, LH, GGA, GGC and GGB) were not significantly different (one-way ANOVAR). The same was true for carapace widths of mature male *E. ovata* (LXR, LRL, GGA and GGC) and immature males of indeterminate species (LXR, LRL, GGD, GG1 and GG5). For immature females, however, comparisons between LXR, LRL, GGD, GGE, GG1 and GG5 showed significant heterogeneity (one-way ANOVAR, $p = 0.001$). Further analysis using the GT2 test (Sokal & Rohlf, 1981) indicated that carapace widths at GGE were significantly greater (at the 5% level) than those at GGD, GG1 and GG5. The explanation for this observation is not clear; no other comparisons were significant.

Carapace widths of *E. ovata* and *E. latimana* for both mature males and mature females were not significantly different, although sample sizes were rather small. For those individuals reared to maturity in the laboratory, it is possible to assign instars on the assumption that maturity is reached in the sixth instar (Seligy, 1971). For *E. ovata* and *E. latimana*, carapace widths of particular instars were very close to those given by Seligy, suggesting that the growth process is similar in both species.

The two species were also examined with regard to three genetic polymorphic systems previously studied in *E.*

Site code	Year	Shade[1] score		Colour morph *lineata* ♀	*lineata* ♂	*redimita* ♀	*redimita* ♂	*ovata* ♀	*ovata* ♂	Spotting[2] + ♀	+ ♂	− ♀	− ♂	Sample size
LH	90	5	MO[3]	21	4	6	0	1	0	27	3	1	1	32
GGA	90	5	MO	72	6	13	0	1	0	81	5	5	1	92
			I	5	0	0	0	0	0	5	0	0	0	5
GGB	90	4	MO	13	1	1	0	0	0	14	1	0	0	15
			I	4	0	0	0	0	0	4	0	0	0	4
GGC	90	4	MO	17	5	5	1	0	0	22	5	0	1	28
			I	2	0	0	0	0	0	2	0	0	0	2
	80		MO	43	0	11	0	1	0	—	—	—	—	55
GGD	90	3	MO	5	6	0	0	0	0	4	6	1	0	11
			IO	3	0	0	0	0	0	3	0	0	0	3
			IL	2	7	0	0	0	0	0	3	2	4	9
			I	3[4]	0	0	0	0	0	0	0	3	0	3
LRL	90	3	MO	28	7	3	1	0	0	30	8	1	0	39
			ML	0	1	0	0	0	0	0	0	0	1	1
			I	9	5	0	0	0	0	6	0	5	3	14
LXR	90	2	MO	15	7	3	1	0	0	16	8	2	0	26
			ML	0	3	0	0	0	0	0	0	0	3	3
			I	17	3	0	0	0	0	8	0	9	3	20
GGE	90	2	MO	1	0	0	0	0	0	1	0	0	0	1
			ML	0	4	0	0	0	0	0	1	0	3	4
			I	7	2	0	0	0	0	2	0	5	2	9
GG1	90	1	MO	0	1	0	0	0	0	0	1	0	0	1
			IO	1	0	0	0	0	0	1	0	0	0	1
			IL	1	5	0	1	0	0	1	1	0	5	7
			I	27	17	0	0	0	0	9	1	18	16	44
	89		ML	7	0	1	0	0	0	2	0	6	0	8
GG5	90	1	MO	0	1	0	0	0	0	0	1	0	0	1
			IO	1	0	0	0	0	0	1	0	0	0	1
			I	24	14	0	0	0	0	5	1	19	13	38
	89		ML	5	0	3	0	0	0	1	0	7	0	8
GG1–5	89	1	ML	30	0	6	0	0	0	7	0	29	0	36

Table 1: Basic data gathered from the ten sampling sites. Sites are presented in order of descending shade score. Site GG1–5 is the total of all spiders collected on Grimes Graves in 1989 and includes sites GG1, GG5 and three populations in between.

[1]Shade score is a subjective assessment made on site, with 5 referring to populations under mature trees with little or no direct sunlight, and 1 referring to populations in very open sites with virtually no shade.

[2]+ = with some spots, − = without spots.

[3]M = Mature, I = Immature (at the time of sampling). O = *E. ovata*, L = *E. latimana*. Immatures of known species were reared to maturity in the laboratory and subsequently identified.

[4]Four immatures failed to reach maturity, one of which escaped before colour/spotting could be scored.

ovata (Oxford, 1983, 1989). All *E. ovata* populations yielding 14 or more mature females had both the *lineata* and *redimita* colour morphs (Table 2). In addition, single females of the *ovata* morph were found at LH and GGA. A comparison of proportions of *lineata* and *redimita* in adults at all sites except GGE, GG1 and GG5 showed them to be homogeneous (Table 2), with mean frequencies of 0.85 and 0.14, respectively. In 1980, during a country-wide survey of colour-morph frequencies in *E. ovata*, scores were made of 55 mature females from the approximate position of GGC. Frequencies of *lineata* and *redimita* in the two samples are very similar (Table 2). The samples of *E. latimana* females taken from a number of pits on Grimes Graves in September 1989 have a *redimita* morph frequency of 0.17, not significantly different from the mean of 0.14 found in *E. ovata* in this area.

The second genetic system, in *E. ovata*, concerns the timing of red-pigment deposition during development (Oxford, 1983). When the pigment of *redimita* and *ovata* morphs is laid down early (third/fourth instar) it affects both sexes equally. However, when the pigment is laid down only in the final, mature instar it affects only females; males genetically *redimita* or *ovata* retain the "juvenile" *lineata* coloration. Thus a comparison of *redimita* frequencies in immatures and mature males with those in mature females enables the presence and frequency of the putative late-developing allele to be assessed (Oxford, 1985b). This analysis was carried out on *E. ovata* from sites LXR, LH, LRL, GGA and GGC. In no individual case was the difference significant but at all five sites mature females showed the higher frequency of *redimita* (binomial probability, $p=0.03$). This comparative test is extremely insensitive when sample sizes are low (Oxford, 1985b) and it is quite possible that the "late" allele is fixed at sites LH and GGA, where no spiders other than mature females were found with the *redimita* pattern. No mature *E. latimana* females were found at any site in the present survey but samples of mature females from GG1 and GG5 are available from 1989. On the assumption that colour-morph frequencies have not changed between the 1989 and 1990 seasons a comparison can be made between immature spiders of both sexes from the present survey and mature females from the year before. Some of the immatures will be *E. ovata* but given the small number reared from GG1, and the fact that all mature females sampled in 1989 were *E. latimana*, the proportion of *E. ovata* in these sites is likely to be small. Spiders were assigned to instars on the basis of their carapace measurements and only those in their fourth instar or beyond were considered in the calculations, since by this stage early developing colour patterns should be established (see above). Taking the pits separately, the comparison of mature females with immatures (both sexes) in GG1 is not significant but adult females had the higher proportion of *redimita*. In GG5 the comparison is significant (Fisher's exact test, $p=0.008$) with 37.5% *redimita* in adult females ($n=8$) but none in immatures ($n=27$). If it is assumed that the colour-morph frequencies in all the Grimes Graves pits are uniform then the comparison of numbers of *redimita* in all females sampled in 1989 with immatures from GG1 and GG5 is also significant ($p=0.007$). Mature females had a frequency of *redimita* of 16.7%, while in immature spiders the frequency was only 1.5%. Thus, in the majority of *E. latimana* genetically *redimita*, red pigment appears to be deposited late in development. The fact that one immature *redimita* male *E. latimana* was taken from GG1 indicates that the allele causing early deposition of red pigment is also present in this species. Unfortunately none of the small number of *E. latimana* females reared in the laboratory changed morph from *lineata* to *redimita* on reaching maturity.

Finally, it has been suggested that the presence and absence of black spots on the dorsolateral margins of the opisthosoma are genetically determined by one or more major loci (Oxford, 1989). In mature *E. ovata*, frequencies of spotting between the sexes within sites were homogeneous. Comparison of spotting with sexes combined between sites is not possible because of the very small numbers without spots, but all are very similar with spotting frequencies varying between 92% (LXR) and 100% (GGB) (Table 2). Combined over sites, males have an overall spotting frequency of 92.6% and females 95.2%. For *E. latimana* numbers of adults are much smaller. Combining all sites, the difference in spotting between the sexes is not significant. However, frequencies of spotting in *E. ovata* and *E. latimana* are vastly different, the former having 94.8% spotted individuals while the latter has only 24% ($\chi^2_{(1)}=111.2$, $p\ll0.001$). This difference is also clearly seen within site GGD, where 92.8% ($n=14$) of *E. ovata* are spotted but only 33.3% ($n=9$) of *E. latimana* (Fisher's exact test, $p=0.005$). In both species, and in both sexes, individuals typically have either five or six spots in each row or none; very few spotted spiders have fewer than five spots.

Discussion

Since *Enoplognatha latimana* was described as a separate species in 1982, a growing number of populations have been discovered in southern England and south Wales (Snazell, 1983; Dobson, 1988; Merrett, 1989 and unpublished county records). Most records are from relatively coastal localities; the present populations are 40 km from the sea and are further inland than any other known *E. latimana* site in Britain (P. Merrett, pers. comm.). The historical and distributional status of *E. latimana* in Britain is unknown. Snazell (1983) re-examined collections of "*E. ovata*" in the British Museum (Natural History) and in private hands without finding any *E. latimana* specimens.

In six of the ten sites sampled here, populations of both *E. ovata* and *E. latimana* were present. It is of interest to ask what the relative frequencies of the species are and whether they vary in a systematic way with habitat. If the phenologies of two species differ markedly, then "relative frequency" is not a meaningful measure. In the present study, where there is considerable overlap between the species' phenologies, relative frequencies are useful but can only be determined accurately when all individuals are fully mature. The optimum time is when all females have established themselves in rolled leaves but before cocoons hatch and adults begin to wander from their retreats, i.e. usually in August. The samples considered here were taken before this time and will tend to overestimate the

proportion of *E. ovata*. Nevertheless, a consideration of identified mature spiders and the frequency of spotting, given that most *E. ovata* in these populations are spotted and most *E. latimana* are unspotted, enables a crude ranking of sites according to relative frequencies. Thus, *E. latimana* is at a very high frequency at GG1, GG5 and GGE, at about 40% in GGD, slightly lower at LXR and lower still at LRL. The other sites, LH, GGA, GGB and GGC, appear to lack this species.

E. latimana is apparently absent from the most shaded and therefore damper sites, and its relative frequency increases with degree of habitat openness (Table 1). This association might not be coincidental since other sites at which *E. latimana* has been found also tend to be unshaded and, as a result, drier. For example, it is reported from duneland in Lancashire (S. Dobson, pers. comm.) and in South Wales (Dobson, 1988), from clifftop vegetation in South Wales and from dry heathland in Dorset (Snazell, 1983). Clearly, this tentative habitat association needs further investigation but *E. latimana* might be found to be widespread in suitable habitats, whether coastal or inland.

The *E. ovata* populations varied greatly in their degree of reproductive advancement, and this too is related to habitat. Sites with a greater degree of shading had a lower proportion of mature males in the adult section of the population, a lower proportion of immatures, and mature females were more swollen with eggs. This contrasts with the situation in Nidderdale, Yorkshire, where the more shaded sites tend to be retarded in this respect (Oxford, 1989 and unpubl.), presumably as a result of lower insolation. It is possible that there are genetic differences between populations which affect development rates, but a more likely explanation hinges on the fact that the weather during the first half of 1990 was exceptionally dry and warm. Under drought conditions, suitable food for *Enoplognatha* is expected to be more abundant and more reliable in shaded, damper habitats than in more open and drier sites. For this reason the growth rates of young spiders in open habitats, in this particular year, might have been slower. There are no indications that the final sizes reached by mature males or females differ between sites. *E. ovata* and *E. latimana* appear to have similar growth patterns in that carapace widths of assigned instars, and of mature males and females, are virtually identical.

Genetically, *E. ovata* and *E. latimana* appear to share all three of the polymorphic systems investigated here. In adults, both species possess colour morphs *lineata* and *redimita* and, where comparisons are possible, there are no differences in frequencies between different *E. ovata* populations or between *E. ovata* and *E. latimana*. The uniformity of colour-morph frequencies in *E. ovata* over linear distances of up to 3.5 km between sites contrasts sharply with the dramatic changes over tens of metres between populations in Nidderdale, Yorkshire (Oxford & Shaw, 1986), despite much greater differences in habitat among the present localities. These observations serve to underline the lack of association between morph frequencies and habitat type repeatedly found in this species (Oxford & Shaw, 1986; Reillo & Wise, 1988a). Comparison of data from GGC with a score of mature females made in approximately the same place ten years previously suggests that colour-morph frequencies in this site are very stable.

Comparisons of colour-morph frequencies in mature males plus immatures with those in mature females allow the detection of a regulatory polymorphism determining the timing of pigment deposition (Oxford, 1983, 1985b). In *E. ovata*, frequencies of "early" and "late" regulatory alleles can vary over very short distances (Oxford, 1985b). In the Grimes Graves area there was no statistical evidence for the presence of the "late" allele within individual populations of *E. ovata*. However, sample sizes were generally small and the statistical test is insensitive to low frequencies of this allele (Oxford, 1985b), and in some sites it could have been fixed. In all possible within-site comparisons mature females had a higher frequency of the *redimita* pattern than mature males plus immatures. This trend is significant and certainly suggests the presence of the "late" allele. In *E. latimana*, no mature females were found. It would have been possible to resample mature females of this species later in the 1990 season but unequivocal identification requires preservation. As females had been removed from sites GG1 and GG5 in 1989 it was considered undesirable to kill more of a species of

Site	Year	Female colour morph (%)			NO	Spotting (%)	N	R.index[1]
		lineata	*redimita*	*ovata*				
E. ovata								
LH	90	75.0	21.4	3.6	28	93.7	32	0.125
GGA	90	83.7	15.1	1.2	86	93.5	97	0.065
GGB	90	92.8	7.1	0	14	100.0	19	0.067
GGC	90	73.9	26.1	0	22	96.4	30	0.214
	80	78.2	20.0	1.8	55	—	—	0
GGD	90	100.0	0	0	8[2]	92.8	14	0.545
LRL	90	90.3	9.7	0	31	97.4	39	0.205
LXR	90	83.3	16.7	0	18	92.3	26	0.308
E. latimana								
GGD	90	100.0	0	0	2	33.3	9	—
GG1–5	89	83.0	17.0	0	36	19.0	36	0

Table 2: Colour and spotting morph frequencies in samples of a sufficient size and in which individuals were identified. Female colour morph is for mature spiders only (sample size = NO). Spotting is based on all individuals in sites containing only one species, but on mature spiders alone in mixed species populations (sample size = N).
[1]R.index is the quotient of (mature males)/(mature males + mature females) (see text).
[2]Including those reared in the laboratory.

unknown national status. Comparisons were therefore made between mature females from 1989 and immature individuals collected in the current survey, although a small proportion of the latter could have been *E. ovata*. Significantly more mature females than immatures were of the *redimita* morph, suggesting the presence of the equivalent of the "late" allele of *E. ovata*. The one immature male *redimita* from GG1 must have been carrying the "early" allele. Thus, on the assumption that the properties of the regulatory polymorphism in *E. ovata* also apply to *E. latimana*, it can be concluded that the latter also possesses a polymorphism for this character. It is desirable that these conclusions are checked by rearing *E. latimana* from early instars to maturity to assess the timing and sexual distribution of pigment deposition.*

In their original description of *E. latimana*, Hippa & Oksala (1982) remark that, of the three species then placed in the *E. ovata* group, this was the only one to have specimens without dorsolateral black spots. Snazell (1983) noted that in the small number of *E. latimana* he had examined the unspotted form was the most common. The tendency for *E. latimana* to be unspotted is also shown in the present data with an overall frequency of the spotted phenotype of 24%. *E. ovata* populations in the same area are homogeneous with respect to spotting and have a mean spotted frequency of 95%. This distinction is also found within the mixed population at GGD, and so does not reflect environmental differences between *E. ovata* and *E. latimana* sites. If the frequencies of spotted and unspotted morphs are determined by natural selection, then it must be operating in different ways on the two species. It should be noted that both species have both morphs and differ only in relative frequencies. Given that frequencies can change between *E. ovata* populations only tens of metres apart (Oxford, 1989), generalisations about species characteristics are unwise until data are obtained from many more sympatric populations.

Of the five species now considered to be within the *E. ovata* group, *E. ovata* and *E. latimana* seem to be the most closely related (Hippa & Oksala, 1983). They share the same three genetic polymorphisms examined here; polymorphisms presumably retained from a common ancestor. An obvious parallel lies in the helicid snails *Cepaea nemoralis* (L.) and *C. hortensis* (Müll.), which also share many visible polymorphisms (Jones, Leith & Rawlings, 1977). As in the case of spotting in *Enoplognatha*, the frequencies of identical morphs may differ in the two snail species in sympatric populations, although the reasons for this are not fully understood (Cain, 1977; Jones, Leith & Rawlings, 1977). It remains to be seen how concordant visible morph frequencies in *Enoplognatha* species are in other mixed populations.

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*Immature *E. latimana*, collected from Grimes Graves in June 1991 and reared in the laboratory, included females which developed the *redimita* pattern only after reaching maturity. This demonstrates conclusively that this species does indeed possess the late-developing allele at the regulatory locus, as predicted on statistical grounds above.

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