Components of variation in population size in the spider *Enoplognatha ovata* (Clerck) *sensu stricto* (Araneae: Theridiidae)

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Summary

Twenty-three populations of the annual spider *Enoplognatha ovata s. str.* were counted in a small area of Nidderdale, Yorkshire, UK for periods of from ten to nineteen years. Methods were developed which enabled estimates of maximum mature female population sizes within sites to be derived from these counts. Population fluctuations over time within sites lie in the approximate range four-fold to fifty-five-fold. About half the overall variation in standardised population sizes is attributed to a between-year component. It is suggested that certain climatic factors, particularly during the immature stages, might contribute to this "year" effect. Correlations in population size between sites are not randomly scattered through the study area, and there is evidence that populations within two major clusters co-vary as a result of human disturbance. Thus, factors influencing population-size variation in *E. ovata* include large scale (climate?), local (disturbance), and site-specific effects.

Introduction

The theridiid spider *Enoplognatha ovata* (Clerck) *s. str.* is an abundant and widespread species in Europe and the coastal regions of North America (Oxford & Reillo, in press). It behaves as a strict annual, with young spiders overwintering low down in the herb layer as second instars (Toft, 1976). During the period April to June the young grow and move higher up the vegetation, maturing in late June to early July. Males die soon after mating. Gravid females build retreats by rolling foliage of broad-leaved plants and within these deposit and guard their, usually single, egg cocoon until the young emerge. Towards the end of August and through September emaciated females wander from their retreats into the general vegetation where they die. This coincides with the final stages of development of the young and their emergence from the cocoon as second instars (the first moult takes place within the cocoon). The young remain in their natal leaf for a variable period before gradually migrating down to the herb layer to overwinter.

E. ovata has been extensively studied over many years as a result of its vivid colour polymorphism (Oxford, 1983; Oxford & Shaw, 1986; Reillo & Wise, 1988, and references therein). Between 1970 and 1988, populations in Nidderdale, Yorkshire, UK were regularly sampled at a number of discrete sites in order to assess spatial patterns of morph frequency variation and to monitor temporal changes in genetic composition (Oxford & Shaw, 1986). This genetical work suggested that there was very little migration even between adjacent sites. Spider densities were high within sites but very low in other habitats between them (Oxford & Shaw, 1986), a result of the requirements of females building nursery retreats. The behaviour of the spider, the timing of the counts and the census method employed enable the mature female

population size at each site to be estimated with some degree of accuracy.

There are very few previous studies of natural fluctuations in the size of spider populations over several generations, and certainly none for the length of time involved here. The present data set, extending over 19 years, therefore offers a rare opportunity to investigate the extent of both spatial and temporal variation in population size in *E. ovata*. Methods are developed for estimating maximum population sizes within sites. These estimates are then used to address the following questions:

1. To what extent do population sizes within a site vary over time?
2. Are fluctuations in population size between sites correlated?
3. What factors might influence population size in this species?

Sites, sampling methods and estimation of population size

Sites and sampling methods

The location of the Nidderdale study area in the UK, and the distribution of sampling sites mentioned here, are shown in Fig. 1 (for further details of the area see Oxford, 1976, 1985; Oxford & Shaw, 1986). The only habitats suitable for *E. ovata* were the verges of roads and tracks, which in most cases were backed by dry-stone walls. A sampling site was defined as a patch of broad-leaved vegetation usually separated from other such patches by rank grass. In the study area, plant species most commonly used for retreats were bramble (*Rubus fruticosus* L. *sensu lato*), raspberry (*Rubus idaeus* L.), hedge woundwort (*Stachys sylvatica* L.) and rosebay willowherb (*Chamaenerion angustifolium* (L.) Scop.). In some cases, a continuous strip of broad-leaved vegetation was arbitrarily divided into two or more contiguous sites. In dense vegetation patches, for example of bramble, leaves chosen by spiders as retreats were always on the surface, possibly so as to receive the maximum insolation and thus reduce the development time of the eggs. A consequence of this was that the vast majority of rolled leaves were easily visible no matter what the vegetation type. Spiders within each sampling site were regarded as separate populations.

In late July or early August, all the vegetation within each site was sampled on one occasion in a standard, methodical and non-destructive way (Oxford, 1976). All sites were counted within a period of five days. Every rolled leaf seen was examined and the presence/absence of a female, the presence/absence of a cocoon and, if a cocoon was present, its developmental state, were recorded. Once most of the females had produced cocoons, sites resampled a few days apart yielded very similar counts. Over the years, spiders were examined in a total of 44 sites within the Nidderdale area (Oxford & Shaw, 1986), i.e. the majority of suitable vegetation patches present when intensive study began in 1979. In this paper only 23 have been considered in detail (Fig. 1). The criteria for inclusion of a site were, (i) it should have been sampled annually for at least the ten-year period 1979–1988, (ii) it should not knowingly have been subjected to repeated human disturbance, (iii) its boundaries

should be clearly defined, and (iv) spider densities within a site within a year should be approximately constant per metre length of verge, to allow adjustments for the spread of vegetation (see below). Nomenclature of sites is alphabetical according to when they were first sampled, and not by geographical position.

Estimation of mature female population size

In all the analyses, total numbers of spiders estimated to be within a site have been used, rather than converting to a density. The reason for doing this is that some parts of the verge width were obviously more suitable for spiders than others. For example, the shorter turf close to the road edge tended not to be frequented, and nor did the very densest parts of bramble patches. Thus the actual area occupied by the spider was difficult to estimate and to compare between sites, and was anyway likely to vary during the life cycle. Since the same length of verge (or an adjusted length — see below) was searched at each site in

Fig. 2: Plot of proportion of females with cocoons (left hand curves) and proportion of cocoons with young in their second instar (right hand curves) against date. $\bigcirc$ = site U, $\bullet$ = site A, $\bullet$ = site AB, $\times$ = site AO and $\blacktriangle$ = site G. Site U was sampled in 1980 and the other sites in 1988.

each year, and since the verge structure remained approximately constant within a site, the site was used as the unit of sampling. In order to estimate maximum mature female population sizes from the number of spiders counted, two scaling factors have to be considered, (i) changes in site (vegetation) length with time, and (ii) the relative maturity of spiders at the time of sampling.

Site length

Not surprisingly, the vegetative characteristics of some sites changed over the almost two decades of study. The beginning and end of each site was marked on the first sampling occasion with plastic tubing wedged into the dry-stone wall, or mapped in relation to landmarks such as field boundaries or telegraph poles. In some sites the broad-leaved vegetation spread outwards from the initial site limits and populations were counted in progressively longer and longer sections of verge. The extent of any spread was monitored over the years and population sizes have been scaled by simple multiplication to the site length measured in the final year, 1988. To do this it had to be assumed that the density of spiders per metre length of site in any one year was constant. In the sites included here, this was approximately the case. At other locations broad-leaved vegetation established itself between sampling sites and gradually encroached upon them. In these cases, only counts of spiders in the length of verge between the two original markers have been used.

Developmental variation

A second necessary adjustment to raw counts stems from the fact that females roll leaves only when
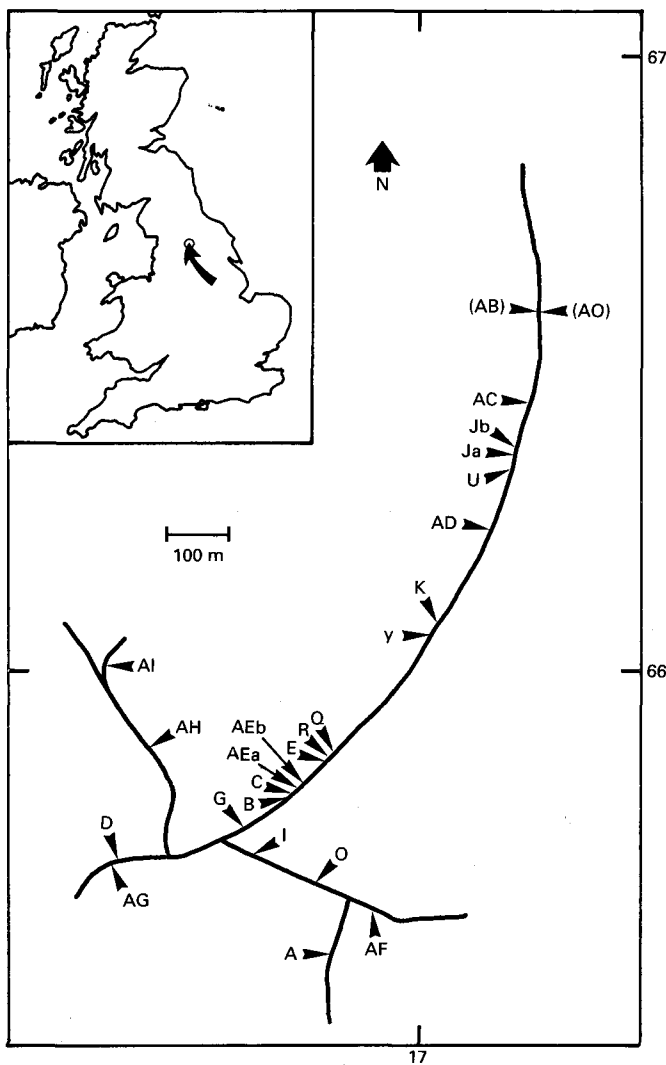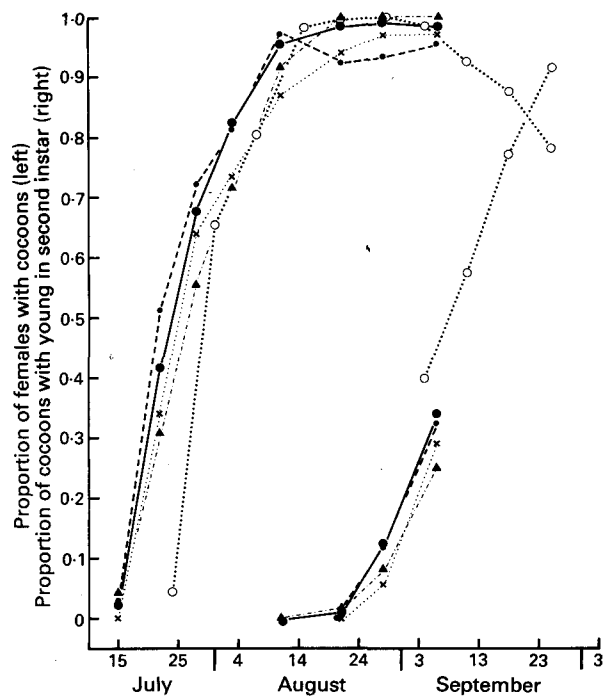

Fig. 1: Map of Nidderdale study area showing positions of sample sites in relation to roads and tracks. Sites in parentheses were used in deriving the relationships between counts and mature female population size but, for various reasons (see p. 193), were not included in the 23 sites considered in detail. Marginal numbers are kilometre squares of the Ordnance Survey (map reference of the extreme south-west corner, SE 163654). Inset shows the location of Nidderdale in the British Isles.

they are gravid and about to deposit cocoons. It follows that in "early" years, when maturation was relatively rapid, by late July or early August a high proportion of females would have been in leaves and available for counting. Conversely, in "late" years a larger fraction of the population would have been missed. One measure of the relative maturity of a population was the proportion of females in leaves who had already deposited cocoons, and this was used to adjust population estimates. Later in the season, females wander from their retreats as mentioned earlier. This loss of adults from the potential sample pool also had to be taken into account.

In order to assess the relationship between the proportion of females in leaves with cocoons and the maximum population size within a site, a series of samples was taken at intervals through the summer at five sites. Site U was sampled in 1980, and sites A, G, AB and AO in 1988 (Fig. 1). Information on the number of spiders counted and the proportion with cocoons is given in Table 1. The proportion of females with cocoons increased rapidly through the latter half of July and reached a plateau of between 95% and 100% by about mid-August (Fig. 2). Numbers of females counted on each occasion also rose steeply to a peak in early August, and then gently declined. The time between the deposition of a cocoon and the emergence of spiderlings in both 1980 and 1988 was at least five weeks (Fig. 2), so it is unlikely that early-maturing females would have left their retreats before late-maturing females became established in theirs. There was a period, therefore, when the entire female population was available for counting. It has been assumed that the highest number of
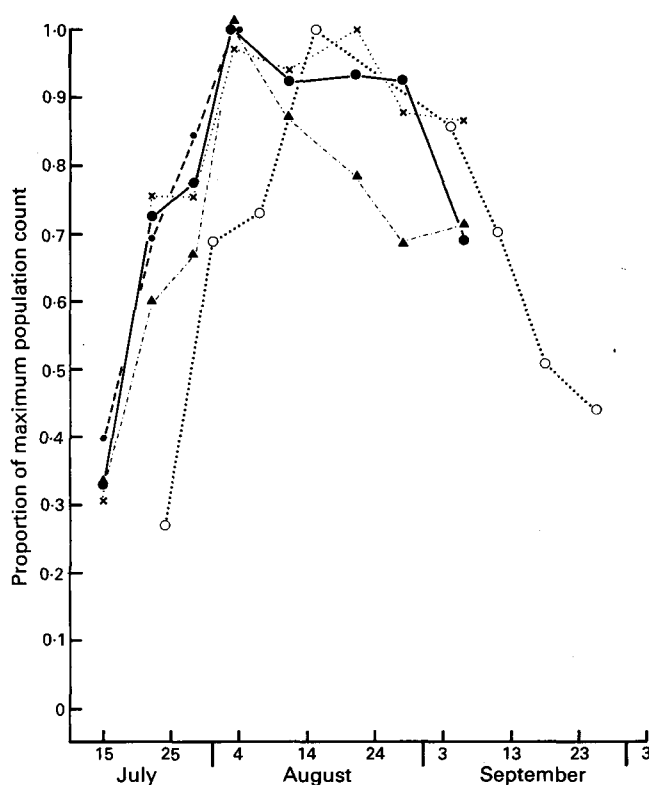

Fig. 3: Plot of counts, as proportion of the maximum count, for each site against date. Symbols as in Fig. 2.

spiders counted within a site during the course of these serial samples represents the true mature female population size. A plot of population size, relative to the peak population size, against time is shown in Fig. 3.

Site U					Site A			
Date	N	P	C	S	Date	N	P	C	S
24.7	47	0.268	0.043	0	15.7	158	0.333	0.025	0
31.7	121	0.691	0.653	0	22.7	343	0.724	0.417	0
7.8	128	0.730	0.804	0	28.7	367	0.774	0.681	0
15.8	175	1.000	0.983	0	4.8	474	1.000	0.823	0
21.8*	108	—	0.991	—	12.8	438	0.924	0.957	0
28.8*	72	—	1.000	—	22.8	443	0.934	0.989	0.013
4.9	150	0.857	0.960	0.399	29.8	440	0.928	0.993	0.125
11.9	123	0.703	0.927	0.575	7.9	382	0.692	0.982	0.342
18.9	89	0.508	0.876	0.771					
25.9	77	0.440	0.779	0.913					

	Site G				Site AB				Site AO		
Date	N	P	C	S	N	P	C	S	N	P	C	S
15.7	23	0.328	0.043	0	39	0.398	0.027	0	20	0.303	0	0
22.7	42	0.600	0.309	0	68	0.694	0.515	0	50	0.757	0.340	0
28.7	47	0.671	0.553	0	83	0.847	0.723	0	50	0.757	0.640	0
4.8	70	1.000	0.714	0	98	1.000	0.816	0	64	0.970	0.734	0
12.8	61	0.871	0.918	0	75**	—	0.973	0	62	0.939	0.871	0
22.8	55	0.786	1.000	0.017	79	—	0.924	0	66	1.000	0.940	0
29.8	48	0.686	1.000	0.082	61	—	0.934	0.121	58	0.879	0.966	0.054
7.9	50	0.714	1.000	0.250	44	—	0.954	0.326	57	0.864	0.965	0.290

Table 1: Numbers of females counted, proportion with cocoons and proportion of cocoons with second instar young in each site. N = number of females counted; P = proportion of maximum population count; C = proportion of females associated with cocoons; S = proportion of cocoons with young in second instar.
*Counts not made by the author. These data have not been used in analyses. **Vegetation was cut back between 4.8 and 12.8 and subsequent counts are therefore unreliable. It is assumed that the count on 4.8 is the maximum, as was the case in sites A and G.

For the first part of the reproductive season, i.e. up to the maximum number found, a plot of the proportion of the maximum population size (P) against proportion of females with cocoons (C) yielded a highly significant linear relationship of the form $P = 0.335 + 0.721C$ ($p \ll 0.001$, $r^2 = 0.88$) (Fig. 4). According to this relationship, by the time 92% of females had cocoons the counted population size equalled the maximum population size, on average. The counted population size then declined as the season progressed, partly as a result of females abandoning their retreats and partly, no doubt, as a consequence of predation, starvation or other causes. Some sources of mortality, e.g. bird predation, may have removed cocoons as well. The appearance of a cocoon changes as spiderlings moult, and their pink exuviae show through the silk wall which by now has been teased thinner by the mother (presumably to aid the release of the young). The proportion of cocoons in which pink exuviae were seen and/or from which the young had emerged was taken as a measure of relative reproductive state in the latter half of the season. It was difficult to separate these two cocoon stages since the process of opening leaves can release the young prematurely. A plot of the proportion of the maximum population size (P) against proportion of cocoons which had pink exuviae and/or from which the young had emerged (S) yielded a significant linear relationship, $P = 0.885 - 0.427S$ ($0.002 > p > 0.001$, $r^2 = 0.65$) (Fig. 4). Thus when pink exuviae first appeared the population count had already dropped to about 88% of its peak value.

These relationships leave a gap between the time when 92% of females had produced cocoons and when second instar spiderlings first appeared. During this period there was no reliable measure of the developmental state of the population, and the observed population size dropped from maximum to 88% of maximum. The mean size of the population over this period was therefore 94% of maximum. Figure 3 suggests that there might have been a plateau in population size before
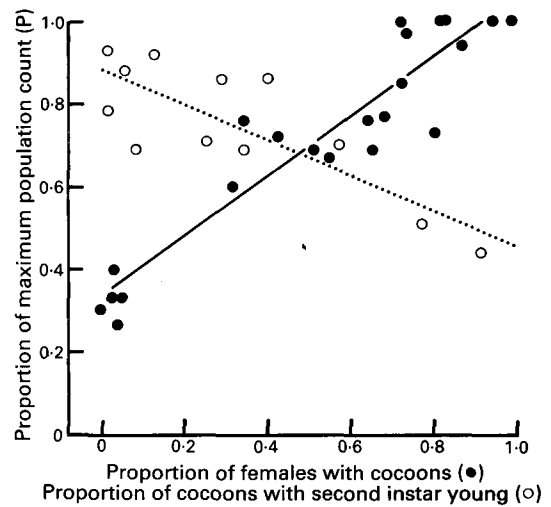

Fig. 4: Plot of proportion of females with cocoons (●) and proportion of cocoons with young in the second instar (○) against counts, as proportions of the highest count, in two phases of the breeding season. Fitted regression lines are shown.

the decline, i.e. the rate of loss within this period was not linear. To allow for the plateau, the mean proportion of 0.94 was arbitrarily increased to 0.96 in order to adjust population counts. That is, if more that 92% of females had cocoons, but none of these cocoons had young in their second instar, it was assumed that the true maximum population size was given by (population count)/0.96.

Analyses of population variation

Using the relationships developed above, and making allowances for any vegetation spread, maximum female population sizes in the Nidderdale sites were estimated for each year (Table 2). Note that in three years the population size in site Jb was so large that subsampling of alternate, metre-wide strips across the verge was used to make spider counts. In some years, adjustments to spider

Year	A	B	C	D	E	G	I	Ja	Jb	K	O	Q	R	U	Y	AC	AD	AEa	AEb	AF	AG	AH	AI
70	162	590	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
71	123	807	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
72	154	357	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
73	218	248	13	114	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
74	323	543	—	80	147	119	60	95	445	—	—	—	—	—	—	—	—	—	—	—	—	—	—
75	—	151	—	—	24	132	78	105	368	170	184	32	21	—	—	—	—	—	—	—	—	—	—
76	564	307	—	227	169	337	182	387	2744*	750	338	230	120	375	—	—	—	—	—	—	—	—	—
77	515	238	—	—	—	—	—	—	—	—	—	—	—	539	—	—	—	—	—	—	—	—	—
78	125	183	—	—	—	—	126	—	—	—	69	—	—	156	—	—	—	—	—	—	—	—	—
79	70	254	74	114	53	48	141	85	226	229	20	99	290	126	107	80	70	80	77	32	27	38	114
80	256	318	33	175	86	328	72	186	208	253	45	84	228	180	544	101	210	69	210	18	151	48	91
81	165	294	91	267	157	212	87	239	455	439	114	104	293	225	479	289	156	123	175	44	61	48	48
82	471	355	83	130	177	227	203	562	1570*	422	394	214	270	409	307	619	401	125	282	178	172	54	73
83	656	822	247	303	401	102	416	770	2479*	295	596	546	621	398	245	579	755	451	724	552	267	57	113
84	894	547	153	160	281	59	164	152	739	171	174	345	476	94	409	153	309	279	445	343	152	75	69
85	320	413	305	128	96	42	133	114	313	210	160	396	440	142	181	171	450	400	484	101	62	114	121
86	186	93	19	183	9	57	42	95	112	65	60	49	27	107	32	118	85	31	62	20	6	32	48
87	306	245	84	112	45	216	71	296	517	136	131	132	214	141	166	107	107	66	187	10	15	30	49
88	456	314	117	99	100	82	64	323	659	246	270	278	325	193	441	224	313	146	209	28	78	3	174
Range	12.8	8.8	23.5	3.8	44.5	8.0	9.9	9.0	24.5	11.5	29.7	17.1	29.6	4.3	17.0	7.7	10.8	14.5	11.7	55.2	44.5	38.0	3.6

Table 2: Estimated maximum population size in each site. * = Total counts estimated from sub-counts in alternate 1 m wide strips of verge. Range = maximum size/minimum size for each site.

counts had very little effect on estimates of maximum population sizes, whereas in other years the effect was large. Given that all counts have now been transformed to estimates of maximum population size, it is possible to investigate population variability and its potential causes.

Population variation between years

Since 1979, all 23 sites were counted each year. Consequently population estimates from sites scored within a year can, in a crude sense, be regarded as "replicates". This enables the total variation in population size to be apportioned into within-year (between site) and between-year components. Before this can be done, however, individual population size estimates, which are for sites of differing lengths and suitability for *E. ovata*, have to be made comparable. The reasons for not simply working in densities have been discussed above. First, for each site, population estimates for 1979 through to 1988 were converted to logarithms (base 10) to reduce the influence of the mean on the variance (Taylor, 1961). Untransformed means and variances were very highly associated (regression of $\log_{10}$ variance on $\log_{10}$ mean, slope $= 2.11 \pm 0.19$ [1 s.d.], $p \ll 0.001$), as has been found by many other authors (e.g. Wolda, 1983; Owen & Gilbert, 1989). In this case, $\log_{10}$ transformation of the population estimates before calculating means and variances reduced, but did not entirely remove, the dependence (regression of variance on mean, slope $= -0.13 \pm 0.06$ [1 s.d.], $p = 0.034$). Indeed, the dependence now became weakly negative (see also Wolda, 1983). The $\log_{10}$ transformed population estimates were then standardised with the function $(n_i - \bar{n})/\text{s.d.}$, where n_i is the population size in year i, $\bar{n}$ is the mean and s.d. is the standard deviation of population sizes within a site over the ten-year period. Standardised population sizes within all sites therefore have zero means and unit standard deviations.

A one-way analysis of variance on these standardised data indicated a highly significant effect of year ($F_{9,220} = 26.7$, $p \ll 0.001$). Thus, 1983 was a good year with high average population sizes, while 1986 was a poor year (Fig. 5). From the mean squares within and between years, it can be estimated that differences between years explain 52.8% of the total variance in population size.

Effect of climate on population size

The highly significant influence of the year on average population sizes in the Nidderdale sites could have several causes, of which the most likely is climate. Possible associations between population size and certain climatic variables were therefore investigated.

Climatic information was abstracted from the Meteorological Office Monthly Weather Reports for two stations, Leeming and Malham Tarn. The former (altitude 32 m) is situated 27 km to the north-east of the study area and the latter (altitude 395 m) 27 km to the west. Monthly figures from January 1969 to June 1988 were recorded for the following eleven variables: mean maximum temperature, mean minimum temperature, mean temperature, highest maximum temperature, lowest minimum temperature,
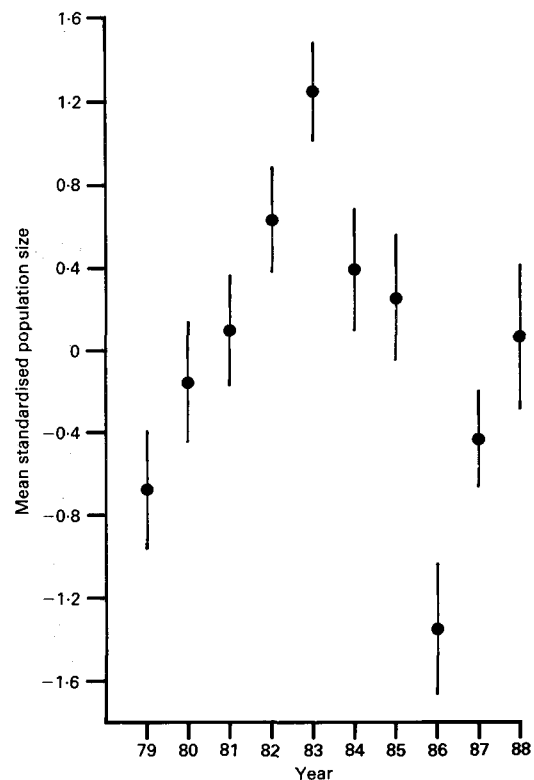

Fig. 5: Plot of means of standardised estimated maximum population size in 23 sites against year. Vertical lines = 95% confidence interval of mean.

temperature range (all in °C), rainfall (mm), number of rain days (days with > 1 mm precipitation), number of snow days (days with snow lying at 0900 h), bright sunshine (daily mean, hours) and grass temperature (number of days with a ground frost). The mean altitude of the two meteorological stations is 213 m, whereas the mean altitude of the Nidderdale sites is about 290 m. These were considered to be sufficiently close to justify averaging values for each climatic variable in each month from the two stations and assuming these means reflected approximately the situation in Nidderdale. Recordings of bright sunshine at Malham Tarn were sporadic, but those that were made showed a very high correlation with values from Leeming ($r = 0.94$, $p \ll 0.001$). For this variable, therefore, only Leeming data were used.

Many of these climatic measures were highly correlated *inter se* and principal component analyses (PCA) were undertaken to derive new, composite and independent variables. Each climatic variable was standardised to have zero mean and unit standard deviation and principal components extracted from the correlation matrix. Because so few populations were censused each year before 1979, analyses were restricted to the years 1979 to 1988. Climatic data analysed in the PCA were monthly means from July 1978 through to July 1988. The snow variable had a value of zero throughout the summer, so PCA was repeated with snow deleted to check whether multiple zeros were seriously affecting the components. The first four principal components, their associated eigenvalues and vector weightings for the two analyses are shown in Table 3. In both analyses the first four components together accounted for 95% or more of the total

Analysis	+ snow variable				− snow variable			
Component	C1	C2	C3	C4	C1	C2	C3	C4
Eigenvalue	6.96	2.15	0.86	0.48	6.46	2.11	0.86	0.33
Cumulative proportion	0.63	0.83	0.91	0.95	0.65	0.86	0.94	0.98
Variable								
Max. temp.	−0.38	0.03	−0.01	0.11	−0.39	−0.05	−0.01	0.01
Min. temp.	−0.36	0.13	−0.07	0.09	−0.38	−0.16	−0.07	−0.20
Mean temp.	−0.37	0.07	−0.04	0.10	−0.39	−0.10	−0.04	−0.09
HMax. temp.	−0.37	−0.03	0.18	0.10	−0.38	0.01	0.18	−0.05
LMin. temp.	−0.35	0.15	−0.24	0.16	−0.37	−0.18	−0.24	0.06
Temp. range	−0.13	−0.34	0.84	−0.07	−0.15	0.34	0.84	−0.22
Rainfall	0.09	0.60	0.35	0.15	0.10	−0.61	0.35	0.10
Rain days	0.10	0.61	0.26	0.06	0.11	−0.61	0.26	0.20
Snow days	0.28	−0.15	−0.01	0.91	—	—	—	—
Sunshine	−0.30	−0.22	0.09	0.27	−0.32	0.20	0.09	0.87
Grass temp.	0.35	−0.16	0.06	0.01	0.36	0.18	0.06	0.30

Table 3: Vector loadings for principal components derived from climatic data. For explanation of variables — see text.

variance. Each component was interpreted by reference to the climatic variables with the highest absolute vector loadings (Table 3). In both analyses the first component (C1) reflected temperature (with all measures except temperature range_weighted approximately equally), the second (C2) rainfall and the third (C3) temperature range. With the snow variable present, C4 was very heavily weighted by snow. When snow was excluded, C5 from the full analysis became C4, reflecting hours of bright sunshine.

As will be discussed below, the standardised mean population sizes shown in Fig. 5 were influenced to some extent by disturbance factors. However, each incident affected a small number of populations and as all have
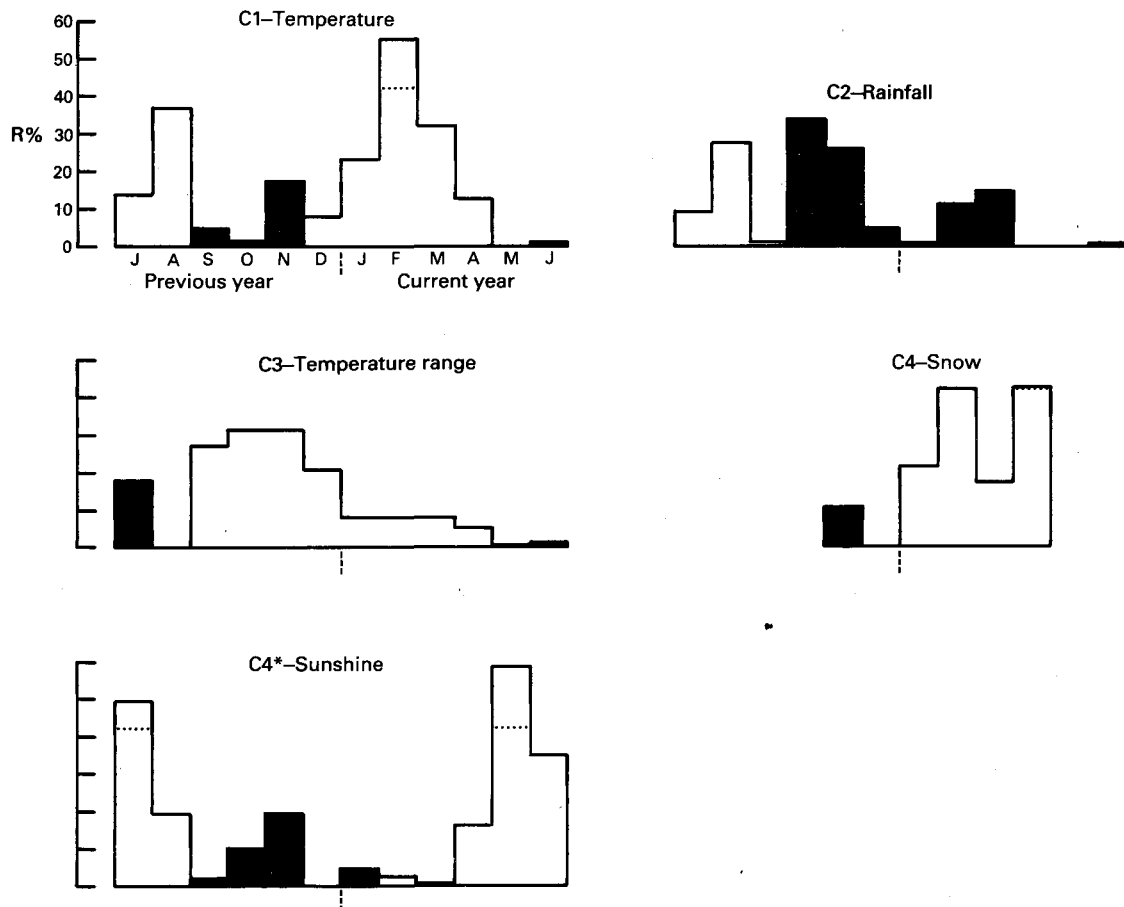

Fig. 6: Percentage of total variance (R%) explained by principal components in multiple regression analyses using three-monthly running means of vector values. C1–C4 are from the full analysis, C4* is from the analysis excluding snow. C4 is shown only for the months in which the snow variable is usually >0. Solid histograms are positive associations and open histograms negative ones. Horizontal dotted lines indicate a proportion of explained variance which marks the 5% significance level. Note that for C1, the signs of the vector loadings (Table 3) are such that a negative association here means that population size is positively related to temperature.

been equally weighted in the calculation of annual means, it was felt justified to seek associations with climatic factors using these means. *E. ovata* seems to be a relatively sedentary spider (Oxford & Shaw, 1986) and so the population size found within a site in year N would be expected to be some function of numbers in year N-1, as well as a function, possibly, of climatic variables. The effect of climate was therefore tested with a multiple regression approach with mean population size in year N as the dependent variable, and mean population size in year N-1 and monthly vector values from the PCA as independent variables (see also Pollard & Lakhani, 1985; Pollard, 1988).

Regressions were run for August in the year before the census to July of the census year, thus covering the total lifespan of the counted adults. Climatic components used were C1 to C4 from the full analysis and C4 from the analysis from which snow was excluded (C4*). Only three of the partial regression coefficients were formally significant, C1 for August (+, $p = 0.028$), C4 for April ($-$, $p = 0.045$) and C4* for July ($-$, $p = 0.033$). Indeed, because of multiple testing, none of these results may actually be significant. Following Pollard (1988), three-monthly running means of the vector values were also calculated and used in identical analyses. This procedure allows for the fact that critical stages in the spider's development might not occur in the same month each year. Here "previous year" months ran from July and the "present year" ended in June. The proportion of the total variance explained by the linear regression component due to weather is plotted by mid-month for the five principal components in Fig. 6. As before, few of the partial regression coefficients were individually significant (at the 0.05 level) but the smoothing effect of using running means produced patterns which are suggestive, although nothing more. In spring, population sizes were positively correlated with warmer temperatures and reduced snow cover. They were also positively correlated with smaller temperature range, hours of sunshine and rainfall during
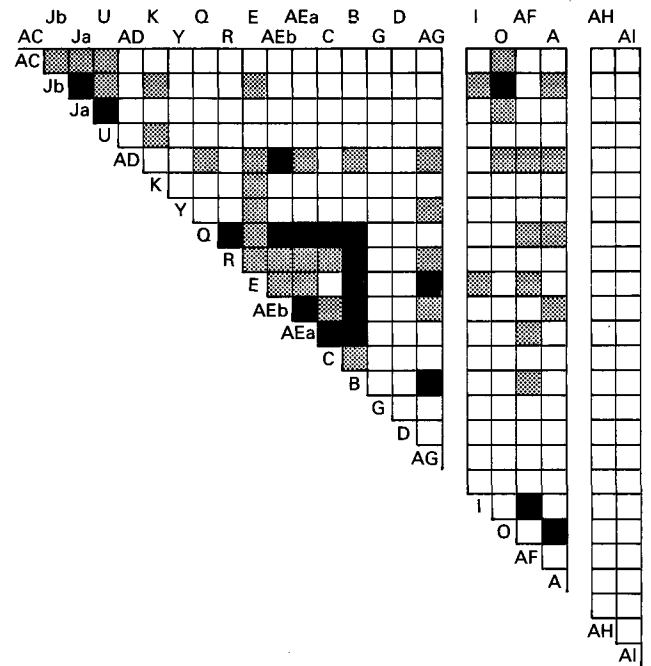

Fig. 7: Correlation matrix of $\log_{10}$ estimated maximum population size in 23 sites for all available years. Dotted squares indicate significance of $0.01 > p > 0.001$, solid squares, $p < 0.001$. The large triangle represents the main road through the study area while the other two sections represent sites along a side road (I–A) and a side track (AH and AI) (see Fig. 1).

autumn. Finally, there was an interesting negative association between population size and hours of bright sunshine through the summer months.

Population variation between sites

Years explained only 53% of the total variance in population size, the remaining 47% being attributable to differences between sites and possibly to site × year interactions. The latter cannot be explored with the present data. To investigate whether variation between sites

Year	Site-group B									Site-group J					
	B	C	E	Q	R	AEa	AEb	Mean	Trans.	Ja	Jb	U	AC	Mean	Trans.
70	1.08	—	—	—	—	—	—	1.08		—	—	—	—	—	
71	1.65	—	—	—	—	—	—	1.65	+	—	—	—	—	—	
72	0.17	—	—	—	—	—	—	0.17	−	—	—	—	—	—	
73	−0.49	−1.79	—	—	—	—	—	−1.14	−	—	—	—	—	—	
74	0.93	—	0.46	—	—	—	—	0.69	+	−1.04	−0.20	—	—	−0.62	
75	−1.39	—	−1.30	−1.81	−2.08	—	—	−1.65	−	−0.90	−0.40	—	—	−0.65	—
76	−0.10	—	0.59	0.46	−0.46	—	—	0.12	+	0.88	1.71	1.36	—	1.32	+
77	−0.56	—	—	—	—	—	—	−0.56	−	—	—	—	—	—	
78	−1.04	—	—	—	—	—	—	−1.04	−	—	—	−0.36	—	−0.36	
79	−0.44	−0.03	−0.53	−0.51	0.36	−0.56	−1.37	−0.44	+	−1.19	−0.91	−0.78	−1.21	−1.02	−
80	−0.04	−0.85	−0.06	−0.70	0.14	−0.73	−0.08	−0.33	+	−0.12	−1.00	−0.08	−0.88	−0.52	+
81	−0.18	0.18	0.52	−0.45	0.37	−0.06	−0.31	0.01	+	0.22	−0.18	0.36	0.58	0.25	+
82	0·16	0.08	0.64	0.38	0.30	−0.04	0.30	0.26	+	1.40	1.12	1.54	1.65	1.42	+
83	1.69	1.19	1.43	1.46	1.07	1.46	1.52	1.40	+	1.83	1.60	1.48	1.56	1.62	+
84	0.95	0.70	1.08	0.93	0.83	0.90	0.89	0.90	−	−0.40	0.40	−1.36	−0.30	−0.43	−
85	0.44	1.40	0.04	1.08	0.75	1.32	1.00	0.86	−	−0.79	−0.57	−0.55	−0.15	−0.51	−
86	−2.27	−1.41	−2.25	−1.32	−1.85	−1.67	−1.65	−1.77	−	−1.04	−1.65	−1.11	−0.67	−1.12	−
87	−0.51	0.10	−0.69	−0.18	−0.08	−0.78	−0.23	−0.32	+	0.52	−0.05	−0.56	−0.80	−0.22	+
88	−0.06	0.43	0.08	0.68	0.47	0.14	−0.08	0.24	+	0.64	0.21	0.06	0.23	0.28	+

Table 4: Standardised population sizes and means for site groups B and J. Trans. (transition) = sign of mean population change from that in the previous year.

was geographically structured, pairwise correlation coefficients between $\log_{10}$ (population size) of all sites in all available years were calculated. To reduce type I errors, only those correlations significant at the 0.01 level or below are shown in Fig. 7. The major feature of Fig. 7 is the clustering of geographically adjacent populations in two regions along the main road through the study area. One region consists of sites AC, Jb, Ja and U (which will be referred to as group J), and the other of sites Q, R, E, AEb, AEa, C and B (group B). Other significant correlations tend to be between scattered sites.

The average behaviour of groups B and J can be compared if population sizes are standardised in the way described previously (p. 197). These standardised values were then averaged for each year across sites within each group (Table 4, Fig. 8). The non-significant correlation between the yearly means of 1974–1976 and 1979–1988, i.e. when more than one site was scored in each of the B and J groups, underlined the lack of *quantitative* association over years ($r = 0.52$, d.f. $= 11$, n.s.). However, it can be asked whether there are *qualitative* associations between groups by considering the ranking of populations and the direction of mean population change from one year to the next. Spearman's rank correlation coefficent between population means for the two groups was just significant ($r_s = 0.565$, d.f. $= 11$, $0.05 > p > 0.02$). Twelve transitions from one year to the next were common to both groups of sites (Table 4). All but one showed concordance in the sign of population trend between the groups ($p = 0.003$, one-tail binomial test). For the discordant comparison (1978–1979), only one population estimate was available in each group in the earlier year. Thus, although the site groups are not quantitatively associated, they do agree as to which

years are good, leading to a population increase, and which are poor, leading to a population decline.

Discussion

The behaviour of spiders often makes the estimation of population sizes relatively easy. For orb-web spinners, for example, counting webs can give an accurate estimate of numbers of individuals present (e.g. Schoener, 1986). In the case of *E. ovata*, webs are difficult to find but nursery retreats are not. One obvious disadvantage of using this feature is that only mature females can be counted. The sex ratio at maturity, determined by raising young from the egg under uncrowded laboratory conditions, is approximately 1:1 (Oxford, 1983). In the field, however, males mature before females and die soon after mating so the sex ratio is constantly changing. The population dynamics of males remains unknown.

Raw counts of females were made by locating all visible rolled leaves. The efficiency of rolled-leaf detection was not quantified but multiple censuses a few days apart gave results which varied by only 5% or less. Searching deeper into vegetation clumps revealed very few additional spiders. The counting efficiency seems to have been high. Greater errors probably arose during the conversion of population counts to estimates of maximum population size using the relationships derived above. The relationship involving the proportion of females with cocoons incorporated data from five sites from different parts of the study area in two years, and the agreement between them was remarkably good. The weaker relationship, involving the proportion of cocoons with second instar young, relied heavily on data gathered from Site U in
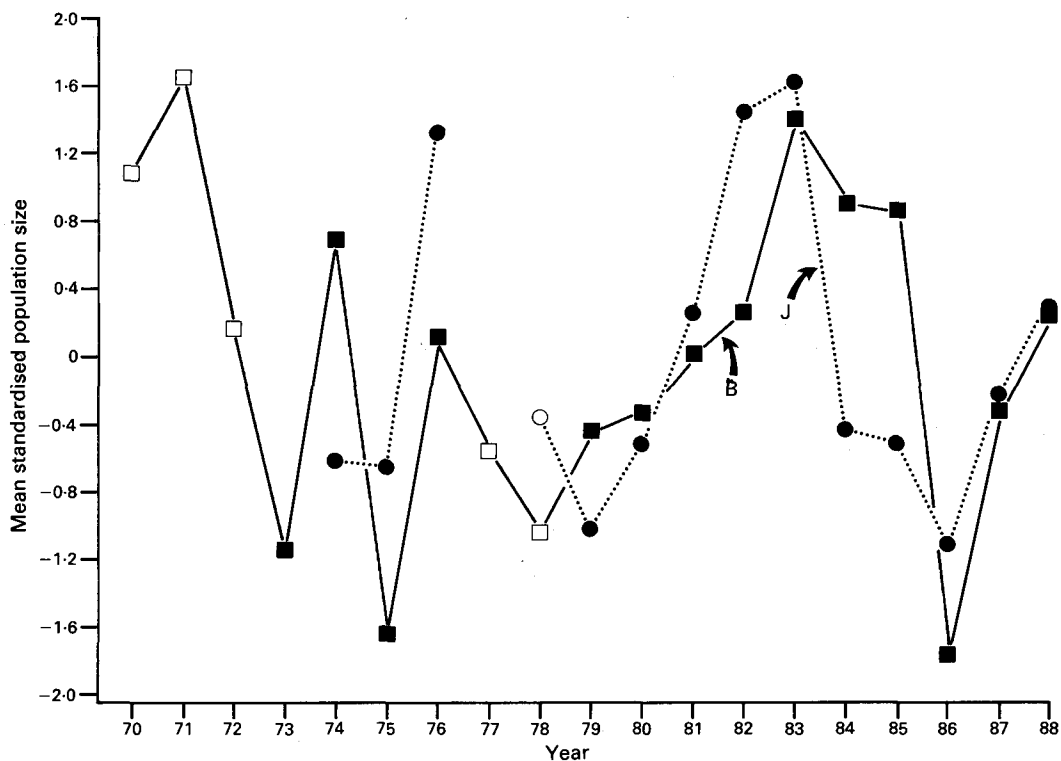

Fig. 8: Plot of mean standardised population sizes for the B (□, ■) and J (○, ●) site groups by year. Open symbols are points based only on one population within a group. Arrows B and J indicate when major disturbances are known to have occurred (see text).

1980. However, this regression equation was used in scaling data in only one year, 1987. Thus, on the whole, estimates of maximum female population size should be reasonably accurate.

Within sites, population sizes varied over time. In terms of raw numbers, maximum population sizes ranged from 3.6 (site AI) to 55.2 (site AF) times the minimum population size (Table 2). These values will be sensitive to the number of years in which a site was counted. A number of other measures of population variability, e.g. the standard deviation of the logarithm of population size, or the coefficient of variation, have been widely used to compare different populations of a species and populations of different species (e.g. Williamson, 1984; Owen & Gilbert, 1989). Recently, McArdle, Gaston & Lawton (1990) and McArdle & Gaston (1992) have described serious problems with these indices, pointing out that they are in fact complex functions of, among other things, mean population size, spatial distribution, size of area sampled and dispersal rates. Comparisons of population variability in *E. ovata* with that of other spiders or other invertebrates are therefore fraught with difficulties.

Standardised population sizes in the 23 sites examined varied both temporally and spatially. Over the ten-year period when all sites were counted, the effect of year accounted for approximately 50% of the overall variance in population size fluctuations. This figure is probably inflated to some extent because population sizes in successive years were not independent, but it is not obvious how the bias can be removed. However, the probability associated with the ANOVAR is so low that the bias would have to be very strong to make a non-significant effect as significant as was found.

Associations between mean population size and climatic variables were sought over this period, although it is recognised that ten years is a very short run for an analysis of this kind. The analyses using running means suggested associations which might have biological significance. Population size correlated positively with warm springs and reduced snow cover. At the beginning of this period the young would be deep in the herb layer. With the advent of milder weather they begin actively to feed and grow (Toft, 1976). Early warmth presumably means an earlier start to this process, possibly removing them from a stage of their life cycle in which mortality is high. It might also be the case that in cold springs food reserves were depleted before feeding commenced. Schaefer (1977a,b) showed that, in four species of spider, mortality of young postembryonic stages contributed most to overall mortality. However, he also demonstrated that winter mortality is low and uncorrelated with winter temperatures in those species with life cycles most like *E. ovata*. The species studied with this Type II life cycle were in different families from *E. ovata* and the extrapolation might not be valid.

Population sizes in Nidderdale were also positively correlated with smaller temperature ranges, hours of sunshine and rainfall in autumn when young spiderlings would be moving down to their overwintering sites. Possibly the supply of food for the young was better under these conditions and they entered winter diapause with greater energy reserves. The negative relationship between population size and hours of bright sunshine through the summer months, if real, is not easy to interpret. These very tentative associations with climatic factors clearly need to be investigated further by studies both in the laboratory and in the field.

Very local factors also had a considerable influence on variation in population size. The correlation matrix (Fig. 7) indicated that population sizes in sites within two geographical areas co-vary; between these groups of sites, however, there was no significant quantitative association. The groups as a whole do agree in the direction of population trends across years, reflecting the influence of year, as discussed above. The most likely explanation for the behaviour of sites within the B and J groups is human disturbance. Between counting populations in 1981 and the spring of 1982 the old growth of bramble was cut back and removed from all sites within the B group. In summer 1982, the B-group mean population size was very low compared with that in the J group (Fig. 8). A second incident, involving a severe cutting back of the road verge, affected sites in the J group before counting in 1984. Here again, mean population size dropped dramatically compared with that of the B group. Lesser disturbances are known which affected individual sites in single years, and doubtless there were others which went unrecorded. In addition, population sizes in some sites, e.g. D, G, AH and AI, showed no correlation whatsoever with those at any other site. Presumably in these cases, extremely site-specific influences of unknown nature had a major impact on population trajectories. Very local effects were almost certainly operating in other sites as well. These effects were uncorrelated with the position of the site or with the structure and species composition of the vegetation present.

During the period studied, it has been shown that population size in *Enoplognatha ovata* was influenced by a year factor (possibly climate), by a local geographical factor (disturbance) and by other, unknown factors which were site-specific. As mentioned in the introduction, the data reported here were a by-product of genetical work and consequently were not gathered with this study in mind. Conclusions must therefore remain tentative; a fuller understanding of the processes controlling population size in this species requires more specific observation and, in particular, experimentation.

Acknowledgements

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