

Studies of colour polymorphism in some marginal populations of the aposematic jersey tiger moth *Callimorpha quadripunctaria*

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Callimorpha quadripunctaria (Lepidoptera, Arctiidae) is both genetically polymorphic for hindwing colour and well protected from predators. Polymorphic populations are, however, only found in the extreme northwest of its extensive distribution in Europe and Asia Minor. Use of a colour analyser confirmed the existence of three reasonably discrete colour classes: bright red, orange and yellow. These could each be subdivided into two further groupings of phenotypes, one of moths of pure colour and the other with a secondary colour. The species is polymorphic in SW England, where it became well established in villages and towns around the Exe estuary in the late 19th century. It now extends about 30 km east and west along the south coast of Devon and up to a similar distance inland along the river valleys. The rate of spread is consistent with the substantial dispersal of up to 500 m detected in a capture-recapture experiment performed at Exeter over the whole flight period in August 1984. This experiment also found no differences in timing of emergence, survivorship or within-habitat movement between the sexes or the colour classes. Males may show a higher rate of emigration than females. The species is polymorphic throughout S Devon. Its stronghold to the west of the Exe basin is characterized by a comparatively uniform morph frequency with 50–65% red, 20–40% orange and 10–20% yellow. Yellow moths have their highest frequency in this area, red moths in the east and west and orange to the north. Adult activity is concentrated in the 2–3 h after dusk. Air temperatures of higher than 15°C are probably critical to pairing which involves sex pheromones released by females. This may be an important factor limiting the species' range. Our results suggest that climatic selection pressures involving non-visual differences in fitness account for the geographical variation. The lack of daytime activity of moths in comparison to that found by other workers on Rhodes and which is likely in other warmer climates suggests the hypothesis that expression of the polymorphism is favoured in the marginal populations of NW Europe by a relaxation of the stabilizing influence on the warning coloration exerted by visual predators.

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INTRODUCTION

The jersey tiger moth *Callimorpha* (= *Euplagia*) *quadripunctaria* (Poda) (Lepidoptera, Arctiidae) is unusual in being both unpalatable and strikingly polymorphic for hindwing colour. The many facets of chemical defence in arctiids, augmented by static displays which may involve stridulation, are reviewed by Rothschild (1961, 1984) and Rothschild *et al.* (1979). The expectation that predators hunting by sight exert stabilizing selection on warning colour patterns (see, for example, Benson, 1972; Sillén-Tullberg, Wiklund & Järvi, 1982) means that visible polymorphism is not expected in aposematic species. The occurrence of a genetic polymorphism involving bright red, orange and yellow colour forms in *C. quadripunctaria* is of additional interest because our examination of museum material shows that the polymorphism is only found in part of its extensive range, namely SW England and NW France. This region is geographically peripheral and probably ecologically marginal for the species. Many workers have suggested that populations in such areas are likely to exhibit differences in their genetic variation in comparison to those of more central ones. The central-marginal model proposes that populations near the centre of a species' range tend to be continuous and at a high density with a high genetic, phenotypic and ecological diversity, whereas those towards the edge are isolated, sparse and chromosomally monomorphic (Mayr, 1963; and for a recent review see Brussard, 1984). The colour polymorphism in *C. quadripunctaria* presents an interesting example of an increase in one form of genetic and phenotypic variation in some marginal populations of a species. This paper reports on a survey of this moth and its polymorphism in SW England and on ecological data obtained principally from a capture-recapture experiment. Our results are used to develop a hypothesis that the colour polymorphism in NW Europe is due to relaxation of stabilizing visual selection on the warning coloration and the existence of climatic selection acting through non-visual differences in fitness.

METHODS

Colour analysis

Many colour forms have been recognized in *C. quadripunctaria*. We scored the colour of the upper surface of the hindwings by eye in the laboratory. Moths were frozen or scored soon after capture because the wing pigments, particularly the red one (Ford, 1937), tend to fade especially in light. Our concept of the nature of the colour phenotypes was developed during initial survey work in 1982 (Liebert, 1983) and 1983. Our refined scoring technique which distinguished six phenotype classes was checked in 1984 using an optical technique to provide a more objective assessment of colour classification. A Melico P.M.5. Colour Analyser was used to measure light reflected from one hindwing from each of 105 moths reared in the laboratory. The moths were from 12 broods (Liebert & Brakefield, in preparation) and covered the range of colour variation found in Devon. Two spots on each wing of about 0.5 mm in diameter were measured. They were located in broad expanses of colour between the black wing markings, one towards the outer edge of the wing and the other in the central region. Standardization of the size and position of the areas measured was achieved by attaching the light pipe sensor of the colour analyser to one eyepiece of a binocular microscope, the other being fitted with a micrometer. Trials showed that measurements of other areas of the wings were unnecessary. Moths were measured in a dark room with a constant tungsten light source. The colour analyser gives readings of the amount of white light absorbed by the wing and of each of the primary colours, blue, red and green. The apparatus is initially standardized by zeroing each colour using a white card. Trials which included worn specimens suggested that some compensation for variability in wing wear or 'general depth' of colour between moths could be achieved by analysing the readings for the primary colours for each wing area transformed as follows. The difference between the overall mean value for white light and that for a particular moth is subtracted from the measurements of each primary colour for that moth. Data for the resulting six variables were then subjected to principal component analysis using the Genstat statistical package.

Field surveys

Samples of *C. quadripunctaria* were obtained during August 1984 and, less extensively, August 1983 from throughout the British distribution of the species in S Devon. Liebert (1983) describes the results of preliminary work in 1982. Collections were made in or around villages and towns by beating or examination of hedges, or by inspection of white walls on which the moths sometimes rest towards the end of hot sunny afternoons. The moth rests with its forewings closed over the hindwings to give an arrowhead shape. The forewings are marked disruptively with white and black stripes. The coloured hindwings are conspicuous in flight. The moths are quite easy to find by eye when a 'search image' has been developed. A few additional samples were collected by other recorders. Numerous correspondents supplied records which helped to define more precisely the distribution of the species.

The capture-recapture experiment

A multiple mark-release-recapture experiment was performed in and around the campus of the University of Exeter to cover the whole flight period in 1984 (essentially August). A total of 648 moths were marked uniquely and released, usually at about midday on the day after capture, at one of four more or less central points in the search area. The release sites were close to trapping areas. The search area was diamond-shaped with a long central axis of about 1100 m and an area of about 0.65 km². Two Robinson mercury-vapour light traps and two Heath portable light traps were fairly evenly spaced along the long axis. The former type of trap was substantially more effective. The traps were inspected regularly each evening until about midnight and again the following morning. The areas to either side of this axis were sampled using assembling traps, inspection of Buddleia bushes and some daytime collecting. The seven assembling traps each contained small numbers of reared virgin females. They consisted of short cylinders of cotton net and were hung in hedges along lanes or on fences at two to four different locations. They were inspected at frequent intervals each evening and any attracted males captured by net. An additional release of 87 marked moths was made on 18 August in a favourable habitat for the species some 350 m distant and across a steep rural valley from one of the outermost light traps. The release was made to provide some information about immigration into the search area.

There are several reasons why this experiment can only provide preliminary estimates of population parameters and why sophisticated methods of data analysis are not appropriate. For example, the moths were released in groups, were from remote as well as local study sites and the sampling intensity was not uniform throughout the search area. Although the total number of days survived by all 'marks' given to moths was quite high (373), the numbers of moths handled, and of recaptures made, were low on many days. These observations suggest that analysis of the capture-recapture data by the deterministic model of Fisher & Ford (1947) is more appropriate than by a stochastic model, such as Jolly's (Bishop & Sheppard, 1973; Sheppard & Bishop, 1973). This analysis excludes the data for recaptures made within 24 h of release (usually < 12 h).

RESULTS

The colour polymorphism

The principal component analysis of the optical data for the 105 moths yields only two important components; the first 'explaining' 78% of the total variance and the second, 18%. The weightings for the blue, red and green variables were similar for each of the wing areas measured. When averaged over these areas the weightings in sequence were -0.04, -0.28 and 0.65 for the first component and -0.70, 0.03 and -0.02 for the second component. Thus the first component reflects the readings for green to some extent contrasted with those for red and the second one reflects the values for blue.

Figure 1 shows a plot of the first two principal components for the 105 moths coded according to our visual scores. There is a good separation of the three main colour classes of bright red, orange and yellow. Moths of each of them are

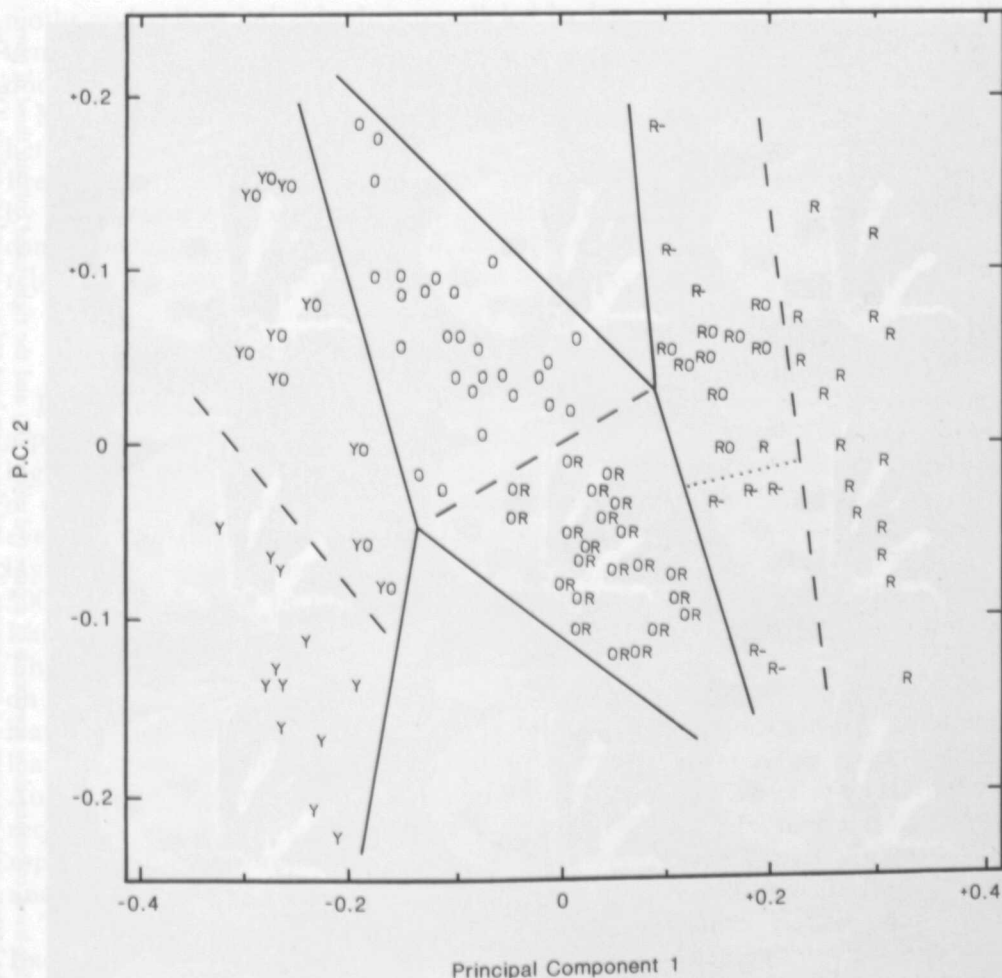


Figure 1. Principal component analysis of colour variation in 105 *Callimorpha quadripunctaria* reared in the laboratory: R, red; RO, red-orange; O, orange; OR, orange-red; Y, yellow; YO, yellow-orange; -, uncertainty about secondary colour. Continuous lines indicate main colour class boundaries and dashed lines, further subdivisions. The dotted line indicates a possible boundary within one of these subdivisions.

illustrated in Fig. 2. Although each of these classes encompasses a range in colour, their reasonably discrete nature means that they can be reliably scored by us in field samples and that some degree of consistency is likely between independent workers who have examined series of standards. More difficulty is encountered with further subdivisions. Figure 1 supports our final visual assessment that each colour class consists of two, or perhaps three, subclasses. For each of the main colours, there is a subclass of moths with comparatively pure colour which is uniform over the wing and one in which secondary colour is present (see Fig. 2. for orange moths). Because of the intergrading of these categories, comparison of their frequency in material scored by other workers is likely to be unreliable. Consequently the data we examine of other recorders and also our own for 1983 will only be analysed with regard to the main classes. The distinction on the dorsal surface of the hindwings between red and orange



Figure 2. Colour variation in *Callimorpha quadripunctaria*. The two left-hand columns show specimens of a pure red colour (R) and the right-hand column those of pure yellow (Y). Columns three and four show orange moths of which the bottom-right specimen is a pure orange (O) and the others have red as a secondary colour (OR). The length of the forewing is 2.5–3 cm.

moths and yellow individuals is paralleled by less intense colour changes on the ventral surface of the hindwings, the inner part of the forewings, and on the dorsal surface of the abdomen.

Most, or perhaps all, of the six colour classes recognized in 1984 are probably heterogenous both with respect to genotype and genotype-phenotype. Preliminary examination of 34 broods indicates that the variation is controlled by segregation of a small number of alleles at each of two, or possibly three, complementary gene loci (Liebert & Brakefield, in preparation). The dominance relationships can be summarized as red > orange > yellow.

Natural history and distribution

In Devon, *C. quadripunctaria* is especially associated with sheltered and warm-aspect lanes radiating uphill from villages or towns. It is characterized by a highly clumped or patchy distribution within a locality. Adults feed on a variety of nectar sources especially Buddleia. Females in an insectary will pair in the evening following eclosion, which usually occurs in the morning. They begin to lay eggs in small batches on the following day, continuing for 1-3 weeks. Over 500 fertile eggs may be laid from a single mating. Eggs hatch in about 14 days. Larvae will feed on a wide variety of herbs and shrubs (see also Walker, 1966). The few larvae found in the field were on *Anchusa* spp. growing in hedgerows or on banks. They overwinter in the second or third instar, often amongst dead leaves. They feed on warmer days. A loose cocoon is spun in moss or dead leaves in June or July, emergence beginning in late July and extending through August with odd individuals up to late September. Our earliest and latest field records of sightings are 20 July and 20 September (a record for 6 July occurs in reports of the Devonshire Association). The later records were all for the cool and wet summer of 1982.

The species was first recorded in Devon at Alphington just southwest of Exeter in 1871 (see, for example, Stidston, 1952: 22). Ford (1975: 35) discusses why this date is likely to be close to the actual year of introduction. The moth apparently quickly became established to the west of the Exe estuary (area III, Fig. 3). It was taken at Starcross (map no. 13) in 1873 where the earliest specimens (1893 and 1894) with full data attached in the British Museum collection were obtained. Moths dating from 1900 to 1909 in the British Museum are from Starcross, Dawlish (14) and Teignmouth (16). Taking its initial site of introduction as halfway between Alphington and Starcross (see star in Fig. 3) the species has now extended its range about 30 km east and 45 km west along the coast. Populations also occur up to about 30 km inland, particularly along the river valleys (Fig. 3). Four records for 1984 from Plymouth to the west may indicate a recent secondary introduction (D. A. Curry and others, pers. comm.).

Our examination of British Museum material also strongly suggests that the colour polymorphism is well established in the Brittany peninsula of NW France. Thus, long series from Cancale (with Mt St Michel) and Rennes included about 100 yellow and orange moths. P. Kirby (pers. comm.) has also seen yellow *C. quadripunctaria* at Quimper and Lorient. Similarly, smaller numbers of moths from the Channel Islands include each form (also D. d'A. Laffoley, pers. comm.). In contrast, several hundred moths from throughout the

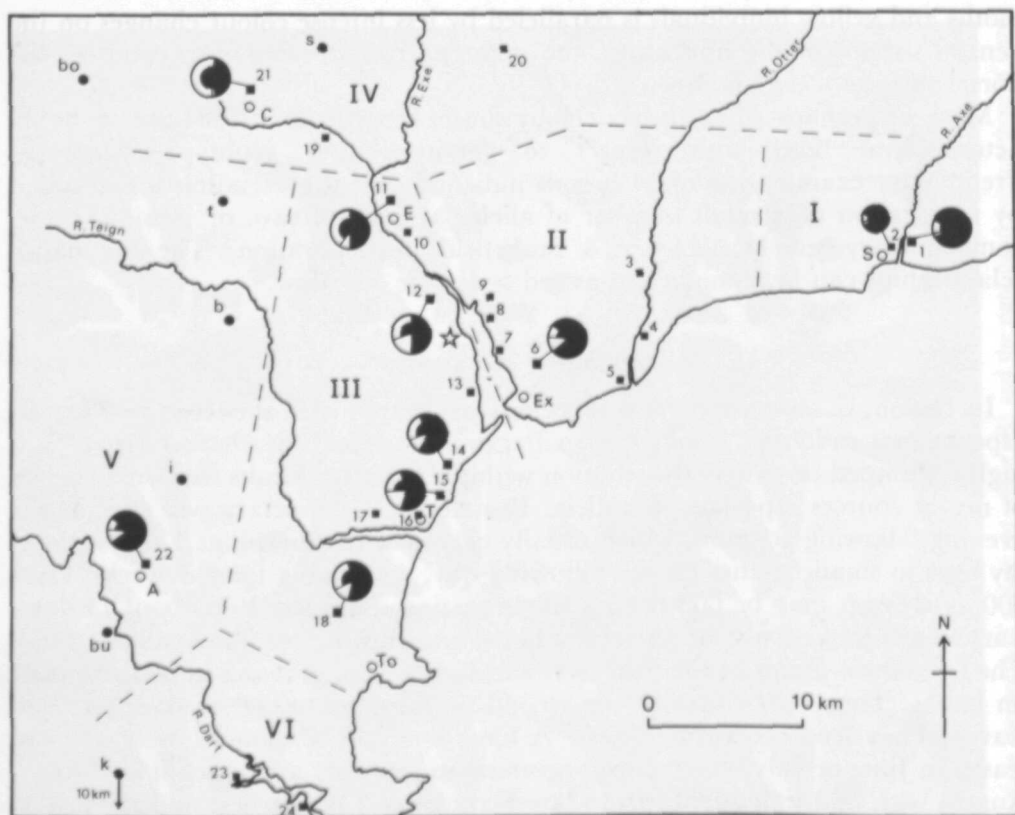


Figure 3. Frequency of the main colour classes of *Callimorpha quadripunctaria* in S Devon in 1984. Pie diagrams show red (in black), orange (halved) and yellow (white) for samples of more than 30 months (23 at site 2). Sampling sites for 1983 and 1984 are squares with map numbers attached given in Tables 1 & 2). Dashed lines and roman numerals indicate area groupings. The star indicates the probable area of introduction. Circles show additional records for peripheral localities; b, Bridford; bo, Bow; bu, Buckfastleigh; i, Islington; k, Kingsbridge; s, Stockleigh Pomeroy; t, Tedburn St Mary. Some main towns: A, Ashburton; C, Crediton; E, Exeter, Ex, Exmouth; S, Seaton; T, Teignmouth; To, Torquay.

rest of the wide species range in Europe south of about 51°N and Asia Minor include yellow specimens only as apparently rare mutants (one each from Austria, Central France and Germany). The other moths all appear to be of the pure red colour but because of fading problems this must be considered uncertain (see also Elger, 1969).

Geographical variation

The frequency data for *C. quadripunctaria* in 1984 are given in Table 1. Those for the large sample from Exeter (University) show no difference between the sexes ($\chi^2 = 7.10$, $df = 5$, $P > 0.1$). The frequency distributions for the three main colour classes in the larger samples ($N > 30$) are highly heterogeneous ($\chi^2 = 65.6$, $df = 16$, $P < 0.001$). Figure 3 indicates that orange and yellow moths are at relatively low frequencies ($< 10\%$) to the east and west and red ($< 45\%$) and yellow ($< 5\%$) inland to the north. Ashburton in the west has particularly high frequencies of the three subclasses with a pure colour while

Table 1. Frequency of the six colour classes and percentage frequency of the three main colour classes in samples of *Callimorpha quadripunctaria* from the sites indicated in 1984 (colour codes and site numbers as in Figs 1 & 3)

Name	Site	No.	Number of moths						Percentage of main classes			Sample size
			R	RO	OR	O	YO	Y	Red	Orange	Yellow	
Axmouth		1	23	10	2	2	0	1	87	11	3	38
Seaton*		2	18	2	2	0	0	1	87	9	4	23
Newton Poppleford		3	7	3	2	1	0	0	77	23	0	13
Otterton		4	0	1	0	0	0	0	—	—	—	1
Exmouth		6	27	4	2	2	1	4	77.5	10	12.5	40
Lymptone		7	7	1	0	1	1	1	73	9	18	11
Exeter (Univ.)		11	120	26	44	70	7	22	51	39	10	289
Exminster		12	30	7	9	13	3	11	51	30	19	73
Dawlish		14	10	11	2	5	2	2	66	22	12.5	32
Holcombe		15	32	21	5	14	3	14	60	21	19	89
Bishopsteignton		17	2	2	0	0	0	2	—	—	—	6
Kingskerswell		18	8	13	6	4	0	5	58	28	14	36
Newton St Cyres		19	5	0	0	1	0	0	—	—	—	6
Bradninch		20	0	0	2	0	0	1	—	—	—	3
Crediton		21	14	3	16	5	0	1	44	54	3	39
Ashburton		22	37	1	0	5	0	6	78	10	12	49
Ashprington		23	1	1	1	1	0	0	70	30	0	10
Dittisham		24	4	1	1	0	0	0				

*Part sample obtained by T. G. Howarth.

Crediton in the north has a very high proportion of orange-red moths (Table 1). Heterogeneity χ^2 tests on the data for the three main colour classes show that the combined samples from areas I, II and V (east and west) are homogeneous ($\chi^2 = 3.80$, $df = 4$, $P > 0.1$) and when pooled are different from that of area IV to the north ($\chi^2 = 37.11$, $df = 2$, $P < 0.001$). The combined sample from the central area III where the species is most abundant is different from both those from the north and the east-west ($\chi^2 = 7.36$, $P < 0.05$, and $\chi^2 = 41.37$, $P < 0.001$, respectively with $df = 2$). The central area is characterized by a relatively uniform frequency distribution of 50–55% red, 20–40% orange and 10–20% yellow. However, the five large samples from this area are heterogeneous particularly when the data for the full six colour classes are analysed ($\chi^2 = 17.66$, $df = 8$, $P < 0.05$ and $\chi^2 = 56.91$, $df = 20$, $P < 0.001$). Figure 3 suggests that there is a clinal increase in orange moths and decline in yellow ones northwards through this area. The increase in orange is associated with a decline in red-orange moths (Table 1). This cline is apparently continued into the northern area. More samples would probably detect clines radiating in all directions from the comparatively uniform frequency of the forms in the centre of the distribution.

The less extensive data for 1983 are given in Table 2. Our own samples provide support for the 1984 results. Thus the small combined sample for areas I and II and that for Ashburton (V) show similarly high frequencies of red moths to the larger ones for 1984. The combined samples for the central area III again show a substantially more uniform frequency distribution of 43% red, 40% orange and 16.5% yellow moths. The two large individual samples from Exeter

Table 2. The frequency of three main colour classes in samples of *Callimorpha quadripunctaria* taken in 1983 from the sites indicated (see Fig. 3)

Site		Number of moths			Percentage frequency			Sample size
Name	No.	Red	Orange	Yellow	Red	Orange	Yellow	
Seaton*	2	7	5	1	54	38	8	13
Seaton	2	5	1	0	—	—	—	6
Budleigh Salterton	5	3	0	0	—	—	—	3
Lympstone	7	5	1	0	91	9	0	11
Exton	8	5	0	0				
Ebford†	9	14	16	1	45	52	3	31
Exeter (misc.)	10	12	9	5	46	35	19	26
Exeter (Univ.)	11	33	35	13	41	43	16	81
Exminster	12	27	26	9	44	42	15	62
Starcross	13	1	0	1	—	—	—	2
Dawlish	14	3	1	1	—	—	—	5
Teignmouth‡	16	127	24	20	74	14	12	171
Kingskerswell§	18	19	4	0	83	17	0	23
Ashburton	22	11	1	1	84	8	8	13

Other recorders: *T. G. Howarth, †S. L. Toyn, ‡D. Laidlaw, §R. Newbold.

(University) and Exminster are both homogeneous with the corresponding 1984 samples ($\chi^2 = 3.49$ and 2.10 , respectively with $df = 2$ and $P > 0.1$). Unfortunately we obtained no samples from the north of the region. Some differences are apparent when the samples of other recorders are examined. Thus the large sample from Teignmouth is different from that from nearby Holcombe in 1984 ($\chi^2 = 5.98$, $df = 2$, $P \cong 0.05$). A similar difference is indicated for Kingskerswell. The frequency of red moths in our combined sample for areas I and II is significantly different from that of other recorders ($\chi^2 = 10.32$, $df = 1$, $P < 0.01$). In each of these cases there is no difference ($P > 0.05$) when the frequency of yellow moths is compared and therefore the heterogeneity appears to result principally from a lack of consistency in scoring the red-orange range of the variation (see section on colour polymorphism). It is probable that without reference to standards, some recorders score only our pure orange as 'orange', and others only our pure red as 'red' moths.

Population dynamics

The data on captures of unmarked *C. quadripunctaria* made between 28 July and 2 September 1984 at Exeter University can be used to examine the timing of emergence of different cohorts of moths. Analysis of plots of cumulative relative frequency, in per cent, on a normal probability scale against date provides estimates of the date by which 50% of each cohort emerged and the standard deviation about this date. The plots did not indicate any substantial departures from normality. The estimates included in Table 3 show no differences in the timing of emergence either between the sexes or among the main colour classes. This conclusion is supported by a corresponding analysis of the daily estimates of number of additions to the population obtained from the capture-recapture data. The peak in number of moths occurs in mid-August with about 95% of first captures occurring over a 3-week period from 6 August.

Table 3. Analysis of the date of capture of unmarked *Callimorpha quadripunctaria* at Exeter in 1984 and estimates of adult population parameters and movement obtained from capture-recapture data. Estimates are given for all moths, the sexes and the main colour classes

Statistic	All moths	Sex		Colour		
		Male	Female	Red	Orange	Yellow
Median date of first capture (August)	—	16.4	17.1	16.6	17.0	15.3
s.d. of capture date (days)	—	5.0	5.2	5.1	5.0	5.8
Total emergence (production)	2692	1762	633	1451	677	93
24-survival rate	0.84	0.84	0.84	0.845	0.77	0.998
Expectation of life (days)	5.7	5.7	5.6	5.9	3.9	—
Total number of releases*	711 (684)	396 (380)	315 (304)	416 (401)	198 (192)	97 (91)
Total number of recaptures*	84 (57)	39 (22)	45 (35)	45 (30)	21 (14)	18 (13)
Percentage recaptured away from release site*	69.0 (80.7)	66.7 (81.8)	71.1 (80.0)	64.4 (76.7)	71.4 (78.6)	77.8 (92.3)

*Values in parentheses exclude moths recaptured and rereleased within 24 h of initial release.

The lack of any earlier emergence by males (protandry) contrasts with that found in many lepidoptera with similar life cycles (see Parker & Courtney, 1983, and references therein). Contributing factors may be remating by females and a restricted period of nights with optimum conditions for female 'calling' of males (see section on adult movement and behaviour). The former explanation is not supported by our laboratory observations or the ineffectiveness of assembly traps in late August. Walker (1966) found more than one spermatophore in some female moths from Rhodes but suggested that they resulted from single copulations.

Table 3 includes estimates of production or total emergence of *C. quadripunctaria* calculated using the formula given by Fisher & Ford (1947). This estimate for all moths suggests that about 41 emerged per hectare. This is probably an overestimate because of dispersal of some moths over a wider area than that searched (see below). The loss of moths due to emigration also means that the estimate for expectation of adult life within the search area of 5.7 days (Table 3) is an underestimate of adult survivorship. The estimates of production suggest that males outnumbered females by more than two to one. This bias is given some support by the captures of unmarked moths (158 males:87 females, excluding assembling areas), but light traps usually tend to attract more males in species of moths, and *C. quadripunctaria* taken on Buddleia or at daytime resting sites show a more even sex ratio (26:22, with recaptures 31:33). Furthermore, our broods reared in 1983 show no evidence of departures from an even sex ratio in all reared moths ($\chi^2 = 1.89$, $P > 0.1$) or for heterogeneity in the sex ratio amongst the larger broods ($N > 25$; $\chi^2 = 3.90$, $df = 4$, $P > 0.1$). Application of Manly's (1973) sensitive iterative method to the data for the known length of life of cohorts of marked moths shows no significant differences

in survivorship among the colour classes (Table 4). The comparison for the sexes approaches significance with females having the higher survival rate. This is not, however, reflected in a difference in the estimates of survival rate (Table 3). Examination of the survivorship curves indicates that females tend to be recaptured after longer periods of time from release, thus whereas 20 of 34 females were recaptured from 5.5 to 13.5 (the longest for any moth) days after capture only six of 22 males were ($\chi^2 = 5.35$, $P < 0.05$). Females were also more likely overall to be recaptured than males ($\chi^2 = 10.81$, $P \cong 0.001$, excluding captures at assembling areas). Such a difference and the apparent bias in favour of males in estimates of production could arise because males are more vagile than females and thus are more likely to emigrate from a habitat.

Table 4. Estimates of daily selective values of females compared to males (m), of orange moths compared to red (R) and of yellow compared to red, orange (O) or all others (R+O) in *Callimorpha quadripunctaria* obtained by the method of Manly (1973)*

	Females (m)	Orange (R)	Yellow (R)	Yellow (O)	Yellow (R+O)
Selective value	1.105	1.028	1.135	1.110	1.128
S.E.	0.055	0.082	0.096	0.108	0.090
t^\dagger	1.91	0.34	1.41	1.02	1.41

*Data are for all new releases except those made over the last 9 days of the experiment and excluding recaptures made within 24 h of release.

† The value of t measures the difference from unity (as for the comparative cohort). All values have $P > 0.05$.

Adult movement and behaviour

There was no heterogeneity between the four release points in the sex ratio or colour frequency distribution of released moths ($P > 0.1$ in each case). Therefore the data can be pooled to examine the proportion of all detected movements which were made away from the release area (Table 3). There is no difference in this proportion either between males and females or between the three main colour classes (e.g. for all data: $\chi^2 = 0.19$, d.f. = 1 and $\chi^2 = 1.14$, d.f. = 2, respectively with $P > 0.1$ for each value). There is thus no evidence of differential movement within the search area. Overall, about 70% of all recaptures were made away from the release area, many several hundred metres distant. The longest movements were seven of about 500 m between one release point and two capture sites. The species does not appear to be very sedentary within our study area and movements into and out of this area are likely. This is emphasized by the fact that of the 87 moths released across a steep valley from the search area two were recaptured within it after 6 and 10 days, respectively.

The capture-recapture data provide preliminary observations about the behaviour and activity of the moths. Females tend to assemble males only when air temperatures are above 15°C after dusk, which is at about 21.00 hours or shortly after in August in Devon (Fig. 4A). The number of males attracted to 'calling' females releasing pheromone peaks sharply after dusk and falls dramatically after about 45 min (Fig. 4B). The moths attracted at temperatures

below 15°C and after 22.00 hours were all during the early part of the experiment when trap success was very low. Our observations suggest that optimum conditions for pairing are high evening temperatures, low wind speed and probably high, very local densities of moths. The data for time of capture at the most successful light trap and at nearby *Buddleia* bushes are less precise since inspection was more infrequent and thus the time of arrival sometimes

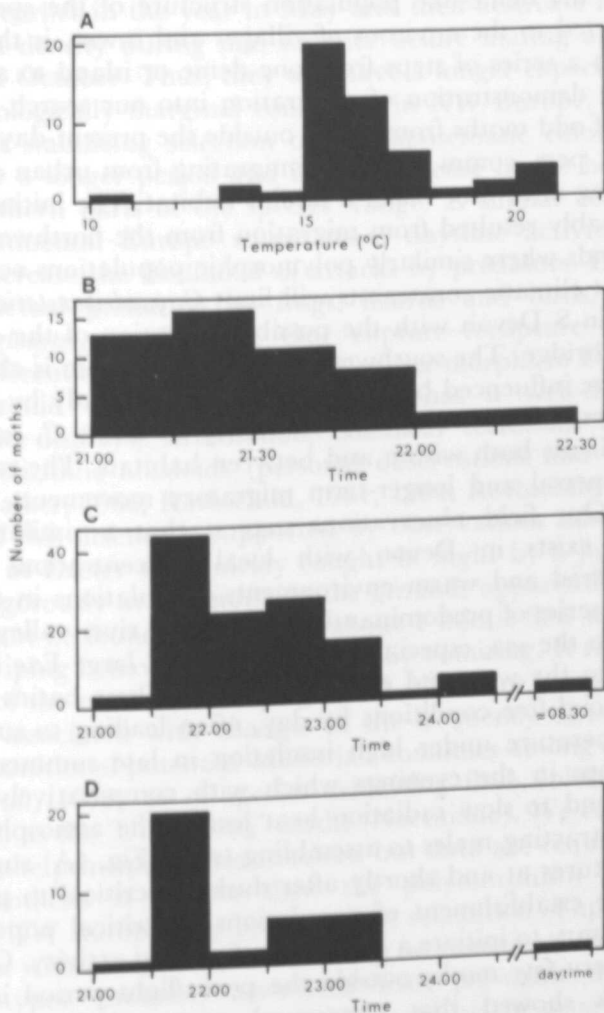


Figure 4. Frequency distributions for captures of *Callimorpha quadripunctaria* at Exeter in 1984. A, Air temperature on arrival of males at assembling traps; B, Time of arrival at assembling traps; C, Time of collection at main Robinson mercury-vapour light trap; D, Time of collection on *Buddleia* flowers near the main light trap. Note that the axes are not always directly comparable.

preceded that of capture by up to about 45 min. However, they clearly indicate that feeding and, more particularly, dispersal activity continue for 1–2.5 h after mating activity ceases (Fig. 4C, D). The data also indicate the predominance of feeding after dusk since the *Buddleia* bushes were inspected on regular afternoon visits and only one moth found (Fig. 4D).

DISCUSSION

Taking 30 km as the average radial distance of spread of *C. quadripunctaria* in Devon over the 113 generations since the first records (Fig. 3), the minimum average displacement per generation can be estimated at about 250–300 m. This is consistent with our findings of quite substantial dispersal by moths, with movements detected of up to about 500 m within a habitat at Exeter. The implication from the deme-like population structure of the species in Devon, where it is restricted to the environs of villages and towns, is that extension of range proceeds in a series of steps from one deme or island to another. This is supported by the demonstration of emigration into our search area at Exeter and the records of odd moths from towns outside the present-day distribution in Devon (J. Heath, pers. comm.). Moths emigrating from urban areas are likely to continue moving until they reach a similar habitat. The initial establishment in Devon presumably resulted from migration from the northwest of France or the Channel Islands where similarly polymorphic populations occur.

We believe that climatic constraints will limit *C. quadripunctaria* to its present-day distribution in S Devon with the possible exception of the coastal strip to the west of Kingsbridge. The southwest peninsula of Britain is characterized by a maritime climate influenced by the gulf stream. The study by Lenau-Jürgens (1971) on Rhodes demonstrated the sensitivity of adult *C. quadripunctaria* to temperature gradients both within and between habitats. The moths exhibited daily vertical dispersal and longer-term migratory movements in response to such gradients. Our field observations suggest that a similar sensitivity of *C. quadripunctaria* exists in Devon with local concentrations of moths in particularly sheltered and warm environments. Populations in this region are associated with a series of predominantly south-facing river valleys and estuaries which are open to the sea, especially the central and large Exe basin sheltered by high ground to the west and east (see Fig. 3). These basins are associated with relatively cloud-free conditions by day, often leading to substantial daily increases in temperature under high insolation in late summer. Cloud cover frequently develops in the evenings which with comparatively high relative humidities will tend to slow radiation heat loss to the atmosphere. Our data obtained when attracting males to assembling traps (Fig. 4A) suggest that high local air temperatures at and shortly after dusk are critical to pairing activity and therefore the establishment of populations. A critical population density may also be necessary to initiate a high level of pairing activity. Our assembling traps attracted very few moths outside the peak flight period in mid-August. Laboratory work showed that ultrasound communication is involved in courtship of the congeneric species *C. dominula* (Brakefield, Laffoley & Liebert, in preparation) and clearly pairing behaviour is complex in many arctiids (e.g. Conner *et al.*, 1980, 1981; Willis & Birch, 1982). A locality in Devon where periodically there is no period of nights in mid-August with favourable conditions and high temperatures from 21.00 to 22.00 hours is likely to be subject to extinction and recolonization cycles.

We spent more than 120 man-hours in 1984 searching for *C. quadripunctaria* in known localities, often in hot and sunny conditions. Over 500 moths were captured but none were seen in flight unless initially disturbed at rest by one of us. Some clearly do move during daylight hours since a few were found feeding

on *Buddleia* and others on white walls late on sunny afternoons. Their main period of mating, feeding and dispersal activity is, however, in the 2–3 h after dusk (Fig. 4). Oviposition in the laboratory often occurs by day so that females resting in hedges may also lay eggs. These observations provide some contrast with those on the Mediterranean island of Rhodes where moths often feed and fly actively by day (Walker, 1966; Elger, 1969; Lenau-Jürgens, 1971; M. Rothschild, pers. comm.). Furthermore, at least in this favourable locality, the moths emerge earlier in the year in May and then aestivate in aggregations of extremely high density during mid-summer before mating and laying eggs in September and October. Thus, they will have a longer expectation of adult life than in the ecologically marginal conditions in NW Europe. This suggests the hypothesis that stabilizing selection on the aposematic colour pattern of the moth acts over a longer period and is more intense in the hot Mediterranean climate of southern parts of the species' range. A similar reasoning probably applies to continental Europe where more daytime activity is likely. Such activity will increase the likelihood of attacks by predators. Elger (1969) notes potential or actual predation by frogs, lizards and birds, especially wrens *Troglodytes troglodytes*, on Rhodes. Our capture-recapture data provide no evidence of differential survivorship of the colour morphs in Devon. In common with other arctiid moths, *C. quadripunctaria* has a well-developed defence involving static displays, stridulation, chemical secretions and odours, and probably pyrrolizidine alkaloids (personal observations and see, for example, Blest, 1964; Walker, 1966; Rothschild, 1961, 1984; Rothschild *et al.*, 1979). The effectiveness of this defence is supported by observations made when a yellow moth released at Exeter was quickly caught in flight by a juvenile robin. The bird pecked vigorously at the moth on the ground, apparently eating the body (which could not be found later). After about 1 min it flew to a perch where a minute's bill wiping behaviour was followed by vomiting. It returned to peck at the remnants of the moth before flying off. A difference in aposematic selection could also be associated with changes in the frequency distribution of colour types in communities of potential Müllerian comimics among other arctiids (see Rothschild *et al.*, 1979) or of species exhibiting flash coloration with bright hindwings such as the 'Underwing' moths (Noctuidae). We consider that this is unlikely to be the principal factor involved but data are required to test it.

If this hypothesis is correct then the polymorphism in the marginal populations of NW Europe may be due to the relaxation of aposematic selection in combination with climatic selection acting on non-visual differences in fitness between genotypes, probably associated with pre-adult development. The occurrence of such climatic selection is indicated by the geographical variation in Devon and especially by the apparent difference in response of the colour morphs along the inland northerly axis of the extension of the species' range from that characteristic of the spread east and west along the coast (Fig. 3). The apparent increase in red moths in both directions along the coast presumably occurs in response to a similar climatic gradient which is different to that existing to the north where orange moths are more frequent. The results of our capture-recapture experiment indicate that there are unlikely to be differential rates of spread among the colour morphs.

This study indicates that colour polymorphism and geographical variation in morph frequency within a marginal region of the distribution of

C. quadripunctaria reflects climatic selection. We suggest that such selection occurs directly in response to the specific conditions of a more northern and maritime climate, and that the expression of colour variation is favoured by a relaxation of the stabilizing influence on the warning coloration exerted by visual predators, associated with changes in adult behaviour in a cooler climate. Laboratory experiments using controlled environments and a more detailed analysis of geographical variation in NW Europe would be useful. The hypothesis concerning aposematic selection could be tested by monitoring the survivorship of cohorts of each colour form transferred from Devon, or of painted or chemically treated (see Ford, 1937) native moths, released in a locality such as Rhodes where only the red form occurs.

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