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The nature of migration in the red admiral butterfly *Vanessa atalanta*: evidence from the population ecology in its southern range

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Abstract. 1. The migrant *Vanessa atalanta* (L.) occurs throughout Europe and North Africa. In autumn, populations emigrate from northern and central Europe to the Mediterranean region to overwinter. In the spring, the northern range is recolonised by migrants from the south. The dynamics of the species in the winter range is poorly known.

2. From 1994 to 1999, adults and immatures of *V. atalanta* were monitored all year round in Mediterranean habitats in north-east Spain.

3. Data showed that the Catalonia lowlands is an area to which *V. atalanta* migrates to breed during the winter. Migrants arrive in October and early November and initiate a period of intensive breeding. Larval development occurs throughout the winter until a first annual generation of adults appears in early spring.

4. Most of the butterflies emerging in the spring emigrate and leave the area without breeding. The data suggest strongly that recolonisation of the northern range is by these butterflies not by wintering adults. Altitudinal migration also seems to be a common phenomenon, allowing a further summer generation of adults to occur at high elevations within the Mediterranean region.

5. The complex phenology of *V. atalanta* in its southern range has evolved as a strategy to track larval resources through space and time. Autumn migration coincides with the greatest availability of the main food plant, *Urtica dioica* L. Late spring migration occurs by the time food quality is decreasing.

Key words. Altitudinal migration, latitudinal migration, Mediterranean, phenology, population ecology, southern range, *Vanessa atalanta*, winter breeding.

Introduction

Though migration by some butterfly species is well established (Williams, 1930, 1958), a detailed understanding is still elusive because of the technical difficulties of studying butterfly migrants (Baker, 1984; Shreeve, 1992). The typical image of true migrants in the north temperate zones is that they simply survive in an overwintering region, then fly north in spring to exploit the temporary availability of high quality resources in summer (Dingle, 1996). This is exemplified by the migrant monarch butterfly *Danaus plexippus* (Malcolm *et al.*, 1993; Brower, 1996) and this same general pattern has been suggested for the red admiral *Vanessa atalanta* (L.) (Benvenuti *et al.*, 1994). Alternatively, some species time their migration to exploit the availability of high quality resources in their winter range, as well as exploiting the availability of northern resources in summer. Some moths and other insects provide good examples of this type of migration (e.g. Riley *et al.*, 1991; Showers, 1997).

Vanessa atalanta is an Holarctic species, found throughout Europe and Africa north of the Sahara (Emmet & Heath, 1990; Tolman & Lewington, 1997). In its northernmost European range, populations are not permanent and its presence depends each year on migration from southern countries (Tucker, 1997). Although records of its directional flights have been documented many times (e.g. Grant, 1936; Lack & Lack, 1951; Williams, 1951; Roer, 1961; Benvenuti *et al.*, 1994), many unanswered questions remain about the migratory

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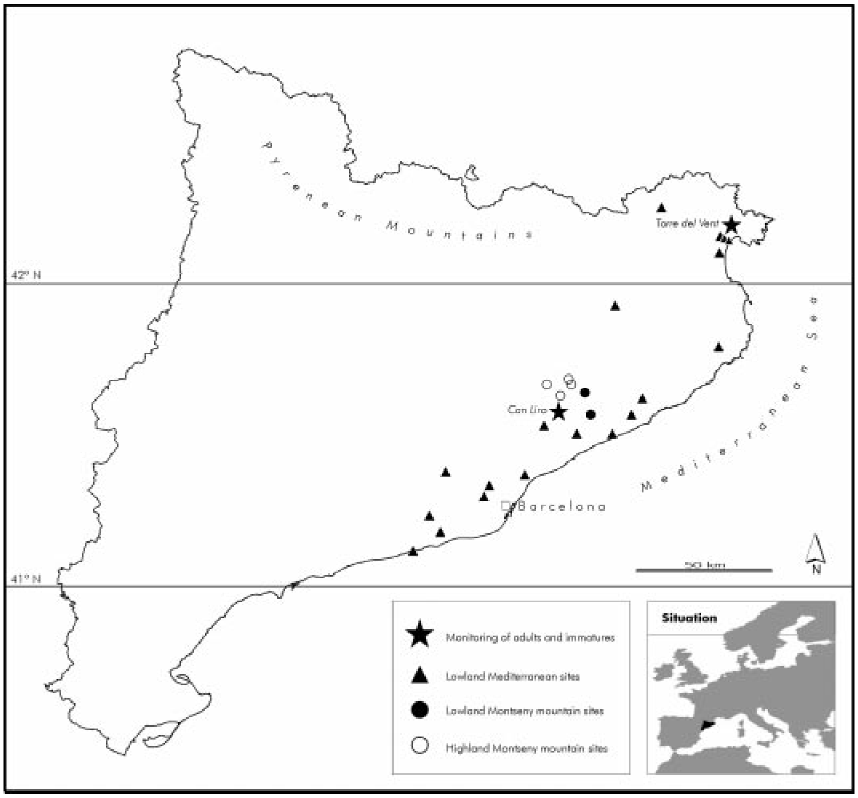

Fig. 1. Location of the two sites where adult and immature *Vanessa atalanta* were monitored all year round (★) and transect routes from the Catalan Butterfly Monitoring Scheme that were used in this study (see text for more details).

pattern of this butterfly (Baker, 1984). In particular, knowledge about its dynamics in the winter range (presumably in the Mediterranean region) is very scarce.

Two recent papers have emphasised the need for an improvement in knowledge of the biology of *V. atalanta* in southern Europe. Bryant *et al.* (1997) investigated how the range margins occupied by four nettle-feeding nymphalid butterflies were conditioned by their thermal requirements for development. *Vanessa atalanta* did not conform to the same pattern as the other three species, apparently because of its migratory status. They acknowledged that uncertainties over the overwintering biology of *V. atalanta* constrained their ability to draw conclusions. Using data from the British Butterfly Monitoring Scheme, Pollard and Greatorex-Davies (1998) analysed the trend of increased abundance of *V. atalanta* in Britain from 1976 to 1996. They suggested that this trend was probably due to increased immigration from southern areas in spring, but lack of knowledge on the precise location of source areas prevented them from reaching more definite conclusions.

In the work reported here, data from various sources are combined to obtain a clear picture of the phenology of this long-distance migrant in typical Mediterranean habitats. This information is used to answer the main question: Does *V. atalanta* simply move south to overwinter and return north to breed in the following spring or does it breed throughout the year (i.e. produce an early spring brood in the south) and exploit high quality resources that are available at different times in the south and in the north of its range?

Materials and methods

As part of the Catalan Butterfly Monitoring Scheme run in Catalonia, north-east Spain, since 1994 (Stefanescu, 2000) and also from a study on mating behaviour of *V. atalanta* (C. Stefanescu, unpublished), abundant information has been obtained on the phenology of this butterfly in its southern European range. Between 1997 and 1999, two stinging nettle *Urtica dioica* patches were selected to monitor the abundance of immature stages all year round.

Estimates of adult relative abundance

Annual abundance. Estimates of adult relative abundance were obtained for the whole year by means of transect counts at two sites ≈ 100 km apart: Can Liro (41°41′16″N, 2°23′07″E) (1995–1999) and Torre del Vent (42°17′31″N, 3°08′00″E) (1997–1999) (Fig. 1). The sites have a Mediterranean climate, with maximum rainfall in autumn and spring, and summer drought (Table 1).

Table 1. Meteorological data and main habitat types at the Torre del Vent and Can Liro sites where both adults and immatures of *Vanessa atalanta* were monitored, and at several sites in the Montseny mountain that were selected to analyse altitudinal patterns of adult abundance. Annual rainfall and mean temperatures show average values for 1994–1999, when most of the butterfly data were collected.

Study site	Altitude (m)	Main habitat type	Annual rainfall (mm)	Mean temperatures (°C)				
				Winter	Spring	Summer	Autumn	All year
Torre del Vent	60	Evergreen oak forest and arable farmland	659.7	9.4	14.0	23.1	15.9	15.6
Lowland site								
Can Liro	310	Evergreen oak forest and arable farmland	645.0	6.8	13.6	23.6	14.6	14.6
Highland sites								
Santa Susanna	750	Montane evergreen oak forest and pastures	911.5	5.1	10.9	20.6	12.1	12.2
El Puig	1000	Beech forest and bracken-dominated grassland	1211.6	4.3	8.4	16.2	9.9	9.7
Turó de l'Home	1675	Heathland	1153.5	1.5	5.7	14.9	7.9	7.5

At Can Liro, an agricultural area in the Montseny mountain surrounded by evergreen oak *Quercus ilex* forest, counts followed the standard British Butterfly Monitoring Scheme methodology (Pollard, 1977; Pollard & Yates, 1993), with some minor adaptations (Stefanescu, 2000). Transects were walked once a week and only those butterflies seen within 5 m in front of the recorder were counted. Only 3% of the possible recording weeks were missed (none in 1996, one in 1995 and 1997, two in 1998, four in 1999) and were estimated as the mean of the preceding and succeeding counts.

Torre del Vent is a small hilltop (60 m a.s.l.) within the Aiguamolls de l'Empordà Natural Park, a flat area extending between the Muga and Fluvià rivers. It constitutes the only prominent topographic landmark within several kilometres and is used as a mating aggregation site by several butterfly species, including *V. atalanta*. A census trail was established from the base to the highest point, and counts of territorial males (cf. Shields, 1967; Brown & Alcock, 1991) were made once a week from March to November and once every 2 weeks from December to February.

Numbers of hilltopping butterflies varied considerably during the day so peak daily counts were used as the measure of abundance. In the first year, up to six transects were walked per day, to identify the daily peak, which occurred ≈ 2–3 h before sunset (cf. Bitzer & Shaw, 1995). Knowledge of this daily pattern enabled the number of transects to be reduced to two or three per day in subsequent years, while ensuring that transects covered the time of peak activity. Missing weeks were again estimated as the mean of the preceding and succeeding counts. Between March and November, 10% of samples were missed due to bad weather (one in 1997, five in 1998, six in 1999). Because sampling was carried out every 2 weeks from December to February, estimates in the winter period accounted for ≈ 50% of the possible recording weeks.

To minimise inter-year variation in the pattern of counts (e.g. advances or delays in adult emergence peaks due to particular meteorological conditions), data were pooled for each of 3 consecutive weeks starting on 1 March (e.g. the first 3 weeks of March were pooled together in the first group, and so on). Thus, for a whole year, data were organised in 17 triads of weeks (except the last group, which comprised the 4 weeks of February). The first triad coincided with the beginning of March to facilitate comparison with data from the Catalan Butterfly Monitoring Scheme.

Both at Can Liro and Torre del Vent, data were pooled across all years and the similarity in the pattern of counts between sites was compared using Spearman's coefficient of rank correlation. Comparisons among years were made at Torre del Vent but not at Can Liro, where small sample sizes meant that triads with zero values were very frequent (ranging from 18 to 64% in a 5-year period). It should be noted, however, that because data points are not strictly independent, significance levels were probably overestimated in these comparisons (see Diggle, 1990).

March–September abundance. Additional data on seasonal abundance were obtained from fixed transect routes throughout Catalonia (Fig. 1) as part of the Catalan Butterfly Monitoring Scheme (Stefanescu, 2000). Sampling began on 1 March and ended on 26 September, thus comprising 30 weeks. Data were used for the period 1994–1999 (except for one site, El Cortalet, where monitoring began in 1988), for 28 transects. Data were excluded whenever $\geqslant 6$ (i.e. 20%) weeks were missed in a given season and when missing counts corresponded to $\geqslant 2$ consecutive weeks.

Seven sites within the Montseny mountain (highest point at 1712 m) constituted a subset of transects that was used to analyse altitudinal patterns of abundance (see Table 1, Fig. 1). Data were pooled into two groups according to their general climate: lowland Mediterranean sites (three transects, including Can Liro) and middle/high mountain sites (four transects). The former were at 150–450 m and were dominated by evergreen oak forests and arable farmland. They have a Mediterranean climate, with rainfall of ≈ 650 mm per year and summer drought. The latter were at 750–1675 m and were dominated mainly by mountain evergreen oak and beech *Fagus sylvatica* forests, heaths, and pastures. They have a Central European climate, with rainfall of ≈ 1200 mm per year and much reduced summer drought.

The remaining 21 transects were used to characterise the pattern of abundance in Mediterranean lowland areas in north-east Spain (Fig. 1). Therefore data from several sites at elevations $\geqslant 450$ m were excluded (see Stefanescu, 2000, for details of recording sites). At present, sampling in the Catalan

Butterfly Monitoring Scheme is highly biased towards Mediterranean habitats (i.e. those with summer drought lasting 1–3 months and rainfall of 350–650 mm per year, depending on the area). Unfortunately, data from the Pyrenees and the pre-Pyrenean area other than Montseny are scarce and do not permit good phenological assessment of *V. atalanta*. As above, data were grouped in triads of weeks and pooled across all available years. Spearman's coefficient of rank correlation was used to assess similarities in seasonal abundance patterns.

Assessment of age population structure

At Torre del Vent, wing-wear condition was recorded in 1998 and 1999 for each territorial male using an arbitrary scale ranging from 1 to 4 (1 = perfect, 2 = fine, 3 = poor, 4 = well worn). Males were observed at perching sites (usually on the ground or on low branches) with the help of 8 × 22 binoculars. This method allowed 75–100% of the males in most of the samples to be classified.

Data from Torre del Vent, Can Liro, and the Catalan Butterfly Monitoring Scheme lowland Mediterranean transects (and also from the monitoring of immature stages, see below) showed several clearly defined oscillations of abundance, highly consistent between seasons and sites. Five such phenological groups were identified (see Results). Age population structure (i.e. proportion of males belonging to the different age classes) was analysed and compared among these phenological groups, using contingency tables. Wing wear is correlated with age (as shown in many previous studies), and males in category 1 were considered to be home-bred. Conversely, the sudden appearance of males belonging to other categories (especially 3 and 4) was indirect proof of the arrival of migratory waves. These data were complemented by records on migration and the monitoring of immature stages.

Records of autumn migration

Migrant *V. atalanta* are easily recognised by their distinctive behaviour: solitary migrant butterflies fly in a straight line at ≈ 1 m above the ground at a mean speed of about 15 km h^{-1} (Roer, 1961; Benvenuti *et al.*, 1994). From 1997 to 1999, observations of autumn migrants were made at Can Liro, using the same procedures as Benvenuti *et al.* (1994). Whenever *V. atalanta* was sighted in a migration flight, it was observed for some time using binoculars until it vanished and its bearing was recorded using a compass. One hundred and sixty-one observations were made. Direction of migrants was analysed for a subset of 126 independent records and uniformity in circular distribution was tested using the Rayleigh test (Zar, 1999).

Estimates of the abundance and development of immatures

Vanessa atalanta is a nettle-feeding specialist. Both *Urtica dioica* and *U. urens* are used as food plants in Catalonia (C. Stefanescu, pers. obs.) but *U. dioica* is by far more abundant throughout the country and is the main host plant. Although eggs are also commonly laid on *Parietaria officinalis*, an abundant herb at disturbed sites, no attempt was made to study immatures on this plant.

From 1997 to 1999, standardised 30-min counts were made every 2 weeks at two *U. dioica* patches in the search for immatures. At Can Liro, the patch (45 m^2) was growing near a stream, within the Butterfly Monitoring Scheme transect route where adults were monitored. The second patch (25 m^2) was located 0.5 km from Torre del Vent (the hilltop site), and was growing on a road margin with a southern aspect. Throughout the recording period, 67 samples were taken out of a possible 72, both at Can Liro and Torre del Vent.

Larvae of *V. atalanta* are very easy to detect due to their habit of concealing themselves within a *tent* of nettle leaves (Tucker, 1997). Each tent found was inspected to determine the larval instar (1 to 5, according to cephalic size). Final-instar larvae sometimes pupate within a conspicuous shelter formed from several nettle leaves spun together with silk but they usually pupate at ground level or even outside the patch. Pupae were seldom found in Can Liro and only very rarely in Torre del Vent, where the overall nettle density was low. On the other hand, eggs are laid on the upper surface of the leaves and are readily located by their bright green colour. They can be mistaken for those of the comma butterfly *Polygonia c-album* but *V. atalanta* lays the eggs preferentially on the middle of the leaf while *P. c-album* lays on the leaf edge. Though egg-laying by *P. c-album* was recorded occasionally in the nettle patch at Can Liro, it is considered that almost all the eggs found (> 99%) belonged to *V. atalanta*.

For each sample, a value representing the mean stage of immatures was calculated according the scale: 0 = egg, 1–5 = larval instars, 6 = pupa. Development of immatures during the autumn and winter period was investigated. Daily temperatures were recorded 100 m from the nettle patch in Can Liro and in a nearby site (El Cortalet) 5 km from Torre del Vent. Because sample size varied among samples (due to mortality and predation on any instar, additional egg-laying, dispersal of full-grown larvae, etc.) and some, but not all, individuals were counted repeatedly throughout their development, it was not possible to undertake a formal statistical analysis between values of mean stage of immatures and temperatures. Instead, the parameters were compared graphically using data from October 1997 to March 1998 (a period with no missing counts), when the number of immatures entering winter was exceptionally high.

Degree-day accumulation (Arnold, 1959) was calculated from daily maximum and minimum temperatures recorded at several sites, using the double triangle method (Sevacherian *et al.*, 1977). The lower and higher thresholds of development were set at 8.3 and 32 °C respectively, following the estimates provided by Bryant *et al.* (1997). According to these authors, 396.5 degree-days are required to complete development from first-instar larva to adult. Calculations were performed with the Degree-Day Utility software (UC IPM, 1990).

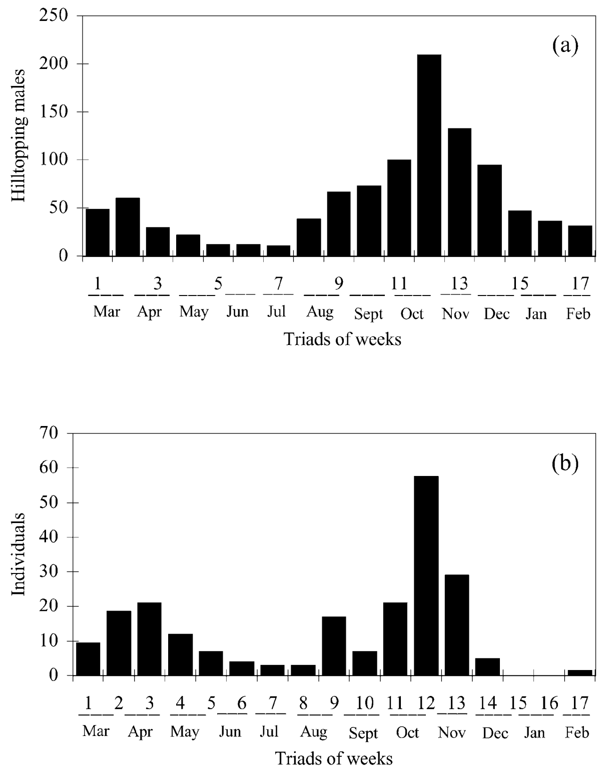

Fig. 2. Seasonal abundance of *Vanessa atalanta* as recorded by weekly transect counts made at (a) a hilltop at Torre del Vent (1997–1999) ($n = 1027$) and (b) Can Liro (1995–1999) ($n = 216$). Data were pooled across all years and for each of three consecutive weeks starting on 1 March.

Assessment of breeding habitat quality

Overall nettle patch quality was assessed once a month. The patch was classified according to two different scales: plant density and foliage quality (cf. Pullin, 1987). Nettle density was scaled from 1 (low) to 3 (high). Foliage quality was scaled from 0 to 4: 0 = senescent plants, 1 = flowering plants, 2 = mature plants prior to flowering, 3 = regrowth plants, 4 = vigorous plants with young leaves. The two measures were multiplied to produce an index of patch availability, ranging from 0 to 12.

Breeding habitat quality is presented as average values for the period 1997–1999. There were inter-year variations, especially due to the heterogeneity of rainfall, but average values are thought to give a good approximation of the usual situation at the sites.

Results

Annual pattern of relative abundance

A first peak of adults was seen in March–April (Fig. 2). Subsequently, numbers decreased and remained very low until a second peak at the end of August–early September. In Torre del Vent, this second peak was not clearly distinct and counts increased steadily from the beginning of August. The strongest increase, however, was in autumn. Thus, October and November counts represented 50 and 43% of the butterflies seen in a whole year at Can Liro and Torre del Vent respectively. Although some butterflies were recorded throughout the winter, numbers remained low or very low from December to February.

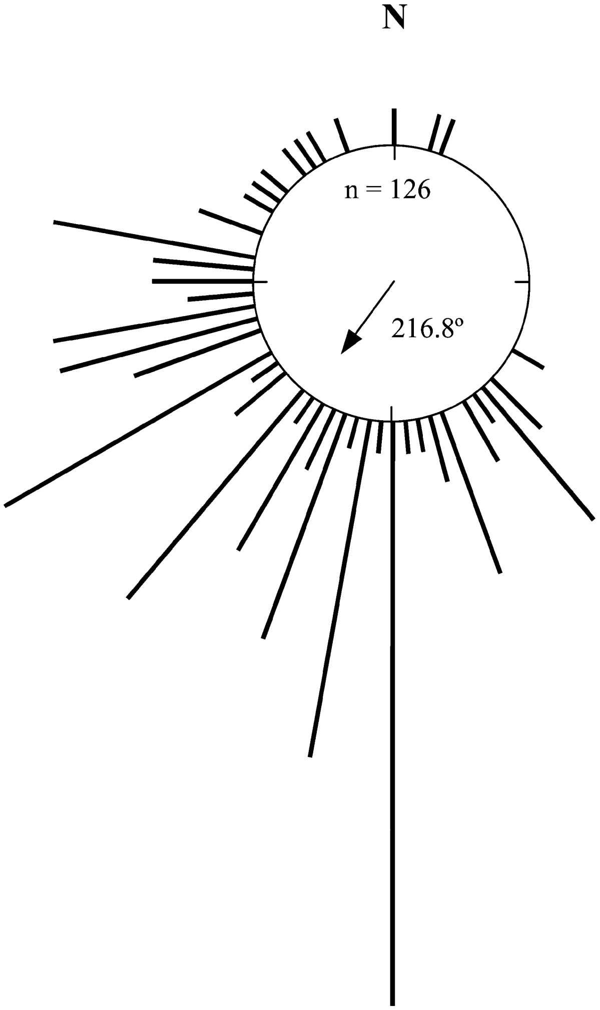

Fig. 3. Flight direction of 126 *Vanessa atalanta* recorded at Can Liro between 30 September and 9 November in 1997–1999. Observations were grouped with a class interval of 5°. The arrow indicates the mean angle of the sample; its length is proportional to the data concentration.

Counts at Can Liro and Torre del Vent were highly correlated (triad counts: $r_s = 0.532$, $n = 17$, $P < 0.05$). Moreover, the seasonal pattern of abundance was consistent between years in Torre del Vent (1997–1998: $r_s = 0.836$, $n = 17$, $P < 0.001$; 1997–1999: $r_s = 0.908$, $n = 17$, $P < 0.001$; 1998–1999: $r_s = 0.676$, $n = 17$, $P < 0.01$).

The autumn migration

In lowland Mediterranean areas, populations increase strikingly in October and early November (Fig. 2), with the

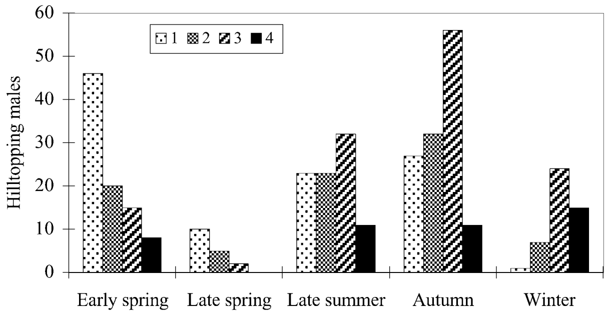

Fig. 4. Wing-wear condition of hilltopping male *Vanessa atalanta* recorded at Torre del Vent in 1998–1999 ($n = 368$), according to an arbitrary scale ranging from 1 to 4 (1 = perfect, 2 = fine, 3 = poor, 4 = well worn). Data were grouped in five phenological categories (see text for more details).

mass arrival of autumn migrants from central and northern Europe (see also Benvenuti *et al.*, 1994) (Table 2, Fig. 3).

The bulk of migration was between 4 and 17 October (70.2% of the records; Table 2). A very similar pattern was observed in 1997 and 1998, while in 1999 migrants arrived slightly later in the season (1997–1998: $\chi^2 = 0$ with Yates correction, d.f. = 1, P = NS, based on distribution of records in triads of weeks; 1997–1999: $\chi^2 = 10.86$, d.f. = 2, $P < 0.01$; 1998–1999: $\chi^2 = 5.63$, d.f. = 2, P = NS).

Pooled data showed a global SSW direction (Fig. 3), with a mean angle $a = 216.8°$, and circular uniformity was rejected strongly (Rayleigh's test: $z = 53.71$, $n = 126$, $P < 0.001$).

Age population structure gives further evidence that the autumn peak was composed mainly of migrants (Fig. 4). Although there was a noticeable contribution from newly emerged males, most of the butterflies were mid- or old-aged. The average value was 2.41 ($n = 126$) and 45% of the males fell into wing-wear class 3.

Overwintering

Autumn migrants commenced reproduction soon after they arrived. Hilltopping activity reached its maximum during the last 2 weeks of October (Fig. 2) while the maximum frequency of egg-laying occurred during late October and early November (Fig. 5).

At Torre del Vent, a coastal site, larval development continued throughout winter, albeit slowly, as shown by the increase in mean stage of immatures from November to March in all three winters. At Can Liro, an inland site, larval growth almost stopped in December and January (Fig. 6). This difference accords with the difference in winter temperatures (December and January mean temperatures in 1997/98: $\bar{x}_{\text{Torre del Vent}} = 9.54 \pm 2.29$ °C, $\bar{x}_{\text{Can Liro}} = 6.21 \pm 2.53$ °C), allowing larval growth at Torre del Vent but not at Can Liro.

Overwintering of adults occurred at both sites, though in low numbers (Fig. 2). Nearly all males seen at Torre del Vent from December to February were very worn and were probably up to 3–4 months old (Fig. 4). Mean wing-wear value was 3.13 ($n = 47$), and only one newly emerged male (class 1) was recorded. Although adults were sighted in Can Liro in all winter months, densities were extremely low.

The early spring emergence

The first annual generation of adults emerged by late March–April, the peak of abundance occurring slightly earlier at Torre del Vent (Fig. 2). This is expected, given the faster development of larvae and pupae at Torre del Vent (Fig. 6). The spring emergence was confirmed at Catalan Butterfly Monitoring Scheme sites (Fig. 7a,c).

Accumulation of degree-days for larval and pupal development during autumn, winter, and early spring was compared with field data. Calculations were made starting on both 15 October and 1 November (Table 3): in most years, eggs laid by the earliest autumn migrants should hatch around 15 October and those laid by the majority of migrants should hatch around 1 November. In general, there was close agreement between expected curves and development of immatures as recorded in the field (Fig. 6) and between predicted dates of emergence and transect counts. At Torre del Vent, the timing of predicted and observed highest counts (expressed as Catalan Butterfly Monitoring Scheme weeks) was 3/3 in 1996/97, 1/4 in 1997/98 (but week 2 was missed), 4/4 in 1998/99. Peak emergences could not be deduced easily from transect data at Can Liro because densities were lower. Even so, there was broad agreement between predictions and field data.

The spring generation consisted predominantly of young butterflies. The average wing-wear value was 1.83 ($n = 89$) and there was a majority of males falling into class 1 (Fig. 4). A few very worn males (probably overwintered) were recorded in March.

The late spring and early summer migrations

Numbers declined rapidly in late spring at lowland Mediterranean sites (Figs 2 and 7a,c). This decrease coincided with an increase at nearby sites located at middle and high elevations (Fig. 7b). Thus, pooled data from lowland and highland sites were correlated negatively, albeit not significantly ($r_s = -0.468$, $n = 10$, P = NS). Predicted accumulation of degree-days (Table 3) showed that the build-up in numbers occurring at highland transects from March to mid June (Fig. 7b) could not be a consequence of local breeding. Even at the lowest, warmest of the mountain transects, temperatures from November to March were usually well below the lower threshold for development, and earliest and peak emergences were predicted to occur during the last 2 weeks of May (Table 3).

The scarcity of butterflies in June–July was also a feature at Torre del Vent (Fig. 2a) and the other Mediterranean lowland transects of the Catalan Butterfly Monitoring Scheme (Fig. 7c). The few males recorded at the hilltop were usually newly emerged, as shown by a low average wing-wear value of 1.53 ($n = 17$).

The very low number of immatures that was found soon after the emergence of the early spring generation indicates that most butterflies left the monitored sites without breeding (Fig. 5).

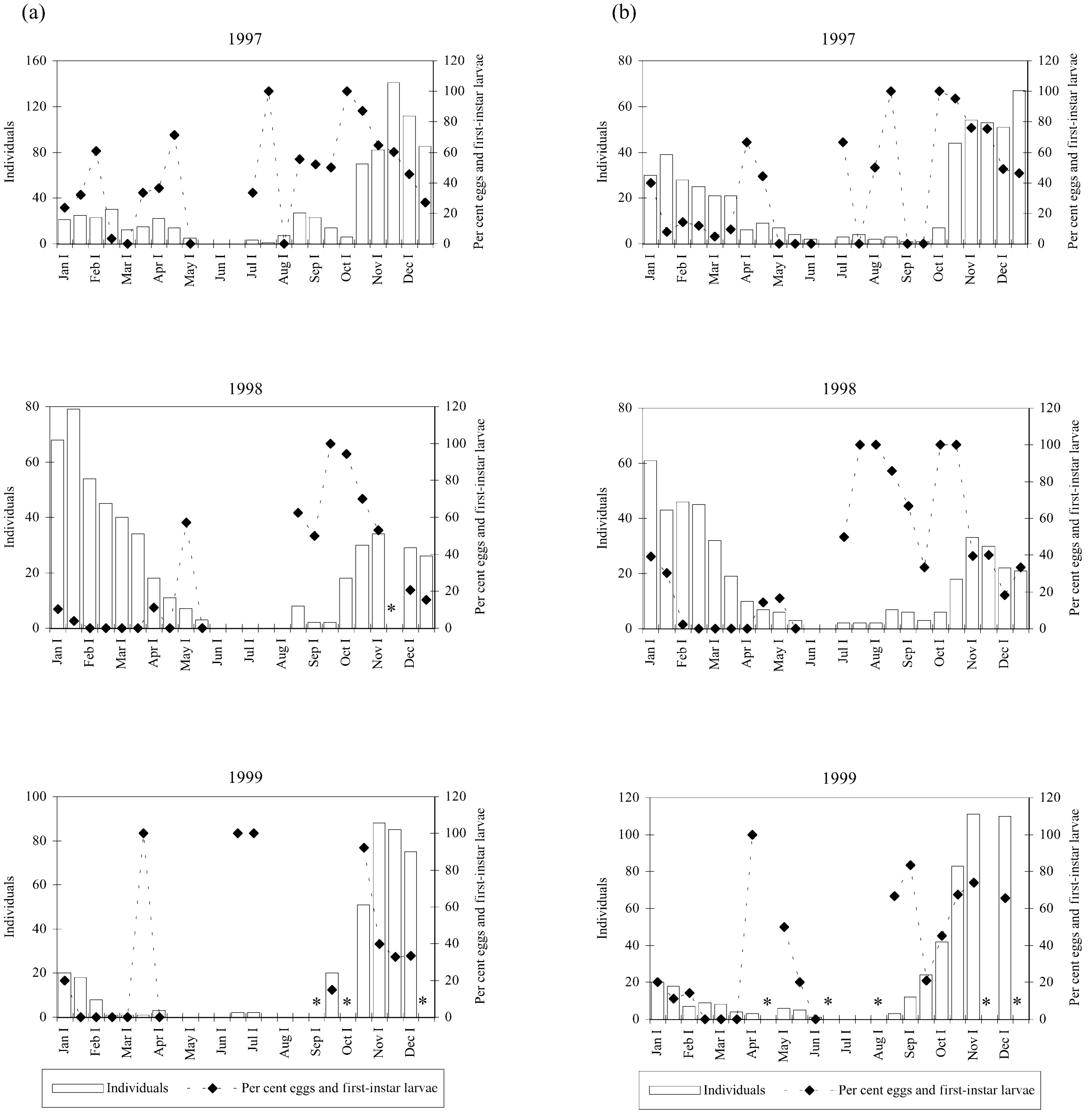

Fig. 5. Seasonal abundance of immatures of *Vanessa atalanta* in standardised 30-min counts made every 2 weeks in two *Urtica dioica* patches at (a) Torre del Vent and (b) Can Liro. The percentage of eggs and first-instar larvae in each sample provides an indication of the timing of major egg-laying activity. *Missing counts.

Mountain breeding and late summer migration

Maximum population levels at middle and high elevations were reached by mid July (Fig. 7b). The summer peak of abundance occurred ≈ 2 months after a first peak was recorded by mid May and is assumed to be the result of local breeding. At El Puig, for example, a site where *V. atalanta* was especially abundant, predicted times of emergence for larvae hatching on 10 May (first day of week 11 in the Catalan Butterfly Monitoring Scheme) were 22 July in 1997, 16 July in 1998, and 11 July in 1999.

Population levels decreased in early August, and by the end of August and the whole of September *V. atalanta* was scarcely recorded at highland transects (Fig. 7b). Conversely, numbers increased at lowland sites during the last 2 weeks of August (Figs 2 and 7a,c) even though immatures on nettle

Table 2. Seasonal distribution of 161 *Vanessa atalanta* recorded at Can Liro during the autumn migration (1997–1999). Triads of weeks and corresponding weeks in the Catalan Butterfly Monitoring Scheme are given to allow comparison with the patterns shown in Figs 2 and 7.

	6–26 September			27 September–17 October			18 October–7 November			8–28 November			
Triad	10			11			12			13			
BMS week	28	29	30	31	32	33	34	35	36	37	38	39	Total
1997	0	0	0	9	42	13	8	12	7	0	0	0	91
1998	0	0	0	4	3	22	8	3	2	0	0	0	42
1999	0	0	0	0	5	15	3	2	0	3	0	0	28
Total	0	0	0	13	50	50	19	17	9	3	0	0	161

Table 3. Predicted dates of first adult emergences (accumulation of degree-days starting on 15 October) and peak emergences (starting on 1 November) in 1997–1999 at Torre del Vent and Can Liro sites where immatures were monitored, and at two middle/high elevation transect routes in the Montseny area (see text for more details).

		1996/97		1997/98		1998/99	
	Altitude (m)	First	Peak	First	Peak	First	Peak
Torre del Vent	60	13 January	16 March	12 January	4 March	20 February	22 March
Can Liro	310	3 April	23 April	3 April	27 April	20 April	5 May
Santa Susanna	750	15 May	22 May	21 May	31 May	23 May	30 May
El Puig	1000	13 June	19 June	21 June	26 June	19 June	25 June

patches were extremely rare during July and early August (Fig. 5). These patterns resulted in a very high correlation between lowland Mediterranean transect counts in the Montseny area and elsewhere ($r_s = 0.867$, $n = 10$, $P = 0.001$; Fig. 7a,c), and a strong opposite pattern of abundance with respect to highland Montseny sites ($r_s = -0.675$, $n = 10$, $P < 0.05$; Fig. 7b,c).

Wing-wear condition in late August–early September was quite heterogeneous (Fig. 4). Old males falling into class 3 were predominant but young individuals were also well represented in the samples because small-scale breeding in late summer occurred in most seasons (Fig. 5). The total number of immatures increased slightly during this period and eggs and first-instar larvae accounted for high percentages before they developed further into a third generation of butterflies by late October–early November (see also Fig. 4).

Changes in breeding habitat quality

The highest nettle quality occurred in autumn and winter (Fig. 8). There were some differences between seasons and sites, mainly due to variability in rainfall (e.g. quality was comparatively low in winter 1998 due to drought in the previous year) and differences in temperature regimes (e.g. at Can Liro, nettles were affected negatively by low temperatures during the coldest months).

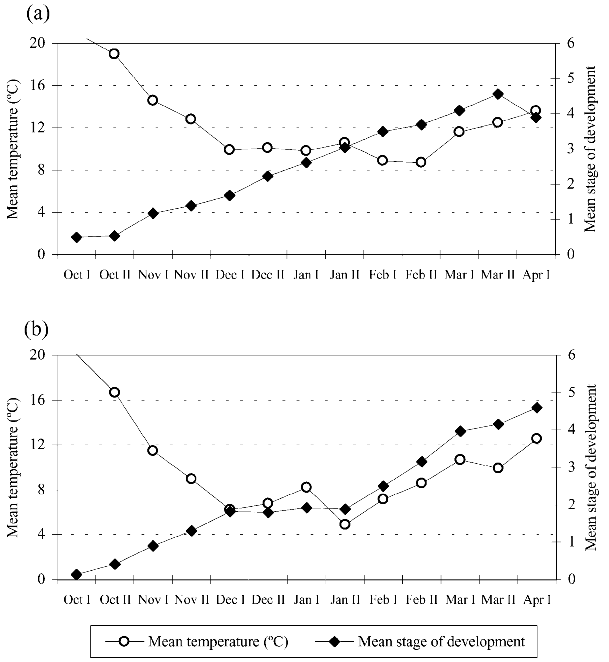

Fig. 6. Mean stage of immatures (0 = egg, 1–5 = larval instars, 6 = pupa) recorded in 2-week samples between October 1997 and April 1998 at (a) Torre del Vent and (b) Can Liro. The mean temperature recorded during each sample interval is also shown.

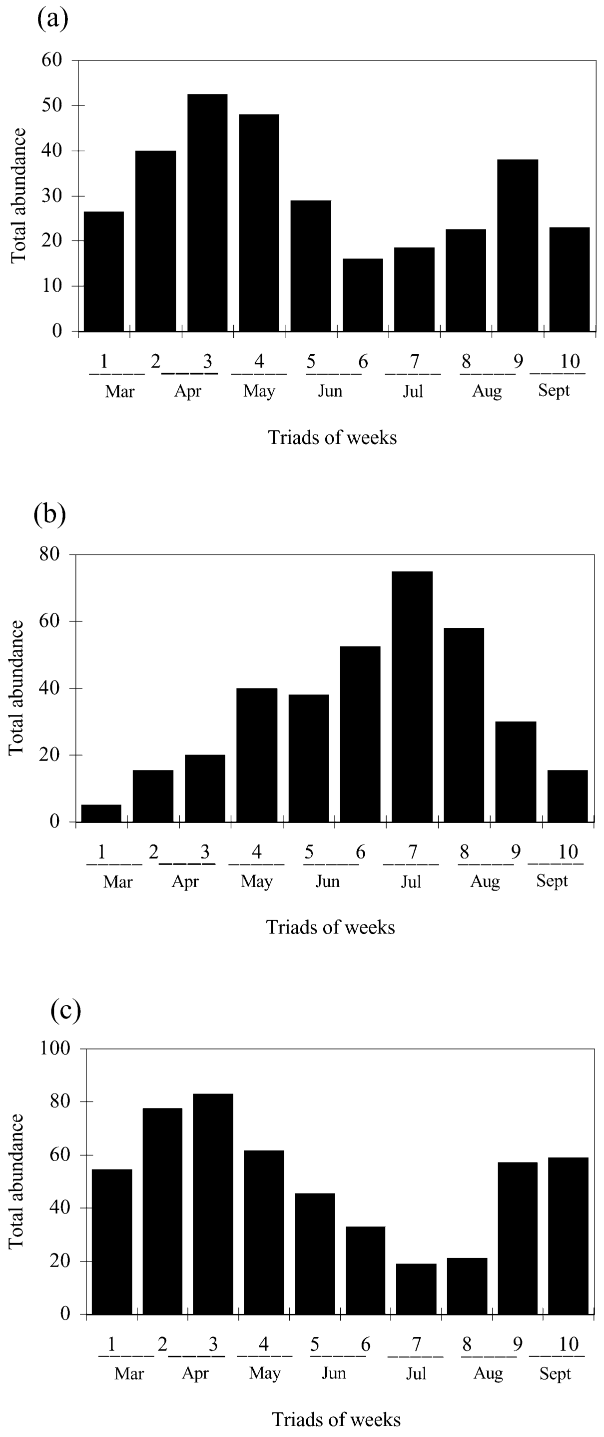

Fig. 7. March–September abundance of *Vanessa atalanta* as recorded by weekly transect counts made at (a) three Mediterranean lowland sites in the Montseny area ($n = 315$ individuals), (b) four middle/high mountain sites in the Montseny area ($n = 350$), and (c) 21 Mediterranean lowland sites throughout Catalonia ($n = 511$). Data were obtained from 1988 to 1999 but available years varied by site.

Patch quality decreased during the spring and reached its lowest values shortly before the summer, however differences in phenology were found between sites. At Torre del Vent, the flowering period was usually in March and patch quality decreased steadily after February until June (Fig. 8a). At Can Liro, patch quality remained high until April, just prior to flowering, but fell to very low levels in May and June (Fig. 8b). This sharp decrease was caused partly by high densities of *Pleuroptya ruralis* Scop. (Lepidoptera: Pyralidae), a nettle specialist moth whose larvae live inside shelters constructed by rolling whole leaves (e.g. Davis, 1991). At Can Liro, this moth was double-brooded (old larvae were found in April–May and again in August–September) and was recorded abundantly in each season (especially the first generation).

Patch quality began to increase during the summer and was high at the beginning of October. Thus, in early autumn, there was the highest seasonal availability, with respect to both plant density and foliage quality (Fig. 8).

Discussion

The work reported here shows that the Catalonia lowlands, and probably the Mediterranean region as a whole, is an area to which adult *V. atalanta* migrate in order to breed in winter. It is

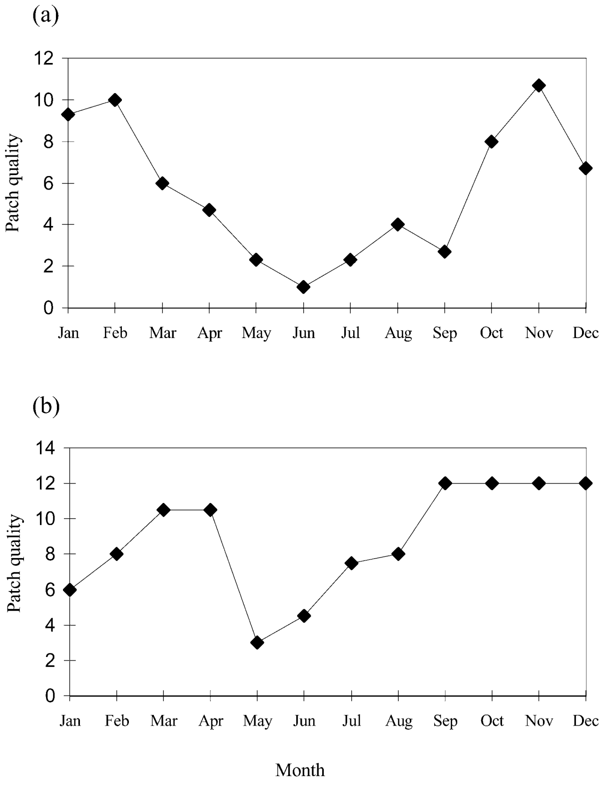

Fig. 8. Seasonal nettle patch quality recorded at (a) Torre del Vent and (b) Can Liro. Patch availability combines qualitative measures of plant density and foliage quality and is scaled from 0 to 12. The curves show average values for 1997–1999.

not a region to which the adults retreat simply in order to hibernate successfully. Although the higher autumn than spring peak gives the appearance that overwintering breeding may lead to a decline in population size, this may not be the case: spring adults apparently emigrated soon after emergence and individuals may have been present for a shorter period than in autumn.

As expected, migration (both latitudinal and altitudinal) is key to understanding the phenology of this butterfly in southern Europe. Another crucial point is that autumn breeding and subsequent development of immatures throughout the winter, produces an early spring generation of adults.

In the Mediterranean region, the most conspicuous event in *V. atalanta* phenology is the mass arrival of autumn migrants from north and central Europe. Depending on the breeding success and population levels reached at northern latitudes, this invasion becomes more or less apparent. In 1997, for example, *V. atalanta* was particularly abundant in The Netherlands and the British Isles (van Swaay & Ketelaar, 2000) and autumn transect counts at two Catalan Butterfly Monitoring Scheme sites also yielded the highest values ever recorded.

As shown here, migrants start to arrive by late September and early October, and the bulk of migration is recorded by mid October (see also Lack & Lack, 1951). The last migrants are usually seen in early November. This temporal pattern is almost identical to that found by Benvenuti *et al.* (1994) in central-northern Italy (42–44°N), at a similar latitude to Catalonia.

Pooled data for autumn migrants showed a mean flight direction of 216°, i.e. towards SSW. This direction differs from the predominantly SSE direction found by Benvenuti *et al.* (1994) for central-northern Italy (but see also Benvenuti *et al.*, 1996). In both cases, however, the preferred direction matched the orientation of the coastline closely, minimising the risk of flying into the open sea, an explanation suggested by Spieth and Kaschuba-Holtgrave (1996) for *Pieris brassicae*.

Regular monitoring, together with circumstantial observations, suggests that most of the butterflies produced in source areas of northern and central Europe, emigrate to the Mediterranean region in autumn (Pollard & Greatorex-Davies, 1998). Although there are records of overwintering adults at northern latitudes (e.g. Archer-Lock, 1989; Emmet & Heath, 1990), it is generally assumed that overwintering is rare and has a negligible effect on numbers in the following season (Pollard & Greatorex-Davies, 1998).

In Catalonia, the arrival of migrants coincided with a period of intensive breeding, and both hilltopping activity and egg-laying increased greatly in October and early November. Adult activity was also recorded regularly in winter months but numbers decreased progressively and only a few, very worn individuals were seen at the end of this period.

This phenological model differs from that in closely related species and may explain why some ecophysiological responses in *V. atalanta* did not fit well to the predictions raised by Bryant *et al.* (1997). *Aglais urticae*, *Inachis io*, and *Polygonia c-album* all overwinter as adults and breed in spring (Emmet & Heath, 1990; C. Stefanescu, pers. obs.). In contrast, adults of *V. atalanta* did not cease their activity completely in winter.

Immatures that hatched from eggs laid in autumn did not enter into a true diapause. Instead, slow growth is still possible whenever temperatures remain above the developmental threshold. In other words, immatures of *V. atalanta* remain active throughout most of the winter, with occasional quiescence and growth retardation (Mansingh, 1971; Leather *et al.*, 1993).

Bryant *et al.* (1997) estimated the developmental threshold in *V. atalanta* at ≈ 8.3 °C though this varied according to instar. Bryant *et al.* (2000) found that larvae of *V. atalanta* do not bask and their body temperature depends largely on ambient temperature. In contrast, the gregarious basking larvae of *I. io* and *A. urticae* achieve body temperatures 20 °C above ambient temperature when direct sunlight is available.

There is close agreement between development threshold estimates and field observations (Fig. 6). At Can Liro, larval growth was arrested completely between December 1997 and January 1998, when the mean recorded temperature was 6.21 °C, but growth continued during the same period at Torre del Vent, where the comparable temperature was 9.54 °C. The same pattern was found in the following two winters and, on the basis of recorded temperatures, should have occurred in most recent years (Table 1).

Using weather data for the period 1997–1999 from Torre del Vent and Can Liro, it was found that eggs hatching by late October and early November are predicted to produce adults between 4 and 22 March and 23 April and 5 May respectively. These predictions were confirmed by field data gathered from transect counts of adults (Fig. 2).

Though spring emergence is observed at many lowland Mediterranean sites (Fig. 7c), most of these butterflies leave their natal patches without breeding. This conclusion is reached from two lines of evidence. First, the age population structure was highly biased towards young individuals. Secondly, in 3 consecutive years, early immatures were scarcely recorded in April–May, following emergence of the first generation of adults.

Both latitudinal and altitudinal migration are likely to account for the disappearance of spring butterflies. Northward migration in March–June has been known to occur at northern latitudes for nearly a century (e.g. Williams, 1930, 1951, 1958; Grant, 1936; Roer, 1961) but is seen rarely in the Mediterranean region (but see Benvenuti *et al.*, 1994). The recolonisation of central and northern Europe that occurs every season implies that at least part of the population overwintering in the Mediterranean region migrates to the north in spring. Data presented here indicate strongly that the offspring of autumn migrants are involved in this northward migration, and give no support to the hypothesis that recolonisation is a result of wintering adults returning to their original breeding grounds (Benvenuti *et al.*, 1994).

This study also gives some evidence of altitudinal migration in *V. atalanta*. Intensive monitoring at several sites in the Montseny mountain seemed to indicate that butterflies emerging at low sites in early spring moved uphill to breed at mid and high elevations (Fig. 7a,b). Accumulation of degree-days at the lowest and warmest mountain site from 15 October predicted first emergences of adults between 15 and 31 May in 1997–1999. Adults recorded at this and higher, colder sites before these dates must have come from the lowlands. Additional evidence comes from circumstantial observations of nettle patches in winter. Due to the low temperatures, nettle leaves were killed and became totally unavailable to young larvae until April or May (C. Stefanescu, pers. obs.), as happens in most of central and northern Europe.

Pooled data from several years and transect routes at mid and high elevations showed that a distinct peak of abundance occurred by mid July, ≈ 2 months after the arrival of the bulk of lowland migrants. This increase in population levels was the result of local breeding and the emergence of the second generation of adults in the same season. Predictions of developmental time from first-instar larva to adult coincided fully with the pattern actually recorded.

Likewise, by the end of summer, this second generation of adults can be assumed to have moved downhill to breed again at lowland sites (Fig. 5). A further third generation thus occurs in October, resulting in a mixing of individuals of different ages when autumn migrants start to arrive (Fig. 4). Alternatively, the increase in population levels in the lowlands by late August may be the result of migrants arriving from south or central France, although this seems unlikely considering the lack of observations of southward flights before October (Table 2).

The pattern found in the Montseny mountain can almost certainly be generalised to most of Catalonia and perhaps to many other mountainous Mediterranean areas. An increase in abundance by late August (unexplained by local breeding) seems to be a common feature at lowland sites in the Catalan Butterfly Monitoring Scheme (Fig. 7c). Though detailed data such as those presented here are not available from other areas, Larsen (1976) suggested that, in the south-eastern Mediterranean, *V. atalanta* may only breed during the winter at lowland sites and from May onwards is mostly found breeding in the mountains.

The complex phenology of *V. atalanta* in the Mediterranean region, involving altitudinal and latitudinal migration, has certainly evolved as a strategy to track larval resources through space and time. Thus, the arrival of migrants in the autumn, with subsequent breeding and larval development in winter, coincides with the major availability (both in quality and abundance) of the main host plant, *U. dioica*. The decrease in food quality (Fig. 8) occurring just after the emergence of the first generation of butterflies might have imposed a very strong selective pressure for migration in late spring and early summer. Thus the pressures involved may be departure from a declining resource, movement towards an improving resource, and movement to and from areas where successful overwintering is possible.

Poleward migration in spring has been reported for many insects in temperate regions, including *V. atalanta*, and is considered to be an adaptive strategy allowing the colonisation of increasingly favourable areas (e.g. Williams, 1958; Johnson, 1995; Pedgley *et al.*, 1995; Dingle, 1996; and references cited therein). On the other hand, altitudinal migration is a less well-known phenomenon, though there is circumstantial evidence for many highly mobile butterflies (e.g. Larsen, 1975; Shapiro, 1975, 1980) and, more recently, it has been described in great detail in a fairly sedentary species (Peterson, 1997). With the available data, however, it is not possible to know whether both types of migration in *V. atalanta* could be the result of the maintenance of genetic variation (some kind of dichotomy) in a presumably panmictic population. This seems unlikely and poses an interesting problem that deserves further investigation and would require an experimental approach to be addressed fully.

The phenological pattern described here for the Mediterranean region should help in understanding several aspects of the ecology of *V. atalanta*, for example those related to changes in abundance in its northern margin of distribution (Pollard & Greatorex-Davies, 1998). Data from several butterfly monitoring schemes are now available (Pollard & Yates, 1993; van Swaay *et al.*, 1997; Stefanescu, 2000) and the integration of all this information will help in understanding the population dynamics of this and other common migrants (see Pollard *et al.*, 1998, for an integrated study of *Cynthia cardui*). These widespread and highly mobile butterflies are important in assessing future changes in phenological and migratory patterns in response to global climate change (cf. Bryant *et al.*, 1997).

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