

Phenology of *Charaxes jasius* (Nymphalidae: Charaxinae) in the north-east Iberian Peninsula

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Summary. Between 1994 and 1997 a population of *Charaxes jasius* (Linnaeus, 1767) was intensively studied in Catalonia (north-east Iberian Peninsula). Phenological data on adults were obtained by means of standardised transect counts and bait traps. Additional data were obtained from a number of transect routes throughout Catalonia, as part of a Butterfly Monitoring Scheme. Data on the immature stages were obtained during a systematic study of eggs and larvae. *C. jasius* is bivoltine, and the phenology is highly coincident in every season over a wide area. The first brood flies from the end of May to mid-July, and the second from the end of July to the end of September or beginning of October. In some years the second brood has a markedly bimodal emergence. Population size is much higher in the second than first brood. Hibernation occurs in the larval stage, usually between November and March, when daily mean temperatures fall below 11.5–13°C. Larvae from any instar may be found at the start of winter, but at the end of this period almost all individuals are in 3rd to 5th instars. Although *C. jasius* is potentially a continuously brooded species, these results indicate that the limitations imposed by thermal conditions set an upper limit of two broods per year in the north-east Iberian Peninsula.

Zusammenfassung. In den Jahren 1994 bis 1997 wurden an einer Population von *Charaxes jasius* (Linnaeus, 1767) in Katalonien (nordöstliche Iberische Halbinsel) Daten zur Phänologie der Imagines mittels standardisierter Transekte und Köderfallen erhoben. Zur Ergänzung dienten Beobachtungen entlang weiterer Transekte in ganz Katalonien im Rahmen eines Tagfalter-Monitoring-Schemas. Phänologische Beobachtungen der Entwicklungsstadien wurden durch systematische Suche erbracht. In Katalonien bildet *C. jasius* zwei Generationen aus, die über das Untersuchungsgebiet synchronisiert sind: von Ende Mai bis Mitte Juli, und von Ende Juli bis Ende September oder Anfang Oktober. In einigen Jahren bilden sich während der zweiten Generation zwei getrennte Populationsmaxima aus. Die zweite Generation ist stets viel individuenstärker als die erste. Die Überwinterung erfolgt als Larve, normalerweise von November bis März, wenn die mittleren Tagestemperaturen unter 11.5–13°C fallen. Zu Beginn des Winters werden Larven aller Stadien angetroffen, am Ende des Winters befinden sich fast alle Tiere im dritten bis fünften Larvalstadium. Obwohl *C. jasius*

eine Art mit potentiell ununterbrochener Generationenfolge ist, begrenzen die Temperaturbedingungen im Nordosten der Iberischen Halbinsel den Lebenszyklus auf zwei Generationen pro Jahr.

Résumé. De 1994 à 1997, une population de *Charaxes jasius* (Linnaeus, 1767) de Catalogne (nord-est de la péninsule ibérique) a été étudiée intensivement. Des données sur la phénologie des adultes ont été obtenues au moyen de comptes standardisés suivant des routes fixées ainsi que des trappes à appât. Un complément de données fût fourni en provenance d'un nombre de routes fixées à travers toute la Catalogne, faisant partie d'un Programme d'Inventarisation des Papillons Diurnes. Une étude systématique des œufs et des chenilles fournit des données quant à la phénologie des premiers états. *C. jasius* est bivoltine, et la phénologie est hautement synchronisée à chaque saison à travers une large région. La première génération vole de fin mai à la mi-juillet, et la deuxième de fin juillet à fin septembre ou début octobre. Certaines années, la deuxième génération montre deux périodes distinctes d'éclosion maximale. La deuxième génération est toujours nettement plus nombreuse que la première. L'hibernation a lieu à l'état larvaire, en général de novembre à mars, quand les températures moyennes journalières descendent en dessous de 11.5–13°C. Des larves à chaque état peuvent être rencontrées au début de l'hiver, mais à la fin de cette période la quasi totalité des individus appartiennent du troisième au cinquième état. Bien que, potentiellement, *C. jasius* soit une espèce à générations multiples et continues, ces résultats indiquent que des limites imposées par les conditions thermales réduisent le nombre de générations à deux par an dans le nord-est de la péninsule ibérique.

Key words: Nymphalidae, Charaxinae, *Charaxes jasius*, phenology, Catalonia, Iberian Peninsula.

Introduction

Charaxes jasius (Linnaeus, 1767) is a widely distributed species in the Afrotropics and a sole representative of the genus in the Mediterranean region (Larsen, 1986; Henning, 1989). The main host plants in the Mediterranean are the mulberry trees *Arbutus unedo* L. and, in the eastern part, *A. andrachne* L. (Higgins & Riley, 1980; Hesselbarth *et al.*, 1995). Other host plants have been recorded from the west and east Mediterranean (e.g. Nel, 1979; Feierabend, 1986; Larsen, 1986; Stefanescu, 1995) but these are only occasionally used.

The adult is bivoltine and has two well-defined broods, the first mainly in June–July and the second in August–September. A partial third brood may occasionally exist, as recorded from the south of the Iberian Peninsula during favourable winters (Verdugo, 1984). The eggs are laid individually on the upper surface of mulberry tree leaves and, depending on temperature, hatch within 8–15 days. They are readily located by their bright

yellow colour and large size (ranging from 1.5 to 2 mm). The larvae, which pass through five instars, are hardly mobile and remain chiefly on the upper surface of the resting leaf, where they spin a silk mat shortly after hatching. In many cases this resting leaf is conserved throughout development. In the last instar, the larvae usually abandon the host plant to pupate in the nearby vegetation. The duration of larval development significantly varies between the first and second brood. Larvae from the first adult brood complete growth in some two months whereas those from the second adult brood take about eight months.

C. jasius has been the subject of previous studies both on morphology and distribution (Agenjo, 1967; Verdugo, 1984; Jugan, 1998), and biology (Castro, 1949; Jauffret & Pujol, 1961; Loritz, 1963; Verdugo, 1984; Sanetra & Peuker, 1993; Hesselbarth *et al.*, 1995). This research, however, is based mainly on data from laboratory breeding but not on systematic field studies covering a long period of time. The present contribution aims at filling this gap and, using data from several populations from the north-east Iberian Peninsula monitored over the last four years, gives precise information on the phenology of the species. The adult flight period and the relative abundance of both annual broods are quantified, and data on larval development in the wild are provided.

Material and methods

Most of the data used in this study were collected at the locality of Fitor (UTM 31TEG04, altitude 200 m), in Catalonia (north-east Iberian Peninsula), between 1994 and 1997 (fig. 1). This site is located in the north of the Gavarres mountain range with a maximum altitude of 535 m. The climate is typically Mediterranean, with maximum rainfall in autumn and spring and summer drought. Temperatures are high in summer and mild in winter (Table 1). The area is siliceous in nature and dominated by Cork Oak (*Quercus suber* L.) with areas of Aleppo Pine (*Pinus halepensis* Mill.) and Stone Pine (*Pinus pinea* L.). The mulberry tree is extremely abundant and constitutes one of the most characteristic plants of the range vegetation (Domínguez *et al.*, 1992). This allows Fitor, together with the rest of the Gavarres,

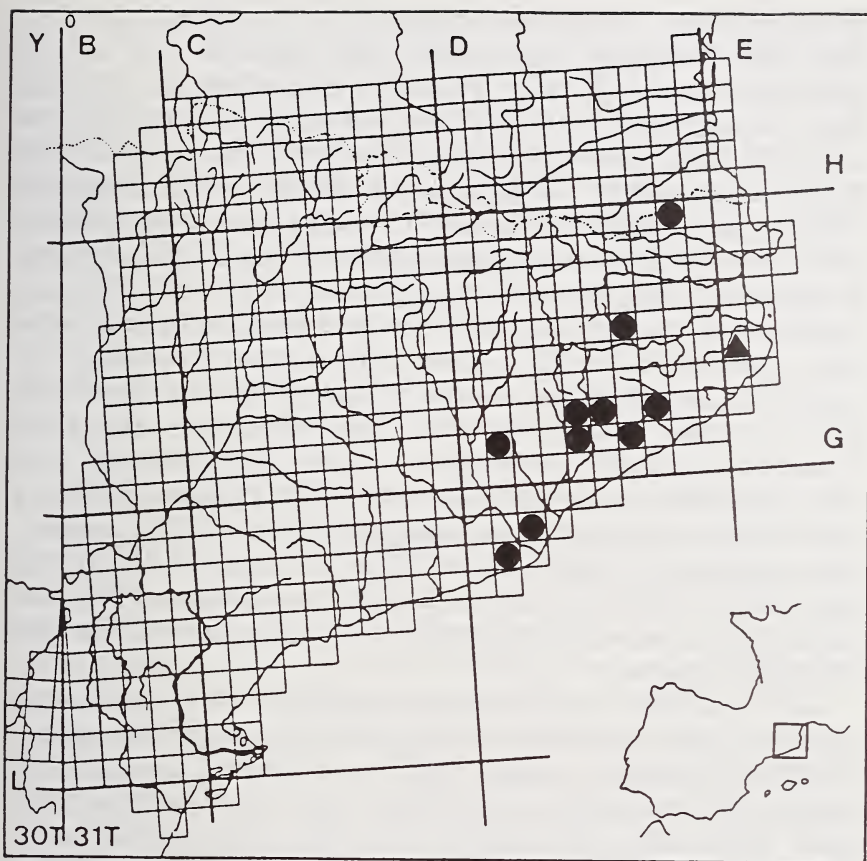


Fig. 1. Location of Fitor (▲) and rest of the BMS sites (●) with breeding populations of *Charaxes jasius*.

to support one of the largest populations of *C. jasius* in Catalonia and possibly in the Iberian Peninsula.

Phenological data both on imagoes and immature stages were obtained at this locality. Monthly mean daily maximum and minimum temperatures and rainfall for the period 1993–1997 were recorded at La Bisbal meteorological station, located at an elevation of 39 m, approx. 6 km from Fitor (Table 1).

Two different methods were used to study the imagoes: species abundance estimates from fixed transect counts and individual captures from bait traps. Transect counts followed the standard

British Butterfly Monitoring Scheme (BMS) methodology (Pollard, 1977; Pollard & Yates, 1993). The transects were walked once a week and only those butterflies seen within 5 m in front of the recorder were counted. At the end of the season, an annual index of abundance was calculated for each brood as the sum of the weekly counts, including a few missing values estimated as the mean of the preceding and succeeding counts (see Pollard, 1977, for more details). Sampling began on March 1st and ended on September 26th, thus comprising a total of 30 weeks. Because some individuals were still on the wing during October in most years, standardised counts were also conducted during that month, but data were not used in the calculations of the annual index to allow direct comparison with data from the other transects (see below). Nevertheless, numbers were usually very low in October and hence the exclusion of these counts had a minor effect in the resulting annual index. Recording was always restricted between 9:00 and 14:00 Spanish Summer Time (7:00 and 12:00 GMT). When the temperature drops below 15°C, the transects were passed through only if sunshine occurred on 75% of transect sections.

Additional data on the seasonal abundance of *C. jasius* were obtained from a number of fixed transect routes throughout Catalonia (north-east Spain) (fig. 1), as part of the Butterfly Monitoring Scheme conducted there since 1994 (Stefanescu, in press). The number of transects with breeding populations of *C. jasius* increased during the four years of the study, from an initial total of 5 in 1994 to 12 in 1997. A collated index of abundance for each brood was calculated from the transect data of the BMS sites (excluding Fitor).

The weighted mean date of the counts (MD), together with the standard deviation about this date (SD), were calculated for each brood and for every year in Fitor and at the rest of the sites, as described by Brakefield (1987) and Pollard (1991). Both measures represent estimates of the mean date and degree of synchronisation of the adult flight period. As in Pollard (1991), the recording weeks were used as the unit of time instead of the day of counts.

The data collected at Fitor with the aid of bait traps for a parallel study on adult behaviour were also used to analyse

phenology at this site. *C. jasius* adults never visit flowers but do, on the other hand, feed avidly on rotting fruit (especially figs), tree sap and animal excrements. This behaviour means they are susceptible to capture in bait traps, as is also the case with other *Charaxes* species (Rydon, 1964; Henning, 1989; Sourakov & Emmel, 1995). During the flight period of the two 1996 and 1997 broods a total of eight Blendon traps (Platt, 1969; Austin & Riley, 1995) were installed along the transect route. The traps were installed 7–12 times during the flight period of each brood. Ripe banana with a trace of anise was used as bait, a combination which proved to be strongly attractive to this species. Traps were installed from 10:00 to 20:00, and the catch has been taken out every hour (except between 13:00 and 17:00 h when the traps were emptied every two hours due to the high number of individuals captured). For each individual sex, in 1997, wing wear using an arbitrary scale ranging from 1 to 5 (1 – mint; 2 – fine but some scales lost; 3 – slight wing damage; 4 – notable wing damage; 5 – strong wing damage) was recorded. Ageing was estimated for either sex by regressing wing wear on date from the beginning to the end of the sampling period and differences between sexes were assessed using covariance analysis.

Data on the immature stages were obtained from the systematic study of eggs and larvae at Fitor, for the period 1996–1997. A series of fixed routes were established in zones where the highest oviposition activity had been observed and were walked every 2–7 days from spring to autumn and approximately every 15 days in winter. The eggs and larvae found were marked with numbered plastic tags situated at the base of the leaf stalk. At each visit the larval instar was noted (from I to V). The low mobility of the larvae made periodical monitoring easy, and losses occurring between samples were attributed to death due to predation or other causes. For each sample, a value representing the mean stage of immatures (MSI) was calculated according to the following scale: 0 – egg; 1–5 – larval instars I – V; 6 – pupa.

Results

At Fitor (as in the other studied localities) *C. jasius* adults have a clearly bivoltine phenology. The flight curves at Fitor for the period 1994–1997 are shown on figure 2. Although important

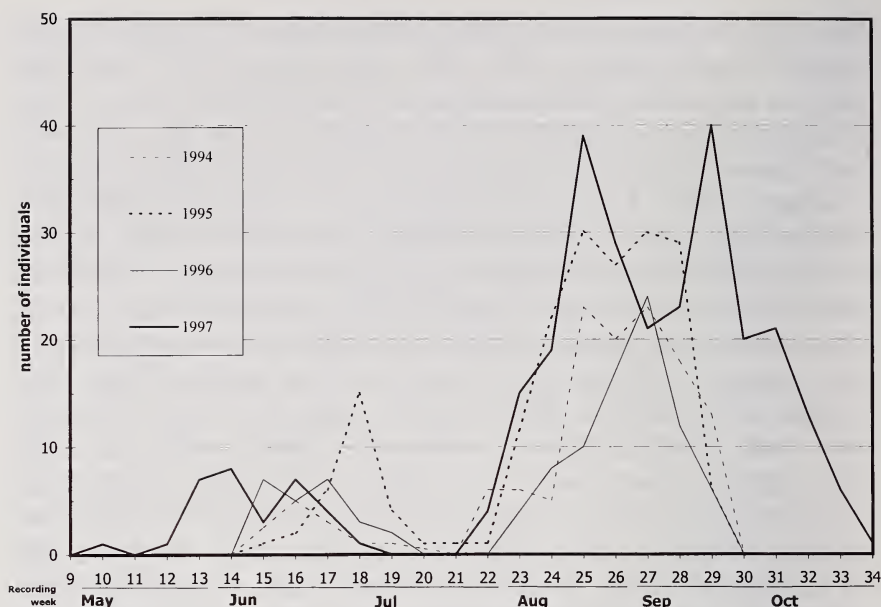


Fig. 2. Seasonal abundance of *Charaxes jasius* adults in 1994–1997 at Fitor site, as recorded by weekly transect counts.

abundance variations exist between years (as detected by changes in the annual index for each brood — see Table 2), the two broods are well separated in time. The first brood flies from the end of May to mid July (weeks 12 to 20), while the second is on the wing from the end of July to the end of September and even October (weeks 22 to 34). Occasionally, the second brood has a bimodal emergence, as can be seen from the flight curve for 1997. This bimodality is reflected perfectly by the data obtained using the bait traps (see below). The apparent bimodality of the first brood of 1997 is in reality an artefact of sampling, due to unfavourable weather conditions (very cloudy and low temperatures) affecting week 15 counts.

In all years the number of the second brood individuals was much higher than that of the first (fig. 2). On average the first brood represented 14.9% of individuals counted throughout the season (range: 10.2–22.9%; Table 2). The relation between the two broods is very similar when data from the rest of the BMS (mean 14.7%; range: 7.5–18.3%) are considered.

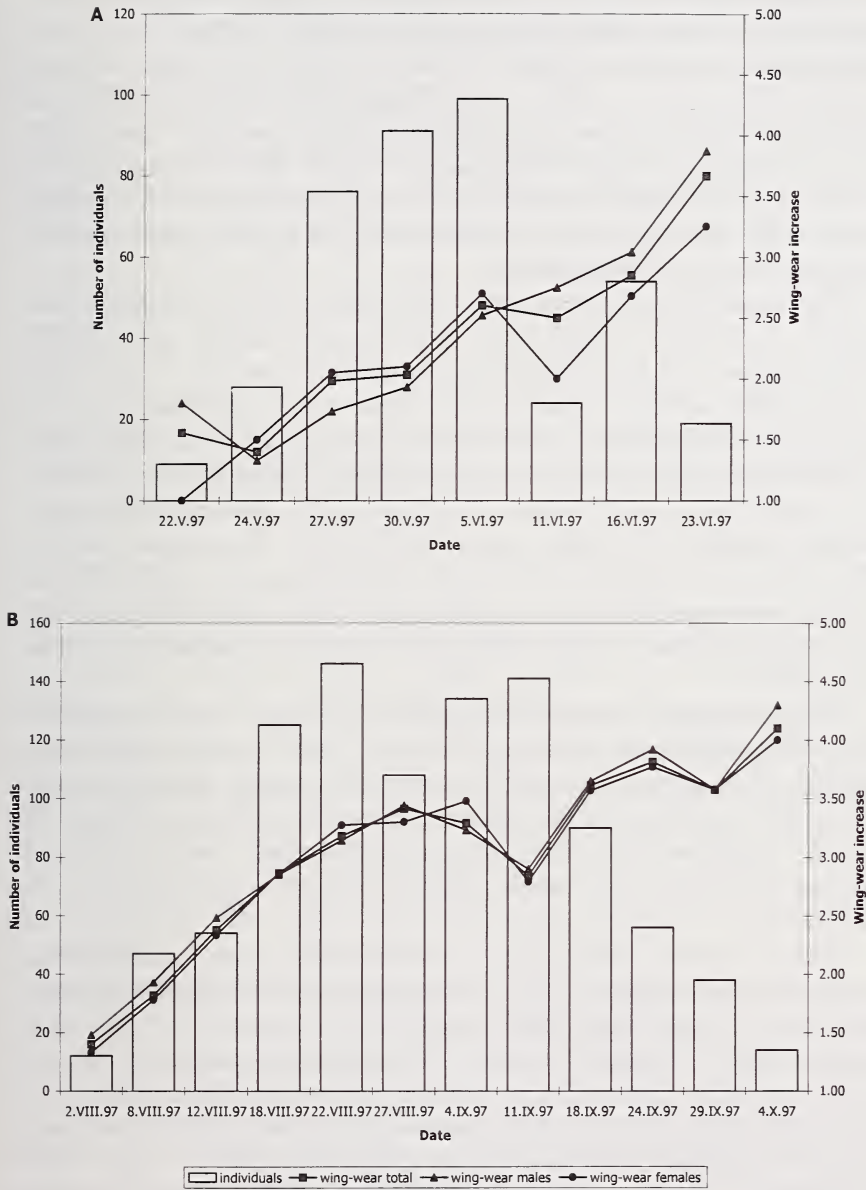


Fig. 3. Ageing of population as detected by wing wear increase from the beginning to the end of sampling in first brood 1997 (A) and second brood 1997 (B). Numbers of butterflies (histograms) are captures in bait traps.

If the results from Fitor are compared to the rest of the BMS network, a remarkable coincidence in flight periods during the four years is observed (Table 2). In only one of the eight broods studied (the first in 1995) a significant difference was observed (t-test, $p < 0.01$) between the MD at Fitor and the rest of the sites. Logically, the great similarity between the Fitor values and those from the BMS resulted in a strong coincidence in the time separating the two annual broods (dif MDs) in a given season and all over the studied area.

Throughout the four years of the study, MD variability was greater in the first brood than in the second. In the whole BMS network the first brood MD oscillated between 14.16 (1997) and 16.68 (1995), that is a difference of two and a half weeks in the flight period maximum. In contrast, the second brood MD varied in little more than half a week from 25.73 (1994) to 26.36 (1996). It should be noted, however, that the MD of the 1997 second brood would be slightly increased if data for counts during October were included. In that year the flight period of the second brood was considerably extended not only at Fitor (fig. 2) but at many localities, where a bimodal emergence pattern was also observed.

With reference to the SD, values are higher for the second than the first brood (Levene test, $p < 0.01$ in the four years tested), indicating that the first brood emergence period is more compact than the second. This is reflected perfectly in figure 2, where it can be seen that the first brood flight period at Fitor oscillates between 5–7 weeks, while for the second this is 7–13 weeks.

Data obtained through the use of bait traps confirm and complement the above results. The number of individuals captured with this methodology (843 in 1996, 1365 in 1997; Table 3) is much higher than the number of individuals detected by the counts, so the phenological data are more reliable. Even so a great coincidence in the period in which population maxima occur can be observed between the two methodologies (cf. figs. 2 and 3, Table 3). There are notable differences, however, with respect to proportions between the first and second broods. In 1996 the first brood represented 36.1% of total captured individuals while in 1997 it was 29.3%, these values being some 1.5–2 times higher than those obtained during transect counts.

For the four sampled broods the sex ratio can be taken as 1:1 (χ^2 -test, $p = 0.11$). However, a predominance of females in the first brood of 1996 ($p < 0.05$) and of males in the second of 1997 ($p < 0.0001$) was found.

Figure 3 shows population ageing for the two 1997 broods. In both cases, wing wear increased with time (first brood: $y = 0.06x + 1.44$, $r = 0.964$, $p < 0.001$; second brood: $y = 0.03x + 1.95$, $r = 0.881$, $p < 0.001$; where y is wing-wear from 1 to 5, and x are the days from the beginning of the first sample). The regression equation slopes of males and females did not differ significantly in either case (ANCOVA, $F_{(1,12)} = 1.326$, $p = 0.27$ and $F_{(1,20)} = 0.009$, $p = 0.93$, respectively). On the other hand, the regression equation slopes pooled for both sexes differed significantly between the first and second brood (ANCOVA, $F_{(1,16)} = 5.326$, $p = 0.035$), suggesting that first brood adults become worn more quickly.

The existence of a bimodal emergence in the second brood of 1997 (fig. 2) is well documented by the bait traps. So, on 4th and 11th September there was a noticeable increase in the number of captures after the decrease that occurred during the last week of August (Table 3). This decrease was not the result of poor weather as all sampling in the second brood was done on hot and sunny days. Moreover, newly emerged specimens appeared in the population towards the second half of the flight period as shown by a noticeable decrease of wing wear (fig. 3). The short time separating the two peaks of abundance (four weeks compared with an average of dif MDs of 10.21 weeks in the period 1994–1997, Table 2) means that the existence of a third brood can be rejected.

Data from the monitoring of immature stages is presented in Table 4. Development of the individuals which give the second brood occurs largely during the second fortnight of June, July and early August. Important differences in development time were observed during the two years of study. Larvae grew faster in 1996 than in 1997, probably because of the higher summer temperatures of 1996 (overall mean temperature of June–July 22.69 and 21.65°C, respectively).

Hibernation occurs in the larval stage. Eggs laid by second brood adults in September and October hatch in two weeks and

Table 1. Monthly mean daily maximum, minimum and overall mean temperatures and rainfall recorded in La Bisbal meteorological station (31TEG04, 39 m) for the period 1993–1997

1993–97	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Mean maximum (°C)	14.17	15.25	18.13	19.86	23.77	26.83	30.43	30.23	25.31	21.85	17.14	14.40	21.45
Mean minimum (°C)	3.97	4.12	5.37	7.57	11.50	15.13	17.64	18.33	14.05	12.09	7.87	5.27	10.24
Overall mean (°C)	9.07	9.68	11.75	13.71	17.63	20.97	24.04	24.28	19.69	16.97	12.50	9.83	15.85
Rainfall (mm)	62.72	39.72	39.04	48.30	34.88	61.76	14.82	59.44	84.44	157.94	86.72	97.20	786.98

the larvae continue growing while temperatures permit. Although larvae in any instar may be found at the inception of winter, at the end of this period almost all individuals are at the third and fourth instars (Table 4). In 1996/1997, larval growth stopped between November and February and was resumed in March. On the other hand, in 1997/1998 the MSI increased continuously, though slowly, all over the winter. Moreover, in 1997/1998 larval populations took about a month longer to reach a MSI value higher than 3.00 and, while 3.5 was reached in the first winter at the end of October, this score was just attained two months later the following season (Table 4).

Discussion

C. jasius has a typically bivoltine phenology in the NE Iberian Peninsula, with a first brood flight period in June and early July and a second in August and September. The second brood is

Table 2. Comparison between data obtained in transect counts at Fitor and the rest of the BMS sites. In brackets, number of sites with breeding populations of *Charaxes jasius*, excluding Fitor; AI – annual index of abundance of first (1) and second (2) broods; MD – mean date of the counts of each brood; SD – standard deviation about this date; dif MDs – difference between MD of the first and second broods; t – t-test values to test for differences in MD between Fitor and the rest of BMS sites for the first (t_1) and second (t_2) broods (significance at: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$)

	AI ₁	AI ₂	MD ₁	SD ₁	MD ₂	SD ₂	dif MDs	t_1	t_2
1994									
BMS sites (n=5)	6	74	16.0	1.41	25.7	1.80	9.7	-0.837	-1.725
Fitor	13	114	16.6	1.36	26.2	1.88	9.6		
1995									
BMS sites (n=8)	22	154	16.7	1.67	25.8	2.18	9.1	-2.852 ***	-0.694
Fitor	30	158.5	17.9	1.17	25.9	1.72	8.1		
1996									
BMS sites (n=11)	28	125	16.5	1.87	26.4	1.94	9.9	-0.081	0.0421
Fitor	24	81	16.5	1.29	26.4	1.56	9.8		
1997									
BMS sites (n=12)	50	264	14.2	1.66	26.3	2.08	12.1	-1.2	-1.73
Fitor	32	210	14.6	1.74	26.6	2.22	12.0		
Average 1994-1997									
BMS sites	26.5	154.2	15.8	1.65	26.0	2.00	10.2		
Fitor	24.8	140.9	16.4	1.39	26.3	1.84	9.9		

Table 3. Capture data of *Charaxes jasius* with bait traps at Fitor in 1996–1997. Columns indicate number of single captures of males and females, number of individuals recaptured and number of unmarked individuals. Sex ratios (see text) are based on single captures of males and females

first generation									
samples	1996	BMS wk	Total	male	female	recapt.	unmark.	% m	% f
1	11.VI.96	15	13	-	-		13	-	-
2	13.VI.96	15	31	-	-		31	-	-
3	15.VI.96	16	108	27	44	19	18	0.38	0.62
4	19.VI.96	16	90	26	34	18	12	0.43	0.57
5	24.VI.96	17	35	8	11	13	3	0.42	0.58
6	1.VII.96	18	19	5	5	9	0	0.50	0.50
7	11.VII.96	19	5	1	3	1	0	0.25	0.75
	Total		301	67	97	60	77	0.41	0.59

first generation									
samples	1997	BMS wk	Total	male	female	recapt.	unmark.	% m	% f
1	22.V.97	12	9	6	3	0	0	0.67	0.33
2	24.V.97	13	28	5	14	1	8	0.26	0.74
3	27.V.97	13	76	23	24	12	17	0.49	0.51
4	30.V.97	13	91	25	27	6	33	0.48	0.52
5	5.VI.97	14	99	28	43	14	14	0.39	0.61
6	11.VI.97	15	24	11	2	3	8	0.85	0.15
7	16.VI.97	16	54	18	16	5	15	0.53	0.47
8	23.VI.97	17	19	6	7	3	3	0.46	0.54
	Total		400	122	136	44	98	0.47	0.53

first generation									
samples	1996/97	BMS wk	Total	male	female	recapt.	unmark.	% m	% f
			701	189	233	104	175	0.45	0.55

second generation									
samples	1996	BMS wk	Total	male	female	recapt.	unmark.	% m	% f
1	10.VIII.96	24	7	5	2	0	0	0.71	0.29
2	17.VIII.96	25	29	17	7	2	3	0.71	0.29
3	21.VIII.96	25	104	39	38	12	15	0.51	0.49
4	26.VIII.96	26	125	48	60	10	7	0.44	0.56
5	2.IX.96	27	131	47	52	12	20	0.47	0.53
6	10.IX.96	28	86	33	32	10	11	0.51	0.49
7	16.IX.96	29	43	17	15	7	4	0.53	0.47
8	28.IX.96	31	17	5	8	2	2	0.38	0.62
	Total		542	211	214	55	62	0.50	0.50
Total 1996 843									
recaptured 115									
unmarked 139									

second generation									
samples	1997	BMS wk	Total	male	female	recapt.	unmark.	% m	% f
1	2.VIII.97	23	12	6	3	1	2	0.67	0.33
2	8.VIII.97	23	47	22	12	0	13	0.65	0.35
3	12.VIII.97	24	54	27	18	3	6	0.60	0.40
4	18.VIII.97	25	125	58	47	8	12	0.55	0.45
5	22.VIII.97	25	146	65	53	11	17	0.55	0.45
6	27.VIII.97	26	108	38	49	12	9	0.44	0.56
7	4.IX.97	27	134	87	16	5	26	0.84	0.16
8	11.IX.97	28	141	64	53	10	14	0.55	0.45
9	18.IX.97	29	90	36	39	6	9	0.48	0.52
10	24.IX.97	30	56	17	23	6	10	0.42	0.57
11	29.IX.97	31	38	16	11	6	5	0.59	0.41
12	4.X.97	32	14	4	7	1	2	0.36	0.64
	Total	965	440	331	69	125	0.57	0.43	
Total 1997 1365									
recaptured 113									
unmarked 223									

second generation									
samples	1996/97	BMS wk	Total	male	female	recapt.	unmark.	% m	% f
			1507	651	545	124	187	0.54	0.46
Total 1996/97 2208									
Total male 840									
Total female 778									

always more abundant than the first, a common feature of bivoltine species at middle latitudes (Pollard, 1984) and, in the case of *C. jasius*, a direct consequence of the high mortality of the hibernating larvae (unpubl. data).

The differences found with respect to the relative abundance of the two broods when transect counts or bait trap data are considered may be attributed to two different reasons. Firstly, the number of second brood individuals is so high that the traps become saturated in the middle part of the day and population size is underestimated. Secondly, the availability of ripe fruit is far greater in August and September than in June and so the traps are more effective during the first brood.

A comparison between a very large population and several other populations monitored within the Catalanian BMS, revealed a highly coincident phenology in every season over a wide area. Thus, no significant differences were detected in the MDs (calculated from transect data) in seven out of eight broods studied. Moreover, the only significant value (first brood 1995) was probably due to an abnormally high count towards the end of the flight period in Fitor, when several individuals were concentrated on excrements along the transect route.

Even though the number of BMS stations with breeding populations of *C. jasius* increased during the four years of the study (from an initial total of five, excluding Fitor, to eleven), the MDs continued to coincide. This synchrony shows that the populations are subject to very similar climatic conditions typical of littoral and prelittoral Mediterranean ecosystems of the NE Iberian Peninsula (fig. 1). This coincidence also indicates that the standardised transect counts used in the BMS provide a very accurate description of the flight period, even though *C. jasius* is ordinarily a scarce butterfly at most sites and correspondingly counts are low.

There is no doubt that the principal conditioner in advance or delay of the flight period between different seasons is temperature and its corresponding effect on the development period of the immature stages (Scriber & Slansky, 1981). A clear example can be seen in the 1997 season, where abnormally high temperatures in March–May (15.5 vs. 14.08°C for the period 1993–1996) and abnormally low for the period June–July (21.65 vs. 22.72°C

for the period 1993–1996) were combined. The first brood advanced slightly more than two weeks with respect to the corresponding mean for 1994–1996, while the second showed the opposite trend as revealed by the highest dif MDs value recorded that year over the whole period (Table 2).

The temperature effect is particularly evident in the case of larvae resulting from the second brood. In 1996/1997 development suspended between November and February, when mean temperatures oscillated between 9.28 and 11.57°C. In contrast, though mean temperatures from December to February were lower (9.2–10.4°C) in 1997/1998, MSI values increased continuously, though slowly, during this period (Table 4). These results seem somewhat contradictory, as they suggest that the species' lower thermal threshold varies depending on the season. Nevertheless, this apparent paradox may arise, in part, from the differences in the timing of the second brood of adults coupled with the highest mortality usually experienced by eggs and young larvae (unpubl. data). As a result of the bimodality of the second brood in 1997 (fig. 2), eggs were found until late November and first instar larvae occurred until late December, that is, one month and a half later than in the previous season (Table 4). The more severe mortality acting on these young stages could lead to an increase of the MSI values during the first half of the winter, even in the case that larvae were in a complete growth arrest. The steady increase of the MSI values during January and February is more difficult to explain, but could also be a consequence of the haphazardly disappearance of older larvae due to predation and the corresponding variation in the size and structure of the samples.

It is interesting to note that an increase in summer temperatures does not always lead to a reduction of larval development time. Thus, the summer of 1994 was the hottest of the period considered but the time separating the two broods was longer than in 1995 (Table 2). Both July and August 1994 were extremely hot: mean maximum temperatures exceeded 31°C and maximum temperatures near 40°C were recorded on several days. These unusually high temperatures can affect caterpillar growth detrimentally in different ways. They may be outside the thermal optimum temperature of the species and hence increase respiratory expen-

diture (e.g. Casey, 1993), but may also affect food quality by dramatically reducing the leaf water content in periods of drought stress (e.g. Slansky, 1993 and references given), as usually happens with the mulberry tree (Castell, 1997).

These results indicate that the restrictions imposed by thermal conditions set an upper limit of two broods per year in the NE Iberian Peninsula. Mean temperatures from December to February are always less than 12.5°C along the littoral and prelittoral (Clavero *et al.*, 1996) and under such circumstances larval growth is much reduced if not completely arrested. This is the usual phenology throughout the rest of the area of distribution including the southern limit in North Africa (Tennent, 1996). Exceptionally, however, a third brood of adults may exist in the south of the Iberian Peninsula in December–January in years with an exceptionally mild winter (Verdugo, 1984). This third brood is also obtained when larvae from the second brood are reared indoors with high temperatures and natural photoperiod (pers. obs.) and, therefore, *C. jasius*, like many other *Charaxes* spp. (Owen & Chanter, 1972), is in fact a potentially continuously brooded species.

The existence of two peaks of butterfly abundance during the second brood in some years (e.g. in 1997, fig. 2), may be confounded with a multivoltine cycle with three broods. The data obtained through the bait traps in 1997 clearly indicate that this bimodal curve is real (Table 3, fig. 3) and is a consequence of a multimodal emergence and not a third brood. The same conclusion is reached for the immature stages, where monitoring never confirmed the existence of a third brood (Table 4). In contrast to other butterflies where bimodal emergence has been established (e.g. *Papilio glaucus* — Hagen & Lederhouse, 1984; *Maniola jurtina* — Goulson, 1993), in the case of *C. jasius* this does not seem to resemble an intrinsic population characteristic repeated annually. It seems more likely that this appears occasionally in response to particular environmental conditions. For example, the unusually cold temperatures recorded at the end of June 1997 could have affected eggs and larvae differentially and thus enhanced differences in the total development time between parts of the population. A similar reasoning was suggested by Dennis (1985) to explain the multimodality within broods in British *Aglais urticae*.

Further laboratory experiments under controlled temperatures would be necessary to assess not only those abiotic factors governing larval development but also the potential variation and plasticity of individual growth. Undoubtedly, this information will help to interpret correctly specific patterns found in natural populations.

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