

Delayed ovarian maturation in the butterfly *Hipparchia semele* as a possible response to summer drought

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ABSTRACT. 1. Several references indicate that the period of flight of the European satyrine butterfly *Hipparchia semele* (L.) (Nymphalidae, Satyrinae) starts earlier in southern latitudes, where summers are longer and drier than in the north. However, summer drought has an adverse effect on the growth of grasses on which larval feeding depends. Growth of the grasses is delayed as long as the drought lasts.

2. From laboratory and field observations in a mid altitude area near the centre of the Iberian Peninsula, a mechanism that can be interpreted as an adjustment of this insect's life cycle to the host plant's phenology has been observed, i.e. delayed gonadal maturation of adult females. This delay is not associated with female diapause. Although the mean delay in oviposition after copulation was 43 days some captive females were able to oviposit much earlier, and this suggests variability in oviposition dates which might have an environmental or a genetic basis.

3. A mechanism of delayed ovarian maturation similar to that of *H.semele* is also known to occur in the satyrine *Maniola jurtina* (L.); it is suggested that this adaptation enables these species to occupy wider geographical ranges than other univoltine satyrines in Europe.

Key words. Life history, phenology, delayed ovarian maturation, summer drought, Lepidoptera, Satyrinae.

Introduction

Mediterranean climates are characterized by hot dry summers and mild rainy winters; because of this, vegetative growth is mainly restricted to the rainy season in Mediterranean areas (Mooney *et al.*, 1974).

At a first glance summer drought seems to be disadvantageous for the reproduction of a number of univoltine summer butterflies of which the larvae feed on grasses, such as many of the

satyrine nymphalids that inhabit mid elevations and lowlands with more or less strict mediterranean climate in southern Europe. Under these conditions, a severe depletion of larval food (i.e. leaves with contents of nitrogen, water and water-soluble carbohydrates adequate for larval growth: Scriber & Slansky, 1981; Bink, 1985) occurs at or before the time when adult insects emerge. In order to synchronize the period of larval feeding with the new growth of grasses, any kind of adaptive phenological behaviour might be expected to operate in such a way that the young larvae are able to start feeding in autumn, when the rain is predictable and favours the growth of host plants. Several mechanisms

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could be involved, and in fact larval and adult aestivation have already been reported for some temperate satyrids (Scali, 1971; Bink, 1985). Most of our knowledge of the biology of European butterflies, however, comes from humid countries, and little is known about the way that the same species behave under different conditions.

The grayling butterfly *Hipparchia semele* (L.) inhabits a large area in Europe from Portugal and the British Isles to south European U.S.S.R., and from the Baltic countries in the north to the Mediterranean shore (southern Spain, Italy, etc.) in the south (Kudrna, 1977). Whereas in the British Isles and The Netherlands the adults emerge in July (Heath *et al.*, 1984; Tinbergen *et al.*, 1942; F. A. Bink, pers. comm.), they have been recorded in June, May and even earlier in the South of Italy (Verity, 1953; E. Balletto, pers. comm.). So, if adult emergence is earlier in southern latitudes where the summer dry period is longer, the insect needs to spend that dry period in a resting stage.

In central peninsular Spain, *H. semele* is widespread in mountains and uncultivated lands, on limestone and chalk as well as on well-drained siliceous soils. Some of the published observations on its seasonal pattern of abundance lead to confusion: while Querci (1932) pointed out that a gradual emergence occurs for 2 months, Monserrat (1976) found that the number of butterflies followed a bimodal curve in summer in the Sierra de Guadarrama, and concluded that two broods actually occurred. The observations by Monserrat (1976) bring to mind the behaviour of *Maniola jurtina* in Tuscany (Scali, 1971) where females aestivate, show delayed ovarian maturation, and follow a bimodal pattern of seasonal abundance. However, aestivation in the last larval instar of laboratory reared *H. semele* from southern France has been recently reported by Bink (1985). The aim of this study was then to assess the general biology and life cycle phenology in an area where a moderate summer drought occurs.

Materials and Methods

The study consisted of a number of field observations on adult phenology, habitat, behaviour and larval food plants, combined with the results of rearing the species in the laboratory under conditions close to the natural.

For field observations, a 30×30 km area at 800–1000 m on the West side of the river Tajo at the level of Entrepeñas Dam (Provincia de Guadalajara, Spain) was selected. The climate can be classified as semi-arid mediterranean, with an average precipitation of 600–700 mm/year, a dry season from mid June to the beginning of September (65–84 days on average), and mean January temperatures usually between 3°C and 6°C (Allué, 1966; Nicolás *et al.*, 1979). The vegetation consists of a varied series of successional stages derived from the *Quercus faginea* Lam. woodland or mixed *Q. faginea*–*Q. rotundifolia* Lam. woods. The distribution of *H. semele* in the area is more or less continuous, and the whole area was taken as a unit. Regular transect samples were carried out at Budia (950 m; 2°46'W, 40°39'N) and Chillarón del Rey (800–850 m; 2°41'W, 40°35'N). Thirteen other sites representing several vegetation types and humidity levels were also visited once or twice a month to ascertain the environmental preferences of the species, as well as to capture male and female adult *H. semele* to be transported to the laboratory.

In the course of the samples (1983–85) the number of male and female butterflies and their activity were recorded. Individuals initially at rest were observed for 1 min and then recorded for 4 min, thus avoiding erroneous recording due to cryptic behaviour shown by disturbed butterflies. The wing wear state of ninety-three males and eighty-two females was recorded during the summer of 1985 (on the scale: 1=newly emerged, to 5=very worn). Additionally, eighty females were captured in places surrounding the main study sites (1984 and 1985) and dissected to ascertain the degree of ovarian maturation, diameter of the widest eggs within the ovarioles, and the presence of spermatophores within the bursa copulatrix.

For rearing, *H. semele* females were kept in 12 or 37 litre voliaries supplied with water and a small pot with diluted apricot jam. Since previous experience showed that caged females do not lay eggs on fresh grass but usually attach them to the floor and walls of the cages, the voliaries were constructed with plastic grid (grid squares approx. 5×5 mm). The butterflies then tended to stick the eggs on the outer surface of the wall by bending the abdomen across the grid. This facilitated egg collection and counting.

The newly hatched larvae were kept either in Petri dishes with fresh grass leaves, or on pots with a mixture of grass species. Usually two or more plants were used simultaneously: *Festuca* spp., *Poa* spp., *Elymus repens* (L.) Gould., *Lolium perenne* L., *Dactylis glomerata* L., *Brachipodium phoenicoides* (L.) Roem. & Schultes. The full-grown larvae were placed in separate jars before pupation. All rearings were made in an outdoor yard in the Universidad Autónoma de Madrid (c. 500 m). Although more than 500 newly born larvae were initially used for rearing, an unexpectedly high larval mortality occurred in the first larval instar every year. This made it necessary to collect some additional larvae and adults in the field (in the case of adults, these were caught only within the first 15 days of the period of adult occurrence in the study area). For caged adults the longevity, date of mating (when known) and number of eggs laid were recorded. Dead females were dissected and examined for the number of eggs remaining and mating condition.

Results

Adult phenology

The adults can be seen from the first week of June to the first week of October, though they are most frequent between 15 June and 20 September. Three males were seen in the last week of May, but none was recorded by this date during transects. Of 339 butterflies recorded 173 were males and 166 females. As an overall trend for the whole period of study, the proportion 1 male:1 female was reached by mid July (Fig. 1).

No evidence for a seasonally bimodal pattern of abundance was found. The estimated wing wear state of the insects along the summer of 1985 suggested that adult emergence occurred over a period of 30–40 days for each sex. No data were available for the first 10 days of August that year, but the adults of both sexes seemed to fall within wear category 3 by the end of July (Fig. 2); the regression coefficients of wing wear state/time did not differ significantly between males and females (F test for the difference between two regression coefficients according to Sokal & Rohlf, 1969: $F_5=3.971$; d.f.=18; $0.1>P>0.05$; regression line for males, $y=0.025x+1.358$; $r=0.85$; $n=93$; females, $y=0.026x+1.437$; $r=0.85$; $n=82$; see also Fig. 2).

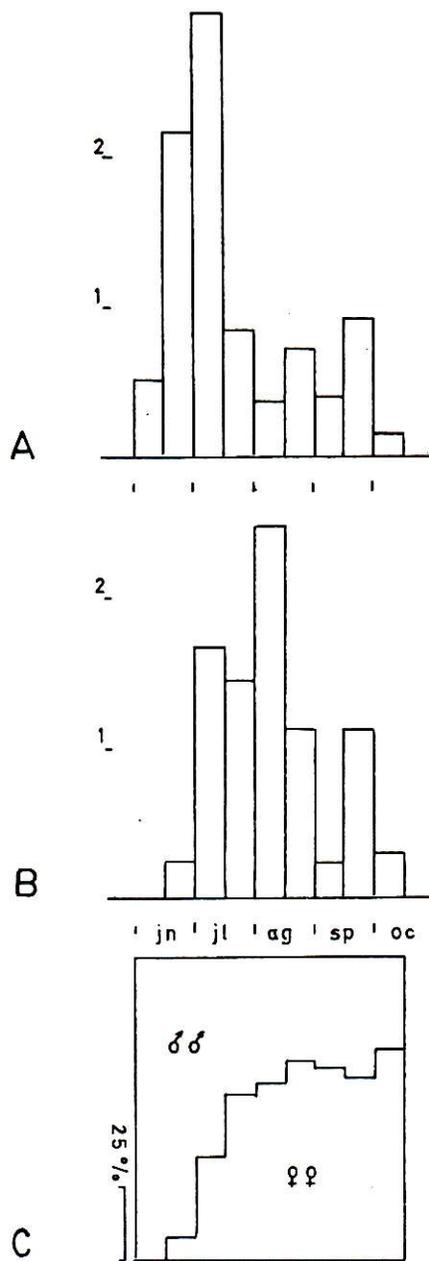


FIG. 1. Relative abundance of adult *H. semele* during its period of flight in the study area (individuals/sample): (A) males, (B) females, (C) proportion males/females.

Timing of oviposition

The first observed oviposition was on 20 August and searching females were often seen during the month of September. Nineteen of

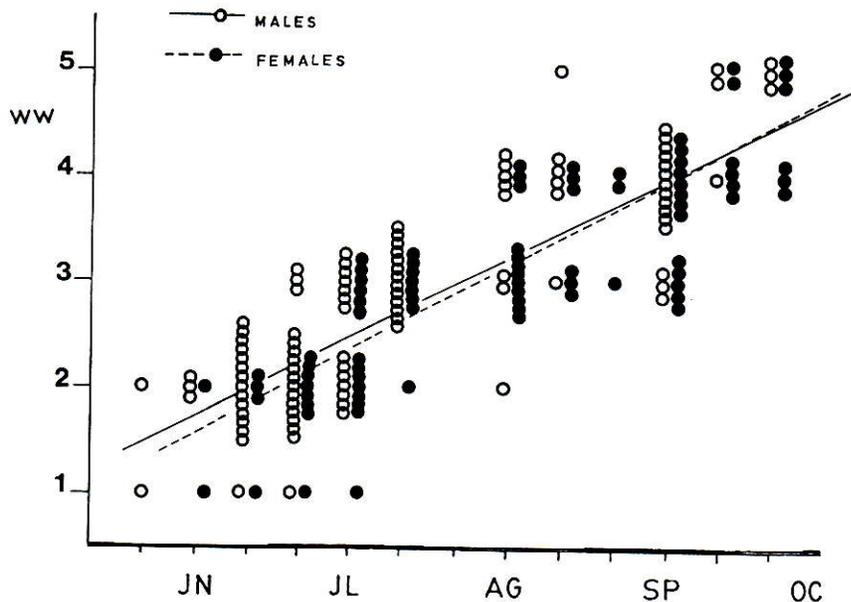


FIG. 2. Estimated wing wear state (ww) of adult *H. semele* during the summer of 1985 in the study area, plotted against dates of capture, and regression lines for both sexes (see text).

these females were followed until they deposited at least one egg. As previously noted by Tinbergen *et al.* (1942), females do not select fresh grass leaves for oviposition (see also Bethune-Baker, 1907, but cf. Wiklund, 1984). After alighting on the ground, they walk for a short distance (5–25 cm) and attach a single egg to the under surface of any solid object, usually dead plant materials such as wilted oak or pine leaves, or small branches lying on the ground. Only in seven cases (total observed=51) was the egg directly laid on a wilted grass stem or blade, never on a fresh one. After laying one egg, the female walks for a variable distance or flies some metres away before laying again. No clear inspection for suitable host plants before alighting was recognized, and in at least two cases the egg was laid more than 50 cm away from the nearest apparent potential larval host.

Results of dissection of field-caught females

Nearly 95% of all females were already mated when captured. Four virgin females were taken, on dates and with estimated wing wear (ww): 15 July 1984 ww=1, 5 August 1984 ww=2, 27 August 1984 ww=3, 15 July 1985 ww=3. Previous dissections showed that newly emerged

females have clearly immature ovaries, the maximum width of the ovarioles ranging between 0.07 and 0.12 mm, while in ovipositing females mature eggs (chorionated, wider than 0.70 mm) are found in the common oviduct. All dissected females appeared to be immature until the end of August, and females with mature eggs in the common oviduct were not found before September (Fig. 3). No females in ages '1' and '2' had mature eggs, and also some of the insects in ages '3' and '4' were immature (Fig. 4).

Adult potential longevity and egg production by captive females

The adult life span reached 2 or 3 months in the laboratory. The maximum for males and females was, respectively, 115 days, mean=70, SD=44, $n=5$, and 110 days, 84 ± 21 , $n=6$.

No female started ovipositing immediately after copulation; for the six reared females, a period of preoviposition longer than 20 days was observed (28–65 days, mean= 43.2 ± 14.3). During this period, females were in general less active than males, but they regularly fed and took water in the voliaries.

The length of the oviposition period reached 73 days in one female (mean= 34 ± 15). For

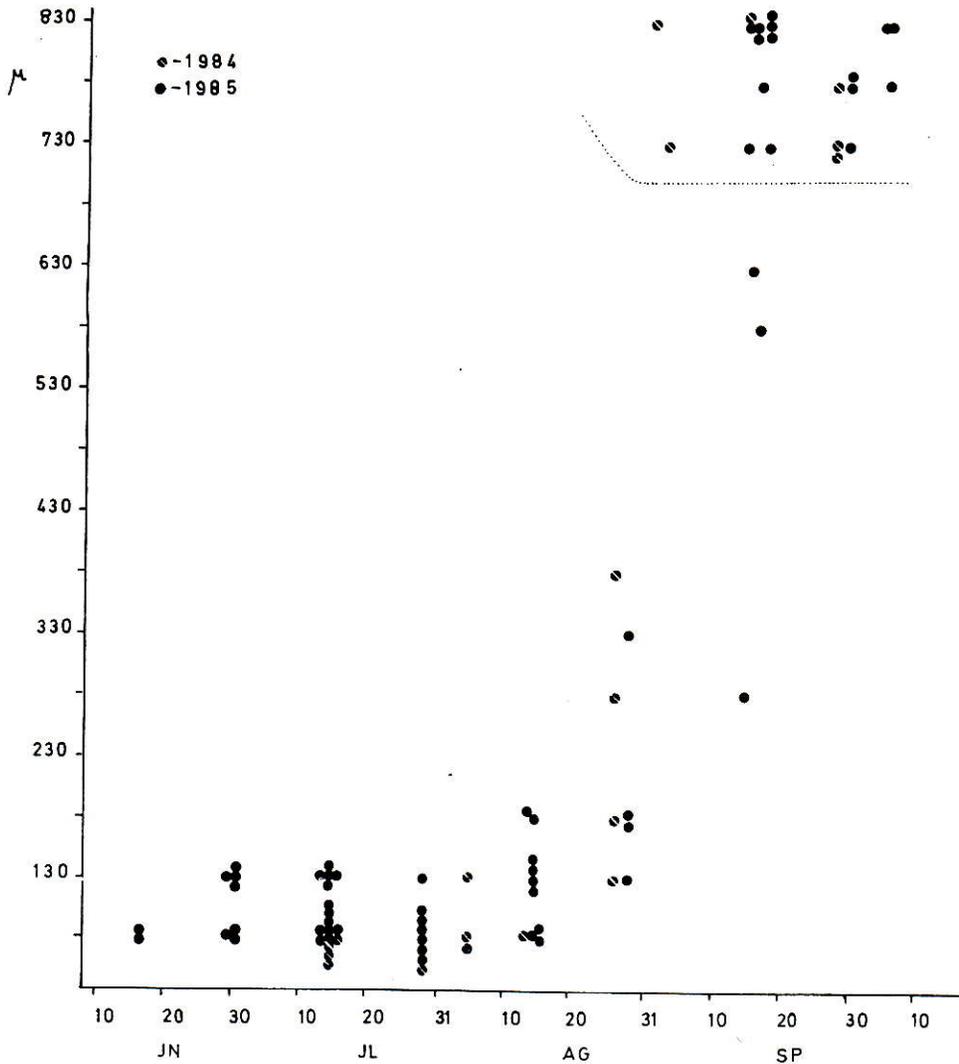


FIG. 3. Maximum diameter (μm) of the eggs contained in the ovaries of female *H. semele* taken in the field, plotted against dates of capture. Ovipositing females are those above the dotted line in the upper right quarter of the graph.

seventeen females (six from rearing, eleven from the field) the mean daily egg rate was 19.3 ± 5.6 eggs/day, the maximum daily egg rates ranging between 31 and 50 a day, and the mean total egg production was 612 ± 244 eggs/female. All females died before depletion of their egg endowment occurred.

Among the females that were taken in to the laboratory, eight behaved in the way described above; three other females, however, started laying between 15 July and 25 July, respectively 12, 15 and 30 days after being caged.

Early stages

The lengths of the immature stages under outdoor conditions were 7–25 days for the egg stage, 250–300 days for the larval stage, and 21–40 days for the pupal stage.

After hatching, the newly born larvae remained quiescent and did not feed on fresh grasses even when they were placed upon young leaves of potted plants. Surprisingly, there was very high mortality during these first days of larval life (many larvae simply died and

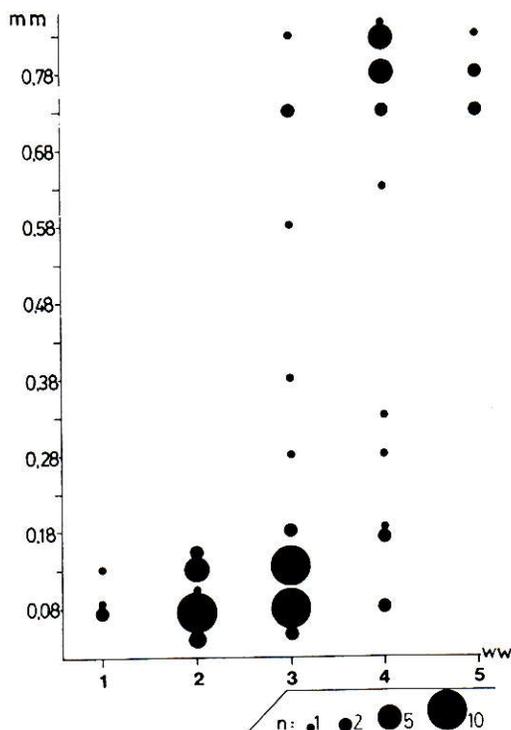


FIG. 4. Relationship between the maximum width of the eggs contained in the ovaries of field-caught females (mm) and their estimated wing wear state (ww).

shrivelled up on apparently suitable grass leaves) and only twenty-six insects survived. These started feeding 15–30 days after hatching (25 September to 20 October).

Once larval feeding had started, no period of diapause or quiescence was observed. Larval growth decreased but did not completely cease during the colder months (December–February), and the last (fifth) instar was reached in April or May. Pupation occurred from 20 April to 20 June. No evidence for larval aestivation in the last larval instar was found in a total of twenty-one individuals. The length of all immature stages (except first instar larvae) seemed to be inversely correlated with temperature; indoor rearing (12–25°C), under natural daylight conditions, of four first instar larvae resulted in adults by the beginning of March (at least 2 months before the usual dates in the field).

Discussion

The data from wild females (no oviposition

observed nor ripe females found until late summer) support the view that female *H. semele* exhibits delayed ovarian maturation parallel to that observed in some of the caged females during the period of study. The length of the delay could be as much as 2 months in some individuals, with a mean of over 1 month after copulation. There is no evidence against late emergence and in fact the period of emergence is probably more than a month for each sex (as previously suspected by Querci, 1932). However, the relationship between the estimated wing wear state and the size of the widest eggs contained in the abdomen of field captured females (Fig. 4) shows that a relatively long female gonadal maturation must be a generalized phenomenon in the area.

An influence of environmental conditions on female gonadal maturation cannot be discounted. Because some captive females (both laboratory raised and brought in from the field) showed earlier onset of oviposition than that observed in the field (and in the other caged individuals) it appears that, at least to some extent, faster ovarian development in these insects might have been favoured by, for example, continuous easy availability of food and water.

The area of the field observations is not under extreme mediterranean climate, summer drought is of moderate length and winter temperatures are relatively low. In extreme mediterranean climates with a long dry season long-delayed oviposition should be even more necessary, while at high altitudes or latitudes this is not so. Thus there is a possibility that the population under study is an intermediate or mixed one, and the ability to oviposit a few days after emerging is still retained, at least in a part of the population or under certain conditions. A situation of this kind has been described for *Maniola jurtina* at intermediate altitudes in Italy (Masetti & Scali, 1972): some females emerge early and aestivate, while others emerge late with no aestivation.

Weissman (quoted by Gilbert & Singer, 1975) explains the occurrence of a second generation of *Coenonympha tullia* (Müll.) whose adult females undergo delayed ovarian maturation to compensate for the inability of the first instar larvae to survive both the long dry summer and a part of the winter in California. The same may apply to *H. semele* in mediterranean areas: with-

out a long period of preoviposition, larval hatching would occur too soon in the season. Although potential egg production is relatively high in *H. semele*, the actual reproductive success is obviously dependent on the number of days of oviposition. Mated females should be expected to reduce their activity before starting to oviposit. Caged females were less active than males, but the results of this work do not support the idea that adult diapause is associated with the slow rate of female gonadal maturation.

Delayed oviposition has been found in several other satyrines that inhabit areas with a more or less pronounced summer drought: *M. jurtina* in Italy (Scali, 1971), *Heteronympha merope* (Fabricius) in southern Australia (Edwards, 1973), *C. tullia* in California (Weissman, *op. cit.*). It has also been suggested in *Kanetisa circe* (Fabricius) and *Pyronia* spp. (Verity, 1919; Scali, 1971), and it probably does in *Hipparchia algrica* (Oberthür) in north-western African mountains: H. Powell (notes by Powell in Oberthür, 1914) was unable to obtain eggs from field-caught females during June and July, but some females laid by the end of August. So, it is possible to envisage it as a convergent adaptation to summer drought, though not restricted to mediterranean areas. Two of the above species (*M. jurtina* and *H. semele*) are among the more widespread European monovoltine satyrines (cf. Higgins & Riley, 1983) and their phenologies – as far as they are known at present – are remarkably similar. It is tempting to hypothesize that delayed ovarian maturation has evolved from a life cycle phenology that was primarily adapted to a particular area or climate and has subsequently allowed these butterflies to occupy a wider geographical range.

A 2 or 3 days period of quiescence in first instar larvae was noticed by Wolfe (1896) from British newly born larvae of this species. It appears to be a quite common phenomenon among European satyrines: *Melanargia*, *Hipparchia*, some *Erebia* (Tilley, 1983; Mansell, 1985; Bink, 1985), *Kanetisa*, *Maniola* and *Coenonympha* (García-Barros, unpubl. data). Because of the large observed mortality of *H. semele* larvae there is some doubt as to whether aestivation did occur in this study. Many satyrines do not lay their eggs directly upon larval hosts, and larvae of some species have been shown to be adapted to endure starvation for several days (Wiklund, 1984; Karlsson &

Wiklund, 1985). The only evidence for a period of larval quiescence in *H. semele* in this study is that the larvae did not feed either on potted grasses or fresh young leaves within Petri dishes (in the dishes, larval feeding is denoted by the presence of faeces and traces of chewing on the leaves, that are easily detected under a binocular microscope at low magnification). The high mortality that was observed every year may indicate the lack of very precise ecological conditions required by the newly born larvae, particularly since they will need no feed for some days. It is possible that further work will reveal that both larval quiescence and resistance to starvation occur together in this species.

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