

The life-history of *Tomares ballus* (Fabricius, 1787) (Lepidoptera: Lycaenidae): phenology and host plant use in southern Spain

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Abstract. The life-history of *Tomares ballus* in southern Spain is described. In Sierra Morena *T. ballus* is monophagous and feeds on flowers and fruits of *Astragalus lusitanicus* (Lam., 1783) (Fabaceae), despite the availability of other potential host plants. The phenological coupling between *T. ballus* and *A. lusitanicus* is considerable in Sierra Morena, whereas the flowering period of the remaining potential host plant species is approximately one month later. In the Guadalquivir Valley butterflies show preferences for *Medicago polymorpha* (L., 1753). Other aspects of the life-history of *T. ballus* are discussed in relation to the morphological and productive features of *A. lusitanicus*.

Introduction

Tomares ballus is a Mediterranean biogeographical component of the Palaearctic butterfly fauna. It is frequently found in some parts of North Africa, the southeastern half of the Iberian Peninsula and a small region in southeastern France, feeding mainly on *Lotus hispidus* (D.C., 1805) (Higgins & Riley, 1980). The other species of the same genus flying in Europe is *T. nogelli* (Henrich-Schaffer, 1851), which flies in Rumania and uses *Astragalus ponticus* (Pallas, 1800) as host plant (Higgins & Riley, 1980). In northern Africa the range of *T. ballus* overlaps that of *T. mauretanicus* (Lucas, 1849) which feeds on *Hippocrepis multisiliquosa* (L., 1753) (Higgins & Riley, 1980; Courtney, 1983).

Despite the recent work by Descimon and Nel (1986), *T. ballus* is not a well known species. The present work focuses on different aspects of the life history of *T. ballus* and its host plants in southern Spain.

Study Area

Field work was carried out in areas located on both sides of the middle of the Guadalquivir River in southern Spain (Córdoba province) (Fig. 1). In the northern zone (Sierra Morena Mountains, SM), soils are mainly siliceous and poorly-developed. A varying degree of human management has affected the composition and structure of the original vegetation. The region is a mosaic of different units, where areas of oak forest (*Quercus rotundifolia* and *Q. suber*)

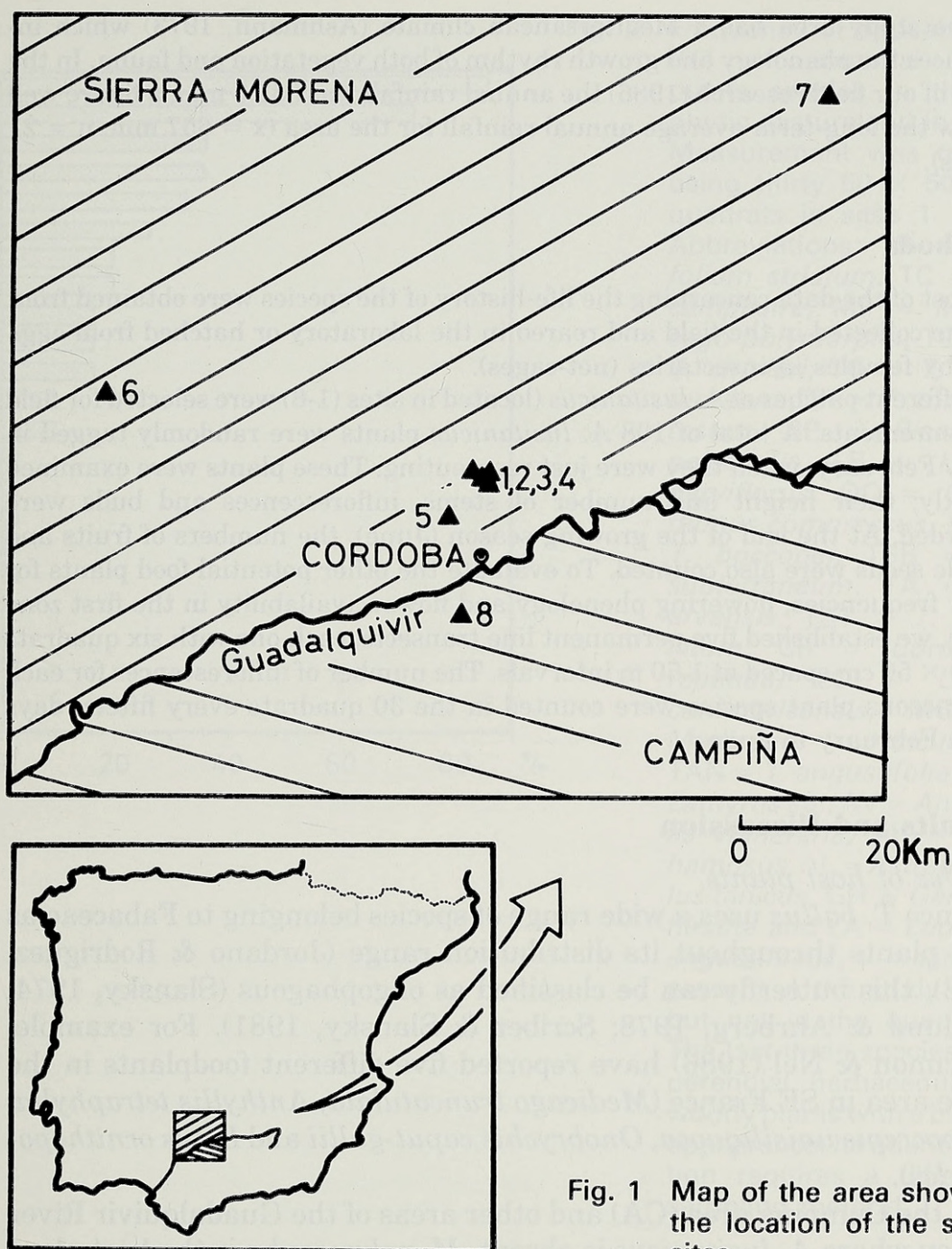


Fig. 1 Map of the area showing the location of the study sites.

alternate with scrubland or therophytic pastureland. Scrubland is mainly composed by Cistaceae (*Cistus ladanifer*, *C. monspelliensis*, *C. salvifolius*), Labiatae (*Rosmarinus officinalis*, *Lavandula stoechas*) and Ericaceae (*Arbutus unedo*, *Erica arborea*). A more detailed description can be found in Gonzalez Bernaldez et al. (1976). Seven different study sites (1-7) were chosen in this area (Fig. 1).

The deep and fertile calcareous soils of the southern zone, located in the Guadalquivir Valley (Campiña, CA), have allowed an intensive agricultural exploitation. The original vegetation has been completely removed and replaced by herbaceous crops (wheat and sunflowers) and olive groves. Only one site (8) was chosen in this area (Fig. 1).

The study area has a Mediterranean climate (Ashmann, 1973) which influences the phenology and growth rhythm of both vegetation and fauna. In the year of our field research (1986) the annual rainfall was 532.5 mm, a figure well below the long-term average annual rainfall for the area ($x = 657$ mm, $n = 21$ years).

Methods

Most of the data concerning the life-history of the species were obtained from larvae collected in the field and reared in the laboratory or hatched from eggs laid by females in insectaries (net-cages).

Different patches of *A. lusitanicus* (located in sites (1-6) were selected for field measurements. A total of 108 *A. lusitanicus* plants were randomly tagged in early February, when they were just resprouting. These plants were examined weekly; their height and number of stems, inflorescences and buds were recorded. At the end of the growing season (June), the numbers of fruits and viable seeds were also counted. To evaluate the other potential food plants for their frequencies, flowering phenology and flower availability in the first zone (SM), we established five permanent line transects, each one with six quadrats of 50×50 cm spaced at 1.50 m intervals. The number of inflorescences for each herbaceous plant species were counted in the 30 quadrats every fifteen days from February to June.

Results and Discussion

1. Use of host plants.

Since *T. ballus* uses a wide range of species belonging to Fabaceae as host plants throughout its distribution range (Jordano & Rodriguez, 1988), this butterfly can be classified as oligophagous (Slansky, 1974; Wiklund & Ahrberg, 1978; Scriber & Slansky, 1981). For example, Descimon & Nel (1986) have reported five different foodplants in the same area in SE France (*Medicago truncatulata*, *Anthyllis tetraphylla*, *Hippocrepis unisiliquosa*, *Onobrychis caput-gallii* and *Lotus ornithopodioides*).

In the Campiña area (CA) and other areas of the Guadalquivir River Valley where *A. lusitanicus* is absent, *M. polymorpha* is the host plant for *T. ballus*. This species is a common papilionaceous legume growing in ditches, river banks and abandoned olive groves. This area (CA) contains a lower number of potential host plant species than pasturelands of the Sierra Morena Mountains (SM).

All oviposition records during 1986 from the CA population were on *M. polymorpha*, despite the fact that *M. sativa* L. was also available, but less abundant. At the time of maximum butterflies density, no *M. sativa* plants with flowers or buds were found.

Eggs are laid on the leaves of *M. polymorpha* usually on the upperside (80%, $n = 24$), and in many cases on plants still without flowers. Despite the abundance of *M. polymorpha* in this zone, where it forms extensive dense patches, considerable overspread egg-laying is exhibited (distance between two successive egg-layings $x = 12.3 \pm 14.5$ m, max. = 49.5, min.

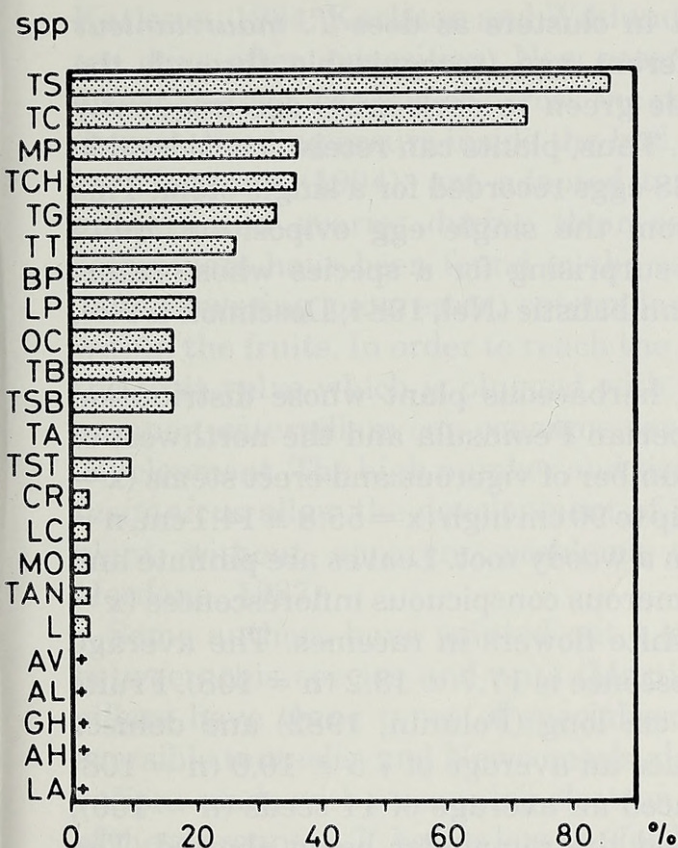


Fig. 2 Frequency of appearance (%) of potential host plants species in thero-phytic pastureland in SM. Measurement was made using thirty 50 × 50 cm quadrats in sites 1 – 3. Abbreviations: TS = *Trifolium striatum*, TC = *T. campestre*, MP = *Medicago polymorpha*, TCH = *T. cherleri*, TG = *T. glomeratum*, TT = *T. tomentosum*, BP = *Biserrula pelecynus*, LP = *Lotus parviflorus*, OC = *Ornithopus compressus*, TB = *T. bocconeii*, TSB = *T. subterraneum*, TA = *T. arvensis*, TST = *T. stellatum*, CR = *Coronilla repanda*, LC = *Lotus conimbricensis*, MO = *Medicago orbicularis*, TAN = *T. angustifolia*, L = *Lathyrus sp.*, AV = *Anthyllus vulneraria*, AH = *A. hamosus*, AL = *Astragalus lusitanicus*, GH = *Genista hirsuta* and LA = *Lupinus angustifolius*, + = species present in the study area but not in the quadrats. The last three species are perennial herbaceous or woody plants with a bushy appearance. Its quantification requires a different sampling method.

= 2, n = 15). Moreover, eggs are usually laid singly. Only one oviposition event of three eggs on a single plant and another of two eggs were observed. This isolated egg-laying pattern is consistent with the one reported by other authors (Nel, 1984; Descimon and Nel, 1986).

The colonies of *T. ballus* in Sierra Morena (SM, study sites 1-7) are restricted in host plant usage, feeding on *A. lusitanicus* despite the availability of different potential host plants (Fig. 2). In 1986, a total of 1962 eggs were counted on *A. lusitanicus* and only one on *Ornithopus compressus*.

Most eggs are laid between the buds of incipient inflorescences (91.13%, n = 1962), but females occasionally lay them on apical or mature leaves or on the main stems of plants. Several are often found on

the same inflorescence, but not in clusters as does *T. mauretanicus* (Courtney, 1983). Eggs of different age (recognizable through the variable color of them, from pale green to dark grey) are frequently found on the same inflorescence. Thus, plants can receive considerable egg loads, up to a maximum of 38 eggs recorded for a single stem. This egg-laying behaviour differs from the single egg oviposition, quite common in Lycaenidae, and is surprising for a species whose caterpillars have been described as cannibalistic (Nel, 1984; Descimon & Nel, 1986).

A. lusitanicus is a perennial herbaceous plant whose distribution includes the southwest of the Iberian Peninsula and the northwest of Africa. Plants show a variable number of vigorous and erect stems ($x = 7.0 \pm 5.02$, $n = 108$) which grow up to 90 cm high ($x = 55.8 \pm 14.1$ cm, $n = 108$). Stems resprout yearly from a woody root. Leaves are pinnate and 8-12 cm long. Stems produce numerous conspicuous inflorescences ($x = 6.5 \pm 2.0$, $n = 108$) of dense white flowers in racemes. The average number of floral buds per inflorescence is 17.7 ± 13.2 ($n = 108$). Fruits are legumes approximately 10 cm long (Polunin, 1982) and dehisce when ripening. Each stem produce an average of 7.5 ± 10.0 ($n = 108$) mature fruits. Ripe fruits produced an average of 11 seeds ($n = 100$), with only 22.4% being viable and the remainder being aborted. The appearance of *A. lusitanicus* is quite different from that of the remaining potential host plants, since all of them are procumbent small herbaceous plants.

This *Astragalus* species is toxic for livestock (Gonzalez Rodriguez, 1980) especially for sheep (Moyano, 1985) but the compound responsible of this toxicity is unknown (Infante et al., 1964; Poyato, 1968; Baraibar, 1982). Thus, plants are avoided by vertebrate herbivores (*Cervus elaphus*, *Oryctolagus cuniculus*), which clearly benefits *T. ballus* survivorship in the SM population, whereas grazing and trample may cause high mortality to larvae feeding on *M. polymorpha* in the CA population. The effects of *A. lusitanicus* allelochemicals on SM *T. ballus* population remain unassessed.

A. lusitanicus grows vigorously following particular shrub vegetation management practices (e.g. fires, plowing). On the other hand, it is scarce in areas with considerable shrub and tree cover. This fact suggests that the suitability of *A. lusitanicus* patches to *T. ballus* colonies may decrease through the years and finally disappear if additional disturbance does not occur; that is, *A. lusitanicus* is a successional or even a fugitive species.

2. Life history of *T. ballus*.

Eggs are roughly spherical with average diameter of 0.54 ± 0.01 mm ($n = 115$). The average weight is 0.0007 ± 0.0005 g ($n = 151$). Our data does not allow to establish any relationship between egg weight and female age, as happens in different satyrid butterflies (Wiklund and

Karlsson, 1984; Karlsson and Wiklund, 1985). Hatching usually occurs ten days after oviposition. New caterpillars make a hole in the bud where the egg was laid or across the petals (in the case of an unopened flower). Feeding occurs inside the bud. Caterpillars, described in detail by Chapman (1904), are adapted to an endophytic life, feeding on anthers and ovaries during their early stages. Sometimes several caterpillars have been found in the same flower.

As flowering progresses, caterpillars feed on the developing seeds within the fruits. In order to reach the seeds, they make a hole through the fruit valve which is plugged with silk from the inner side. In this manner, caterpillars can consume several fruits before finishing their development. The high number and size of inflorescences and fruits of *A. lusitanicus* allow the development of several caterpillars on the same plant without apparent problems of competition or cannibalism (Jordano, 1987).

Some authors have pointed out a possible mutualistic relationship between this species and ants (Martin Cano, 1982). *T. ballus* caterpillars have three types of specialized organs: porous cupola glands, eversible tentacles and Newcomer's gland (Martin Cano, 1982). Observations made with a scanning electron microscope confirm the presence of these organs in *T. ballus* larvae (Jordano, unpubl.). However, we have never observed any type of interactions between this species and ants in the study area. This supports the observations made by Descimon and Nel (1986). In spite of this, caterpillars and pupae introduced in artificial nests of *Cataglyphis hispanica*, a carnivorous ant species, were not attacked by the ants (Jordano, unpubl.), as happens with *Artogeia rapae* larvae.

During 1985, twenty five third and fourth instars larvae were collected in the field. Of them, 36% showed evidence of attack by parasitoids. Every parasitized larvae contained a considerable number of parasitoids ($x = 16.8 \pm 6.2$, $n = 8$) belonging to an undescribed species of a small wasp of the genus *Cotesia* (Braconidae, Microgastrinae, Cotesiini). Parasitoids killed the larvae within 4-7 days. During this time, larvae lost on the average 48.8% of their weight ($n = 9$). The endophytic habits of larvae and their specialized feeding behavior, likely provide some protection against parasitoids. The larvae are exposed to parasitoid attacks only when they have to move from one consumed flower or fruit to another.

The larvae of the wasps parasitoid come outside the caterpillars to pupate in small cocoons and imagos emerged during the same spring. Therefore they have more than one generation per year and probably are not specific to *T. ballus*.

Larval development of *T. ballus* lasts about two months in laboratory conditions with no precise light or temperature regulation ($x = 58.1 \pm 3.5$ days, $n = 18$). Males and females have development periods of similar lengths.

Caterpillars reach a maximum weight over 0.30 g (female max. weight = 0.40 g; male max. weight = 0.35 g). However, weight losses occur after reaching maximum weight during prepupal phase, during which larvae stop feeding. In the prepupal phase caterpillars leave the plant on which they have developed, searching for a place to pupate. As a result, the final weight of caterpillars before pupation is considerably lower than their maximum weight, ranging between 0.20-0.25 g (females max. final weight = 0.26 g; males max. final weight = 0.24 g). Weight loss during the prepupation phase was about 30% of maximum weight ($x = 30.4\% \pm 7.6$, $n = 12$).

Pupation occurs in the soil, generally partially buried or under stones. Pupae are brown without rugosities or maculations. We did not find any myrmicophilous or sound producing organs. In a random sample of pupae obtained in the laboratory, females were found to weigh significantly more than males (females, $x = 0.17 \pm 0.02$ g, $n = 27$; males, $x = 0.14 \pm 0.03$ g, $n = 27$; $F = 10.94$, $p < 0.01$).

Diapause occurs in the pupal stage and imagos emerge the following year. Notwithstanding, some pupae did not produce imagos, continuing in diapause and giving imagos two years later. This fact suggests that a cold exposure for interrupting diapause might be necessary, as has been reported for other species (Templado & Alvarez, 1985).

Female butterflies were larger (CVL mean = 15.85 ± 1.07 , $n = 8$; WS mean = 29.30 ± 1.60 mm, $n = 6$) than males (CVL mean = 14.38 ± 0.67 mm, $n = 9$; WS = 27.70 ± 1.32 , $n = 9$) (CVL = costal vein length, WS = wing span).

Longevity of imagos in the field has not been assessed, but it ranged between 18 and 22 days in insectaries.

Potential female fertility was approached by dissecting the abdomen of virgin butterflies just emerged from the pupae and counting their eggs and oocytes (Dunlap Pianka et al. 1977; Ehrlich & Ehrlich, 1978; Dunlap-Pianka, 1979). Values ranged between 317 and 584 eggs per female ($x = 456.2 \pm 102.0$, $n = 5$).

3. Phenology.

T. ballus is univoltine and one of the first species which can be seen every year at the study area, excluding those which spend the winter as imagos (eg. *Gonepteryx rhamni*, *G. cleopatra* and *Nymphalis polychloros*). It is on the wing from early February until the end of April, with a peak flight around mid-March. Slight between-year variations are observed, depending on weather conditions. Isolated individuals have been observed as early as the end of January and as late as May.

Data of study sites 1-3 displays the flowering phenology of the potential host-plant species living in the same zone as *A. lusitanicus* (Fig. 3). The flowering period of the latter species occurs earlier than that of the remaining ones except for *Trifolium subterraneum* (whose flowering and underground ripening characteristics excludes it as a suitable host plant).

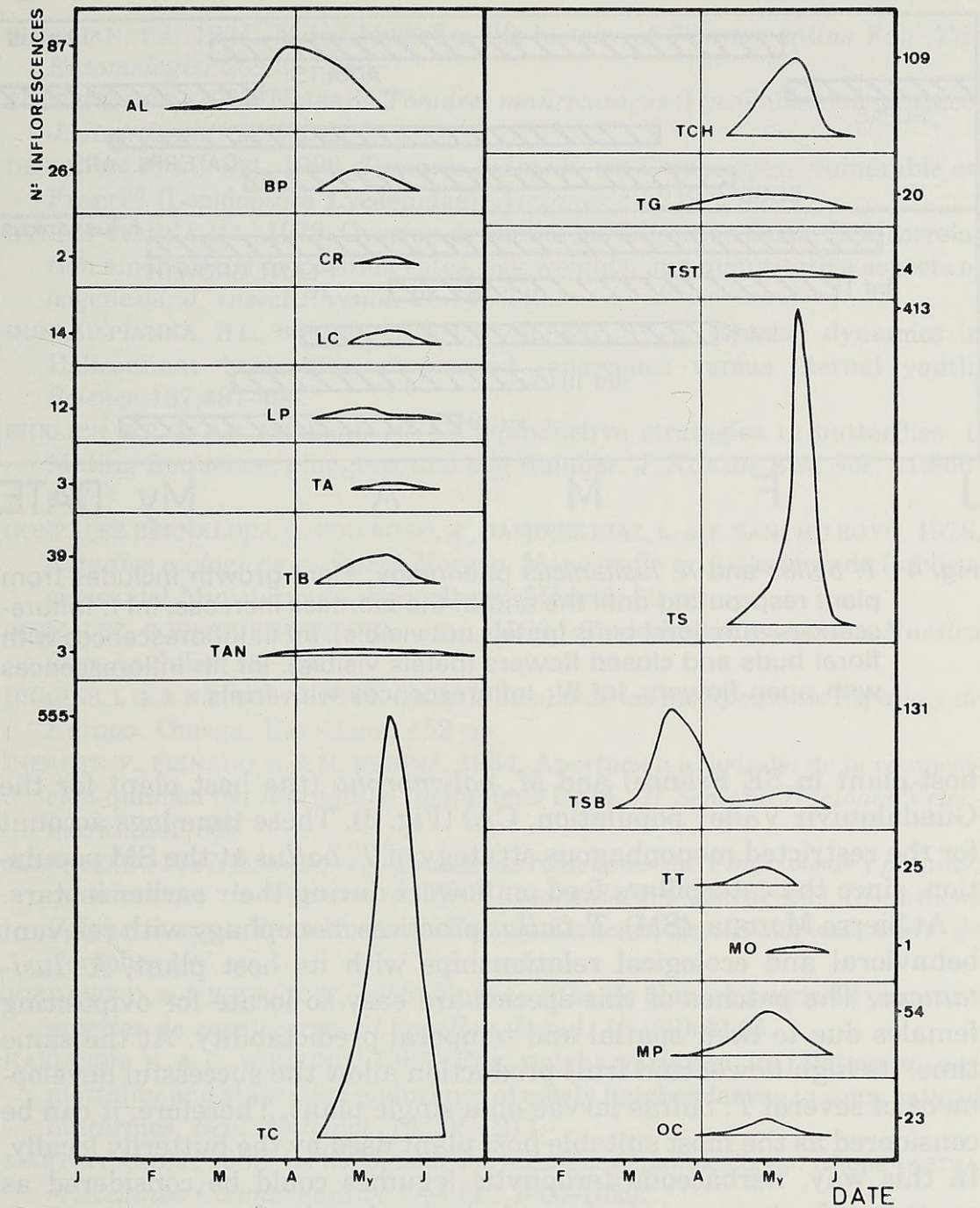


Fig. 3 Flowering phenology of potential *T. ballus* host plants (Fabaceae) growing in the study area. Inflorescences were counted in thirty 50 × 50 cm quadrats every fifteen days. The central line on the graphs show *T. ballus* egg laying peak. Notice the phenological coupling between *T. ballus* egg laying peak. Notice the phenological coupling between *T. ballus* and *A. lusitanicus* and in a lesser extent with *T. subterraneum*. Abbreviations as in Fig. 2.

Figure 4 shows the comparative phenology of *T. ballus* and of *A. lusitanicus* at the study area (SM). The flight period of *T. ballus* and, more specifically, its maximum egg laying activity, is coincident with the flowering peak of *A. lusitanicus* (Jordano, 1987), whereas the flowering peak of the remaining potential host plants occurs at least one month later (Fig. 3). This is the case of *Anthyllis tetraphylla* (the main

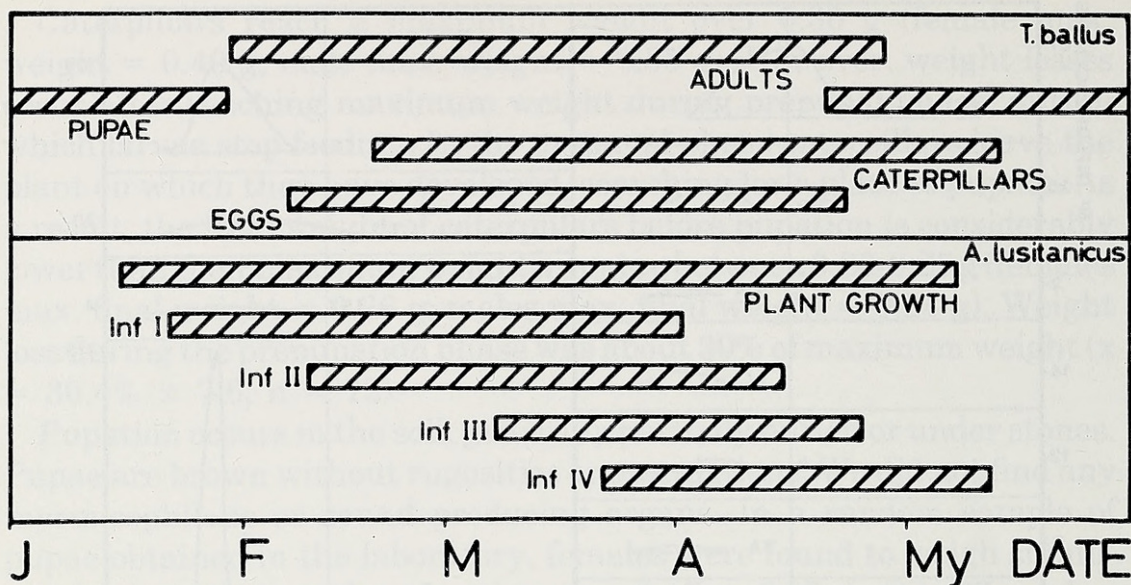


Fig. 4 *T. ballus* and *A. lusitanicus* phenology. Plant growth includes from plant resprouting until the end of the biomass increase. Inf I: Inflorescences with floral buds (petals not visible). Inf II: Inflorescences with floral buds and closed flowers (petals visible). Inf III: Inflorescences with open flowers. Inf IV: Inflorescences with fruits.

host-plant in SE France) and *M. polymorpha* (the host plant for the Guadalquivir Valley population, CA) (Fig. 3). These time lags account for the restricted monophagous strategy of *T. ballus* at the SM population, since the caterpillars feed on flowers during their earlier instars.

At Sierra Morena, (SM), *T. ballus* practices monophagy with relevant behavioral and ecological relationships with its host plant, *A. lusitanicus*. The patches of this species are easy to locate for ovipositing females due to their spatial and temporal predictability. At the same time, its high flower and fruit production allow the successful development of several *T. ballus* larvae on a single plant. Therefore, it can be considered as the most suitable host plant used by the butterfly locally. In this way, herbaceous terophytic legumes could be considered as secondary hosts in areas where *A. lusitanicus* is absent.

Acknowledgements. We wish to thank H. Descimon, A.M. Shapiro, P. Jordano and two anonymous referees for helpful suggestions on an earlier draft of this work. M. and R. Zamora provided facilities to work in "Villa Alicia". Financial support was provided by grant 3126/83 of the Caicyt to J.F.H.

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