

# Egg-laying by the butterfly *Iphiclides podalirius* (Lepidoptera, Papilionidae) on alien plants: a broadening of host range or oviposition mistakes?

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## Abstract

*Egg-laying by the butterfly Iphiclides podalirius (Lepidoptera, Papilionidae) on alien plants: a broadening of host range or oviposition mistakes?— Iphiclides podalirius is an oligophagous butterfly which feeds on plants of the Rosaceae family. In 2002 and 2005 in NE Spain, we recorded for the first time oviposition on two alien plant species, Cotoneaster franchetii and Spiraea cantoniensis. To ascertain if this unusual behaviour represents a broadening of host range or, alternatively, an oviposition mistake, larval performance on the new plants was investigated in the laboratory and compared with performance on the most common host plants used in the study area. Although larval performance on common hosts differed to some extent, the use of a wide range of plants of different quality at population level may in fact respond to the so-called "spreading of risk" strategy in variable environments. On the other hand, larval performance and survival to adulthood were so low on the two new hosts that our observations probably represent a case of maladaptive oviposition behaviour. This may be due to an evolutionary lag between the newly introduced plants and the insect, although other possible explanations are also taken into account.*

Key words: Lepidoptera, Swallowtail butterflies, *Iphiclides podalirius*, Alien plants, Host plant range, Oviposition mistakes.

## Resumen

*Ovoposición de la mariposa Iphiclides podalirius (Lepidoptera, Papilionidae) en plantas exóticas: ¿ampliación del rango de plantas nutricias utilizadas o errores de puesta?— Iphiclides podalirius es una mariposa oligófaga que se alimenta de plantas de la familia Rosaceae. En 2002 y 2005 se observó, por primera vez en el noreste de España, la puesta sobre dos plantas exóticas, Cotoneaster franchetii y Spiraea cantoniensis. Para poder discernir si este comportamiento inusual representa una ampliación del rango de las plantas nutricias utilizado o, por el contrario, se explica como un error de ovoposición, se investigó el desarrollo larvario sobre estas nuevas plantas en el laboratorio y se comparó con el desarrollo sobre las plantas nutricias más ampliamente utilizadas en la zona de estudio. Aunque se observaron diferencias significativas en el tiempo de desarrollo y el peso pupal entre las plantas nutricias habituales, la utilización de todas ellas por parte de una misma población podría responder a una estrategia de "repartir el riesgo" en un ambiente heterogéneo. Por el contrario, la supervivencia larval, el tiempo de desarrollo y el peso pupal fueron tan bajos en las dos nuevas plantas estudiadas que nuestras observaciones constituyen muy probablemente un ejemplo de comportamiento mal adaptado. Ello podría responder a la existencia de un desajuste evolutivo entre las plantas introducidas y el insecto, si bien otras posibles explicaciones son también consideradas y discutidas.*

Palabras clave: Lepidoptera, Papiliónidos, *Iphiclides podalirius*, Plantas exóticas, Plantas nutricias, Errores de ovoposición.

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## Introduction

Colonisation of new hosts by phytophagous insects has received much attention in evolutionary and ecological research, as not only is it thought to represent one of the driving forces behind speciation processes, but it may also have marked consequences for the populations of both the insects and the plants concerned (e.g. Strong et al., 1984; Feder, 1998). For butterflies in particular, many studies have focussed on the incorporation of alien plants into the butterfly's host plant range and the effects this has on aspects such as geographical or habitat range expansion (e.g. Gutiérrez & Thomas, 2000; Shapiro, 2002), population dynamics (e.g. Tabashnik, 1980; Shapiro & Masuda, 1980) and the evolution of population adaptive traits (e.g. Singer et al., 1993; Camara, 1997).

Colonisation events are almost invariably initiated by ovipositing females which have to decide whether or not a plant is acceptable as an oviposition site. For most species, this decision involves two steps: firstly, and mainly based on visual and volatile chemical cues, she has to decide whether or not to land on the potential host plant; and, secondly, once she has landed on the plant, she has to decide whether or not to oviposit on a basis of the stimulants and deterrents perceived by chemoreceptors located in the tarsi, antennae, proboscis and ovipositor (Feeny et al., 1983; Renwick & Chew, 1994). However, oviposition must be accompanied by the capacity of eggs to hatch and larvae to develop into adults on the new host plant. Observations of oviposition on new plant species must therefore be complemented by data on the development of immature stages before such behaviour can be regarded as indicative of the broadening of a butterfly's range of hosts.

The present study was motivated by field observations of egg-laying by the scarce swallowtail butterfly *Iphiclides podalirius* (L.) on two alien plants that had not been previously reported in the literature as host plants. In this paper we describe the results of laboratory rearing experiments with both the most common host plants used by this butterfly and the two potential new hosts, and discuss the implications of our findings.

## Material and methods

### Study species

*Iphiclides podalirius* is an oligophagous butterfly belonging to the family Papilionidae that feeds on woody plants of the Rosaceae family. According to Tolman & Lewington (1997), species in the genus *Prunus* (including most cultivated species) are preferred in Europe, although other trees in the genera *Pyrus*, *Crataegus*, *Sorbus* and even *Amelanchier* are also used. In Catalonia (north-east Iberian peninsula), the following are the most common host plants: blackthorn *Prunus spinosa* L., fruit trees of

the genus *Prunus* (*P. dulcis* (Miller), *P. avium* (L.), *P. domestica* L. and *P. persica* (L.)), pear tree *Pyrus communis* L. and hawthorn *Crataegus monogyna* Jacquin. More rarely, oviposition has been recorded on apple *Pyrus malus* L. and apricot trees *Prunus armeniaca* L. and, in other parts of Spain, on *Sorbus aucuparia* L. (M. L. Munguira, pers. comm.). However, data on larval development on these plants in the wild are not available.

Eggs are laid singly under the leaves of the plants mentioned above, with a predilection for those growing in hedges or in isolated stands. They hatch after one to four weeks, according to temperature. Caterpillars are highly sedentary, especially in the first instars. They spend most of their time on a silk cushion spun on the surface of the leaf selected as a resting site—normally the one on which the egg was laid—and move only to feed upon nearby leaves. Therefore, female choice when egg-laying is crucial for the subsequent survival of the larva.

*I. podalirius* overwinters in the pupal stage and is usually multivoltine in the Iberian Peninsula. The adult is highly mobile and populations have an open structure (i.e. the breeding areas have no distinct boundaries) as in many other Papilionidae (e.g. Lederhouse, 1983). Mating takes place at special sites selected by males for territorial establishment, mainly hilltops that may be far away from egg-laying sites.

### Field observations

Observations of oviposition on hitherto unrecorded plants were made at two different Catalan sites: Can Liro (Sant Pere de Vilamajor, 41° 41' 16 N 2° 23' 07 E, 310 m a.s.l.) and Montjuïc (city of Barcelona, 41° 21' 97 N 2° 09' 79 E, 95 m a.s.l.).

At Can Liro, a searching female was followed on 20 VIII 2002 until she detected a medium-sized shrub (ca. 2 m tall) of *Cotoneaster franchetii* Bois growing in isolation in a sunny hedgerow. She then engaged on a more stationary flight, carefully inspecting the outer branches before landing on one of them, curved her abdomen under the leaf and laid an egg. She immediately moved away in search of another potential host.

In the city of Barcelona, in the Parc de Petra Kelly (Montjuïc), a female was observed on 29 VIII 2002 carefully inspecting a shrub of *Spiraea cantoniensis* Lour. (ca. 2 m tall) and laying at least seven eggs on the underside of the leaves of the outer branches. In another visit three years later, on 26 VIII 2005, one additional egg and four first instar larvae were found on the same shrub. Finally, on 2 IX 2005, two first instar larvae and two eggs were also found on a small shrub (ca. 75 cm tall) of *S. cantoniensis* in Can Liro.

Both *C. franchetii* and *S. cantoniensis* are exotic shrubs of the family Rosaceae, widely used as ornamental plants in Catalan gardens and urban parks. *C. franchetii* is originally from western China and *S. cantoniensis* from eastern Asia.

### Rearing experiments

Two "common-garden" experiments were designed to compare larval growth and survival on some of the most common host plants and also on *Cotoneaster franchetii* and *Spiraea cantoniensis*. All the material used for these experiments was collected at Can Liro. In the first experiment (April–June 1998), larvae hatching from 88 naturally laid eggs on *Prunus spinosa*, *P. domestica*, *P. persica* and *Crataegus monogyna* were randomly assigned to these four host plants, and larvae were reared in an environmental chamber maintained at a constant temperature of 24°C under a photoperiod of 16L:8D. In the second experiment (April–May 2005), a total of 72 eggs were collected from the same host plants and the corresponding larvae were divided among *P. spinosa* (used as a control as a host plant known to be optimum for larval growth), *C. franchetii* and *S. cantoniensis*. Rearing took place in the same environmental chamber, under the same conditions.

In both experiments, eggs belonged to many different females and represented a good sample of the genetic diversity of the population. Eggs about to hatch were placed individually on Petri dishes lined with moist paper and with fresh supplies of the food plant. Food for the larvae was collected from plants growing wild at Can Liro. In the case of *C. franchetii*, we used the same individual on which oviposition had actually been recorded on 2002. Food plants were replaced every other day in the 1998 experiment and every day in the 2005 experiment to maintain humidity and leaf turgor. Furthermore, to prevent any chamber effect, the relative position of Petri dishes was changed every day in both experiments.

Larvae and pupae were checked daily and their performance was measured by means of three variables: survival to adulthood, development time and pupal weight (measured at the second day of the pupal stage). Wing length and sex of adult butterflies were also recorded.

Unfortunately, ovipositions on *S. cantoniensis* (recorded on three occasions) and, especially, on *C. franchetii* (recorded only once) were such rare events that we could not use eggs being laid on these alien plants in the field when performing our second rearing experiment. We were therefore unable to test to see whether possible individual variation in host-choosing tendencies (i.e. females preferring the new hosts) is correlated with physiological variation in larvae in host adaptation (but see Discussion). However, we tried to minimise this problem by collecting and rearing indoors on the same individual plant the six immature larvae found on *S. cantoniensis* in August 2005, and by comparing the outcome of this small-scale rearing experiment with the results of our second experiment. Additionally, we marked the position of the eggs from the other two oviposition events on *S. cantoniensis* and recorded their fate in the wild in subsequent visits.

### Results

#### Larval survival

Experiment 1 showed no significant differences in survival between the four common host plants ( $\chi^2 = 4.62$ ,  $df = 3$ ,  $p = 0.20$ ; fig. 1A). Survival ranged from 90.5% on *P. spinosa* to 63.6% on *C. monogyna*, with intermediate values of 77.3% and 69.6% for *P. persica* and *P. domestica*, respectively. It should be noted, however, that some of the larvae reared on *C. monogyna* produced crippled adults; given that this may be a common phenomenon in the wild, survival on *C. monogyna* may be somewhat overestimated in figure 1a. Most mortality on these common hosts occurred in the final instars, especially in the prepupal and pupal stages. One exception was *P. domestica*, on which 3 out of 7 recorded losses corresponded to the first instar larvae.

In contrast with the previous results, we found striking differences in survival to adulthood between the common host plant *P. spinosa* and the two new tested plants ( $\chi^2 = 59.15$ ,  $df = 2$ ,  $p < 0.001$ ; fig. 1B). Survival was nearly 100% on *P. spinosa*: all 22 larvae used in the experiment pupated successfully and only one pupa died. On the contrary, only 2 out of 25 larvae reached adulthood when reared on *C. franchetii* and none survived on *S. cantoniensis*. Most mortality on the new hosts occurred in the first instar: 100% on *S. cantoniensis* and 84% on *C. franchetii*. Of the four larvae that moulted successfully to the second instar on *C. franchetii*, two died in both the fourth and fifth instars.

#### Development time

Although males tend to develop faster than females (C. Stefanescu & J. Jubany, unpubl. data; see also Lederhouse et al., 1982), a significant difference for total development time (in days) was only found between males and females reared on *P. domestica*; therefore, we decided to pool the data for both sexes in subsequent analyses.

Development time differed strongly between the four common hosts ( $F = 35.79$ ,  $df = 3.61$ ,  $p < 0.001$ ; fig. 2A). However, most of this variation was accounted for by the lower development rate on *C. monogyna*, which was roughly 80% of that recorded on the other three hosts (which showed no significant differences in Tukey *post-hoc* multiple comparisons). On *Prunus* species, development time to adulthood ranged from 41.3 to 44 days, while on *C. monogyna* lasted 53.3 days.

Unexpectedly, development time on *P. spinosa* was shorter in the second experiment than in the first experiment (36.3 days vs. 43.1 days;  $t$ -test = 6.54,  $df = 38$ ,  $p < 0.001$ ). Perhaps this was due to the fact that the food was replaced every day instead of every other day in the second experiment, thus being overall of better quality. Moreover, the rearing experiment in 2005 took place towards the

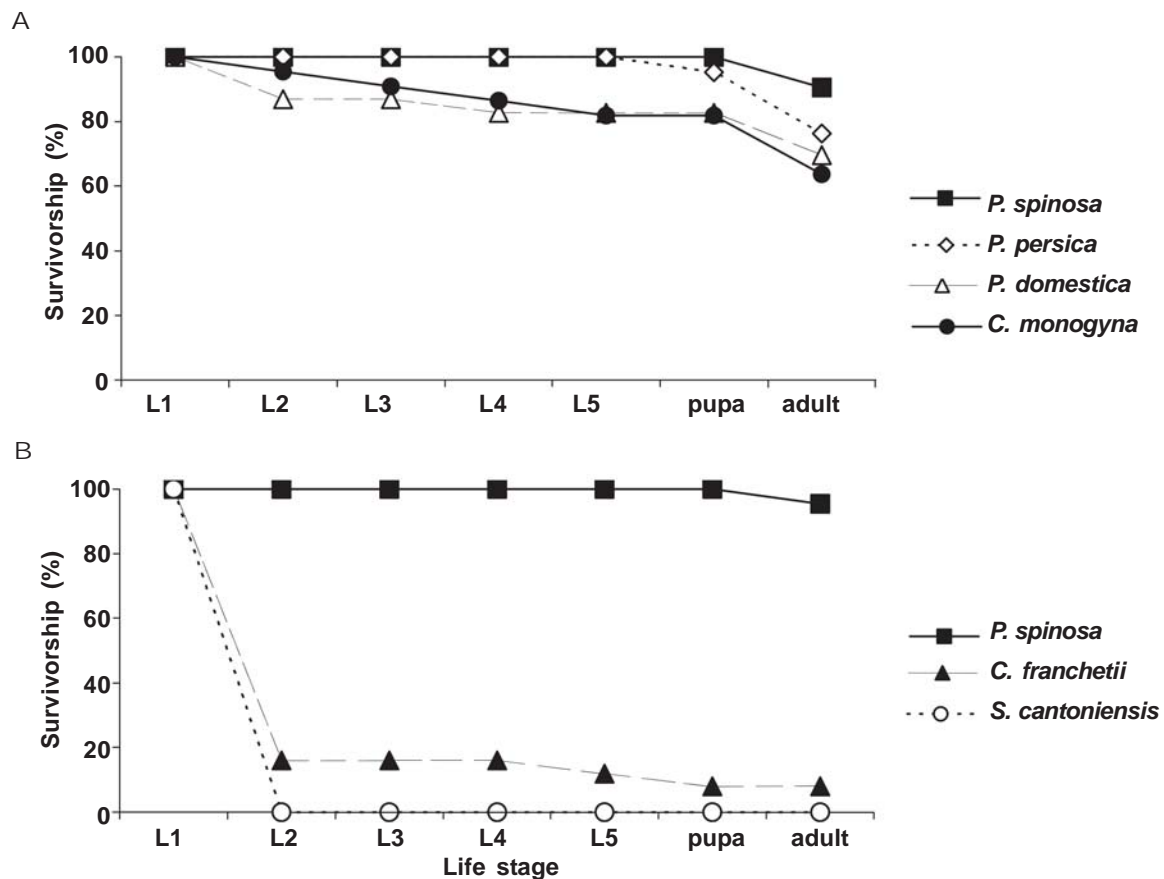


Fig. 1. Survivorship curves of *Iphiclides podalirius* when reared: A. On the four common hosts *Prunus spinosa* ( $n = 21$ ), *P. domestica* ( $n = 23$ ), *P. persica* ( $n = 22$ ) and *Crataegus monogyna* ( $n = 22$ ) (experiment 1); and B. On *Prunus spinosa* ( $n = 22$ ) and on the two new plants *Cotoneaster franchetii* ( $n = 25$ ) and *Spiraea cantoniensis* ( $n = 25$ ) on which oviposition was recorded in the wild (experiment 2). Symbols show the percentage of individuals alive at the beginning of each stage.

Fig. 1. Curvas de supervivencia para *Iphiclides podalirius* criado: A. Sobre cuatro plantas nutricias comunes *Prunus spinosa* ( $n = 21$ ), *P. domestica* ( $n = 23$ ), *P. persica* ( $n = 22$ ) y *Crataegus monogyna* ( $n = 22$ ) (experimento 1); B. Sobre *Prunus spinosa* ( $n = 22$ ) y dos plantas nuevas *Cotoneaster franchetii* ( $n = 25$ ) y *Spiraea cantoniensis* ( $n = 25$ ), cuya ovoposición tuvo lugar en la naturaleza (experimento 2). Los símbolos representan el porcentaje de individuos vivos al inicio de cada fase.

beginning of the season and so the leaves of *P. spinosa* might have been in better condition than in 1998.

Most importantly, the second experiment showed that larvae reared on *C. franchetii* developed at a much lower rate than those reared on *P. spinosa* (fig. 2B). Thus, total development time to adulthood was almost twice as long for *C. franchetii* (65 days for *C. franchetii* vs. 36.3 days for *P. spinosa*;  $t$ -test = 13.03,  $df = 21$ ,  $p < 0.001$ ). These differences were observed in all the developmental stages except for the pupal stage (although only two pupae survived on *C. franchetii*), which lasted about the same for both hosts ( $t$ -test = 1.19,  $df = 21$ ,  $p = 0.25$ ; fig. 2B).

#### Pupal weight

Given that *I. podalirius* males are regularly smaller in size and weight than females (as confirmed by highly significant  $t$ -tests in pair-wise comparisons for all hosts), pupal weights were analysed separately for both sexes.

Experiment 1 showed a significant effect of host in pupal weight for both males ( $F = 5.31$ ,  $df = 3,32$ ,  $p < 0.004$ ; fig. 3) and females ( $F = 3.45$ ,  $df = 3,32$ ,  $p < 0.03$ ; fig. 3). In general, larvae reared on *P. domestica* and, especially, on *P. persica* produced heavier pupae than those reared on *P. spinosa* and *C. monogyna*. Multiple comparisons indicated that, in females, the mass achieved on *P. spinosa* was

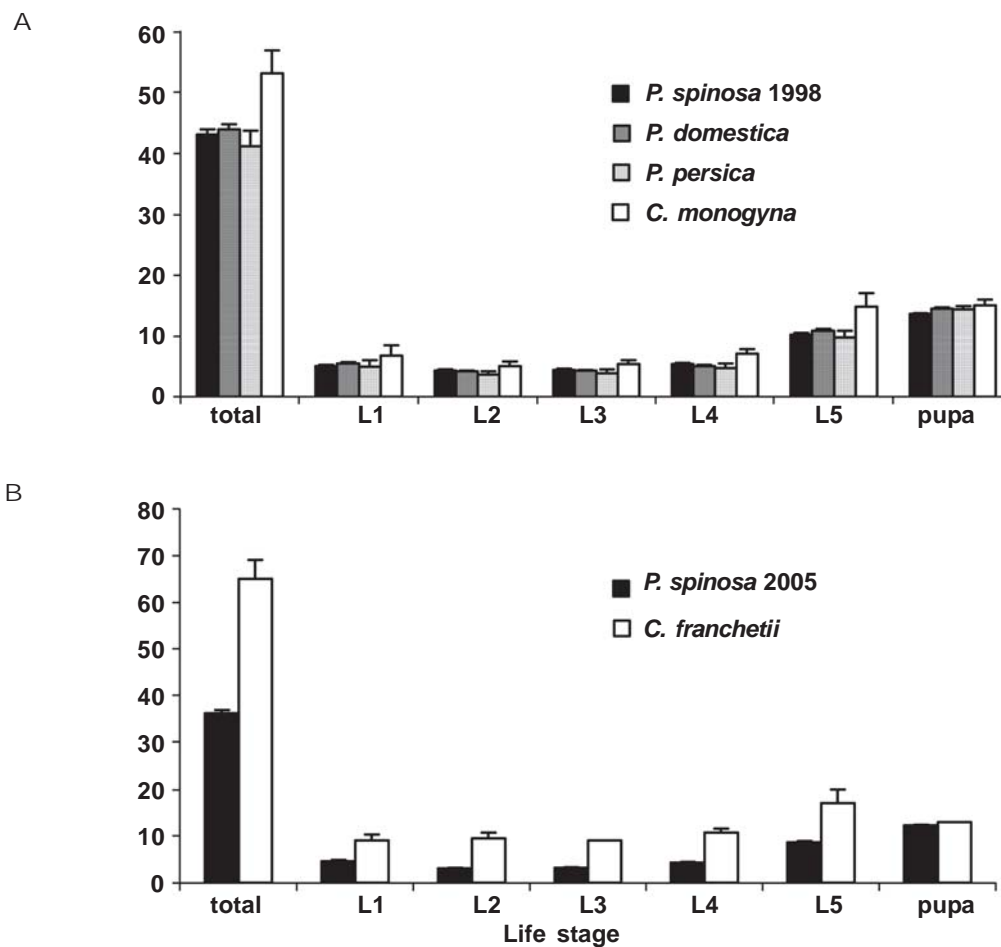


Fig. 2. Mean values ( $\pm$  SE) of total development time (from egg hatching to adult eclosion) and development time for each larval instar and the pupal stage: A. On the four common hosts *Prunus spinosa*, *P. domestica*, *P. persica* and *Crataegus monogyna* (experiment 1); B. On *P. spinosa* and *C. franchetii* (experiment 2). Sample sizes in experiment 1: *P. spinosa*,  $n = 21$  for L1–L5,  $n = 19$  for pupa and total; *P. domestica*:  $n = 19$ – $20$  for L1–L5,  $n = 16$  for pupa and total; *P. persica*:  $n = 20$ – $21$  for L1–L5,  $n = 16$ – $17$  for pupa and total; *C. monogyna*:  $n = 18$ – $21$  for L1–L5,  $n = 14$  for pupa and total. Experiment 2: *P. spinosa*:  $n = 22$  for L1–L5,  $n = 21$  for pupa and total; *C. franchetii*:  $n = 4$  for L1–L3,  $n = 3$  for L4,  $n = 2$  for L5, pupa and total.

Fig. 2. Valores medios ( $\pm$  EE) del tiempo total de desarrollo (desde la eclosión del huevo hasta la eclosión del adulto) y tiempo de desarrollo para cada fase larvaria y la de pupa: A. Sobre las cuatro plantas nutricias comunes *Prunus spinosa*, *P. domestica*, *P. persica* y *Crataegus monogyna* (experimento 1); B. Sobre *P. spinosa* y *C. franchetii* (experimento 2). Tamaños de la muestra en el experimento 1: *P. spinosa*:  $n = 21$  para L1–L5 y  $n = 19$  para pupa y total; *P. domestica*:  $n = 19$ – $20$  para L1–L5,  $n = 16$  para pupa y total; *P. persica*:  $n = 20$ – $21$  para L1–L5,  $n = 16$ – $17$  para pupa y total; *C. monogyna*:  $n = 18$ – $21$  para L1–L5,  $n = 14$  para pupa y total. Experimento 2: *P. spinosa*:  $n = 22$  para L1–L5,  $n = 21$  para pupa y total; *C. franchetii*:  $n = 4$  para L1–L3,  $n = 3$  para L4,  $n = 2$  para L5, pupa y total.

significantly lower than on the other three hosts, while in males it was lower on *C. monogyna* and *P. spinosa* than on *P. persica*.

There were no differences in pupal mass on *P. spinosa* between experiments 1 and 2. On the other hand, pupal weights of the only two males

that survived on *C. franchetii* (0.54 and 0.64 g) were much lower than those values recorded on *P. spinosa* (fig. 3). Despite the very small sample size, a pair-wise comparison indicated that the observed difference cannot be explained by chance ( $t$ -test = 3.24,  $df = 8$ ,  $p = 0.012$ ).

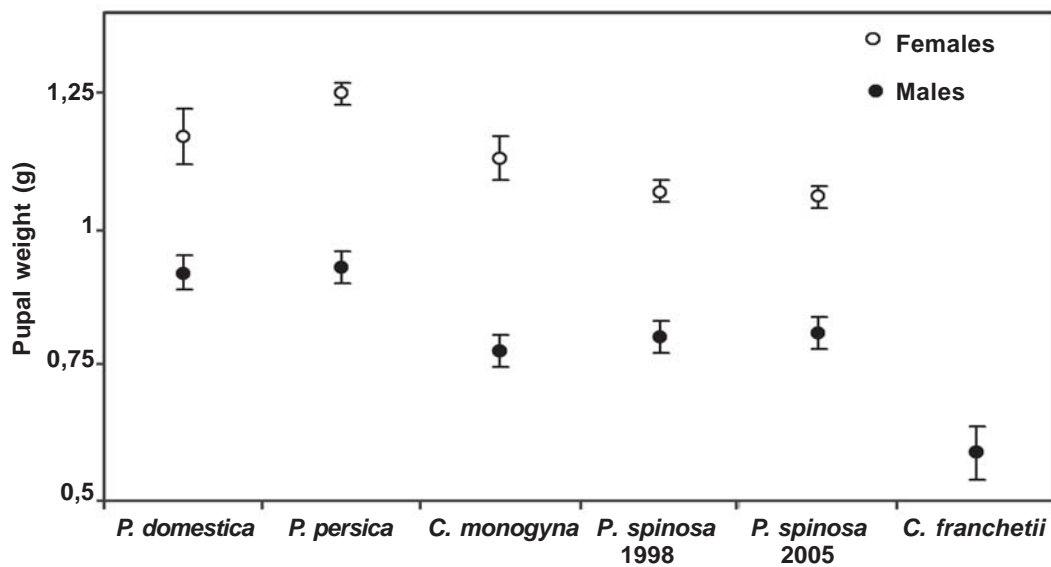


Fig. 3. Pupal weights ( $\pm$  SE) of males and females reared on the four common hosts *Prunus spinosa* (data shown for experiments 1 and 2), *P. domestica*, *P. persica* and *Crataegus monogyna*, and the alien plant *Cotoneaster franchetii*.

Fig. 3. Pesos de las pupas ( $\pm$  EE) de los machos y las hembras criados sobre las cuatro plantas nutricias *Prunus spinosa* (se incluyen los datos para los experimentos 1 y 2), *P. domestica*, *P. persica* y *Crataegus monogyna*, y la planta exótica *Cotoneaster franchetii*.

## Discussion

*Iphiclides podalirius* is an oligophagous species, feeding on a wide range of plants belonging to the Rosaceae family. The diversity of host plants used by *I. podalirius* is maintained at a local scale, in what Wiklund & Ahrberg (1978) have termed a polyphagic strategy within the species' oligophagy. This strategy might seem somewhat puzzling in view of the findings of our laboratory experiment, showing significant differences in larval performance between some of the most commonly used hosts. Thus, it is apparent that *Crataegus monogyna* is a poorer host than *Prunus spinosa*, *P. domestica* and *P. persica* and larvae feeding on this plant tended to have lower survival rates, to develop at a slower rate and to produce generally smaller pupae. On the other hand, host quality was similar in the three *Prunus* species. Although females achieved lower pupal weights on *P. spinosa* than on *P. persica* and *P. domestica*, the predictable loss of adult fecundity (e.g. Hinton, 1981, but see Leather, 1988) might be compensated by the highest survival to adulthood recorded on the former host.

It is possible that there exists a correlation between the host plant preference of ovipositing females and larval physiological variation in host adaptation that went unnoticed in our "common garden" experiment. However, this seems unlikely in a species that uses a variety of hosts

sympatrically and shows an open population structure and a non-resource mating system (i.e. hill-topping behaviour). Under this scenario, gene flow among individuals using different hosts is predictably too high to allow a host-associated differentiation within a population. Moreover, although experiments on oviposition preference have not yet been conducted (and thus no hierarchy of oviposition preference has been established; cf. Wiklund, 1981; Thompson, 1993), direct observations of egg-laying females in the wild seem to indicate that thresholds of acceptance of alternative plants are usually very low (C. Stefanescu, pers. obs.). For instance, consecutive oviposition events of individual females on two or three different hosts growing side by side in the same hedgerow are a common phenomenon.

We believe that the most plausible scenario to account for the use of a wide range of hosts of different quality at a local scale is provided by the so-called "spreading of risk" strategy in variable environments (Den Boer, 1968). In particular, considering that immature stages are subject to extremely high mortality rates due to predation and parasitism (Stefanescu, 1999, 2000; Stefanescu et al., 2003; see also Feeny et al., 1985), we suggest that females may achieve a greater success by ovipositing on many different plants, even if they are poor hosts.

This rather generalist behaviour may help to explain the recent incorporation of the American native *Prunus serotina* in the host diet of a German population of *I. podalirius* (Landeck et al., 2000) and also our observations of egg-laying on the two alien plants *C. franchetii* and *S. cantoniensis*. However, larval performance on these two latter hosts was so low that we might ask if our observations do not represent, in fact, a case of maladaptive oviposition behaviour. Although survival to adulthood was recorded on *C. franchetii*, larval performance was extremely poor on this plant, at least when compared with that on a wide range of common hosts. Moreover, our rearing experiment seemed to indicate that *S. cantoniensis* is toxic to larvae, which invariably die in their first instar when feeding on this plant. This seems to be corroborated by the fact that not a single larva was found alive one week later in a careful inspection of the plants on which oviposition was naturally recorded in 2002 and 2005, and also by the death during their first instar—as occurred in all 25 larvae from our second experiment—of all five larvae collected on *S. cantoniensis* in 2005 and reared indoors. In light of these results, egg-laying on *S. cantoniensis* may be considered one more example to add to the list of oviposition mistakes documented in the literature (e.g. Chew, 1977; Larsson & Ekblom, 1995; Graves & Shapiro, 2003).

Many authors have discussed the apparent paradox of oviposition on non-hosts or on hosts that confer very poor offspring fitness (e.g. Courtney, 1982; Thompson, 1988; Mayhew, 1997; Nylin et al., 2000). In the context of the present study, a likely explanation is that an evolutionary lag exists between the newly introduced plants and the local insect. Indeed, because of the increasing spread of exotic plants throughout most of the world's ecosystems, this has become a fairly common phenomenon (e.g. Graves & Shapiro, 2003). Given enough time, however, it is expected that the use of toxic or very poor host plants (such as *S. cantoniensis* and *C. franchetii*, respectively) will disappear as a result of natural selection: if oviposition preference responds primarily to selection, then the plants will be excluded from the diet; if the first-responding trait is larval performance, then the plants will be incorporated into the insect's diet (Singer, 2003). As commented above however, in the case of *I. podalirius* gene flow between populations is so strong that it makes the existence of local adaptations, for example towards particular hosts, highly unlikely.

There are of course, other possible (not necessarily exclusive) explanations accounting for our observations. For example, low specificity in the oviposition preference hierarchy—as seems to be the case at least in some females of *I. podalirius* (see above)—may facilitate oviposition on low-ranked host plants or even lethal plants in the absence of the preferred hosts (cf. Wiklund, 1981). This may be particularly likely in secondary habitats, such as urban areas and gardens, where

common host plants are scarce or non-existent and have been replaced by alien, but still phylogenetically related and chemically similar, plants. Although our observations in the city of Barcelona fit this scenario very well, oviposition on *S. cantoniensis* and *C. franchetii* in Can Liro, where preferred host plants are very abundant and commonly used by *I. podalirius*, points to some other explanation. In the case of *C. franchetii*, at least, it may be argued that the pressure to 'spread the risk' could be so strong as to favour oviposition on such a poor host. Future field experiments would enable us to test this hypothesis and help to elucidate whether this alien plant can be regarded as a true host for *I. podalirius* or not.

In a more general context, we believe that observations such as the ones reported here are of great interest in the study of the evolution of insects' host range and add further data to the increasingly important phenomenon of colonisation of newly introduced plants by local fauna (cf. Strong et al., 1984; Nylin & Janz, 1999).

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