

Bird predation on cryptic larvae and pupae of a swallowtail butterfly

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*Cryptic coloration in Lepidopteran larvae and pupae has presumably evolved because of a selective pressure exerted by accurate visual predators, most likely birds. To what extent birds are primary predators of swallowtail butterflies (Papilionidae) is, however, a controversial subject. Experimental work has shown that birds ignore or reject unpalatable larvae with warning colours, but their impact on those species with cryptic larvae is still largely unknown. In a study of the population ecology of the Scarce Swallowtail butterfly *Iphiclides podalirius*, predation of larvae and pupae by the Great Tit *Parus major* was recorded on several occasions. Direct observations, together with indirect evidence, indicate that the impact of this bird on the butterfly population was very important and, on an evolutionary timescale, may have represented a strong selective pressure favouring the cryptic coloration of larvae and pupae. Moreover, the data presented conclusively demonstrate the total ineffectiveness of the larval osmaterium as a defence mechanism against predation by the Great Tit.*

Key words: Great Tit, *Parus major*, Scarce Swallowtail butterfly, *Iphiclides podalirius*, predation, NE Spain

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INTRODUCTION

Butterfly larvae and pupae are often subject to very heavy mortality as a result of parasitism and predation by both invertebrates and vertebrates (e.g. Warren 1992). Swallowtail butterflies (family Papilionidae), in particular, have been the subject of several detailed

studies aimed at determining their main predators (Feeny *et al.* 1985, Scriber *et al.* 1995). Available information shows that birds are indeed important predators of the pupal stage (West & Hazel 1982) and it has even been hypothesised that green pupae evolved from the ancestral brown condition as a result of the natural selection imposed

by visual predation by birds (Hazel & West 1996).

Evidence of the impact of birds on larvae is, however, somewhat contradictory. For example, Dempster *et al.* (1976) investigated the population biology of the European Swallowtail butterfly *Papilio machaon* in England, and were able to record the Reed Bunting *Emberiza schoeniclus*, Sedge Warbler *Acrocephalus schoenobaenus* and Bearded Tit *Panurus biarmicus* taking larvae, but no further details were given by these authors. However, in a set of experimental studies involving the same butterfly, wild-caught Great Tits *Parus major* and hand-raised Blue Tits *Parus caeruleus* and Quails *Coturnix coturnix*, Wiklund and co-workers found that almost all larvae were ignored or immediately released after being seized in the bill by the birds (Järvi *et al.* 1981, Wiklund & Järvi 1982, Wiklund & Sillén-Tullberg 1985). These authors concluded that the larvae of *P. machaon* were unpalatable, and suggested that their distasteful substances lie in the outer parts of the body, thereby enabling them to survive tasting by predators without any further injury. Moreover, the coloration of later instars of this species consists of a striking combination of green with black stripes interrupted with red spots, hence larvae display a typical aposematic pattern (Bowers 1993).

In contrast to *P. machaon*, the larvae of a number of other swallowtail butterflies are extremely cryptic on their hostplants. Heinrich (1993) suggested that both the impressive patterns of camouflage and the activity patterns in cryptic (and palatable) Lepidopteran larvae have evolved because of a selective pressure exerted by accurate visual predators, most likely birds. Indeed, many field studies centred on tits (Paridae) indicate not only that they take huge numbers of caterpillars, especially during the breed-

ing season (e.g. Gibb 1955, Cowie & Hinsley 1988, Blondel *et al.* 1991), but also that their breeding success seems to correlate with caterpillar abundance (e.g. Perrins 1991, Seki & Takano 1998). In addition, enclosure experiments have shown the negative effect of bird predation on caterpillar density in control plots (e.g. Holmes *et al.* 1979, Attegrim 1989). Moreover, although caterpillars face a vast array of invertebrate enemies (e.g. predatory wasps and parasitoids), many of these display very little visual discrimination and rely mainly on scent to locate their prey (Heinrich 1993). Therefore, according to Heinrich's hypothesis, birds should have been important potential predators of cryptic swallowtail larvae.

From 1996 to 1999, in NE Spain, an investigation was undertaken into the population ecology of immature stages of the Scarce Swallowtail butterfly *Iphiclides podalirius*, a species with cryptic larvae and pupae. In this paper I report a study designed to quantify the impact of bird predation on larvae and pupae and interpret the results in the context of Heinrich's hypothesis, as a complement of a general study focused on invertebrate predators and parasitoids on the butterfly population (Stefanescu *et al.* in press).

MATERIAL AND METHODS

Study species

Iphiclides podalirius is a swallowtail butterfly widespread in the Palaearctic region. It feeds on different woody plants belonging to the family Rosaceae, notably blackthorn *Prunus spinosa*, fruit trees of the genus *Prunus*, and hawthorn *Crataegus monogyna* (Tolman & Lewington 1997). In NE Spain, the species is partially trivoltine. Adults of the first generation appear from pupae which

have overwintered and emerge in early spring; butterflies of the second and partial third generation fly from the end of June to the beginning of September. Eggs are laid singly on hostplants, with a predilection for those growing in hedgerows.

The caterpillars are highly sedentary: they live on a silk cushion on the upper surface of a leaf selected as a resting site, and only move to feed upon nearby leaves. First instar larvae are black with two transversal white marks, a common pattern in most swallowtail butterflies, often interpreted as a bird-dropping mimesis (Edmunds 1974). Next instars are green with yellow stripes and constitute an excellent example of cryptic larvae on their hostplants. At the end of their development, after three to six weeks, larvae can measure up to 5 cm and weigh as much as 1.5 g, and they may use small twigs instead of leaves as resting sites.

Caterpillars from the first generation, as well as those from the second generation that develop directly into a third generation, usually pupate on the host plant, and green pupae are well hidden among branches and foliage. Caterpillars of the third generation and those of the second generation with no direct development always leave their host plant and become brown pupae, which hibernate hidden among ground vegetation (usually amongst dry grasses). Pupation behaviour has been studied in detail over the last five years and shows a remarkably stable pattern. Whether pupation occurs on the hostplant or among the litter, larvae entering the prepupal stage begin a wandering phase in search of a pupation site mostly at 10-12 a.m. (57.6% observations, $n = 92$); the initial time of the wandering phase has never been recorded before 9 a.m. and in under 15% of cases before 10 a.m. (Stefanescu *in prep.*). Therefore, disappearance of mature larvae from the

monitored hostplants before 9 a.m. was attributed to predation.

Study system

The study was carried out in Can Liro (Sant Pere de Vilamajor, 41°41'16''N 2°23'07''E, 310 m a.s.l., NE Spain), an agricultural area surrounded by evergreen holm oak *Quercus ilex* forest, in the lower sections of the Montseny hills.

Most observations were performed, in June-July 1999, at a hedgerow consisting of 14 small blackthorns with heights ranging from 35 cm to 65 cm (hereafter referred to as Hedgerow 2, following Stefanescu *et al. in press*). These were young shoots resulting from the cutting, in February 1999, of a dense old blackthorn hedge. Following very high levels of oviposition by first generation butterflies, the locations of all eggs or larvae found were marked with plastic tags, and were periodically revised. In the period 2-25 June, larvae were checked twice daily: in the early morning, at 7:00-9:00 a.m., and just before night, at 9:00-10:00 p.m. Thus it was possible to record the disappearance of several mature larvae in the early morning that had still been present the evening before; because wasps and other diurnal invertebrate predators are largely inactive until the heat of the morning builds up, bird predation was considered to be the probable cause of these disappearances. To confirm this assumption, regular observations of birds foraging in the hedgerow were undertaken on 12, 24, 28 June and 6 July. From a vantage point, birds were observed with binoculars at 6:30-7:30 a.m., coinciding with the period of their greatest activity shortly after dawn.

In addition, a number of green direct-developing pupae were artificially manipulated in an experiment aimed at determining the main pupal predators.

Twelve pupae were placed in naturally simulated positions on the hostplants, or released as old larvae that had been kept inside protective sleeves—as a defence against predators—until their development was completed, and then allowed to select a pupation site. The fate of these pupae was recorded, as well as the approximate time of disappearance, if they were subject to predation.

A few other data were obtained in another hedgerow consisting of four blackthorn bushes, two peach trees and a hawthorn growing between two fields (henceforth referred to as Hedgerow 1). Their height ranges were 180-200 cm (trees) and 50-215 cm (bushes).

Circumstantial observations also suggested that birds could be important predators of overwintering pupae. In order to improve further on this information, during the winters of 1997-98 and 1998-99 birds foraging in Hedgerow 1 and in an adjacent alfalfa field *Medicago sativa* harbouring overwintering pupae were observed with binoculars for variable periods from inside a house, on 30 occasions. Birds were grouped into three classes according to the regularity of their appearance in censuses: regular foragers (>50% of censuses), common foragers (10-50% of censuses) and occasional foragers (<10% of censuses).

RESULTS

Larval predation

In June 1999, altogether 59 larvae were monitored in Hedgerow 2 (Fig. 1). Later stages (i.e. larvae of instars 4-5, the most likely to be preyed upon by birds) increased steadily until 10 June (Fig. 1a), when five 4- and six 5-instar larvae were recorded on the hostplants at 10:00 p.m. On 11 June, however, two 5-instar larvae had disappeared before 7:30 a.m. and

between 9:30 and 10:00 a.m., respectively. A third larva left the hostplant to pupate at 1:00 p.m.

On 12 June, at 8:00 a.m., three 4- and one 5-instar larvae from a total of five old larvae that were present on a small blackthorn the evening before had already disappeared. Indirect evidence of predation was provided by the presence of a blot of body fluids of the 5-instar caterpillar at its resting site on the twig. A few minutes later, a Great Tit was seen arriving at the hedgerow, directly alighting on the blackthorn, hopping a couple of times on the branches, capturing the single 4-instar larva that still remained and flying away with the larva in its bill. At 9:00 a.m. a Great Tit appeared again. The bird hopped around on a couple of shoots before hopping to a third blackthorn, where it found a 5-instar caterpillar, gripped it with its bill, and flew away. Observations stopped at this point, but during the day the only two 4- and 5-instar larvae still present in the hedgerow disappeared, presumably as a result of Great Tit predation.

The disappearance of six 2- and four 3-instar larvae was recorded on 14 June (Fig. 1a). This represented a significant increase in the proportion of losses of young larvae vs. young larvae alive, with respect to what was recorded in each of the previous five 2-day periods, in which the mortality of young larvae had remained unchanged (2-12 June: $G = 1.8$, d.f. = 4, $p > 0.7$; 2-14 June: $G = 13.9$, d.f. = 5, $p = 0.016$). Although no direct observations were available on 14 June, these results suggest that young larvae could have been captured by the Great Tit once older ones were no longer available.

Moderate numbers of larvae were still present by mid-June (Fig. 1b); because most 3-instar larvae were moulting to the fourth instar, old larvae again became increasingly common. Until 24 June, dis-

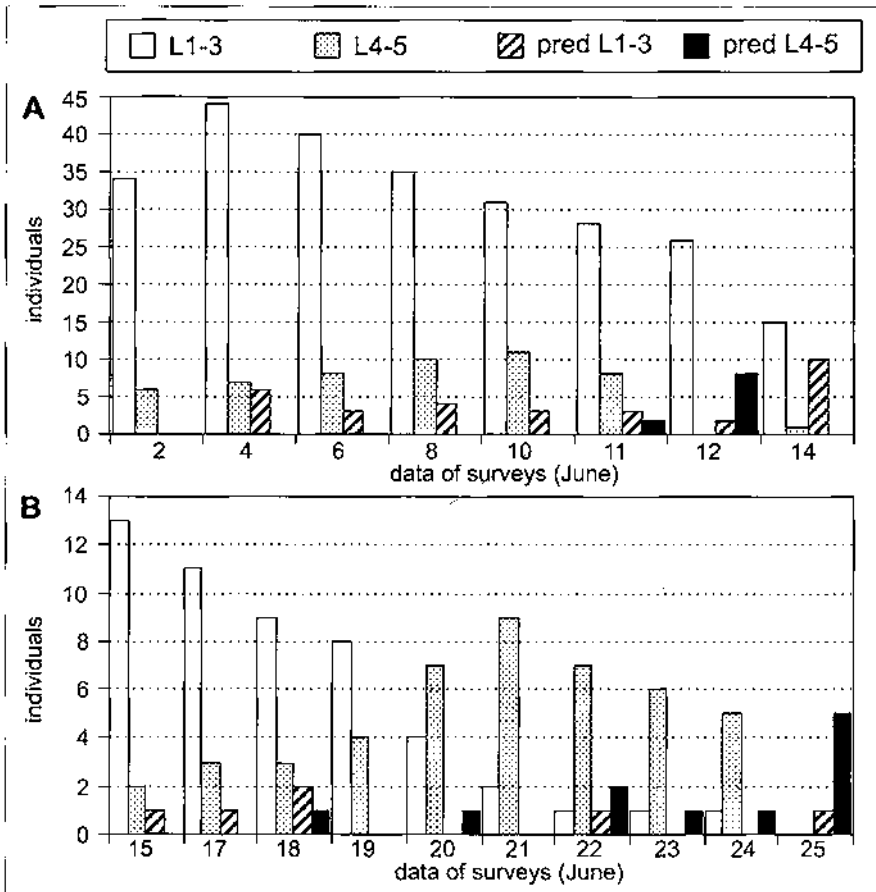


Figure 1. Young (instars 1-3) and old (instars 4-5) larvae of *Iphiclides podalirius* present on blackthorns in Hedgerow 2 in (A) 2-14 June 1999, and (B) 15-25 June 1999, and losses (attributed to predation) recorded during the same periods. For a given date, "L1-3" and "L4-5" refer to the larvae present in the early morning count, and "pred L1-3" and "pred L4-5" to the larvae recorded as lost though still present in the previous count (usually carried out at 9:00-10:00 p.m. of the previous evening). Note that the sum of young and old larvae present on a given date plus the ones that have disappeared since the previous count does not necessarily correspond to the exact number of larvae recorded on the preceding date, because of the appearance of some new first instar larvae when hatching from the eggs.

Figura 1. Larves joves (estadis 1-3) i adultes (estadis 4-5) d'Iphiclides podalirius presents als aranyoners del marge 2 al (A) 2-14 juny de 1999, i (B) 15-25 juny de 1999, i baixes (atribuïbles a depredació) enregistrades durant aquests períodes. Per a una data determinada, "L1-3" i "L4-5" es refereix al nombre de larves presents durant el comptatge realitzat al matí, i "pred L1-3" i "pred L4-5" a les larves desaparegudes però encara presents en el comptatge anterior (que normalment es feia a les 9:00-10:00 h de la nit anterior). Noteu que, per a una data determinada, la suma de larves joves i adultes presents més les que van desaparèixer des del comptatge anterior no necessàriament es correspon amb el número exacte de larves presents en la data anterior, a causa de l'aparició de larves de primer estadi a mesura que aquestes anaven eclosionant de l'ou.

appearance was recorded in a few cases but no direct observations were made. On that day, a Great Tit arrived in the hedgerow at 6:52 a.m. and began a careful exploration of several shoots. At 6:55 a.m. the single 5-instar larva present at the time was detected and captured. The Great Tit flew away to a nearby tree, hammered the larva several times against a branch while holding it in its bill-tip (as described in Gosler 1993, p. 40), and ate it in 2-3 minutes. Immediately after this, on a second visit, a prepupa artificially positioned the day before was found and captured. As before, the prey was eaten on a nearby tree. Observations stopped at this point. On the following day, at 7 a.m., all larvae (one 3-instar plus five 4-instar) had disappeared (Fig. 1b).

In summary, all but one of the 59 larvae monitored in Hedgerow 2 were, almost certainly, preyed upon before reaching the pupal stage. Almost all (>85%) of the 21 larvae predated as 4- or 5-instars disappeared between 9:00 p.m. and early morning (i.e. before the start of any activity of potential invertebrate predators of old larvae). On the other hand, based on additional observations during the course of the four-year study, it is assumed that a large proportion of the 37 larvae that disappeared in 1- to 3-instars were taken by predators other than the Great Tit (e.g. ants, spiders, earwigs, coccinellid larvae, etc.). However, the sudden increase of mortality experienced by young larvae on 14 June may also be a consequence of a change in the foraging behaviour of the Great Tit (see Discussion).

Pupal predation (green direct-developing pupae)

The first observation of a bird preying on a green pupa naturally occurring on a

hostplant was made on 14 June. A Great Tit arrived in Hedgerow 1 at 10:30 a.m., hopped to a blackthorn and quickly found and seized the single pupa that was there. Immediately, the bird flew away with the pupa in its bill. No remains were found other than the broken silken girdle that had attached the pupa to the substrate.

Further observations were made in the course of the experimental work involving pupae artificially placed in Hedgerow 2 between 17 June and 9 July. All 12 pupae quickly disappeared (elapsed time before disappearance: 2.54 ± 2.18 days, range: 0-7), probably as a result of systematic predation by the Great Tit. The first five pupae were glued to slender twigs, well camouflaged against leaves between 17-22 June, and all were recorded as lost on 23 June at 10:00 a.m. A prepupa that was placed under a leaf on the evening of this same day was preyed upon by a Great Tit at 7:00 a.m. on 24 June (see "Larval predation").

Though no pupae nor larvae were present in Hedgerow 2, on 28 June observations from the vantage point were resumed. In the period 6:45-7:05 a.m., two Great Tits were seen searching very thoroughly through three blackthorns and a peach tree in Hedgerow 1, without finding the only naturally occurring pupa.

On 3 and 4 July three more pupae were placed in Hedgerow 2. Because they were still alive on 5 July at 10:00 p.m., observations were repeated on 6 July and predation by a Great Tit was recorded again. The bird arrived at 6:45 a.m. and inspected several saplings until it located and seized a pupa, which was eaten on a nearby tree immediately afterwards. On a second visit, another pupa was taken and the bird flew away with it in its bill. Observations stopped at this point. In the evening, the third pupa had already disappeared, leaving no trace other than the broken girdle. The experiment ended

when three more pupae glued to the hostplants were recorded as lost before 8:00 a.m. on the following day.

Pupal predation (brown diapausing pupae)

In the course of the study 88 overwintering pupae were monitored. Of these, only 8 (9.1%) successfully eclosed, the rest being subject to several mortality factors, including physiological death (Stefanescu *in prep.*). Only in one case, in January 1999, was predation by the Great Tit confirmed by direct observation. However, most of the pupae could have been preyed upon by birds, as was suggested by field observations (Table 1). The Great Tit and a number of other bird species were regular foragers in both Hedgerow 1 and the alfalfa field and spent long periods on the ground thoroughly searching the vegetation surrounding the pupal sites. Furthermore, in winters 1997-98 and 1998-99 nearly half (41.7%) of all losses were confirmed as occurring in cases in which intense foraging by the Meadow Pipit *Anthus pratensis*, Song Thrush *Turdus philomelos*, Sardinian Warbler *Sylvia melanocephala* and Great Tit had been recorded around the pupae on the same day or the day before. In all these cases, no pupal remains were found other than the broken girdle and, occasionally, the caudal segment. Alternatively, pupae could have disappeared as a result of predation by small mammals, the most probable predator being the shrew *Crocidura russula*. This was the only mammal species trapped in the area in December 1997.

DISCUSSION

This study shows that insectivorous birds, particularly the Great Tit, can be

	Hedgerow	Alfalfa field
<i>Anthus pratensis</i>		+++
<i>Troglodytes troglodytes</i>	+	
<i>Prunella modularis</i>	+	
<i>Erithacus rubecula</i>	+++	
<i>Phoenicurus ochruros</i>	++	
<i>Turdus merula</i>		++
<i>Turdus philomelos</i>		+++
<i>Sylvia melanocephala</i>	+++	
<i>Sylvia atricapilla</i>	+	
<i>Phylloscopus collybita</i>	+++	+++
<i>Aegithalos caudatus</i>		++
<i>Parus caeruleus</i>	++	
<i>Parus major</i>	+++	+++
<i>Catulus glandarius</i>	+	+
<i>Pica pica</i>		++
<i>Sturnus vulgaris</i>	++	++
<i>Passer domesticus</i>		+++
<i>Passer montanus</i>		+++
<i>Fringilla coelebs</i>		+++
<i>Carduelis carduelis</i>		+
<i>Emberiza cia</i>		+

Table 1. Bird species recorded in winters 1997/98 (15 censuses) and 1998/99 (15 censuses) foraging in Hedgerow 1 and/or the alfalfa field where the overwintering pupae of *Iphiclides podalirius* were located. +++: regular foragers (>50% of censuses); ++: common foragers (10-50% of censuses); +: occasional foragers (<10% of censuses).

Taula 1. Ocells observats durant els hiverns de 1997/98 (15 mostratges) i 1998/99 (15 mostratges) mentre s'alimentaven al marge 1 i/o al camp d'alfals on hi havia les pupes hivernants d'Iphiclides podalirius. +++: visitants regulars (>50% dels mostratges); ++: visitants comuns (10-50% dels mostratges); +: visitants ocasionals (<10% dels mostratges).

important predators of larvae and pupae of *I. podalirius*. Direct observations of predation were relatively scarce, but indirect evidence (especially a highly consistent pattern in the timing of disappearance of prey items that mainly occurred before any activity of other potential di-

urnal predators began) strongly suggested that most losses recorded in June-July 1999 were indeed a consequence of bird predation, shortly after dawn. On the other hand, they can hardly be attributed to the shrew, the only small mammal trapped by night in the area, as records of this species climbing into trees and shrubs are extremely rare (A. Arrizabalaga com. pers.).

Furthermore, the very high mortality experienced by overwintering pupae may also be partially attributed to bird predation. Since actual predation by a Great Tit was only recorded in a single occasion, this assumption relies once again on indirect evidence, as for example the broken girdle left after a pupa had disappeared (consistent with traces found in confirmed cases of bird predation) and the regular presence of several bird species foraging for very long periods in close vicinity of pupae. Some birds searched for seeds in mixed flocks (House Sparrow *Passer domesticus*, Tree Sparrow *Passer montanus*, Chaffinch *Fringilla coelebs*, Goldfinch *Carduelis carduelis* and Rock Bunting *Emberiza cia*; cf. Cramp & Perrins 1994) or mainly preyed on moving insects from a perching site (Robin *Erithacus rubecula* and Black Redstart *Phoenicurus ochrurus*; cf. Cramp 1988), but others such as the Meadow Pipit, Blackbird *Turdus merula*, Song Thrush and Sardinian Warbler fed primarily on invertebrates on the ground (cf. Cramp 1988, 1992), and, in addition to the Great Tit, should be considered as potential serious predators of overwintering pupae.

The present study also suggests that insectivorous birds could have really serious consequences on the butterfly population in question. Thus, all but one of the larvae recorded in June 1999 in one hedgerow were preyed upon within a very short period, probably as the result of the

foraging activity displayed by a breeding pair of Great Tits that were present in the area. Once the birds found the habitat patch, they visited it repeatedly and quickly exhausted the supply of larvae. The same was true when pupae were artificially placed on the hostplants, as none survived and all quickly disappeared.

Interestingly, massive disappearance was first recorded in 4- and 5-instar larvae but, as soon as these were exhausted, 2- and 3-instars also disappeared in high numbers, probably as the result of Great Tit predation. A very similar situation was reported by Tagaki *et al.* (1995) in an experimental study with *Papilio xuthus* larvae and Japanese Tree Sparrows *Passer montanus saturatus*. Once the prey habitat was discovered, Tree Sparrows captured all those larvae artificially placed on several citrus trees, starting with those of 4- and 5-instars, before turning to the smaller 3-instar larvae after the bigger larvae had been depleted. These authors considered that birds selected first the most profitable prey items in terms of energy expenditure and reward, a common finding in the context of classical optimal foraging theory (Crawley & Krebs 1992).

What the data presented here conclusively demonstrate is the total ineffectiveness of the osmaterium as a defence mechanism against predation by the Great Tit. This orange, red or yellow gland present in Papilionidae larvae is everted from behind the head when the larva is disturbed, releasing several toxic and/or repellent substances (Honda 1981). However, in this study, there was not a single case in which a change of behaviour by the bird was observed after the prey had been seized and the osmaterium presumably everted. The same was found by Takagi *et al.* (1995) in the interactions between Tree Sparrows

and *P. xuthus*, and in the experimental work by Leslie & Berenbaum (1990) with Quails and larvae of three swallowtail species. In the latter study, *Papilio polyxenes* and *P. cresphontes*, the two species with aposematic coloration (similar to that exhibited by *P. machaon*) were invariably rejected, while *P. glaucus*, with a much more cryptic green coloration, was always consumed. Moreover, rejection was exactly the same whether *P. polyxenes* larvae were tested with and without functional osmaterium. Järvi *et al.* (1981) also found that larvae of *P. machaon* were ignored or immediately rejected whether they were offered to the Great Tits intact and alive, or dead and decapitated, and so these authors concluded that the osmaterium was not primarily a defence against bird predation. On the contrary, the effectiveness of the osmaterium against several invertebrate predators (notably ants and spiders) has been demonstrated in many studies (e.g. Honda 1983, Damman 1986, Takagi *et al.* 1995) and has been confirmed with field observations in the case of *I. podalirius* (pers. obs.).

The distastefulness of aposematic swallowtail larvae seems to be related to the presence of toxic and/or repellent allelochemicals sequestered from the foodplants (e.g. furanocoumarins contained in Rutaceae and Apiaceae) and allocated on their cuticle (Leslie & Berenbaum 1990, Berenbaum 1995). On the other hand, cryptic swallowtail larvae may feed on different hostplants (e.g. *I. podalirius* on Rosaceae, *P. glaucus* on at least half a dozen plant families, including trees belonging to the Rosaceae) and seem to be palatable. Further experimental work would be very useful to continue investigating what seems to be an essential difference in the defensive mechanisms of the two groups of swallowtail butterflies. Meanwhile, the

evidence so far available coincides with the view of Heinrich (1993) and indicates that palatable swallowtail larvae must rely on crypsis as their primary defensive mechanism in order to avoid detection by bird predators and thus enhance their chances of survival.*

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RESUM

Predació per ocells sobre les larves i les pupes d'Iphiclides podalirius

Presumiblement, la coloració críptica de les larves i pupes dels lepidòpters és una resposta evolutiva a la pressió selectiva exercida pels depredadors dotats d'un bon sentit visual, particularment els ocells. Fins a quin punt els ocells són depredadors importants dels papilioníds és, tanmateix, un fet debatible. Alguns treballs experimentals han demostrat que els ocells ignoren o rebutgen les larves no comestibles i amb coloracions d'advertència, però es desconeix com responen en front les larves amb coloracions críptiques. En un estudi sobre l'ecologia de la papallona Iphiclides podalirius es va poder comprovar com la Mallerenga Carbonera Parus major depredava les larves i pupes en diverses ocasions. A partir d'observacions directes i indirectes es pot concloure que l'impacte d'aquest ocell sobre la població estudiada va ser molt important i se suggereix que, evolutivament, aquest factor ha representat una forta pressió selectiva afavorint la coloració críptica de

les larves i pupes d'aquesta papallona. D'altra banda, les dades que es presenten demostren la inefectivitat de l'osmèteri de les larves com a mecanisme defensiu en front la Mallerenga Carbonera.

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