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Oviposition and Larval Preferences of *Zerynthia polyxena* (Denis & Schiffermüller, 1775) (Lepidoptera: Papilionidae) at its Northern Range Margins

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Abstract: *Zerynthia polyxena* is a western Palaearctic species listed in the EU Habitats Directive (Natura 2000). This study describes its oviposition and larval preferences at two ruderal habitats in southern Slovakia, near its northern distribution margin. The females preferred oviposition at tall and richly-leafed shoots of the regionally used single host plant *Aristolochia clematitis* L. Caterpillars were generally located at the same positions as egg batches, mainly at the underside of leaves of richly-leafed plants.

Key words: butterfly conservation, egg lying strategy, larval ecology

Introduction

The host plant choice is a crucial parameter in the life cycle of herbivorous insects, including butterflies (e.g. Batary et al. 2008, Friberg et al. 2015, Osvath-Ferencz et al. 2016). However, studies of butterfly host plant choice typically explore female oviposition strategies (e.g. Dennis 1996, Gamberale-Stille et al. 2019) rather than preferences of larvae and their ability to exploit a suitable host plant (Tsuji et al. 2018). The oviposition process is influenced by diverse factors: butterfly genetics (Wiklund 1975), chemical stimulants produced by plants (Thompson & Pellmyr 1991, Renwick & Chew 1994, Sachdev-Ghupta et al. 1993), access to a suitable habitat (Konvicka et al. 2003), weather conditions (Dennis & Hardy 2018) and quantity and parameters of host plants (Dennis 1996, Lang & Otto 2015). Offspring survival depends on the female's judgment in selecting the proper habitat for its development (Rausher 1979a), which is known as *Mother Knows Best Paradigm* (Thompson 1988, Garcia-Robledo & Horvitz 2012).

Larval hosts of the butterfly genus *Zerynthia* Ochsenheimer, 1816 (Papilionidae) are plants of the family Aristolochiaceae, a group known to contain toxic alkaloids and aristolochic acids (Rothschild et al. 1972). These chemicals are detected by female tarsal chemoreceptors that are known to stimulate the oviposition process in related species (Sachdev-Ghupta et al. 1993, Renwick & Chew 1994). The suitability of a microhabitat can be characterised by

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many factors. One of these is light density (Clench 1966) as adult females are highly dependent on direct sunlight, which influences their movements and distribution within biotopes. The abundance of host plants and their size as well as quality and amount of foliage may also affect oviposition (Porter 1992, Dennis 1996, Ellis 2003, Örvössy et al. 2014). Generally, a close link between oviposition preferences of females and larval performance is expected (Wiklund 1975, Rausher 1979b). However, deviation from this correlation may be caused by various factors such as predation or parasitism affecting larval fitness more than growth performance (Thompson & Pellmyr 1991). Larval diet is crucial for fitness and significantly affects larval growth rates (Wiklund 1975, Gamberale-Stille et al. 2014). In some cases, larvae may re-evaluate the suitability of the host-plant of their "mothers" and abandon unsuitable plants (Nylin et al. 2000). An extreme case in butterflies are some Nymphalidae: Satyrinae, where "mothers" lay their eggs near the host plant (Bergman 2000) and, thus, the caterpillar's survival directly depends on the larval choice.

Zerynthia polyxena (Denis & Schiffermüller, 1775) is a western Palaearctic species, distributed from south-eastern France and northern Italy through the southern half of Europe (reaching eastern Austria, south-eastern Czechia and southern Slovakia) to Anatolia, Ukraine and southern Russia up to Kazakhstan and the Urals. The univoltine adults fly in spring (April – May) throughout their range and deposit eggs singly or in small groups. The larvae develop communally in early instars. The overwintering pupae are attached singly on lower parts of plant stems or tree bark. It develops on *Aristolochia* spp., sometimes using multiple species within a single region (Slancarova et al. 2015), of which only *Aristolochia clematitis* occurs in Central Europe. This plant occurs in diverse habitats with nitrogen-rich soil, i.e., vineyards, humid grasslands, wetlands, wastelands and forest edges (Barca 2018, Örvössy et al. 2014). While the butterfly is rather common in countries further south, the agricultural changes in landscapes, river regulations and intensive urbanisation negatively affect the amount of suitable habitats at the northern edge of its range. Therefore, it is listed in various national red lists (Kulfan & Kulfan 2001). The IUCN Red List classifies it as the least concern species with decreasing tendency (Van Swaay et al. 2010). It is also listed in the EU Habitats Directive (NATURA 2000) (Numa et al. 2016).

The main aims of our study are (1) to determine host-plant factors influencing oviposition pref-

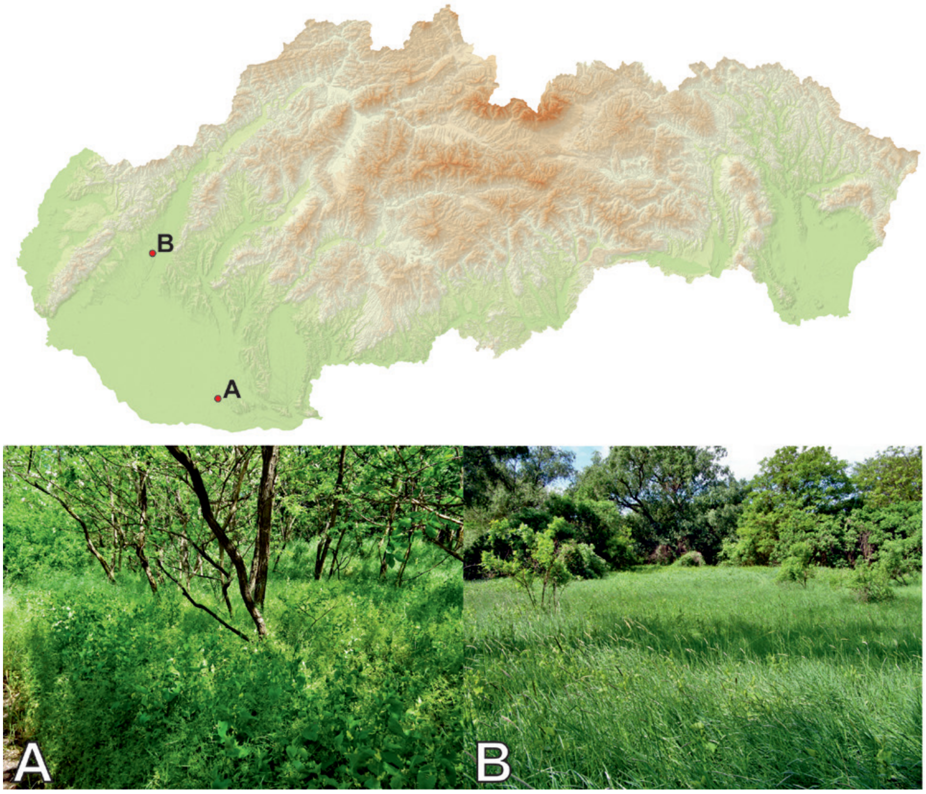

Fig. 1. Map of Slovakia with the location of the sites where *Zerynthia polyxena* oviposition patterns were studied. A – Bajč; B – Hlohovec.

erences of *Z. polyxena* females and (2) to compare preferences of caterpillars for host plant parameters, such as size or shape of the host plant. The obtained data could help to improve the efficiency of conservation of these vulnerable butterflies in their northern range of distribution and highlight the existence of potential regional differences in their bionomy.

Materials and Methods

The data were collected during two seasons (2013 and 2014), from April to June, on two sites in southern Slovakia, Central Europe.

Site 1, near the village of Bajč (N 47°56´, E 18°11´, altitude 113 m), a narrow (≈10 m width) edge separating a young deciduous forest and intensively cropped fields (oilseeds and wheat). The forest was formed mostly by exotic black-locust (*Robinia pseudoacacia*) mixed with (*Quercus* spp.) (i.e., *Chelidonium*-*Robinion* plant association). There were patches of thorny shrubs (*Rosa canina*), coarse grasses (*Poa* spp., *Festuca* spp.) and nitrophilous forbs (*Galium aparine*, *Urtica dioica*) including monodominant patches of *Aristolochia clematitis*.

Site 2, Soroš, a part of the town of Hlohovec (N 48°26´, E 17°47´; altitude 140 m), an alluvium along the river Váh. It was covered by a mosaic of shrub willow (*Salix alba*) belonging to union *Salicion cinereae*, drier thorny shrublands (*Rosa canina*, *Rubus caesius*) and nitrophilous tall-stem formations (dominated by *Aristolochia clematitis*, *Calystegia sepium* and *Urtica dioica*). The habitat was mainly open and sunny, only a part with higher concentrations of shrubs was shaded and seasonally flooded by the river.

The Site 1 thus may be considered as representing half-shaded woodland edge conditions whereas the Site 2 represents open alluvial habitat. At each site, 500 randomly selected shoots of host plants were marked using red fibre and individually checked at two-weeks intervals, obtaining six visits in total between appearance of the first adults and the termination of the larval period. We recorded the total number of eggs on each occupied host plant (*eggs_per_shoot*), the maximum count per leaf (*eggs_per_leaf*) and their *position* (three categories: upper/lower side, stem). We also measured the following explanatory variables of each occupied plant: *shoot height* (cm), *flowering* status (yes/no), number of *leaves*, length of the *longest leaf* (cm) and number of *occupied leaves*.

After the larvae hatched, we tried to locate them during the visits. When the larvae had reached the 3rd to 5th instar, we recorded their locations as these might differ from the females' choice (= egg =-laying). For each larva found, we recorded its *position* (three categories: upper/lower side of leaf, stem), *shoot height*, and *longest leaf* length.

For the analysis of egg numbers, *eggs_per_shoot* and *eggs_per_leaf* were the response variables and *locality*, *position*, *shoot height*, *flowering*, number of *leaves*, length of *longest leaf* and *occupied leaves* were the predictors. For larvae, the response variable was the number per leaf (*larvae_per_leaf*) and the predictors were *locality, position*, *shoot height* and number of *leaves.* We analysed the data using generalised linear models with Poisson distribution implemented in R 3.3.1. We first used single predictor test and then a model with multiple predictors for each response variable with stepwise forward selection, tested using Cp and F tests.

Results

During the surveys, we found 29 plants (5.8% of the sampled plants) with 327 eggs in Bajč (mean/median per occupied plant: 11.3±7.7SD/10, range 1–34) and 20 plants (4.0%) with 219 eggs in Hlohovec (mean/median per occupied plant: 10.9±6.7SD /11, range 1–22). Subsequently, we located 73 caterpillars on 49 plants in Bajč and 72 caterpillars on 43 plants in Hlohovec.

In the single-term tests (Table 1) for *eggs_per_shoot*, *locality* had no effect. Significantly more eggs were found on the underside of leaves (followed by the upper side and the stem). Plants with more eggs had more occupied leaves, and more eggs were found at taller plants with more leaves and greater longest leaf length. The final model, which included the egg position and the longest leaf length, explained >50% of the variation in the data. For *eggs_per_leaf*, the pattern in batch position was as described above, with taller shoots and shoots with longer leaves having more eggs, and plants in Bajč hosted marginally larger batches than those in Hlohovec. The difference between the locations entered the final model together with the longest leaf length. The two predictors explained ≈27% of the variation.

For caterpillars (Table 1), locality had no effect. The preference for the underside was retained (n = 80) but considerably higher proportions than for the eggs were on the upper side (47), on the stem (20) or outside the plant (8). More caterpillars were found on taller plants with more leaves. The multiple regression model contained additive factors for position and number of leaves.

Table 1. Overview of generalised linear models used to evaluate factors influencing female oviposition preferences in *Zerynthia polyxena*.

	Egg per plant						Egg per leaf					
	Direction*	**df**	**Deviance**	**%Dev**	**F**	**p**	**Direction***	**df**	**Deviance**	**%Dev**	**F**	**p**
Null model		48	2466					75	2064.7			
Locality* A*		47	2464.7	0.05	0.02	0.878	B>H	74	1985.5	23.21	2.95	0.090
Position* B**	UN>UP>S	45	1526.8	38.09	9.23	<0.0001	UN>UP>S	73	1826.1	25.95	4.77	0.011
***Shoot height* C**	+	47	1420.7	42.39	34.58	<0.0001	+	74	1985.3	19.49	2.96	0.089
***Flowering* D**		47	2443.6	0.91	0.41	0.515		74	2050.2	16.86	0.53	0.471
***Leaves* E**	+	47	2075.3	15.84	8.85	0.005		74	2047.1	16.99	0.64	0.428
***Longest leaf* F**	+	47	2055.7	16.64	9.38	0.003	+	74	1611.3	21.95	20.82	<0.001
***Occupied leaves* G**	+	47	1819.2	26.23	16.71	<0.001		74	2044.0	17.11	0.75	0.390
Final: B+C		44	1112.4	54.87	4.06	0.012		A+F	1509.6	26.89	4.92	0.030

*Positive signs (+) indicates increasing response. **B – locality Bajč; H – locality Hlohovec. *** Position on leaves: UP – dorsal; UN – underside; S – stem.

Table 2. Overview of generalised linear models used to evaluate factors affecting host plant preferences of *Zerynthia polyxena* larvae.

	Direction*	**df**	**Deviance**	**%Dev**	**F**	**p**
Null model		275	118.82			
***Locality* A**		274	118.56	0.22		0.601
Position* B**	UN>UP>S	273	99.08	0.23	27.21	<<0.001
***Shoot height* C**	+	274	117.39	1.20	3.34	0.069
***Leaves* D**	+	274	110.85	6.71	19.70	<<0.001
Final: B+D		272	91.11	0.01	23.80	<<0.001

*Positive signs (+) indicates increasing response. *** Position on leaves: UP – dorsal; UN – underside; S – stem.

Discussion

At two Slovakian sites of *Zerynthia polyxena*, near the northernmost geographical range margin of the species, we found a shared preference for oviposition on tall and richly-leafed *Aristolochia clematitis* shoots. The caterpillars were located at the same positions as egg batches, i.e. on the underside of the leaves and on tall and richly-leafed plants.

At both study sites, the proportion of egg-bearing shoots was remarkably similar and low, ≈5%. In studies on *Z. polyxena*, this information is rarely reported, probably because the growths of *A. clematitis* are typically dense, with many shoots per unit area, while the proportion of occupied shoots is usually low, which precludes researchers to determine the proportions. Batary et al. (2008) sampled 120 circles of radius of 5 m in clearings of *Populus* sp. and *Robinia pseudoacacia* plantations in central Hungary with "an average of 775 food-plant shoots" per circle and detected 597 eggs. This gives the proportion of occupied shoots >0.6% (597 / 775*120), as some of the eggs were laid in small batches. Örvössy et al. (2014), in the same region, recorded 922 eggs along 23 6 x 40 m transects through "large food plant patches". In Greek Thrace, Slancarova et al. (2015) first measured a number of occupied plants and then supplemented this by measuring "a high number" of unoccupied plants: 57/315 occupied/unoccupied *A. rotunda*, 23/148 *A. pallida*, 8/116 *A. clematitis* and 1/98 *A. hirta* plants. This gives ≈7% *A. clematitis* (or ≈13% of all *Aristolochia* spp.) shoots bearing eggs, clearly an inflated number due to the method used for the collection of data. In any case, the number of shoots occupied by eggs ranges from less than 0.5 % to 7 % among the previous studies, suggesting that the mere amount of host plants is not the limiting factor for *Z. polyxena* at its sites and that the plant trait selection probably plays a role.

Only two localities were surveyed for this study, the edge of an invasive tree stand and the urban floodplain of a regulated river represent heavily human-altered biotopes that are still quite common in densely-populated and intensively-farmed southern Slovakia. This results into nationally favourable status of the species (European Environment Agency 2012). The same applies for the *Robinia – Populus* plantations clearings and hummocks in central Hungary (≈140 km SE from our sites), from which high densities of both host plant and the butterfly have been reported (Batary et al. 2008, Örvössy et al. 2014). Accounts from countries further south, Slovenia (Čelik et al. 2012) and Greece – Thrace (Slancarova et al. 2015), described the occurrence in more natural biotopes (river valleys with non-intensive cultivation) but, in both cases, the host plants were abundant.

Regarding habitat types, our results complement previous findings describing the preferences of egg-laying females for sun-exposed host plant patches (Čelik et al. 2012, Örvössy et al. 2014). One of our localities, Bajč, was a partially shaded woodland edge. The occurrence of eggs and larvae there points to suitability of partially shaded patches with high host plant abundances for oviposition. The results of Slancarova et al. (2015) from Greece, where *Z. polyxena* utilised *Aristolochia* spp. with contrasting shade tolerance (shade-tolerant *A. hirta* and sun-requiring *A. pallida*), also document a flexibility of this butterfly with respect to sun exposure.

The preference for oviposition on taller shoots with longer/larger leaves on both studied sites is another case of the frequently observed preferences for large prominent host plant shoots, observed in various butterfly species of several families, e.g. Pieridae (Porter 1992), Riodinidae (Turner et al. 2009) and Nymphalidae (Pschera & Warren 2018). This preference is detected for all *Z. polyxena* populations studied so far (Batary et al. 2008, Slancarova et al. 2015) as well as for the closely related *Z. cassandra* (Geyer, 1828) (Vovlas et al. 2014, Cini et al. 2019), *Z. cerisy* (Godard, 1824) (Dennis 1996) and other Parnassiinae feeding on Aristolochiaceae, i.e. *Archon apollinus* (Herbst, 1798) (Slancarova et al. 2015). Laying eggs mainly on the underside of leaves is also in agreement with previous studies (Dennis 1996, Batary et al. 2008, Vovlas et al. 2014, Slancarova et al. 2015), probably protects the eggs from unfavourable factors such as desiccation (Tsuji et al. 2018) or attacks by parasitoids (Watanabe et al. 2018). These two aspects of mother choice had to be optimised by natural selection.

Despite the long coevolution between butterflies and their host plants, mistakes in the mothers' choice may occur (Dethier 1959). Therefore, larvae should also possess their own “choice mechanism” in order to improve their survival. As in previous studies (Örvössy et al. 2014, Slancarova et al. 2015), we found more *Z. polyxena* larvae on taller and richly-leafed *Aristolochia* shoots. As in the case of eggs, the majority of larvae were found at undersides of leaves. The plant shoots were considerably smaller during the time of our search for eggs than when we searched for the larvae. As in other Lepidoptera, young larvae first feed at spots where they emerged from eggs and later disperse to other shoots (Jones 1987, Mauricio & Bowers 1990, Tsuji et al. 2018). Larval selection of larger shoots ensures more food and hence less intraspecific competition for larvae (Kivelä & Välimäki 2008) and richer foliage provides better cover against detection by natural enemies (Sei & Porter 2003, Örvössy et al. 2014). Regarding larval preference for underside of the leaves, it apparently follows mothers` oviposition patterns, possibly for the same reasons such as protection from direct sun and predation. This, however, does not exclude occasional basking in direct sun, which may accelerate larval development (Porter 1982).

In conclusion, both ovipositing females and feeding caterpillars utilise large and prominent shoots of *Aristolochia clematitis* at the northern limits of the geographical range of *Z. polyxena*. It corroborates earlier findings from more central parts of the range, and also suggests that besides mere host plants presence, large and prominent shoots must be available for the butterfly to flourish. This may pose a management problem, given that the nitrogen-rich, essentially ruderal and insular *A. clematitis* patches are sometimes controlled by mowing relatively early in spring. To maintain *Z. polyxena* sites, cutting of ruderal grasslands containing the host plants, including host-plant patches in riparian habitats, on railway verges or along field margins, should be postponed to late season, i.e. July or later, when the larvae are already pupated.

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