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# TAXONOMIC REVIEW OF *EUPHYDRYAS MATURNA* (LINNAEUS, 1758) (LEPIDOPTERA, NYMPHALIDAE) WITH DESCRIPTION OF A NEW SUBSPECIES FROM DOBROGEA (ROMANIA) AND NOTES ON CONSERVATION BIOLOGY

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Taxonomy, geographical range and subspecific subdivision of *Euphydryas maturna* are considered. The isolated population from Dobrogea is described as *E. maturna opulenta* ssp. n. based on external and genital characters. The separation is also supported by the significant genetic differentiation based on 17 allozyme loci. The Dobrogea population was shown to be highly differentiated from the nearby populations in the Carpathian basin. This population may therefore be an relict population and possibly also an evolutionarily significant unit. Its conservation is of high concern as are many other butterfly species inhabiting sparse deciduous forests. With 2 tables and 18 figures.

Key words: Melitaeini taxonomy, biogeography, *Euphydryas maturna* subspecies, genital characters, conservation biology

### INTRODUCTION

### Phylogenetic subdivision of Euphydryas

Species of the genus *Euphydryas* SCUDDER, 1872 (sensu lato) (Nymphalidae, Melitaeini) have a Holarctic distribution. Eight species occur in the Palaearctic region and six in the Nearctic region (HIGGINS 1978). They form a monophyletic group within the Melitaeini clade as opposed to the *Chlosyne–Phyciodes–Melitaea* monophylum (ZIMMERMANN *et al.* 2000, WAHLBERG *et al.* 2003). The subdivision of this genus was often discussed. HIGGINS (1978) has elevated this group to tribal status and subdivided it into four genera: *Euphydryas* SCUDDER (1 species) and *Occidryas* HIGGINS, 1978 (4 species), both are exclusively North American, *Eurodryas* HIGGINS, 1978 (4 species, which are exclusively Palaearctic) and *Hypodryas* HIGGINS, 1978 consisting of one North American and four Palaearctic species. This subdivision was also adopted in some official lists (e.g. Habitat Directive Annex II–IV). In contrast, several authors considered *Euphydryas* forming a single genus within the tribe Melitaeini (EHRLICH *et al.* 1975, BRUSSARD *et al.* 1985, SCOTT 1986, BRITTEN *et al.* 1993, KARSHOLT & RAZOWSKI 1996). According to molecular phylogenetic surveys (ZIMMERMANN *et al.* 2000) the monophyly of three species groups was supported from the four genera proposed by HIGGINS (1978). They found, however, a fairly low level of differentiation within the *Euphydryas* s.l. clade and argued that this group is also rather distinct from other Melitaeinae genera morphologically. They have shown the monophyly of the subgenus *Euphydryas* s. str. and the polyphyly of *Occidryas* within *Euphydryas* s.l. According to these surveys *Hypodryas* and *Eurodryas* should also be relegated to subgenus status because they describe monophyletic subclades within *Euphydryas* s.l. Therefore, we follow the recommendation of these authors hereafter and consider *Hypodryas* as a subgenus of *Euphydryas*, and *E. (H.) maturna* as the widely distributed Palaearctic sister species of the Palaearctic boreo-(Siberian)-montane *E. (H.) ichnea* (BOISDUVAL, 1833).

#### Taxonomy of Euphydryas maturna

Euphydryas maturna (LINNAEUS, 1758) is a Euro-Siberian polytypic species with large distribution in E and NE Europe. Western and Southern Central Europe is populated by the nominotypic subspecies (type locality Southern Sweden, HIG-GINS 1950). Specimens with dark colouration and reduced yellowish markings have been described as E. maturna urbani (HIRSCHKE, 1901) from the humid prae-Alpine valleys of Upper Bavaria and Salzburg. The population of the Bialowieza forest is also typifyed by large size and dark colouration (E. maturna adamczewskyi KRZYWICKI, 1967). Populations of the western Balkan Peninsula were separated as E. maturna idunides (FRUHSTORFER, 1917), this subspecies also occurs in SW Transdanubia in Hungary and adjacent territories. The ecomorph of sub-Mediterranean habitats in Southern and Central Transdanubia has been described as E. maturna ornivora VARGA, 1968 (in VARGA & SÁNTHA 1973) with reference to the food-plant Fraxinus ornus in these habitats. The sometimes strong populations of the Eastern Carpathian Basin have been separated from the nominotypic subspecies as E. maturna partiensis VARGA et SÁNTHA, 1973. NE European and Siberian populations are often mentioned (HIGGINS 1978, LUKHTANOV & LUKH-TANOV 1994) as E. maturna staudingeri (WNUKOVSKY, 1929; nom. nov. pro Melitaea maturna var. uralensis STAUDINGER, 1871, praeoccupied by M. arduinna uralensis EVERSMANN, 1844). E. maturna tenuireticulosa VARGA et SÁNTHA, 1973 can be considered as junior synonym (syn. n.) of this subspecies.

In recent publications, the subspecific subdivision of *E. maturna* has not been accepted (TUZOV *et al.* 1997, TSHIKOLOVETS *et al.* 2002, TSHIKOLOVETS 2003). Bulgarian *E. maturna* collected in Dobrogea and Ludogorie regions has been mentioned by ABADJIEV (1995) and ABADJIEV and BESHKOV (2003) as *E.* 

*maturna maturna*. Surprisingly, the taxonomic separation of *E. maturna partiensis* has also been questioned though specimens outside Bulgaria have not been surveyed. Therefore, it is of taxonomic importance to study specimens from Dobrogea and compare them to large collection materials from the Carpathian Basin and other parts of Europe.

# **Euphydryas maturna opulenta** RÁKOSY et VARGA, ssp. n. (Figs 1–4, 6–7)

Holotype: female, Romania, Dobrogea N, Ciucurova, 44° 54' N, 28° 28' E, 275 m, 04. 06. 1994., leg. et coll. L. RÁKOSY (Cluj-Napoca, deposited at the Zoological Museum of the Babeş-Bolyai University).

Paratypes: 21 males and 28 females from the same locality, 04. 06. 1994 and 28. 05. 2000, leg. L. RÁKOSY, G. STANGELMAIER and CH. WIESER, in colls L. RÁKOSY, G. STANGELMAIER, Z. VARGA (deposited at the Zoological Collection of the Dept. Evolutionary Zoology, University of Debrecen) and CH. WIESER.

Description: The largest form of the species, fore wing length of males is 21.5-25.5 mm (N = 7, mean: 23.57 mm), of females is 24-28 mm (N = 11, mean: 26.5 mm). The colouration of the upperside is dark and contrasting. Sexual dimorphism in colouration is not expressed. Males have very pointed apex of fore wings, females are broader winged, often huge. The reddish submarginal stripe is vivid reddish-orange and narrow. Other reddish parts of the pattern are vividly coloured, relatively small and sharply bordered by the very dark, blackish-brown pattern. The light spots on the males are often whitish with considerable individual variation, on the females they are vivid ochreous orange. The underside of wings is ochreous orange with strongly contrasting dark pattern and relatively large light marginal lunules (Figs 1–2).

Diagnosis and comparison with other subspecies. The most conspicuous characters of the new subspecies are the significantly larger size and rich, contrasting colouration, especially in females. The mean length of fore wing is 23.57 mm in 7 males (21.5–25.5 mm), compared to 20.42 mm (18.5–23.5 mm) in 26 males from different localities of the Carpathian Basin; 26.5 in 11 females (24–28 mm) compared to 23.82 mm (23–24.5 mm) in 20 females from different localities of the Carpathian Basin. There is a considerable individual variation in all populations of *E. maturna*. The light parts of the wings are more restricted and contrasting in the new subspecies while they are more extended and less contrasting in most other forms of the Carpathian Basin, especially in males. The submarginal reddish stripe is also often rather restricted in females of the new subspecies, but it is often very broad in females of other populations, even in dark specimens. The new subspecies shows the most similarity to the relatively large and vividly coloured specimens from Southern Transdanubia which were relegated to *E. maturna idunides*. This external similarity was, however, not confirmed by the genetic data.

Characters of male and female genitalia. The whole male genitalia of *E. maturna opulenta* is robust and very strongly sclerotised, the uncus is relatively short and thick; it seems to be robuster than in other subspecies (Figs 6–11). The slender and elongate shape of uncus of *E. maturna idunides* (FRUHSTORFER, 1917) seems to be a good distinctive character (Fig. 14). Valvae are more triangular than in other subspecies, processus posterior is trifide, it shows overlapping variation in differ-



**Figs 1–5.** *Euphydryas maturna opulenta* RÁKOSY et VARGA, ssp. n.: 1–2 = holotype (female), 1 = upperside, 2 = underside, 3–4 = male in natural habitat, 3 = upperside, 4 = underside, 5 = habitat, near Ciucurova, N Dobrogea



**Figs 6–13.** Genital slide of *Euphydryas maturna* and *E. cynthia* spp.: 6–7 = *E. m. opulenta* RÁKOSY et VARGA, ssp. n. (male, paratypes), 8–9 = *E. m. partiensis* VARGA et SÁNTHA, 1973 (male, paratypes), 10 = *E. m. idunides* (FRUHSTORFER, 1917) (male), 11 = *E. m. maturna* (LINNAEUS, 1758) (male), 12 = *E. cynthia leonhardi* (FRUHSTORFER, 1917), Rila Mts (male), 13 = *E. cynthia drenovskyi* (RÖBER, 1926), Pirin Mts (male) (scale bars = 1 mm)

ent populations. The upper arm of processus is short and thick in *E. maturna opulenta*, more slender and curved in *E. maturna idunides* (Fig. 15). We could not find in female genitalia any significant differences from other subspecies. Similar level of subspecific differentiation was also observed in the male genitalia of *E. cynthia leonhardi* (FRUHSTORFER, 1917) and *E. cynthia drenovskyi* (RÖBER, 1926) (Figs 12–13).

Distribution and bionomy. The new subspecies was discovered by the first author in northern Dobrogea and later also found in the Macin Mts. The habitat is a damp ash-alder-willow gallery forest where butterflies are locally abundant along a broad, sunny forest glide (Figs 3–5).

Re-consideration of the subspecies described by VARGA et SÁNTHA (1973): Other populations from the Carpathian Basin did not show conspicuous external features with the exception of the butterflies from Southern Transdanubia which has been relegated to *E. maturna idunides* (VARGA et SÁNTHA, 1973). Unfortunately, recent genetic data could not confirm this separation (PECSENYE *et al.* 



Fig. 14. Variability and subspecific differences in shape of uncus of *Euphydryas maturna* spp.: A–C = *E. m. opulenta* ssp. n. (Dobrogea); D–H = *E. m. partiensis* (E Hungary, Guthi forest); I–J = *E. m. maturna* (Wien: Rohrwald); K–O = *E. m. idunides* (SW Hungary, Drava lowland)



**Fig. 15.** Variability in shape of processus posterior of *Euphydryas maturna* spp.: A-C = E. *m. opulenta* ssp. n. (Dobrogea); D-H = E. *m. partiensis* (E Hungary, Guthi forest); I-L = E. *m. idunides* (SW Hungary, Drava lowland)



Fig. 16. Distribution of Euphydryas maturna in Eurasia and in SE Europe

2005, 2007). Thus, further studies are needed, first of all from the north-western part of the Balkan Peninsula (Croatia, Bosnia). The subspecific separation of *E. maturna partiensis* has also been disputed by ABADJIEV and BESHKOV (2003). However, there are some morphological (shorter and more rounded shape of fore wings in males, more diffuse and homogenous orange-reddish colouration of females (more details see: in VARGA & SÁNTHA 1973) and also certain bionomical differences (habitat, food plants) that can support this subdivision. More extended structural (genitalia) and genetic (allozymes) surveys are required to solve this problem.

# GENETIC POLYMORPHISM OF *EUPHYDRYAS MATURNA* IN THE CARPATHIAN BASIN

#### Enzyme studies

Enzyme polymorphism was used to survey genetic variation of *E. maturna* populations. Allozyme polymorphism was studied 25 samples of 19 populations (Table 1) by vertical polyacrylamide gel electrophoresis at 19 loci: aldehyd oxidase (*Aox*), aconitase (*Acon*), esterase (*Est-1, Est-2*), glutamate dehydrogenase (*Gdh*), glutamate oxalacetat transaminase (*Got*),  $\alpha$ -glycerophosphate dehydrogenase (*acpdh*), hexokinase (*Hk*), isocitrate dehydrogenase (*Idh*), leucine amino peptidase (*Lap*), lactate dehydrogenase (*LdH-1, LdH-2*), malate dehydrogenase (*Mdh*), malic enzyme (*Me*), phosphoglucose isomerase (*Pgi*), phosphoglucomutase (*Sod-1, Sod-2*).

Thoraxes were homogenised in 400  $\mu$ l extraction buffer and these samples were used to study *Got*,  $\alpha$ *Gpdh*, *Hk*, *Idh*, *LdH-1*, *LdH-2*, *Mdh*, *Me*, *Pgi*, *Pgm*, *Sod-1*, *Sod-2*. Abdomens were homogenised also in 400  $\mu$ l of extraction buffer and these samples were used to analyse *Acon*, *Aox*, *Est-1*, *Est-2*, *Gdh*, *Lap* and *6Pgdh*. The extraction buffer, the electrophoresis buffer systems and running conditions together with the staining solutions were slightly modified after BERECZKI *et al.* (2005). Genotypes of the different individuals were scored according to their enzyme pattern.

Alternative alleles were found at 15 loci in at least one population. Nevertheless, the population sample collected in Dobrogea was completely monomorphic at 8 loci out of the total 17. There was one diagnostic allele at the *Idh* locus in this population, which did not occur in any other population investigated. In addition, there were other loci (especially Pgm) contributing much to the differentiation between the Dobrogea and the other *E. maturna* populations.

		specificits.			
Species	Geographic region	Population	Year	Abbrev.	No.
E. aurinia	Transdanubia (W HU)	Gödörháza (wet meadow)	2004	4aGod	20
		Bakony Mts	2005	5aBak	18
E. maturna	Nyírség (NE lowland)	Őmböly, forest glide	2005	5mFeO	40
			2006	6mFeO	44
		Fényi forest (fringe)	2005	5mFeII	40
			2006	6mFeII	56
		Fényi forest (clearing)	2005	5mFeI	21
			2006	6mFeI	56
		Fényi forest (glide)	2005	5mFeIII	29
		Bátorliget	2005	5mBat	42
		Guthi forest A (fringe)	2005	5mGutA	39
			2006	6mGutA	43
		Guthi forest B (glide)	2006	6mGutD	47
	Bereg-Szatmári Plain	Fülesd forest (fringe)	2002	2mFul	15
		Lónyai forest (glide)	2006	6mLon	29
	N Hungary	Novaj (forest glide)	2001	1mNov	23
		Sajólád (forest glide)	2004	4mSaj	43
		Girincs (forest glide)	2004	4mGir	33
		Feldebrő (forest glide)	2006	6m Feld	30
	Körös region	Sebesfoki forest	2001	1mSeb	23
		Gyula, town forest	2001	1mGyV	56
		Gyula, town forest	2006	6mGyV	18
		Gyula, Körös forest	2001	1mGyK	17
		Gyula, Körös forest	2006	6mGyK	33
	Transdanubia (W HU)	Herend (forest glide)	2005	5mBak	32
		Őrtilos (Dráva gallery)	2005	5mOrt	23
	Romania	Dobrogea	2006	6mDob	19

 Table 1. Genetic samples examined: species, countries (regions), sites, years, codes, numbers of specimens.

# Statistical analyses

Genotype and allele frequencies were calculated on the basis of banding patterns. Allele frequencies were used to estimate Cavalli-Sforza and Edwards chord distances (CAVALLI-SFORZA & EDWARDS 1967) and a UPGMA dendrogram was constructed on the basis of the distance matrix (SNEATH & SOKAL 1973). To support the nodes of the dendrogram nonparametric bootstrap (FELSENSTEIN 1985)

153

was computed with 3000 bootstrap replicates. The percentage of replicates where each node is still supported is given on the dendrogram. PAST ver.1.56 (HAMMER *et al.* 2006) was used to calculate chord distances, process the dendrogram and carry out the bootstrap.

Figure 17 demonstrates that the Dobrogea sample is clustered in a distinct branch of the dendrogram separated from all other *E. maturna* populations studied. The result of the PCA analysis was fairly similar (Fig. 18). The sample originating



Cavalli-Sforsa & Edwards chord distance

**Fig. 17.** UPGMA dendrogram constructed based on Cavalli-Sforza and Edwards chord distances. The outgroups are two *Euphydryas aurinia* populations from Western Hungary. 6mDob is the sample collected in the Dobrogea population in 2006; all other samples originated from various Hungarian populations

from the Dobrogea population showed again a clear separation from all the other populations along the first axis. This axis explained 26.3 % of the total genetic variation. The differences in the allele frequency distribution at the Pgm locus contributed most to this axis.

These results demonstrate the relative genetic isolation of the Dobrogea population from other adjacent populations of *E. maturna* and also support its subspecific status.

#### DISCUSSION

ZIMMERMANN *et al.* (1999, 2000) suggested some interesting biogeographical hypotheses on the basis of the phylogenetic relationships among the species within the *Hypodryas* clade. *Euphydryas cynthia* ([DENIS et SCHIFFERMÜLLER], 1775) was shown to be the most basal species with its conspicuous disjunct distribution in the Alps and in the high mountains of the eastern Balkans (HIGGINS



Fig. 18. The results of PCA. The points represent the samples; polygons indicate those samples that originate from the same population. The first two axes explained 43.2% of the total genetic variation

1978, VARGA & SCHMITT 2008). They suggested that this species might have been isolated from the ancestral Hypodryas subclade during an earlier glacial period. Unfortunately, the trichotomy of E. (H.) iduna (DALMAN, 1816), E. (H.) gillettii (BARNES, 1897), and E. (H.) maturna + E. (H.) ichnea (BOISDUVAL, 1833) has not been resolved. They supposed that their ancestral population might have been split into 3 populations during the same glacial period. They have only found one difference in the COI sequence between the species pair E. maturna and E. ichnea, which may have diverged fairly recently. Unfortunately this hypothesis has not been supported by any evidence concerning possible differentiation between the Siberian E. ichnea (= intermedia MÉNÉTRIES, 1859) and the European E. ichnea wolfensbergeri (FREY, 1880). These two taxa show a long-distance disjunction from Southern Siberia to the Alps as opposed to the much larger and continuous Euro-Siberian distribution of E. maturna. Thus, we think that no final conclusion can be drawn before the phylogeographic analysis of the three entirely different disjunct patterns of E. cynthia (Alps - Balkans), E. iduna (Arctic Eurasia - Caucasus - Altaj - Sajan massifs) and E. ichnea (Siberian mountains - Alps) is not carried out. ZIMMERMANN et al. (1999, 2000) also supposed that this species survived the latest glacial period in a single refuge and suffered a severe population bottleneck, which might have resulted in the surprisingly strong homogeneity of the 2 E. maturna COI sequences. It is obvious that this hypothesis must be tested by analysing several different genetic loci in many different populations. Our first results showed that E. maturna populations are generally well differentiated from each other although they do not show any evident geographic pattern of regional differentiation in the Carpathian basin. Therefore, the Dobrogea population might be a postglacial marginal isolate without closer phylogeographical connections to other SE European populations of the species.

## CONSERVATION BIOLOGY AND BIONOMY

## Conservation status, habitats, bionomy, food plants and life cycle

Euphydryas maturna belongs to the most significant European butterflies from conservation biological points of view. Although about 20% of the European butterfly species are threatened to some extent (VAN SWAAY et al. 2010), only one species is qualified as Regionally Extinct (RE Aricia hyacinthus), three species are as Critically Endangered (CE Pieris wollastoni, Coenonympha phyrne, Pseudochazara cingovskii), twelve species as Endangered (E Pieris cheiranthi, Colias myrmidone, Gonepteryx maderensis, Lycaena helle, Phengaris (Maculinea) arion, Plebejus zuellichi, Polyommatus humedasae, Turanana taygetica, Boloria improba, *Coenonympha oedippus, Pararge xyphia, Pseudochazara euxina*) and twenty-two species as Vulnerable (VU, e.g. also *Euphydryas maturna*). These recent evaluations are partly in contradiction with the Annexes II–IV of the Habitats Directive.

Some of these threatened species inhabit light-penetrated, sparse deciduous forests or forest-scrub-grassland mosaics, mostly in continental temperate Europe as *Parnassius mnemosyne*, *Leptidea morsei*, *Euphydryas maturna*, *Coenonympha hero* and *Lopinga achine*. The number of declining woodland species is, however, considerably higher (VAN SWAAY & WARREN 1999, BENES & KONVIČKA 2002, VAN SWAAY *et al.* 2010). Open woodlands suitable for these butterflies had been maintained for centuries by historical forest management, such as coppicing and forest pasture (WARREN 1985, 1987, BUCKLEY 1992, SPARKS *et al.* 1994, KONVIČKA & KURAS 1999, BERGMAN 2001, KONVIČKA *et al.* 2005, BENES *et al.* 2006, FREESE *et al.* 2006). In contrast, large-surface clear-cutting and high-forest management creates unsuitable conditions for these species (WARREN & KEY 1991, GREATOREX-DAVIES *et al.* 1993, MEGLÉCZ *et al.* 1997, 1999, WAHLBERG *et al.* 2003, FREESE *et al.* 2006, LIEGL & DOLEK 2006).

*Euphydryas maturna* shows a significant restriction in its range and a severe decline in population size all over Europe, with the exception of some areas in Eastern Europe (Ukraine, Russia, probably also Belarus, south-eastern Finland) where the species is often qualified as widely distributed and frequent (WAHL-BERG 1998, 2001*a*, TSHIKOLOVETS *et al.* 2002, TSHIKOLOVETS 2003). It has become extinct from Belgium and Luxembourg and the decline fluctuates between 75–99% in Austria, Czech Republik, France, Germany and Sweden (HASLETT in: VAN HELSDINGEN *et al.* 1996, VAN SWAAY & WARREN 1999). In addition to these general tendencies, local populations exhibit many differences in habitat selection, initial food plant and food plant after hibernation (EBERT & RENNWALD 1985, WEIDEMANN 1985, ELIASSON 1991, VARGA 1995, WAHLBERG 1998, WAHLBERG & ZIMMERMANN 2000, PECSENYE *et al.* 2005, FREESE *et al.* 2006).

In Central Europe (Austria, Czech Republik, Germany) the initial food-plant is frequently *Fraxinus excelsior*, or rarely *Ligustrum vulgare* (FREESE *et al.* 2006). Larvae mostly hatch in mid- or end of June and they have a one-year life cycle with aestivation and hibernation. The food plant preference of larvae after hibernation is different from site to site. They feed on herbaceous plants with iridoid glycosids. Mostly on *Plantago lanceolata* and *Veronica* spp. In northern populations (Finland) the initial food plant is often herbaceous Scrophulariaceae (*Melampyrum pratense, Veronica longifolia*) the caterpillars have also been reared on *Fraxinus excelsior, Lonicera xylosteum* and *Melampyrum pratense* (WAHLBERG 1998, 2001*a,b*, WAHLBERG & ZIMMERMANN 2000). Females alighted were also observed on *Epilobium angustifolium, Anthriscus sylvaticus, Filipendula ulmaria,*  *Rubus idaeus, Melampyrum sylvaticum* but without oviposition. The number of eggs in egg clumps varied between 119 and 321 (WEIDEMANN 1985, 1988, EBERT & RENNWALD 1991, pers. obs. of VARGA). Larvae hatch in these Northern populations late July to mid-August and they hibernate two times.

Populations of the Carpathian Basin and SE Europe are similar to the Central European populations in many respects though they can use several Fraxinus species. In lowland riverine gallery forests F. angustifolia (incl. subsp. pannonica) is the most important food plant while in thermophilous white oak forests F. ornus can serve for oviposition (KOVÁCS 1970, pers. comm., VARGA & SÁNTHA 1973). In some continental lowland oak forests of E Hungary Ligustrum vulgare was regularly observed as initial food plant of E. maturna (VARGA, mscr. NATURA 2000 monitoring report). Nests of gregarious young larvae were mostly observed on sunny forest fringes with southern and south-eastern exposition. Nests were mostly found on young Fraxinus trees in semi-shadowed position between 1.5-4 m. Oviposition on Ligustrum occurs between 0.5-1 m, usually on the under surface of the leaves. Too narrow glides or fringes with northern exposition are unsuitable both for the butterflies and larval nests. After hibernation feeding larvae were mostly found on Veronica hederaefolia and they could be easily reared on this food plant, while V. chamaedrys was neglected (VARGA, mscr. NATURA 2000 monitoring report). Butterflies are only moderately sedentary. Males have a patroulling or posting behaviour alternatively (VARGA 1995). It is unclear, however, how the density of the population can influence the proportion of these behaviour types. It is also poorly known whether density pressure can motivate the butterflies to move from habitat to habitat.

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