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Behavior and oviposition preferences of a black-veined white, *Aporia crataegi* (Lepidoptera: Pieridae)

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Abstract

We studied the behavior and oviposition preferences in *Aporia crataegi*. The study was conducted in a network of dry karst meadows with hedgerows consisted mainly of host plants (*Crataegus monogyna*; *Prunus spinosa*, *Prunus mahaleb*, *Rosa* sp.) between them. We recorded 15 different behaviours that we divided into six categories: (1) behaviours connected to flight (9 different behaviors), resting (2 behaviors); and (3) feeding, (4) courtship, (5) copula and (6) oviposition with one behaviour each. Males proved to spend most of their time on wings patrolling, while females were more sedentary, but still actively flying and searching for nectar sources and oviposition sites. Differences in behaviour between the sexes were less prominent during the morning but increased during the midday and afternoon, as the males became more active but females were resting and feeding more, probably after searching for host plants and egg-laying earlier in the day. Most commonly, *C. monogyna* was chosen for oviposition by females, but we found a single oviposition site on *P. mahaleb* as well. Females lay their eggs in clusters of an average size (AVG±SD/SE) of 34.4±12.8/2.05 eggs, and from a single to up to seven oviposition sites were recorded per host plant. Since the number of eggs in each recorded plant with four or more oviposition sites exceeded an upper limit of eggs laid by a single female reported in literature, females either can lay more eggs or more than one female chose the same host plant. Occupied host plants had similar characteristics as the ones occupied with larvae; females preferably choose smaller shrubs, exposed to the sun with a high percentage (>50%) of a leaf litter coverage underneath them.

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Introduction

Butterflies that exploit different habitats in their adult and juvenile stages are either highly mobile or require different habitat types nearby. During the lifetime of an adult, animals can express different behaviours that can change among different habitat patches (Jugovic *et al*., 2017a). These changes are related to the differential abundance of nectar sources and include thermoregulation and intra- and interspecific communication (Shreeve *et al.,* 2009).

In butterflies, a pattern of flight interacting with resting or basking is important in thermoregulation (Van Dyck and Matthyssen, 1998) as insects are ectothermic organisms. Before each flight, a butterfly has to increase the temperature of the muscles (Josephson, 1981; Heinrich, 1993) above the ambient temperature (up to 34-37°C in several temperate butterflies: Vielmetter, 1958; Douwes, 1976; Rutowski *et al*., 1994; Dreisig, 1995; Van Dyck and Matthysen, 1998) to excess a required minimal value that enables flight and other activities connected to flight. In some species, wing flapping is required to activate the muscles and increase the energy that can be then invested in take-off. This method is energetically costly hence some butterfly species regulate the energy levels by basking (Casey, 1988; Dennis, 1993; Van Dyck and Matthyssen, 1998). There are three general ways of basking in adult butterflies: (i) dorsal basking with widely open wings and their upper (dorsal) side oriented towards the sun, (ii) lateral basking with wings closed and their lower (ventral) side oriented towards the sun, and (iii) reflectance, in which butterflies sunbathe their upper wings but the wings are not widely open (Kingsolver 1985). When a butterfly needs to cool down it can either change the position to be parallel to the sunlight or can move into a shadow (Kingsolver, 1985). Besides behavior, wing morphology is also important in thermoregulation as wings can transfer energy towards the body. Thermic features (*e.g.* absorption) differs among butterfly species (Van Dyck and Matthyssen, 1997) and several other factors influence the flight performance, the size of an insect being one of the most outstanding ones. Insects can produce myogenic heat when flying; this heat is sufficient only in large insects as in larger insects it is lost slowly by convection. High convective heat loss and negligible endogenous heat production is on the other hand characteristic for most of small insects. Nevertheless, small insects need less time to warm up (Shelly and Ludwig, 1985; Heinrich, 1986; Heinrich, 1993). Wing coloration is another important factor in flight performance, and melanism is reported to increase in cooler environments (Watt, 1968; Guppy, 1986). Nevertheless, coloration and wing patterns can also be used for mate signaling or predator avoidance and evasion (Dennis *et al*., 1986; Ho *et al*., 2016). It has been noticed that even small differences in colors can affect which behavior will prevail in different ecotypes (*e.g. Pararge aegeria*: Van Dyck and Matthyssen, 1998).

Restoring energy in butterflies is important for investments in other activities. Feeding is therefore very important in highly active and mobile species, which can invest their energy in dispersal, searching for mates, courtship and copulating. Sexual dimorphism in behavior is common in butterflies as females usually need to seek for appropriate oviposition sites, while males invest more in female seeking. In males, most of their flying activities are connected to mate-locating behavior; most commonly males either actively search for females (patrolling) or wait for them at particular sites (perching) (Scott, 1974). Perching males are often recognized as more territorial, display short flights and are often involved in fights with other individuals (Van Dyck and Matthyssen, 1998). Regarding the oviposition sites, some species (i) lay their eggs directly on the larval host plant (when there is a necessity for quick development or host plants are not abundant) or close by, while (ii) others (especially those that have abundant host plants in the area or overwinter as eggs and larvae later feed on herbaceous plants) are not so choosy and often leave the larvae to seek for their host plant (review in Wiklund, 1984). In species, where females lay their eggs directly on the host plants, females usually detect a suitable host plant if it is visually apparent, but can frequently alight on an unsuitable plant before finding the appropriate one (Wiklund, 1984). The number of eggs laid per batch is different among the species and can be laid singly or in groups (clusters). It has been reported that the optimal size of egg clusters is tightly related to egg densities and can result in different rates of survival in later stages (Ito *et al*., 1982); in some species females lay their eggs singly (or in small groups) but distribute their eggs over a large area (cf. Janz *et al*., 2005).

In *Aporia crataegi*, adults inhabit dry karst meadows where they feed on various nectar sources but need shrublands for their juvenile stages (Jugovic *et al*., 2017a,b). This species needs different species of Rosaceae as its host plants (Merrill *et al*., 2008); among them, numerous species are cultivated and hence this pierid was treated as an economically important pest in the past (*e.g.* Ruszkowski, 1960; Wilbert, 1960; Grichanov, *et al*. 2004) despite its population decline during the modern times (*e.g.* Kuussaari *et al*., 2007; Asher *et al*., 2001; Jugovic *et al*., 2017a).

Data on the behavior of this species is known from the records during mark-release-recapture studies (Jugovic *et al*., 2017a), however focused recordings of the species behavior remains to be studied. Jugovic *et al*. (2017a) noticed behavioral differences between the sexes; males spent their time on wings and patrolling for the females about 1.6 times more frequently than females, while they were resting much less than females. Feeding was approximately equally frequent in both sexes. Courtship and copula were detected but rare, while oviposition was not recorded despite five seasons of mark-release-recapture study (in years 2012, 2013, 2015, 2017, 2018; Jugovic *et al*., 2017a, Jugovic, unpubl.). Moreover, the trends in behavioral differences between the habitat patches were similar for both sexes. For example, pronounced flying recorded in pasture and overgrown areas with low and high densities of nectar and host plants, respectively, were explained as a more time-consuming food searching (Jugovic *et al*., 2017a). In females, a pronounced flying behavior in such sites can also serve to spread their eggs over a larger area (Garcia-Barros and Fartmann, 2009). On the opposite, flight was less frequently observed at dry karst meadows with rich nectar sources (Jugovic *et al*., 2017a). Available data on the feeding behavior suggest that *A. crataegi* is an opportunistic feeder (Jugovic *et al*., 2017a, Stefanescu and Traveset, 2009).

Ovipositing behavior and selection of ovipositing plants have only rarely been studied in *A. crataegi*. It is however known that females lay yellow eggs on larval host plants in large groups (up to ca. 100) and larvae hatch after approximately two weeks. They live gregariously in a silken web from which they emerge to feed and hibernate within the silky nest during the winter. In spring, they continue to live gregariously, feed and grow, then they spread around before they pupate (Emmet and Heath, 1989; Merrill *et al*., 2008). Merill *et al*. (2008) studied the elevation distribution of *A. crataegi*, also by searching for oviposition sites. They found out that at lower elevations, the north side (expected to correspond to cooler microclimates) of host plants was more frequently selected while at higher elevations the north side was less frequently selected. A study on the larval preferences of *A. crataegi* (Jugovic *et al*., 2017b) suggests that in the area investigated in the present study, larvae feed on four host plants (commonly on *Crataegus monogyna* and *Prunus spinosa*, and very rarely on *Prunus mahaleb* and *Rosa* sp.) and prefer smaller host plants exposed to the sun on dry karst meadows over pastures and overgrown areas.

In the present study, we focused on the behavior of *A. crataegi* by tracking the animals during three time-intervals (morning, midday, afternoon) and searching for the oviposition sites to fill in the missing gap in knowledge. We addressed these further questions: (1) do males and females express different behaviors, (2) do the behavior change during the day, (3) do females seek host plants for oviposition and (4) what are their preferred oviposition sites? We hypothesized that (1) females as in many other butterflies are more sedentary (Jugovic *et al*., 2018) whereas males are more mobile and use patrolling as a mate-locating strategy (Čelik *et al*., 2009). We predicted that (2) due to lower morning temperatures butterflies will express more sedentary and feeding behaviors (activities related to restoration of energy) while during the day other activities will be more pronounced (Jugovic *et al*., 2018). We also predicted that (3) females will seek for host plants for oviposition and (4) that the habitat and microhabitat conditions of the oviposition sites will be similar to those preferred by larvae (Jugovic *et al*., 2017b).

Materials and Methods

Study site

The study was conducted on a single habitat patch of *A. crataegi* near Rakitovec (SE Slovenia, Municipality of Koper) that was selected from three habitat patches where mark-release recapture and study of larval preferences were studied in 2012 and 2013, respectively (*i.e.* patches named R1, R2, Z in Jugovic *et al.*, 2017a,b). The patch R2 (45°28′ 52″ N, 13°56′35″ E; Jugovic *et al.*, 2017a,b) was selected due to high densities of butterflies in relation to other two patches, and abundance of two most commonly used host plants (*C. monogyna* and *P. spinosa*; Jugovic *et al.*, 2017b). The peak total seasonal density in 2012 was 72 (95% CI: 55-88) butterflies per hectare for the three patches together and peak density of captures was 32.4 males and 26.4 females per hectare in the selected patch which was at least two times higher than at any other studied patch that year (Jugovic *et al.*, 2017a). Density of *C. monogyna* and *P. spinosa* in R2 were 30.9 and 33.0 plants per hectare (derived from Jugovic *et al.*, 2017b).

The selected site (5.18 ha) is a dry karst meadow in a depression at an elevation of 500-520 m a.s.l. and is subdivided into small subpatches by hedgerows that are constituted mainly of *C. monogyna* and *P. spinosa*.

Field work

In the period from 18th May until 22nd June 2017 we tracked the individual animals and recorded their behaviors. Before the data collection for the statistical analysis, animals were randomly tracked to fulfil the list of possible behaviors. Additional behaviors that were not recorded during this time but were recorded during the mark-release-recapture study in 2012 (Jugovic *et al.*, 2017a) were added to the list. For statistical analysis, animals were tracked during three time-intervals: in the morning (8:30 - 10:30 am), midday (11:30 am - 13:30 pm), and afternoon (14:30 - 16:30 pm). Each male and female were tracked for 5 and 20 minutes, respectively; when the animal was too quick to follow tracking time was shorter; however only data for butterflies that were tracked over two minutes were included in data analysis. Females were tracked for a longer period than males because we tried to detect oviposition beside other more frequent behaviors. Observations were carried out only on sunny, non-windy days with the highest air temperature over 20°C (mornings were always cooler than middays and afternoons). The recorded data included the sequence of behaviors and the duration of each behavior (in seconds), divided by males and females, and three time-intervals.

Since oviposition was rarely recorded during the animal tracking, we then searched for oviposition sites on the host plants to enlarge the dataset. For each host plant we then recorded geographic coordinates (Garmin Oregon 200, precision ≤5 m) and eight parameters on the macrohabitat level (Table 1) that described the general environmental conditions or were related to spatial location, regardless of whether animals were present or not. When an oviposition site was found, four additional microhabitat parameters were recorded (Table 1). Additionally, the side of the leaf on which eggs were located (upper side or under side) was recorded for egg batches. Finally, the number of eggs per oviposition site and the number of oviposition sites per each host plant were also counted.

Statistical analysis

A list of different behaviors was compiled and an ethogram was constructed. The relative duration of each behavior was presented. Regarding the behavior frequencies, we tested for possible differences (Likelihood ratio statistics, Chi-square test for homogeneity, significance accepted at $P<0.05$) in behaviors between males and females (whole dataset and separately for each part of the day) and three parts of the day (separately for males and females). Standardized residuals (SR) were used to define the significant contributors to the total Chi-square value; only cells with $|SR|>2.0$ were treated as significant.

Before the analysis of the oviposition preferences, macro- and microhabitat parameters were categorized in evenly wide groups for the purpose of Chi square testing. We first compared eight parameters at the macrohabitat level recorded from occupied and unoccupied (control) host plants. Also here, the likelihood statistics ($P<0.05$) with SRs was used to conclude possible significant differences between two groups of host plants. For the three plant dimensions (Table 1), also a one-way T-test between occupied and unoccupied host plants was performed (significance was accepted at $P<0.05$). After that, oviposition preferences at the microhabitat level were assessed by testing the egg-batch distribution for homogeneity. The Pearson Chi-square test was used and the significance level was set at $P<0.05$.

An average number of eggs laid in a group with standard error, standard deviation and range of values (min-max) was calculated for each host plant species. To detect a possible correlation between the number of oviposition sites and the number of laid eggs per host plant we calculated a linear correlation between the two parameters.

Table 1. A list of recorded parameters at oviposition sites (OS) of *A. crataegi*.

Parameter	Type	Levels
Macrohabitat level		
Host plant height (cm)	Continuous	5 (45-65 cm; 65-85 cm; 85-105 cm; 105-125 cm; >125 cm)
Host plant shortest diameter (cm)	Continuous	4 (0-40 cm; 40-80 cm; 80-120 cm; >120 cm)
Host plant longest diameter (cm)	Continuous	5 (10-35 cm; 35-60 cm, 60-85 cm; 85-110 cm; >110 cm)
Aspect	Categorical	5 (Flat, N [305°≤azimuth<45°]; E [45°≤azimuth<135°]; S [135°≤azimuth<225°]; W [225°≤azimuth<305°])
Light conditions	Categorical	3 (sun, half shade, full shade)
Herbal layer (% of coverage underneath)	Continuous	4 (0-25 %, 25-50 %, 50-75 %; 75-100 %)
Other shrubs (% at 5×5 m^2 around the host plant)	Continuous	4 (0-25 %, 25-50 %, 50-75 %; 75-100 %)
Leaf litter (% of coverage underneath)	Continuous	4 (0-25 %, 25-50 %, 50-75 %; 75-100 %)
Microhabitat level		
Distance of OS from the ground, cm	Continuous	5 (25-36 cm; 36-47 cm; 47-58 cm; 58-69 cm; 69-80 cm)
Distance of OS from the tip of the branch, cm	Continuous	5 (0-10 cm; 10-20 cm; 20-30 cm; 30-40 cm; 40-50 cm)
Distance of OS from the tip of the leaf, mm	Continuous	5 (0-2 mm, 2-4 mm, 4-6 mm, 6-8 mm, 8-10 mm)
No. of leaf from the tip of the branch	Counted	5 (0-5; 6-10; 11-15; 16-20; 21-25)

Results

Behavior

During the present study, we recorded 15 different behaviors of *A. crataegi* in total that we divided into six categories: (1) behaviors connected to flight (nine behaviors), (2) feeding, (3) resting, (4) courtship, (5) copula and (6) oviposition (Table 2). Flying behaviors were most diverse and in some cases include also individuals with whom the observed individual was in contact. Courtship and copula necessarily included a pair of a male and a female, whereas oviposition is limited to females. Additional behavior that could be assigned to a resting category was observed: up to over 10 (or even more) animals of both sexes aggregated together on a single herbaceous plant (*e.g. Trifolium* sp.) and stayed so during the night, as these aggregates could be detected early next morning.

Only one copula (during midday) was observed but was tracked for 20 minutes, and for most of the time (90%) the pair was still and resting on vegetation (Poaceae, *Knautia illyrica*) but was flying for 45 seconds (3.8 %). During the flight, the female was leading and dragging a male with her.

Oviposition was observed only once (during midday): before the oviposition took place, a female flew around a few host plants (*C. monogyna*), obviously searching for the suitable ovipositing site. We were recording its behavior for 15 minutes. A female was circling (in flight) around smaller host plants with frequent landing and resting (usually flapping with wings in the meantime) in between; when the female found a suitable site, started to bend the abdomen towards the host plant's leaf and laid eggs immediately afterwards. The first egg-laying occasion lasted for 172 seconds and was followed by a 9-seconds long pause and another (shorter) egg-laying occasion (21 seconds) at the same leaf. After a longer resting that followed the second oviposition, the female flew away in a quick flight. This female laid 48 and 10 eggs during the first and second observed oviposition, respectively.

Regarding the duration of behavior categories, we noticed that in males flying behaviors were most common (58% of all behaviors, most commonly in quick flight on long distances: 30%), while females flew only for a quarter of their time (28%). Feeding in both sexes was also frequent (28% and 25% of the time in males and females, respectively). Other common behaviors in females were also resting (20 % of the time) and courtship (26 %), however in males these two behaviors (8% and 6%, respectively) were less frequent.

In terms of behavior categories regarding the three parts of the day (morning, midday, afternoon) and sex, the frequencies of the behaviors were statistically different between the sexes and parts of the day ($P<0.001$). Feeding was the only behavior that is similarly common in both sexes (Table 3: data for the whole day together). There were also differences in behavior between the sexes during each of the three parts of the day ($P<0.05$; Table 3).

Contrary we found no statistical differences in behavior frequencies among the three parts of the day in males ($P>0.05$). Nevertheless, such a difference was found in females ($P<0.01$; Table 4). During the midday time females were observed to be involved in courtship more frequently than expected (SR=1.7) but during the afternoon they were feeding more frequently than expected (SR=1.9).

Oviposition

Although four species of Rosaceae (*Crataegus monogyna*, *Prunus spinosa*, *Prunus mahaleb*, and *Rosa* sp.) were recorded as host plants in the wider area of the present study, oviposition sites were observed only at *C. monogyna* (N=13) and exceptionally at *P. mahaleb* (N=1; excluded from the further statistical analysis due to a single case, where the number of laid eggs in a single cluster was 26). Eggs were laid on the upper side of the leaves without exceptions. Females chose smaller host plants (T-test: height, $P<0.01$, shortest diameter, $P<0.05$, longest diameter, $P>0.05$) than the randomly chosen unoccupied control plants (Figure 1). Further, chosen plants did not differ from control ones ($P>0.05$) in the cover of herbal layer and leaf litter underneath the host plants, and other shrubs' cover around the investigated shrubs (5×5 m quadrant with

Table 2. A list of 15 different behaviours in *A. crataegi* divided in six categories. Since copula and oviposition were scarcely observed, only behaviour categories 1-4 were statistically analysed (+: behaviour present but scarce; <0.5 %). Values truncated to the nearest integers. *data from mark-release-recapture study in 2012 (Jugovic *et al.*, 2017a).

Behaviour category	Abbr.		Behaviour	Abbr.	Males (%)	Females (%)
1. Behaviours connected to flights	(F)	1	Slow flight on short distances	(Fls)	22	11
		2	Quick flights, long distances	(Flf)	30	14
		3	Another *A. crataegi* individual chases the observed individual	(Cs1)	1	2
		4	An individual of another butterfly species chases the observed individual	(Ca1)	1	+
		5	Observed individual chases another *A. crataegi* individual	(Cs2)	3	+
		6	Observed individual chases individual of another butterfly species	(Ca2)		
		7	Chasing of three or more butterfly individuals	(C3)	1	1
		8	Two *A. crataegi* individuals approch each other in flight, almost interaction	(Is)	+	+
		9	Observed individual approaches to an individual of another butterfly species, almost interaction (and *vice versa*)	(Ia)	+	+
2. Feeding	(Fe)	10	Feeding	(Fe)	28	25
3. Resting	(R)	11	Resting	(R)	8	21
		12	*Aggregating in groups in herbaceous plants before the sunset, preparing to overnight	(A)	+	+
4. Courtship	(Cp)	13	Courtship	(Cp)	6	26
5. Copula	(Co)	14	Copula	(Co)	+	+
6. Oviposition	(O)	15	Oviposition	(O)		+

an investigated plant in the center). There was also no statistically significant difference in aspect (P>0.1) of occupied and control host plants, however, the difference is expressed in light conditions (P<0.01) meaning that all plants with oviposition sites were exposed to full sun.

In occupied host plants we noticed significant deviations in data from uniform distribution (Table 5) in all eight measured parameters (P<0.05). Ovipositing females preferred smaller host plants (height, shortest and longest diameters) on sunny places exposed to south or east with herbal vegetation and leaf litter underneath exceeding 50% of coverage but with a low percentage of coverage by other shrubs (mostly <50%) nearby.

Females most commonly laid the eggs on *C. monogyna* 47 to 58 cm (P<0.05) above the ground, in distance from the tip of the branch less than 10 cm (P<0.01) which corresponds to the 7th bundle of leaves or less from the tip of the branch (P<0.05). The position of eggs on the leaf surface was in most cases similar (P>0.05) and these data are uniformly distributed.

On average, females laid 34.4±12.8/2.05 (AVG ± SD/SE) eggs in a group ranging from 5 to 58 (most commonly 30-50 eggs) on the upper side of a leaf (number of observed oviposition sites = 39; Figure 2a). There were only four cases when females laid 10 or fewer eggs. We never recorded a single female to lay eggs at more than one ovipositing site. The highest number of ovipositing sites recorded on a single plant was seven, and this case was observed only once, resulting also in the highest number of eggs (N=261) per plant. In general, the number of eggs per plant increased with the number of ovipositing sites on it (P<0.001; Figure 2b).

Discussion

This study showed that behavior in *A. crataegi* from SW Slovenia is sexually related: males fly more and rest less than females, and the behavior changes during the day. Females were only rarely observed to lay eggs and the observations were almost exclusively recorded on a single species (*C. monogyna*) out of four host plant species in the area (Jugovic *et al*., 2017b). Chosen oviposition sites are in line with main conclusions on larval preferences from the same area (Jugovic *et al*., 2017b), meaning that most probably larvae do not spread around shortly after they are hatched.

Table 3. Absolute (N) and relative (%) frequencies of four behaviour categories in males and females of *A. crataegi* in SW Slovenia in 2017. Likelihood ratio statistics (LR) are shown for comparison of absolute frequencies between males and females in total data set (a), and between males and females for the morning (b), midday (c) and afternoon (d) observations.

		(a) Total						(b) Morning						(c) Midday						(d) Afternoon					
		Males (705)			Females (608)			Males (155)			Females (145)			Males (447)			Females (163)			Males (103)			Females (300)		
		N	%	SR	N	%	SR	N	%	SR	N	%	SR	N	%	SR	N	%	SR	N	%	SR	N	%	SR
% per behaviour	Flight	446	63.3	*2.2*	301	49.5	*-2.4*	98	63.2	0.6	80	55.2	-0.7	286	64.0	0.9	83	50.9	-1.6	62	60.2	1.5	138	46.0	-0.9
	Feeding	226	32.1	-0.9	222	36.5	1.0	50	32.3	0.1	46	31.7	-0.1	136	30.4	0.2	47	28.8	-0.3	40	38.8	-0.5	129	43.0	0.3
	Resting	26	3.7	*-2.7*	55	9.0	*2.9*	5	3.2	-1.8	16	11.0	1.8	20	4.5	-1.7	20	12.3	*2.8*	1	1.0	-1.8	19	6.3	1.1
	Courtship	7	1	*-2.9*	30	4.9	*3.1*	2	1.3	-0.4	3	2.1	0.4	5	1.1	*-2.3*	13	8.0	*3.7*	0	0.0	-1.9	14	4.7	1.1
% per sex	Flight		59.7			40.3			55.1			44.9			77.5			22.5			31.0			69.0	
	Feeding		50.4			49.6			52.1			47.9			74.3			25.7			23.7			76.3	
	Resting		32.1			67.9			23.8			76.2			50.0			50.0			5.0			95.0	
	Courtship		18.9			81.1			40.0			60.0			27.8			72.2			0.0			100.0	

Significant contributions (standard residuals, |SR|>2) are marked in italics. χ^2 for the above categories are as follows: a) LR=47.21, df=3, P<0.001; b) LR=7.92, df=3, P<0.05; c) LR=29.52, df=3, P<0.001; d) LR=17.57, df=3, P<0.001.

Table 4. Absolute (N) and relative (%) frequencies of four behaviour categories in males (a) and females (b) of *A. crataegi* in SW Slovenia in 2017. Likelihood ratio statistics (LR) are shown for comparison of absolute frequencies between the three daily intervals (morning, midday and afternoon) observations

		(a) Males									(b) Females								
		Morning (155)			Midday (447)			Afternoon (103)			Morning (145)			Midday (163)			Afternoon (300)		
		N	%	SR	N	%	SR	N	%	SR	N	%	SR	N	%	SR	N	%	SR
% per behaviour	Flight	98	63.2	0.0	286	64.0	0.2	62	60.2	-0.4	80	55.2	1.0	83	50.9	0.3	138	46.0	-0.9
	Feeding	50	32.3	0.0	136	30.4	-0.6	40	38.8	1.2	46	31.7	-1.0	47	28.8	-1.6	129	43.0	1.9
	Resting	5	3.2	-0.3	20	4.5	0.9	1	1.0	-1.4	16	11.0	0.8	20	12.3	1.4	19	6.3	-1.6
	Courtship	2	1.3	0.4	5	1.1	0.3	0	0.0	-1.0	3	2.1	-1.6	13	8.0	1.7	14	4.7	-0.2
% per part of the day	Flight		22.0			64.1			13.9			26.6			27.6			45.8	
	Feeding		22.1			60.2			17.7			20.7			21.2			58.1	
	Resting		19.2			76.9			3.8			29.1			36.4			34.5	
	Courtship		28.6			71.4			0.0			10.0			43.3			46.7	

χ^2 for the above categories are as follows: a) LR=7.91, df=6, P>0.05; b) LR=19.51, df=6, P<0.01.

Behavior

Behaviors connected to flight were expectedly most diverse of all recorded behaviors as butterflies rely on flight for most of their activities, since (1) males and females should be able to find each other and mate, (2) females should find a suitable oviposition site that enables the larvae to locate their host plants, and (3) adults should be able to locate nectar plants in order to live long enough to perform both of the above activities (Wiklund, 1981). Despite the highest proportion of all recorded behaviors (males 58%, females 28%), flying activity in *A. crataegi* males is relatively low in comparison to some other males of Pierid and Nymphalid butterflies (*e.g. Pieris napi*, *Antocharis cardamines*, *Melanargia galathea*; all with >70% of their time spent in flight, followed by *Maniloa jurtina* and *Pyronia tytonius*; mostly with >60%; Dennis and Shreeve, 2003). On the other hand, males in another Nymphalid *Lasiommata megera* expresses a similar proportion of flight behaviors (ca. 60%, but with a wide range; Dennis and Shreeve, 2003). The most common flying behavior in *A. crataegi* is flight over long distances (behavior 1 in Table 2) proving that this butterfly is highly mobile species (Jugovic *et al*., 2017a). This behavior arguably serves for dispersion over a large area enabling the species to overcome longer distances over an unsuitable matrix (Jugovic *et al*., 2017a) in search for mating opportunities (males; Dennis and Shreeve, 2003), suitable oviposition patches (females; Jugovic *et al*., 2017b) and nectar sources (both sexes; Jugovic *et al*., 2017a). While on a suitable habitat patch, males express their patrolling behavior while searching for females, and females search for suitable host plants for oviposition (behavior 2). The same slow flight is often related to feeding that involves flying from one nectar plant to another within a patch. Nevertheless, no perching behavior was recorded in this species. On a species level, perching was predominant in a lightly colored Belgian *Pararge aegeria* ecotype, while another ecotype of darker males is mostly patrollers (Van Dyck and Matthyssen, 1998). The warmer climate in Slovenia and larger body size (see references in Introduction) of *A. crataegi* arguably contribute to a substantial increase of body temperature and can compensate for their light (white) coloration. Further, a complete lack of records for *A. crataegi* basking can also be linked to their large body size and warm climate, and heating up

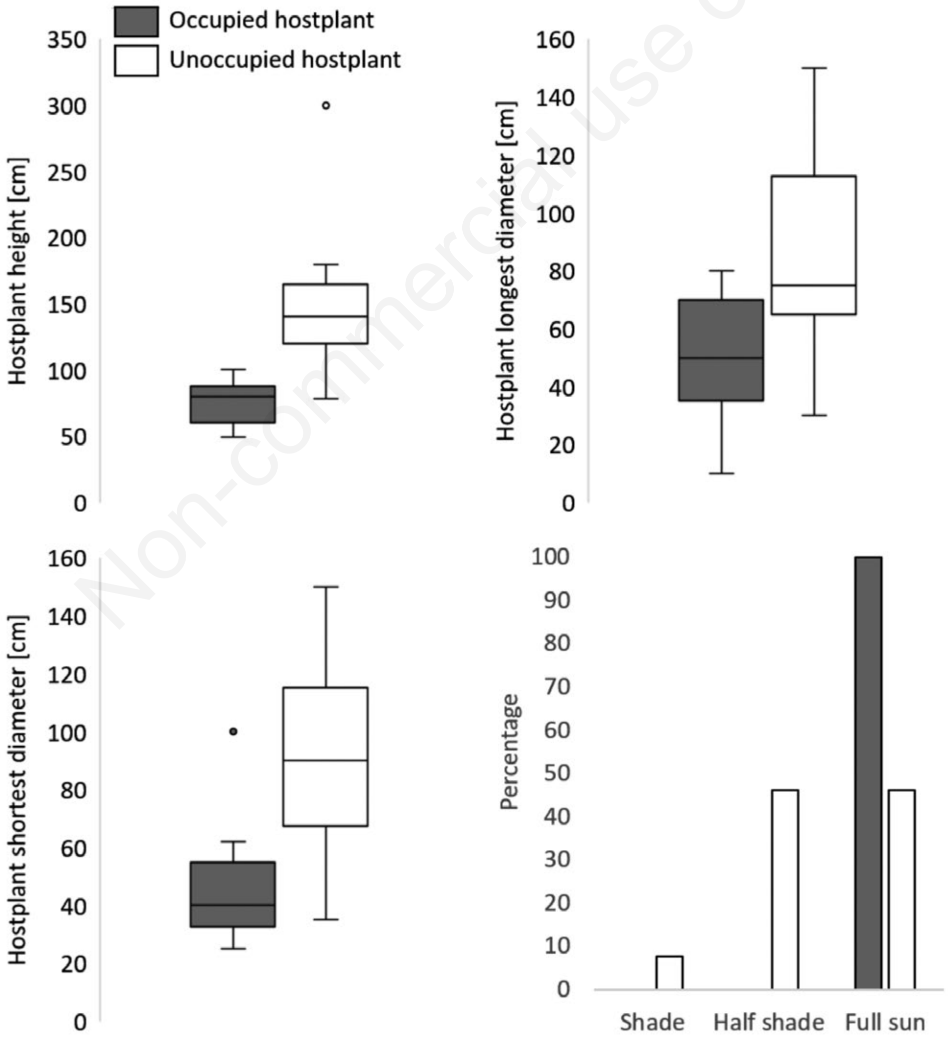

Figure 1. Box-plot diagrams for distribution of three dimensions (height, longest and shortest diameters) in occupied and unoccupied host plants (*C. monogyna*; ANOVA: height – P<0.001; shortest diameter – P<0.05; longest diameter – P>0.05) and the distribution of light conditions (shade, half shade, full sun) at occupied and unoccupied host plants of *A. crataegi* in SW Slovenia in 2017.

during resting and/or feeding could sufficiently supply the energetic demands of a butterfly. Interactions between the butterflies can be expressed in a way that the observed specimen is chased by other *A. crataegi* butterflies, which is twice as often in females than males, and in most of these cases a male follows a female, probably trying to mate afterwards (behaviors 3 and 5 in Table 2). As shown during our study, other butterfly species can also chase *A. crataegi* butterflies; chasing the individuals of other butterfly species can be a result of expressed territoriality (*e.g. Hypolimnas bolina*: Kemp, 2000; *V. atalanta:* Shields, 1967; Dimock, 1978; Swanson, 1979; Bitzer and Shaw, 1979; Alcock, 1984; Opler and Krizek, 1984; Brown and Alcock, 1991; *C. pamphilus*: Wickman, 1985a,b). In the vast majority of the observed interactions, *Melanargia galathea* that was at its peak in June chased the *A. crataegi* butterflies. Without targeting observations, true territoriality in some butterfly species however, remains controversial, as some butterflies may approach other specimens merely to identify their species and sex (Scott, 1974; Suzuki, 1976). Territoriality in butterflies is often associated with perching (on rocks, trees, shrubs, hilltops, or on flat ground and waiting for females to fly by) rather than patrolling behavior. Since in *A. crataegi*, no perching behavior was recorded and long-distance movements (patrolling in males) are prevailing, this is arguably not a territorial species, which also proves scarce observations on chasing other butterfly species (behavior 6), and moreover, aggregating before the sunset. Also, few observations on the interaction of three or more butterflies most probably uncover attempts of the males to recognize conspecific females (behavior 7). When the recognition is instant, no actual interaction is needed (behaviors 8 and 9). The latter two behaviors are less frequent than the behaviors connected to an actual interaction (behaviors 3-7) indicating that actual interaction is often needed for butterflies to recognize the other specimens' identity.

The second most common behaviors are feeding and courtship in males and females, respectively, with feeding in females closely behind. In *A. crataegi*, feeding is well expressed as this butterfly species is quite large and needs energy to perform all the activities. Since it can live for a long period (up to 21 with an average of 7.1-7.5 days; Jugovic *et al*., 2017a), restoration of energy loses is necessary. Although there is no statistically significant difference in feeding between males and females, the gathered energy is most probably differently distributed in each sex. While females have to maturate eggs, males exploit this energy for actively patrolling and additional locating of nectar sources. Females are larger and weaker fliers; hence the proportion of resting is much larger in females than in males. Females are much more often seen involved in courtship as many males attempt to mate with a single female, checking her readiness to mate. Copulae were seen more often by chance (*e.g.* Jugovic *et al*., 2017a, unpubl. data) than as a result of individual tracking. A pair can persist in a copula for more than

Table 5. Results of Chi-square tests for homogeneity for analysing the distribution of ovipositing sites (OS) of *A. crataegi* at two levels.

	χ^2	df	P	Eggs laid
Habitat level				
Host plant height	9.69	4	*	commonly 40–90 cm
Host plant shortest diameter	10.08	3	*	commonly 30–70 cm
Host plant longest diameter	9.69	4	*	commonly 30–70 cm
Aspect	11.23	4	*	commonly south or east
Light conditions	26.0	2	***	only under full sun
Herbal layer	8.23	3	*	commonly >50% covered
Other shrubs	8.23	3	*	<75% of coverage
Leaf litter	20.54	3	***	>50 % of litter coverage
Microhabitat level				
Distance of OS from the ground	11.64	4	*	commonly 47-58 cm
Distance of OS from the tip of the branch	42.67	4	***	≤10 cm
Distance OS from the tip of the leaf	6.00	4	NS	
No. of leaf bundles from the tip of the branch	12.41	4	*	≤7

***P<0.001; **P<0.01; *P<0.05; NS, not significant.

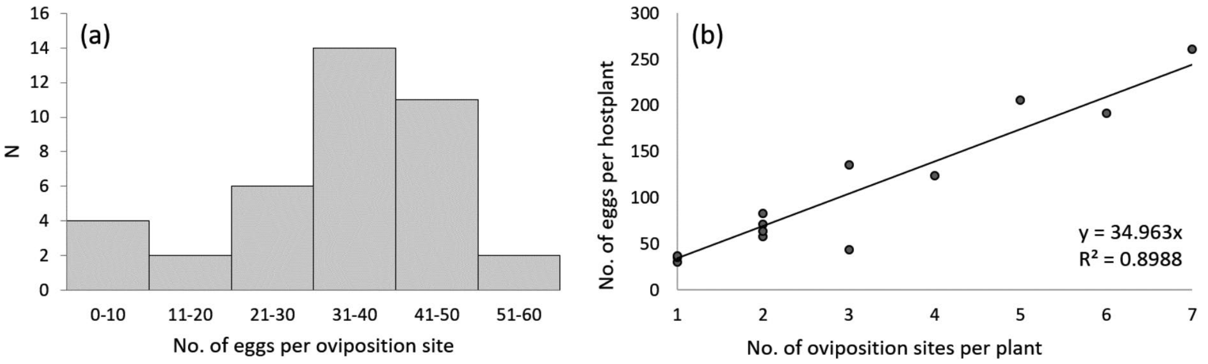

Figure 2. The distribution of batch size classes per oviposition site (a) and a linear relationship between the number of oviposition sites per host plant (*C. monogyna*) and the number of eggs per host plant of *A. crataegi* in SW Slovenia in 2017.

half an hour and the pair usually rests on vegetation during that period. When disturbed, a pair can fly over shorter distances until it rests again. During these flights, females are the strongest fliers of the pair and usually drag males with them (Jugovic, personal observations). While this behavior in Pieridae is rare, it has already been observed for the herein studied species. In other pierid species with an exception of *Gonepteryx rhamni* and *Leptidea sinapis* in which neither sex exhibits any tendency to take flight when disturbed during copulation, the male always carries the female when flying in copula (Wiklund and Forsberg, 1991). During the mark-release-recapture study (Jugovic *et al*., 2017a; personal observations), careful handling and marking of the animals did not result in breaking the copulating pair apart. In some cases, a pair with at least one already marked individual was found, which indicates the marking procedure does not negatively impact the reproduction of this species.

Interestingly, differences in behavior between males and females are more pronounced at midday and in the afternoon than in the morning. Although the distribution of behavior frequencies did not depart from the expected values during the morning hours, a large difference was found in resting between males and females. Females prove to be more sedentary (resting SR=1.8), while males started to fly and search for females already during this period of the day (resting SR=-1.8; absolute difference of 3.6). The difference between males and females considering the same behavior further increases during the midday (males SR=-1.7; females SR=2.8, absolute difference 4.5) but decrease in the afternoon (males SR=-1.7; females SR=1.1, absolute difference 2.8). This result together with increased sexual difference in flying performance during the midday in the opposite direction (males SR=0.9; females SR=-1.6, absolute difference 2.5) and afternoon (males SR=1.5; females SR=-0.9, absolute difference 2.4), where males are much more frequently observed in flight than females, indicates that the intensity of patrolling increases with increased temperature (Wickman, 1985b; see also Kingsolver, 1983). Although frequencies of feeding behavior do not deviate from the expected values, it has been noticed that in males feeding is more pronounced in midday than in females, while in females it is much more pronounced in the afternoon. This may be the result of a quicker energy loss in males owing to their higher activity while in females a pronounced feeding in the afternoon is necessary to recover from courtship, copulating, searching for suitable oviposition sites and egg-laying earlier in the day.

Oviposition

Oviposition sites were mainly recorded on *C. monogyna* but exceptionally also on *P. mahaleb*. Despite the latter being observed only once during the present study, this case can support one of the ovipositing behavior (Wiklund, 1984); females usually detect larval host plants visually when they are apparent but if the color cue is important (*Pieris brassicae*; Ito *et al*., 1982), a female can also lay eggs on another substrate similar to the most suitable host plant. This could be the case of the recorded oviposition site on *Prunus mahaleb* during our study. Although also larvae had been exceptionally found on this plant [only 0.6 % (N=2) of occupied host plants were represented by this species, N=362: Jugovic *et al*., 2017b] no traces or direct observations of feeding on it were seen (Jugovic, personal observations). No egg clusters were found on *P. spinosa* despite being equally abundant as *C. monogyna* at the site. Nevertheless, shrubs of *P. spinosa* there are larger than shrubs of *C. monogyna* (Jugovic *et al*., 2017b) and grow in denser groups. The difference in size can play an important role in the selection of a site for oviposition by a female since smaller shrubs well exposed to the sun are preferentially chosen.

Female preferences for specific sites on a host plant level and its surrounding have been already reported in *A. crataegi* and other Pieridae (*e.g*. Merill *et al*., 2008; Čelik, 2013). In our case, the vast majority of parameters (11 out of 12) significantly departed from homogeneity. From those, most departing parameters (with P<0.001) were light conditions, coverage with leaf litter and distance of oviposition site from the tip of the branch. These results are all in line with the study on larval preferences of *A. crataegi* on *C. monogyna*, where larvae were detected mostly on full sun (83%), some findings were in half shade (17%), but none were in full shade (in *P. spinosa*, the percentages are 83.5, 16.0 and 0.5%, respectively; data derived from Jugovic *et al*., 2017b; Jugovic, unpublished). Since all oviposition sites were found at the full sun, the small discrepancy between the two studies can be attributed to that larvae are mobile while eggs are attached to a leaf. Still, a requirement for a warm microhabitat during the juvenile stages is confirmed as larvae were observed to bask (Jugovic *et al*., 2017b). Moreover, same authors argued that ground conditions probably reflect general micro-climate conditions experienced by the plants and this feature may be used as a cue for egg-laying females despite no strong support for this variable was found in the study of larval preferences (Jugovic *et al*., 2017b). All the host plants with oviposition sites in the present study, however, had a large proportion of a leaf litter coverage (>50 %) underneath, while the unoccupied plants could have also lower values of this parameter. Despite the small sample size in the present study, the results supported outcome of the previous study on larval microhabitat selection (Jugovic *et al*., 2017b). Further, short distance of oviposition sites from the end of the branches (*i.e*. from the edge of the host plant) again corroborates with short distance of larval webs from the edge of the host plant, confirming need for warmer microhabitats at more exposed sunny places with a small share of coverage with other shrubs that would make shade nearby. Finally, while aspect was not a certain predictor for the presence of larvae, we noticed that females chose mostly south (46% of cases) or east aspects (38%), and host plants were only rarely oriented towards west (8%) or without aspect (on a flat ground, 8%) but never towards north, all that indicating possible avoidance of cooler microhabitats (cf. Merill *et al*., 2008; Jugovic *et al*., 2017b).

Following the literature data that a single female lays up to ca. 100 eggs during her lifetime (Emmet and Heath, 1989; Merrill *et al*., 2008), and that we never found more than 58 eggs per an oviposition site (data exclusively for *C. monogyna*; for a single record of oviposition site on *P. mahaleb* see Results), we believe that a single female lays eggs at least at two sites, but arguably at even more. Unfortunately, we could not record whether this happens on the same host plant or the female flies away to another plant before continues with egg-laying. During our study, a single female that was observed laying the eggs flew far away from the host plant at which the eggs were laid. This observation would be in line with a risk-spreading strategy (Garcia-Barros and Fartmann, 2009) to increase the chances of survival of the offspring. Nevertheless, recordings of several oviposition sites per a single plant do not completely preclude the possibility that at least some separate egg clutches are laid by a single female, although this could also result from several egg-laying females. If the upper limit of ca. 100 eggs per female (*e.g*. Merill *et al*., 2008) is correct, then more females have to choose the same individual host plant at least in cases where the number of eggs per plant exceeded this upper limit. In this case, some females necessarily chose already occupied host plants. The upper limit per plant was in our case exceeded in each plant where we observed four or more oviposition sites. On the other hand, fewer than four egg clutches could be laid by a single female, especially if the number of oviposition events is linked to the number of spermatophores receipted by a single female. Usually one or two, but up to three spermatophores are reported for a Swedish population of *A. crataegi* (Wiklund and Forsberg, 1991). If chemical and visual cues are important in choosing a host plant (*e.g.* as in *Pieris brassicae*: Renwick and Radke, 1988), this could mean two possible explanations: (1) females that lay eggs on occupied host plants are able to sense (through visual and/or chemical cue) a suitable host plant but they neglect eggs laid there before, or (2) eggs that are already laid (and sensed by an approaching female) additionally attract an egg-laying female.

References

ALCOCK J., 1984 - Convergent evolution in perching and patrolling site preferences of some hilltopping insects of the Sonoran Desert. - Southwest. Nat. 29: 475-480.

ASHER J., WARREN M., FOX R., HARDING P., JEFFCOATE G., JEFFCOATE S., 2001 - The millennium atlas of butterflies in Britain and Ireland. Oxford University press, Oxford.

BITZER R.J., SHAW K.C., 1979 - Territorial behavior of the Red Admiral, *Vanessa atalanta* (L.) (Lepidoptera: Nymphalidae). - J. Res. Lepid. 18: 36-49.

BROWN W.D., ALCOCK J., 1991 - Hilltopping by the Red Admiral Butterfly: mate searching alongside congeners. - J. Res. Lepid. 29: 1-10.

CASEY T.M., 1988 - Thermoregulation and heat exchange. - Adv. Insect Physiol. 20: 119-146.

ČELIK T., VREŠ B., SELIŠKAR A., 2009 - Determinants of within-patch microdistribution and movements of endangered butterfly *Coenonympha oedippus* (Fabricius, 1787) (Nymphalidae: Satyrinae). - Hacquetia 8: 115-128.

ČELIK T., 2013 - Oviposition preferences of a threatened butterfly *Leptidea morsei* (Lepidoptera: Pieridae) at the western border of its range. - J. Insect Conserv. 17: 865-876.

DENNIS R.L.H., PORTER K., WILLIAMS W.R., 1986 - Ocellation in *Coenonympha tullia* (Müller) (Lepidoptera: Satyridae). II. Population differentiation and clinal variation in the context of climatically induced antipredator defence strategy. - Entomol. Gaz. 37: 133-172.

DENNIS R.L.H., 1993 - Butterflies and climate change. Manchester University Press, Manchester.

DENNIS R.L.H., SHREEVE T.G., 2003 - Does the Marbled White butterfly *Melanargia galathea*(L.) (Papilionoidea: Satyrinae) behave like a 'white'? - School of Biological and Molecular Sciences, Oxford Brookes University, Headington, Oxford. 7 p.

DIMOCK T.E., 1978 - Notes on the life cycle and natural history of *Vanessa annabella* (Nymphalidae). - J. Lepid. Soc. 32: 88-96.

DOUWES P., 1976 - Activity in *Heodes virgaureae* (Lep., Lycaenidae) in relation to air temperature, solar radiation, and time of day. - Oecologia 22: 287-298.

DREISIG H., 1995 - Thermoregulation and flight activity in territorial male graylings, *Hipparchia semele* (Satyridae), and large skippers, *Ochlodes venata* (Hesperiidae). - Oecologia 101: 169-176.

EMMET A.M., HEATH J., 1989 - The moths and butterflies of Great Britain and Ireland, vol 7, part 1. Harley Books, Colchester.

GARCIA-BARROS E., FARTMANN T., 2009 - Butterfly oviposition: sites, behaviour and modes. In: Settele J, Shreeve T, Konvicka M, van Dyck H, eds. Ecology of butterflies in Europe. Cambridge University press, Cambridge, p 513.

GRICHANOV I.Y., OVSYANNIKOVA E.I., SAULICH M.I., 2004 - Interactive agricultural ecological atlas of Russia and neighbouring countries. Economic plants and their diseases, pests and weeds. Available from: http://www.agroatlas.ru/en/content/pests/Aporia_crataegi/map/. Accessed: 2 February 2019

HEINRICH B 1986 - Comparative thermoregulation of four montane butterflies of different mass. - Physiol. Zool. 59: 616-626.

HEINRICH B., 1993 - The hot-blooded insect. Strategies and mechanisms of thermoregulation. Springer, Berlin, Heidelberg, New York.

HO S., SCHACHAT S.R., PIEL W.H., MONTEIRO A., 2016 - Attack risk for butterflies changes with eyespot number and size. - R. Soc. Open Sci. 3: 150614, 13 pp.

ITÔ, Y., TSUBAKI, Y., OSADA M., 1982 - Why do *Luehdorfia* butterflies lay eggs in clusters? – M. Res. Popul. Ecol. 24: 375.

JANZ N., BERGSTRÖM A., JOHANSSON J., 2005 - Frequency dependence of host plant choice within and between patches: a large cage experiment. - Evol. Ecol. 19: 289-302.

JUGOVIC J., ČRNE M., LUŽNIK M., 2017A - Movement, demography and behavior of a highly mobile species: a case study of *Aporia crataegi* (Lepidoptera: Pieridae). - Eur. J. Entomol. 114: 113-122.

JUGOVIC J., GRANDO M., GENOV T., 2017B - Microhabitat selection of *Aporia crataegi* (Lepidoptera: Pieridae) larvae in a traditionally managed landscape. - J. Insect Conserv. 21: 307-318.

JUGOVIC J., ZUPAN S., BUŽAN E., ČELIK T., 2018 - Variation in the morphology of the wings of the endangered grass-feeding butterfly *Coenonympha oedippus* (Lepidoptera: Nymphalidae) in response to contrasting habitats. - Eur. J. Entomol. 115: 339-353.

KEMP D.J., 2000 - Contest behavior in territorial male butterflies: does size matter? - Behav. Ecol. 11: 591-596.

JOSEPHSON R.K., 1981 - Temperature and the mechanical performance of insect muscle. In: Heinrich B, ed. Insect Thermoregulation. New York: John Wiley and Sons; pp 19-44.

KINGSOLVER J.G., 1983 - Ecological significance of flight activity in *Colias* butterflies: implications for reproductive strategy and population structure. - Ecology 64: 546-551.

KINGSOLVER J.G., 1985 - Butterfly thermoregulation: organismic mechanisms and population consequences. - J. Res. Lepid. 24: 1-20.

KUUSSAARI M., HELIÖLÄ J., PÖYRY J., SAARINEN K., 2007 - Contrasting trends of butterfly species preferring semi-natural grasslands, field margins and forest edges in northern Europe. - J. Insect Conserv. 11: 351-366.

MERRILL R.M., GUTIÉRREZ D., LEWIS O.T., GUTIÉRREZ J., DÍEZ S.B., WILSON R.J., 2008 - Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. - J. Anim. Ecol. 77: 145-155.

OPLER P.A., KRIZEK G.O., 1984 - Butterflies East of the Great Plains. Johns Hopkins University Press, Baltimore.

RENWICK J.A.A., RADKE C.D., 1988 - Sensory cues in host selection for oviposition by the cabbage butterfly, *Pieris rapae*. - J. Insect. Physiol. 34: 251-257.

RUSZKOWSKI A., 1960 - Niestrzep glogowiec (*Aporia crataegi* L.). - Prace Naukowe Instytutu Ochrony Roslin 2: 87-142.

RUTOWSKI R.L., DEMLONG M.J., LEFFINGWELL T., 1994 - Behavioural thermoregulation at mate encounter sites by male butterflies (*Asterocampa leilia*, Nymphalidae). - Anim. Behav. 48: 833-841.

SCOTT J.A., 1974 - Mate-locating behavior of butterflies. - Am. Midl. Nat. 91: 103-117.

SHELLY T.E., LUDWIG D., 1985 - Thermoregulatory behavior of the butterfly *Calisto nubile* (Satyridae) in a Puerto Rican forest. - Oikos 44: 229-233.

SHIELDS O., 1967 - Hilltopping. - J. Res. Lepid. 11: 99-127.

SHREEVE T., KONVIČKA M., VAN DYCK H., 2009 - Functional significance of butterfly wing morphology variation. In: Settele J, Shreeve T, Konvička M, Van Dyck H, eds. Ecology of Butterflies in Europe. Cambridge University Press, Cambridge. pp. 171-188.

STEFANESCU C., TRAVESET A., 2009 - Factors influencing the degree of generalization in flower use by Mediterranean butterflies. - Oikos 118: 1109-1117.

SUZUKI Y., 1976 - So-called territorial behavior of the small copper, *Lycaena phlaeas daimio* Seitz (Lepidoptera: Lycaenidae). - Kontyû Tokyo 44: 193-204.

SWANSON H.F., 1979 - Butterfly Revelations. Rollins Press, Inc., Orlando, Florida.

VAN DYCK H., MATTHYSSEN E., 1998 - Thermoregulatory differences between phenotypes in the speckled wood butterfly: Hot perchers and cold patrollers? - Oecologia 114: 326-334.

VIELMETTER W., 1958 - Physiologie des Verhaltens zur Sonnenstrahlung bei dem Tagfalter *Argynnis paphia* L.: I. Untersuchungen im Freiland. - J. Insect Physiol. 2: 13-37.

WATT W.B., 1968 - Adaptive significance of pigment polymorphisms in *Colias* butterflies. I. Variation of melanin pigment in relation to thermoregulation. - Evolution 22: 437-458.

WICKMAN P.O., 1985a - Territorial defence and mating success in males of the small heath butterfly, *Coenonympha pamphilus* (L.) (Lepidoptera: Satyridae). - Anim. Behav. 33: 1162-1168.

WICKMAN P.O., 1985b - The influence of temperature on the territorial and mate locating behaviour of the small heath butterfly, *Coenonympha pamphilus* (L.) (Lepidoptera: Satyridae). - Behav. Ecol. Sociobiol. 16: 233-238.

WIKLUND C., 1981 - Generalist vs. specialist oviposition behaviour in *Papilio machaon* (Lepidoptera) and functional aspects on the hierarchy of oviposition preferences. - Oikos 36: 163-170.

WIKLUND C., FORSBERG J., 1991 - Sexual size dimorphism in relation to female polygamy and protandry in butterflies: a comparative study of Swedish Pieridae and Satyridae. - Oikos 60: 373-381.

WIKLUND C., 1984 - Egg-laying patterns in butterflies in relation to their phenology and the visual apparency and abundance of their host plants. - Oecologia (Berlin) 63: 23-29.

WILBERT E.L., 1960 - *Apanteles pieridis* (Bouché) (Hym., Braconidae), ein Parasit von *Aporia crataegi* (L.) (Lep., Pieridae). - Entomophaga 5: 183-211.