



Movement, demography and behaviour of a highly mobile species: A case study of the black-veined white, *Aporia crataegi* (Lepidoptera: Pieridae)

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Abstract. We studied the demography, movement, behaviour and choice of nectar plants by adults of *Aporia crataegi*. This study was done in a dense network of different types of habitats (total size of study area 16.26 ha) from open landscape to shrubland, the latter being a result of abandonment of traditional agricultural practices such as extensive mowing and grazing. Total population size was estimated to be approximately 1700 and 2700 for females and males, respectively. Median and maximum distances moved by males were 134 and 3493 m, and by females 138 and 3165 m, respectively. The average lifespan was ca. 7.1 and 7.5 days, with maximum recorded lifespans of 21 and 17 days for males and females, respectively. The greater capture probability recorded for males indicates their high activity, as they spend most of their time in flight patrolling and searching for mates. A parabolic recruitment curve and protandry were also recorded. Both sexes are highly mobile. The spatial distribution of both sexes was roughly similar. The adult behaviour differed in different habitats, with more time spent feeding and resting when nectar plants were plentiful and more time spent flying when they were rare. Although adults utilized nine nectar sources, only two were recorded in over 80% of all the feeding occasions. In order to re-establish open grassland with some shrubland, traditional and mosaic management of the landscape should be revived at least to some extent.

INTRODUCTION

The Mediterranean region, although being under heavy anthropogenic pressure and climate change, remains the stronghold for many European species of wildlife. Although there is only a limited amount of data on long-term trends in the numbers of species of butterflies in the Mediterranean region (Stefanescu et al., 2011a), it reveals alarming trends especially for species inhabiting open types of habitat such as shrubland and grassland (Stefanescu et al., 2011b). Although habitat specialists are undoubtedly declining more than habitat generalist species in temperate and Mediterranean regions (Warren et al., 2001; Stefanescu et al., 2011b; Pennekamp et al., 2014), the decline in generalists should be taken seriously as it usually underestimates the potential risk of extinctions (Van Swaay et al., 2011).

Agricultural activities strongly affect the layout and biodiversity of landscapes. During the last few decades, the intensification of agricultural practices and abandonment of traditional management has dramatically changed landscapes (Zeiler, 2000; Stefanescu et al., 2004). In a mosaic landscape, the destruction of habitats due to the abandon-

ment of traditional management and their fragmentation are two major threats that result in a decrease in the size of habitats and their connectivity (Polus et al., 2006). Therefore, it is crucial to maintain a dense network of suitable habitats that enable wildlife to disperse (Thomas et al., 1992; Mousson et al., 1999; Bergman & Landin, 2001; Anthes et al., 2003; Polus et al., 2006).

A typical butterfly inhabitant of mosaic landscapes (e.g., Tolman & Lewington, 2008; Verovnik et al., 2012), is the black-veined white, *Aporia crataegi* (Linnaeus, 1758). Although the larvae of this species are polyphagous (Kuussaari et al., 2007) and thus should not be very susceptible to habitat destruction, this butterfly species is no exception to the general rule of recent population decrease. This species is usually treated as common and widespread but has suffered several declines in some parts of its distribution in the past. In Great Britain (in 1920s) and recently in the Czech Republic and The Netherlands, its decline is significant (Asher et al., 2001). It is no longer a resident species in Great Britain, where it was once common in the south and the populations there were frequently strengthened by

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immigrations from the continent. Some declines have also been noticed in Central Europe, e.g., in Austria, where it is critically endangered (Koschuh & Gepp, 2004). Despite unexplained local extinctions and the obvious decline in this species, it is still listed as of Least concern (LC) in the European Red List of Butterflies (Van Swaay et al., 2010).

In Slovenia, its area of occupancy throughout the country declined at least by 15% during the last 25 years (Verovnik et al., 2012), leaving the populations outside the southern region, on predominantly carbonate bedrocks, scarce and isolated. In the southern region, however, the maintenance of open and semi-open habitats ceased with the abandonment of traditional grazing, and dry and semi-dry grasslands are now rarely maintained by extensive mowing (Jogan et al., 2004; Kaligarič, 2005) or grazing (Kaligarič, 2005). As a consequence they become overgrown followed by pioneer forests (Jogan et al., 2004; Kaligarič, 2005; Jugovic et al., 2013).

Movement of adults, demographic parameters and behaviour of butterflies can be much altered when habitats change (Merx & Van Dyck, 2005; Brückmann et al., 2011; Weyer & Schmitt, 2013; Pennekamp et al., 2014) and this also significantly affects the genetic structure of the population (e.g., Krauss et al., 2004). It is therefore important to understand (1) whether in a given mosaic landscape a species is capable of moving between patches and to persist as a metapopulation, (2) how it utilizes food resources, and (3) how the distribution of resources and the opposite sex affect behaviour. For conservation purposes, it is therefore indispensable to have knowledge of the ecology of the species in a wide range of habitats in a region.

Here we present a one-season study of a population of *Aporia crataegi* in south-western Slovenia where its distribution is continuous. Our aim was to estimate (1) demographic parameters, behaviour and movements within and between three sites with different types of habitats and (2) utilization of nectar plants.

MATERIAL AND METHODS

Study species

Aporia crataegi is a widespread Palearctic species inhabiting most of Europe and Asia between 40–70°N, including Japan (Tolman & Lewington, 2008). Its flight period lasts from April to July, depending on location and weather conditions (Tolman & Lewington, 2008; Verovnik et al., 2012). In Europe, this species inhabits different habitats, but predominantly dry grassland, woodland edges and shrubland (Tolman & Lewington, 2008), where larval hostplants (e.g., *Prunus* spp., *Crataegus* spp.) and nectar plants (Asher et al., 2001) occur. Females lay their eggs on a host plant in groups of 100–200. Larvae feed on the leaves of the host-plant during summer and overwinter in silky webs. In spring, they continue feeding in a group, but become solitary and spread before pupating and transforming into adults (Merill, 2008).

Study sites

The study sites of a total size of 16.26 ha are located in south-western Slovenia (45°28'52.80"N, 13°56'35.03"E) at altitudes between 500 and 620 m a.s.l. on carbonate bedrock at the edge of the Karst (part of the Natura 2000 site). The three sites near the villages of Rakitovec (sites R1 and R2) and Zazid (site Z) are situated between 1430 and 3160 m (measured from edge to edge) apart (Fig. 1). Site R1 (5.32 ha) is extensive dry grassland. Two different habitats (henceforth habitat patches) characterize this site: while its southern part (patch R1A) lies in a depression and is mowed once or twice a year, its northern part (patch R1B)

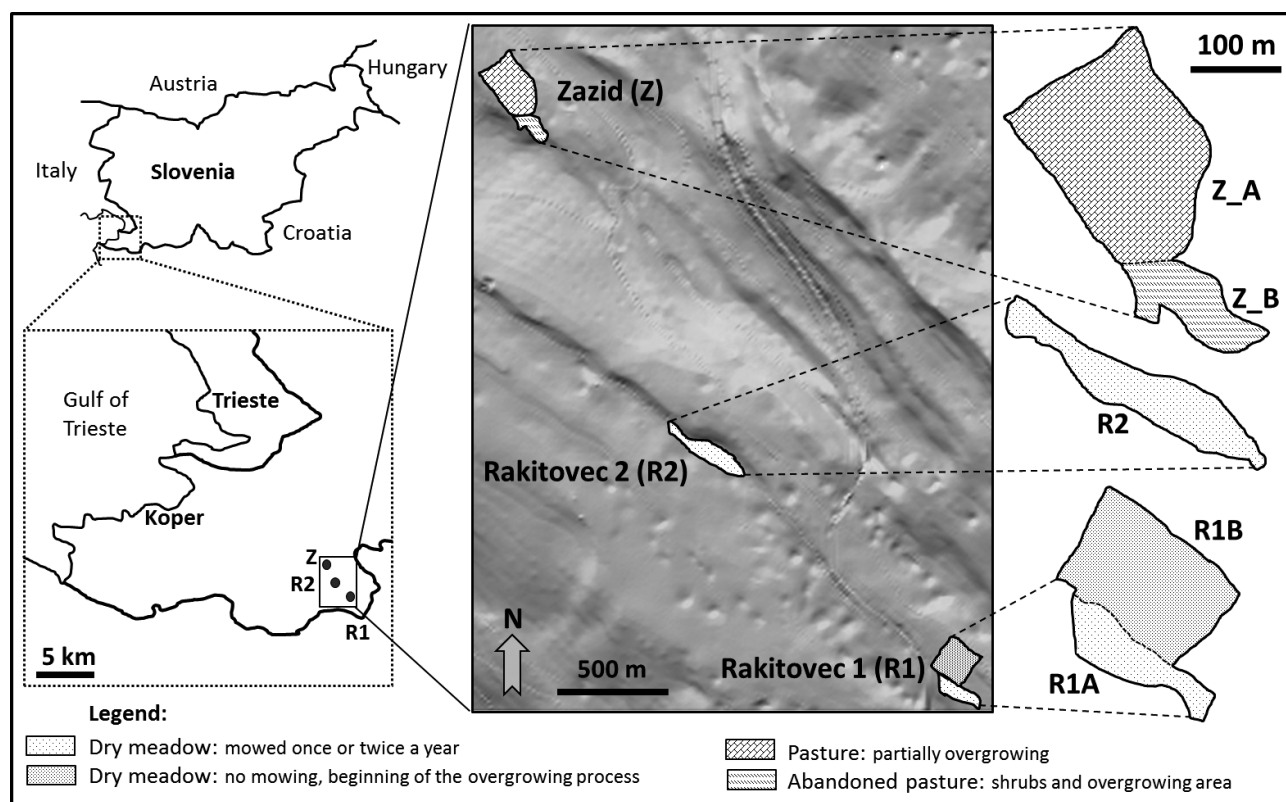


Fig. 1. Geographic position (inset) and types of habitats at three MRR study sites (Rakitovec 1, Rakitovec 2 and Zazid) for *Aporia crataegi* in SW Slovenia.

is on a south facing slope. The slope is not currently mowed and is becoming overgrown (Jugovic et al., 2013, 2014). Mowing of the southern R1A started between our visits on 18th and 21st June, and continued until 55% of the patch was mowed by the time of our last visit on 29th June (see Jugovic et al., 2013 for details). Site R2 (5.18 ha) lies in an elongated depression orientated in a NW–SE direction and is mowed once or twice a year (Jugovic et al., 2013, 2014). Mowing of R2 started between our visits on 14th and 18th June, and continued until 55% of the site was mowed by the time of our last visit on 29th June (see Jugovic et al., 2013, for details). Site Z (5.76 ha) is a dry grassland, where there were two habitat patches: the northern three quarters (Z_A) was an extensive pasture for cattle, while the southern quarter (Z_B) was abandoned and in a late stage of being overgrown (Jugovic et al., 2013, 2014). The study sites are surrounded by pioneer forests predominantly of *Pinus nigra* or by hedges. In the hedges, host plants of *Aporia crataegi* (e.g., *Crataegus monogyna*, *Prunus spinosa*) were abundant (Jugovic et al., 2013, 2014).

Mark-release-recapture

This study was done from 15th May to 29th June 2012, at two to four day intervals. Two longer intervals were from 8th to 14th June and from 21st to 26th June as the weather prevented another sampling occasion in between. Altogether, the populations were sampled on 16 occasions (Table 1). Each butterfly was netted and individually marked with a black permanent marker and released immediately at the same location. Prior to netting, the behaviour of each butterfly was recorded (flying, resting, feeding, in copula or courtship). The other data collected included each butterfly's individual mark, sex, exact locality and time (date, hour) of capture (Garmin Oregon 200, precision ≤ 5 m). When feeding or resting, the plant species were also recorded.

We initially recorded some movements between the three sites, hence the data (capture histories) were pooled for the study of demographic parameters. For the calculation of daily survival probability (ϕ or ϕ), recruitment rates (probability of entrance; ρ or b), capture probability (p) and the estimate of seasonal (or total) population size (N), we used the POPAN formulation in program MARK 8.0 (White & Burnham, 1999), which implies the existence of a superpopulation. This method can also generate derived parameters, such as daily population sizes (N_t) and daily number of births (B_t). The POPAN approach (Schwarz & Arnason, 1996) seems to be suitable for butterflies, as their population sizes are changing on a daily basis mainly due to recruitment from pupae and deaths of adult animals. This method is often used in ecological studies of butterflies and other insects (e.g., Öckinger & Smith, 2008; Čelik et al., 2009; Čelik 2012; Weyer & Schmitt, 2013; Pennekamp et al., 2014).

Following Čelik (2012) and Schtickzelle et al. (2003), a two-step procedure was used in MARK to select the models with the best fit to the data. Firstly, data were analyzed using the Cormack-Jolly-Seber (CJS) module, modelling for ϕ and p . Secondly, the best-fitting models were used within the POPAN module. The best models were selected based on Akaike Information Criterion corrected for small sample size (AICc) (Burnham & Anderson,

2002), which chooses models with $AICc < 2$. A goodness-of-fit test for the global or most parameterized model ($\phi(g^*t) p(g^*t)$) was also run in the CJS module, using the median \hat{c} -hat approach. The resulting estimate of \hat{c} -hat was then used to correct for overdispersion in the global model in both steps of the procedure (CJS and POPAN analyses).

In the modelling process within the CJS module both ϕ and p were allowed either to be constant (·); vary according to group (g); with time in a factorial (t) or linear (tlin) way; or even be arranged in an additive ([g+t], [g+tlin]) or interactive manner ([g*t], [g*tlin]), thus resulting in 64 possible models. In POPAN the parameter of entrance included eight basic and three additional structures ([tlin+tlin²], [g+tlin+tlin²], [g*[tlin+tlin²]]). The best models were used to calculate daily survival probability, capture probability, total population size, daily population sizes and daily number of births using the procedure of model averaging (weighted average of selected best models).

The results of the last four samples (from 18th June to 29th June) were not included in the MARK analysis, due to lack of recaptures for both males and females marked on 18th June or later. Daily population sizes and daily number of births for these occasions were calculated using the method proposed by Nowicki et al. (2005: 205–206). Negative values were corrected to 0.

The highest population densities (number of specimens per hectare) in a season were estimated for the days with peak abundance (calculation of highest daily population size) and separately for the sexes. The estimates of total population densities were derived from the total population size divided by the total area (in ha). To assess the relative difference in the densities of the animals at the three sites, the numbers of males and females captured were calculated for each of the sites on the days of peak abundance. The relative difference in densities in the habitat patches was calculated in the same way (dry meadows at R1A and R2 were treated separately).

We have used the following formula to assess average lifetime expectancy: $e_{avg} = (1 - \phi)^{-1} - 0.5$ (Nowicki et al., 2005). The formula is suitable for animals that emerge in groups in the early hours of the morning (Nowicki et al., 2005). We recorded the longest life span for males and females.

Behaviour

To define whether males and females behave differently, Pearson Chi square test of homogeneity was used. We compared the distribution frequencies of five behavioural types between the sexes, and accepted differences at $p < 0.05$. We then tested for possible differences in behaviour in the five habitat patches, using Likelihood ratio statistics, again at $p < 0.05$. Standardized residuals were used to assess the relative contributions of the cells to the overall Chi square value. Significant contribution was accepted when the absolute value of the standardized residual for the cell was ≥ 2.0 (see Čelik, 2013).

To assess the use of nectar sources, we tested whether males and females differed in their choice of nectar plants. Likelihood statistics were used, with a Chi square test accepted as significant when $p < 0.05$ (see Čelik, 2013).

Table 1. Summary of the data collected on the numbers of males and females of *Aporia crataegi* caught in SW Slovenia during sampling in 2012.

Sampling occasion	1	2	3	4	5	6	7	8	9	10	11	12	13*	14*	15*	16*
Date	15.5.	18.5.	22.5.	24.5.	25.5.	28.5.	30.5.	1.6.	4.6.	6.6.	8.6.	14.6.	18.6.	21.6.	26.6.	29.6.
Interval (days)	3	4	2	1	3	2	2	3	2	2	6	4	3	5	3	
No. of males	9	32	19	65	90	147	176	148	159	234	232	161	51	14	1	0
No. of females	0	1	0	3	7	23	16	34	47	69	136	165	34	21	5	8
Total no.	9	33	19	68	97	170	192	182	206	303	368	326	85	35	6	8

* The last four sampling occasions were not included in the analysis as no marked butterflies were recaptured.

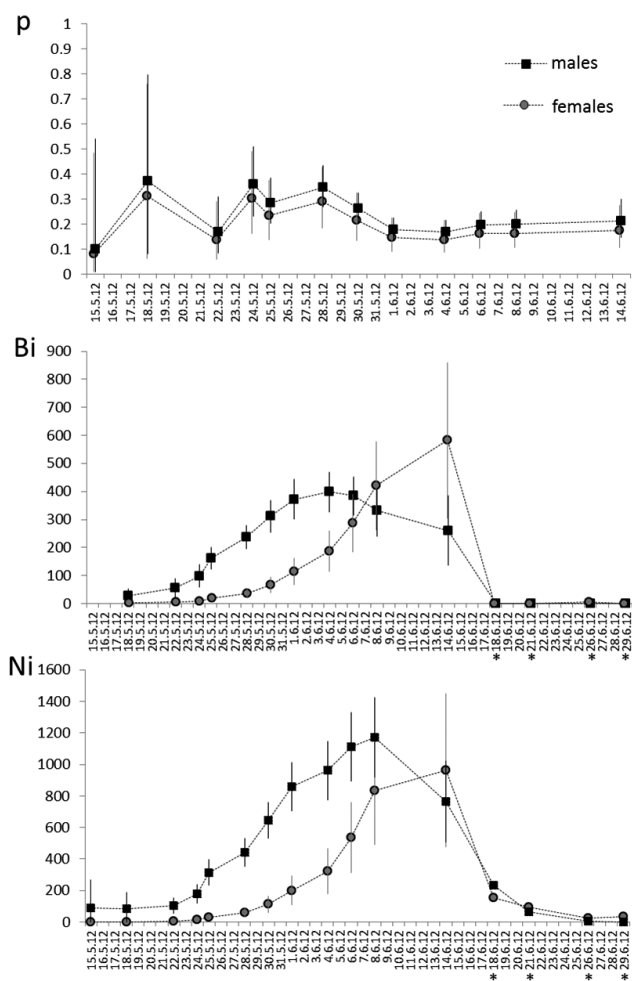


Fig. 2. Estimates of the daily catchability (p), daily recruitment (B_i) and daily population sizes (N_i) of *Aporia crataegi* in SW Slovenia in 2012, based on the average of the best three models in the POPAN module in programme MARK. The error lines represent 95% confidence intervals. Daily recruitment values are shown for the final days of each interval. Asterisks denote the sampling dates that were omitted from the POPAN analysis and the values for B_i and N_i were calculated manually (see Methods).

Movements

The distance between consecutive captures was measured as a straight line connecting two consecutive points of capture (ArcGIS 10.0; ESRI, Redlands, CA, USA). We calculated median, mean and maximum distances moved by males and females, and the distance per day by dividing the distance between the consecutive captures by the number of days in between. We tested the medians for possible differences between males and females (Mann-Whitney U test, $p < 0.001$), and between the distances measured on each recapture occasion (1st vs. 2nd vs. 3rd ... 7th in males and 1st vs. 2nd vs. 3rd in females; Kruskal-Wallis test, $p < 0.001$).

The inverse cumulative percentages of individuals travelling certain distances, of 50 m intervals, were fitted to a negative ex-

ponential function (NEF), where probability of an individual (P) moving distance D (in km) is $P = e^{-kD}$; k is the dispersal constant describing the shape of the exponential function, where the expected distance (D') between two consecutive captures is given by $D' = 1/k$ (Hill et al., 1996). We also fitted our data to an inverse-power function, where probability of an individual moving a certain distance D (in km) is given by: $P = CD^{-n}$, in which C and n are scaling constants (Hill et al., 1996). These models can be used by conservation practitioners to rank the dispersal abilities of species (Pennekamp et al., 2014). The slopes with their standard errors of the resulting fitted distributions were assessed using the linear regression $\ln P = -kD$ in NEF and $\ln P = \ln C - n \ln D$ in IPF and compared between sexes using t-test in regression (Soper, 2016).

For both functions (NEF, IPF), numbers (with 95% confidence intervals) and percentages of animals capable of moving a certain distance were calculated from the estimates of the population sizes of males and females using model averaging of the best models with $AICc < 2$.

Statistical analyses were performed using MS Excel 2010 and SPSS statistical package ver. 20.0 (IBM SPSS Inc., 1989, 2011).

RESULTS

Demographic parameters

Altogether 1711 butterflies (1184 males and 527 females) were marked. Of these, 363 males (30.7%) and 52 females (9.9%) were recaptured at least once. The first males were captured on 15th May and the first female two days later, and the next females were not recorded until 24th May. Most males (234 or 13.7% of all males) were caught on 6th June and most females (165; 31.3% of all females) eight days later (Table 1). On the last sampling occasion on 29th June, only eight females and no males were recorded. No butterflies were recorded after that.

The median \hat{c} -hat approach indicated a slight overdispersion of the data (\hat{c} -hat = 1.3). This was then corrected for in both modelling steps: CJS and POPAN. Using the POPAN formulation, we calculated best-fit models based on $AICc$. Table 2 reports best three models, with $\Delta AICc < 2.0$. All three models indicated a constant survival and the possibility that it was sex-specific (indicated by one model). Model averaging therefore gave a moderately different daily survival rate for males (0.8686; 95% confidence interval 0.8404–0.8925) and for females (0.8759; 95% confidence interval 0.8197–0.9164). Capture probability was time-dependent and presumably differed between sexes (Fig. 2). Recruitment rate was always sex-specific and followed a parabola, being lowest at the beginning ($b_{1 \text{ males}} = 0.0099$; $b_{1 \text{ females}} = 0.0012$), and highest at the peak of the season (for males around 1st June, $b_8 = 0.146$; for females 14th June, $b_{12} = 0.337$). A later decrease, however, was indicated only for males ($b_{11 \text{ males}} = 0.0955$), since the recruitment rate could not be calculated for the period after 14th June due to a lack

Table 2. The best supported POPAN models based on the Akaike information criterion ($AICc$), their likelihood, number of parameters and Q Deviance. All models with a $\Delta AICc < 2$ are shown.

Model	QAICc	Delta QAICc	AICc Weights	Model Likelihood	Num. Par.	Q Deviance
1. $\varphi(.) p(g+t) b(g^*(tlin+tlin^2)) N(g)$	2118.321	0	0.424	1	21	-4740.7
2. $\varphi(.) p(t) b(g^*(tlin+tlin^2)) N(g)$	2118.983	0.663	0.305	0.718	20	-4738.0
3. $\varphi(g) p(g+t) b(g^*(tlin+tlin^2)) N(g)$	2119.664	1.343	0.217	0.511	22	-4741.4

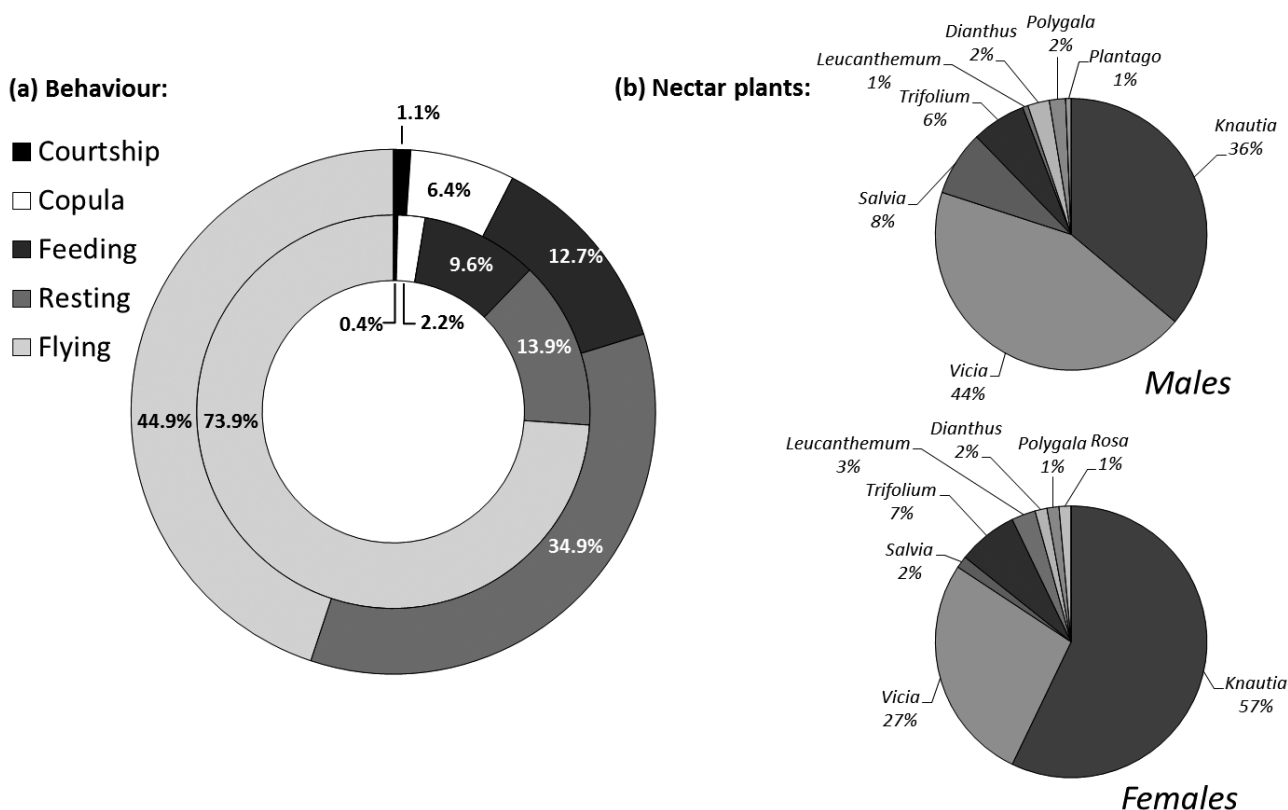


Fig. 3. (a) Percentage of the different behaviours recorded for males (inner circle) and females (outer circle) of *Aporia crataegi* and (b) their choice of nectar plants in SW Slovenia.

of recaptures. Daily number of births also followed this pattern (Fig. 2). Estimated total population sizes were different for males and females. The estimate for males was 2730 (95% confidence interval 2385–3074) and considerably lower for females: 1732 (95% confidence interval 1101–2363). Daily population sizes (Fig. 2) changed in a parabolic way, with peaks on 8th and 14th June for males and females, respectively.

Highest total daily population densities occurred on 8th and 14th June for males and females, respectively, reaching 72 males and 59 females per hectare. Dates of the peak numbers captured were mainly congruent with the highest daily population densities, however not for all sites or

habitat patches (Table 3). The relative numbers of captures on peak days were approximately three (males) to five (females) times higher at R2 than R1, and six (females) to seven (males) times higher at R2 than at Z. Considering the peak numbers of males and females captured, the dry meadow on the slope at R1 (habitat patch R1B) was 3.6 to 3.7-times less densely populated than the dry meadow in a depression (R1A) and the pasture at Z (patch Z_A) was subsequently (in males) to slightly more (1.75-times in females) densely populated than the overgrown area (patch Z_B) nearby (Table 3).

The average life span of the females (7.5 days) was slightly longer than that of the males (7.2 days). The longest life span recorded for males was 21 days (28th May–18th June) and 17 days for females (28th May–14th June).

Table 3. Peak total daily population densities (95% confidence intervals in brackets) of males and females of *Aporia crataegi* (derived from MRR data), and peak daily densities of captures at the three sites and five patches.

	Site/patch	Males/ha	Date	Females/ha	Date
Peak daily population density	Total	72 (55–88)	8 th June	59 (29–89)	14 th June
	R1	11.1 ^a	6 th June	4.9 ^b	6 th June
	R1A	20.0	6 th June	13.0	6 th June
	R1B	5.5	6 th June	3.5	6 th June
Peak density of captures	R2	32.4	8 th June	26.4	14 th June
	Z	4.7	8 th June	4.3 ^c	6 th June
	Z_A	4.4	8 th June	4.9	6 th June
	Z_B	4.2	8 th June	2.8	6 th June

Peak densities of captures on days of peak population density (8th and 14th June for males and females, respectively) were: ^a8.5, ^b4.7, and ^c0.5 individuals/ha.

Behaviour

There were significant differences in the behaviour of males and females (Pearson Chi-square = 158.494, df = 4, p < 0.001) and in the behaviour of males (LR = 170.662, df = 16, p < 0.001) and females (LR = 126.365, df = 16, p < 0.001) among the five habitat patches. Females spent much more time than expected resting and copulating (standard residuals = 8.0 and 3.8, respectively), while males spent less time than expected in these two activities (std. res. –4.8 and –2.3, respectively). Males spent more time flying and patrolling for the opposite sex (std. res. = 3.6) and females spent less time flying than expected (std. res. = –5.9). Frequencies of feeding did not deviate significantly from the expected values for either sex (std. res. absolute

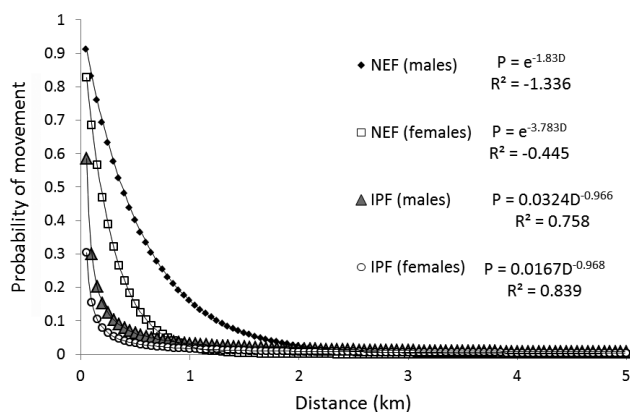


Fig. 4. Probability of males and females of *Aporia crataegi* moving a certain distance derived from NEF and IPF, which were based on distances between consecutive captures (in the formula, P represents a probability of moving a certain distance, D).

value < 2.0). The difference in behaviour between the sexes was most clearly expressed in flying time, as males were recorded 1.6 times more frequently flying (73.7%) than females (46.1%; Fig. 3).

In both habitat patches at site Z, both sexes usually spent longer than expected flying [std. res.: $Z_A_{\text{males}} = 3.3$; $Z_B_{\text{males}} = 2.2$; $Z_A_{\text{females}} = 4.8$; $Z_B_{\text{females}} = 1.9$ (close to significance)] and less time feeding (std. res.: $Z_A_{\text{males}} = -3.5$; $Z_B_{\text{males}} = -2.5$; $Z_A_{\text{females}} = -2.7$; $Z_B_{\text{females}} = -0.4$) and resting (std. res.: $Z_A_{\text{males}} = -3.9$; $Z_B_{\text{males}} = -2.3$; $Z_A_{\text{females}} = -2.9$; $Z_B_{\text{females}} = -1.5$). The opposite was recorded at R2, where males and females were recorded feeding (std. res.: males = 4.9; females = 1.5) and resting (std. res.: males = 3.4; females = 3.3) more, and flying (std. res.: males = -3.3; females = -3.6) significantly less frequently than expected. A significantly lower frequency of feeding was recorded also at R1A (std. res.: males = -2.4; in females absolute value < 2) and R1B (std. res.: males = -3.6; females = -2.8), and the same trend was recorded for resting [std. res. insignificant but always negative for both patches and sexes: (-1.2)–(-1.8)]. There were no significant deviations from expected frequencies for other types of behaviour. Nevertheless, we recorded more and less copulating events than expected for females at R1A (std. res.: 1.9, close to sig.) and Z_A (std. res.: -1.9, close to sig.), respectively.

Nectar plants

In total, nine species of plants were recorded as nectar plants for the black-veined white. Although there was a significant difference in the choice of nectar sources by males and females (LR = 17.795, df = 8, $p = 0.023$), two of the most frequently recorded nectar plants (*Knautia illyrica* and *Vicia* aggr. *cracca*) accounted for 80% and 84% of the feeding occasions for males and females, respectively. While these two species were visited similarly by males (*Knautia*: 36%, *Vicia*: 44%), females visited *K. illyrica* much more often (57%) than *V. cracca* aggr. (27%). *Salvia pratensis* and *Trifolium nigra* were visited on 14% and 9% of feeding occasions, leaving only 6% and 7% for the other four plant species for males (*Leucanthemum* sp., *Dianthus sanguineus*, *Polygala nicaensis*, *Plantago* sp.) and females

(*Leucanthemum* sp., *Dianthus sanguineus*, *Polygala nicaensis*, *Rosa* sp.), respectively (Fig. 3). Interestingly, the vast majority of the species of nectar plants (75% for males and 87.5% for females) have blue or violet flowers.

Movements

Males moved between sites more frequently (21 movements) than females (1 movement), however most of the inter-site movements were between the closest sites, R1 and R2 (1.43 km apart; 13 males, of which 9 were in the direction of R2, and a movement of a single female to R1), and much less between the sites furthest apart, R1 and Z (3.16 km apart; only males: two to Z and three in the opposite directions). A single movement was recorded for a male that moved from R2 to Z (1.77 km apart).

Median, mean and maximum distances moved by males were 134, 640 and 3493 m, and by females the respective values were 138, 604 and 3166 m. Median distances did not differ significantly ($U = 6214.0$, $p = 0.832$) between the sexes. Mean daily movement was insignificantly different ($U = 8665.5$, $p = 0.139$) for males (Median = 19.6 m) and females (13.3 m), and no significant difference was detected between successive captures (Kruskall Wallis test, $\chi^2 < 3.6$ and $p \geq 0.2$ in both sexes).

NEF and IPF functions fitted the data for males and females well ($p < 0.001$). Fitting NEF to the mobility data (Fig. 4) resulted in the following equations: $P = e^{-1.83D}$ for males and $P = e^{-3.783D}$ for females (where P is a probability of moving a certain distance, D). The expected distances (D') between consecutive capture points were 546 and 250 m for males and females, respectively. The estimated probabilities (in % of individuals) of long-distance movements were 16.04% (males) and 2.28% (females) for 1 km, 0.01% (males) and $6.10 \cdot 10^{-7}\%$ (females) for 5 km and $1.13 \cdot 10^{-16}\%$ (males) and $3.72 \cdot 10^{-15}\%$ (females) for 10 km (Appendix 1). More than 3% of males (approx. 3.1%) and females (approx. 3.3%) reached distances up to 1.9 and 0.9 km, respectively. The regression slopes for males and females did not differ ($t = 1.61$, $df = 94$, $p = 0.108$). The IPF function $P = 0.0324D^{-0.966}$ was recorded for males and $P = 0.0167D^{-0.968}$ for females. The estimated probabilities (in % of individuals) of long-distance movements based on the IPF were: 3.24% (males) and 1.24% (females) for 1 km, 0.68% (males) and 0.35% (females) for 5 km, and 0.35% (males) and 0.18% (females) for 10 km. The regression slope was steeper for females ($t = 5.91$, $df = 94$, $p < 0.001$). IPF predicted a higher probability of movement of distances over 1.1 km for females and over 2.3 km for males.

DISCUSSION

Demography, habitat characteristics, behaviour and movements

Typically for MRR studies on butterflies, the number of males marked was much higher than of females (Kuras et al., 2003; Fric et al., 2009; Junker & Schmitt, 2010; Ćelik, 2012). Moreover, obvious protandry and the parabolic trend in the daily population sizes are other typical char-

acteristics of many univoltine species of butterfly. Most likely, the difference in capture probability can be attributed to the difference in the activity of the sexes. While males spend much more time flying, patrolling and searching for females, the latter are more sedentary. Constant survival rates recorded for both sexes may be connected to the relative robustness of this species in terms of its ability to survive changes in weather. Despite the two rainy days on 1st–2nd June, no decline in daily recruitment rate or daily population size was detected during this period or shortly after. Since the decline in daily population sizes started ten (males) to four (females) days before mowing started (Jugovic et al., 2013), we could not connect these two events. It is however possible that the complete lack of recaptures of females after 14th June was influenced by mowing. Furthermore, bad weather around 11th June could have negatively affected the adults (mostly females) emerging from pupae or prevented them from flying after emergence. Mowing might have also forced adult females to emigrate due to the destruction of nectar plants, and further prevented some of the last females from emerging from pupae. These possible causes are reflected in an overall male biased sex ratio. Nevertheless, mowing occurred only on R2 and R1B, and approximately half of the two patches were not mowed until the end of the flying season (Jugovic et al., 2013). Estimated mobility indicated that males are capable of covering larger areas and invest a lot of energy in moving, which may be reflected in their slightly shorter average lifetime. That the longest lifetime was recorded for males can thus only be an artefact due to their higher detectability.

We most likely covered the whole flying season in 2012, as no butterflies were detected before or after the reported 37 and 43 days for males and females, respectively. Since the area studied lies within the stronghold region of this species in Slovenia (Verovnik et al., 2012), we believe the estimated density of the adults is amongst the highest for this country. Nevertheless, big differences in densities among different types of habitats indicate that not all the habitat patches studied are equally suitable for this species. The density of individuals seem to be higher in extensively managed meadows that are both rich in nectar plants and surrounded by a hedge with larval host plants (e.g., high density at R2 where there is a high abundance of both nectar and host plants; Črne et al., 2013).

While behavioural differences between the sexes were prominent, males and females showed similar trends in their behavioural differences between different habitats (pastures vs. overgrown areas). For females, the pronounced flying recorded in habitat patches Z_A (pasture) and Z_B (overgrown area; both with low density of nectar plants and high density of host plants compared to the three other patches, field observations) could serve to spread their eggs over a larger area (cf. Janz et al., 2005), while in males it can be due to lower density of females and thus more intense patrolling. The opposite was recorded at the site with the highest density of nectar sources (R2). An alternative explanation for the increased flying behav-

our would be that where less food is available, adult butterflies might also have to spend more time searching for food. These differences in behaviour are most commonly explained by the following: (1) males and females should be able to find each other and mate, (2) females should lay their eggs in a way that enable their 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). The utilization of nectar from nine species of plants corresponds to the most abundant plant species that were flowering during the flying period and suggests that *A. crataegi* is an opportunistic feeder. This assumption is in line with the conclusions of Stefanescu & Traveset (2009) for the family Pieridae as a whole. The authors attribute *A. crataegi* an intermediate level of generalization, but closer to generalist species. The intermediate level of specialization corresponds well with our data; although nine species of nectar plants were utilized, only two (*K. illyrica*, *V. cracca* aggr.) accounted for over 80% of all feeding occasions.

We therefore believe that a dense network of permanent dry karst meadows contributes most to the overall high density of this species, and for population stability should be maintained (Čelik, 2012). Differences in density of captures between the habitat patches, however, indicate that in karst meadows an abundance of nectar plants is the most important determinant of this species abundance (e.g., Hardy et al., 2007). In these habitats, the number of marked animals seems to be positively associated with the number of species of nectar plants. Although the two main host plants (*P. spinosa*, *C. monogyna*) were present throughout the study area (pers. observ.), their density did not seem to determine adults abundance. Since this species is highly mobile (Clausen et al., 2001), with $\max_{\text{males}} = 3497$ m and $\max_{\text{females}} = 3165$ m confirmed by this study, one would not necessarily expect the larval and adult habitats of *A. crataegi* to overlap spatially. Considering the 1% probability of movements assessed using IPF, movements up to 3.35 (males) and 1.65 (females) kms are probable, and in our case were attributed to 24–31 males and 11–24 females, respectively. This dispersal ability roughly corresponds to that of the highly mobile *Euphydryas aurinia* assessed by Zimmermann et al. (2011), where 1% of the individuals achieved distances of at least 2.15 (males) and 1.8 km (females). The 1% probability is assumed to be sufficient to maintain a metapopulation of *E. aurinia* in a fragmented landscape (Zimmermann et al., 2011). Despite the striking difference in the long-distance dispersal ability of the sexes (males with a high and females with a low ability), *A. crataegi* is a butterfly with a high dispersal ability, indicating that individuals of both sexes utilize large areas. In addition, the insignificant differences in the daily distance travelled by the sexes also supports this idea, as do the insignificant differences in distances between consecutive captures for both, males and females. In general, IPF is preferred over NEF owing to its superiority in predicting rare long distance events (Baguette et al., 2000; Baguette, 2003; Weyer & Schmitt, 2013; Pennekamp et al., 2014)

and its independence of marking effort (Fric & Konvicka, 2007; Pennekamp et al., 2014). Considering the density of recordings of this species at the Karst Edge (Verovnik et al., 2012) and the estimate of the 1% moving probability from the IPF, this species should constitute a metapopulation that stretches at least throughout the whole of this region and its surroundings, which is an area of approximately 140 km².

Implications for conservation

Aporia crataegi is a polyphagous species with the habitats of adult and juvenile stages overlapping only slightly. While adult butterflies require open habitats (Stefanescu & Traveset, 2009) rich in nectar plants, females should also be able to locate host plants for their larvae (e.g., Koschuh & Gepp, 2004) that are common in the later successional stages of their habitats. *A. crataegi* is also capable of moving long distances; therefore the quality of the matrix in a fragmented landscape should be appropriate for butterflies searching for mates or new habitats. Firstly, adult and larval habitats should be close enough for the butterfly to easily move between them, and secondly, there should be a dense network of open habitats with nectar plants for them to exploit. These sites could then act as stepping stones between adult and larval habitats, and facilitate the dispersion of adults and persistence of a species in a fragmented landscape. Since the abandonment of traditional management of karst meadows and pastures in southern Europe (i.e., extensive grazing and mowing), these areas are becoming overgrown and as a result open and semi-open areas are in severe decline. Occasional late mowing (once or twice a year) or extensive grazing would therefore slow down succession and significantly contribute to the persistence of open areas that can support higher numbers of species than woodland (Balmer & Erhard, 2000; Schmitt & Rákósy, 2007). This kind of traditional management should not include the use of fertilizers and pesticides, and other disturbing factors such as urbanisation and colonization by non native species. This study clearly emphasises that only the preservation of areas that are large enough to include not only all the appropriate habitats, but also a suitable matrix of them (Bergman et al., 2004, 2007; Liivamägi et al., 2014) may be crucial for the persistence and dynamics of a metapopulation and the long term existence (Thomas & Jones, 1993) of this highly mobile species. This, however, can be achieved within large areas where nature conservation is high on the priority list, and Natura 2000 areas could well serve this purpose.

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Appendix 1. Estimated percentage and number of *Aporia crataegi* individuals (NEF and IPF models) moving certain distances. Basis for individual measurements were estimates for population size of males (N = 2730) and females (N = 1732), with their 95% confidence intervals (males: N⁻–N⁺ = 2385–3074; females: N⁻–N⁺ = 1101–2363).

	Distance (km)	Males				Females			
		% individuals	N individuals	N ⁻	N ⁺	% individuals	N individuals	N ⁻	N ⁺
NEF	0.05	91.26	2491.29	2176.46	2805.21	82.77	1433.51	911.26	1955.77
	0.1	83.28	1442.35	916.88	1967.83	68.50	1186.46	754.21	1618.71
	0.2	69.35	1201.15	763.55	1638.75	46.93	812.76	516.65	1108.86
	0.3	57.75	1000.28	635.86	1364.70	32.15	556.76	353.92	759.60
	0.4	48.09	833.00	529.52	1136.48	22.02	381.39	242.44	520.34
	0.5	40.05	693.69	440.97	946.42	15.08	261.26	166.08	356.45
	1	16.04	277.84	176.62	379.06	2.28	39.41	25.05	53.77
	2	2.57	44.57	28.33	60.81	0.05	0.90	0.57	1.22
	5	0.01	0.18	0.12	0.25	6.10 10 ⁻⁷	1.06 10 ⁻⁵	6.72 10 ⁻⁶	1.44 10 ⁻⁵
	10	1.13 10 ⁻⁶	1.95 10 ⁻⁵	1.24 10 ⁻⁵	2.67 10 ⁻⁵	3.72 10 ⁻¹⁵	6.44 10 ⁻¹⁴	4.10 10 ⁻¹⁴	8.79 10 ⁻¹⁴
IPF	0.05	58.52	1597.73	1395.82	1799.05	30.35	525.61	334.12	717.10
	0.1	29.96	817.91	714.55	920.98	15.51	268.70	170.81	366.59
	0.2	15.34	418.71	365.80	471.47	7.93	137.36	87.32	187.41
	0.3	10.37	283.01	247.25	318.68	5.36	92.77	58.97	126.57
	0.4	7.85	214.35	187.26	241.36	4.05	70.22	44.64	95.80
	0.5	6.33	172.78	150.95	194.56	3.27	56.58	35.97	77.19
	1	3.24	88.45	77.27	99.60	1.67	28.92	18.39	39.46
	2	1.66	45.28	39.56	50.99	0.85	14.79	9.40	20.17
	5	0.68	18.69	16.32	21.04	0.35	6.09	3.87	8.31
	10	0.35	9.57	8.36	10.77	0.18	3.11	1.98	4.25