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ORIGINAL PAPER

Potential metapopulation structure and the effects of habitat quality on population size of the endangered False Ringlet butterfly

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Abstract The False Ringlet (*Coenonympha oedippus*) is a European butterfly species, endangered due to the severe loss and fragmentation of its habitat. In Hungary, two remaining populations of the butterfly occur in lowland Purple Moorgrass meadows. We studied a metapopulation occupying twelve habitat patches in Central Hungary. Our aim was to reveal what measures of habitat quality affect population size and density of this metapopulation, estimate dispersal parameters and describe phenology of subpopulations. Local population sizes and dispersal parameters were estimated from an extensive mark–release–recapture dataset, while habitat quality was characterized by groundwater level, cover of grass tussocks, bush cover, height of vegetation and grass litter at each habitat patch. The estimated size of the metapopulation was more than 3,000 individuals. We estimated a low dispersal capacity, especially for females, indicating a very low probability of (re)colonization. Butterfly abundance and density in local populations increased with higher grass litter, lower groundwater level and larger area covered by tussocks. We suppose that these environmental factors affect butterfly abundance by determining the microclimatic conditions for both larvae and adult butterflies. Our results suggest that the long-term preservation of the studied metapopulation needs the maintenance of high quality habitat patches by appropriate mowing regime and water regulation. Management also should facilitate dispersal to strengthen metapopulation structure with creating stepping-stones or gradually increase habitat quality in present matrix.

Keywords *Coenonympha oedippus* · Dispersal · Habitat management · Mark-recapture · Population size · Purple Moorgrass meadow

Introduction

The biodiversity crisis currently seems to appear more critical among butterfly species than other species (Thomas 1991; Thomas et al. 2004). Butterfly populations disappear more rapidly than bird or plant populations due to short life and lack of dormant propagules (Thomas et al. 2004). However, Hambler et al. (2011) suggested that long-term extinction rates are similar amongst birds and butterflies, but the latter react more rapidly to changes in habitat quality or climate. In Europe, the decline is attributed to habitat destruction, agricultural intensification or abandonment and climate change (Thomas 1991; Thomas and Morris 1994; Warren et al. 2001; Hanski 2003; Parmesan 2003). As European landscapes have long been human dominated, many species rich habitat types rely on low-intensity agricultural use typical of earlier agronomic eras, now requiring conservation-oriented habitat management

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to maintain them. Around 50 % of butterfly species live in such semi-natural managed grasslands (Erhardt and Thomas 1991), where management is necessary to maintain their current populations (van Swaay and Warren 1999; van Swaay 2002).

Wet meadows are seriously threatened by the above factors (Halada et al. 2011), and have become one of the most endangered habitat types in Europe. Habitat degradation and fragmentation of wet meadows have caused the decline of several butterflies (van Swaay and Warren 1999; Nowicki et al. 2007; Skórka et al. 2007), including the False Ringlet (*Coenonympha oedippus*) (van Swaay et al. 2010). Most of its European populations are threatened by habitat loss (isolation and fragmentation) and habitat degradation, especially land drainage, abandonment and changes in habitat management. Populations also suffer from the spread of invasive weeds (*Solidago* spp.) and encroachment of bushes after abandonment, collection of butterflies, development of built-up areas and climate change (van Swaay and Warren 1999; Čelik and Verovnik 2010; Örvössy et al. 2010; Šašić 2010; Sielezniew et al. 2010).

In order to stop further decline and promote the long-term survival of the species, suitable habitat management is required. Development of a proper management action plan should be based on a survey that describes which factors influence the metapopulation structure of the species under consideration and determine the parameters of the best available habitat's quality.

Generally, two main approaches exist to explain the variation of population size and predict survival of butterfly species: metapopulation theory and the habitat quality approach (Thomas et al. 2001). Metapopulation theory assumes that patch size and isolation are the main factors that influence population size and persistence in a habitat patch (Hanski and Glipin 1997), which has been supported by several studies (e.g. Thomas and Hanski 1997; Thomas et al. 1998; Nowicki et al. 2007). This approach has been used for several butterfly species due to their high sensitivity to fragmentation (Baguette and Nève 1994; Hanski 1998; Fischer et al. 1999; Öckinger 2006; Hovestadt et al. 2011). However, the metapopulation approach has some limitations in continuous landscapes, where habitat patch definition is not exact and resources of butterflies do not spatially overlap (Dover and Settele 2009).

The resource limitation approach offers an alternative to avoid the problems of patch definition, continuity of landscapes and sparse location of resources in the matrix (Dennis et al. 2006). It determines the habitat based on necessary resources, and emphasises the importance of the habitat quality (Vanreusel and Van Dyck 2007). The resource limitation approach is part of the wider and more traditional habitat quality approach, which is the analysis of habitat quality in light of the habitat requirements of a certain species (Oostermeijer and van Swaay 1998; Skórka et al. 2007). Such studies usually include surveys to determine appropriate habitat management. Using both metapopulation and habitat quality approaches in the same study, it is possible to predict population size or density (Thomas et al. 2001; Sawchik et al. 2003; Rabasa et al. 2008) and in some cases patterns of site occupancy more reliably than by the conventional separation (Lenda and Skórka 2010; Sanford et al. 2011). Furthermore, this double approach is particularly relevant in the study area, as the False Ringlet lives in a fragmented habitat complex where habitat quality varies considerably. Efforts to maintain the small and isolated populations by conservation management are hampered by a lack of knowledge about the habitat requirements of this species. Hence, a suitable management regime would facilitate the long-term survival of the species. Therefore, our study aims were (i) to gain information about the population structure: discriminate clusters based on phenology, asynchrony of subpopulations and movement pattern of the species, and (ii) to determine whether and how habitat quality affect its population size and density.

Materials and methods

Species

The distribution area of the False Ringlet covers the whole Palaearctic region (Gorbunov 2001; Bozano 2002). The locations of European populations are more or less identified, while there is little information about the Asian populations. The current geographical distribution of the species is highly fragmented, and colonies in the European part are highly isolated (Kudrna 2002). The species has experienced more than 80 % population decline across its European range in recent decades, and has become extinct in Slovakia, Bulgaria and Switzerland (van Swaay and Warren 1999; Dušej et al. 2010). The False Ringlet is considered as "near threatened" by IUCN (2011), and is listed in Annex II and IV of the Habitats Directive and Annex II of the Bern Convention. Although the size and distribution of the European populations are declining at several localities, some populations seem to be stable. The largest and most stable populations exist in Italy (Bonelli et al. 2010). Highly isolated populations are still present in France (Lhonoré and Lagarde 1999), Liechtenstein (Staub and Aistleitner 2006), Austria (Aistleitner et al. 2006), Slovenia (Čelik and Verovnik 2010), Croatia (Kučinić et al. 1999; Šašić 2010), Hungary (Örvössy et al. 2010), Poland (Sielezniew et al. 2010) and Russia (Gorbunov 2001). Outside Europe, *C. oedippus* is very abundant in the Transbaikalia, northern Altai, Chuluunbaatar and in the Mongolian Altai, while populations are more scattered in the West Siberian lowlands (Gorbunov and Kosterin 2007, Bräu et al. 2010). The European populations generally occupy semi-open wet habitats: Purple Moorgrass (*Molinia coerulea*) meadows, bogs, wet heathlands, sedge communities at marginal zones of swamps and forest meadows (Bräu et al. 2010; Čelik and Verovnik 2010; Örvössy et al. 2010; Šašić 2010; Sielezniew et al. 2010). There are some populations in the Mediterranean parts of Europe that occur in dry habitats (Čelik 2004; van Halder et al. 2008), but also with a high coverage of Purple Moorgrass. In Hungary, the species has been recorded in several locations, but its original habitats have disappeared or decreased in size. There are only two remaining metapopulations, the current study site at Ócsa, Central Hungary (Örvössy et al. 2010) and one in the Fertő-Hanság National Park, Western Hungary (András Ambrus pers. comm.)

Based on earlier studies of within-habitat movements, this species was considered sedentary with weak flight ability (Lhonoré and Lagarde 1999; Celik et al. 2009). Its oviposition is not selective, as females lay their eggs on different plant species or on grass litter (Bräu et al. 2010). After emergence, young polyphagous larvae feed on monocotyledonous species, especially on Purple Moorgrass (Bräu et al. 2010). Larvae hibernate in the tussocks of grass, continue feeding during spring and pupate in early May (Bräu et al. 2010). Imagoes emerge in June–July, and the flight period lasts 4–5 weeks.

Study site

Our study area was situated next to the town of Ócsa, Central Hungary, and belongs to the Duna-Ipoly National Park. All potential habitat patches were mapped around the two known inhabited patches based on a rough field survey of the vegetation and aerial photos. Altogether, 31 potential habitat patches were surveyed for the presence of the False Ringlet butterfly in June and July 2006; the species' presence was recorded in 16 patches with 12 patches of higher densities. These twelve study patches were isolated from each other by 0.01–3.2 km, separated by softwood forest groves, shrubs, grasslands or agricultural areas (Fig. 1). They varied in size from 0.14 to 1.66 ha. The examined patches were all wet meadows with the ground water level close (0.1–2.0 m) to the surface, and vegetation was dominated by mainly Purple Moorgrass and other Poaceae and *Carex* species with few nectar sources for the butterflies (Örvössy et al. 2010). Forests and shrubs surrounded these meadows. The traditional management of the area was extensive mowing for haymaking. Most of the studied patches had been abandoned without any or with very limited mowing; traditional once a year mowing is still carried out only in three patches (c, d, e on Fig. 1.). The abandoned patches have experienced weed invasion and scrub encroachment.

Sampling

We carried out an extensive mark-release-recapture survey in the twelve habitat patches between the 5th and 28th of June 2007. The butterflies were individually marked using permanent pens on the underside of their hindwings. Each patch was visited every other day. In order to standardize the sampling effort, the duration of each visit depended on the size of the patch; as a standard, the surveyor spent

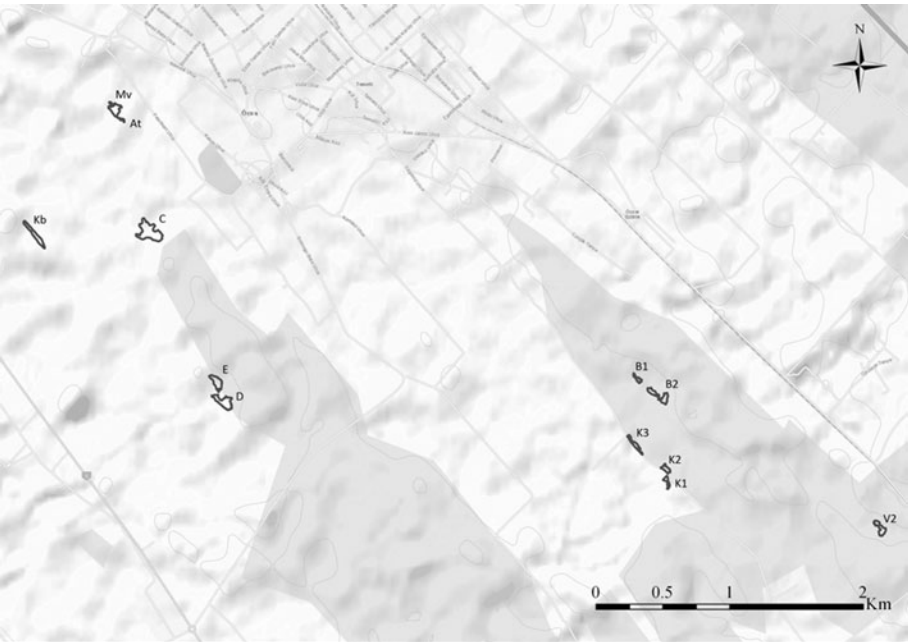


Fig. 1 The twelve study habitat patches of the False Ringlet metapopulation complex at Ócsa in 2007 using ESRI World Topographic Map

60 min in a 0.5 ha patch. We observed and caught butterflies occasionally (1–3 times) in the four additional locations, these data were included only in the Virtual Migration 2 model (see below), as the model require information about all the known habitat patches. We measured the quality of each habitat patch in randomly distributed 2 × 2 m quadrats (3–7 quadrats per habitat patch depending on their size). Height of vegetation (5 measures per quadrat), height of grass litter (5 measures per quadrat), number of flowers/nectar sources (all flowers of forbs) were measured in all quadrats. The arithmetic mean values of each parameter were used in the analyses. Height of vegetation was measured excluding bushes, from the ground to the surface of grass plants (Poaceae and Carex species mainly). Grass litter was a thick layer of dead leaves, we measured its height from the ground. The thickness of this layer is largely influenced by mowing and hay removal. The area covered by tussocks and percentage of bush cover were estimated for each habitat patch. Area covered by tussocks is a parameter which can be connected to earlier management, as intensive mowing destroys tussock structure (Bartoš et al. 2011). Also tussock structure may have an effect on larval survival by providing hibernating sites in case of high groundwater level. The groundwater level was measured after the flight period by hand-dug wells (5 cm diameter) in each patch. Therefore, the relationship between population size or density of the species and the groundwater level should be treated only as a guideline.

Statistical analysis

The mark-release-recapture dataset was analysed in two steps, and separately for each of the twelve habitat patches. First, we fitted a Cormack–Jolly–Seber (CJS) model to each dataset with time- and sex-dependent parameters (survival rate and recapture probability). We tested for the goodness of fit by a bootstrap GOF test and a χ^2-based GOF test (‘Release’) (Lebreton et al. 1992). Then we performed a model selection based on AIC values to reach the most parsimonious model (Burnham and Anderson 2002). Secondly, we fitted a Jolly–Seber (JS) model with a set up for survival rate and encounter probability as in the most parsimonious CJS model. Model selection was performed again to find the best parameterization (the JS model had two additional parameters: population size N, which can be sex-dependent, and proportional recruitment *pent*, which can be time- and sex-dependent). Daily population size was a derived parameter of the JS model. Average lifespan was calculated from the survival rate of the CJS model ($1/-\ln(Phi)$, Cook et al. 1967). All analyses were carried out using MARK 5.1 software (White and Burnham 1999).

The Virtual Migration 2 programme (Hanski et al. 2000) was used to estimate the following dispersion and population parameters for both sexes: within-patch mortality, migration rate per one-hectare patch, scaling of migration with patch size, distance-dependence of migration, mortality during migration and scaling of immigration into a patch. This programme can handle the problems of different number of dispersal events and capture probability between males and females. Parameter estimation was conducted using 1,000 randomizations in simulated annealing followed by 5,000 intelligent randomizations to converge on the optimum (Hanski et al. 2000). One parameter was fixed, as there were no significant difference between scaling of immigration and scaling of emigration. Confidence intervals for the parameters were estimated based on likelihood ratio tests, we used 2,000 evaluations. Replicate runs were conducted to check for convergence of parameter estimates and confidence intervals.

The relationship between butterfly quantity and habitat quality parameters was analysed with “General Additive Models, for Location, Scale and Shape”, without any smoothing effect, only for exploiting the availability of lognormal dispersion. Two response variables were used in the analyses: total population size (the estimated number of all individuals during a flight period in each habitat patch) and the maximum observed density of individuals (observed number of individuals divided by the minutes spent in each habitat patch during the peak day of the flight period). For both dependent variables we fitted a general additive model with lognormal error distribution, without any smoothing effect. Predictor variables were standardized: height of vegetation, height of grass litter, number of flowers/nectar sources, area covered by tussocks, percentage of bush cover, area and groundwater level. We applied a backward-stepwise model selection based on AIC values. These analyses were performed using gamlss package (Stasinopoulos et al. 2012) of R (2.12.2) statistical software (R Development Core Team 2011).

Results

In 2007, due to the hot weather, butterflies emerged earlier than usual; the first observation was on the 3rd of June, the mark-release-recapture was carried out between the 5th and 28th of June. Altogether, 1,496 butterflies (914 males and 582 females) were marked, during 2,052 capture events. The maximum daily butterfly density ranged between 0.09 and 1.72 observed individual per minute per patch, total population size per patch varied between 24 and 1,055 individuals (Table 1). We had sufficient data in ten habitat patches for estimation of the daily population size and survival. The daily survival (SE) varied between 0.22

(0.18) and 0.79 (0.02) for males and 0.82 (0.04) and 0.87 (0.08) for females. The changes in estimated daily population size in the habitat patches are shown in Fig. 2. In all patches protandry was observed, i.e. males emerged earlier than females (Fig. 2). Average lifespan (SE) varied between 0.7 (0.5) and 7.3 (0.3) days (Table 1). The timing of the highest daily population size varied in the ten habitat patches; there were 6 days difference between first and last peaks in the number of individuals. Highest daily population size was observed on the 5th and 6th of June in patch C, D, E, Mv, and between the 10th–12th of June in patch B1, B2, K1, K2, K3, V2. The two groups of patches were separated by relatively large distances and differed in size (Fig. 1). The estimated total number of individuals in the metapopulation was slightly over 3,000, which was calculated for ten habitat patches, where the total estimated number of individuals (SE) varied between 24 (6.7) in patch E and 765 (73.5) males and 290 (28.6) females in patch B2.

As the butterflies were individually marked in twelve patches regularly and in four additional ones occasionally, we had information about the dispersal among habitat patches. Altogether, 48 dispersal events (37 males and 11 females) were detected between habitat patches. Females moved less frequently and shorter distances than males. For males, the longest observed movement was 5.8 km, while the longest observed movement by a female butterfly was less than 0.5 km. The Virtual Migration 2 model showed that one dispersal parameter differed significantly between males and females; distance-dependence of migration was stronger in the case of females (Table 2). The Virtual Migration 2 model's goodness-of-fit test showed that model fit was poor only in two habitat patches (C, V2) for males and in three habitat patches (K1, M, V2) for females (Table 3).

The maximum daily density was significantly affected by the groundwater level and by the area covered by tussocks following the minimal adequate general additive model (Table 4). The density of butterflies was higher in habitats where the groundwater level was lower, and the area covered by tussocks was larger, groundwater level had a stronger effect (Table 4). The depth of groundwater level and the height of grass litter, based on general additive model (Table 4), affected the estimated total population size. The population size was larger in habitat patches where the groundwater level was lower and the grass litter was higher, both parameters had almost equal influence on population size (Table 4).

Discussion

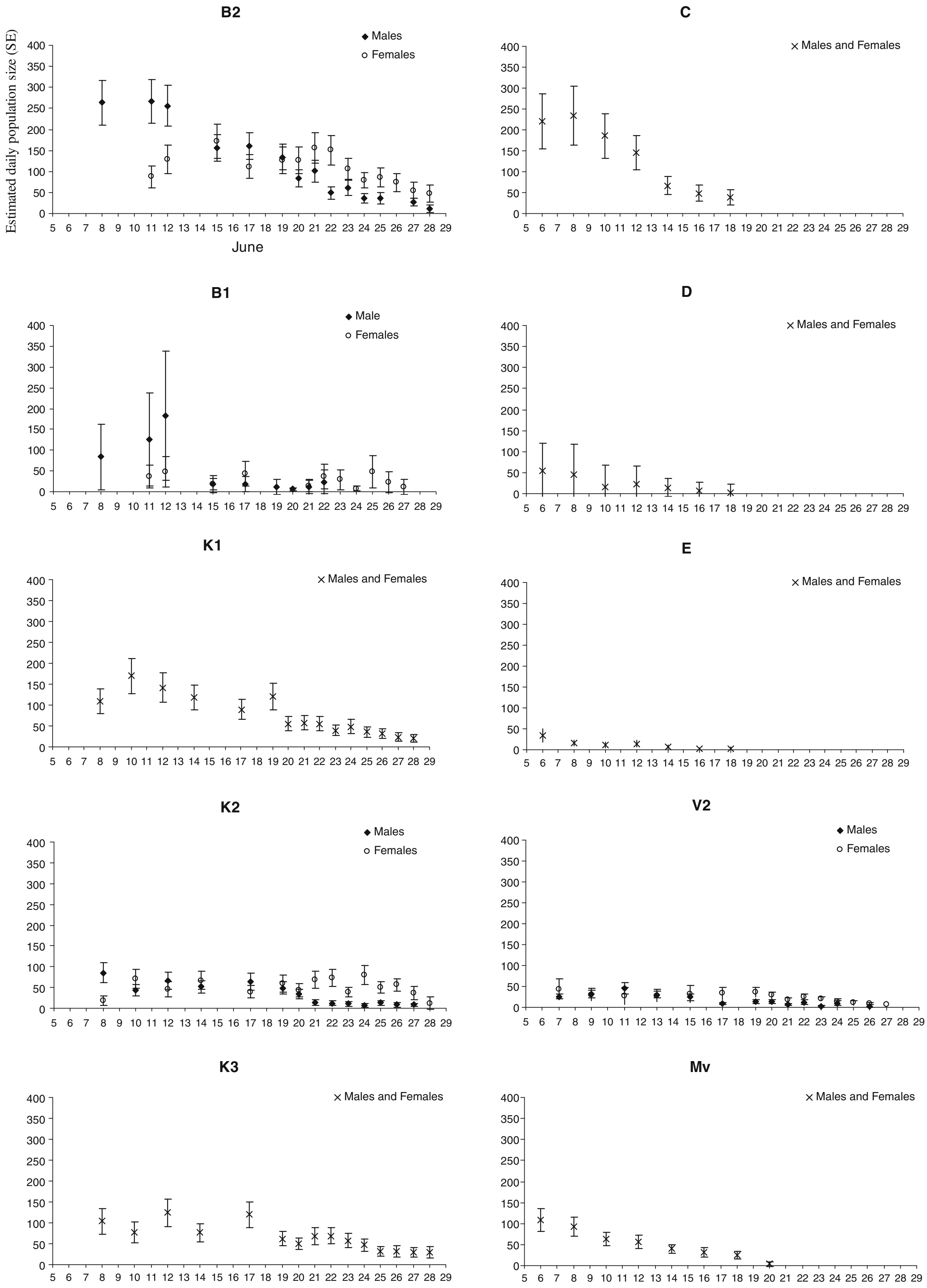
Metapopulation structure

The metapopulation of the False Ringlet at Ócsa, Hungary, is larger both in area and population size than earlier

Table 1 Summary data of the mark-release-recapture dataset, and derived parameters from Cormack–Jolly–Seber model (capture probability, Lifespan) and Jolly–Seber model (total population size)

Habitat patch	Area (ha)	Number of captured individuals		Number of recaptured individuals		Capture probability		Lifespan (SE) (day)		Maximum daily density	Total population size (SE)	
		m	f	m	f	m	f	m	f	Captured individual/ minute	m	f
B1	0.14	46	33	3	4	0.62 (0.76)	0.079 (0.05)	0.7 (0.5)	7.3 (0.4)	0.83	42.0 (<0.1)	93.4 (35.9)
B2	0.53	322	205	79	75	0.15 (0.02)		4.2 (0.3)	7.3 (0.3)	0.95	765.3 (73.5)	289.9 (28.6)
C	1.66	137	82	19	10	0.18 (0.06)		2.8 (0.3)		0.27	384.4 (77.0)	236.3 (49.5)
D	0.79	38	46	5	9	0.34 (0.11)		2.5 (0.4)		0.33	55.9 (12.2)	
E	0.54	16	20	3	5	0.30 (0.13)		3.4 (0.4)		0.17	23.7 (6.7)	
K1	0.16	141	87	19	21	0.19 (0.04)		2.8 (0.3)		1.72	336.8 (53.0)	164.1 (26.6)
K2	0.21	187	128	26	39	0.35 (0.10)	0.16 (0.03)	1.5 (0.4)	5.0 (0.3)	1.42	302.7 (30.9)	
K3	0.27	115	65	24	22	0.17 (0.03)		4.2 (0.3)		0.78	225.7 (33.1)	114.4 (19.3)
M	0.53	85	54	24	12	0.27 (0.06)		4.0 (0.3)		0.48	102.7 (7.4)	
V2	0.42	89	110	39	52	0.30 (0.04)	3.7 (0.3)	6.9 (0.3)		0.46	94.4(7.4)	
At	0.04	7	3	4	0					0.60		
Kb	0.57	7	10	5	0					0.09		

Here we present the most parsimonious models, in some cases gender differences appeared in parameter values (m: male, f: female). The Cormack-Jolly-Seber models were for each patches: B1, K2 [*Phi*(g), *P*(g)]; B2, V2 *Phi*(g),*P*()]; C, D, E, K1, K3, Mv [*Phi*(),*P*()]. The number of marked and recaptured butterflies was not large enough for model parameter estimation with Cormack–Jolly–Seber nor with Jolly–Seber method in patch At and Kb. The Jolly–Seber model did not fit for males of patch B1, due to low recapture rate


B2
◆ Males
○ Females
Estimated daily population size (SE)
400
350
300
250
200
150
100
50
0
5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29
June
C
× Males and Females
B1
◆ Male
○ Females
D
× Males and Females
K1
× Males and Females
E
× Males and Females
K2
◆ Males
○ Females
V2
◆ Males
○ Females
K3
× Males and Females
Mv
× Males and Females

◀ **Fig. 2** Estimated daily population sizes (±SE). Estimation was based on MRR dataset analysis with a Jolly-Seber model. The best model was gender dependent in patch B1, B2, K2 and V2, hence males and females are illustrated separately, while in the other patches estimated daily population sizes were illustrated jointly for males and females. The Jolly-Seber model did not correctly fit for males of patch B1, therefore SE values are large

Table 2 Parameter estimates from the Virtual Migration 2 model (95 % confidence intervals in parentheses) for False Ringlet within the 12 study and 4 additional meadow patches

	Male parameter value	Female parameter value
Within-patch mortality	0.096 (0.000; 0.231)	0.112 (0.000; 0.180)
Emigration constant	0.140 (0.032; 0.266)	0.071 (0.011; 0.201)
Scaling of emigration	−0.189 (−0.463; −0.000)	−0.000 (−0.545; 0.000)
Distance dependence	**1.026 (0.654; 1.554)**	**0.210 (0.000; 0.625)**
Migration mortality	3.896 (0.000; 8.239)	14.546 (0.000; 58.531)
Scaling of immigration	–	–

Distance dependence differed significantly between males and females. Significant differences between sexes are shown in bold. Scaling of emigration and immigration did not differ significantly; therefore, scaling of immigration was a fixed parameter

estimations suggested (Bálint and Máté 2004), but it is divided into small subpopulations. This indicates that the population complex may be vulnerable due to small subpopulation sizes. Spatial isolation of the subpopulations raises the possibility of a metapopulation structure. The attributes of classic metapopulations include colonization-extinction dynamics, fast turnover rate, sufficient dispersal among habitat patches, asynchronous dynamics of the local populations, and strict distinction between habitat and hostile matrix (Hanski and Glipin 1997; Hanski 1998; Bourn et al. 2000). Our results suggest that female dispersal is very low, hence, probability of recolonization is low, and a fast turnover rate is unlikely (Hanski and Glipin 1997). While females move only among the closest habitats, there is evidence that males are able to move between all the examined habitat patches. Similar gender differences in dispersal were also observed in an Italian population (Bonelli et al. 2010). In a Slovenian habitat complex the maximum observed dispersal movement was less than 340 m (Čelik and Verovnik 2010), whereas a Croatian study shows no dispersal even among close habitat patches (<450 m; Šašić 2010).

Spatial asynchrony in demography of local populations can also be frequently detected in metapopulation dynamics (Sutcliffe et al. 1997). In the studied metapopulation, there were two groups of habitat patches with 6 days difference between the peaks of the estimated daily

Table 3 Virtual Migration 2 model goodness-of-fit test for each habitat patch separately for males and females

Habitat	Males						Females					
	Residents		Emigrants		Immigrants		Residents		Emigrants		Immigrants	
	Q	df	Q	df	Q	df	Q	df	Q	df	Q	df
B1	0.44	23	0.12	11	0.28	11	0.32	22	0.03	11	0.11	10
B2	1.36	23	0.54	11	0.28	11	0.41	22	0.23	11	0.10	10
C	**1,418.37**	13	**1,418.36**	6	0.01	6	0.04	13	0.03	6	0.02	6
D	0.03	13	0.01	6	0.02	6	0.03	13	0.02	6	0.01	6
E	0.01	13	0.01	6	0.01	6	0.02	13	0.01	6	0.01	6
K1	2.17	23	0.23	11	0.15	11	**34.32**	22	0.10	11	32.51	10
K2	0.72	23	0.20	11	0.19	11	32.95	22	32.54	11	0.11	10
K3	0.77	23	0.17	11	0.19	11	1.66	22	0.07	11	0.12	10
M	0.01	13	0.00	6	0.01	6	**208.29**	13	**208.27**	6	0.02	6
V2	**1,422.41**	23	0.06	11	**1,418.55**	11	**213.90**	23	0.10	11	**208.37**	11
At	0.01	13	0.00	6	0.01	6	0.01	8	0.00	1	0.01	1
Kb	0.00	13	0.00	6	0.01	6	0.02	13	0.00	6	0.01	6
A	0.00	1	0.00	0	0.00	0	0.00	1	0.00	0	0.00	0
Bt	0.00	1	0.00	0	0.00	0	0.00	1	0.00	0	0.00	0
S	0.00	1	0.00	0	0.00	0	0.00	1	0.00	0	0.00	0
V1	0.00	1	0.00	0	0.00	0	0.00	1	0.00	0	0.00	0

Significant ($p > 0.05$) lack of fit are shown in bold

Table 4 Results of general additive model analyses showing the minimal adequate models for maximum density and total population size of the False Ringlet

Dependent variable	AIC of basic model with intercept only	AIC of lowest AIC model	Explanatory variables	Parameter estimates (SE)
Maximum density	17.03	−1.21	Groundwater level	**0.67 (0.09)**
			Area covered with tussocks	**0.39 (0.09)**
Total population size	143.00	131.86	Groundwater level	**0.59 (0.14)**
			Height of grass litter	**0.66 (0.15)**

Groundwater level, area covered by tussocks and height of grass litter are significantly related with the density and total population size of False Ringlet

Significance of estimated parameters in all cases: $p < 0.001$

population sizes. The first peak occurred in the largest, more open patches on the western side of the study area, while the latest peak was in the smaller, more closed habitat patches on the eastern side (Fig. 2.). In this case, the distance between the two groups and difference between habitat characteristics (such as area and shading) may together have caused the asynchrony among subpopulations. This asynchrony is probably not large enough to save a subpopulation from environmental perturbations, such as unfavourable weather conditions, but can strengthen the metapopulation, as the two groups of patches are separated by time and distance. Dispersal among habitat patches is possible, as patches inhabited by the metapopulation have soft rather than sharp habitat boundaries. Several male butterflies were spotted in between habitat patches, indicating that the matrix is suitable for longer persistence, although, female dispersal is more limited. These differences in dispersal distances may be a result of sex-specific effects of unfavourable matrix environment on flight speed, as was shown by Turlure et al. (2011) in *Boloria* butterflies. Dispersal was not even among patches, and the VM2 model did not fit in some patches. Those patches probably differed in habitat quality, affecting dispersal pressure (Baguette et al. 2011).

According to these results, the metapopulation of False Ringlet at Ócsa is consisted of two groups of habitat patches that can aid the long-term survival of each other, although we did not observe any female dispersal between the two groups. Female dispersal was limited to very short distances, but male dispersal might have been also controlled by habitat quality, alongside patch area and distance. Our results indicate that creating stepping-stones or corridors for females between habitat patches may have a positive effect on female dispersal and therefore strengthen the metapopulation. Although, to reveal the metapopulation structure, the long-term study of patch occupancy and local population asynchrony is necessary, while a genetic study would help to assess the present and past possibilities of dispersal.

Habitat quality, requirements and management

Habitat patches differed in several ways, in area, quality and earlier and current management. Patches in the same size were very different in the number of marked individuals (Table 1). Habitat patch B2 has a large subpopulation versus patch E or Kb. While the small number of marked individuals in patch Kb can be explained by its distance from the core habitat patches, the centrally located patch E must be of lower quality as it only supports a small population. In addition, there are differences in the lifespan of males and females among the habitat patches. Lifespan is calculated from apparent survival probability, which is negatively related with dispersal from a given patch. Greater dispersal can be caused by several factors, including lower habitat quality, males searching for female and density dependent dispersal (Baguette et al. 2011). In this case, male butterflies in patch B1 have a very short estimated lifespan, which is probably a result of a combination of poor model fitting and a high emigration rate, and not a locally high death rate. A high emigration rate of males in this patch may be the result of a low number of females in that patch. Overall, male dispersal was greater than female dispersal, explaining the lower apparent survival and so shorter lifespan of males. The shorter estimated lifespan, compared to other studies (Čelik and Verovnik 2010; Örvössy et al. 2010) is probably the consequence of dispersal among local habitat patches.

Determination of habitat quality in the patches and the requirements of the species can help determine proper habitat management, which can facilitate long-term persistence of the subpopulations. Three variables of habitat quality were of particular importance: groundwater level, height of grass litter and the area covered by tussocks. Our expectation was that higher water level increases habitat quality for the subpopulations, as the species lives in wet meadows and the local and several other European populations are suffering from the effects of land drainage (Čelik and Verovnik 2010; Örvössy et al. 2010; Šašić 2010;

Sielezniew et al. 2010). In contrast to this, we found that the patches with lower groundwater level were inhabited by larger and denser subpopulations. However, we have to acknowledge that this phenomenon is only true at this range of groundwater level, as the surrounding unoccupied drier uninhabited areas were not included in the study. In the light of the fact that there are plans to increase the groundwater level in the area, this is an especially important result. The groundwater level may have a detrimental negative effect on larval survival by changing vegetation structure and microclimate. Rapid and drastic increases of groundwater level should be avoided, as this could destroy the habitat as well as the population. An earlier study on *Coenonympha tullia* showed that larvae can climb up to high positions during flooding (Joy and Pullin 1996). Therefore maintaining tall vegetation is important for larval survival in areas subject to flooding. During winter and early spring the area can be covered by water and the existence of dry areas can be crucial for the survival of larvae. Adult False Ringlet butterflies locally may prefer semi-open habitats with bushes (Čelik and Verovnik 2010; Örvössy et al. 2010; Šašić 2010; Sielezniew et al. 2010), because bushes develop well where the groundwater is not so high and provide a better microclimate for the butterflies in hot summers. More specifically, the groundwater level should be high enough to maintain the *Molinietum* vegetation for the species, but sufficiently low to allow larval survival and the presence of bushes for adult preferences.

Although the presence of bushes might increase the size and density of subpopulations, encroachment of bushes due to abandonment of these wet meadows can destroy the habitats in the study area and in other European locations as well (Bräu et al. 2010; Čelik and Verovnik 2010; Örvössy et al. 2010; Šašić 2010; Sielezniew et al. 2010). Regular mowing can prevent the spread of weeds, such as *Solidago* spp. and encroachment of bushes, but also has a negative effect on tussock structure and amount of grass litter (Bartoš et al. 2011).

Structured vegetation with tussocks and large amounts of grass litter were among the most important factors affecting population density and size in the study area. The maximum daily density was higher in habitat patches where tussocks covered a large proportion of the patch, and the estimated population size increased with the height of grass litter. This could be the consequence of larvae overwintering inside the tussocks and grass litter (Bräu et al. 2010). Traditionally, infrequent (once yearly) mowing by hand in autumn maintained these semi open meadows. Too frequent mowing could lead to the loss of grass litter and of tussock structures, while lack of mowing would result in the overgrowing of the area (Skórka et al. 2007). For future prospects, a mowing experiment would help to reveal what kind of management can maintain an optimal habitat quality. Before that, there is an urgent topic to examine. The water level is going to be increased on the area to halt decades of slow desiccation. This process will rearrange the metapopulation structure: patch location, habitat size and quality, dispersal possibilities etc. Following this process would answer some questions about how this metapopulation reacts to habitat changes and its precise structure.

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