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ORIGINAL PAPER

Oviposition site selection of the Alcon blue butterfly at the northern range margin

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Abstract Female oviposition decisions in insects may strongly affect offspring growth and survival, and thus determine population performance. In this study, we examined oviposition site selection in the xerophilous ecotype of the endangered myrmecophilous butterfly *Phengaris* (=*Maculinea*) *alcon* (Lepidoptera, Lycaenidae) in Estonia, at the northern distribution margin of both the butterfly and its host plant, *Gentiana cruciata* L. Egg distribution on individual host plants appeared to be highly uneven: plants carrying high egg loads contrasted to a high proportion of host plants without any or with a few eggs. Host plant use for oviposition was strongly dependent on plant characteristics and environmental context. Host plant height relative to the surrounding vegetation rather than the absolute height of host plants was a key factor determining the use of particular host plant individuals for oviposition. In particular, plants protruding above surrounding vegetation had a higher probability of being used for oviposition, and carried more eggs. Additionally, the number of eggs laid on individual host plants was positively associated with the presence of flowers and the number of shoots. More aggregated host plants received fewer eggs than those with less conspecifics around. Feeding damage by wild herbivores, found in a substantial proportion of the butterfly's host plants, strongly reduced the number of eggs on individual plants. Our results underline the need to assure that butterfly's host plants do not become overgrown by surrounding vegetation. Best practices for opening vegetation around host plants may need further studies that explicitly account for butterfly's host ants—their abundance in relation to vegetation height and their response to opening vegetation.

Keywords Phengaris rebeli · Oviposition preference · Habitat requirements · Microclimatic conditions · Peripheral populations · Social parasite

Introduction

One of the major concerns for conservation biology today is the fast decrease of global biodiversity (e.g. Pereira et al. 2010; Cardinale et al. 2012). Populations of numerous species have significantly declined or even gone extinct, mainly as a consequence of habitat loss and fragmentation (e.g. Tscharntke et al. 2002; Fahrig 2003; Van Swaay et al. 2005; Thomas et al. 2009; Van Dyck et al. 2009). Nevertheless, there are many cases where population declines have resulted from inappropriate management of existing habitats (Balmer and Erhardt 2000; Waring 2001; Konvička et al. 2008). Narrowly specialized species, and those occurring at low densities, are expected to be particularly vulnerable in this regard.

The adequacy and effectiveness of habitat management practices often require detailed information on geographic variation in species' ecological requirements. In the case of insects, ecological factors controlling female oviposition decisions are one of the key elements to consider. Egg-laying choices of a female largely determine the environment in which her progeny will grow, thus strongly affecting offspring growth and survival (e.g. Bergström 2005; Küer and Fartmann 2005; Doak et al. 2006). Quite naturally, in herbivorous insects, such as butterflies, a suitable oviposition substrate is primarily determined by host plant species.

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However, many additional factors may affect actual availability and suitability of a host plant for oviposition. Host plant size (e.g. Wiklund 1984; Heisswolf et al. 2005; Küer and Fartmann 2005) and apparency (e.g. Chew and Courtney 1991), its nutritional quality (e.g. Baylis and Pierce 1991), microclimatic conditions (e.g. Shreeve 1986) as well as the presence of mutualists (e.g. Pierce and Elgar 1985) and natural enemies (e.g. Wiklund and Friberg 2008) have all been shown to play a role in oviposition site selection. Because of these additional restrictive factors, a considerable proportion of potentially suitable host plants may remain unused by female butterflies. Consequently, knowledge of plant characteristics affecting oviposition decisions is fundamental for developing management practices that by increasing the proportion of suitable host plants, would enhance persistence of small, host plant limited populations.

Peripheral populations deserve particular attention in this regard as they hold key insights into the limits of realized niches (Holt and Keitt 2005; Bahn et al. 2006). In particular, the northern distribution limits of many insect species, butterflies among them, have been shown to be primarily determined by temperature rather than host plant distribution (Virtanen and Neuvonen 1999; Mattila et al. 2011). This means that populations at their northern range margins are likely to face climatic conditions that are more restrictive for their growth and development than conditions in more central populations of their distribution range. Accordingly, peripheral populations often appear to be ecologically divergent from more central populations (Moritz et al. 2012; Krehenwinkel and Tautz 2013; Bridle et al. 2014). We also might expect herbivorous insects to differ in their oviposition behaviour, e.g. in microclimatic preferences during egg-laying. Accounting for region-specific ecological requirements is therefore particularly essential for successful conservation of peripheral populations, but could also be valuable for understanding species' biogeography and evolutionary ecology (e.g. Settele et al. 2005).

The endangered, obligatorily myrmecophilous butterfly Alcon blue, *Phengaris alcon* (Denis and Schiffermüller, 1775), stands out for its complex life cycle (e.g. Thomas et al. 1989). Female butterflies lay their eggs on specific host plants where (functionally) monophagous caterpillars pass through their first three instars feeding on developing flowers and seeds. In the fourth (final) instar, the caterpillars drop to the ground where they are adopted by ants from the genus *Myrmica* Latreille, 1804. They complete their development in ant colonies as obligatory parasites. Population performance of these butterflies thus depends on two specific, spatially overlapping, resources; both of which can be limiting (e.g. Clarke et al. 1998; Meyer-Hozak 2000). Within populations, *P. alcon* as well as most other *Phengaris* species are highly specialized both in their

host plant and host ant use. However, among geographically distant populations, substantial intraspecific variation occurs in host use (e.g. Elmes et al. 1998; Steiner et al. 2003; Arnaldo et al. 2011; Casacci et al. 2011; Czekes et al. 2014) and, thus inevitably, in many related ecological aspects, oviposition site selection among them. Moreover, the existence of two different ecotypes (xerophilous and hygrophilous; *P. alcon* X and *P. alcon* H, hereafter) in this species (Als et al. 2004; Bereczki et al. 2005, 2006; Fric et al. 2007; Sielezniew et al. 2012) adds another dimension of intraspecific ecological variation.

In this study, we examined host plant use for oviposition in the xerophilous ecotype of *P. alcon* (*P. rebeli* auct. nec Hirschke, 1904, see Als et al. 2004; Pech et al. 2004; Bereczki et al. 2005; Pecsenye et al. 2007) at the northern distribution margin of the species (Northern Estonia). The species occurs in the study region in small (sub)populations, confined to small isolated habitat patches in a landscape dominated by relatively intensive agriculture (Vilbas et al. 2016) and therefore requires urgent conservation attention. The species has expanded to its present northern range margin relatively recently, whereas a further expansion of its range to the north with warming climate is unlikely. This is because its sole host plant in the region, *Gentiana cruciata* L. (Kukk and Kull 2005; GBIF Backbone Taxonomy 2016), also reaches its northern range margin in Estonia, and a northward shift of the plant is unexpected due to lack of suitable habitats (calcareous grasslands) at higher latitudes. Although the egg-laying behaviour of *P. alcon* has attracted considerable attention (e.g. Dolek et al. 1998; Van Dyck et al. 2000; Küer and Fartmann 2005; Nowicki et al. 2005; Árnyas et al. 2006; Van Dyck and Regniers 2010; Czekes et al. 2014; Wynhoff et al. 2015; Osváth-Ferencz et al. 2016), the results obtained from different regions, and for different ecotypes of the species, are somewhat inconsistent, and such information at the species' northern range margin is lacking. To ascertain the main drivers of host plant use for oviposition in the northernmost *P. alcon* X populations, we evaluated the relative importance of various host plant related factors potentially affecting the butterfly's selection of particular oviposition sites. We discuss our results in the context of practical conservation of this species.

Materials and methods

Study species and research area

Only the xerophilous ecotype of *P. alcon* is known to occur in Estonia. The butterfly inhabits a few small areas in the northern and central parts of the country, where it occurs on nutrient-poor xerothermic and calcareous

grasslands. In the study region, *Gentiana cruciata* L. is the sole larval host plant of the species. As for host ants, the caterpillars have been documented to complete their development exclusively in the colonies of *M. schencki* Viereck in Estonian populations (Vilbas et al. 2016). Adults are on the wing from the beginning of July to the end of August.

Host plant use for oviposition was investigated in the largest known population of *P. alcon* X in Estonia, in a 13.2 ha calcareous grassland in the Pandivere Upland (Fig. 1). This grassland harbours one of the largest *G. cruciata* populations in the region, with an estimated 400 *G. cruciata* plants, corresponding to an average density of approximately 30 plants/ha. The landscape surrounding the study area is dominated by arable land and forest, in which calcareous grasslands form a mosaic of small discontinuous patches.

Data collection

Data on the distribution of eggs on host plants were collected in a sampling area of 300×150 m (i.e. 4.5 ha, Fig. 1). In the beginning of September 2014, shortly after the flight period of the butterfly, we counted all *P. alcon* X eggs (either as live eggs or egg shells) on all host plants within the sampling area. The distinctive and resilient egg shells of the butterfly are firmly attached to the host plants (Thomas et al. 1991), facilitating detailed field studies of host plant use for oviposition even after eggs have hatched. For each host plant individual, we recorded the following data: (a) number of shoots, (b) average height of the shoots, (c) average height of the vegetation surrounding the host plant [using the method described by Stewart et al. (2001)], (d) presence/absence of flowers, and (e) host plant patchiness (number of *G. cruciata* shoots within a 1 m radius around the focal plant). Besides these parameters,

Fig. 1 Location of the study site in Estonia, Northern Europe (*above*) and a map illustrating the distribution of *Gentiana cruciata*, the sole host plant of *Phengaris alcon* X, in the study site (*below*)
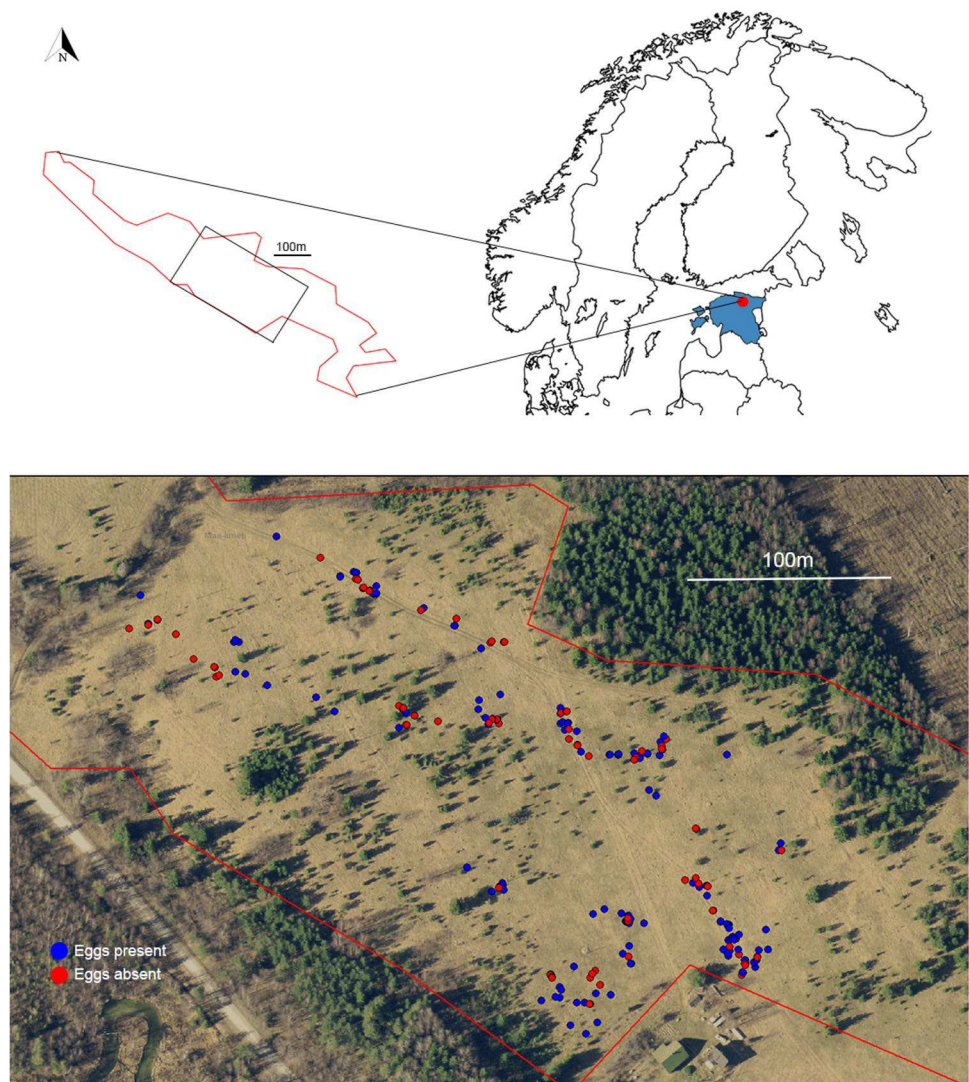
for each host plant individual we calculated the difference between the height of its tallest shoot and average height of the surrounding vegetation to describe host plant apparency for ovipositing butterflies. Finally, we documented damage caused by wild herbivores to individual shoots (shoot damaged/undamaged).

Statistical analyses

At least partly, qualitative (presence-absence of eggs on particular host plants) and quantitative (number of eggs on the plant, once it is used for oviposition) patterns of oviposition site use reflect two fundamentally different aspects of oviposition—host plant searching/finding and host plant use for oviposition once it has been found. To decouple factors governing these oviposition steps, we analysed factors determining host plant use for oviposition in two steps. In the first step, a generalized linear model (GLM) with binomial errors (logistic regression) was applied to assess the factors affecting oviposition site use at the level of presence–absence of *P. alcon* eggs. In the next step, we only used the subset of plants with eggs to ascertain the factors affecting the number of eggs laid on host plants. For this purpose, a GLM model with a Poisson error structure was applied. The following predictor parameters entered the model in both cases: (a) host plant apparency, (b) host plant patchiness, (c) number of shoots, (d) average height of the shoots, and (e) presence/absence of flowers (see also Table 1). To identify collinearity between predictor variables, we calculated a variance inflation factor (VIF) for each variable. None of our VIF values exceeded 1.8, whereas collinearity among variables is considered to become problematic at VIF > 3 (Zuur et al. 2010). Best models (see below) were statistically tested to assess spatial autocorrelation in the model residuals. Moran's I was used for this purpose. In addition, best models were checked visually for spatial autocorrelation (both Pearson and deviance residuals). As spatial autocorrelation was not significant in the models, we used non-spatial models.

An Information-theoretic approach was employed for model selection and multimodel inference. Candidate models were ranked using Akaike information criteria corrected for small sample sizes (AIC_C). For each particular model, the difference between its AIC_C value and AIC_C value of the best model was calculated (ΔAIC_C), ΔAIC_C of the best model being zero. The models with $\Delta AIC_C \leq 2$ were considered to be close to the best model (Burnham and Anderson 2002). The ΔAIC_C values were used to calculate Akaike weights for each model. To infer the relative importance of predictor variables, model averaging was conducted across models with all possible combinations of variables. The relative importance for each variable was calculated by summing Akaike weights across all the models containing that particular variable—the larger the sum for a particular variable, the more important it was considered relative to other variables (Burnham and Anderson 2002). All the analyses were performed in R version 3.1.1 (R Development Core Team 2014), using *MuMIn* (model selection and model averaging; Bartoń 2013) and *Ape* (assessing spatial autocorrelation; Paradis et al. 2004) packages. Plants that were damaged by herbivores were not incorporated in any of these analyses. However, to assess potential effects of herbivore browsing on oviposition patterns, separate analyses were carried out to compare egg numbers on damaged vs. undamaged shoots.

Results

Altogether 295 *G. cruciata* plants (66 plants/ha) with 918 shoots were examined for *P. alcon* X eggs (Fig. 1). In total, 2,733 eggs on 192 plant individuals (65% of all plants) were found, i.e. average egg count per plant was 14.2. The number of eggs found on individual plants was highly variable, ranging from 1 to 123 eggs. Just 10.5% of all plants carried half of all eggs. More than 98% of eggs were located in the upper 20% of the shoots. Leaves were the most preferred oviposition substrate, receiving 68.5% of all eggs (54.6 and 13.9% on the adaxial and abaxial surfaces, respectively). Flowers carried 30.4% and stalks the remaining 1.1% of eggs.

Table 1 Mean parameter values (and bootstrap confidence intervals) for host plants with/without eggs of *Phengaris alcon* X

Variable	Eggs present		N	Eggs absent		N
	Mean	95% CI		Mean	95% CI	
Host plant apparency* (cm)	12.9	(12.3, 13.5)	167	5.8	(4.5, 7.1)	87
Host plant patchiness**	4.0	(3.3, 4.7)	167	5.5	(4.3, 6.6)	87
Number of shoots per plant	3.1	(2.9, 3.3)	167	2.5	(2.1, 2.8)	87
Average host plant height (cm)	25.0	(23.8, 26.1)	167	20.5	(19.3, 21.9)	87

*Difference between the height of the tallest shoot of the host plant individual and average height of the surrounding vegetation

**Number of *G. cruciata* shoots within 1 m radius around focal host plant

Table 2 Best models predicting presence-absence of eggs *Phengaris alcon* X on individual host plants

Model rank	Host plant apparency	Host plant patchiness	Number of shoots	Host plant height	Presence of flowers	AIC$_C$	ΔAIC$_C$	Akaike weight
1	+	+	−	−	−	238.0	0	0.229
2	+	−	−	−	−	238.8	0.84	0.150
3	+	+	+	−	−	239.9	1.89	0.089

Models are ranked by Akaike information criteria

+/− indicate presence/absence of particular variables in the models

Table 3 Relative importance of the variables predicting presence-absence of *Phengaris alcon* X eggs on host plant individuals, as based on model averaging

Predictor variable	Relative importance
Host plant apparency	1.00
Host plant patchiness	0.59
Number of shoots	0.29
Host plant height	0.27
Presence of flowers	0.27

Presence-absence of *P. alcon* X eggs on individual plants was best explained by a model containing host plant apparency and host plant patchiness. Host plant apparency was also present in other top-ranked models (Table 2), whereas the presence of other variables in top-ranked models was less consistent. Accordingly, based on model averaging over all 32 models, host plant apparency was the only predictor with high relative importance (RI = 1, Table 3). It was followed by host plant patchiness, while other variables (number of shoots, average height of the host plant and presence of flowers) had much lower relative importance (Table 3). With regard to variables of higher importance, *P. alcon* X was more likely to oviposit on host plants that were protruding from the surrounding vegetation, and those being spatially less clumped / more isolated (Table 1).

The number of eggs laid by *P. alcon* X on individual host plants was best explained by two models that carried virtually all Akaike weight (w_i = 0.999). Both models contained host plant apparency, host plant patchiness,

number of shoots and presence of flowers as predictor variables (Table 4). Accordingly, all these four variables achieved very high relative importance values from model averaging (Table 5). The average height of host plant shoots was present in one of the two top-ranked models and had thus lower relative importance in predicting the number of eggs laid on host plants. More specifically, the number of eggs on host plant individuals was positively associated with host plant apparency, number of shoots and the presence of flowers. Also, less clumped host plants received relatively more eggs than those with more conspecifics around. As an illustration of the latter point, host plant individuals with no conspecifics within 3 m radius carried almost twice as many eggs as those with at least one other host plant individual within 3 m radius (15.6 vs. 8.7, respectively). In regard to predictor variables, there was a significant positive relationship between host plant apparency and mean number of flowers per plant shoot ($F_{1,253}$ = 64.8, p < 0.00001).

Eighty-one shoots in 41 plants (8.8 and 13% of all shoots and plants, respectively) had their upper parts missing, with clear signs of browsing by (wild) herbivores. Significant differences between damaged and undamaged shoots were detected both at the level of presence–absence of eggs and numbers of eggs. In particular, shoots that had been damaged had significantly lower probability of carrying butterfly eggs (Fisher's exact test: p < 0.0001). Consistently, damaged shoots had 3.5 times less eggs than undamaged ones (Welch's two-tailed *t* test: t = 4.36, df = 6.3, p = 0.004). Interestingly, herbivore browsing was more severe in plants with fewer conspecifics around (2.2 shoots within 1 m radius, on average,

Table 4 Best models predicting the number of eggs laid by *Phengaris alcon* X on individual host plants

Model rank	Host plant apparency	Host plant patchiness	Number of shoots	Host plant height	Presence of flowers	AIC$_C$	ΔAIC$_C$	Akaike weight
1	+	+	+	−	+	2456.4	0	0.680
2	+	+	+	+	+	2457.9	1.51	0.319

Only plants in which at least one egg had been laid were considered in this analysis. Models are ranked by Akaike information criteria

+/− indicate presence/absence of particular variables in the models

Table 5 Relative importance of the variables predicting number of eggs laid by *Phengaris alcon* X on individual host plants, as based on model averaging

Predictor variable	Relative importance
Host plant apparency	1.00
Host plant patchiness	1.00
Number of shoots	1.00
Presence of flowers	1.00
Host plant height	0.68

around damaged plants and 4.5 shoots around undamaged plants: $F_{1,293} = 8.5$, $p = 0.004$).

Based on the number of eggs counted, we could assess the size of the population examined. In particular, taking into account that a female *P. alcon* lays 100–150 eggs (Hochberg et al. 1992; Meyer-Hozak 2000) with a sex ratio of approximately 1:1 (e.g. Meyer-Hozak 2000), and that we counted eggs on about three-fourths of all *G. cruciata* individuals, the size of the population can be estimated to be about 50–70 individuals.

Discussion

The number of eggs laid per host plant strongly varied in the xerophilous ecotype of *Phengaris alcon* at its northern distribution margin. While more than one-third of host plant individuals remained completely unused, a bare 10% of most egg-loaded plants carried nearly half of all eggs. A closer examination indicates that the butterflies' oviposition patterns are strongly linked to plant characteristics and environmental context. In particular, more conspicuous host plants and those isolated from other conspecifics had a higher probability of being used for oviposition and carried more eggs than less conspicuous plants and those with a more aggregated spatial distribution. The number of eggs laid was also notably higher on plants with flowers and a greater number of shoots. Eggs were mainly deposited on the uppermost organs of the plants, close to the flower buds and stalks. Also, our results indicate that wild herbivore feeding may be an important factor influencing the fate of laid eggs, and thus population performance of *P. alcon*.

Oviposition on tall, visually conspicuous plants is a frequently documented pattern in butterflies (e.g. Thompson and Price 1977; Courtney 1982; Porter 1992; Nowicki et al. 2005), and *P. alcon*, regardless of the ecotype, appears to be no exception (e.g. Nowicki et al. 2005; Árnyas et al. 2006; Wynhoff et al. 2015). However, our results show that host plant height relative to the surrounding vegetation rather than height of host plants per se is the main factor

that determines the use of particular host plant individuals for oviposition. In fact, without exceptions, all plants carrying eggs were higher than the surrounding vegetation. Perhaps the most straightforward interpretation of this result is that such plants are visually more easily detectable for the butterflies. Shoots above surrounding vegetation have also been proposed to provide better protection from predators (e.g. orb-webbing spiders; Küer and Fartmann 2005).

Alternatively, plants protruding above surrounding vegetation, and thus receiving more solar radiation, may offer more favorable microclimatic conditions for the development of butterfly eggs and newly-hatched larvae (Thomas 1991; Küer and Fartmann 2005). If this is the case, then host plant apparency should be particularly influential determinant of oviposition decisions in northern populations like ours. We also might then expect to see latitudinal variation in within-plant egg distribution, with individuals of northern populations laying proportionally more eggs on the upper side of the leaves. However, neither of these predictions seem to hold. Like in Estonian populations, host plant apparency has been reported to be a strong determinant of oviposition patterns throughout most of the species' European range (Germany: Dolek et al. 1998; Meyer-Hozak 2000; Lithuania: Oškinis 2012; Hungary: Árnyas et al. 2006; Romania: Osváth-Ferencz et al. 2016). Moreover, the available data on *P. alcon* X provide no evidence of latitudinal differences in within-plant egg distributions. Contrary to expectations, the proportions of eggs laid on the upper and lower surfaces of the leaves are astonishingly similar (55–60% of all eggs on the upper surface, 10–14% on the lower surface) in different regions (Estonia, Lithuania, Hungary), despite a latitudinal distance of more than 1500 km (this study, Árnyas et al. 2006; Oškinis 2012). Thus at the plant scale, microclimatic conditions seem to have little influence on oviposition decisions in this butterfly.

In the quantitative model of oviposition site use, host plant patchiness, number of shoots and presence of flowers were other predictor variables receiving high relative importance. Somewhat surprisingly, less aggregated host plants, i.e. those with fewer conspecifics growing in the near vicinity, carried higher numbers of eggs than more clumped plants. As a plausible explanation, this oviposition pattern may reflect low within-habitat movement in this species, resulting from high time stress set by a short life span combined with a high egg load (Körösi et al. 2008). Accordingly, it has been shown that, once the suitable host plant is found, *P. alcon* females tend to show highly stereotypic oviposition behaviour by repeatedly climbing up and down to lay their eggs on neighbouring shoots (Van Dyck and Regniers 2010). It is likely that in clumped plants, females exhibiting such behaviour lay their eggs on shoots of multiple closely spaced plants, resulting, however, in

fewer eggs per plant (see also Capman et al. 1990). This same egg laying behaviour may also explain why plants with higher number of shoots carried more eggs than those with fewer shoots.

P. alcon X has been shown to lay its eggs on host plants irrespective of the presence or density of host ant colonies (Thomas and Elmes 2001). This, however, implies that the observed accumulation of a high share of eggs on a relatively small proportion of host plants may have direct negative consequences for the butterfly population. In particular, a medium-sized host ant colony (*Myrmica schencki* in our population: Vilbas et al. 2016) gives rise to a maximum of 4–5 adult butterflies (Elmes et al. 1991). In our previous study (Vilbas et al. 2016), we showed that, in this population, larvae on a single host plant can typically be adopted by ants of no more than one colony, on average (we counted 18 *M. schencki* colonies in the vicinity of 29 host plants). In this case, if all eggs laid were to survive to adults, the optimal number of eggs on a single host plant should be up to five. In our population, however, more than 50% of the eggs located on individual plants in which the number of eggs was at least four times higher (i.e. >20, up to 123). By strongly exceeding the carrying capacity of *Myrmica* colonies around such plants, individuals from these heavily overcrowded host plants may thus exhibit high density-dependent mortality when adopted by ant colonies. Small populations like ours (50–70 individuals, see "Results" section) should be especially vulnerable to such losses.

In a considerable proportion of shoots inspected, their uppermost organs had been cut off, most likely due to browsing by wild herbivores, such as European roe deer (*Capreolus capreolus*), a species repeatedly observed in the study area during fieldwork. Herbivore damage had a strong negative effect on the presence and number of butterfly eggs. In particular, the notable 13% of all host plants with signs of herbivore feeding carried <0.5% of all eggs. Intriguingly, herbivore damage was particularly severe on more isolated host plants which, when undamaged, received more eggs than more aggregated plants (see above). Naturally, when acting after butterflies have laid their eggs, large herbivores could eat the eggs with plant organs. However, damaged plants may also become less detectable or less attractive for egg-laying butterflies. Indeed, browsed shoots were, on average, 3.5 cm shorter and had approximately 3 times less flowers than undamaged shoots. The detrimental effects of wild herbivores on *P. alcon* X populations are not necessarily rare: a similar cascade of interactions has also been reported in a Hungarian population of the butterfly (Árnyas et al. 2006).

Several guidelines and suggestions on how to manage *P. alcon* X habitats can be derived from the results of this study. Most importantly, it is essential to assure that the butterfly's host plants do not become overgrown by surrounding vegetation: otherwise, a high proportion of host plants may remain completely unavailable for oviposition. A positive relationship between host plant apparency and mean number of flowers per plant shoot indicates that overgrown plants also provide fewer resources for butterfly larvae and they have reduced reproductive success. Lower detectability of such plants for pollinators may lead to a further reduction in the seed set. Moreover, *Myrmica schencki*, the host ant of the butterfly in our populations (Vilbas et al. 2016) has been considered to be one of the most thermophilous ant species (Elmes et al. 1998), which may mean that high vegetation is unsuitable for the host ant as well. Nevertheless, further studies are needed to determine best practices for opening vegetation around host plants. Host ants are a key factor to consider here—their abundance in relation to vegetation height and their response to opening vegetation. Besides mowing and small-scale sod cutting (WallisDeVries 2004), carefully thought out grazing has been suggested as a tool to manage *P. alcon* X habitats (Maes et al. 2004). Nevertheless, care must be exercised because of direct (consumption of eggs and larvae) and indirect (consumption of flower buds and flowers, reduction of plant apparency) negative effects of grazing on the butterfly. As showed in this study, even wild herbivores can cause substantial damage to host plants. Spatial (exclosures to protect host plants) or temporal (grazing in late autumn after the larvae have left the plants) restrictions should therefore be applied to grazing regimes.

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