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Inhabiting warm microhabitats and risk-spreading as strategies for survival of a phytophagous insect living in common pastures in the Pyrenees

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Abstract. The breakdown of the transhumant grazing system in the Spanish Pyrenees has led to a severe decline in the area of pastures. However, in the high mountain zone there are still large areas of species-rich grasslands. The aim of this study was to assess the oviposition preferences of the shrub-feeding Blue-spot hairstreak, *Satyrium spini* (Denis & Schiffermüller, 1775), in montane common pastures in the Spanish Pyrenees and recommend a way of managing these grasslands that favours this species. Our study showed that females of *S. spini* laid their eggs on Dwarf buckthorn (*Rhamnus pumila* Turra) and Alpine buckthorn (*R. alpina* L.), which are novel host plant records for Spain. A warm microclimate was of crucial importance for egg-laying. Occupied plants grew mostly at sparsely vegetated grassland sites where there were large patches of bare rocks, stones or gravel. Most egg batches were laid close to the ground and 75% consisted of only one egg. The number of batches per *R. pumila* plant was higher on east-, south- and west-facing slopes than on north-facing slopes. Presence of eggs and the number of egg batches per *R. pumila* plant were best explained by a long sunshine duration. At high altitudes particularly warm microhabitats seem to be more important for *S. spini* than at lower altitudes in Central Europe. We assume that the preference for unusually warm microhabitats is explained by the cold climatic conditions near the altitudinal range limit of the species. That most of the eggs were laid singly and not in small batches as in Central Europe might be a risk-spreading strategy to cope with the harsh climatic conditions and the high inter-annual variation in weather conditions in the high mountain zone in the Pyrenees. The best way to maintain open grasslands for *S. spini* and other thermophilous grassland species in the high mountain zone of the Pyrenees is to use the traditional combination of sheep and cattle grazing.

INTRODUCTION

During recent decades, the worldwide rate of species extinctions has risen continuously and is now estimated to be 100 to 1000 times higher than the natural background extinction (Pimm et al., 1995). In terrestrial ecosystems, the most important driver of this process is land-use change (Sala et al., 2000). On a global scale it is expected to have the largest impact on biodiversity by the year 2100 and to be even more important than other factors like climate change or nitrogen deposition.

The transition from traditional land-use to modern agriculture mostly entails two contrasting processes: intensified use of productive sites that can be cultivated mechanically and abandonment of marginal land (Foley et al., 2005; Henle et al., 2008; Kleijn et al., 2009). Both phenomena often have adverse effects on species richness. Intense exploitation of agricultural land occurs mainly in lowlands with fertile soils and sufficient rainfall or irrigation water, whereas abandonment of land is typical of mountain areas (Caraveli, 2000; MacDonald et al., 2000). Declines in habitat and species diversity due to cessation of traditional land use have been reported for several European mountain ranges (MacDonald et al., 2000; Tasser & Tappeiner, 2002; Bezák & Halada, 2010).

The causes and consequences of land-use change are particularly well studied in the Spanish Pyrenees (García-Ruiz & Lasanta-Martínez, 1990; García-Ruiz et al., 1996; Poyatos et al., 2003; Lasanta-Martínez et al., 2005; Vicente-Serrano et al., 2005). The traditional agricultural systems have undergone dramatic changes since the beginning of the 20th century (García-Ruiz & Lasanta-Martínez, 1990; Lasanta-Martínez et al., 2005). Decreases in rural populations, losses of winter pastures in the Ebro basin and the development of tourism, which partially replaced agriculture as the main source of revenue, have led to the breakdown of the transhumance system (= seasonal movement of shepherds and their livestock). This in turn caused a severe decline in sheep numbers which in some areas decreased by 90% in the course of the last century and many summer pastures have become abandoned, particularly those that were less productive and remote. However, at high altitude in the Pyrenees there are still large areas of grassland with a very diverse fauna and flora (Gómez et al., 2003; García-González et al., 2008). Our study area in the upper part of the Aísa Valley (western Spanish Pyrenees) is such a biodiversity hotspot (Isern-Vallverdú, 1990; García-González et al., 1991).

Butterflies are a charismatic and species-rich insect group. Because they respond rapidly to environmental

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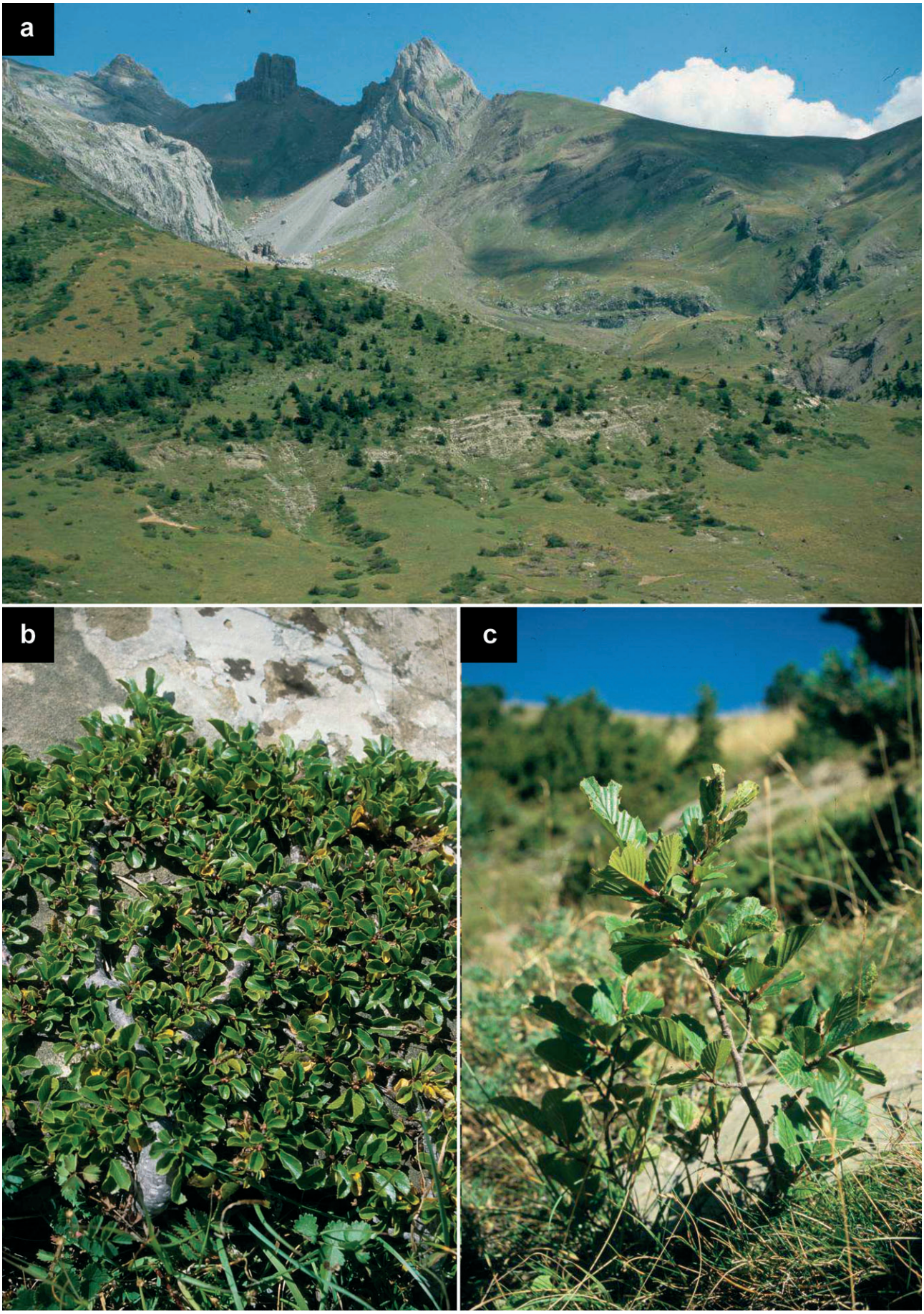

Fig. 1. View of the common pastures in the study area (a), *Rhamnus pumila* (b) and *R. alpina* (c) host plants of *Satyrium spini*.

changes they are often used as bioindicators (Watt & Boggs, 2003; van Swaay et al., 2006). The most important biotope for European butterflies, including threatened species, is grassland (van Swaay et al., 2006). The Blue-spot hairstreak, *Satyrium spini* (Denis & Schiffermüller, 1775), is a monophagous species that in temperate lowlands (Ebert & Rennwald, 1991; Fartmann, 2004; Hermann, 2007) and high mountain ranges (Huemer, 2004) is associated with species-rich dry grasslands. Although its host plants (*Rhamnus* species) are widespread (e.g. Villar et al., 1997) *S. spini* is not common in the Spanish Pyrenees (Abós Castel, 1988; García-Barros et al., 2004; C. Stefanescu, pers. comm.). Unlike for Central Europe (Weidemann, 1982; Koschuh et al., 2005; Hermann, 2007) there is no information on the oviposition habitats of this species in southern Europe (cf. García-Barros & Fartmann, 2009), which might explain its scattered distribution throughout the Pyrenees.

The aim of this study was to assess the oviposition preferences of the shrub-feeding hairstreak butterfly *S. spini* in high mountain common pastures of the Spanish Pyrenees and recommend a way of managing grasslands that favours this species. In particular we considered the following questions:

(i) Which environmental factors determine the egg-laying preferences of this species?

(ii) What are the implications for nature conservation in the light of the ongoing agricultural changes in the Pyrenees?

MATERIAL AND METHODS

Study area

The study area (42°44′N, 0°35′W) is located in the western Spanish Pyrenees, about 20 km north of Jaca (province Huesca) in the Aísa Valley. It is approximately 200 ha in size and situated in the high mountain zone (1470–1780 m a.s.l.) in the eastern part of the Natural Park Valles Occidentales (Sánchez, 2007). The climate is oro-Mediterranean with a mean annual temperature of 5.5°C, a mean summer temperature of 13.5°C and a mean winter temperature of –0.6°C (values given for an altitude of 1780 m a.s.l.). Mean annual precipitation varies with altitude between 1200 and 2000 mm (Badía Villas et al., 2002). Within the study area calcareous grasslands used as common pastures for cattle and sheep dominate. These grasslands developed as a result of livestock husbandry with tree cutting or burning and replaced native woodlands (García-Ruiz & Lasanta-Martínez, 1990). The inclinations and aspects of the hillsides in this valley are very variable. On the steeper slopes there are large areas of bare rocks and sparsely vegetated screes (Fig. 1a).

Study species

The Blue-spot Hairstreak, *Satyrium spini* (Denis & Schiffermüller, 1775), is a lycaenid butterfly with a range extending from South-west, South and Central Europe to Western Asia. It is absent from the British Isles, Scandinavia and the oceanic regions of Central Europe (Ebert & Rennwald, 1991). *S. spini* occurs in most parts of the Iberian Peninsula, but mainly in the mountain ranges (García-Barros et al., 2004). *S. spini* is a univoltine species with a flight period ranging from July to August in the Spanish Pyrenees (Abós Castel, 1988). Females lay their eggs usually in small batches on various species of buckthorn (*Rhamnus* spp.) (Tolman & Lewington, 1998; Koschuh et al., 2005; Hermann, 2007). The larvae spend the winter within the egg shell and hatch in spring (Ebert & Rennwald, 1991; Hermann, 2007).

TABLE 1. List of the parameters included in the microhabitat analyses. GLM – Generalized Linear Model, MWU – Mann-Whitney *U* test, t – *t* test.

Variable	Factor levels	Statistical method
Response variable		
Host plant occupancy	2[a]	GLM (Binomial)
Egg batches per plant	metric	GLM (quasi-Poisson)
Predictor variable		
Microclimate		
Aspect	4[b]	Fisher's exact test
Sunshine duration (h)[1]	metric	GLM[2], t
Vegetation height (cm)[3]		
Shrub layer (< 0.5 m)	metric	GLM[4], MWU
Field layer	metric	GLM, MWU
Vegetation cover (%)[3]		
Shrub layer (< 0.5 m)	metric	GLM[4], MWU
Field layer	metric	GLM[5], MWU
Mosses/lichens	metric	GLM, MWU
Litter	metric	GLM, MWU
Cover of bare ground (%)		
Bare soil	metric	MWU
Gravel	metric	MWU
Stones	metric	MWU
Rocks	metric	MWU
Total	metric	GLM[5], MWU
Host plant cover (%)	metric	GLM, MWU

[1]Accuracy: ¼ h; [2]For most months, values of sunshine duration were inter-correlated. Therefore the mean of the values for all the months of a year was used; [3]Height and cover of trees and taller shrubs were excluded from the analysis as they had zero values in more than 95% of the samples; [4]Height and cover were inter-correlated. For GLM analysis, the principal component of both was used; [5]Cover of field layer and total cover of bare ground were intercorrelated. For GLM analysis, the principal component of both was used; [a]Occupied = 1, unoccupied = 0; [b]North = 1, East = 2, South = 3, West = 4.

Two potential host plants of *S. spini* occur in the pastures of the Aísa Valley: Dwarf buckthorn (*Rhamnus pumila* Turra) and Alpine buckthorn (*R. alpina* L. ssp. *alpina*). *R. pumila* is a dwarf shrub with a reptant habit, mostly growing on calcareous rocks in mountainous regions in Southern Europe (Villar et al., 1997; Aeschimann et al., 2004). *R. alpina* is a shrub that can reach 4 m in height and grows on dry, base-rich and nutrient-poor soils in the mountains of South-western Europe (Villar et al., 1997; Aeschimann et al., 2004). On the southern slope of the Pyrenees both *Rhamnus* species mainly occur in the high mountain zone between 1200 and 2500 m a.s.l. (Villar et al., 1997).

Sampling design

In August 2010 we searched both of the potential host plants, *Rhamnus pumila* and *R. alpina*, for eggs of *S. spini*. We aimed to sample all aspects within the study area with the same intensity and therefore spent 45 min searching for eggs on north-, east-, south- and west-facing slopes, respectively. The time spent searching was measured using a stop-watch, which was on

when searching a *Rhamnus* plant and off when walking to another plant.

For each host plant that was checked for eggs we noted its status [with eggs (hereafter referred to as "occupied") or without eggs (hereafter referred to as "unoccupied")], the number of egg batches found, the number of eggs per batch and several environmental parameters (Table 1). For each egg batch we noted its position on the host plant and the height above the surface of the ground (rock or ground). Vegetation structure was recorded in an area of 50 × 50 cm (hereafter called "microhabitat") around each egg batch (Table 1). Potential daily sunshine duration was recorded for every month of the year using a horizontoscope (Tonne, 1954). Inclination and aspect were measured using a compass with inclinometer. The total amount of time spent sampling was one week.

Data analysis

If data were normally distributed (Shapiro-Wilk test) and variances were homogenous (Levene test), parameters on occupied and unoccupied host plants were compared using a *t* test. Otherwise, a Mann-Whitney *U* test was used. For categorical variables Fisher's exact test for small sample sizes was applied.

In addition to this, we used Generalized Linear Models (GLM) with different response variables (Table 1) for a more detailed analysis of the *R. pumila* microhabitats. All explanatory variables were checked for inter-correlations using Spearman's correlation coefficient before being entered into the models. Principal components were calculated and entered into the models for variables with correlation coefficients >|0.5|. As our count data showed overdispersion, we corrected the standard errors using quasi-Poisson GLMs. Non-significant predictors were excluded from the final models by stepwise backward-selection using the drop1 command. This command automati-

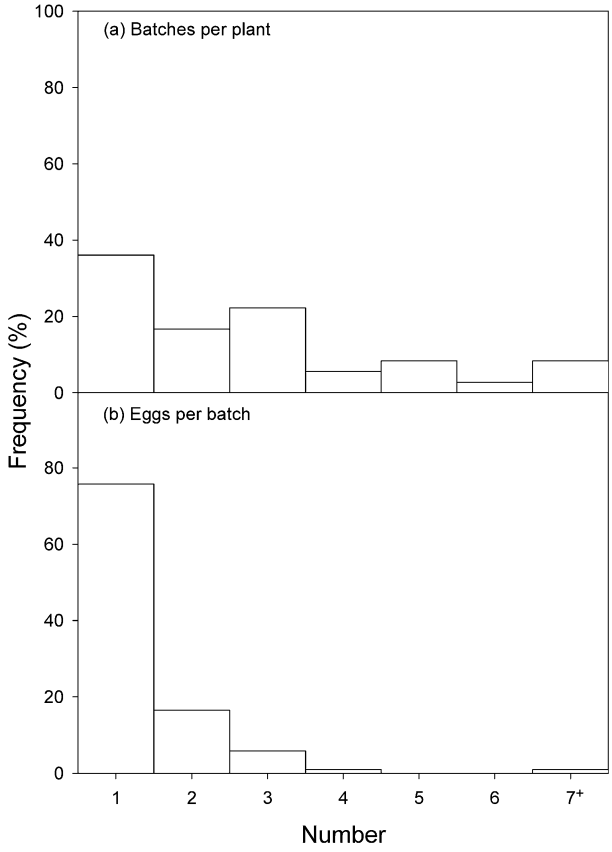

Fig. 2. Frequency distribution of the number of egg batches per plant (mean ± SE = 2.9 ± 2.4) (a) and eggs per batch (mean ± SE = 1.4 ± 0.9) (b) ($N_{batches}$ = 103; N_{eggs} = 142).

TABLE 2. Mean values ± SD of all numerical environmental parameters on occupied and unoccupied host plants of *Satyrium spini* in the Aísa Valley. Comparison of mean or median values was done using *t* test (t) and Mann-Whitney *U* test (MWU), respectively; n.s. = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Parameter	*Rhamnus pumila*			*R. alpina*	*R. p.* vs. *R. a.* [1]
	Occupied (N = 36)	Unoccupied (N = 16)	*P* (test)	Occupied (N = 11)	*P* (test)
Microclimate					
Sunshine duration (h)	6.5 ± 1.7	5.1 ± 2.4	* t	6.6 ± 1.7	n.s. t
Vegetation height (cm)					
Shrub layer (< 0.5 m)	6.4 ± 13.7	3.4 ± 9.8	n.s. MWU	30.9 ± 13.6	*** MWU
Field layer	4.1 ± 3.3	4.8 ± 4.3	n.s. MWU	7.8 ± 4.4	** MWU
Mosses/lichens	0.5 ± 0.7	0.4 ± 0.6	n.s. MWU	0.1 ± 0.2	n.s. MWU
Litter	0.1 ± 0.2	0.3 ± 1.0	n.s. MWU	0.0 ± 0.2	n.s. MWU
Vegetation cover (%)					
Shrub layer (< 0.5 m)	1.5 ± 4.1	2.7 ± 10.0	n.s. MWU	26.4 ± 16.6	*** MWU
Field layer	16.5 ± 19.2	15.5 ± 20.3	n.s. MWU	27.5 ± 27.3	n.s. MWU
Mosses/lichens	1.1 ± 1.7	2.7 ± 0.9	n.s. MWU	0.5 ± 1.5	n.s. MWU
Litter	0.4 ± 1.7	0.7 ± 10.0	n.s. MWU	2.7 ± 9.0	n.s. MWU
Cover of bare ground (%)					
Bare soil	1.1 ± 2.2	0.2 ± 0.6	* MWU	0.9 ± 3.0	n.s. MWU
Gravel	6.5 ± 11.7	4.8 ± 10.0	n.s. MWU	29.5 ± 29.4	** MWU
Stones	6.1 ± 14.2	1.6 ± 2.4	n.s. MWU	24.3 ± 34.5	* MWU
Rocks	51.0 ± 24.1	59.5 ± 27.0	n.s. t	14.1 ± 26.4	*** MWU
Total	65.3 ± 22.6	66.1 ± 24.7	n.s. MWU	71.6 ± 23.4	n.s. MWU
Host plant					
Height (cm)	.	.	.	43.2 ± 22.3	.
Cover (%)	16.8 ± 11.2	17.7 ± 13.4	n.s. MWU	31.8 ± 17.5	** MWU

[1] Occupied *Rhamnus pumila* and occupied *R. alpina* plants were compared.

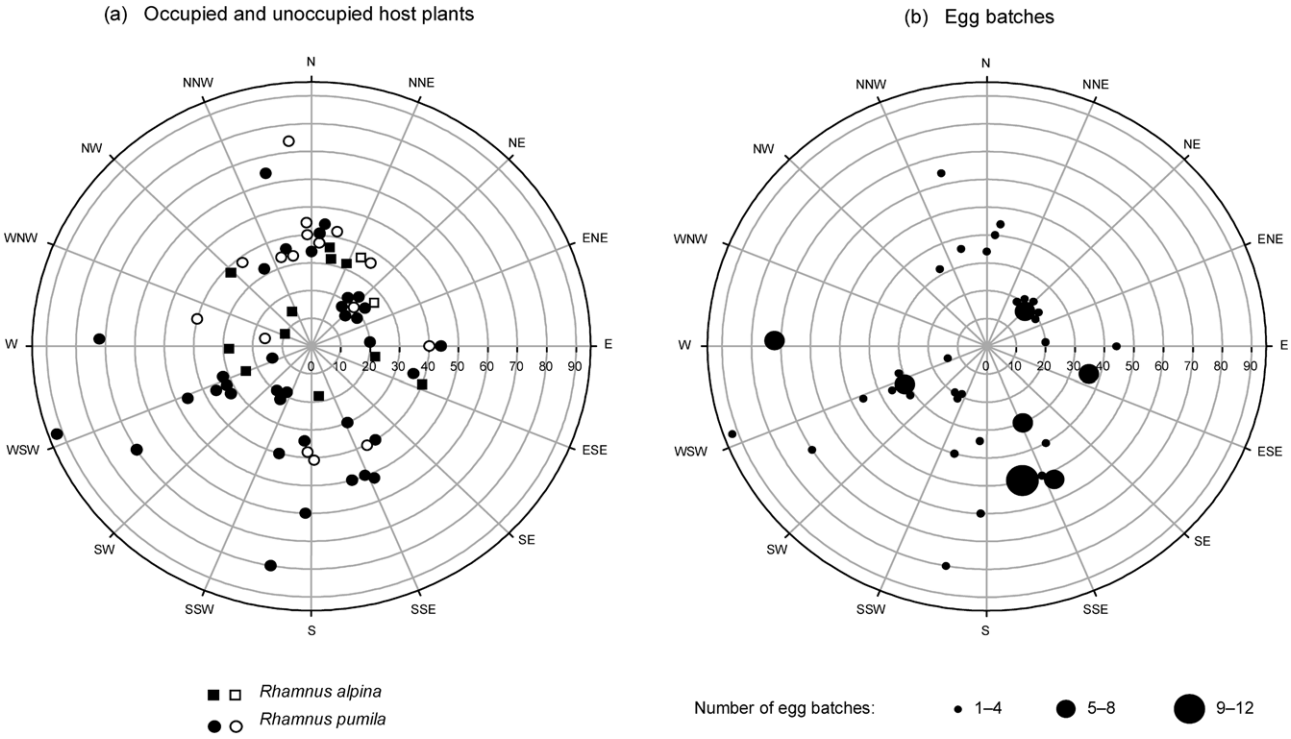

Fig. 3. Polar plot of aspect and slope (°) where *Rhamnus* host plants grew that were used for oviposition by *Satyrium spini* (black symbols) and those that were not (white symbols) (a) and the number of egg batches per *Rhamnus pumila* plant (b).

cally drops each explanatory variable in turn, and each time assesses the significance of the dropped variable by likelihood ratio tests (type III tests). Only explanatory variables significant at the 5% level were retained in the final models.

Significance tests and correlation analyses were performed using SigmaPlot 11.0 and GLM analyses were conducted in R 2.12.2 (R Development Core Team, 2011).

RESULTS

In total we surveyed 52 *R. pumila* (36 occupied vs. 16 unoccupied) and 13 *R. alpina* plants (11 vs. 2) (Table 2). Altogether we found 103 egg batches on 36 *R. pumila* and 40 on 11 *R. alpina* (Fig. 2, Table 2). Usually, occupied host plants had one up to three batches (75% of the cases); four to twelve batches per host plant rarely occurred (25%) (Fig. 2). Females usually laid their eggs singly (76%) or in small groups of two or three eggs (22%). Egg batches of four to eight eggs were rare exceptions (2%). Mean size of the egg batches did not differ between *R. pumila* (mean ± SD = 1.4 ± 0.9) and *R. alpina* (mean ± SD = 1.5 ± 0.9) (Mann-Whitney *U* test: $U = 1881.0$, $P = 0.30$). Eggs were deposited on twigs and in twig forks. Due to its reptant growth, batches on *R. pumila* were always situated very close to the surface of the ground (mean ± SD = 2.0 ± 2.1 cm). Eggs on *R. alpina* were found from 1 to 57 cm above ground with three quarters of them between 5 and 15 cm (mean ± SD = 10.5 ± 10.0 cm). Eggs were laid at significantly different heights on the two host plants (Mann-Whitney *U* test: $U = 445.5$, $P < 0.001$).

Typically, the microhabitats of occupied *R. pumila* were very sunny and sparsely vegetated rocks, solitary boulders or screes in the pastures (Fig. 1b, Table 2). The sites were dominated by bare rocks and vegetation usually covered less than one fifth of the ground. Microhabitats of occupied *R. pumila* were – compared to unoccupied ones – characterized by a significantly longer sunshine duration and cover of bare soil. Microhabitats of occupied *R. alpina* had similar characteristics and were mostly found on screes and river banks (Fig. 1c, Table 2). However, shrub height and cover, field layer height, host-plant cover and the cover of gravel and stones were significantly higher, while that of rocks was significantly lower.

Although occupied plants of both *Rhamnus* species were found in areas with a wide range of aspects and inclinations, most occupied *R. pumila* occurred on east-, south- and west-facing slopes (Fig. 3a, Table 3). This difference in aspect between occupied and unoccupied *R. pumila* plants was slightly not significant ($P = 0.06$). However, the number of batches per *R. pumila* plant was

TABLE 3. Absolute and relative frequencies of the nominal variable aspect in occupied and unoccupied *Rhamnus pumila* microhabitats. Results of Fisher's exact test using absolute frequencies: occupied vs. unoccupied: $P = 0.06$; number of egg batches vs. unoccupied: $P < 0.001$.

Aspect	Occupied (N = 36)		Unoccupied (N = 16)		Egg batches (N = 103)	
	N	%	N	%	N	%
North	6	16.7	9	56.3	9	8.7
East	9	25.0	2	12.5	23	22.3
South	12	33.3	3	18.8	44	42.7
West	9	25.0	2	12.5	27	26.2

TABLE 4. Results of the Generalized Linear Model analysis used to determine the association of several environmental parameters (predictor variables, Table 1) with the presence of egg batches in *Rhamnus pumila* microhabitats (a) and the number of egg batches per *R. pumila* plant (b). Non-significant predictors were excluded from the final model by stepwise backward selection ($P > 0.05$). Sample sizes: 36 occupied microhabitats, 16 unoccupied microhabitats, 103 egg batches.

Variable	Estimate	SE	*Z*	*P*
a) Presence of egg batches				
Sunshine duration	0.030	0.014	2.213	< 0.05
Pseudo R^2 [Nagelkerke's] = 0.14				
b) Egg batches/plant				
Sunshine duration	0.021	0.007	2.930	< 0.01
Pseudo R^2 [Nagelkerke's] = 0.36				

significantly higher on plants in those aspects than on north-facing slopes (Fig. 3b, Table 3).

The importance of unshaded sites that receive large amounts of direct solar radiation is confirmed by the results of the GLM analyses (Table 4). Potential daily sunshine duration was the only significant parameter explaining the presence of egg batches on *R. pumila* [Pseudo R^2 (Nagelkerke's) = 0.14] and the number of egg batches per *R. pumila* plant [Pseudo R^2 (Nagelkerke's) = 0.36].

DISCUSSION

This study on the oviposition habitats of *S. spini* in high mountain common pastures of the Spanish Pyrenees showed that females used *R. pumila* and *R. alpina* for oviposition. Both species represent novel host plant records for Spain (cf. Munguira et al., 1997). Occupied plants grew mostly at sparsely vegetated grassland sites with large patches of bare rocks, stones or gravel. Most of the egg batches were laid close to the ground, on the reptant *R. pumila* directly above the rock surface (mostly < 2 cm) and on the taller *R. alpina* mostly within 15 cm above ground. In three quarters of the cases the batches contained only one egg. The number of batches per *R. pumila* plant was highest on east-, south- and west-facing slopes and least on north-facing slopes. Presence of eggs and the number of egg batches per *R. pumila* plant were best explained by a long sunshine duration.

These findings indicate that a warm microclimate is of crucial importance for *S. spini*. Although the two host plants of *S. spini* have completely different growth forms, all egg-laying sites exhibit roughly the same characteristics that ensure favourable microclimatic conditions. Based on the results of this study we conclude that there are three main factors that contribute to the relatively high temperatures in the oviposition habitats of *S. spini*:

(i) By preferring sunny locations on east-, south- and west-facing slopes, females make sure that the eggs and larvae receive large amounts of direct solar radiation.

(ii) Large patches of bare ground around the host plants further warm up the near-ground air layer (cf. Stoutjesdijk & Barkman, 1992).

(iii) The eggs are laid close to the ground in the boundary layer where wind speed is lowest and air temperatures are highest (cf. Porter, 1992).

The importance of a warm microclimate for the immature stages has been described for many thermophilous butterfly species (García-Barros & Fartmann, 2009) and has already been shown for *S. spini* in Central European lowlands and low mountain ranges (Koschuh et al., 2005; Hermann, 2007; Löffler et al., 2013). In our study area, however, warm microhabitats are likely to be even more important than in Central Europe. At the lower altitudes in Central Europe, where the climate is mild (Ellenberg & Leuschner, 2010), this species lays its eggs at heights of up to 1.3 m above the ground and the occurrence of bare ground, rocks or gravel is not a prerequisite for egg-laying (Löffler et al., 2013). We assume that the preference for unusually warm microhabitats is explained by the harsh climatic conditions near its altitudinal range limit in the Pyrenees. The growing season is rather short with 80–150 days (Aldezabal Roteta, 2001), and the mean summer temperature of 13.5°C is relatively low (given for an altitude of 1780 m a.s.l.) (Badía Villas et al., 2002). Some other studies also indicate that butterflies compensate for the cooler climate near their cool range margins by occupying relatively narrow and hot niches (Thomas, 1993; Thomas et al., 1998; Merrill et al., 2008).

S. spini is known to deposit its eggs usually in small batches (Hermann, 2007). Koschuh et al. (2005) and Löffler et al. (2013) showed for low mountain ranges in Eastern Austria and lowlands in Central Germany, respectively, that 25% of the batches consisted of one egg and 75% of two or more eggs. Surprisingly, in our study the ratio was reversed with 76% of the eggs laid singly. Dispersing the eggs in space rather than concentrating them in a few localities has often been considered as a strategy of risk-spreading (García-Barros & Fartmann, 2009). In line with this, we interpret the oviposition of single eggs by a female in our study area as a strategy to increase the survival rate of the offspring under unfavourable and poorly predictable climatic conditions. The climate in the high mountain zone of the Spanish Pyrenees is characterised by relatively short and cool summers, long and cold winters (see above), high velocity winds in winter causing snowdrift and damaging the vegetation (pers. observ.) and an overall large inter-annual variation. In contrast, weather conditions at the lower altitudes in Central Europe are not as harsh and more predictable. For *Hamearis lucina*, small egg batches are also thought to constitute a risk-spreading strategy to cope with unfavourable climatic conditions along a geographic gradient (Anthes et al., 2008). However, to verify this assumption it is necessary to undertake further studies on batch size and survival rates of *S. spini* eggs and larvae along a climatic gradient.

Implications for conservation

Based on the results of this study we conclude that the preservation of open grasslands with small buckthorn plants growing in very sunny and warm locations is crucial for the long-term survival of *S. spini*. Abandonment of common pastures in the Spanish Pyrenees with subsequent shrub encroachment and reforestation would lead to shading of the host plants and a loss of habitat for *S. spini* (cf. Löffler et al., 2013) and probably many other thermophilous grassland species (Steffan-Dewenter & Tscharntke, 2002; WallisDeVries et al., 2002; Stefanescu et al., 2011). Areas above the climatic timberline might be too cold and suitable habitats at lower elevations in the Pyrenees, where the opposed processes of agricultural intensification and abandonment are even more accentuated than in high mountain areas (García-Ruiz & Lasanta-Martínez, 1990; Lasanta-Martínez et al., 2005), are probably scarce. Sites where the vegetation structure remains open without any kind of management (e.g. floodplains, extremely steep slopes) are few in number and mostly of small size (pers. observ.).

The best way to maintain an open landscape and preserve the species-rich and structurally diverse vegetation of the high mountain common pastures is the traditional combination of sheep and cattle grazing. Sheep are known to be selective grazers and have a homogenising effect on the vegetation (Rook et al., 2004), but also contribute to the maintenance of some specific plant species and communities of high conservation value (Sebastià et al., 2008). Cattle in contrast do not select particular plant species and thus, enhance vegetation heterogeneity (Sebastià et al., 2008) and are effective in controlling shrub encroachment even at moderate stocking densities (Casasús et al., 2007). Several recent studies have documented positive effects of cattle grazing on species richness of plants and insects (e. g. Pykälä, 2003; Pöyry et al., 2004; WallisDeVries et al., 2007). Besides, cattle are the farm animals preferred by local farmers for economic reasons (García-Ruiz & Lasanta-Martínez, 1990) and if conservation policies are to be effective they should be based on economically profitable measures. Where livestock grazing alone is not sufficient to counteract reforestation, mechanical removal of shrubs and trees should be done like in former (and partially recent) times, when woody species were cut by farmers for firewood and in order to keep the pastures open.

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