Ecol Res (2008) 23: 259–269
DOI 10.1007/s11284-007-0376-x

ORIGINAL ARTICLE

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Connectivity compensates for low habitat quality and small patch size in the butterfly *Cupido minimus*

Received: 20 March 2006 / Accepted: 21 February 2007 / Published online: 12 April 2007

Abstract Habitat size, habitat isolation and habitat quality are regarded as the main determinants of butterfly occurrence in fragmented landscapes. To analyze the relationship between the occurrence of the butterfly *Cupido minimus* and these factors, patch occupancy of the immature stages in patches of its host plant *Anthyllis vulneraria* was studied in the nature reserve Hohe Wann in Bavaria (Germany). In 2001 and 2002, 82 *A. vulneraria* patches were surveyed for the presence of *C. minimus larvae*. The occurrence was largely affected by the size of the food plant patches. In a habitat model that uses multiple logistic regression, the type of management and habitat connectivity are further determinants of species distribution. Internal and temporal validation demonstrate the stability and robustness of the developed habitat models. Additionally, it was proved that the colonization rate of *C. minimus* was significantly influenced by the distance to the next occupied *Anthyllis* patch. Concerning long-term survival of (meta-) populations in fragmented landscapes, the results show that lower habitat quality may be compensated by higher connectivity between host plant patches.

Keywords Butterfly · *Cupido minimus* · Dispersal · Habitat model · Habitat size · Habitat quality · Habitat isolation · Species persistence

Introduction

In metapopulation biology, habitat size and isolation are assumed to be the most important factors for the occurrence and long-time survival of butterflies in fragmented habitats (Hanski and Gilpin 1991; Thomas et al. 1992; Hanski 1994a). Theoretical (Hanski 1994a; Hanski and Thomas 1994) and empirical studies (Harrison 1991; Hanski et al. 1994; Hill et al. 1996) among Lepidoptera have demonstrated that the greater the patch size and the connectivity to other occupied patches, the higher the colonization probability (Wilcox 1980; Hovestadt 1990; Poethke et al. 1996). Extinction rates of local populations are higher in small and isolated patches.

However, recent studies have demonstrated that habitat quality might also be a good determinant of lepidopteran occurrence and may improve the comprehension of metapopulation dynamics (Kuussaari et al. 1996; Dennis and Eales 1997; Thomas et al. 2001; Wahlberg et al. 2002). For example, Dennis and Eales (1997) asserted that patch occupancy of *Coenonympha tullia* was as successfully explained by habitat quality as by habitat size and isolation together. In the study of Thomas et al. (2001), habitat quality was the best predictor for the occurrence of three butterfly species in comparison to isolation and patch size. Further, Thomas et al. (1998) showed that within the genus *Maculinea*, increasing extinction rates due to habitat loss and

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Electronic supplementary material The online version of this article (doi:10.1007/s11284-007-0376-x) contains supplementary material, which is available to authorized users.

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isolation could be much reduced—in a preconditioned minimum area—if the habitat quality was optimized. According to Thomas et al. (2001), variation in habitat quality is the missing third parameter in metapopulation dynamics beside the conventional spatial parameters of isolation and area.

Habitat models are widely used to specify functional relationships between the occurrence of a species and its environment (Guisan and Zimmermann 2000; Austin 2002) and to quantify habitat requirements (Morrison et al. 1998). In this study, we developed habitat models based on presence–absence data using logistic regression (Trexler and Travis 1993; Guisan and Zimmermann 2000) to test: (1) which of three factors—patch size, patch quality and isolation—best explains species distribution, and (2) to what extent they are responsible for species persistence. The study species, the Small Blue *Cupido minimus* (Fuessli 1775) (Lepidoptera: Lycaenidae), is widely distributed in Europe, but has declined sharply in many countries during the last decades (Asher et al. 2001). Therefore, the results of our study may enhance our understanding of the (meta-) population biology of *C. minimus* and help in choosing effective conservation strategies.

To estimate the predictive performance of habitat models, they should be transferred to independent data (Manel et al. 1999; Guisan and Zimmermann 2000; Pearce and Ferrier 2000a, b; Reineking and Schröder 2003). In addition to using internal validation techniques, we tested our habitat models also under different landscape conditions by externally validating the models in space and time.

Methods

Study species

The Small Blue *C. minimus* colonizes poor, arid and often calcareous grasslands with kidney vetch (*Anthyllis vulneraria*) as feedstock (Ebert and Rennwald 1991; Weidemann 1995). The larvae feed only on *Anthyllis vulneraria* in the study area. *C. minimus* is a xerothermophilic species (Blab and Kudrna 1982) and is univoltine. The flight period in the study area lasts from the beginning of May until the beginning of July.

C. minimus occurs in Europe from Spain to Scandinavia, and also across Asia and Mongolia. While the distribution is assumed to be stable in many European countries, there is a particularly serious decline in north-western Europe ($>50\%$ decrease in distribution in 25 years; Asher et al. 2001, pp. 145–146). In Germany, Weidemann (1995) described the decline of this species in many regions during the last decades, and *C. minimus* is regarded as 'near threatened' (Pretscher 1998). Agricultural intensification as well as abandonment are regarded as the main causes for the decline (e.g. Kudrna 1986; Feldmann et al. 2000).

Field work and identification of relevant habitat factors

The main study area, about 21 km^2, is the nature reserve 'Hohe Wann' in Northern Bavaria, Germany (50°03′N, 10°35′E). The mean annual temperature is 8.8°C, and the mean annual precipitation 650 mm (Deutscher Wetterdienst 2002). The region is highly structured through the geological (Trias: Middle Keuper), geomorphological and microclimatic heterogeneity of the landscape. While the leveled areas (plateaus, valleys) are in intensive agricultural use, the slopes are used extensively or are fallow land. Thus, on the one hand, the landscape is characterized by a small-scale mosaic of crop fields, fallow land and intensively managed meadows and on the other hand by poor grassland, thermophilic fringes, hedges and forests.

As the recording of *C. minimus* is most reliable accredit out by searching for the eggs and larvae in the flower heads of *A. vulneraria* (Hermann 2000), in 2000 all patches of kidney vetch ($n = 82$) were mapped in the study area and subsequently plotted in aerial photographs (scale 1:3,500). *Anthyllis* patches were considered as separate if they were at least 10 m apart. The size of small patches was measured in the field, for larger patches a Geographic Information System (GIS, ESRI-ArcView 3.2) was used. During the main flight periods in 2001 and 2002 the incidence of the immature stages of *C. minimus* was recorded in all *Anthyllis* patches. If the species was not detected at the first sampling occasion, the patch was searched for a second time at the end of the flight period. Each patch was scanned for eggs and larvae in time periods proportional to its area, with a maximum of 15 min per patch. The patch sizes range from 1m^2 to 6,300 m^2. Additionally, further parameters of the habitat quality of the *Anthyllis* patches were recorded in the field: vegetation structure (e.g. plant cover, vegetation height) of the different vegetation strata and of the *Anthyllis* plants, succession parameters (degree of bush encroachment) and the management regime (four different categories). Insolation parameters are exposition, inclination and scale of shading. The habitat type (three different categories) was detected from a vegetation map (see Table 1 for more details). The complete survey of the *Anthyllis* sites in the main study area enabled us to calculate patch isolation and connectivity. The distance to the next occupied *Anthyllis*-patch was used as a simple measure of isolation. Moreover, the connectivity S_i according to Hanski (Hanski 1994b; Moilanen and Nieminen 2002) was calculated:

$$S_i = \sum_{j \neq i} p_j \cdot \exp(-\alpha \cdot d_{ij}) \cdot A_j^b \tag{1}$$

S_i = patch connectivity, p_j = occupancy of patch i [0 or 1], α = parameter scaling the effect of distance on dispersal success, d_{ij} = distance between patch i and j measured from center to center [km], A_j = size of patch j [m^2], b = scaling of immigration

Table 1 Habitat parameters of the *Anthyllis vulneraria* patches (estimation of the vegetation cover according to LONDO 1976)

Parameter	Unit/categories
Anthyllis patch size	[100 m^2]
Cover of *Anthyllis*	Cover [%]
Height of *Anthyllis*	[m]
Habitat type	Extensively managed meadow/ mesoxerophytic grassland/ thermophilic fringes
Type of management	Mown grassland/cattle grazed meadows/shepherding/ fallow land
Date of first management	Until 15th June/until 15th July/ until 15th August/after 15th August/fallow
Inclination	[°]
Sine exposition	[1]
Cosine exposition	[1]
Scale of shading	Unshaded/partly shaded/largely shaded
Cover of bush encroachment	Cover [%]
Height of bush encroachment	[m]
Cover of shrub layer	cover [%]
Height of shrub layer	[m]
Cover of lower herb layer	Cover [%]
Height of lower herb layer	[m]
Cover of upper herb layer	Cover [%]
Height of upper herb layer	[m]
Cover of moss layer	Cover [%]
Cover of bare ground	Cover [%]
Connectivity S	Scale of connectivity after Hanski (1994b)
Distance to the next occupied patch	[m]

Based on the results of Leon-Cortes et al. (2003) and Krauss et al. (2004) on *C. minimus* in Britain and Germany (Lower Saxony) respectively, as well as on the result of a colonization experiment with two artificial *Anthyllis* patches in the main study area (Binzenhöfer; unpubl. data) an average dispersal distance of 200 m was estimated. Consequently, we used $\alpha = 5$ and according to Krauss et al. (2004), $b = 1$, assuming a proportional rise of emigration rate with increasing patch area.

To test the transferability of the habitat models under different geographical conditions (Dennis and Eales 1999; Schröder and Richter 1999; Schröder 2000; Fleishman et al. 2003), an additional study area with *C. minimus* occurrence was chosen in 2002: the nature reserve Leutratal near Jena in Thuringia (50°52'N, 11°34'E). This study area (0.5 km^2) is characterized by shell-limestone slopes (lower Triassic limestone) of the river Saale valley covered with mesoxerophytic grassland in combination with semi-arid grasslands and thermophile fringes at different successional stages (Heinrich et al. 1998; Hirsch et al. 1998). Normally, the grassland is mown in late summer (not before the end of July) or autumn. The climate is warmer (mean annual temperature is 9.3°C) and dryer (mean annual precipitation 587 mm) compared to our main study in Northern Bavaria (Heinrich et al. 1998).

Using an identical sampling protocol to that used in the main study area, 39 *Anthyllis* patches were found here, with patch sizes ranging from 1 m^2 to 1,500 m^2.

Statistical analyses

The relationships between the occurrence of *C. minimus* and the parameters patch size, connectivity (or isolation) and habitat quality of the patches were analyzed using logistic regression. All statistical analyses were performed with R 2.2.0 (R Core Development Team, http://www.r-project.org) using the packages Hmisc and Design provided by F. Harrell.

Model selection

First, univariate analyses were conducted, in order to examine the importance and relevance of each explanatory variable (Hosmer and Lemeshow 2000) before entering these parameters into a multiple model. Parameters with P-values > 0.2 were excluded from the analysis (Hosmer and Lemeshow 2000). The influence of the remaining variables was quantified by their odds ratios, which is a measure to estimate the effect of a predictor by specifying the ratio of odds between the presence or absence of a species when the value of the explanatory variable is altered by one unit. Further, the number of habitat parameters was reduced to avoid strong multicollinearity between the predictor variables. If there was a strong correlation between two explanatory variables (Spearman rank correlation $r_s > 0.5$, see also Fielding and Haworth 1995; Binzenhöfer et al. 2005), only the parameter that correlated most strongly with the incidence was selected for further modeling. For variable selection prior to estimating multiple models, we applied stepwise backward selection (Hosmer and Lemeshow 2000) with the Akaike Information Criterion (AIC) as a selection criterion (Burnham and Anderson 2002, Reineking and Schröder 2006). Since the biases and shortcomings of stepwise variable selection are known (e.g. Whittingham et al. 2006) we acknowledged model uncertainty by comparing our "final" model with a set of almost equally good models resulting from AIC-based best subset regression (cf. Tables 5 and 6, electronic appendix).

Model evaluation

Different kinds of performance criteria can be used to evaluate a habitat model. Nagelkerke's (1991) R^2_N quantifies the proportion of variance explained by the model. Values exceeding 0.4 indicate a good calibration (Backhaus et al 2000; Steyerberg et al. 2001). Model discrimination describes the ability to correctly separate occupied from unoccupied habitats. Due to the failure to use all information of the classifier (Fielding and Bell

Table 2 Occupancy by *C. minimus* larvae and spatial characteristics of the *Anthyllis vulneraria* patches in the training area (2001 and 2002) and the test area (2002)

	Training area		Test area
	Hohe Wann 2001	Hohe Wann 2002	Leutratal 2002
Number of patches	82	65	39
Occupied patches [%]	45 (55%)	53 (82%)	39 (100%)
Empty patches [%]	37 (45%)	12 (18%)	–
Mean patch size [m^2] [min./max.]	643 [1/6300]	792 [1/6300]	299 [1/1500]
Mean patch size of occupied patches [m^2] [min./max.]	1118 [1/6300]	936 [1/6300]	299 [1/1500]
Mean distance [m] to the next occupied patch [min./max.]	182 [11/1025]	203 [11/1025]	42 [20/115]

1997), a threshold-independent measure for discrimination was applied, namely the area under the receiver operating characteristic curve (AUC). AUC-values above 0.7 describe an acceptable discrimination, values between 0.8 and 0.9 indicate a good discrimination, and values above 0.9 an excellent discrimination (Hosmer and Lemeshow 2000). For the comparison of different alternative models we used AIC. The model with the lowest AIC represents the best compromise between goodness of fit and the lowest number of predictors (Burnham and Anderson 2002).

Model validation

To test the accuracy and transferability of the final habitat models, we applied internal as well as external validation methods to get an unbiased estimate of model performance (Verbyla and Litvaitis 1989; Guisan and Zimmermann 2000). The models were internally validated by means of bootstrapping with 1,000 bootstrap replicates (Reineking and Schröder 2003, Peppler-Lisbach and Schröder 2004). To judge the quality of the model predictions, independent, external data were used. We collected data in a 2nd year in the main study area and in a second study area. Following Schröder (2000), we applied the significance test according to Beck and Shultz (1986) to verify the transferability in space and time, whereby the evaluation is deemed successful if the AUC-values of the model transferred significantly exceed a critical AUC-value (here: $\mathrm{AUC_{crit}} = 0.7$; cf. Bonn and Schröder 2001). Because of 100% patch occupancy in the second test area, we were not able to calculate AUC-values and to execute this transferability test for spatial validation. Therefore, we checked the plausibility of estimated occurrence probabilities compared to the prevalence.

Effects of geographical parameters on population dynamics

Based on the 2-year survey of the immature stages of *C. minimus*, the influence of geographical parameters on the extinction rate and the colonization rate was tested. The effects of the geographical parameters on the colonization and the extinction events were analyzed by logistic regression.

Results

Prevalence and spatial patch characteristics

In the nature reserve Hohe Wann, the prevalence of the pre-imago stages of *C. minimus* increased from 55% in 2001 to 82% in 2002 (see Table 2), whereas the number of the *Anthyllis* patches decreased in the same period by about 21% (2001: $n = 82$, 2002: $n = 65$). Eleven and four *Anthyllis* patches were found in 2001 and 2002 respectively with only one or two plants. In both years three of them were occupied with eggs or larvae from *C. minimus*. Their distances to the next occupied patch were less than 100 m (2001: 11–73 m, 2002: 62–78 m). We detected *C. minimus* larvae in each of thirteen patches larger than 1000 m^2. The mean distance to the next occupied *Anthyllis patch* was 182 m in 2001 and 203 m in 2002. In 2001 and 2002 the most isolated habitat was 1,025 m away from the next *C. minimus* population with sizes of 500 m^2 and 588 m^2 respectively.

In the study area Leutratal, eggs or larvae occupied all 39 patches in 2002. The distance between the patches ranged from 20 to 115 m. The two largest *Anthyllis* patches measured 1,500 m^2, the smallest 1 m^2.

Effects of environmental factors on the occurrence of *Cupido minimus*

Selection and relevance of single parameters

After parameter reduction on the basis of univariate regression analyses and Spearman rank correlations, only six variables remained for further modeling (see Table 3 for significance levels, R^2_N and odd ratios). Patch size yielded the highest explanatory power ($R^2_N = 0.39$). The odds ratio of *C. minimus* nearly doubled for each 100-m^2 area of larval food plants. Management regime had also a great influence on species occurrence. The most adequately managed sites are those with extensive shepherding, followed by mown grasslands, cattle-

Table 3 Results of univariate logistic regression models, significance (*P*-value), bootstrapped Nagelkerke's R^2 (R^2_N), bootstrapped AUC and odds ratios of the significant habitat parameters

Predictor variable	*P*	AUC	R^2_N	Categories	Odds ratio (e^{β})
Anthyllis patch size	< 0.001	0.784	0.39		1.8 (per 100 m^2)
Type of management	0.004	0.667	0.11	Fallow land	Reference category
				Mown grasslands	6.8
				Shepherding	31.5
				Cattle grazed meadows	1.1
Date of first management (inclusive squared term)	0.014	0.617	0.09	Until 15th June/until 15th July/until 15th August/after 15th August/fallow fit by unimodal response model (see Fig. 1)	
Habitat type	0.010	0.672	0.11	Thermophilic fringes	Reference category
				Extensively managed meadows	6.4
				Mesoxerophytic grasslands	2.4
Connectivity ($\alpha = 5, b = 1$)	0.005	0.680	0.10	Scale of connectivity after Hanski	11.4
Shrub layer cover	0.194	0.539	0.01		0.3 (per 10%)

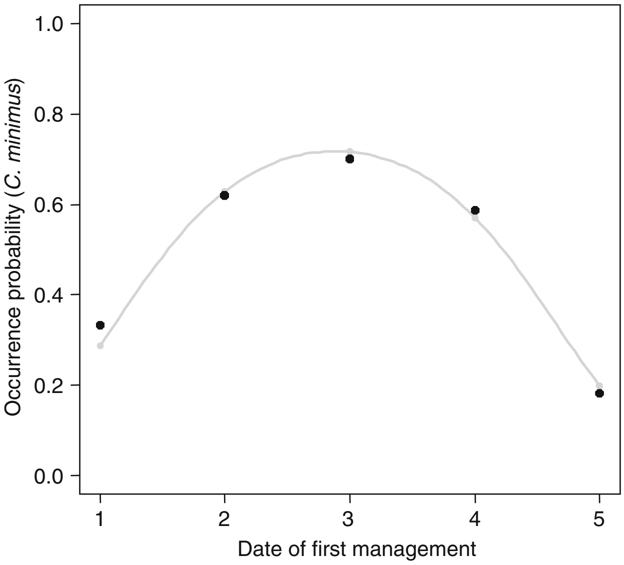

Fig. 1 In a univariate model, the parameter 'date of first management' can be considered either as a numeric or as a categorical predictor. The values of the predictor (*x*-axis) represent: 1 = until 15th June; 2 = until 15th July; 3 = until 15th August; 4 = after 15th August; 5 = fallow. *Black* Predicted occurrence probabilities of *C. minimus* for this variable taken as a categorical predictor, *grey* unimodal response curve considering the predictor as numeric

grazed meadows and fallow land. The parameter 'date of first management' showed a unimodal response (Fig. 1), whereas the period between middle of July and middle of August resulted in the highest predicted probabilities. Very early farmed sites (before 15th June) and particularly fallow land featured the lowest predicted probabilities. Within the parameter habitat type, the odds ratio was six fold higher for the extensively managed grassland and doubled for the mesoxerophytic meadow in comparison with the thermophilic fringes. Connectivity had a positive effect on the occurrence of *C. minimus*. Cover of shrub layer showed a negative, but slight influence on occurrence.

Multivariate effects of environmental factors on habitat suitability for *Cupido minimus*

As habitat suitability is not specified by one parameter alone, a multiple logistic regression analysis was performed to investigate the influence of different combinations of predictors on *C. minimus* occurrence.

Logistic regression with backward selection resulted in a model that considers the predictors '*Anthyllis* patch size', 'connectivity' and 'date of first management' (Table 4; Fig. 2). The performance criteria indicate a good calibration and discrimination of the model after bootstrapping. Patches exceeding sizes of 50 m^2 (log-value 1.699) enhance the predicted probability independently of habitat connectivity and date of first management. At sites greater than 1,800 m^2 (log-value 3.255), the occurrence probability is 100% (Fig. 2a, c for lowest connectivity). For the highest connectivity value in the main study area (1.04) but for unfavorable date of first management an occurrence probability between 41% and 45% is already predicted for very small sites (10 m^2). For optimal date of first management and the highest connectivity value, an occurrence probability of 85% is estimated independently of *Anthyllis* patch size (Fig. 2b).

Therefore, and as already demonstrated in the univariate models, the factor patch size plays the most important role for explaining *C. minimus* occurrence. In the multiple model the variance is mainly explained by patch size. Including the other two predictor variables and the interaction term, R^2_N increased from 0.39 to 0.46 and the AUC-value from 0.784 to 0.853 (Table 4).

Finally, we compared our 'final' model to a set of alternative models having a similarly good fit in terms of AIC, which were derived from an all-possible subset procedure. Each of those considered '*Anthyllis* patch size' and 'connectivity, but also 'habitat type' or 'management type' (cf. Tables 5 and 6, electronic appendix). Estimated regression coefficients (and standard errors) resemble the ones presented in Table 4.

Table 4 Regression coefficients, standard errors, and performance criteria of the multiple habitat model after internal validation by means of bootstrapping with 1,000 replicates: Nagelkerke's R^2 (R^2_N) and the area under the receiver operating characteristic curve (AUC)

Model parameter [coefficients (standard errors)]	R^2_N	AUC
Anthyllis patch size [0.3993 (0.2429)], connectivity [2.2142 (1.1288)], date of first management [3.1530 (1.8995)], square of date of first management [−0.5191 (0.2999)], interaction *Anthyllis* patch size * connectivity [2.9965 (2.0124)], intercept [−5.5522 (2.8357)]	0.463	0.854

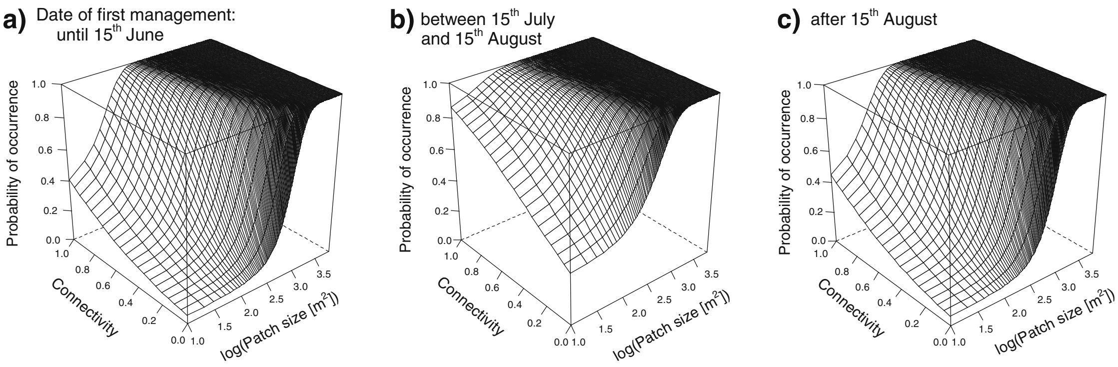

Fig. 2 Response curves corresponding to the habitat model of the premature stages—response variable: predicted probabilities of the occurrence of *C. minimus* (*z*-axis). Predictors: patch size ($\log_{10}$ transformed), connectivity and date of first management

Transferability of model results

The generality of the habitat models was tested by transferring them in time. The transferability in time (from 2001 to 2002) of both habitat models was significant (AUC = 0.891 significantly exceeding $\mathrm{AUC}_{\mathrm{crit}} = 0.7$, with $P < 0.0001$). Validation by spatial model transfer was not possible applying this transferability test, since *C. minimus* was recorded in all *Anthyllis* patches in the Leutratal; which corresponds with the high occurrence probabilities (mean: 0.749 ± 0.237 SD, min: 0.307, max: 1) predicted for this area.

Effects of spatial landscape structure on population dynamic processes

The total extinction rate of *C. minimus* from 2001 to 2002 was 10% (eight extinction events), of which six patches went extinct due to patch eradication and two local *C. minimus* populations went extinct in persistent patches. The abandoned *Anthyllis* sites were 263 m and 1,025 m from the next occupied patch and 64 m^2 and 500 m^2 in size. Due to the small sampling size (only two 'real' extinction events), statistical analysis was not feasible.

All in all, 16 (25%) of the persistent patches were (re)colonized for the first time in 2002. Within univariate logistic regression the distance to the next occupied patch was found to affect colonization ($P < 0.04$, $R^2_N = 0.21$). The most distant patch, which was newly colonized, was 534 m apart from the next occupied patch and 180 m^2 in size. Though the influence of patch size on colonization rate was positive, it was not significant ($P < 0.09$, $R^2_N = 0.14$). No relationship was found between colonization and connectivity ($P < 0.76$, $R^2_N = 0.005$).

Discussion

Effect of single environmental factors on habitat suitability for *Cupido minimus*

The influence of habitat quality factors

The target species was restricted to three habitat types: extensively managed meadows, mesoxerophytic grasslands, and thermophilic fringes. In contrast to Ebert and Rennwald (1991), *C. minimus* was predominantly recorded in extensively managed meadows and not in mesoxerophytic grasslands. This may be explained by the fact that many *Anthyllis* plants in the study area grew at locations which were cleared of bushes no more than a few years ago. Therefore, many patches are currently just in a transitional stage between extensively managed meadows and mesoxerophytic grasslands. This is because a higher number and cover of typical species of mesoxerophytic grassland still have to immigrate at first, contrary to *Anthyllis vulneraria*, which is a pioneer on immature soils. Thermophilic fringes are the habitat type with the lowest prevalence in the nature reserve

Hohe Wann. This effect could be traced back again to the fact that the cover of bush encroachment due to the extensive management is normally very high in fringes, and this habitat type therefore is suboptimal as larval food plant and probably for the xerothermophilic butterfly, too. The weak, but negative relationship between cover of shrub layer and *C. minimus* occurrence in the present study also corroborates this effect. Further, population size of *C. minimus* is negatively correlated with cover of shrub layer as demonstrated by Krauss et al. (2004) in a study near Göttingen in southern Lower Saxony (Germany). These results correspond with the studies of Ebert and Rennwald (1991) and Weidemann (1995), who regard early or initial successional stages as habitats for *C. minimus*.

The date of first management also influenced the occurrence of *C. minimus*. The highest predicted probabilities were found at sites first managed between middle of July and middle of August, after the majority of the larvae have already hatched out. Sites farmed very early (until 15th June) and fallow land are most inappropriate, because the former, as a rule, have fertile soils and will be managed several times a year. Thus, the immature stages of *C. minimus* will be damaged on the larval food plant. Furthermore, as pioneers are weak competitors, *Anthyllis vulneraria* will be swamped out as a result of strong bush encroachment (see above).

In addition, the type of management explains the species occurrence. *C. minimus* most strongly benefited from extensive shepherding. Conspicuously less suitable were mown grasslands, followed by cattle-grazed meadows. In agreement with management time the lowest occurrence probabilities were found on fallow grounds. To sum up, pasturing—if possible with avoidance during the development phase of the immature stages—seems to be the most adequate management method for *C. minimus*, if management does not occur too frequently or too intensively (e.g. with cattle). Under these conditions, on the one hand there still remain sufficient flowering *Anthyllis* plants for egg deposition or nectar, and on the other hand bare ground will be generated, which again promotes this pioneer plant. Consequently, abandoned farmland negatively affects *C. minimus* occurrence. The study results correspond greatly with recommendations from other authors. According to Feldmann et al. (2000), *C. minimus* habitats should not be mown or intensively grazed before the beginning of July. Also, according to Ebert and Rennwald (1991), overgrazing and wrong time-phased (at the development-phase of the immature stages) or repeated mowing per year should be avoided. Asher et al. (2001) advocated an adopted, extensive grazing regime in summer time and recommended pasturing in autumn or winter. From their point of view, periodic ground disturbance may be essential on sites that cannot be grazed, as seeds of *Anthyllis vulneraria* can only germinate on bare ground. Ebert and Rennwald (1991) as well as Weidemann (1995) also highlight the potential importance of sites without natural cover for *Anthyllis* settlement and for *C. minimus* survival (like slopes with sparse vegetation or rural roads). Likewise, in the present study areas of such locations are occupied by *C. minimus*.

The influence of patch size and habitat connectivity

In the univariate as well as in the multiple models, patch size and habitat connectivity were shown to be important factors for explaining *C. minimus* occurrence. Patch size explained a large amount of variance in the distribution of *C. minimus* in the host plant patches of different sizes. Such a positive area-incidence relationship has been found in a number of studies on butterflies (e.g. Wahlberg et al. 1996, Dennis and Eales 1999) and other insects (e.g. Hanski 2001, Biedermann 2003) in fragmented landscapes. In addition, habitat connectivity is influencing the presence of *C. minimus*. This interconnection is indirectly affirmed by Asher et al. (2001). In their study, the extinction risk of *C. minimus* populations was strongly increased by isolation of small habitat patches. In our study, the variable with the highest explanatory power was *Anthyllis* patch size, which is confirmed by the investigations of Krauss et al. (2004). The high importance of food-plant availability, due to the strong dependency of immature stages on the host plants, might be the limiting factor for butterfly distribution (Thomas et al. 2001). According to Krauss et al. (2004), connectivity nevertheless did not play a significant role in determining the population size of *C. minimus*. The authors found *Anthyllis* patches isolated up to 4.4 km, but they were occupied by *C. minimus*. Presumably connectivity plays an important role for the persistence of *C. minimus* populations whenever the conditions are suboptimal. While our study mainly took place in Keuper soil with only a small proportion of lime, the study of Krauss et al. (2004) was performed in soils of shell-limestone with a high proportion of lime, where *Anthyllis vulneraria* has its main distribution (Oberdorfer 2001). Thus, the density of food plants and of *C. minimus* adults is much higher in shell-limestone regions such as the second study area Leutratal. There, but also near Göttingen, all *Anthyllis* patches were occupied by *C. minimus* without exception. Our results show that classical metapopulation dynamics (extinction and/or (re)colonization events: 25% of patches re-colonized in 2002) occur when habitats are too fragmented, i.e. when connectivity falls below a certain threshold—a threshold which due to smaller distances wasn't reached in the test area. These smaller distances were at least partly due to rather good edaphic conditions.

Furthermore, logistic regression analyses conducted by Leon-Cortes et al. (2003, p. 473) confirmed that *C. minimus* in North Wales usually went extinct when host plants were at low densities. In a mark–release–recapture study of *C. minimus* in chalk grassland in southern Belgium, Baguette et al. (2000) did not observe butterfly movements between habitat patches which were more than 762 m apart, although within their study exchange could theoretically have been observed with distances between 1,334 m and 2,568 m. Maybe the management between the Belgium habitats is too intensive (mainly fertilized grassland), and consequently dispersal corridors are not available. In general, according to Dennis and Eales (1997), habitat quality and patch size may be more influential factors for butterfly occurrence than isolation. But in areas where site eradication and fragmentation have progressed further, connectivity falls below a certain threshold, and isolation is likely to be a more prominent factor (Dennis and Eales 1999), as is the case in our main research area.

Multivariate effects of environmental factors on habitat suitability for *Cupido minimus*

Multiple regression analyses resulted in a final habitat model including three significant habitat factors (see Table 4). In addition to the two landscape parameters patch size and connectivity, date of first management was the only factor among all habitat quality predictors which remained in the multiple model presented here. Alternative models with similar performance considered habitat type or management type instead of date of first management, but do not change our interpretation. The preferred land-use type, shepherding, in the study area mostly occurs on poor grasslands (extensively managed meadows or mesoxerophytic grasslands) during an optimal timeframe, and prevents a high shrub cover. Obviously, the date of first management is a good surrogate for the real factors driving habitat quality of *C. minimus*.

In the final model, *Anthyllis* patch size, connectivity and date of first management determine the patch occupancy of the study species. Model calibration and discrimination of the model are evaluated as “good”. However, in the multiple model of Krauss et al. (2004) only patch size remained as a predictor. This may be explained by the fact that (1) the habitat factors investigated did not consider the management methods, and (2) the habitat conditions are probably optimal, and hence the isolation effect did not significantly affect occurrence (see above). The relationship between incidence, patch size, connectivity (or isolation) and habitat quality is also known for other butterflies (Thomas and Harrison 1992; Hanski 1994b; Hill et al. 1996; Thomas and Hanski 1997; Dennis and Eales 1999; Gutierrez et al. 2001; Thomas et al. 2001) and other insects (beetles: Roslin and Koivunen 2001; grasshoppers: Kindvall and Ahlen 1992; Appelt and Poethke 1997; Kuhn and Kleyer 1999; leafhoppers: Biedermann 2000, 2004). Patch size affects species presence because the habitat size is correlated with population size, and large populations will become extinct less frequently (Wilcox 1980; Hovestadt 1990; Poethke et al. 1996). Connectivity is important for patch occupancy, as the colonization probability of an unoccupied patch decreases with increasing isolation (Hanski 1994b). According to Leon-Cortes et al. (2003), the number of eggs and larvae of *C. minimus* is significantly correlated with the number of inflorescences per *Anthyllis* plant, which is a result of habitat quality. Thomas et al. (2001) have demonstrated that—in addition to isolation and patch size—habitat quality is a major determinant of species survival. The persistence of three different butterfly species was two to three times better explained by variations in habitat characteristics than by site isolation. According to these authors, the three factors operate at different hierarchical levels. While habitat quality contributes more to species persistence, patch size and isolation more strongly influence the recolonization of empty habitats. For instance, patch occupancy and extinction of the butterfly *Speyreira nokomis apacheana* were best modeled by measures of habitat quality, rather than by patch size and isolation (Fleishman et al. 2002).

If habitat quality is high, small and isolated habitats are also suitable for butterflies (Thomas et al. 2001). This conclusion is affirmed by the investigations of Krauss et al. (2004), who detected 100% patch occupancy of *C. minimus* in spite of great variances in patch size and isolation. In the two investigation years of the present study, the prevalence of this species constitutes 55% and 82% in the Hohe Wann, probably due to the comparatively unfavorable habitat conditions. In contrast, in the nature reserve Leutratal, with optimal geological formation and soil type for host plant settlement, all potential habitats were occupied. This comparison supports in turn the statement of Thomas et al. (2001) that habitat quality is the third parameter affecting (meta-)population dynamics.

The final habitat model shows a very good transferability in time. In contrast, the high patch occupancy was the reason why spatial validation did not work. However, this fact in particular highlights the general validity of the presented model. *Anthyllis vulneraria* grows on extensively managed shell-limestone slopes in such high densities that the maximum distance to the next *Anthyllis* patch is only 115 m, and thus lower than the assumed mean dispersal distance of 200 m. The ubiquity of *C. minimus* in the nature reserve Leutratal could therefore be ascribed to high habitat quality, large *Anthyllis* sites and high connectivity.

Population structure and population dynamics of *Cupido minimus*

The results of our 2-year survey of *C. minimus* in the main study area indicate a metapopulation structure (Hanski and Gilpin 1991; Hanski and Gilpin 1997; Reich and Grimm 1996). The species occupied discrete host-plant patches separated by non-habitat and showed turnover in its incidence. Furthermore, population dynamics are assumed to be asynchronous, as indicated by the simultaneous occurrence of local extinction and (re)colonization events. In their study of *C. minimus* in southern Belgium, Baguette et al. (2000) also classified the network of colonies as a metapopulation. Only two of three habitat patches were colonized due to low dispersal ability and high habitat isolation.

In our study, the patch occupancy of *C. minimus* increased about 25% from 2001 to 2002, although the host-plant distribution decreased by about 21%. Asher et al. (2001) also report large fluctuations of *C. minimus* populations from year to year, possibly in relation to flowering cycles in the host plant. Leon-Cortes et al. (2003) suggest that food plant dynamics strongly affect *C. minimus* persistence. The high colonization rate, in spite of the host-plant decline, in our study presumably results from the management history, rather than from recording bias in the previous year. The newly emerging foodplant patches, due to the clearing of bushes a few years ago, were colonized with a delay, since *A. vulneraria* have to be 1 to 5 years old before they flower (Sterk et al. 1982). As a result of the newly emerged *Anthyllis* patches, the extinction events of *C. minimus* are low (3%) in comparison to colonization events. This again supports the statement of Baguette et al. (2000) that conservation of this species implies the creation of more proximate suitable patches.

Contrary to the occurrence probability of *C. minimus*, no relationship was found between colonization rate and connectivity. However, there was a significant correlation between colonization rate and distance to the next occupied patch. This result may be traced back to the fact that the two attributes integrate different time frames and operate at different levels of population dynamic processes. Colonization is influenced by the regional process of immigration and occurs from one year to the next. On the other hand, patch occupancy is more affected by processes at the local level (like birth and death), or by events dating back some time ago (e.g. management history, climatic disasters).

Connectivity and the distance to occupied patches are crucial factors, which must be considered together with dispersal capabilities of a species in order to build up an adequate habitat network for the persistence of a metapopulation (Baguette et al. 2000). In the main study area, the maximum distance between one *C. minimus* colony and the next one was 1,025 m. Immigration into habitat patches was observed over distances of several hundred meters (534 m maximum) from occupied patches. In mark–recapture studies in Great Britain some movements over 1 km were detected, and vagrants 17 km from known colonies were recorded (Asher et al. 2001). However, the great majority of *C. minimus* individuals in a population is very sedentary. Based on a colonization experiment with two artificial *Anthyllis* patches in the present main study area (Binzenhöfer; unpubl. data) an average dispersal distance of 200 m was estimated. In Southern Belgium, 91% of the marked individuals remained in the same habitat during the flight period (Baguette et al. 2000), and the adults of the mark–recapture experiment in the UK rarely moved more than 40 m (Asher et al. 2001).

Conclusions

Our study demonstrates that *Anthyllis* patch size had the strongest effect on the occurrence of *C. minimus*, also when occasionally very small food plant patches were occupied. A further important factor for the occurrence was habitat quality, in which date of first management was especially important. The results show that lower habitat quality may be compensated by higher connectivity between the host plant patches to ensure long-term survival of (meta-)populations in fragmented landscapes.

Acknowledgments We thank Zdenek Fric, Ferenc Kassai and Alban Pfeifer for field assistance. Many thanks to two anonymous referees and the editor Yoh Iwasa for their constructive comments on the manuscript. This study is part of the MOSAIK-project, and is financially supported by the German Federal Ministry of Education and Research (BMBF, grant 01LN0007).

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