Landscape Ecology (2006) 21:989–1001
DOI 10.1007/s10980-005-6057-7

Research article

Occurrence pattern of *Pararge aegeria* (Lepidoptera: Nymphalidae) with respect to local habitat suitability, climate and landscape structure

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Received 19 July 2005; accepted in revised form 18 December 2005

Key words: Butterfly, Distribution, Fragmentation, Habitat quality, Logistic regression, Occurrence probability, Predictive habitat model

Abstract

Distribution patterns of wild species are affected by environmental variables, such as climate, anthropogenic land use or habitat quality, which act simultaneously at different scales. To examine the relative importance of particular factors and scales on population response we investigated the speckled wood butterfly *Pararge aegeria* (L.) as a model organism occupying semi-natural habitats. Its distribution was recorded in 23 study sites (5×5 km) over a 2 year study period. The sites were located in agricultural landscapes within seven Temperate European countries. Environmental predictors were mapped at a local and a regional scale. Logistic regression models were then developed to represent humid (beneficial) and dry (adverse) weather conditions during larval development. The humid year model predicted that *P. aegeria* is equally but generally not very dependent on local and regional factors, resulting in generally high occurrence probabilities. In contrast, the dry year model predicted severe restrictions of *P. aegeria* to both high quality patches and landscapes with beneficial structural and climatic preconditions. As both models resulted in entirely different predictions, our study showed that the sensitivity of *P. aegeria* to local and landscape features might change, and that factors of less importance could easily become limiting factors. The results stress that high quality landscape is important at both the local and regional scale even for species that are considered relatively robust. They also sound a note of caution when predictions about population response for management purposes are based on just a single or a few year(s) of observation.

Introduction

Biodiversity is adversely affected by human induced changes in land use that operate over a broad range of spatial scales (Tilman and Kareiva 1997; Opdam et al. 2003). Factors which function simultaneously at different scales determine the local occurrence of species (Cushman and McGarigal 2002; Jeanneret et al. 2003). Hence, it is a major aim in both theoretical and applied ecology to understand the effects and interactions of environmental factors on the distribution of organisms

(Lawton 1996; Hanski and Gilpin 1997; Gaston and Blackburn 1999; Rushton et al. 2004).

Habitat quality, corresponding to the requirements of a particular species, is expected to be of major importance at the local scale (Duelli 1997; Shreeve et al. 2004). However, data of such high resolution are costly both to obtain and update. At coarser scales, climatic factors (Pollard, Rothery, and Yates 1996; Hill, Thomas, and Huntley 1999; Warren et al. 2001) as well as landscape structure (Hanski 1999; Thomas and Kunin 1999) affect the persistence of natural populations. Landscape composition (i.e. amount and number of habitats present) is one key factor (e.g. Wagner et al. 2000), but also landscape configuration (i.e. spatial arrangement and connectivity of habitat) has a strong impact on local populations (Hanski and Gilpin 1997). Environmental predictors like climate data and landscape structure are now easy to obtain thanks to the increasing development of Geographical Information Systems (GIS) and digital cartography. However, these data are often focused on land use which might not reflect the precise habitat requirements of a particular species. Investigating the relative importance of site- and species-specific local habitat quality, climate and landscape structure at coarse scales of resolution is therefore of great interest to theoretical and applied ecology as well as conservation management.

Butterflies are excellent model organisms for investigations of (meta-) population response to habitat quality (Wettstein and Schmid 1999), landscape composition (Summerville and Crist 2001), landscape configuration (Hanski and Gilpin 1997; Baguette et al. 2003) and matrix properties (Chardon et al. 2003; Jeanneret et al. 2003). We selected the speckled wood *Pararge aegeria* (L.) as a model organism because it occupies natural and semi-natural habitats subjected to massive alteration as a result of changes in anthropogenic land use. *Pararge aegeria* is essentially a species of woodlands and their margins (Settele 1999). Larvae feed on a variety of grass species (Shreeve 1986a) and the butterfly overwinters as either larvae or pupae (Hesselbarth et al. 1995). *Pararge aegeria* can have two or three generations per year. The flight periods of the different generations overlap but two distinct peaks in phenology occur around May and August (Ebert and Rennwald 1991). *Pararge aegeria* is an apparently sedentary species which usually remains in one particular woodland area (Shreeve 1992). Nevertheless, there is also evidence for considerable mobility, at least for some individuals, since it is currently expanding its range northwards due to climate warming in Europe (Shreeve 1995; Parmesan et al. 1999). A higher percentage cover of woodland is shown to increase the rate of expansion (Hill et al. 2001) due to its preference for dispersal along linear woody features (e.g. tree rows, hedgerows) or between woodland patches (Chardon et al. 2003).

In the present study we focus on the impacts of climate, landscape structure and local habitat quality in agricultural landscapes on the distribution of *P. aegeria*. At the landscape level of 5×5 km we did not develop our model for specific habitat requirements of *P. aegeria* but focused instead on a coarse landscape classification (arable fields, woody elements, herbaceous elements). However, at the local scale the habitat requirements of *P. aegeria* were considered within a radius of 250 m when evaluating local habitat quality. The following questions were addressed: (1) Which environmental factors are appropriate for describing the effects of land use on the distribution of *Pararge aegeria*? (2) How important are factors operating on local scales compared to regional scale factors? (3) Is this relation invariant?

Methods

Study sites and environmental variables

Our study is based on data generated and compiled in the EU research project 'Greenveins' (Bugter et al. 2001). *Pararge aegeria* was investigated at 485 survey points in 23 study sites of 5×5 km located within arable landscapes. The sites were distributed among seven European countries: France, Belgium, The Netherlands, Switzerland, Germany, Czech Republic and Estonia (Figure 1). The sites were predominantly agricultural (between 40% and 98% agricultural area), flat (thus potentially suitable for intensive arable agriculture), located below 400 m a.s.l., and representative of the surrounding landscape. Together they covered a wide range of both agricultural land-use intensity and landscape structure (see Herzog et al. 2006).

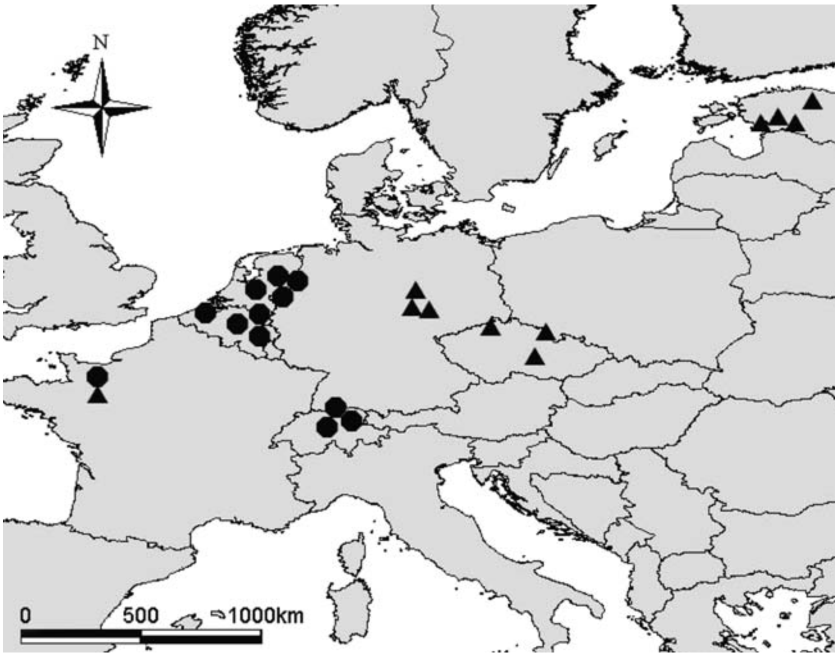

Figure 1. Geographical location of study sites. Circles: surveyed in 2002. Triangles: surveyed in 2003.

We recorded environmental data about the regional and local landscape structure (focusing on semi-natural elements), climatic factors, and the weather conditions during the survey years. The landscape structure was evaluated from habitat maps with a spatial resolution of 1×1 m (D. Bailey, submitted manuscript). The maps were digitized from orthophotos using ArcGIS software (ESRI 2003). The habitats were mapped according to an adaptation of the EUNIS classification system (available at http://eunis.eea.eu.int/habitats.jsp) and these were then aggregated into woody, herbaceous or arable habitats (Table 1). A further coarser level of aggregation classified the study sites into semi-natural habitats (including ecotone structures along arable fields such as headlands or hedgerows) and non-habitat (arable land, urban areas). In order to consider the specific habitat requirements of *P. aegeria* at the local scale we additionally recoded the maps into optimal, suboptimal and unsuitable habitats (Table 1). Variables describing regional and local landscape structure were measured using the maps. At the regional scale, percentage cover, mean patch size, number of patches, largest patch index, edge density, proximity index and Euclidean nearest neighbor distance were computed for semi-natural, woody and herbaceous habitats using ArcGis and FRAGSTATS analysis (McGarigal and Marks 1995). At the local scale, percentage cover of optimal, suboptimal, and arable habitats were used to evaluate local habitat suitability for *P. aegeria*.

To account for the geographical gradient covering our study we considered longitude, latitude and corresponding climatic variables (monthly temperature, precipitation and humidity data recorded over the last 25 years) at study site level. Climatic variables were obtained from globally interpolated climate data with a spatial resolution of 0.5 degrees (available at http://climate. geog.udel.edu/~climate). The interpolations are based on the Global Historical Climatology Network (Peterson and Vose 1997) and on Legates and Willmott's (1990a and b) station records of monthly mean air temperature and total precipitation. For weather conditions during the survey years (temperature and precipitation) we assigned the study sites (in some cases more than one site) to the nearest weather station and used weather data at a monthly resolution.

Field surveys for occurrence of Pararge aegeria

A stratified random sampling design (Hirzel and Guisan 2002) was applied. Up to 10 high quality,

Table 1. Habitat classification.

Habitat	Habitat class	*P. aegeria*
Scrubby woodland edges	Woody	Optimal
Broadleaved hedgerows	Woody	Optimal
Woodland fringes, tall forb habitats	Woody	Optimal
Mixed deciduous and coniferous hedgerows	Woody	Suboptimal
Temperate scrub habitats	Woody	Suboptimal
Temperate scrub heathlands	Woody	Suboptimal
Broadleaved deciduous woodlands	Woody	Suboptimal
Fruit and nut orchards	Woody	Suboptimal
Mixed deciduous and coniferous woodlands	Woody	Suboptimal
Grassy margins	Herbaceous	Not suitable
Coniferous hedgerows	Woody	Not suitable
Line of trees	Woody	Not suitable
Mires, bogs, fens	Herbaceous	Not suitable
Grasslands, tall forb habitats	Herbaceous	Not suitable
Coniferous woodlands	Woody	Not suitable
Arable land, urban areas, water bodies	Not suitable	Not suitable

Habitat class: focusing on the landscape; *P. aegeria*: focusing on the species.

10 medium quality and 10 low quality survey points were selected randomly from the digitized habitat maps. The quality of the survey points was assessed according to habitat suitability within a radius of 100 m. Potentially suitable habitats were considered to be internal and external woodland edges, woodland fringes and broadleaved hedgerows as well as other habitat types with some kind of woodland aspects (Table 1). The actual number of points recorded depended on the amount and distribution of potential habitat and ranged between 10 and 30 spots per study site. Single points were spaced at least 500 m apart to avoid double counting. The presence or absence of *P. aegeria* within a radius of 50 m around each point was recorded within a 10 min period and additionally the number of individuals present was roughly estimated. All survey points of a given study site were monitored on the same day. Census days lay well within the flight period of the second generation between July and August (Ebert and Rennwald 1991). To ensure comparability among sites, surveys were carried out by experienced entomologists under standardized conditions that allowed for high butterfly activity. For example, sites were visited in the morning and afternoon on sunny, non-windy days and the higher temperatures around midday were avoided. Twelve sites were recorded in 2002 and the remaining 11 sites in 2003 (Figure 1).

Statistical analysis

Pre-analysis for scale of local influence and spatial autocorrelation

We recorded the environmental variables at two spatial scales: the regional level (study site) and the local level (survey point). To assess the scale of local influence we calculated the percentage of optimal and suboptimal habitat (as defined in Table 1) within circular areas of varying size around each survey point. Mark-release-recapture studies of *P. aegeria* report on average recapture distances of less than 50 m and maximum distances of about 170 m (in a few cases up to 2200 m; Van Dyck et al. 1997; Merckx and Van Dyck 2005). We tested diameters of 50, 125 and 250 m. Larger areas were not considered to avoid substantial overlap between the points and interdependency of the local environmental predictors. Logistic regression models on the presence–absence data of *P. aegeria* revealed that the radius of 250 m performed the best according to the deviance ratio and it was hence used for the further analyses.

Linear model statistics are confounded by spatial autocorrelation, as this contradicts the assumption of independence among samples replicated through space (Legendre and Legendre 1998). Therefore, we checked whether the butterfly data were autocorrelated. Semivariograms (Legendre and Legendre 1998) showed no overall trend for an increase or decrease in dissimilarity among survey points. Hence, no spatial autocorrelation was evident.

Occurrence pattern analysis

Since the estimation of abundance data came from numerous field-workers across Europe, we relied on the more robust presence–absence data for model building. In field surveys, not observing a butterfly does not necessarily mean that it is absent, but it indicates at least a very low abundance.

A potentially resulting bias in the data was avoided by the standardized survey protocols. The presence–absence data were analyzed using a generalized linear mixed effects model (GLMM) via penalized quasi-likelihood estimation (PQL; Breslow and Clayton 1993). This allowed the study site effect to be accounted for as a random variable. Thus, the survey point data were considered to be nested within study sites. All other variables were treated as fixed effects. A binomial error distribution with a logit link function was used in all statistical analyses (Crawley 2002; Quinn and Keough 2002). These models were implemented in the glmmPQL-routine in the R statistical software package (R Development Core Team 2004; Venebles and Ripley 2002). The environmental variables were standardized to mean 0 and unity standard deviation to avoid problems of collinearity between main factors and interaction terms and to make the coefficient estimates comparable in terms of importance (Quinn and Keough 2002). To allow for curvilinear relationships between each environmental variable and the presence–absence data we incorporated both the linear and quadratic terms of the environmental variables. The models were simplified by stepwise removing variables manually to reduce the Akaike's Information Criterion (AIC; Sakamoto et al. 1986; Rushton et al. 2004) and to eventually contain only effects significant at the 5% level (Crawley 2002).

Several statistical methods have been developed to evaluate model performance (Fielding and Bell 1997; Manel et al. 2001). Since no external data set was available to validate our models externally, we used the Area Under the Curve (AUC) of a Receiver Operating Characteristic (ROC) plot for internal validation. AUC is a powerful, threshold-independent measure of overall fit that varies between 0.5 (for a chance performance) to 1.0 for a perfect fit (Fielding and Bell 1997; Cumming 2000; Manel, Williams and Ormerod 2001; Gibson et al. 2004). We calculated the AUC using SPSS software. The results are reported as AUC ± its standard error obtained by bootstrapping.

Results

The occurrence of *P. aegeria* was analyzed simultaneously at both the local (survey points) and regional (study sites) spatial scales. The analysis of optimal and suboptimal habitat patches at the local scale using a logistic regression model showed that a combination of optimal and suboptimal habitat variables contributed most significantly to the occurrence of *P. aegeria*. Thus, 'suitable local habitat' was used to describe local habitat quality and was the only factor from the local scale retained in further models.

In the initial model for all data only the factors 'survey year', 'mean precipitation' and their interaction remained significant in addition to 'suitable local habitat'. Different sites were surveyed in 2002 and 2003 and these differed significantly in certain aspects (Table 2). The sites surveyed in 2003 were located more east- and northwards with the corresponding climatic conditions (i.e. lower mean annual temperature and precipitation), and were characterized by a lower number of woody patches. There were no differences in landscape composition (percentage of woody, herbaceous and all semi-natural habitats) or local level factors (i.e. percentage of suitable local habitat) between the sites surveyed in 2002 and 2003. However, there were striking differences between the years regarding the summer weather conditions during larval development of *P. aegeria*. The summer of 2002 was relatively humid with an average monthly precipitation of 85.5 mm in June, July and August which is not significantly different from the long-term mean (average 82.6 mm; $p = 0.76$, *t*-test). In 2003 the summer was significantly dryer (average 41.5 mm) compared to both the long-term mean (average 68.1 mm) and the study sites surveyed in 2002 (both $p < 0.001$, *t*-test; Table 2). Another major difference was that the mean abundance of *P. aegeria* per occupied survey point was significantly lower in study sites surveyed in 2003 (Table 2). The discrepancies in the environmental preconditions required the data for the 2 years to be analyzed separately and are reflected by differences in the final two best models (Table 3). Both models were indicated by the AUC values to be of high accuracy (2002 AUC = 0.84 (± 0.024); 2003 AUC = 0.84 (± 0.024)).

Beneficial conditions (2002)

Pararge aegeria is predominantly a woodland species. The study sites surveyed in 2002 were

Table 2. Average characteristics (mean ± standard error) of study sites surveyed in 2002 and 2003.

Factor	Variable	2002	2003	*p*
Geographical position	Latitude	50.4 (±0.6)	53.5 (±1.3)	**0.027**
	Longitude	5.9 (±0.7)	16.6 (±2.8)	<**0.001**
Climate	Mean annual temperature (°C)	9.3 (±0.2)	7.2 (±0.6)	**0.002**
	Mean monthly precipitation (mm)	72.2 (±0.4)	53.7 (±0.2)	<**0.001**
	Mean temperature 6, 7, 8 (°C)	16.4 (±0.2)	16.3 (±0.2)	n.s.
	Mean precipitation 6, 7, 8 (mm)	82.6 (±4.4)	68.1 (±2.5)	**0.007**
Weather in survey year	Mean precipitation 6, 7, 8 (mm)	85.5 (±10.1)	41.5 (±4.5)	<**0.001**
Landscape structure	Woody patches	747 (±88.2)	382 (±78.0)	<**0.001**
	Woody elements (%)	12 (±2.1)	17 (±2.9)	n.s.
	Semi-natural elements (%)	25 (±3.6)	30 (±4.4)	n.s.
	Woody elements (%)	12 (±2.1)	17 (±2.9)	n.s.
	Euclidean nearest neighbor (m)	13 (±1.4)	18 (±4.0)	n.s.
Local habitat quality	Suitable local habitat (%)	15 (±2.6)	23 (±3.3)	n.s.
Abundance *P. aegeria*	Abundance per survey point	3.7 (±0.3)	1.8 (±0.2)	<**0.001**
Study sites	Number of study sites	12	11	
Survey points	Number of survey points	291	194	

Climate data are based on monthly resolution over the last 25 years. 6, 7, 8: months June, July, August. Woody patches: number of woody patches (woodland, scrub and hedgerows). Suitable local habitat: frequency of optimal and suboptimal habitat within a circle of 250 m radius around a survey point. Euclidean nearest neighbor: mean Euclidean nearest neighbor distance between the semi-natural elements of a study site. In bold: significant factors (*t*-test).

characterized by beneficial conditions for this species such as a humid climate, a high number of woody patches and also humid weather conditions during larval development. These conditions coincided with high abundance of *P. aegeria* in occupied patches (mean abundance = 3.7 individuals per occupied survey point, 95% CI: 3.1–4.3; Table 2). Under these conditions, both local and regional factors had a similar but low effect on the occurrence probability, indicated by similar standardized coefficients of the model (Table 3). The results show that the probability of *P. aegeria* occurrence is a function of the factor 'suitable local habitat' around a survey point and the regional factor 'mean Euclidean nearest neighbor' distance of semi-natural elements within a study site (Figure 2). High amounts of suitable local habitat increased the occurrence probability, but even at low levels of local habitat availability increasing occurrence probabilities were predicted for study sites with larger mean Euclidean nearest neighbor distances between semi-natural habitats. However, a generally high probability of occurrence indicated that the impacts of both factors were very low.

Adverse conditions (2003)

In contrast to 2002, the sites surveyed in 2003 reflected adverse conditions for *P. aegeria*: a low long-term mean annual precipitation, fewer woody patches and very dry weather conditions during larval development. These conditions coincided with a low abundance of *P. aegeria* (mean abundance = 1.8 individuals per occupied survey point, 95% CI: 1.4–2.1; Table 2). Positive effects were observed for the factors: 'suitable local habitat', 'long-term mean monthly precipitation' and the number of 'woody patches' (Table 3). For means of convenience 'long-term mean monthly precipitation' will be referred to in the text as 'precipitation'. The standardized coefficient estimates indicated that precipitation had the most important effect on the occurrence of *P. aegeria*, followed by the number of woody patches and the interaction between the number of woody patches and suitable local habitat. The occurrence probability was highly dependent on all three environmental factors, as a predicted probability of 'one' was only achieved when all factors were near their maximum (Figure 3).

The significant interaction between suitable local habitat and woody patches illustrated a change in the relative importance of local habitat availability as a function of the number of available woody patches (Table 3; Figure 3a).

Relative importance of local habitat

Plotting the occurrence probability of *P. aegeria* as a function of the number of woody patches and

Table 3. Generalized linear mixed effects models of *Pararge aegeria* occurrence for humid and dry conditions during larval development.

Variable	Std. Coeff.	Std. Error	DF	*t*-value	*p*
Humid conditions (2002)					
Intercept	0.58	0.30	278	1.950	0.052
Euclidean nearest neighbor	0.97	0.29	10	3.393	0.007
Suitable local habitat	0.94	0.22	278	4.284	< 0.001
Dry conditions (2003)					
Intercept	− 3.39	0.50	181	−6.829	< 0.001
Mean monthly precipitation	1.62	0.38	8	4.301	0.003
Woody patches*Local habitat	0.94	0.33	181	2.872	0.005
Woody patches	0.91	0.25	8	3.586	0.007
Suitable local habitat	0.47	0.30	181	1.557	0.121

The environmental variables are ranked by their relative importance according to the standardized regression coefficients (Std. Coeff.). Std. Error: standard error. DF: numerator degrees of freedom; for N total see Table 2. Euclidean nearest neighbor: mean Euclidean nearest neighbor distance between semi-natural habitat patches. Suitable local habitat: percentage of optimal and suboptimal habitat within a radius of 250 m. Woody patches: number of woody patches. Woody patches*Local habitat: Interaction term of the number of woody patches and suitable local habitat.

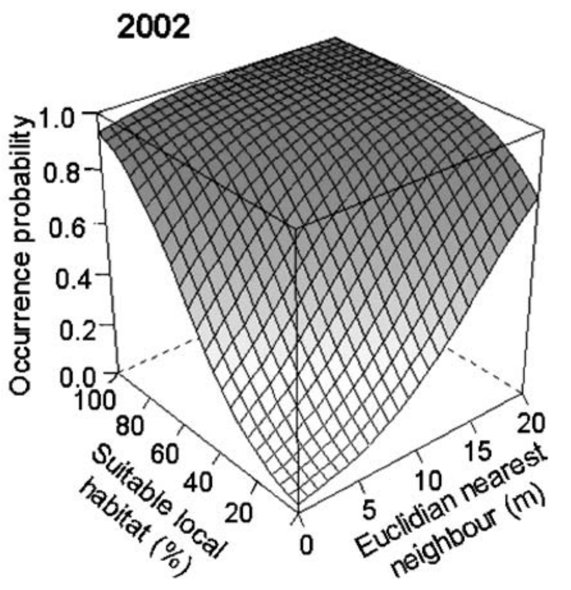

Figure 2. Occurrence probability of *Pararge aegeria* under beneficial conditions as a function of the availability of suitable local habitat (local factor; 250 m radius) and the mean Euclidean nearest neighbor distance of semi-natural habitats (regional factor; 5 × 5 km). The probability surface was calculated on the basis of the logistic model presented in Table 3.

precipitation revealed a strong positive effect of both factors for sites surveyed in 2003 (Figure 4a). To illustrate the relationship of all variables (occurrence probability, suitable local habitat, woody patches and precipitation) in a 3D-plot, we had to keep one variable constant (in this case suitable local habitat). In Figure 4a we chose to set the value of the proportion of suitable local habitat to its mean across all study sites (15%) to illustrate the occurrence probability for average local conditions. However, the interaction observed between local habitat suitability and the number of woody patches (Table 3) indicated that the shape of the surface for predicted probability will differ with the amount of suitable local habitat. Therefore, we calculated the relative importance of local factors as the difference in predicted occurrence probability for the minimum (0%) and maximum (83%) amount of suitable local habitat. Local habitat suitability was important within landscapes where the predicted occurrence probability of *P. aegeria* was high for patches with a maximum amount of suitable local habitat but low in patches with a minimum amount of suitable local habitat. By way of contrast, local habitat suitability was of low importance in landscapes where small differences in occurrence predictions of *P. aegeria* were observed for patches with high or low amounts of suitable local habitat.

The response surface of the relative importance of suitable local habitat as a function of the number of woody patches and precipitation exhibited two peaks (Figure 4b): One in study sites with a high number of woody patches and low precipitation, and the second in study sites with a low number of woody patches and high precipitation. Local habitat was not important in study sites with both a low number of woody patches and low precipitation and was of minor importance in study sites with both a high number of woody patches and high precipitation.

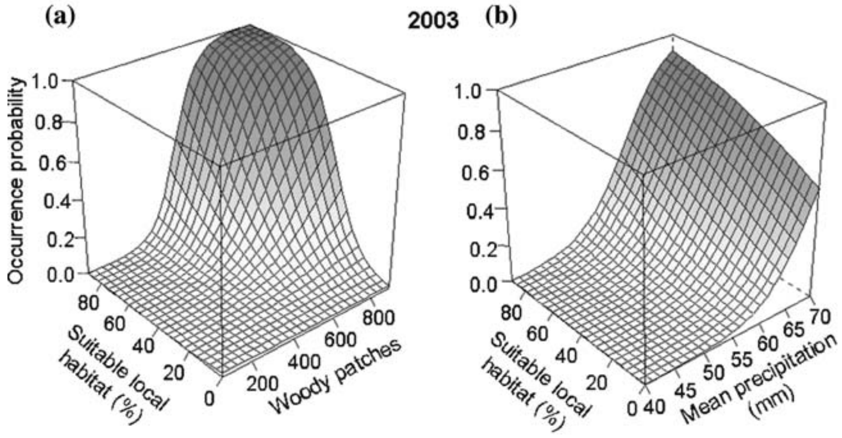

Figure 3. Occurrence probability of *Pararge aegeria* under adverse conditions. Surfaces were calculated on the basis of the logistic model presented in Table 3. (a) Dependence on the availability of suitable local habitat (local factor) and the number of woody patches (regional factor). The value of mean monthly precipitation was set to its mean across all study sites (54 mm). (b) Dependence on the availability of suitable local habitat (local factor) and the long-term mean monthly precipitation (regional factor). The value of woody patches was set to its mean across all study sites ($n = 382$).

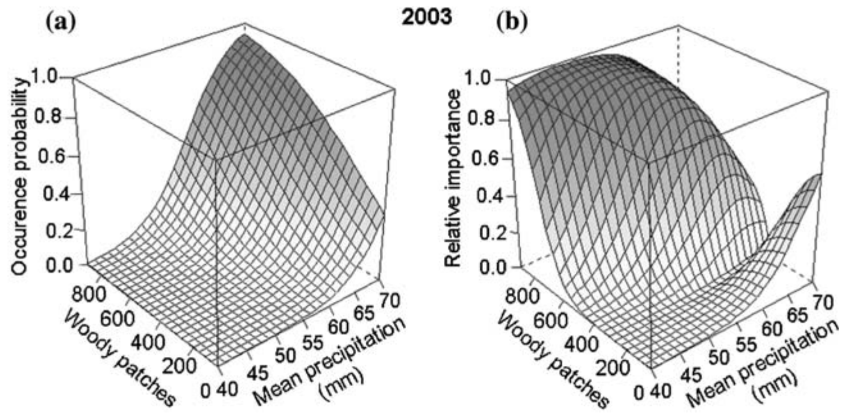

Figure 4. (a) Occurrence probability of *Pararge aegeria* under adverse conditions depending on the number of woody patches and long-term mean monthly precipitation. The surface was calculated on the basis of the logistic model presented in Table 3. The value of suitable local habitat was set to its mean across all study sites (15%). (b) Relative importance of local habitat availability (local factor) depending on the number of woody patches and long-term mean monthly precipitation (both regional factors). The relative importance was calculated as the difference in predicted occurrence probability for the minimum and maximum amount of local habitat.

Discussion

The data for our analysis were obtained from eastern and western regions of Temperate Europe that were surveyed in two different years under differing environmental conditions. Nevertheless, some generic patterns were apparent with respect to differences in weather conditions and the ecology of the butterfly. Microhabitat selection as well as larval development of *P. aegeria* is temperature and humidity sensitive (Shreeve 1984; Shreeve 1986b; Merckx et al. 2003). Humid conditions are regarded as optimal, while arid conditions are unfavorable for the development of the butterfly (Hesselbarth et al. 1995). Drought is thought to have a direct influence on egg mortality (Wiklund and Persson 1983) and an indirect influence through desiccation and wilting of food plants (Pollard 1988; Roy et al. 2001). Temperature and precipitation in the summer of 2002 were well within the average range of climatic variation, but the summer of 2003 was extremely dry. Such arid conditions most likely affect the appearance of the second generation of *P. aegeria*. The consequences for the occurrence of imagos can be illustrated by the observation (unquantified) of several *P. aegeria* individuals in two German study sites with adequate habitat composition in 2002, but none being recorded during the survey period in 2003. The outstanding relevance of the remarkably dry summer of 2003 is also supported by an observed decrease in the abundance of the butterfly *Hesperia comma* (L.), who's larvae feed also on several grass species (Settele 1999). Populations across Germany decreased between 82% and 91% compared to the previous year as a consequence of desiccation of food plants (Ralf Bolz, Silvaea Biome Institute, personal communication).

Consequently, the distribution patterns of *P. aegeria* differed significantly between the humid and the dry year. In humid years, *P. aegeria* is predicted to occur nearly everywhere, exhibiting equally low dependence on both habitat quality at the local scale and the mean Euclidean nearest neighbor distance of semi-natural elements at the regional scale. The positive relationship between predicted occurrence probability and the mean Euclidean nearest neighbor distance of semi-natural habitats is curious and we could see no reason why *P. aegeria* should benefit from larger distances between the semi-natural habitats. However, collinearity among explanatory variables might obscure the ecological interpretation of the statistical models, and causality should be inferred with caution (MacNally 2000, 2002). Therefore, we analyzed correlations between the Euclidean nearest neighbor distance of semi-natural habitats and the other environmental variables. Euclidean nearest neighbor distance was correlated most strongly with latitude ($r = 0.86$), followed by certain landscape metrics (proximity index of semi-natural habitats, $r = 0.80$; proximity of herbaceous habitats, $r = 0.66$; Euclidean nearest neighbor distance of herbaceous habitats, $r = 0.65$). Therefore, the predicted increase of occurrence probability with Euclidean nearest neighbor distance of semi-natural habitats might be in fact a function of latitude and the corresponding changes in climate (increasing humidity) from continental to Atlantic conditions (see Figure 1).

Our results indicate that under general beneficial conditions such as 'normal' humidity during larval development the local abundance and occurrence probability of *P. aegeria* is high. These findings are supported by Merckx and Van Dyck (2005) who report on similarly high abundance estimates for *P. aegeria* in the very same Belgian study site (Hoegaarden) and survey year 2002 (Merckx and Van Dyck: 0.19 individuals per minute; our estimate: 0.22 individuals per minute). High local abundance might lead to density dependent dispersal which has been previously demonstrated for other butterfly species (Kuussaari et al. 1996; Brunzel 2002; Mennechez et al. 2004). Petit et al. (2001) reported that as population size of the butterfly *Proclossiana eunomia* increases, males leave the habitats. If this also applies to *P. aegeria*, whose males also exhibit territorial behavior (Davies 1978; Shreeve 1984), it is likely that males disperse from high quality habitats with high densities of butterflies to lower quality habitats. Hence, beneficial environmental conditions and corresponding high local abundances may cause a decoupling of *P. aegeria* occurrence from local and regional factors due to density dependent dispersal supported by territoriality ('spillover effect'). Under such conditions, *P. aegeria* is expected to occur even in patches with only a minimum amount of its favored habitats, namely scrubby woodland edges and hedgerows regardless of the regional landscape structure.

Totally different patterns, however, are apparent for dry years and we interpret the observed low average local abundance of *P. aegeria* to be a consequence of adverse environmental conditions such as drought during larval development. In contrast to humid years, the impacts of regional and local factors on the occurrence of *P. aegeria* are high in dry years and restrict the butterfly to shadier, more wooded habitats and landscapes. Under such restrictions, climatic preconditions (long-term mean monthly precipitation), landscape structure (number of woody patches), and local habitat suitability increase in importance and might even become limiting factors that represent the specific carrying capacity of the landscape (Hanski and Ovaskainen 2000). The precipitation during larval development in summer on the other hand affects the growth potential of the population. In dry years, regional factors seem to dominate over local habitat quality and even patches of the highest local quality are predicted to be empty when the number of woody patches or the long-term mean monthly precipitation is low. We conclude that critical weather conditions either slow larval development and cause very low population densities so that incidence is missed, or that unfavorable weather in combination with disadvantageous climatic and landscape preconditions causes local extinction.

The combination of local and regional factors within a landscape seems to determine their relative importance for the occurrence probability of *P. aegeria*. In our study, local habitat quality was of major importance for the occurrence of the butterfly in sites where only one regional factor was high and the other was low. Thus, high local habitat quality compensated either a regional low number of woody patches or a dry climate. In sites where both regional factors were high, local habitat quality was of minor importance and occurrence probability was generally high as both regional factors compensated for low local habitat quality. In study sites where both regional factors were low, local habitat quality had obviously no effect as *P. aegeria* was totally absent from the site and local habitat quality could not compensate for low quality at the regional level.

Based on the statistical analysis, we would predict *P. aegeria* to show a high colonizing potential even in low quality patches under beneficial conditions, but to be restricted to high quality patches and landscapes under adverse conditions. This may be indicative of intrinsic metapopulation patterns. Most butterfly species, which, like *P. aegeria*, live in landscapes subject to massive alteration may form metapopulations in response to anthropogenic habitat fragmentation (reviews in Thomas and Hanski 1997; Cowley et al. 2000; but see Shreeve et al. 2004). Metapopulations are regarded as spatially structured populations consisting of distinct subpopulations that are separated by unhabitable space and connected by dispersal. Their persistence at larger scales depends on a compensation of local extinction by recolonization. In a spatially realistic metapopulation model, dispersal is a function of the landscape context (Hanski and Gilpin 1997). Our study stresses the importance of high quality landscape conditions at both regional and local scales even for a common species like *P. aegeria* that appears to be tolerant to low quality landscape structure. The alleged less importance of landscape quality could even turn into a limiting factor if other environmental factors such as climate or incisive singular events affect *P. aegeria*. When events that drastically affect population demography occur, such as extreme weather conditions in summer, butterflies can be expected to respond more sensitively to landscape structure. Such extreme events may occur more frequently and pronounced in future due to climate change (IPCC 1998) and also at the margins of the species range. Hence, an increased sensitivity to landscape features might explain the observed pronounced differences in the rate of range expansion in landscapes that differ only slightly, but significantly, in the percentage cover of suitable habitat (3.6% and 2.7% of woodland; Hill et al. 2001).

Conclusions

Pararge aegeria is a common yet interesting species for conservation concerns as butterflies in general experience increased population and regional extinction (Thomas et al. 2004). Recent studies suggest that apparently common species may decline just as much as rare species (Thomas and Abery 1995; Cowley et al. 1999; Summerville and Crist 2001). Climate and land use change and a likely altered species sensitivity to landscape structure and other environmental factors may also change the future status of currently common species (Leon-Cortes et al. 1999). Hence, population-level conservation is a matter of great urgency for all species no matter of their present incidence. However, the marked differences between the models for humid and dry years in our study sound a note of caution when predicting population response on the basis of single or few year(s) observations. They also indicate potential difficulties for conservation management since single environmental events, such as increased drought (related to climate change), affecting the demography of species might also change species sensitivity and thus the population response to landscape features dramatically. Hence, generalizations to future scenarios, landscapes at the distribution margins or recommendations about thresholds might be, in the majority of cases, overoptimistic.

Acknowledgements

Many thanks to Raphael De Cock, Mart Meriste, and Isabella Sedivy for butterfly survey. We kindly thank Josef Settele for habitat classification according to the requirements of *Pararge aegeria* and Isabel Augenstein, Nicolas Schermann and Riccardo De Filippi for the GIS work. We are grateful to Roland Brandl, Jana Verboom, and two anonymous referees for discussion and comments on the statistics and ecology. Funding was received from the Energy, Environment and Sustainable development Programme (FP5) of the European Commission within the project "Greenveins" (contract number EVK2-CT-2000-00082).

References

Baguette M., Mennechez G., Petit S. and Schtickzelle N. 2003. Effect of habitat fragmentation on dispersal in the butterfly *Proclossiana eunomia*. Comptes Rendus Biologies 326: 200–209.

Breslow N.E. and Clayton D.G. 1993. Approximate inference in generalized linear mixed models. J. Am. Stat. Assoc. 88: 9–25.

Brunzel S. 2002. Experimental density-related emigration in the cranberry fritillary *Boloria aquilonaris*. J. Insect Behav. 15: 739–750.

Bugter R.J.F, Burel F., Cerny M., Edwards P.J., Herzog F., Maelfait J.P., Klotz S., Simova P., Smulders R. and Zobel M. 2001. Vulnerability of biodiversity in the agro-ecosystems as influenced by green veining and land-use intensity: the EU project GREENVEINS. In: Mander U., Printsmann A. and Palang H. (eds), Development of European landscapes. Proceedings of the International Association for Landscape Ecology. Publicationes Instituti Geographici Universitatis Tartuensis 92, Tartu, pp. 632–637.

Chardon J.P., Adriaensen F. and Matthysen E. 2003. Incorporating landscape elements into a connectivity measure: a case study for the Speckled wood butterfly (*Pararge aegeria* L.). Landscape Ecol. 18: 561–573.

Cowley M.J.R., Thomas C.D., Thomas J.A. and Warren M.S. 1999. Flight areas of British butterflies: assessing species status and decline. Proc. Roy. Soc. Lond. Ser. B – Biol. Sci. 266: 1587–1592.

Cowley M.J.R., Wilson R.J., Leon-Cortes J.L., Gutierrez D., Bulman C.R. and Thomas C.D. 2000. Habitat-based statistical models for predicting the spatial distribution of butterflies and day-flying moths in a fragmented landscape. J. Appl. Ecol. 37: 60–72.

Crawley M.J. 2002. Statistical Computing: An Introduction to Data Analysis using S-Plus. John Wiley & Sons, Chichester.

Cumming G.S. 2000. Using between-model comparisons to fine-tune linear models of species ranges. J. Biogeogr. 27: 441–455.

Cushman S.A. and McGarigal K. 2002. Hierarchical, multi-scale decomposition of species-environment relationships. Landscape Ecol. 17: 637–646.

Davies N.B. 1978. Territorial defence in the speckled wood butterfly (*Pararge aegeria)*: The resident always wins. Anim. Behav. 26: 138–147.

Duelli P. 1997. Biodiversity evaluation in agricultural landscapes: an approach at two different scales. Agri. Ecosyst. Environ. 62: 81–91.

Ebert G. and Rennwald E. 1991. Die Schmetterlinge Baden-Württembergs: Tagfalter II. Ulmer, Stuttgart (Hohenheim).

ESRI ArcGIS. [8.x] 2003. Redlands. Environmental Systems Research Institute, California.

Fielding A.H. and Bell J.F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24: 38–49.

Gaston K.J. and Blackburn T.M. 1999. A critique for macroecology. Oikos 84: 353–368.

Gibson L.A., Wilson B.A., Cahill D.M. and Hill J. 2004. Spatial prediction of rufous bristlebird habitat in a costal heathland: a GIS-based approach. J. Appl. Ecol. 41: 213–223.

Hanski I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos 87: 209–219.

Hanski I. and Gilpin E.M. 1997. Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, London.

Hanski I. and Ovaskainen O. 2000. The metapopulation capacity of a fragmented landscape. Nature 404: 755–758.

Herzog F., Steiner B., Bailey D., Baudry J., Billeter R., Bukáèek R., de Blust G., de Cook R., Dirksen J., Dormann C.F., de Filippi R., Frossard E., Liira J., Schmidt T., Stöckli R., Thenal C., van Wingerden W. and Bugter R. 2006. Assessing the intensity of temperate European agriculture at the landscape scale. Eur. J. Agron. 24: 165–181.

Hesselbarth G., Van Oorschot H. and Wagener S. 1995. Die Tagfalter der Türkei. Selbstverlag Sigbert Wagener, Bocholt.

Hill J.K., Collingham Y.C., Thomas C.D., Blakeley D.S., Fox R., Moss D. and Huntley B. 2001. Impacts of landscape structure on butterfly range expansion. Ecol. Lett. 4: 313–321.

Hill J.K., Thomas C.D. and Huntley B. 1999. Climate and habitat availability determine 20th century changes in a butterfly's range margin. Proc. Roy. Soc. Lond. Ser. B – Biol. Sci. 266: 1197–1206.

Hirzel A. and Guisan A. 2002. Which is the optimal sampling strategy for habitat suitability modelling. Ecol. Model. 157: 331–341.

IPCC 1998. The Regional Impacts of Climate Change: An Assessment of Vulnerability. Cambridge University Press, Cambridge.

Jeanneret P., Schupbach B. and Luka H. 2003. Quantifying the impact of landscape and habitat features on biodiversity in cultivated landscapes. Agri. Ecosyst. Environ. 98: 311–320.

Kuussaari M., Nieminen M. and Hanski I. 1996. An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia*. J. Anim. Ecol. 65: 791–801.

Lawton J.H. 1996. Patterns in ecology. Oikos 75: 145–147.

Legates D.R. and Willmott C.J. 1990a. Mean seasonal and spatial variability global surface air temperature. Theor. Appl. Climatol. 41: 11–21.

Legates D.R. and Willmott C.J. 1990b. Mean seasonal and spatial variability in gauge-corrected, global precipitation. Int. J. Climatol. 10: 111–127.

Legendre P. and Legendre L. 1998. Numerical Ecology. Elsevier, Amsterdam.

Leon-Cortes J.L., Cowley M.J.R. and Thomas C.D. 1999. Detecting decline in a formerly widespread species: how common is the common blue butterfly *Polyommatus icarus*? Ecography 22: 643–650.

Manel S., Williams H.C. and Ormerod S.J. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. J. Appl. Ecol. 38: 921–931.

Mac Nally R. 2000. Regression and model-building in conservation biology, biogeography and ecology: the distinction between – and reconciliation of – 'predictive' and 'explanatory' models. Biodiv. Conserv. 9: 655–671.

Mac Nally R. 2002. Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. Biodiv. Conserv. 11: 1397–1401.

McGarigal K. and Marks B.J. 1995. FRAGSTATS: Spatial pattern analysis program for quantifying landscape structure. PNW-GTR-351. Gen. Tech. Rep, Portland, Oregon, USA.

Mennechez G., Petit S., Schtickzelle N. and Baguette M. 2004. Modelling mortality and dispersal: consequences of parameter generalisation on metapopulation dynamics. Oikos 106: 243–252.

Merckx T. and Van Dyck H. 2005. Mate location behavior of the butterfly *Pararge aegeria* in woodland and fragmented landscapes. Anim. Behav. 70: 411–416.

Merckx T., Van Dyck H., Karlsson B. and Leimar O. 2003. The evolution of movements and behavior at boundaries in different landscapes: a common arena experiment with butterflies. Proc. Roy. Soc. Lond. Ser. B – Biol. Sci. 270: 1815–1821.

Opdam P., Verboom J. and Pouwels R. 2003. Landscape cohesion: an index for the conservation potential of landscapes for biodiversity. Landscape Ecol. 18: 113–126.

Parmesan C., Ryrholm N., Stefanescu C., Hill J.K., Thomas C.D., Descimon H., Huntley B., Kaila L., Kullberg J., Tammaru T., Tennent W.J., Thomas J.A. and Warren M. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399: 579–583.

Peterson T.C. and Vose R.S. 1997. An overview of the global historical climatology network temperature data base. Bull. Am. Meteorol. Soc. 78: 2837–2849.

Petit S., Moilanen A., Hanski I. and Baguette M. 2001. Metapopulation dynamics of the bog fritillary butterfly: movements between habitat patches. Oikos 92: 491–500.

Pollard E. 1988. Temperature, rainfall and butterfly numbers. J. Appl. Ecol. 25: 819–828.

Pollard E., Rothery P. and Yates T.J. 1996. Annual growth rates in newly established populations of the butterfly *Pararge aegeria*. Ecol. Entomol. 21: 365–369.

Quinn G.P. and Keough M.J. 2002. Experimental Design and Data Analyses for Biologists. Cambridge University Press, Cambridge.

R Development Core Team 2004. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Roy D.B., Rothery P., Moss D., Pollard E. and Thomas J.A. 2001. Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. J. Anim. Ecol. 70: 201–217.

Rushton S.P., Ormerod S.J. and Kerby G. 2004. New paradigms for modelling species distributions? J. Appl. Ecol. 41: 193–200.

Sakamoto Y., Ishiguro M. and Kitagawa G. 1986. Akaike Information Criterion Statistics. D. Reidel Publishing Company, Dordrecht/Tokyo.

Shreeve T.G. 1984. Habitat selection, mate location, and microclimatic constrains on the activity of the speckled wood butterfly *Pararge aegeria*. Oikos 42: 371–377.

Shreeve T.G. 1986a. Egg-laying by the speckled wood butterfly (*Pararge aegeria*): the role of female behavior, host plant abundance and temperature. Ecol. Entomol. 11: 229–236.

Shreeve T.G. 1986b. The effect of weather on the life cycle of the speckled wood butterfly *Pararge aegeria*. Ecol. Entomol. 11: 325–332.

Shreeve T.G. 1992. Monitoring butterfly movements. In: Dennis R.L.H. (ed.), The Ecology of Butterflies in Brittain. Oxford, Oxford University Press, pp. 120–138.

Shreeve T.G. 1995. Butterfly mobility. In: Pullin A.S. (ed.), Ecology and the Conservation of Butterflies. Chapman and Hall, London, pp. 37–45.

Shreeve T.G., Dennis R.L.H. and Van Dyck H. 2004. Resources, habitats and metapopulations – whither reality? Oikos 106: 404–408.

Settele J. 1999. Die Tagfalter Deutschlands. Ulmer, Stuttgard.

Summerville K.S. and Crist T.O. 2001. Effects of experimental habitat fragmentation on patch use by butterflies and skippers (Lepidoptera). Ecology 82: 1360–1370.

Thomas C.D. and Abery J.C.G. 1995. Estimating rates of butterfly decline from distribution maps – the effect of scale. Biol. Conserv. 73: 59–65.

Thomas C.D. and Hanski I. 1997. Butterfly metapopulations. In: Hanski I. and Gilpin M.E. (eds), Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, London, pp. 359–386.

Thomas C.D. and Kunin W.E. 1999. The spatial structure of populations. J. Anim. Ecol. 68: 647–657.

Thomas J.A., Telfer M.G., Roy D.B., Preston C.D., Greenwood J.J.D., Asher J., Fox R., Clarke R.T. and Lawton J.H. 2004. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. Science 303: 1879–1881.

Tilman D. and Kareiva P. 1997. Spatial Ecology. Princeton University Press, Princeton.

Van Dyck H., Matthysen E. and Dhondt A.A. 1997. The effect of wing colour on male behavioural strategies in the speckled wood butterfly. Anim. Behav. 53: 39–51.

Venables W.N. and Ripley B.D. 2002. Modern Applied Statistics with S. 4th ed. Springer, New York.

Wagner H.H., Wildi O. and Ewald K.C. 2000. Additive partitioning of plant species diversity in an agricultural mosaic landscape. Landscape Ecol. 15: 219–227.

Warren M.S., Hill J.K., Thomas J.A., Asher J., Fox R., Huntley B., Roy D.B., Telfer M.G., Jeffcoate S., Harding P., Jeffcoate G., Willis S.G., Greatorex-Davies J.N., Moss D. and Thomas C.D. 2001. Rapid respones of British butterflies to opposing forces of climate and habitat change. Nature 414: 65–69.

Wettstein W. and Schmid B. 1999. Conservation of arthropod diversity in montane wetlands: effect of altitude, habitat quality and habitat fragmentation on butterflies and grasshoppers. J. Appl. Ecol. 36: 363–373.

Wiklund C. and Persson A. 1983. Fecundity, and the relation of egg weight variation to offspring fitness in the speckled wood butterfly *Pararge aegeria*, or why don't butterfly females lay more eggs? Oikos 40: 53–63.