*Evolutionary Ecology Research*, 2002, **4**: 993–1004

# Range sizes in butterflies: correlation across scales

Martin Brändle,* Sabine Öhlschläger and Roland Brandl

*Department of Animal Ecology, Faculty of Biology, Philipps-University of Marburg,*
*Karl-v.-Frisch Str. 1, D-35032 Marburg, Germany*

## ABSTRACT

We assessed the importance of body size, niche measures, resource availability, life-history traits and population parameters for geographical range sizes of butterflies on a regional (Germany, Baden-Württemberg) and European scale. In univariate analyses we found that body size, habitat range, host range, altitudinal distribution, host distribution, the number of generations, dispersal ability and population size were all positively related to range sizes on the two geographic scales. These results were more or less similar in cross-species and phylogenetically controlled analyses. Hierarchical partitioning suggested that habitat range, host range and host distribution influence distributional range size on the regional scale. Body size, clutch size, dispersal ability and population size explained very little additional variance. On the European scale, the importance of altitudinal distribution increased and the importance of host range declined. Our analyses demonstrate that the processes which influence distributional range size of butterflies differ in their importance across scale.

*Keywords*: body size, butterflies, distribution, geographical scale, life-history traits, macroecology, niche breadth.

## INTRODUCTION

Over the last decade, macroecology has generated considerable insights into patterns of geographic range sizes of species and associated processes (Brown, 1995; Gaston and Blackburn, 2000). Despite considerable progress, there are still some outstanding issues. First, there is a strong taxonomic bias because most studies have focused on mammals and birds (e.g. Brown, 1995; Blackburn *et al.*, 1996; Gaston and Blackburn, 2000) and, secondly, the effects of geographical scale remain relatively unexplored (Gaston, 1994; Blackburn and Gaston, 1998). We consider the latter issue and investigate processes that may shape the geographic range sizes of species on two spatial scales. The following processes have been proposed to influence range sizes of species on ecological time scales:

1. *Body size.* Large species need larger home ranges and thus more space to build up viable populations. Therefore, populations of large species need more area for persistence. Furthermore, large species are more mobile than small ones and, consequently, may

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* Author to whom all correspondence should be addressed. e-mail: braendle@mailer.uni-marburg.de

appear at more places. However, the argument that large species need more space and thus need larger range sizes for their persistence may be not valid for small-bodied insects: even the largest insects may be able to maintain viable populations in rather small areas (Loder *et al.*, 1998).

2. *Niche breadth.* Brown and co-workers (Brown, 1984, 1995; Brown *et al.*, 1995, 1996) have proposed that niche breadth is intimately correlated with range size. Species with a broad niche should be able to cover larger geographical ranges. Since home range size increases with a steeper slope than daily energy requirement, larger species need less energy per area. This allows larger species to use resources with a low energy content (Brown and Maurer, 1989). Therefore, large species should be less specialized than smaller ones and large species should be able to exploit a broader range of habitats, which should lead to a larger range size. This chain of arguments rests on physiological patterns in mammals. Although this idea was applied to butterflies by Thomas and Mallorie (1985) and to moths by Lindström *et al.* (1994), the physiological background is obscure. Nevertheless, there is a correlation between body size and degree of polyphagy in several phytophagous insect taxa (Wasserman and Mitter, 1978; Loder *et al.*, 1998; Brändle *et al.*, 2000).
3. *Resource availability.* Species that utilize widespread resources should themselves be widespread (e.g. Hanski *et al.*, 1993; Quinn *et al.*, 1997, 1998; Gregory and Gaston, 2000).
4. *Vital rates.* There is a robust correlation between abundance and geographic range size. Abundance is correlated with many life-history traits (Brown, 1995; Gaston and Blackburn, 2000). Life-history traits influence the intrinsic rate of increase as well as the carrying capacity. This should generate a correlation between life-history traits and range size.
5. *Metapopulation dynamics.* Dispersal ability and population size are hypothesized to affect a species range size through metapopulation dynamics (Hanski *et al.*, 1993). Mobile species are more likely to immigrate into empty and suitable habitat patches and are also more likely to colonize new patches (Hanski *et al.*, 1993). Furthermore, common species produce more migrants and are less prone to go extinct. Thus, one expects mobile and common species to occupy more places.

At present, there is little information on which spatial scales the described processes may operate. Here, we use the range sizes of European butterflies on two spatial scales to analyse patterns of range sizes in relation to body size, niche measures, resource availability and life-history traits. Butterflies have several advantages for such an analysis. Most importantly, butterflies are phytophagous insects. Thus, the number of plant species used by the caterpillar is a straightforward and easy measure of dietary niche breadth. Measuring dietary niche breadth is much more difficult in other taxa, such as birds (e.g. Brandl *et al.*, 1994). Secondly, butterflies are the favourite group of amateur entomologists. An impressive body of information exists on their natural history, which has already attracted the attention of macroecologists (see also Cowley *et al.*, 2001). Using butterflies, we address the following important question: Do the patterns of correlations between range sizes versus body size, niche measures and other traits of species show differences across spatial scales?

## MATERIAL AND METHODS

### Geographic range sizes of species

For Germany, the most precise distributional information about butterflies is available for Baden-Württemberg ($3.5 \times 10^4$ km$^2$, $11 \times 11$ km grids, total 293 grids; Ebert and Rennwald, 1991a,b). Distributional information is available for 116 butterfly species (excluding the Hesperiidae). Range size was estimated by counting the number of occupied grids; for simplicity, from hereon called regional distribution. On the European scale, we analysed maps published in Higgins and Riley (1993); note that these maps are very similar to those produced by Tolman and Lewington (1997). We arbitrarily divided the area into fifty-four $450 \times 450$ km grids, of which 46 grids cover land area (about $10^6$ km$^2$). A grid was counted as occupied when at least touched by the distributional range of a species. We ignored the Canary Islands and the Azores. In total, we extracted range sizes for 337 species. Our range size measures on the two scales are measures of occupancy and there are two bounds: zero and the maximum number of available grids. Hence, both measures of geographical range size may be expressed as percentages and the arcsine square root transformation is appropriate for statistical analysis (see also Williamson and Gaston, 1999).

### Body size

We estimated body size as the midpoint between minimum and maximum forewing length (in millimetres), as reported by Higgins and Riley (1993), which is a good measure of body size (e.g. Gaston and Reavey, 1989; Hawkins and Lawton, 1995). From a statistical point of view, body size distributions are skewed and $\log_{10}$-transformated body size data approach a normal distribution (Novotný and Kindlmann, 1996).

### Niche breadth measures

First, we considered the range of habitats utilized by the caterpillars as a measure of habitat range. For a subset of 122 species, Weidemann (1995) lists the distribution of caterpillars across 29 habitats defined by plant communities. We used the total number of habitats utilized as a measurement of a species' habitat range. For statistical analysis, habitat range was $\log_{10}$-transformed as the distribution was considerably skewed. Secondly, we considered the number of plant species used by the caterpillars as a measure of dietary niche breadth. On the European scale, we distinguished between four categories (e.g. Gaston and Reavey, 1989): 1 = species with caterpillars restricted to a single host species, 2 = species restricted to a single host genus, 3 = species restricted to a single host family, 4 = species that use more than one host family. Information was extracted from Higgins and Riley (1993) and corrected for apparent errors using information in Ebert and Rennwald (1991a,b), Schweizerische Bund für Naturschutz (1988), Koch (1991) and Weidemann (1995). On the regional scale, we used the detailed data on larval host species provided by Ebert and Rennwald (1991a,b). Here we used the total number of larval hosts, irrespective of taxonomic affiliations between host plant species, as a measure of host range (for alternatives, see Symons and Beccaloni, 1999). Before the statistical analyses, the regional measure of host range was $\log_{10}$-transformed. Thirdly, we considered the altitudinal distribution of species as a measure of their tolerance to different climates. This may be viewed as a habitat envelope in which a butterfly species is able to survive. The Schweizerische Bund für Naturschutz (1988) reports the distribution of butterfly species across 13 altitudinal categories. We used the span of altitudinal categories (minimum = 1, maximum = 13) as a surrogate for the climate tolerance of a species. Niche measures are compromised, as rare species are bound to be found in only a few categories (Gaston, 1994; Gaston and Blackburn, 2000). However, data on butterflies are the most precise when compared with other insect taxa (e.g. Hawkins and Lawton, 1995) and our data on distribution and niche were extracted from different sources, which mitigates the danger of bias and the non-independence of data.

### Resource availability

We were only able to quantify resource availability on the regional scale. We estimated the distribution of larval food-plants as reported by Sebald *et al.* (1992a,b, 1994a,b, 1996a,b, 1998a,b). On a grid system, these authors provide distribution maps for each vascular plant species that occurs in Baden-Württemberg [11 × 11 km grids, total 312 grids (*Note*: differences in grid number compared with the butterflies is due to different counting of grids located at the country border)]. For each butterfly species, we counted the total number of grids in which at least one larval food plant species has been reported to occur. As for the estimation of geographical range size of the butterflies, the arcsine square root transformation is appropriate for statistical analysis (see above).

### Life history and other traits of species

First, we considered the average number of generations per year listed in Ebert and Rennwald (1991a,b), Koch (1991), Weidemann (1995), Schweizerische Bund für Naturschutz (1988) and Higgins and Riley (1993). Secondly, we considered clutch size as listed in Weidemann (1995). We distinguished between five categories: 1 = < 60 eggs, 2 = 60–130 eggs, 3 = 130–250 eggs, 4 = 250–500 eggs, 5 = 500–1000 eggs. Thirdly, we used dispersal ability and population size as given by Bink (1992). Each species was ranked on a scale from 1 to 9, where low numbers indicate low dispersal ability and small populations, and high numbers indicate good dispersal and larger populations.

### Statistical analysis

Species are linked by their phylogeny (Felsenstein, 1985; Harvey and Pagel, 1991). Although geographical range size appears to be independent of phylogeny (Gaston, 1998), phylogenetic conservatism of body size and life-history traits is strong (e.g. Harvey and Pagel, 1991). Thus, we conducted two types of analyses: (i) a cross-species approach, using species as independent data points; and (ii) a phylogenetically controlled approach, using phylogenetic independent contrasts. We used the method suggested by Pagel (1992) as implemented in the program CAIC (Crunch-option; Purvis and Rambaut, 1995). Since a fully resolved phylogeny of European butterflies is not available, we were forced to use taxonomic affiliation to estimate phylogenetic relations. For the relationships among families and subfamilies, we used Janz and Nylin (1998, fig. 1). All other relationships were as according to Karsholt and Razowski (1996). We assumed all branch lengths to be equal (see Martins and Garland, 1991). The assumption incorporated into the calculation of contrasts assumes that all lineages make the same proportional changes. Thus, the magnitude and sign of the standardized contrasts should be independent of the estimated value of the character at the node at which the contrast was taken (Freckleton, 2000). We checked this assumption for all the traits considered by regressing the independent contrasts against their estimated nodal values. We found no significant positive correlations ($P > 0.05$).

Relationships among traits were explored using correlation analysis and regression analyses. We always used the largest set of species available for each type of analysis. Note that, for phylogenetic independent contrasts, the regression lines have to pass through the origin (Garland *et al.*, 1992; Pagel, 1992).

Macroecological studies are confounded by complex interrelationships between independent variables. To estimate the importance of the different independent variables for distributional range sizes, we applied hierarchical partitioning, a technique that has recently found its way into ecology (Chevan and Sutherland, 1991; MacNally, 2000). The aim of hierarchical partitioning is not to identify a single optimal model and it does not generate a predictive equation. Rather, all possible regression models are used to estimate the average independent effect of a given independent variable on the dependent variable (MacNally, 2000). Sometimes statistically significant independent effects can be suppressed by antagonistic joint effects. This technique is designed for such scenarios, converting antagonistic effects into negative joint contributions (Chevan and Sutherland, 1991). A major drawback of the method is that there is currently no simple way to assign statistical significance to the independent contribution of an explanatory variable. Thus, we also computed multiple regression models applying the backward-elimination technique.

## RESULTS

### Regional scale

Using species as independent data points, in univariate correlation analyses most of the independent variables were positively correlated with distributional range size (Table 1). The only exception was clutch size. After controlling for phylogeny, the results changed somewhat: body size and population size failed to reach the 10% significance level, whereas clutch size did (Table 1). Note that, due to the many polytomies in our phylogeny, the number of contrasts was much less than the number of species. In a hierarchical partitioning using species as data, four variables had some influence on regional range size (Fig 1, upper left): habitat range, host range, resource availability and dispersal. All other independent variables were only of minor importance. With phylogenetic independent contrasts (Fig. 1, upper right), the results changed somewhat: the importance of habitat range, host range and resource availability remained, but altitudinal range also became important. We found only moderate agreement in the patterns of independent and joint effects between the cross-species and the phylogenetically controlled approaches (independent effects: Spearman rank correlation, $r_s = 0.66$, $P = 0.06$; joint effects: $r_s = 0.48$, $P = 0.19$).

### European scale

Using species as independent data points, in univariate correlation analyses most of the independent variables were positively correlated with distributional range size measured

**Table 1.** Cross-species analysis ($r_{raw}$) and phylogenetically controlled analysis ($r_{con}$) of correlations of range sizes of butterflies on a regional scale (Germany, Baden-Württemberg) and on the European scale (Europe) against body size, niche measures, resource availability, life-history traits and population parameters

| | Dependent variables | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Regional scale | | | | European scale | | | |
| Independent variables | $n$ | $r_{raw}$ | $n$ | $r_{con}$ | $n$ | $r_{raw}$ | $n$ | $r_{con}$ |
| Body size | 115 | 0.22* | 44 | −0.14 | 335 | 0.12* | 86 | 0.24* |
| Habitat range | 111 | 0.43*** | 44 | 0.60*** | 122 | 0.48*** | 46 | 0.54*** |
| Host range | 104 | 0.54*** | 43 | 0.60*** | 145 | 0.21* | 55 | 0.35** |
| Altitudinal distribution | 112 | 0.29** | 43 | 0.43** | 174 | 0.54*** | 56 | 0.62*** |
| Resource availability | 102 | 0.49*** | 43 | 0.66*** | — | — | — | — |
| Generations | 116 | 0.37*** | 44 | 0.49** | 327 | 0.35*** | 84 | 0.31** |
| Clutch size | 109 | −0.06 | 44 | 0.35* | 118 | −0.11 | 46 | 0.20 |
| Dispersal ability | 105 | 0.39*** | 41 | 0.33* | 121 | 0.34*** | 47 | 0.33** |
| Population size | 105 | 0.27** | 41 | −0.11 | 121 | 0.38*** | 47 | 0.39** |

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

on the scale of Europe (Table 1). As in the analysis of the regional range size, clutch size was an exception. Cross-species hierarchical partitioning (Fig. 1, lower left) suggested that habitat range, altitudinal range, the number of generations, dispersal ability and population size have some importance for the distributional range sizes on the European scale. In a phylogenetically controlled analysis, the results changed again (Fig. 1, lower right): the importance of dispersal ability, population size and the number of generations declined, whereas the importance of altitudinal range and habitat range increased. Again, the agreement between the two approaches was not strong (independent effects: $r_s = 0.33$, $P = 0.42$; joint effects: $r_s = 0.60$, $P = 0.12$).

## Comparisons between scales

The geographical range size of species was positively correlated across scale ($n = 116$, $r = 0.62$, $P < 0.001$; Fig. 2). This result did not change when we corrected for phylogeny ($n = 52$ contrasts, $r = 0.68$, $P < 0.001$). We also calculated the correlation of geographic range sizes of butterflies in Britain (Hodgson, 1993) to their range sizes on our regional and European scales. In both cases, we found a significant correlation (Britain *vs* Baden-Württemberg, $n = 51$, $r = 0.64$, $P < 0.001$; Britain *vs* Europe, $n = 51$, $r = 0.66$, $P < 0.001$; contrasts: Britain *vs* Germany, $n = 26$, $r = 0.61$, $P < 0.001$; Britain *vs* Europe, $n = 28$, $r = 0.61$, $P < 0.001$; range size measures arcsine square root-transformed). Moreover, when we computed a multiple regression using distribution in Germany and in Europe as independent variables, both explained a significant part of the variance in the geographic range size of British butterflies (total explained variance, $r^2 = 0.54$, $P < 0.001$; standardized regression coefficient range size in Germany, $\beta = 0.42$, $P < 0.001$; standardized regression coefficient

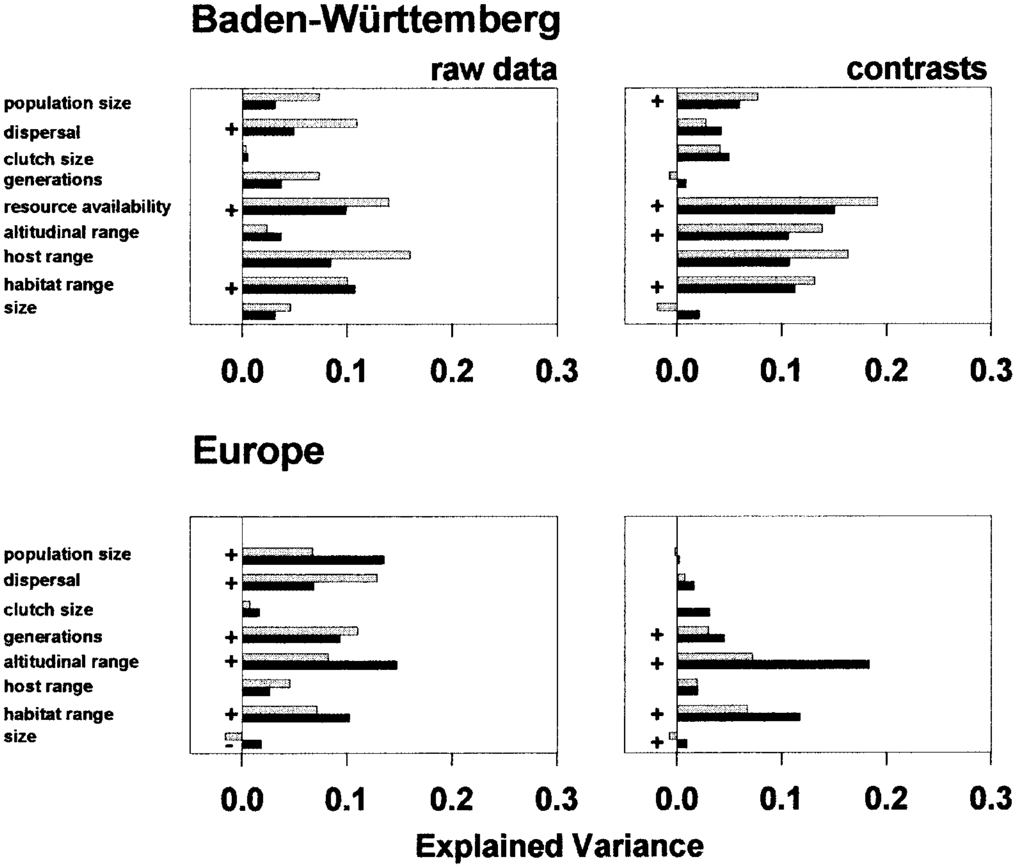

**Fig. 1.** Summary of the results of four separate hierarchical partitions. The graphs show the importance of independent variables for distributional range size. The upper row presents the analysis of range sizes on a regional scale (Baden-Württemberg in southern Germany); the lower row presents the analysis of range sizes on the European scale. The left-hand panels present the results for the raw data; the right-hand panels present the results for the phylogenetic independent contrasts. Black bars indicate independent effects, grey bars joint effects. The abscissa indicates the explained variance equivalent to $r^2$-values. Statistically significant effects after eliminating non-significant variables in multiple regression analyses are indicated by a plus or minus sign (positive or negative standardized regression coefficient).

range size in Europe, $\beta = 0.43$, $P < 0.001$; contrasts: total explained variance, $r^2 = 0.70$, $P < 0.001$; standardized regression coefficient range size in Germany, $\beta = 0.45$, $P = 0.002$; standardized regression coefficient range size in Europe, $\beta = 0.51$, $P < 0.001$).

Despite the correlation of range sizes across scale, we found little agreement in the patterns of univariate correlation coefficients across scale: for species as well as contrasts, the correlation coefficients listed in Table 1 showed no significant rank correlation (species: $r_s = 0.36$, $P > 0.3$; contrasts: $r_s = 0.38$, $P > 0.3$). Similarly, there was little agreement only in the independent contributions and the joint effects shown in Fig. 1 across scales: for species

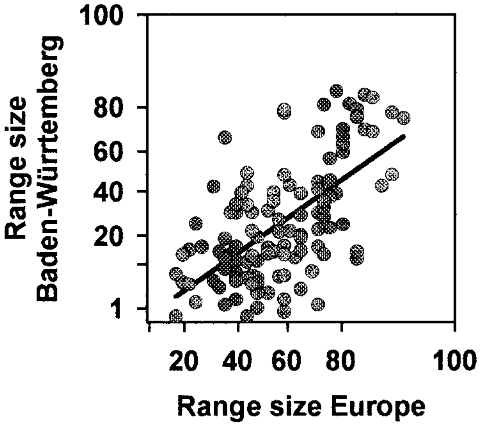

**Fig. 2.** Correlation of range size on a regional scale (Baden-Württemberg in southern Germany) with range size on the European scale. Note that the axes are arcsine square root transformed.

as well as contrasts, the correlation coefficients showed no significant rank correlation (independent contributions: species, $r_s = 0.31$, $P > 0.3$; contrasts, $r_s = 0.33$, $P > 0.3$; joint effects: species, $r_s = 0.35$, $P > 0.3$, contrasts, $r_s = 0.55$, $P > 0.1$).

## DISCUSSION

The results of our analyses can be summarized as follows: First, on each of the two scales, there is no simple single variable that predicts most of the variance in the range size of butterflies. Secondly, independent of scale, body size is only a weak predictor of the range size of butterflies. In birds and mammals, a positive correlation between body size and range size has sometimes been found (e.g. Brown and Maurer, 1989). The relationship is, however, weak in many other taxa and our study supports this view. Thirdly, on the regional scale, niche measures and resource availability are the most important parameters for the distributional range size of butterflies. On the European scale, physiological tolerance increases in importance.

We wish to draw attention to some restrictions of our data set and the analyses about which we are aware. First, the power of the phylogenetic approach is sometimes poor, especially on the European scale. This is due to the many polytomies in the tree as well as missing data. Secondly, the analyses among scales are not strictly comparable. Our measure of host range conducted on the regional scale counts the number of recorded hosts, whereas on the regional scale our measure incorporates the taxonomic affiliation of hosts (see Symons and Beccaloni, 1999). Thirdly, we ignored other processes hypothesized to influence geographical range sizes, for example voltinism, flight period, development time and larval growth rate (Dennis *et al.*, 2000). Fourthly, we ignored historical processes. Present-day ranges are not only the outcome of ecological processes, but of processes during the Pleistocene and the Holocene (Dennis, 1993; Dennis *et al.*, 1998). Despite these drawbacks, some of the variables considered in our analyses showed some influence on distributional ranges sizes; also, the percentage of variance accounted for by a single variable never reached 30% (Fig. 2).

Until now, few studies have attempted to distinguish between niche breadth and resource availability. For British birds, Gregory and Gaston (2000) found more support for the resource availability hypothesis than for the niche breadth hypothesis. In our analysis on the regional scale, we measured three niche dimensions (habitat range, altitudinal range, host range) and were able to quantify the spatial availability of host plants. Host range and resource availability showed similar independent contributions to distributional range sizes, although only resource availability remained significant in the multiple regression analysis. Unfortunately, we have no data on the distribution of larval food plants on the European scale. Thus, more data summarizing resource availability on different scales are required for an analysis of the importance of the niche breadth and the resource availability hypotheses in the context of scale. Nevertheless, our regional data do demonstrate that resource availability influences the range sizes of butterflies (see also Cowley *et al.*, 2001).

Although there was a robust correlation between the range sizes of butterflies on the two spatial scales, the patterns of correlations of range size with the independent variables were different between scales. In general, from small to large scale, the importance of dietary niche breadth decreases, whereas that of physical tolerance increases:

1. The importance of altitudinal range is more pronounced on the large spatial scale. This appears to make intuitive sense. From the north to the Mediterranean basin, butterflies are confronted with quite different climates. On the local scale, variations in climate are much less pronounced and physiological tolerance may be of minor importance. Note also that Gutierrez and Menendez (1995) found that some butterfly species occupy a narrower range close to its margin than near the geographic core.
2. Dietary niche breadth is of more importance on the regional scale than on the European scale. Biotypes offer an explanation. As demonstrated several times, insect species show shifts in their food preference across space (see examples in Zwölfer, 1970; Wiklund, 1982; Leather, 1991; Thompson, 1994). On small spatial scales, the mobility of butterfly species may generate gene flow between populations and thus may prevent local adaptation. However, on large spatial scales, populations may be able to adapt to certain food plants according to the particular circumstances of that area. Thus, host switches allow species to distribute across large areas and range sizes are only marginally influenced by host range.

Overall, our results suggest that the importance of processes that determine geographic range size changes across scale. But what causes the correlation of range sizes across scale? With the data we have at hand, we are unable to offer a convincing hypothesis.

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