Mobility costs and energy uptake mediate the effects of morphological traits on species’ distribution and abundance

STEFAN PINKERT 1,2,5 NICOLAS FRIESS 3 DIRK ZEUSS 3 MARTIN M. GOSNER 4, ROLAND BRANDL 1 AND STEFAN BRUNZEL 2

1 Faculty of Biology, Animal Ecology, Philipps-University Marburg, Marburg 35043 Germany
2 Faculty of Landscape Architecture, Biodiversity and Conservation, University of Applied Sciences Erfurt, Erfurt 99085 Germany
3 Faculty of Geography, Environmental Informatics, Philipps-University Marburg, Marburg 35043 Germany
4 Forest Entomology, Swiss Federal Research Institute WSL, Birmensdorf 8903 Switzerland

Citation: Pinkert, S., N. Friess, D. Zeuss, M. M. Gossner, R., Brandl and S., Brunzel. 2020. Mobility costs and energy uptake mediate the effects of morphological traits on species distribution and abundance. Ecology 101(10):e03121. 10.1002/ecy.3121

Abstract. Individuals of large or dark-colored ectothermic species often have a higher reproduction and activity than small or light-colored ones. However, investments into body size or darker colors should negatively affect the fitness of individuals as they increase their growth and maintenance costs. Thus, it is unlikely that morphological traits directly affect species’ distribution and abundance. Yet, this simplification is frequently made in trait-based ecological analyses. Here, we integrated the energy allocation strategies of species into an ecophysiological framework to explore the mechanisms that link species’ morphological traits and population dynamics. We hypothesized that the effects of morphological traits on species’ distribution and abundance are not direct but mediated by components of the energy budget and that species can allocate more energy towards dispersal and reproduction if they compensate their energetic costs by reducing mobility costs or increasing energy uptake. To classify species’ energy allocation strategies, we used easily measured proxies for the mobility costs and energy uptake of butterflies that can be also applied to other taxa. We demonstrated that contrasting effects of morphological traits on distribution and abundance of butterfly species offset each other when species’ energy allocation strategies are not taken into account. Larger and darker butterfly species had wider distributions and were more abundant if they compensated the investment into body size and color darkness (i.e., melanin) by reducing their mobility costs or increasing energy uptake. Adults of darker species were more mobile and foraged less compared to lighter colored ones, if an investment into melanin was indirectly compensated via a size-dependent reduction of mobility costs or increase of energy uptake. Our results indicate that differences in the energy allocations strategies of species account for a considerable part of the variation in species’ distribution and abundance that is left unexplained by morphological traits alone and ignoring these differences can lead to false mechanistic conclusions. Therefore, our findings highlight the potential of integrating proxies for species’ energy allocation strategies into trait-based models not only for understanding the physiological mechanisms underlying variation in species’ distribution and abundance, but also for improving predictions of the population dynamics of species.

Key words: capital-income breeder continuum; distribution–abundance relationship; metabolic ecology; population density; propensity for nectar foraging; range size; resource availability; size–abundance relationship; thermal melanism hypothesis; wingbeat frequency.

INTRODUCTION

Within the last decades, morphological traits have increasingly been used to understand and predict variation in the distribution and abundance of species (Brown et al. 2004, Violle et al. 2007, White et al. 2007, Angert et al. 2011) as well as species’ responses to climate change (Angert et al. 2011, Zeuss et al. 2014, Estrada et al. 2016, MacLean and Beissinger 2017). The presumed role of morphological traits for explaining species’ distributions and abundance stems from the idea that these traits determine the physiological performance of individuals and ultimately the vital rates of populations (Brown et al. 2004, Violle et al. 2007, White et al. 2007). Classic examples for relationships between morphological traits and physiology that can influence the distribution (e.g., range size or occupancy) and abundance of species include effects of body size on metabolic rate, fecundity, and dispersal ability (Damuth 1981, Honěk 1993, Gillooly et al. 2001, 2002, Brown et al.
2004, White et al. 2007). However, morphological traits generally leave a large part of variation in the distribution and abundance of species unexplained and the causes of this unexplained variation remain poorly understood (Blackburn et al. 1993, 2006, White et al. 2007).

Ectotherms depend on thermal energy from their environment for activity and for maintaining fundamental physiological processes (Gillooly et al. 2001, 2002, Heinrich 2013). Ectotherms therefore evolved adaptations to the temperature regimes in which they live (Clusella-Trullas et al. 2007, Zeuss et al. 2014, 2017, Pinkert et al. 2016, Shelomi and Zeuss 2017, Heidrich et al. 2018, Stelbrink et al. 2019). Two of the most important morphological traits that influence the physiology of ectotherms are their body size and melanization (True 2003, Clusella-Trullas et al. 2007, Angilletta et al. 2010, Heinrich 2013, Pinkert and Zeuss 2018). Larger species retain body heat more efficiently than smaller species owing to their lower surface-area-to-volume ratio (Bergmann 1848, Angilletta et al. 2010), and darker colored species heat up faster than lighter colored species because they absorb more solar radiation (Kalmus 1941, True 2003, Clusella-Trullas et al. 2007). Other benefits include enhanced immunocompetence of larger species (Vainio et al. 2004) and enhanced UV protection and pathogen resistance of darker species (True 2003). Because of these functions, individuals of larger and darker ectothermic species often have a higher fitness than smaller and lighter colored individuals (Honěk 1993, Roff and Fairbairn 2013). However, an investment into body size or melanization is energetically costly (Gillooly et al. 2001, Talloen et al. 2004). For instance, large or dark-colored insects require more energy for their growth (Gillooly et al. 2002, Talloen et al. 2004, Angilletta et al. 2010). These higher costs during the development are, in turn, carried over from larval to adult life stages through the body fat reserves (Boggs and Freeman 2005, Boggs 2009, Arrese and Soulages 2010), which might have subsequent negative effects on the fitness of individuals (Kingsolver 1995, Roff and Fairbairn 2013).

Here, we argue that current attempts to understand how the distribution and abundance of species is affected by morphological traits, such as body size and color darkness, often fail to recognize differences in energy allocation strategies among species, as they consider these effects to be direct (Violle et al. 2007). Species might, for instance, compensate an investment into body size or melanin, by allocating less energy to growth, maintenance, or mobility (Boggs and Freeman 2005, Boggs 2009). Thus, although the energetic costs of mobility generally increase with increasing body size, they can be considerably reduced by enhancing the efficiency of locomotion through morphological adaptations (e.g., lower body size to wing size ratios; Betts and Wootton 1988). Such adaptations are especially relevant for ectothermic organisms because mobility costs constitute the main fraction of their energy expenditure (Nagy et al. 1999, Niven and Scharlemann 2005) and particularly for flying ectotherms because mobility costs increase exponentially with wingbeat frequency of species (Bartholomew and Casey 1978, Full 1997). While the energy expanded per wing beat is similar between closely related species, the wing beat frequency can considerably differ among them (Casey et al. 1985) and comparisons of different proxies showed that wing beat frequency is an important predictor of mass-corrected metabolic rate (e.g., 88% of metabolic rate explained; Darveau et al. 2005). In addition, due to the importance of color-based thermoregulation in ectotherms for reaching body temperatures that enable flight (Kalmus 1941), dark coloration could lead to a higher mobility and lower energetic requirements of adults, if the costs of melanization are compensated during larval development (e.g., via reduction of the body size of adults, Talloen et al. 2004).

Alternatively, instead of reducing maintenance and mobility costs, species may increase their energy uptake to compensate an investment into body size or melanin (Boggs and Freeman 2005, Boggs 2009). Differences in energy uptake among species are related to a broad spectrum of morphological, ecological and life-history traits (Tiple et al. 2009, Arrese and Soulages 2010, Ohgushi et al. 2012, Stevens et al. 2012, Pelisson et al. 2013). Thus, species that do not forage as adults (i.e., capital breeders) are often smaller, have shorter lives and produce less offspring than those that take up concurrent energy (i.e., income breeders), because they need to pay for dispersal and reproduction from their energy reserves (Tammaru and Haukojoa 1996, Stephens et al. 2009, Ohgushi et al. 2012). These ecological differences, which are conceptualized in the capital–income breeder continuum hypothesis, set up evolutionary contrasts that allow the classification of energy allocation strategies among species (Ohgushi et al. 2012, Stevens et al. 2012). However, in the absence of easily measured proxies for the mobility costs and energy uptake of species, energy allocation strategies have been studied for only a few species and mostly under laboratory conditions (Hill and Pierce 1989, Buckley 2008, Pelisson et al. 2013, Llndres et al. 2015). Moreover, their importance for species distribution and abundance remains unexplored (Tammaru and Haukojoa 1996, Stephens et al. 2009).

To exemplify the importance of the energy allocation strategies for determining the distribution and abundance of ectothermic species, we use butterflies as model taxon. Butterflies are popular among enthusiast and professional entomologists, which has resulted in a unique pool of ecological knowledge and long-term monitoring data on this group, especially for the European continent. Although the adult life stage comprises a rather small fraction of the total lifetime of individuals (Bink 1992; ~21% [median] including diapause), we consider only data on adult butterflies, because dispersal and reproduction are limited to the adult life stage and
because the adult morphology should be more strongly associated with the fitness of individuals (Boggs and Freeman 2005). To assess the energy allocation strategies of butterfly species associated with the main components of energy allocation, we propose two easily measured proxies: the wingbeat frequency as a proxy for mobility costs, assuming that species with a lower wingbeat frequency (higher flight efficiency) have lower mobility costs, and the propensity for nectar foraging based on in situ images of adult butterflies as a proxy for energy uptake.

Here, we address two main questions. First, we test whether traits associated with the main energy allocation strategies of species mediate the effects of morphological traits on distribution and abundance (Hypothesis 1). We do this by integrating current theoretical and empirical support for single effects among the considered variables into a generalized framework following the assumptions of trait-based theory (Fig. 1). If the effects of morphological traits on the distribution and abundance of species are generally mediated by energy allocation strategies, we expect that their direct effects will be weaker compared to indirect effects via mobility costs and energy uptake. Second, we test whether the energetic costs of morphological traits of species can be compensated by reducing mobility costs or increasing energy uptake during the adult life stage (Hypothesis 2). If the negative effects of morphological traits on the distributions and abundances of species differ depending on the abilities of species to compensate energetic costs, we expect that interactions between morphological traits and mobility costs negatively affect the distribution and abundance of species, whereas interactions between morphological traits and energy uptake will have a positive effect.

**Materials and Methods**

**Proxies for mobility costs and energy uptake**

As a proxy for the energetic costs of mobility, we measured the wingbeat frequency of 316 individuals of 102 butterfly species using high-speed camera footage taken during the years 2013–2017 at different sites in Central Europe (a total of 793,896 frames or 2,646 s; for details and an example film clip, see Video S1 and Appendix S1: Supporting Methods). Wingbeat frequencies of individuals in Hz were calculated as wingbeat counts of each scene divided by its length (in s). Subsequently, for each species, we averaged wingbeat frequencies across individuals (median, 3 individuals; minimum, 1 individual; maximum, 9 individuals). To integrate across the peak and normal mobility costs of a species, we averaged wingbeat frequencies during in situ and escape flight (Fig. 2c). When only normal or peak wingbeat frequencies were available for a species (i.e., for 1 and 43 species, respectively), we used values that were predicted based on the relationship between these two variables (Appendix S1: Fig. S2). Furthermore, while filming, we also recorded the ambient temperature to evaluate whether the wingbeat frequency of species was temperature dependent. However, the correlation between these two variables was not significant (Appendix S1: Fig. S3).

Adult butterflies are mainly generalist nectarivores (Günter and Rennwald 1991a:95–102 and 148–181). To obtain a proxy for the energy uptake of adult butterflies, we therefore assumed that nectar quantity rather than nectar quality is important. In other words, species that spend more time collecting nectar during a given time span should take up more energy than species that spend less time collecting nectar. This simplification is reasonable as sugar concentrations of flowers visited by butterflies are similar because of two important constraints. First, the sweetest nectar offers the highest reward for pollinators. Thus, competition between co-occurring flowering plants maximizes the sugar concentration of their nectar (Krenn 2010). Second, as an increase in sugar concentrations is associated with an increase in viscosity, the upper limit of the sugar concentration of flowers is defined by the “foraging” technique of their pollinators, which is active sucking, in the case of butterflies (Kim et al. 2011). Following an approach that has been successfully applied to extract data on geographical variation in phenotypic traits (Leighton et al. 2016), we counted how often individuals were observed collecting nectar on flowers based on the results of a Google Images search. To avoid potential bias of the access point, which could result from Google’s search algorithms, we used the international homepage (i.e., google.com) and searched for the scientific name of a butterfly species. Of the first 100 hits, only images of clearly identifiable and living adult individuals were used for further analyses (links are available from Dryad Digital Repository, Pinkert et al. 2020). We assigned each image a value of 1 or 0 depending on whether the individual was observed foraging or not (i.e., whether the proboscis was inside the flower or not), and a value of 0.5 if it sat on a flower but the proboscis was not visible. Hence, to avoid potential observer biases (e.g., the preference of the photographers for taking pictures of butterflies on flowers), butterflies that clearly only sat on flowers were not considered as foraging. Finally, we averaged these values for each species (Appendix S1: Supporting Methods and Fig. S4). A rarefaction analysis showed that standard deviations calculated for an increasing number of randomly sampled images of species remained constant at 0.04 for sample sizes above 32 images (Appendix S1: Supporting Methods and Fig. S4). This suggests that our results are not affected by differences among locations and conditions of these observations and, although we used all images sampled for further analyses, it indicates that a relatively small number of images are already sufficient to provide a robust estimate for the propensity of nectar foraging of a species. The reliability of our approach was further
confirmed by a positive relationship between image-based estimates and expert classifications of the nectar-foraging propensity of species ($P < 0.001$, $\rho = 0.31$, $n = 436$; for details and the comparison, see Appendix S1: Supporting Methods and Fig. S5). Furthermore, multiple regressions confirmed that wingbeat frequency negatively and that nectar foraging propensity positively affects the reproduction of species in terms of a higher number of eggs (data for 89 species taken from Bink [1992]; $R^2 = 0.30$; estimate $\pm$ SE: wingbeat $= -0.443 \pm 0.165$, $P < 0.01$; nectar foraging $= 0.332 \pm 0.069$, $P < 0.001$).

**Morphological traits**

Estimates of the color darkness, body size and wing size of a species were calculated based on scanned dorsal drawings of European butterfly species taken from Tolman and Lewington (2008). In our study, we considered only data for females because their investment into body size and color darkness should directly influence reproduction, whereas the morphology of males may be biased by sexual selection (Clutton-Brock and Parker 1992). However, note that both the body size and color darkness of butterfly species are highly positively correlated between sexes (Zeuss et al. 2014, 2017, Shelomi and Zeuss 2017). Color darkness and body volume data were taken from Zeuss et al. (2014, 2017). Specifically, we used the inverted average RGB (i.e., color lightness) of pixels of the basal third of the wings and the body as an estimate of the color darkness of a species (Zeuss et al. 2014, Stelbrink et al. 2019). Specifically, we used the sum of volumes of each pixel row of images of the body surface (Shelomi and Zeuss 2017, Zeuss et al. 2017; $\pi \times (1/2 \text{length of pixel row})^2 \times \text{pixel edge length in cm}$). In addition, we calculated the wing size of images as the number of pixels of the four wings $\times$ pixel area in cm$^2$. All functions used for the image analysis are provided in the R package png (Urbane 2013).

By comparing image-based estimates of body volume and wing area of species with data on the intra-specific variation in their wing span (data taken from Bink [1992] and Willner [2016]), we confirmed that both estimates are representative mean trait values (Appendix S1: Fig. S6). To evaluate the uncertainty that might result from intraspecific variation in size

---

**Fig. 1.** Generalized framework of predicted effects of morphological traits of species on their distribution and abundance via proxies for mobility costs and energy uptake. Examples for supported single effects are as follows: L1, Betts and Wootton (1988); L2, Talloen et al. (2004); L3, Tiple et al. (2009); L4, Corben (1983); L7, Betts and Wootton (1988); L8, Boggis and Freeman (2005); L9, Stevens et al. (2012); L12, L13, L14, Friess et al. (2017); L15, Brändle and Brandl (2001). These effects have been integrated into our framework in accordance with the main assumption of trait-based theory that components of the energy budget mediate the effects of morphological traits on the distribution and abundance of species. Arrows indicate the direction of putative causality as currently supported (solid lines) or hypothesized in the Introduction section (dashed lines). Specifically, we hypothesized that species compensate for the costs of morphological traits by reducing mobility costs (L6 or L7) or increasing energy uptake as adults (L3 or L5) or both. The costs of melanization might be either directly compensated during the adult life stage (L5, L6) or indirectly via the interaction between body size and allocation components (L3, L4, or L1 and L7), as an investment into melanin negatively affects larval growth (L2). A successful compensation should have a positive effect on species distribution and/or abundance (L8, L9, L10, or L11). Two arrows with opposing direction indicate unresolved causal relationships (L12). Avail., availability.
Intraspecific variation in wingbeat frequency

Butterfly phylogeny

Species traits

Phylogenetic signal

FIG. 2. Summary of the data on 102 European butterfly species that have been used in the study: (a) phylogeny, (b) morphological traits and proxies for the mobility costs and energy uptake of butterflies, (c) intraspecific variation in normal (black) and peak (orange) wingbeat frequencies (316 individuals, i.e., females and males are pooled), and (d) the phylogenetic signal in the presented traits of 102 European butterfly species. Trait values in panel b are centered on the overall mean of each trait and scaled to standard deviations, with red dots indicating relatively low and black dots indicating relatively high trait values. In panel c, values on the left indicate the number of individuals per species filmed. Traits in panels b and c are ordered according to the phylogeny. Horizontal bars in panel d indicate the strength of the phylogenetic signals of traits (Pagel’s lambda) calculated based on branch length from the phylogeny of all European butterfly species. All phylogenetic signals were significant at $P < 0.001$. Box plots in panel c show median values (solid black line in the center) with two whiskers extending from the front (first quantile) to the back of each box (third quantile). In the box plots, extreme data points that are more than 1.5 times the interquartile range outside the box are indicated by points. Copyrights for the icon of Lasiommata meara in panel c are held by S. Pinkert.
estimates, we calculated the results of the confirmatory path analysis that tested for indirect effects (Fig. 3, Model 2) 1,000 times using body volume and wing area estimates that were randomly drawn from a normal distribution (Chown and Gaston 2010) inside the species- and trait-specific range (i.e., the cube intraspecific variation in the wing span for body volume and the square for wing area). This analysis indicated that our
conclusions are robust to intraspecific variation in body and wing size (Appendix S1: Fig. S1). Standardized effect sizes of paths were generally higher for image-based estimates of mean trait values compared to randomly drawn size estimates (e.g., values measured for a single individual per species under different temperatures). Furthermore, using data on the annual mean temperature aggregated across the range of species, we confirm that the considered morphological traits are not affected by temperature (estimate ± SE: color darkness = 0.006 ± 0.017, P > 0.05; body size = 0.0123 ± 0.029, P > 0.05; wing size = −0.029 ± 0.020, P > 0.05; temperature data available online). That conclusions are robust to intraspecific variation in body

Distribution and abundance of species

Regional distributions (i.e., regional occupancy) were estimated based on gridded distribution data of species across Europe [in a grid of cells with a size of 50 km × 50 km, CGRS; data taken from Schweiger et al. (2014)]. For each species, regional distributions were calculated by dividing the number of grid cells in which it was present by the total number of grid cells (1,720 grid cells).

To calculate the local distribution and abundance of species (i.e., local occupancy and population density), we used survey data for butterfly species assessed as part of the Biodiversity Monitoring Switzerland during the years 2003–2016 (data available online). The monitoring scheme involved the counting of butterflies at 520 regularly placed sites (in a grid of cells with a size of 5 × 5 km) along transects of 2.5 km length. Transects were visited four to seven times each year during comparable weather conditions. Although regional and local distributions of species should be strongly related (Brändle and Brandl 2001), we also considered local distributions of species in our analysis to account for differences in the spectrum of regionally and locally available habitats that can result in negative distribution–abundance relationships (Gaston and Lawton 1990). Species abundances were calculated as the average number of individuals per occupied transect and year. Note that this abundance measure is not correlated with the number of generations per year (Appendix S1: Fig. S7).

Habitat availability

We were particularly interested in the importance of functional traits of species (i.e., intrinsic drivers) of their distribution and abundance. However, it is well known that the distribution and abundance of phytophagous insects is mainly driven by the availability of their habitat (Curtis et al. 2015, Friess et al. 2017). To account for the potential effect of habitat availability on the distribution and abundance of species, we used gridded distribution

Statistical analyses

The distributions of all variables were reviewed and transformed if necessary (for model residuals and histograms of variables see Appendix S1: Fig. S8–S9). To normalize the data, nectar-foraging propensity, habitat availability, local distribution, and regional distribution were logit-transformed, and wingbeat frequencies, body volume, color darkness, wing area, number of eggs, and local abundance were log−trans-formed. By assessing the phylogenetic signal of species traits based on the phylogeny of all European butterflies (Zeuss et al. 2014) using functions of the R package phytools (Revell 2017), we showed that wingbeat frequency, nectar-foraging propensity, and all morphological traits considered in the analyses carried a strong phylogenetic signal (Fig. 2d). To meet the general assumption of statistical tests that all data points are independent from each other, we therefore accounted for the phylogenetic relationship of species in all models (component models of piecewise structural equation models as well as single and multiple regressions) by fitting generalized least-squares models including a Brownian correlation structure with function of the R package nlme (Pinheiro et al. 2017).

We tested whether mobility costs and energy uptake mediate the effects of morphological traits on the distribution and abundance of species (Hypothesis 1) using confirmatory path analyses (Shipley 2004) as implemented in the R package piecewiseSEM (Lefcheck 2017). This approach allows us to fit a set of linear mixed-effects models in a single causal framework to test hypotheses about relationships of interacting variables and for evaluating the direct and indirect effects of predictor variables on the responses. Specifically, we fitted two main model sets as the basis for confirmatory path analyses (Fig. 3, Table 1; Appendix S1: Table S1). In the first path analysis, we tested for direct effects of morphological traits on the distribution and abundance of species. In the second path analysis, we tested for direct effects of morphological traits on mobility costs and energy uptake, and for direct effects of mobility costs and energy uptake on the distribution and abundance of species (Fig. 1). Both path analyses included a direct

6 https://www.worldclim.org/
7 www.biodiversitymonitoring.ch
Table 1. Summaries of piecewise structural equation models.

| Response       | Abundance_{CH} | Distribution_{CH} | Distribution_{EU} | Habitat availability_{CH} | Body size | Color darkness | Wing size | Nectar foraging | $R^2$ |
|----------------|----------------|-------------------|-------------------|--------------------------|-----------|----------------|-----------|-----------------|-------|
| Model 1        |                |                   |                   |                          |           |                |           |                 |       |
| Abundance_{CH} | +7.60*         |                   |                   |                          |           |                |           |                 | 0.28  |
| Distribution_{CH} | +5.99*         |                   |                   |                          |           |                |           |                 | 0.28  |
| Distribution_{EU} | +3.84*         |                   |                   |                          |           |                |           |                 | 0.35  |
| Body size      |                |                   |                   |                          |           |                |           |                 | 0.01  |
| Wing size      |                |                   |                   |                          |           |                |           |                 | 0.01  |
| Model 2        |                |                   |                   |                          |           |                |           |                 |       |
| Abundance_{CH} | +8.21*         |                   |                   |                          |           |                |           |                 | 0.37  |
| Distribution_{CH} | +5.81*         |                   |                   |                          |           |                |           |                 | 0.24  |
| Distribution_{EU} | +4.52*         |                   |                   |                          |           |                |           |                 | 0.35  |
| Nectar foraging|                |                   |                   |                          |           |                |           |                 | 0.31  |
| Wingbeat       |                |                   |                   |                          |           |                |           |                 | 0.77  |
| Body size      |                |                   |                   |                          |           |                |           |                 | 0.01  |
| Wing size      |                |                   |                   |                          |           |                |           |                 | 0.65  |

Notes: Standardized effect sizes ($z$ scores) of predictors and explained variance ($R^2$) of models that do not account and models that account for the phylogenetic relationship of species) from models that test for direct effects of morphological traits on the distribution and abundance of 102 European butterfly species (Fig. 3, Model 1) and indirect effects via proxies for mobility costs and energy uptake (Fig. 3, Model 2). Models correspond to the path diagrams in Fig. 2. The subscripts CH and EU refer to variables for Switzerland and Europe, respectively. *$P < 0.001$; †$P < 0.01$; ‡$P < 0.05$.

Effect of habitat availability on the local distributions of species and direct effects of local abundance on local distribution and vice versa.

Although most of the predicted relationships were significant for the model including mobility costs and energy uptake, Fisher’s C statistics indicated that some relevant paths were missing. Following Shipley (2004), we therefore added the most important and significant predictor variables (highest effect size) one at a time to the models and repeated the evaluation of the conditional independence claims until this criterion was met (Appendix S1: Table S2). Based on this model evaluation, three missing paths were added to the models: an effect of body size on local abundance, an effect of regional distribution on local abundance and an effect of wingbeat frequency on regional distribution. In a second step, least important and insignificant paths were removed one at a time. Wingbeat frequency and nectar-foraging propensity were added to the first path analysis (Fig. 3, Model 1) when calculating the Akaika information criterion (AIC) and AIC corrected for sample size (AIC$_c$; function sem.aic of the R package piecewiseSEM; Lefcheck 2017), to obtain a nested model structure that allows the comparison of the goodness of fit between both models. Multicollinearity among predictor variables was evaluated by calculating the variance inflation factor from variance-covariance matrices of phylogenetic generalized least-squares models (Zuur et al. 2009). For all our models, variance inflation factors smaller than 3 indicated minor collinearity among predictor variables (Appendix S1: Table S2).

To test whether species compensate an investment into body size and melanization by reducing their mobility costs or increasing energy uptake as adults (Hypothesis 2), we investigated the effects of interactions between morphological traits and components of the energy budget on the distribution and abundance of species using generalized least-squares models that included a Brownian correlation structure to account for the phylogenetic relatedness of species. We repeated the calculation of the models including our image-based estimate of energy uptake with the expert-based nectar-foraging classification and obtained similar results (Appendix S1: Table S3).

Results

Mediation of the effects of morphological traits on distribution and abundance

We tested our first hypothesis, that the effects of morphological traits on the distribution and abundance of species are mediated by energy allocation strategies, by fitting two different piecewise structural equation models that integrated the complex interdependencies of the considered morphological traits. In models that tested for direct effects, we found that none of the considered morphological traits had a significant effect on the distribution and abundance of species, except for a weak positive effect of color darkness on local distribution (Fig. 3, Model 1). In models that accounted for differences in species’ energy allocation strategies, however, all morphological traits significantly affected the distribution and abundance of species via wingbeat frequency and nectar-foraging propensity (Fig. 3, Model 2). In both models, local habitat availability positively affected local distribution, local distribution positively affected regional distribution, and regional distribution negatively affected local abundance (Fig. 3, Table 2). Furthermore, local distribution and abundance positively
affected each other. Component models in which we accounted for species’ energetic strategies explained 18% more of the variance in local distribution and abundance than models that tested for direct effects of morphological traits (Table 1).

In models that tested for indirect effects (i.e., that accounted for species’ energy allocation strategies), body size positively affected the wingbeat frequency and the nectar-foraging propensity of species (Fig. 3). Body size-controlled wing size strongly negatively affected the wingbeat frequency and the nectar-foraging propensity of species. Color darkness strongly positively affected the wingbeat frequency and weakly negatively affected the nectar-foraging propensity of species, but color darkness also strongly negatively affected body size. Thus, color darkness had, in addition, weak indirect negative effects on the wingbeat frequency and the nectar-foraging propensity of species via body size. Among the three considered morphological traits body size had the strongest total effects (i.e., the product of coefficients along an indirect path) on the local abundance and distribution (positive) and wing size had the strongest total effect on the regional distribution (negative, Appendix S1: Fig. S10).

Species with higher wingbeat frequencies generally had both lower local abundances and smaller regional distributions than species with lower wingbeat frequencies, and species with a higher nectar-foraging propensity had higher local abundances than species with a lower nectar-foraging propensity (Fig. 3). In addition to its indirect effects on the distribution and abundance of species, body size also had a negative direct effect on local abundance. The expected effects of nectar-foraging propensity and wingbeat frequency on local distribution and of nectar-foraging propensity on local abundance were not significant. Total effect sizes indicated that wingbeat frequency and nectar-foraging propensity were consistently among the most important predictors species’ distribution and abundance (Appendix S1: Fig. S10).

**Compensatory strategies of species**

We tested our second hypothesis, that species compensate an investment into body size and melanization by reducing their mobility costs or increasing energy uptake as adults, by evaluating interactions between morphological traits and mobility costs as well as energy uptake on the distribution and abundance of species. In single and multiple regressions, interactions between body size as well as wing size and wingbeat frequency negatively affected the distribution and abundance of species, while interactions between body size as well as wing size and nectar-foraging propensity had a positive effect. However, except for the effect of the interaction between color darkness and nectar-foraging propensity on local distribution, the effects of color darkness did not support the assumption that species compensate an

---

**Table 2. Summary of phylogenetic least-squares models that test for compensatory interactions.**

| Response     | Response and allocation components | Morphological trait | Single regressions | Multiple regressions |
|--------------|------------------------------------|--------------------|-------------------|---------------------|
| Abundance\textsubscript{CH} nectar foraging | body size | $-0.37 \pm 0.21$ | 0.083 | 0.10 | $-0.43 \pm 0.19$ | 0.028 | 0.23 |
| Abundance\textsubscript{CH} wingbeat | color darkness | $-0.17 \pm 0.29$ | 0.547 | 0.01 | $-0.13 \pm 0.03$ | $< 0.001$ | 0.17 |
| Abundance\textsubscript{CH} nectar foraging | wing size | $-0.61 \pm 0.36$ | 0.096 | 0.09 | $-0.10 \pm 0.05$ | 0.042 | 0.06 |
| Abundance\textsubscript{CH} nectar foraging | body size | $-0.10 \pm 0.05$ | 0.043 | 0.06 | $+0.95 \pm 0.41$ | $< 0.001$ | 0.022 |
| Abundance\textsubscript{CH} wingbeat | color darkness | $-0.45 \pm 0.26$ | 0.091 | 0.07 | $-1.11 \pm 0.44$ | $< 0.001$ | 0.013 |
| Abundance\textsubscript{CH} nectar foraging | wing size | $-0.33 \pm 0.04$ | 0.196 | 0.02 | $-0.04 \pm 0.04$ | 0.290 | 0.01 |
| Abundance\textsubscript{CH} nectar foraging | body size | $-0.04 \pm 0.04$ | 0.290 | 0.01 | $+0.09 \pm 0.07$ | 0.236 | 0.01 |

*Notes:* Coefficient estimates ($\pm SE$) and $P$ values of predictors as well as explained variance from single ($R^2$) and multiple ($R^2$) regression models that test for the effects of interactions between morphological traits and allocation components on the distribution and abundance of 102 European butterfly species. In multiple regressions, predictors with the highest $P$ value were removed stepwise until the remaining effects were significant at $P < 0.05$. Significant compensatory interactions ($P < 0.05$) are shown in boldface type. The subscripts CH and EU refer to variables calculated for Switzerland and Europe, respectively. Note that an investment into color darkness is compensated during larval development (Fig. 3, Model 2), so that, in adults, its interactions with allocation components are the reverse of what would be expected for a direct compensation via mobility costs and energy uptake.
investment into melanization directly by reducing wingbeat frequency or increasing nectar-foraging as adults (but see the indirect effects in Fig. 3). The effects of interactions between morphological traits and allocation components explained between 8% and 18% of the variance in the distribution and abundance of species in single regressions and between 18% and 23% of the variance in multiple regressions (Table 2).

**Discussion**

Our study aimed at integrating energy allocation strategies into trait-based models for understanding the physiological mechanisms underlying variation in the distribution and abundance of species. Using a generalized ecophysiological framework centered on mobility costs and energy uptake of butterfly species, we demonstrate that the energy allocation strategies associated with these physiological traits are of fundamental importance for mediating the effects of morphological traits on distribution and abundance. We show that most of the effects of morphological traits on species’ mobility costs and energy uptake reflect compensatory strategies. Thus, larger species generally have wider distributions and are more abundant than smaller species if they compensate their investment by reducing mobility costs or increasing energy uptake, whereas an investment into melanin is indirectly compensated via a reduction in body size during development (Fig. 1, Table 2). Consequently, the proxies for species’ energy uptake and mobility costs that accounted for these complex and in part contrasting effects of morphological traits were important first-order predictors of species population dynamics. Species with a low wing beat frequency and those with a high nectar-foraging propensity as adults were more abundant and had larger range sizes and both easily measured proxies of the components of the energy budget considerably improved predictions of species’ distribution and abundance.

In line with several previous studies that reported weak and insignificant size-abundance relationships for other ectothermic taxa (Blackburn et al. 1993, 2006, Friess et al. 2017), we show that body size does not directly affect the abundance of European butterfly species (Fig. 3, Model 1). By contrast, accounting for species’ energetic strategies revealed several important and in part contrasting effects of body size on species’ distribution and abundance (Fig. 3, Model 2). Thus, larger species generally have higher abundances and wider distributions if they compensate an investment into body size by reducing the mobility costs or enhancing energy uptake (Table 2). Integrating these two main components of the energy budget, furthermore established a direct negative effect of body size on the abundance of species that likely reflects the increase in maintenance costs associated with an increase in body size (not explicitly modeled as it lacks appropriate data; Brown et al. 2004, White et al. 2007). In the context of previous studies (Blackburn et al. 1993, 2006, Friess et al. 2017), our results thereby highlight that species’ energy compensation strategies largely explain the scatter in size-abundance relationships and that accounting for these strategies might be more important in ectotherms than in endotherms because of their comparatively low maintenance costs (Nagy et al. 1999).

Following the considerations for body size, darker colored species should have wider distributions and higher abundances if they compensate the energetic costs of melanization via mobility costs and energy uptake. Our results show that darker colored species have higher wingbeat frequencies and forage less (Fig. 3), resulting in lower abundances and smaller distributions (see Appendix S1: Table S10 for total effects). We thereby demonstrate that the costs of melanization are not compensated during the adult life stage. Instead, an investment into melanin during development seems to be partly compensated by a smaller size of adults (negative effect on larval growth, see also Talloen et al. [2004]), which ultimately reduced the mobility and maintenance costs of species (Fig. 3). This carry-over of the energetic costs of color darkness during larval development, to adults, and the trade-off between color darkness and body size suggests a major role of melanization for constraining the development and body size of ectothermic species. Our results stress the importance of incorporating these interdependencies for understanding the mechanisms underlying equivocally supported geographical patterns in the body size of ectotherms (Shelomi 2012, Zeuss et al. 2017). In addition, the finding that adults of darker colored species have generally higher wingbeat frequencies and forage less than lighter colored species (see direct effects in Fig. 3, Table 2), underlines the functional significance of melanin-based heat gain for the physiology of ectotherms (Talloen et al. 2004, Roff and Fairbairn 2013) as well as the need for integrating both color darkness and body size into biophysical models to improve forecasts of species’ responses to climate change (Buckley and Kingsolver 2019).

For dispersal and reproduction, adult insects rely to a varying degree on body fat allocated from concurrent energy uptake as adults (income breeders) and larval fat reserves (capital breeders; Boggs and Freeman 2005, Boggs 2009, Arrese and Soulages 2010). Therefore, mobility costs, which constitute the main fraction of the lifetime energy expenditure of ectothermic taxa (Full 1997, Nagy et al. 1999), and the propensity for concurrent foraging should represent important determinants of the distribution and abundance in insects. Our results indicate that larger or lighter colored butterfly species have lower wingbeat frequencies and higher nectar-foraging propensities, placing their energy allocation strategies at the income end of the capital–income-breeder continuum (Fig. S9). These species partly compensate the costs of an investment into body size and melanin (both traits have overall a negative effect on distribution and abundance) with an enhanced flying efficiency and
concurrent energy uptake as adults. This in turn positively effects their distribution and abundance both directly and indirectly via the dynamic distribution-abundance relationship (Fig. 3). However, despite differences in distribution and abundance between species with high and low mobility costs or energy uptake (capital vs. income breeders), it is important to note that these strategies can be similarly successful. For instance, community-wide analyses indicated that the foraging propensity of species is linked to differences in species life-histories including the timing (Tammaru and Haukioja 1996, Ohgushi et al. 2012, Pellissin et al. 2013) and length of periods of activity (Tammaru and Haukioja 1996, Stephens et al. 2009). We showed that the distribution and abundance of butterfly species is constrained by the availability of their habitat but modulated by differences in their energetic strategies of species (Fig. 3). Thus, together with the finding that species’ mobility costs and nectar-foraging propensity carried strong phylogenetic signals (Fig. 2; Appendix S1: Table 1), our results establish a link between species’ population dynamics and the evolution of energy allocation strategies that contribute to the partitioning of locally available resources among species through time.

Although we consider the presented model an important step towards a generalized ecophysiological framework that helps understanding and predicting the distribution and abundance of species, we are aware of two limitations. First, by using mean trait values of species we did not account for intraspecific variation. Such variation can increase the probability of false negative results and decrease the strength of the effects of morphological traits on mobility costs and energy uptake (Bolnick et al. 2011). We showed that intraspecific variation in morphological traits does not affect our conclusions (Appendix S1: Fig. S1), but it is, nevertheless, likely that the predictive power of the models will improve if morphological traits of individuals are directly measured at the respective locations and times. Second, although our framework can readily be extended, some allocation components of a species were not considered in our analysis as we lacked appropriate data. Thus, further studies may also include larval growth or larval energy uptake and not only the flying efficiency, but also the flying activity of species to improve the estimation of mobility costs.

CONCLUSIONS

In conclusion, our study supported the hypothesis that mobility costs and energy uptake mediate contrasting effects of morphological traits on the distribution and abundance of species and we demonstrate that these contrasting effects largely offset each other when the differences in species’ energy allocation strategies are not taken into account. We thereby exemplify that assuming direct effects of morphological traits on species’ distribution and abundance can lead to a critical underestimation of the functional significance of morphological traits and to false mechanistic conclusions. As from a physiological perspective there is nothing unique to European butterflies, our results highlight the general potential of easily measured proxies of species’ energy allocation strategies for predicting the population dynamics of ectothermic species. Thus, mobility costs of species may not only be assessed based on wingbeat frequencies of flying taxa, such as bees and flies (Corben 1983), but also based on the running speed of ground-dwelling taxa (Full 1997), such as carabid beetles and reptiles. Other proxies for the energy uptake of species may be obtained by assessing the duration of plant–animal interactions of nectarivores (Memmott et al. 2007), based on observational data and data from camera traps. These data are readily available for a broad spectrum of organisms and hence provide a promising alternative to the substantially cost- and time-intensive measurement of, for instance, field metabolic rates and energy time budgets. Therefore, we are convinced that the classification of species’ energy allocation strategies based on such easily measured proxies will facilitate rigorous assessments of the importance of the capital–income-breeder continuum for differences in species’ life histories and population dynamics and that its integration into mechanistic models (Kearney and Porter 2009, Buckley et al. 2010) will improve the accuracy of trait-based predictions of the distributions and population trends of species.

ACKNOWLEDGMENTS

We sincerely thank Susanne Fritz and Lauren Buckley for comments on an earlier version of the manuscript. We also thank Helga and Dietrich Wagler, Hermann-Josef Falkenhahn, Armin Six, and Lothar Feisil for classifying the propensity for nectar foraging of butterfly species based on their experience, and Dieter Schneider for species identification and counting nectar foraging individuals based on Google images. N. Friess was supported as a doctoral student by the Rudolf and Helene Glaser Foundation organized in the “Stifterverband für die deutsche Wissenschaft.” N. Friess and R. Brandl were partly supported by the Hessen State Ministry for Higher Education, Research and the Arts, Germany through the LOEWE priority project Nature 4.0 – Sensing Biodiversity. We acknowledge the Swiss Federal Office for the Environment (FOEN) and the National Data- and Information-Centre of the Swiss Flora (Info Flora) for the permission to use the data from their monitoring programs.

LITERATURE CITED

Angert, A. L., L. G. Crozier, L. J. Rissler, S. E. Gilman, J. J. Tewksbury, and A. J. Chunco. 2011. Do species’ traits predict recent shifts at expanding range edges? Ecology Letters 14:677–689.

Angilletta, M. J., B. S. Cooper, M. S. Schuler, and J. G. Boyles. 2010. The evolution of thermal physiology in endotherms. Frontiers in Bioscience E 2:861–881.

Arrese, E. L., and J. L. Soulages. 2010. Insect fat body: energy, metabolism, and regulation. Annual Review of Entomology 55:207–225.

Bartholomew, G. A., and T. M. Casey. 1978. Oxygen consumption of moths during rest, pre-flight warm-up, and flight in relation to body size and wing morphology. Journal of Experimental Biology 76:11–25.
Memmott, J., P. G. Craze, N. M. Waser, and M. V. Price. 2007. Global warming and the disruption of plant–pollinator interactions. Ecology Letters 10:710–717.
Nagy, K. A., I. A. Girard, and T. K. Brown. 1999. Energetics of free-ranging mammals, reptiles, and birds. Annual review of Nutrition 19:247–277.
Niven, J. E., and J. P. W. Scharlemann. 2005. Do insect metabolic rates at rest and during flight scale with body mass? Biology Letters 1:346–349.
Ohgushi, T., O. Schmitz, and R. D. Holt. 2012. Trait-mediated indirect interactions: ecological and evolutionary perspectives. Cambridge University Press, Cambridge, UK.
Péllisson, P.-F., M.-C. Bel-Venner, D. Giron, F. Menn, and S. Venner. 2013. From income to capital breeding: when diversified strategies sustain species coexistence. PLoS ONE 8:e76086.
Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, R Core Team. 2017. nlme: linear and nonlinear mixed effects models. R package version 3.1-313. CRAN.R-project.org/package=nlme.
Pinkert, S., R. Brandl, and D. Zeuss. 2016. Colour lightness of dragony, assemblages across North America and Europe. Ecography 40:1110–1117.
Pinkert, S., N. Friess, D. Zeuss, M. M. Gossner, R. Brandl, and S. Brunzel. 2020. Mobility costs and energy uptake mediate the effects of morphological traits on species’ distribution and abundance. Dryad Dataset. https://doi.org/10.5061/dryad.0k6dj9x5
Pinkert, S., and D. Zeuss. 2018. Thermal biology: melanin-based energy harvesting across the tree of life. Current Biology 28:887–889.
Revell, L. J. 2017. phytools: An R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution 3:217–233.
Roff, D. A., and D. J. Fairbairn. 2013. The costs of being dark: The genetic basis of melanism and its association with fitness-related traits in the sand cricket. Journal of Evolutionary Biology 26:1406–1416.
Schweiger, O., A. Harpke, M. Wiemers, and J. Settele. 2014. CLIMBER: Climatic niche characteristics of the butterflies in Europe. ZooKeys 367:65–84.
Shelomi, M. 2012. Where are we now? Bergmann’s rule sensu lato in insects. The American Naturalist 180:511–519.
Shelomi, M., and D. Zeuss. 2017. Bergmann’s and Allen’s rules in native European and Mediterranean Phasmatodea. Frontiers in Ecology and Evolution 5:25.
Shipley, B. 2004. Analysing the allometry of multiple interacting traits. Perspectives in Plant Ecology, Evolution and Systematics 6:235–241.
Stelbrink, P., S. Pinkert, S. Brunzel, J. Kerr, C. W. Wheat, R. Brandl, and D. Zeuss. 2019. Colour lightness of butterfly assemblages across North America and Europe. Scientific Reports 9:1760.
Stephens, P. A., I. L. Boyd, J. M. McNamara, and A. I. Houston. 2009. Capital breeding and income breeding: their meaning, measurement, and worth. Ecology 90:2057–2067.
Stevens, V. M., A. Trochet, H. van Dyck, J. Clobert, and M. Baguette. 2012. How is dispersal integrated in life histories: a quantitative analysis using butterflies. Ecology Letters 15:74–86.
Talloen, W., H. van Dyck, and L. Lens. 2004. The cost of melanization: Butterfly wing coloration under environmental stress. Evolution 58:360–366.
Tammarsu, T., and E. Haukioja. 1996. Capital breeders and income breeders among Lepidoptera: consequences to population dynamics. Oikos 77:561–564.
Tiple, A. D., A. M. Khurad, and R. L. H. Dennis. 2009. Adult butterfly feeding–nectar flower associations: Constraints of taxonomic affiliation, butterfly, and nectar flower morphology. Journal of Natural History 43:855–884.
Tolman, T., and R. Lewinton. 2008. Collins butterfly guide: the most complete field guide to the butterflies of Britain and Europe. Third edition. Harper Collins Publisher, London, UK.
True, J. R. 2003. Insect melanism: the molecules matter. Trends in Ecology & Evolution 18:640–647.
Urbanek, S. 2013. png: Read and write PNG images. R package version 0.1-7. CRAN.R-project.org/package=png.
Vainio, L., H. Hakkarainen, M. J. Rantala, and J. Sorvari. 2004. Individual variation in immune function in the ant *Formica exsecta*: Effects of the nest, body size and sex. Evolutionary Ecology 18:75–84.
Viole, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional! Oikos 116:882–892.
Wasserthal, L. T. 1975. The role of butterfly wings in regulation of body temperature. Journal of Insect Physiology 21:1921–1930.
White, E. P., S. K. M. Ernst, A. J. Kerkhoff, and B. J. Enquist. 2007. Relationships between body size and abundance in ecology. Trends in Ecology & Evolution 22:323–330.
Willner, W. 2016. Taschenlexikon der Schmetterlinge Europas. Quelle & Meyer, Wiesbeckheim, Germany.
Zeuss, D., R. Brandl, M. Brändle, C. Rahbek, and S. Brunzel. 2014. Global warming favours light-coloured insects in Europe. Nature Communications 5:4847.
Zeuss, D., S. Brunzel, and R. Brandl. 2017. Environmental drivers of voltinism and body size in insect assemblages across Europe. Global Ecology and Biogeography 26:154–165.
Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York, USA.

**Supporting Information**

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ccy.3121/suppinfo

**Data Availability Statement**

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.0k6dj9x5. These data sets include aggregated data for the butterflies of Switzerland and their host plants that were used under license for the current study, but restrictions apply to the availability of the raw distribution and abundance data (available at request from Biodiversity Monitoring Switzerland and Info Flora Database).