

Movements and flight morphology in the endangered Large Blue butterflies

Communication

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Abstract: Movements and flight morphology of the endangered Large Blue butterflies *Phengaris teleius* and *P. nausithous* in southern Poland were studied with mark-release-recapture surveys and GIS analyses. Most individuals moved relatively small distances (<40 metres) within their habitat patches. Distances covered by both species were positively related to season progression and wing length, and negatively related to body mass. *P. teleius* movement distances slightly exceeded those of *P. nausithous*. In addition, females moved longer distances than males, although the difference was significant only in *P. teleius*. Morphological traits appeared to be good indicators of the inter-specific and inter-sexual differences in mobility. While *P. teleius* individuals were heavier than *P. nausithous* ones, they had considerably longer wings, which may explain longer movements in the former species. Similarly, females were heavier than males in both species, but they invested more in wing size, which is likely to compensate for the negative impact of body mass on movement distances. Our results indicate that combination of GIS analysis of movement distances recorded with mark-release-recapture methods and morphometric measurements taken in field during non-lethal handling of captured individuals proved useful for studying the mobility potential of the endangered insect species.

Keywords: *Dispersal • Maculinea • Metapopulation • Mobility • Morphometric measurements*

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1. Introduction

In light of global biodiversity loss, understanding factors affecting animal mobility has grown in importance, due to many species living in increasingly fragmented landscapes [1-3]. Higher mobility increases the probability of colonisation of vacant habitat patches as well as the chances of rescue effects for declining local populations, and thus enhances viability of entire metapopulations [1]. In turn, information on within-patch movements offers insight into space and resource use by individuals living in local populations [4,5]. It is also

believed that within-patch mobility may be useful for assessing potential for inter-patch dispersal [4,6].

In recent years, growing attention has been given to heterogeneity in mobility among individuals and how it is affected by morphological traits. Studies on butterflies indicate that variation in individual mobility, reflected by flight speed and acceleration capacity, can be related to differences in certain morphological parameters, particularly body mass and wing loading [7,8]. Furthermore, it has been found that individuals from populations that were newly established through colonisation events are larger and have relatively

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longer wings than those from more resident populations [9–11]. Similarly, butterflies living in highly fragmented landscapes - where the probability of reaching other habitat patches is low - are characterised by shorter wings and lower dispersal potential than those living in more continuous landscapes [12]. Increasing habitat fragmentation may also bring changes in relative investment in various body parts [13]. However, almost all the aforementioned and related studies assessed dispersal potential indirectly (e.g. through flight speed or acceleration capacity). What is lacking is knowledge of relationships between morphological traits and real distances covered by individuals [8].

Profound knowledge of individual mobility is especially valuable in the case of endangered species occurring in highly fragmented landscapes. In Europe, insects inhabiting semi-natural grasslands are among the most endangered animals [14,15]. Butterflies of the genus *Phengaris* (= *Maculinea*) are regarded as sensitive indicators of grassland biodiversity and as umbrella species, the conservation of which is likely to enhance numerous other co-occurring species in their habitats [16,17]. They have a highly specialised myrmecophilous lifestyle and depend on two crucial resources: specific foodplants and *Myrmica* host ants, the colonies of which are parasitised by *Phengaris* larvae [16,18].

In the present study we examined within-patch movements of two Large Blue butterflies: *P. teleius* (Bergsträsser, 1779) and *P. nausithous* (Bergsträsser, 1779), in relation to their morphological traits. In particular, we were interested in (1) determining within-patch movement distances covered by both species occurring sympatrically in the same habitats, (2) assessing inter-sexual differences in their movements, and (3) evaluating if morphological traits may explain variation in movement distances among individuals.

2. Experimental Procedures

2.1 Field sampling

The study was carried out in a wet meadow complex in Kraków, southern Poland, where large metapopulations of *P. teleius* and *P. nausithous* occupy patches of their *Sanguisorba officinalis* foodplant [19]. Three foodplant patches were chosen for intensive mark-release-recapture surveys conducted throughout the adult flight period from early July till mid August of 2002–2004 [20]. Patch K17 was the largest (8.77 ha; maximal dimension: 500 m) and surrounded by built-up areas, high reeds and forest fragments. The two smaller patches (K18: 1.06 ha; max. dimension: 180 m; K9: 0.65 ha; max. dimension 90 m) were located close to each other

and were surrounded mostly by meadows without *S. officinalis* and high reeds. A more detailed description of the study sites can be found elsewhere [20,21]. Patch K9 was investigated only in 2003. Captured butterflies were marked with individual numbers written on their hind wings and immediately released. The geographic position of each capture was recorded with Garmin 12 XL GPS units, allowing ca. 3 m precision. Distances covered by the butterflies were calculated as straight lines between consecutive capture points. Only the distance between the first and the second capture was analyzed to avoid pseudoreplication.

The wing length, body mass and thorax width of recaptured individuals were measured directly in the field. Wing length was defined as the longest dimension of the forewing, *i.e.* from its basis to the tip, and it was measured to the nearest 0.5 mm with specially adapted millimeter paper scales. Thorax width was measured using a Mitutoyo 7313 pressure-sensitive thickness gauge with 0.01 mm precision. Following these measurements, the butterflies were placed in small bags and weighed with an Acculab PP2060D balance to the nearest 1 mg. However, it should be mentioned that sample size marginally differed among the three traits as several butterflies escaped while measurements were taken and, additionally, we sometimes had to abandon recording thorax width in order to maintain a constant capture effort during periods of high butterfly abundance.

2.2 Statistical analysis

A general linear mixed model (GLMM) was used to test the effects of species and sex on butterfly movement distances. The season progression (expressed as the number of days from July 1st) and time between captures were included in the model as continuous covariates. In the first step, the model was built with all the main effects and interaction terms, including year and patch ID as random factors. Patch ID had to be nested in year as patch K9 as surveyed only in 2003. In the final model all the main effects and significant interactions were retained. The distributions of movement distances were highly positively skewed and ln-transformation was applied to achieve their normality [22,23].

GLMMs were also applied to test the effects of butterfly morphology on distances covered by individual butterflies. The models were built separately for each trait: body mass, wing length and thorax width. In each case they included the effects of species, sex, season progression, time between captures and interaction terms; nonsignificant interactions were again removed from final models. In the models for wing length and thorax width, body

mass was used as a covariate to control for its effect. As previously, year and patch ID nested within year were assigned as random factors.

Finally, in order to evaluate inter-specific and inter-sexual differences in relative investment in the investigated morphological traits, we built three further GLMMs with body mass, wing length, and thorax width as dependent variables. The two latter models, apart from the effects of species and sex as well as their interaction, also included body mass as a covariate to account for possible allometries. All the statistical analyses were performed using JMP 8 software (SAS 2006).

3. Results

The distances covered by both species were short relative to patch dimensions. The majority of movements were below 40 m, and the maximum movement distances - recorded at patch K17 - were 423 m for *P. teleius* and 515 m for *P. nausithous*. There was a clear effect of species, with longer distances being covered by *P. teleius* individuals (Table 1). Apart from this, movement distances increased significantly with season progression, although the increase was rather gradual (slope \pm SE: 0.011 \pm 0.003). The main effects were modified by the significant interaction between species and gender (Table 1). Females of *P. teleius* moved

longer distances than males, while for *P. nausithous* the inter-sexual difference was not significant (Figure 1).

The investigated morphological traits were positively correlated with one another (Table 2), but body mass and wing length had opposite effects on distances covered by butterflies. The GLMMs applied for testing the effects of morphological traits (Table 3) explained 20% and 15% of the variance in individual movement distances in the case of body mass and wing length respectively, but only 5% in the case of thorax width. After controlling for

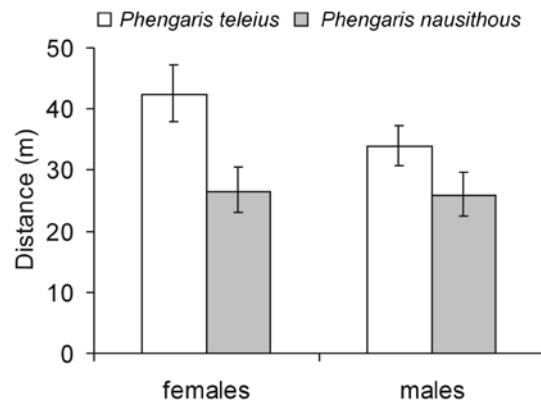


Figure 1. Within-patch movement distances (mean values with 95% confidence intervals) of *Phengaris teleius* and *P. nausithous*.

Effect	df	F	P
Species	1, 928.5	9.712	0.002
Sex	1, 1316	1.831	0.176
Season progression	1, 1207	10.449	0.001
Time span between captures	1, 1221	3.519	0.061
Interaction: species*sex	1, 1192	4.228	0.041
Random effects	estimate (SE)	z	P
Year	0.003 (0.023)	0.13	0.897
Site(year)	0.034 (0.008)	4.25	<0.001

Table 1. Results of the general linear mixed model (GLMM) analysis of factors affecting within-patch movement distances covered by *Phengaris teleius* ($n=373$ females and $n=457$ males) and *P. nausithous* ($n=230$ females and $n=265$ males), (total $n=1325$ butterflies).

Trait	Body mass	Wing length	Thorax width
Body mass	---	0.432 *** (312)	0.187 * (142)
Wing length	0.335 *** (240)	---	0.455 *** (146)
Thorax width	0.131 n.s. (131)	0.410 *** (136)	---

Table 2. Matrix of Pearson's correlation coefficients among the investigated morphological traits of *Phengaris teleius* (in top-right half) and *P. nausithous*. (in bottom-left half). Sample sizes are given in parentheses. Significance levels: *** - $P<0.001$; * - $P<0.05$; n.s. - non-significant.

the effects of species and sex, we found that movement distances were negatively related to body mass (slope ± SE: -0.006 ± 0.002 , $n=552$ individuals; Table 3, Figure 2a) and positively to wing length (slope ± SE = 0.113 ± 0.029 , $n=552$ individuals; Table 3, Figure 2b). In turn, thorax width had no apparent effect on the distances covered by butterflies (slope ± SE = 0.091 ± 0.162 , $n=273$ individuals; Table 3).

The results concerning inter-specific and inter-sexual differences in morphology are presented in Table 4. We found that *P. teleius* adults were significantly heavier than *P. nausithous*, and females were significantly heavier than males regardless of the species. Even with the effect of body mass accounted for, *P. teleius* had relatively longer wings and wider thoraxes than *P. nausithous*, whereas females surpassed males in wing length but not in thorax width (Figure 3).

4. Discussion

Our results showed relatively low within-patch movement of *Phengaris* butterflies, which is in fact characteristic of most Lycaenidae [7]. Most distances were only a few tens of meters and, particularly at the largest of the investigated patches, were much shorter than the patch dimensions. This supports the hypothesis that *Phengaris* butterflies do not move freely within their habitat patches, instead tending to establish home ranges [24,25].

The analysis also revealed that despite occurring sympatrically in the same habitats, *P. teleius* and *P. nausithous* differ in within-patch mobility, with the former species covering longer distances. This indicates that a single *P. teleius* individual utilises more space within a

habitat patch than a single *P. nausithous*. Consequently, while setting conservation targets concerning the size of habitat patches, it is advisable to prioritise *P. teleius* requirements, as patches large enough for this species should also be suitable for *P. nausithous*. Stricter spatial requirements may be responsible for the rarity of *P. teleius* relative to *P. nausithous* in recent decades in many regions of Central and Western Europe [15,26,27],

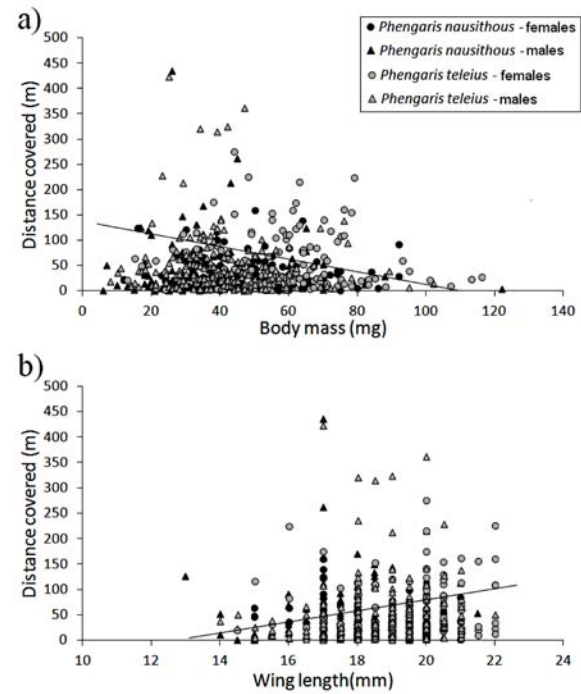


Figure 2. The effect of (a) body mass and (b) wing length on distances covered by *Phengaris* butterflies. The regression line is fitted to all data points (regardless of butterfly species and sex).

Effect	Distances (Body weight)			Distances (Wing length)			Distances (Thorax width)		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Body mass	1, 546	4.421	0.036	1, 544	10.080	0.002	1, 266	1.732	0.189
Wing length	-	-	-	1, 544	12.368	<0.001	-	-	-
Thorax width	-	-	-	-	-	-	1, 266	0.259	0.622
Species	1, 543	16.745	<0.001	1, 520	9.095	0.004	1, 266	8.437	0.004
Sex	1, 542	4.222	0.040	1, 542	2.903	0.089	1, 266	4.336	0.038
Season progression	1, 546	7.037	0.008	1, 540	7.990	0.005	1, 266	1.928	0.166
Time span between captures	1, 546	2.636	0.105	1, 544	2.342	0.127	1, 266	0.154	0.695
Random effects	estimate (SE)	<i>z</i>	<i>P</i>	estimate (SE)	<i>z</i>	<i>P</i>	estimate (SE)	<i>z</i>	<i>P</i>
Year	0.448(0.582)	0.770	0.441	0.510(269)	1.288	0.198	not estimated	-	-
Site(year)	0.983(0.474)	2.074	0.038	0.201(156)	1.896	0.058	not estimated	-	-

Table 3. The final general linear mixed models for the effects of morphological traits (in bold) on the distances covered by butterflies; the interaction between species and sex was nonsignificant in all cases. The effect of body mass was included in models for wing length and thorax width to control for allometry. Other potentially confounding factors were included in all models.

despite much higher host ant specificity of the latter species [18].

Interestingly, a recent metapopulation-scale analysis of dispersal in *Phengaris* butterflies occurring sympatrically in the Czech Republic showed considerably higher emigration rate and longer inter-patch movements in *P. nausithous* compared to *P. teleius* [28]. Although it is tempting to interpret the discrepancy in the findings of the above study and the present one as a manifestation of differences in mobility between the two study areas, in reality the patterns of higher within-patch mobility in *P. teleius* and higher inter-patch dispersal in *P. nausithous* appear fairly consistent (see review in [29]). This suggests that there is no direct relationship between the levels of within-patch mobility and inter-patch dispersal of different species.

By contrast, the inter-sexual differences in mobility are concordant for both intra- and inter-site movements (this study; [28]). Higher mobility of females has been reported in many insects [5,30–32] and seems related to oviposition behaviour. Laying eggs in different fragments of a habitat patch or in different patches helps to maximise offspring survival, and thus female fitness, through risk spreading [2]. Distribution of butterfly males within a habitat patch is usually affected by the microdistribution and density of freshly emerged (receptive) females [33,34]. Since the females emerge in specific sites the distribution of males may be constrained to these sites, which may in turn result in their lower flight distances. The increase of movement distances with season progression recorded in our study may be explained in a similar way. Habitat quality is likely to deteriorate toward the end of the season—in particular, this may refer to the quality of foodplants for ovipositing females.

Two of the investigated morphological traits proved useful in understanding within-patch mobility potential. While body mass, wing length and thorax width were positively correlated with one another, they had different impacts on distances covered by butterflies. Movement distances were negatively related to body mass and positively to wing length. The same pattern has been recorded in several butterfly species [7,11]. In turn,

even though the thorax houses flight muscles [35,36], and its mass or volume positively correlated with flight performance in other butterflies [8,35,37], it had no influence on the movement distances of *Phengaris* adults in our study.

Body mass and wing length appeared to be good indicators not only of individual variability, but also of

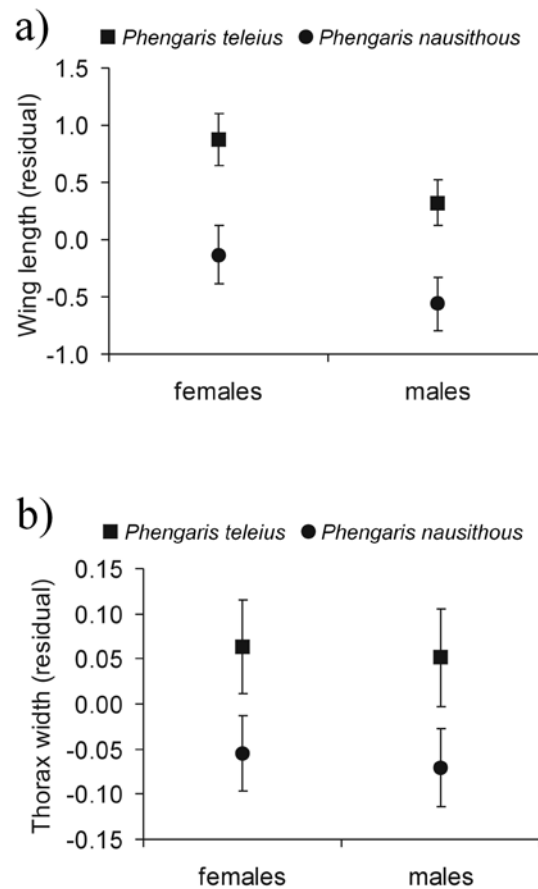


Figure 3. Inter-specific and inter-sexual differences in (a) wing length and (b) thorax width of the investigated butterflies. Values shown (means with 95% confidence intervals) represent residuals not explained by the allometric relationship with body mass.

Trait	<i>P. teleius</i>		<i>P. nausithous</i>		Inter-specific difference		Inter-sexual difference	
	females	males	females	males	F	P	F	P
body mass [mg]	56.1±1.6 (133)	40.7±1.2 (179)	50.9±1.6 (109)	36.9±1.4 (133)	9.856	0.002	104.694	< 0.001
wing length [mm]	19.5±0.13 (141)	18.8±0.11 (192)	18.4±0.12 (112)	17.7±0.13 (138)	60.290	<0.001	4.841	0.028
thorax width [mm]	2.13±0.04 (61)	2.07±0.03 (85)	2.00±0.05 (71)	1.89±0.05 (66)	10.991	0.001	0.928	0.336

Table 4. Morphological characteristics of *Phengaris teleius* and *P. nausithous*. Mean values with SE are given, together with sample sizes in parentheses. The results of the general linear mixed models (GLMMs) for the effects of species and sex are also presented; the interaction between species and sex was nonsignificant in all cases. The effect of body mass was controlled for in the models for wing length and thorax width.

the inter-specific and inter-sexual differences in mobility. Despite *P. teleius* being heavier than *P. nausithous* the former had relatively longer wings, which may explain its longer movement distances. Similarly, females in both species were heavier than males, but they invested disproportionately more in wing size, which compensates for the negative impact of body mass on the distances covered.

Since getting direct estimates of butterfly mobility is a laborious task [38], there has been growing interest in finding morphological traits that could serve as proxies for dispersal ability [39,40]. The results of our study indicate that body mass and wing length are promising traits in this respect, although their predictive powers were relatively low, which is a common problem for most proxies of mobility [39]. Nevertheless, while body mass and wing length can provide only general information about butterfly movement distances, this can be enough for many purposes, e.g. for inter-specific comparisons in order to set conservation priorities. Therefore, a combination of GIS-based assessment of movement distances with the analysis of morphological traits measured in the field as applied in the present study provides a useful tool for studying

butterfly mobility. Incorporating body mass and wing size measurements into mark-release-recapture surveys is particularly recommendable when dealing with endangered species since these measurements can be taken without killing or prolonged handling of the study organisms [37].

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