

Emigration propensity and flight performance are decoupled in a butterfly

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Abstract. Dispersal, defined as any movements potentially leading to gene flow, is a major process driving a species' capacity to cope with human-induced environmental modifications. However, the dispersal process is multi-causal, which currently hinders predictions regarding a species' resilience to global change. We used a multifaceted approach to disentangle the relative importance of a suite of dispersal-related factors in the butterfly *Lycaena tityrus*, including condition- (morphology and behavior) and context- (environmental) dependent factors. Experiments were conducted at an experimental platform dedicated to study dispersal, the Metatron, to record emigration propensity in two-patch experimental metapopulations under different environmental conditions. The butterflies' individual condition was subsequently assessed in the laboratory. Individual condition did not generally influence emigration propensity. We detected a significant sex bias in emigration propensity, being generally higher in females than in males, but in a context-dependent manner. The environmental context affected emigration propensity, which was higher when habitat quality was poor. Our results show that emigration is not random in *L. tityrus*, but is rather an active process triggered by sex and habitat quality. Our main finding was that individual condition, and particularly flight ability measured by a performance test, was not related to emigration propensity in experimental metapopulations. Our results may have important implications for forecasting future species distributions, as deteriorating environmental contexts are likely to increase emigration whatever the individual condition is.

Key words: climate change; condition; context dependence; dispersal; flight ability; *Lycaena tityrus*; Metapopulation; Metatron; movement.

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INTRODUCTION

Dispersal, often defined as any movements potentially leading to gene flow (Ronce 2007), is a complex process serving different functions and involving a variety of underlying mechanisms (Bowler and Benton 2005, Bonte et al. 2012, Matthysen 2012). The multi-causality of

dispersal has been fully appreciated in recent years (reviewed by Matthysen 2012), suggesting that complex interactions between several factors influence the dispersal process (Skórka et al. 2013, Legrand et al. 2015). As a next step, it seems important to disentangle the relative importance of the multiple factors relevant to dispersal, including individual condition (e.g.,

morphology and behavior) and the environmental context (e.g., habitat quality and weather; Legrand et al. 2015, Turlure et al. 2016). Also, growing evidence indicates that dispersal is not a fixed but a highly plastic trait (Ronce 2007). In invertebrates, for instance, flight behavior is influenced by food availability (Saastamoinen et al. 2010) and weather conditions (Niitepõld et al. 2009). Consequently, organisms may collect information on their current environment, which may feed back on their dispersal decision (Cote and Clobert 2007, Clobert et al. 2009, Baguette et al. 2011, Nowicki et al. 2014).

Dispersal is of crucial importance for ecological and evolutionary processes, ranging from metapopulation dynamics through metacommunity regulation to gene flow and speciation (Clobert et al. 2012). Dispersal also is of utmost importance in driving a species' capacity to respond to human-induced global change like climate change or habitat loss and fragmentation (Cote and Clobert 2007, Travis 2013). Persistence under changing conditions requires to either stay and adapt to the new conditions or to leave by moving along with the waves of change (Berg et al. 2010). In the latter case, dispersal is a key process allowing individuals to track their shifting climate niche (resulting in species range shifts; Warren et al. 2001, Hickling et al. 2006) or to maintain metapopulation connectivity (Baguette et al. 2013).

Within this framework, we here use a multifaceted approach to disentangle the relative importance of factors potentially affecting dispersal, including both individual condition (morphology and flight performance) and environmental context. As a study organism, we used the Sooty Copper butterfly *Lycaena tityrus*, a currently northward expanding species (Brunzel et al. 2008, Settele et al. 2008), rendering the investigation of its movement drivers particularly interesting in the current era of climate change. We first examined the influence of different environmental factors on the first step of the dispersal process, that is, the propensity to leave a habitat patch (emigration propensity; see Bonte et al. 2012 for a thorough description of dispersal as a three-step process). In recent studies on butterflies, environmental conditions have been shown to have a strong influence on emigration and dispersal rates. Habitat quality and weather conditions are especially likely to

prevail over the individual phenotype in butterflies' dispersal decisions (Cormont et al. 2011, Legrand et al. 2015, Kuussaari et al. 2016). We used the Metatron, a unique experimental platform designed to study dispersal in terrestrial organisms in experimental metapopulations (Legrand 2012). Second, we measured flight performance (here: time in flight under stress) to examine connections between emigration propensity under semi-natural conditions and physiological flight performance under laboratory conditions (Ducatez et al. 2012, Legrand et al. 2015). Third, we assessed individual variation in several morphological parameters (e.g., thorax–abdomen ratio, wing loading, and fat content) that may be associated with movement ability (Skórka et al. 2013, Legrand et al. 2016). Note that morphological differences may have important consequences for flight performance (Arnold 1983, Gilchrist 1990, Berwaerts et al. 2002), and even for dispersal and colonization success in butterflies (Hill et al. 1999, Sekar 2012). For instance, sexes may differ in flight or dispersal ability / behavior due to differential selection pressures or strategies (Gilchrist 1990, Berwaerts et al. 2002, Ducatez et al. 2014). Males often show traits associated with increased flight ability and have been shown to be more active than females in many butterfly species (Berwaerts et al. 2002, 2008, Ducatez et al. 2014). Nevertheless, females could be the more dispersive sex (Fischer et al. 1999) as (1) single mated females are, in contrast to males, able to found a new population; and (2) females may emigrate more readily to escape from male harassment or as a risk-spreading strategy by distributing their eggs over a wider area (Hill et al. 1999, Hopper 1999, Trochet et al. 2013).

The main aim of this study was to disentangle the relative importance of individual condition versus environmental context in shaping dispersal decisions. In particular, we test the following hypotheses: (1) Context-dependent variables are better predictors for dispersal than condition-dependent variables. Specifically, emigration rates will increase if habitat quality is poor (Cormont et al. 2011, Legrand et al. 2015, Kuussaari et al. 2016); (2) condition-dependent factors (e.g., morphology) are related to flight performance rather than emigration propensity; (3) sexes differ in both flight performance and dispersal propensity, with males having a better flight

performance (related to morphology) while females have a higher dispersal propensity (risk-spreading strategy; Hill et al. 1999, Hopper 1999, Trochet et al. 2013).

METHODS

Study organism

Lycaena tityrus (Poda, 1761) is a widespread temperate-zone butterfly ranging from Western Europe to Central Asia (Ebert and Rennwald 1991). This species is currently expanding its range toward higher latitudes and altitudes, which is assumed to be largely driven by anthropogenic climate change (Brunzel et al. 2008, Settele et al. 2008). The species is bivoltine with two discrete generations per year in most parts of its range, although populations with one or three generations per year occur. Overwintering takes place as half-grown larvae. The principal larval host plant is *Rumex acetosa* L. (Polygonaceae), but several congeneric *Rumex* species are utilized as well (Ebert and Rennwald 1991, Tolman and Lewington 1998, Settele et al. 2008). Adults are nectar feeders (Ebert and Rennwald 1991). For the following experiments, a total of 35 freshly eclosed, mated females from a bivoltine German population, located within the core distribution area (vicinity of Greifswald, northeastern Germany; 54°02' N, 13°26' E), were caught in June 2015. Wild-caught females were transferred to a climate chamber at Greifswald University for egg laying.

Animal rearing

Caught females were kept at 26°C, 60% relative humidity, and a L18:D6 photoperiod. For oviposition, females were placed separately in translucent 1-L plastic pots covered with gauze and were provided with *Rumex acetosa* (oviposition substrate), fresh flowers, water, and a highly concentrated sucrose solution (for adult feeding). Deposited eggs were collected daily and transferred, separated by female, to small plastic boxes and kept under the same conditions used for oviposition. After hatching, larvae were placed in groups of 10–15 individuals in larger, transparent plastic boxes (500 mL), containing moistened filter paper and fresh cuttings of *R. acetosa* in ample supply. Boxes were checked daily, and larvae were supplied with fresh food as necessary. Larval time was on average 15.5 ± 0.3 d (see Fischer

and Fiedler 2000a for more information on life-history data for *L. tityrus*). Resulting pupae were transferred to a climate cabinet set to 15°C (60% r.h., L18:D6) in order to retard further development (pupal time at 15°C is ~26 d). Once most larvae had pupated, pupae were transferred to the Station for Theoretical and Experimental Ecology (SETE) of the CNRS in Ariège, southwestern France. There, pupae were randomly divided into three groups and also initially kept at 15°C. In total, pupae were kept at 15°C for about 3 weeks. Three days before the start of the respective experiment (see *Metatron setup and experimental design*), pupae were transferred to warmer conditions (26–28°C) to facilitate quick and synchronized adult eclosion. After adult eclosion, butterflies were individually marked by writing a number on their left hindwing using a water-proof felt-tip pen. Sexes were kept separately until the start of experiments. Butterflies were collected over three eclosion days to reach sufficiently high numbers, being fed with flowers and a highly concentrated sucrose solution. Consequently, butterflies were 1–3 d old upon their release into the Metatron (see *Metatron setup and experimental design*).

Metatron setup and experimental design

The Metatron is an experimental platform consisting of interconnected mesh cages (patches) operated by the Station for Theoretical and Experimental Ecology (SETE) of the CNRS (Fig. 1). It allows for the manipulation of spatial and environmental factors in a semi-natural environment (Legrand 2012). Each cage is 200 m³ (10 × 10 × 2 m) large and is covered by insect-proof gauze. The ground within the cages is covered by natural vegetation. We carried out three experiments in the Metatron as outlined below. Each experiment involved two-patch experimental metapopulations, consisting of a departure and an arrival cage, connected by a single, S-shaped corridor (19 m long). To start the experiments, butterflies were released into the departure cage, in which they could either stay or which they could leave through the corridor leading to the arrival cage. Thereafter, butterfly positions were monitored through several recapture sessions. To allow for an appropriate discrimination between dispersers and resident individuals, corridors were designed to be challenging as indicated by corridor entries

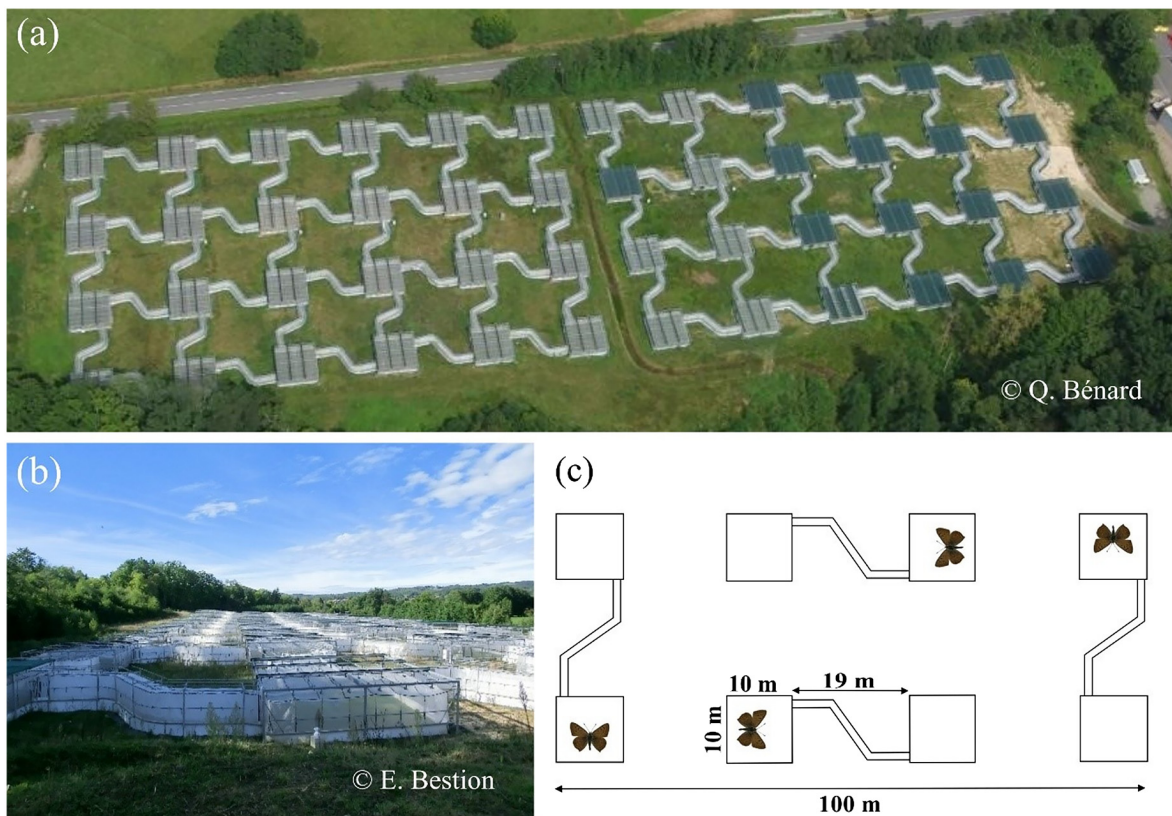


Fig. 1. (a) Aerial photograph of the Metatron (photograph taken by Quentin Bénard). Each Metatron cage is 200 m^3 ($10 \times 10 \times 2 \text{ m}$), fenced by tarps near the ground and an entomological net above. The cages are connected by 19 m long, S-shaped narrow corridors. The experiments were performed on the right-hand cages of the photograph. (b) Side view photograph of cages and corridors (photograph taken by Elvire Bestion). (c) Experimental design of experiment 3. We released 447 butterflies into four departure cages (butterfly pictures on the scheme) with different treatments, each connected to an initially empty arrival cage with beneficial conditions.

representing $<2\%$ of the total vertical surface area of patches (Legrand 2012). Moreover, the S-shape of the corridor prevented dispersing butterflies to see the arrival cage. Emigration propensity was scored as the number of butterflies leaving the departure cage, that is, being re-captured either in the arrival cage or corridor at least once. The number of repeated dispersers, that is, butterflies moving back and forth between the cages more than once, was low ($\sim 2\%$ of all butterflies). The vegetation within both cages and the corridors was cut (turf height 10 cm) prior to the start of experiments to allow for the manipulation of host and nectar-plant availability.

Throughout all experiments, arrival cages had identical conditions with resources and sunny conditions being available, while no resources were

available within the corridors. In the first two experiments, we tested the effect of one environmental factor each, by using four cages to create 2 two-patch metapopulations per experiment. Hence, one replicate per treatment was used. In the third experiment, we investigated both environmental factors to test for additive / interactive effects. Here, we used a total of eight cages, that is, 4 two-patch metapopulations (Fig. 1c). In experiment 1, we exclusively manipulated resource availability, that is, one of the departure cages entailed 25 pots with flowering nectar plants and additionally 20 pots with host plants, while the other entailed only a very limited number of flowering nectar plants (four pots, no access to host plants). All cages were exposed to full sunlight (sunny), conditions suitable for high flight activity.

In experiment 2, we exclusively manipulated solar radiation. Here, individuals in both departure cages had access to an equal though limited number of flowering nectar plants (eight pots, no access to host plants). One departure cage provided sunny and the other one shady and therefore cooler conditions. Shady conditions were achieved through closing motor-driven shutters positioned above the cages (Legrand 2012).

In experiment 3, we manipulated both resource availability and solar radiation. Two of the departure cages contained resources (25 pots with flowering nectar plants and 20 pots with host plants), while the other two entailed only a limited number of flowering nectar plants (see *Experiment 1*; hereafter referred to as “no resources” for simplicity). Per resource type, one cage provided sunny and the other one shady conditions. Consequently, we had four types of departure cages: (1) resources and sun, (2) resources and shade, (3) no resources and sun, and (4) no resources and shade. Between all experiments, cages were swapped, hence using different departure and arrival cages for similar treatment combinations. Experiments were conducted between the 15 and 29 July 2015.

We released 138 and 150 butterflies into the two departure cages in experiment 1, 92 and 102 butterflies in experiment 2, and 107, 108, 113, and 119 butterflies into the four cages in experiment 3 ($n = 929$ in total; see Table 1 for further information on sample sizes and sex ratios). In general, *L. tityrus* is a rather sedentary species, which can occur in high local densities in high-quality habitat patches (personal observation; cf. Fischer et al. 1999, Fischer and Fiedler 2001a). In experiments 1 and 2, all butterflies were 2 d old upon release into the Metatron, while in experiment 3, age

ranged between 1 and 3 d. The release of butterflies took place as a single event at 9 a.m. on the first day of each experiment. Recapture sessions started in the afternoon (3 p.m.) of the same day and thereafter were repeated twice a day (between 9 a.m. and 12 a.m. and 3 p.m. and 6 p.m., except under rainy conditions). The position (i.e., departure cage, corridor, or arrival cage) of each individual was recorded for each session for the following 2.5 (experiments 1 and 2) or 3.5 (experiment 3) days. The short observation periods resulted from high mortality within the Metatron due to biotic (predators, e.g., spiders) and abiotic (e.g., heat and thunderstorms) factors (mortality rates: experiment 1 = 70%, experiment 2 = 53%, experiment 3 = 83%; see Table 1 for cage-specific mortality rates). Mortality rates were assessed at the end of each experiment. Under natural conditions, lifespan in copper butterflies typically ranges between 7 and 10 d (Fischer et al. 1999, Fischer and Fiedler 2000b, Karl and Fischer 2009). In experiment 3, butterflies found dead were replaced but only within the first 24 h to allow for an appropriate time to emigrate (for information on the numbers of replaced butterflies, see Table 2). During the last recapture session, all remaining butterflies were caught and subjected to a flight performance test. As *L. tityrus* is a native species in Ariège where the Metatron is located, special care was taken to prevent the escape of butterflies to control the risk of admixture between experimental and wild individuals.

Flight performance test

Butterflies were tested for flight performance using a well-established assay (cf. Ducaitez et al. 2012). Each individual was placed into a plastic chamber (30 × 16 × 14 cm), which was

Table 1. Information on sample size, sex ratio, dead butterflies, and mortality rates for all experiments and treatment combinations.

Experiment	Initial sample size	Resources	Sun	Males	Females	Sex ratio M:F (%)	Dead butterflies	Mortality rate (%)
1	138	+	+	70	68	51:49	91	66
	150	–	+	78	72	52:48	111	74
2	92	Few	+	45	47	49:51	50	54
	102	Few	–	49	53	48:52	53	52
3	107	+	+	53	54	50:50	90	83
	108	+	–	54	54	50:50	80	74
	119	–	+	58	61	49:51	105	88
	113	–	–	55	58	49:51	99	88

Table 2. Information on the number of butterflies in the analyses, replacements, and emigrations for all experiments and treatment combinations.

Experiment	Resources	Sun	Butterflies in analysis	Replaced butterflies	Replaced butterflies in analysis	Emigrations	Female emigrations/females	Male emigrations/males
1	+	+	47	0	0	7	5/30	2/17
	–	+	39	0	0	15	11/33	4/6
2	Few	+	42	0	0	2	2/31	0/11
	Few	–	49	0	0	18	16/41	2/8
3	+	+	18	3	0	6	6/10	0/7
	+	–	28	8	5	5	4/18	1/10
	–	+	14	5	1	5	2/9	3/5
	–	–	14	4	1	8	7/12	1/2

perforated at its base and fixed to a rapid agitator (Vortex 4 digital, IKA, Staufen, Germany). After a habituation period of 30 s, the vortex was switched on to strongly shake the chamber, preventing the butterfly from holding onto the walls. Thus, during the test, butterflies had to fly or were lying uncomfortably at the bottom of the shaking chamber. The time an individual butterfly spent flying was recorded for 60 s, with higher values reflecting a better flight performance. Performance tests were performed at $22 \pm 0.5^\circ\text{C}$, mimicking summer (July) conditions in Greifswald. After the performance test, butterflies were frozen in liquid nitrogen for later analyses of morphology.

Morphological analyses

To test for associations between emigration propensity in the Metatron or flight performance and other traits, we measured several morphological traits. Therefore, frozen butterflies were back-transferred to Greifswald University. First, adult body mass was determined to the nearest 0.01 mg (CPA225D, Sartorius, Göttingen, Germany). Then, wings, heads, and legs were removed. Thorax and abdomen were separated and afterward weighed. Abdomen fat content was measured following Fischer et al. (2003) but using the less poisonous acetone instead of dichloromethane. Abdomens were first dried to constant weight for two days at 70°C . Abdomen dry mass was measured. Afterward, fat was extracted twice, each time for 48 h using 1 mL of acetone ($\text{C}_3\text{H}_6\text{O}$) per butterfly. Solutions were exchanged between both fat extractions. Then, abdomens were again dried for two days at 70°C , after which the fat-free dry mass was measured. Absolute (mg) and relative (%) fat content

were determined as the mass difference between abdomen dry mass and the remaining dry mass after the two fat extractions. Forewing area and length (from basis to apex) were measured using digital images of left forewings (captured from ventrally with a digital USB microscope [VMS 004, Veho, Southampton, England] mounted on a microscope stand [DP-M14, OiTEZ, Hongkong, China]) and NIS elements software 3.22.15 (Nikon, Tokyo, Japan). Wing loading was calculated as total body mass divided by forewing area, and wing aspect ratio as $4 \times \text{forewing length}^2$ divided by the forewing area (Berwaerts et al. 2002). Thorax–abdomen ratio was calculated by dividing thorax by abdomen mass.

Statistical analyses

Statistical analyses were conducted separately for each experiment. To analyze variation in morphological traits, we built general linear mixed models (GLMMs) with the respective morphological trait as response variables; resource availability, sun, and sex as fixed explanatory variables; and family as a random variable. In experiment 3, age was used additionally as a covariate (i.e., a continuous explanatory variable; note that in experiments 1 and 2 all individuals were 2 d old; see above). Owing to strong inter-correlations among traits, total body mass, abdomen mass, absolute fat content, and wing area were excluded from further analyses ($r > 0.660$; Appendix S1: Table S1). To determine the predictors of individual flight performance and emigration propensity (departure cage left: yes/no), we built generalized linear models (GzLMs) with either a normal error distribution and a log-link function (for flight performance as response variable) or a binomial error

distribution and logit-link function (for emigration propensity as response variable). Data were analyzed using the same explanatory variables as above for morphological traits, and additionally using thorax mass, thorax–abdomen ratio, relative fat content, wing length, wing aspect ratio, and wing loading (and flight performance for emigration propensity) as covariates. Only butterflies where both emigration propensity and flight performance data were available were used for the analyses. All above models were selected by a stepwise backward elimination of non-significant factors with P -values >0.1 . Note that an Akaike's information criterion approach yielded identical results. All statistical tests were performed with Statistica 12.0 (StatSoft, Tulsa, Oklahoma, USA). All means are given ± 1 Standard error (SE).

RESULTS

Experiment 1

Significant sex differences were found for all morphological traits except from thorax mass, absolute fat content, forewing length, and wing loading (Appendix S1: Table S2; see Results of general linear mixed models). These differences indicated that females had on average higher abdomen and adult body masses, a lower relative fat content, thorax–abdomen ratio and wing aspect ratio, and a larger wing area than males (Table 3). A significant effect of resource availability was found for thorax mass only, which was higher in individuals released into departure

cages with resources. However, resource availability was involved in significant interactions with sex for total body mass, abdomen mass, thorax–abdomen ratio, absolute fat content, and wing loading. These interactions indicate that differences between sexes were more pronounced in or restricted to individuals being released into cages with resources (Table 3). Differences among families were significant for thorax mass, relative and absolute fat content, wing length, and wing area, and tendencies were found for total body mass and wing aspect ratio (Appendix S1: Table S2).

Emigration propensity in the Metatron was significantly affected by resource availability only; no covariate was included in the final model (Table 4a). Individuals with no access to resources showed a higher emigration propensity (38% of 39 vs. 15% of 47; Fig. 2a). Flight performance was significantly affected by resource availability, wing length, aspect ratio, and family (Table 4b). Individuals that were released into a departure cage with resources flew longer than individuals that were released into a departure cage without resources ($38.4 \pm 4.7 > 23.4 \pm 6.5$ s; Fig. 2b). Flight performance was negatively correlated with wing length but positively with aspect ratio. Thus, butterflies with shorter wings and a higher aspect ratio had a better flight performance.

Experiment 2

Significant sex differences were found for all morphological traits except from thorax mass,

Table 3. Morphological traits of *Lycaena tityrus* in relation to sex and the presence of resources in the departure cage for experiment 1.

Trait	Resources		No Resources	
	Males	Females	Males	Females
Adult body mass (mg)	29.2 ± 0.98^A	37.3 ± 1.20^B	28.1 ± 3.04^A	32.4 ± 1.45^A
Thorax mass (mg)	15.2 ± 0.62^A	14.3 ± 0.40^A	12.6 ± 1.10^A	13.2 ± 0.57^A
Abdomen mass (mg)	7.9 ± 0.76^A	16.7 ± 0.71^B	10.3 ± 2.71^{AC}	13.3 ± 0.82^C
Thorax–abdomen ratio	2.1 ± 0.20^A	0.9 ± 0.03^B	1.7 ± 0.34^A	1.0 ± 0.04^B
Fat (mg)	0.4 ± 0.10^{AB}	0.5 ± 0.04^B	0.3 ± 0.16^{AB}	0.3 ± 0.04^A
Fat (%)	13.3 ± 2.67^A	8.8 ± 0.60^{AB}	12.9 ± 4.27^A	5.5 ± 0.56^B
Wing length (mm)	14.7 ± 0.17^A	14.8 ± 0.13^A	14.2 ± 0.39^A	14.9 ± 0.14^A
Wing area (mm ²)	80.8 ± 1.85^A	88.1 ± 1.51^B	75.7 ± 4.20^A	89.1 ± 1.62^B
Wing loading	36.2 ± 1.08^A	42.3 ± 1.01^B	37.7 ± 4.55^{AB}	36.1 ± 1.21^A
Wing aspect ratio	10.7 ± 0.10^A	10.0 ± 0.05^B	10.7 ± 0.13^A	10.0 ± 0.05^B

Notes: Given are mean + 1 standard error. Group sample sizes are 17 for fed males, 6 for unfed males, 30 for fed females, and 33 for unfed females. Different superscript letters indicate significant differences among groups.

Table 4. Results of generalized linear models for the effects of resources, sex (both fixed), family (random) and thorax mass, thorax–abdomen ratio, relative fat content, wing length, wing aspect ratio, and wing loading (and flight performance for emigration propensity; covariates) on (a) emigration propensity (logit-link function and binomial error distribution) and (b) flight performance (flight duration in a vortex; log-link function and normal error distribution) in the butterfly *Lycaena tityrus* (experiment 1).

Factor	df	Odds ratio	95% CI	Parameter estimate	SE	Wald χ^2	<i>P</i>
(a) Emigration							
Resources	1	0.230	0.008–0.674			7.1	0.0075
(b) Flight performance							
Resources	1			–0.27	0.09	8.8	0.0030
Wing length	1			–0.34	0.13	6.9	0.0088
Aspect ratio	1			0.34	0.17	4.2	0.0399
Family	6					16.2	0.0127

Notes: Models were constructed by a stepwise backward elimination of non-significant factors. Only final models are presented. Significant *P*-values are given in bold. Blanks result from the use of different statistical models in (a) and (b). CI, confidence interval; SE, standard error.

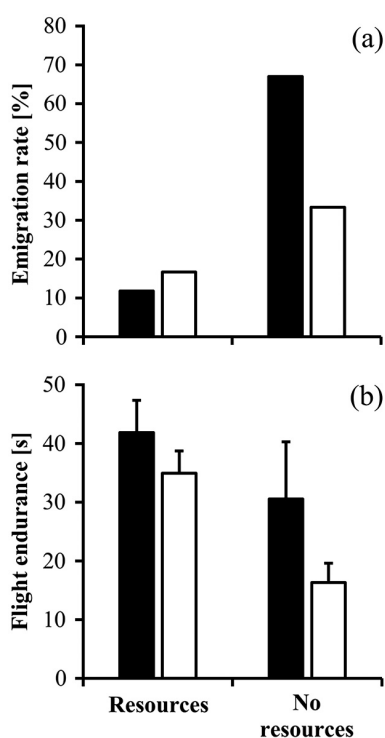


Fig. 2. Emigration propensity (%), (a) and flight performance (mean + 1 standard error), (b) of *Lycaena tityrus* in relation to the presence or absence of resources in the departure cage in experiment 1. Males: filled bars; females: open bars.

relative fat content, and forewing length (Appendix S1: Table S3; see Results of general linear mixed models). Females had on average higher abdomen and adult body masses, a lower

thorax–abdomen ratio, a higher absolute fat content, a larger wing area, a higher wing loading, and a lower wing aspect ratio than males (Table 5). A significant effect of sunshine conditions was found for abdomen mass, thorax–abdomen ratio, and absolute and relative fat content. Individuals that were released into sunny cages had on average a lower abdomen mass, concomitantly a higher thorax–abdomen ratio, and a lower absolute and relative fat content. Furthermore, significant sun-by-sex interactions were found for abdomen mass, thorax–abdomen ratio, relative fat content, and wing loading (Appendix S1: Table S3). They show that sexual differences were more pronounced under sunny as compared to shady conditions, except for relative fat content (Table 5). Differences among families were significant for thorax mass, wing length, and wing area (Appendix S1: Table S3).

Emigration propensity was significantly affected by sunshine conditions only (Table 6a). Individuals showed a higher emigration propensity when released into a shady rather than sunny departure cage (36.7% of 49 > 4.8% of 42; Fig. 3a). Flight performance was significantly positively correlated with thorax–abdomen ratio. Hence, a higher thorax–abdomen ratio led to a better flight performance. Additionally, the interaction between sun and sex tended to influence flight performance (Table 6b), suggesting that males had a better flight performance when released into shady departure cages whereas there was no difference between the sexes when released into sunny departure cages (Fig. 3b).

Table 5. Morphological traits of *Lycaena tityrus* in relation to sex and sunshine conditions in the departure cage for experiment 2.

Trait	Sun		Shade	
	Males	Females	Males	Females
Adult body mass (mg)	27.8 ± 0.61 ^A	40.0 ± 1.53 ^B	32.2 ± 2.68 ^{AB}	39.4 ± 1.94 ^B
Thorax mass (mg)	14.9 ± 0.49 ^A	14.8 ± 0.54 ^A	13.7 ± 0.90 ^A	14.3 ± 0.59 ^A
Abdomen mass (mg)	7.0 ± 0.74 ^A	19.2 ± 1.00 ^B	13.0 ± 2.28 ^{AB}	19.2 ± 1.32 ^B
Thorax–abdomen ratio	2.3 ± 0.22 ^A	0.8 ± 0.03 ^B	1.4 ± 0.30 ^C	0.8 ± 0.05 ^B
Fat (mg)	0.2 ± 0.07 ^A	1.0 ± 0.15 ^B	1.2 ± 0.26 ^B	1.1 ± 0.11 ^B
Fat (%)	11.6 ± 2.86 ^A	15.2 ± 1.43 ^A	29.1 ± 3.24 ^B	18.4 ± 1.30 ^A
Wing length (mm)	14.9 ± 0.14 ^A	14.8 ± 0.12 ^A	14.5 ± 0.15 ^A	14.8 ± 0.13 ^A
Wing area (mm ²)	82.9 ± 1.49 ^{AB}	88.5 ± 1.64 ^B	77.4 ± 1.66 ^A	88.8 ± 1.57 ^B
Wing loading	33.7 ± 1.08 ^A	45.0 ± 1.30 ^B	41.5 ± 2.97 ^{AB}	43.8 ± 1.65 ^B
Wing aspect ratio	10.8 ± 0.06 ^A	9.9 ± 0.03 ^B	10.9 ± 0.12 ^A	9.9 ± 0.05 ^B

Notes: Given are mean + 1 standard error. Group sample size is 11 for males and 31 for females at sunny, and 8 for males and 41 for females at shady conditions. Different superscript letters indicate significant differences among groups.

Table 6. Results of generalized linear models for the effects of sun, sex (both fixed), family (random) and thorax mass, thorax–abdomen ratio, relative fat content, wing length, wing aspect ratio, and wing loading (and flight performance for emigration propensity; covariates) on (a) emigration propensity (logit-link function and binomial error distribution) and (b) flight performance (flight duration in a vortex; log-link function and normal error distribution) in the butterfly *Lycaena tityrus* (experiment 2).

Factor	df	Odds ratio	95% CI	Parameter estimate	SE	Wald χ^2	<i>P</i>
a) Emigration							
Sun	1	0.089	0.019–0.419			9.4	0.0022
b) Flight performance							
Thorax–abdomen ratio	1			0.23	0.10	5.4	0.0206
Sun × Sex	1			0.14	0.08	2.9	0.0870

Notes: Models were constructed by a stepwise backward elimination of non-significant factors. Only final models are presented. Significant *P*-values are given in bold. Blanks result from the use of different statistical models in (a) and (b). CI, confidence interval; SE, standard error.

Experiment 3

Significant sex differences were found for all morphological traits measured except from thorax mass, relative fat content, and forewing length (Appendix S1: Table S4; see Results of general linear mixed models), indicating that females had on average higher abdomen and total body masses, a lower thorax–abdomen ratio, a higher absolute fat content (mg), a larger wing area, a higher wing loading, and a lower wing aspect ratio than males (Table 7). A significant effect of resource availability was found for relative and absolute fat content only, showing that individuals that had access to resources had a lower relative (7.9 ± 0.6% vs. 15.1 ± 1.4%) and absolute (0.31 ± 0.03 mg vs. 0.70 ± 0.08 mg) abdomen fat content. Effects of sunshine conditions, in contrast, were non-significant throughout, as was the case for all interaction

terms. Differences among families were significant for wing aspect ratio only. A significant effect of age was found for wing area only, indicating that older butterflies had larger wings than younger ones (thus, larger butterflies eclosed first; Appendix S1: Table S4).

Emigration propensity was significantly affected by relative fat content and the three-way interaction between resources, sex, and sun (Table 8a). Butterflies with a higher relative fat content had a higher emigration propensity (14.3 ± 1.2% vs. 8.8 ± 0.9%). The significant three-way interaction shows that males were more dispersive than females only if a lack of resources coincided with sunny conditions (60% of 5 vs. 22% of 9). Under all other conditions, females were the more dispersive sex (resources + sun: 60% of 10 vs. 0% of 7; resources + shade: 22% of 18 vs. 10% of 10; and

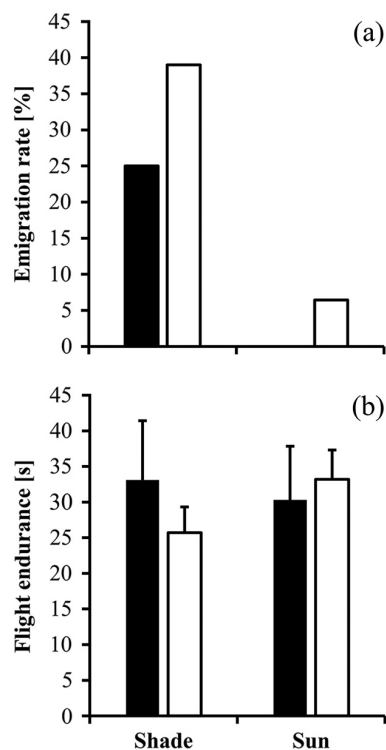


Fig. 3. Emigration propensity (%), (a) and flight performance (mean + 1 standard error, (b)) of *Lycaena tityrus* in relation to having experienced sunny or shady conditions in the departure cage in experiment 2. Males: filled bars; females: open bars.

Table 7. Morphological traits of *Lycaena tityrus* in relation to sex for experiment 3.

Trait	Males	Females
Adult body mass (mg)	27.9 ± 0.98 ^A	37.2 ± 1.31 ^B
Thorax mass (mg)	14.9 ± 0.06 ^A	14.3 ± 0.04 ^A
Abdomen mass (mg)	7.1 ± 0.04 ^A	16.9 ± 0.09 ^B
Thorax–abdomen ratio	2.3 ± 0.14 ^A	0.9 ± 0.04 ^B
Fat (mg)	0.2 ± 0.04 ^A	0.6 ± 0.06 ^B
Fat (%)	11.2 ± 1.41 ^A	10.5 ± 0.91 ^B
Wing length (mm)	14.5 ± 0.16 ^A	14.8 ± 0.11 ^A
Wing area (mm ²)	78.5 ± 1.70 ^A	86.8 ± 1.19 ^B
Wing loading	35.6 ± 0.87 ^A	42.3 ± 1.35 ^B
Wing aspect ratio	10.8 ± 0.07 ^A	9.9 ± 0.04 ^B

Notes: Given are mean + 1 standard error. Group sample size is 24 for males and 49 for females. Different superscript letters indicate significant differences among groups.

no resources + shade: 58% of 12 vs. 50% of 2). Additionally, sex and the interaction between resources and sex tended to influence emigration propensity. Females tended to have an overall

higher emigration propensity than males (39% of 49 > 21% of 24). The resource-by-sex interaction shows that females tended to have a higher emigration propensity than males if resources were present in the departure cage, while it was the other way around if no resources were present (Fig. 4a). Consequently, emigration propensity increased much more strongly in males than in females when no resources were present. Flight performance in the vortex was significantly affected by thorax–abdomen ratio, wing loading, and family (Table 8b). Flight performance was positively correlated with thorax–abdomen ratio and wing loading. Hence, a higher thorax–abdomen ratio and wing loading increased flight performance.

DISCUSSION

Our study revealed that flight performance was linked to morphological traits, such as a high thorax–abdomen or aspect ratio (i.e., condition). In contrast, emigration propensity was not affected by individual condition under semi-natural conditions. We found a sex-biased emigration propensity, which was generally higher in females, but dependent on the environmental context. For instance, without resources emigration propensity was higher in males. Furthermore, the environmental context affected emigration propensity, which was higher in conditions indicative of poor habitat quality such as shade and a lack of resources. Furthermore, we found several sex-specific differences in morphology. We start our discussion with variation in morphological traits, as these have been implied to affect flight ability in insects and may thus underlie variation in emigration propensity.

Sexual differences in morphological traits

Morphological traits measured were, as expected, strongly affected by sex. Our results showed consistently that females were heavier than males, which is usually explained by fecundity selection for large body size in females, as both traits are often positively related (Honek 1993, Blanckenhorn 2000). In accordance with this relationship, mass differences between the sexes were caused by pronounced variation in abdomen mass (with a concomitantly higher absolute fat content under favorable conditions),

Table 8. Results of generalized linear models for the effects of resources, sun, sex (all fixed), family (random) and age, thorax mass, thorax–abdomen ratio, relative fat content, wing length, wing aspect ratio, and wing loading (and flight performance for emigration propensity; covariates) on (a) emigration propensity (logit-link function and binomial error distribution) and (b) flight performance (flight duration in a vortex; log-link function and normal error distribution) in the butterfly *Lycaena tityrus* (experiment 3).

Factor	df	Odds ratio	95% CI	Parameter estimate	SE	Wald χ^2	<i>P</i>
(a) Emigration							
Resources × Sun × Sex	1					5.4	0.0201
Fat	1	0.827	0.733–0.933			9.5	0.0020
Resources × Sex	1					3.3	0.0698
Sex	1	3.960	0.822–19.063			2.9	0.0861
(b) Flight performance							
Thorax–abdomen ratio	1			0.60	0.12	23.5	<0.0001
Wing loading	1			0.04	0.01	13.5	0.0002
Family	5					15.3	0.0091

Notes: Models were constructed by a stepwise backward elimination of non-significant factors. Only final models are presented. Significant *P*-values are given in bold. Blanks result from the use of different statistical models in (a) and (b). CI, confidence interval; SE, standard error.

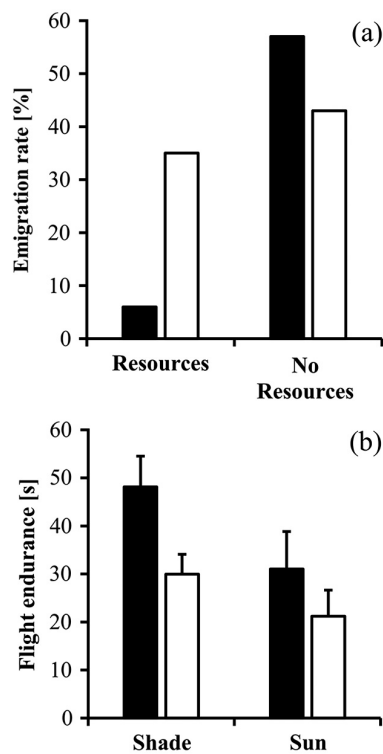


Fig. 4. Emigration propensity (%), (a) in relation to the presence or absence of resources and flight performance (mean + 1 standard error), (b) in relation to having experienced sunny or shady conditions in the departure cage in *Lycaena tityrus* (experiment 3). Males: filled bars; females: open bars.

enabling high fecundity and large amounts of storage reserves to fuel egg production in females (Eaton 1988, Tammaru et al. 1996, Berwaerts et al. 2002). Relative fat content typically is higher in males in order to fuel flight activity (Zera et al. 1998, Karl and Fischer 2008).

The females' higher mass found here results in a higher wing loading compared with males, which has been shown to increase the energetic costs of flight (Wickman 2009, Saastamoinen et al. 2012). In this study, males and females also differed clearly in wing morphology. Despite similar wing lengths, females showed larger wing areas resulting from having wider wings, while those of males are more elongated as evidenced by a higher wing aspect ratio (see also Dudley 2000, Hassall 2015). Thorax mass, by contrast, did not differ among sexes, demonstrating that males have relatively larger thoraxes than females, resulting in a consistently increased thorax–abdomen ratio, which may in turn increase flight capacity (Berwaerts et al. 2002, Karl et al. 2008). The above sex-specific differences in morphology may result from differential selective pressures favoring flight performance in males (Van Dyck and Wiklund 2002, Berwaerts et al. 2006). As male *L. tityrus* are territorial, a good flight performance might be useful to succeed in competition for mates or in territorial disputes with rival males (Ebert and Rennwald 1991, Fischer and

Fiedler 2000a). We were not able to verify this in a flight performance test, which is discussed below (see Section *Study limitations*).

Environmental differences in morphological traits

Effects of environmental conditions were less consistent than the above sexual differences. Storage reserves, namely fat content, were reduced if resources were present in the departure cages in experiment 3. We assume that this counterintuitive result stems from butterflies remaining largely inactive with regard to routine movements when being deprived of food in order to save energy and to endure the critical phase of resource limitation (Saastamoinen and Hanski 2008). Furthermore, females need nectar for egg production in copper butterflies, without which less energy will be allocated to reproduction (Arrese and Soulages 2010, Karl et al. 2011). Both mechanisms result in a reduced consumption of storage reserves, at least initially (note here the young age of the butterflies tested). The above interpretation of an important impact of activity on storage reserves is further supported by the fact that the highest mean fat content was found in individuals being deprived of food under shady conditions, as a lack of solar radiation will further reduce butterfly activity (Wickman 2009, Kuussaari et al. 2016). Furthermore, experiment 2 yielded identical results, as individuals released into sunny cages had on average a lower abdomen mass, a higher thorax–abdomen ratio, and a lower fat content. However, in experiment 1 the above patterns did not prevail, for which we have no explanation.

In experiments 1 and 2, sexual differences were more pronounced when individuals had access to food or when they were exposed to sunny conditions. The former indicates that females gained more mass when having access to food, probably as a result of egg maturation (Karl et al. 2011). The latter indicates that males lost more mass and fat under sunny conditions compared to females, which may reflect their high flight activity under such conditions.

Effects on emigration propensity

A lack of resources needed for adult feeding and oviposition caused, as expected, a higher emigration propensity. Thus, individuals apparently showed a higher motivation to leave the departure patch in search for vital resources.

Also, emigration propensity was higher under shady as compared to sunny conditions. This is intriguing, since shade or a lack of opportunity for sun basking will certainly reduce overall flight activity (Fischer and Fiedler 2001b). Butterflies require high muscle temperatures between 30° and 38°C for flight activity, which is achieved through basking in the sun (Watt 1995, Wickman 2009). Taken together, these findings clearly suggest that emigration in *L. tityrus* is not merely driven by chance effects, rather butterflies can accurately assess patch quality and actively decide to leave a patch in case of degraded habitat quality. Such conditional, context-dependent behavior allows escape from patches of unfavorable quality (Matthysen 2012). Accordingly, directed flight has been observed to occur more often in unsuitable habitats (Dennis 2004).

Interestingly, we found sex-biased emigration propensity, which additionally depended on environmental conditions in the departure cage. In experiment 3, females tended to have a higher emigration propensity in general and showed a clearly higher emigration propensity than males if resources were present. This accords well with our expectations and is likely caused by male harassment and risk spreading in females. When being confronted with a lack of resources, both sexes increased emigration rates. However, this increase was much more pronounced in males, such that under these conditions, males were more likely to emigrate than females. This is likely caused by males searching for appropriate sites to establish a territory, which typically cover dense patches of flowering nectar plants (Ebert and Rennwald 1991, Fischer and Fiedler 2001b). The fact that male emigration was most strongly promoted when a lack of resources coincided with sunny conditions probably indicates that males took advantage of beneficial conditions during flight to search for territories. However, sex differences were not significant in experiments 1 and 2, although a similar trend was observed in experiment 2 (not attaining significance) and to some extent even in experiment 1.

The impact of condition on emigration propensity was remarkably low. Only one instance of relative fat content had once a significant impact (experiment 3), indicating a positive association between fat and emigration propensity. Note that flight performance was never included into the

models, reinforcing the above notion that emigration in *L. tityrus* is in the first place governed by motivation (i.e., context) rather than flight ability. These findings agree with other studies on butterflies, clearly demonstrating the importance of habitat quality and weather conditions on emigration propensity (Conradt et al. 2001, Cormont et al. 2011, Legrand et al. 2015). In contrast, dispersal modes in lizards, which constitute other intensively studied model organisms, are mainly related to social context (Le Galliard et al. 2003, Cote and Clobert 2010, Baguette et al. 2014). Here, dispersal most likely occurs as a single event soon after birth, whereas dispersal in butterflies and probably other insects appears to be unrelated to age (Baguette et al. 2014), which showed no association with emigration propensity in our study.

Variation in flight performance

In contrast to emigration propensity, variation in flight performance was principally determined by morphological traits, namely thorax–abdomen ratio, aspect ratio, and wing loading and length. This suggests that differences in flight performance indeed can be readily explained by morphological differences as has been repeatedly suggested (Van Dyck and Wiklund 2002, Berwaerts et al. 2006). Accordingly, higher thorax–abdomen ratios have been shown to increase flight capacity as thorax mass is associated with the amount of flight musculature (Srygley and Chai 1990, Berwaerts et al. 2002). Aspect ratio is known to influence aerodynamic aspects of flight (Dudley 2000, Hassall 2015), and high ratios have been shown to increase flight ability and acceleration (Betts and Wootton 1988, Berwaerts et al. 2002, Berwaerts and Van Dyck 2004). High wing loadings might increase flight costs but have nevertheless been associated with fast flight, which could explain their positive influence on flight performance (Betts and Wootton 1988). Shorter wings might reflect a smaller size in general and therefore potentially increased maneuverability and elevated performance in the vortex test. Regarding the influence of environmental conditions on flight performance, we only found a negative effect of a lack of resources in the departure cage in experiment 1. This is consistent with the results discussed above (see Section *Environmental differences in morphological traits*) and might be attributed to the lower fat content of the individuals.

Study limitations

Conducting research using an experimental platform under semi-natural rather than natural conditions has many advantages but is still accompanied by some potential biases and limitations. Therefore, the results obtained should be extrapolated to natural systems carefully (Legrand 2012). First, the experimental habitat patches obviously do not resemble a perfect natural habitat well, especially in terms of size and population density, which may in turn affect emigration rates. Nevertheless, local patterns have been shown to predict large-scale patterns (Levey et al. 2005). The focus of our study was to compare effects of different contexts and of condition on emigration propensity, with the results showing mostly clear and reasonable patterns. Furthermore, note that *L. tityrus* can sometimes occur in high densities along suitable habitat patches.

Second, high mortality rates restricted our observations to the first days of adult life and additionally lowered final sample sizes. Reasons might be the high numbers of predators (e.g., spiders and mantids) and extreme weather events during the experiments (e.g., thunderstorms and heat). In general, conditions of the study site differed from those experienced by the native population during summer, for instance, with regard to average (native: 16.7°C vs. experimental: 19.4°C; Deutscher Wetterdienst 2018) and extreme temperatures (native: 33°C vs. 38.2°C; Deutscher Wetterdienst 2018). Consequently, we started with high initial sample sizes, but nevertheless had to confront partly low and unbalanced final sample size available for analyses. We still think that the patterns found are reliable, as most of the treatment conditions were replicated in different experiments and similar conditions revealed similar results. Additionally, cages were swapped between the experiments to minimize cage effects. Also, note that adult lifespan in copper butterflies is relatively short, typically ranging between 7 and 10 d in nature (Fischer et al. 1999, Karl and Fischer 2009).

Third, flight performance was measured after the experiments on emigration propensity, which could have influenced the results obtained. For instance, we did not find differences between sexes, although a better flight performance in males has been shown for the study species in previous experiments (Reim et al. 2018a, b, see

Fig. 4b for a non-significant tendency). This was potentially caused by the males' high flight activity in the cages (e.g., for mate location or territorial defense) and hence an increased consumption of storage reserves, which in turn were no longer available for the flight performance test.

CONCLUSIONS

Despite study limitations, our results show clear patterns which likely bear biological significance, confirming that using the experimental platform was appropriate (Legrand 2012, Legrand et al. 2015). In summary, we show that, first, males and females differed substantially in morphology, with males showing traits typically associated with better flight performance. However, we were not able to verify this in the performance test (see *Study limitations*). Second and more interestingly, the traits underlying increased flight performance (i.e., condition) did not affect emigration propensity. Instead, we found sex-biased emigration propensity, which was dependent on the environmental context. For instance, although females showed traits associated with diminished flight performance, they tended to show a higher emigration propensity in general, which was especially increased when resources were present. Without resources, emigration propensity was higher in males, which were probably searching for suitable sites to establish a territory. This indicates that flight performance and the first step of dispersal, that is, the actual consequence of dispersing, do not necessarily equate, and casts doubt on the intuitive assumption of a general, positive relationship between the two. Note that the study design did not allow examination of other stages of dispersal. Thus, we cannot assess the effects of flight performance on dispersal success. Third, environmental conditions (i.e., the context) affected condition, flight performance, but also emigration propensity. Notably, conditions indicative of poor habitat quality such as shade and a lack of resources promoted emigration. This suggests that emigration in *L. tityrus* is not merely a random process but is governed by an active decision in a context-dependent manner, following an accurate assessment of patch quality. In summary, our results suggest that emigration propensity in this butterfly is a highly plastic, context-dependent trait triggered largely by

habitat quality rather than by individual condition. This result supports the findings in other butterfly species (Cormont et al. 2011, Saastamoinen et al. 2012, Legrand et al. 2015). Besides abiotic factors, resource availability, and harassment, this may also involve density dependence (Enfjäll and Leimar 2005, Trochet et al. 2013). In previous studies, both positive (emigration increases with population density) and negative density-dependent dispersal have been demonstrated, the former being likely a result of social interactions (e.g., male harassment) whereas the latter might be induced by mate scarcity (Hanski 1994, Baguette et al. 1996, 1998, Kuussaari et al. 1998, Enfjäll and Leimar 2005). Importantly, deteriorating habitat quality promoted emigration propensity (Legrand et al. 2015), which should be considered when trying to forecast future species distributions. For instance, climate change is likely to reduce habitat quality, but this will simultaneously likely increase emigration propensity and thereby potentially facilitate range shifts in flying insects (Travis 2013).

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