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# Movement Patterns Differ between Sexes and Depend on Weather Conditions in the Butterfly *Lycaena tityrus*

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**Abstract** Habitat loss and anthropogenic climate change are important threats to biodiversity conservation. Owing to the concomitantly deteriorating habitat quality, individuals are often forced to disperse to new habitats, rendering dispersal an ecologically important process. However, dispersal ability may differ within and among populations, and is further dependent on environmental conditions. We therefore studied sexual differences in and environmental effects on movement patterns in the sooty copper butterfly *Lycaena tityrus*. As predicted, males were more active and covered longer distances than females, presumably owing to mate location and territorial disputes. Males alighted more often on flowers than females, probably to fuel their high flight activity, while females showed a high affinity to host-plants for egg-laying. Our findings provide a striking example of sex-related differences in animal behavior, as revealed by the use of customary smartphones, which apparently can comprise suitable means to reveal biologically significant behavioural patterns. More problematic than the technical device used seems to be the challenge of following individual butterflies for long enough in the field, such that any extrapolations to dispersal seem difficult.

**Keywords** Animal behavior · dispersal · environmental context · flight activity · mate location · sexual differences

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## Introduction

Human impact, driving habitat loss and fragmentation as well as climate change, is all pervasive on Earth (e.g. Forester and Machlist 1996; Sanderson et al. 2002). Owing to the concomitantly deteriorating habitat quality, individuals are often forced to disperse to new habitats (e.g. Hanski 1998), although the likelihood to reach these is often low due to reduced habitat availability and fragmentation (Fernández-Chacón et al. 2014). Dispersal is therefore important for dealing with environmental variation (Cote and Clobert 2007; Travis et al. 2013), as it may allow individuals to track their shifting climate niche (Warren et al. 2001; Hickling et al. 2006) and to maintain metapopulation connectivity (Hanski and Gilpin 1997; Baguette et al. 2013).

Despite its concomitant ecological importance, the motivation as well as the ability to disperse may differ strongly among and within populations (Van Dyck and Baguette 2005; Baguette and Van Dyck 2007; Ducatez et al. 2014; Bestion et al. 2015). Factors that may affect dispersal ability include morphology, physiology, and overall condition (Bowler and Benton 2005; Bonte et al. 2012; Therry et al. 2014). Moreover, sexes may differ in dispersal behavior. In insects, females are often the more dispersive sex (e.g. Fischer et al. 1999) as (1) single-mated females are, unlike males, able to found a new population (Hill et al. 1999; Hanski et al. 2002, 2004), (2) females may need to escape from male harassment (Hovestadt and Nieminen 2009; Trochet et al. 2013) or as (3) they pursue a risk spreading strategy by distributing their eggs over a wider area (Hopper 1999). In addition to such intrinsic factors, dispersal is also affected by external factors such as prevailing weather conditions (Legrand et al. 2015). In general, dispersal increases with rising temperature and solar radiation but decreases with increasing cloud cover, rainfall, and wind speed (Kuussaari et al. 2016).

Against this background, we here investigate (within-patch) movement patterns in the temperate-zone butterfly *Lycaena tityrus*. Focussing on movement patterns rather than dispersal per se was due to the fact that dispersal is very difficult if not impossible to observe directly in flying insects (Riley and Smith 2002; Cant et al. 2005). We thus argue that knowledge on movement patterns is an important first step for a better understanding of dispersal, as movement may eventually result in dispersal. For instance, flight track length has been shown to be associated with flight metabolic rate and PGI genotype, parameters that are in turn known to be related to dispersal (Niitepõld et al. 2009). Butterflies are suitable models to study movement for several reasons. First, they exhibit large variation in dispersal ability and their natural history is well known (Stevens et al. 2010). Second, they are sensitive indicators of habitat change and therefore ecosystem quality (Murphy et al. 1990; van Swaay 1990; Erhardt and Thomas 1991). Third, as pollinators they play an important role in ecosystems by providing pollination services, the lack of which may cause a loss of plant diversity (Potts et al. 2010). Fourth, as herbivores they may be particularly threatened by climate change, due to effects on the quality and phenology of host-plants as well as on the butterflies themselves (Roy and Sparks 2000).

Specifically, we explore within-patch mobility to test the hypotheses that (1) movement patterns differ among the sexes, and that (2) movement is strongly affected by prevailing weather conditions. As *L. tityrus* males are territorial (Ebert and Rennwald 1991; Fischer and Fiedler 2000a), we predict that males are more active than females (due to mate location, inspection flights, territorial disputes), while females are expected to move further away from the point of first encounter than males due to straighter flight trajectories (see above). We further predict that activity is positively related to beneficial (warm, sunny) weather conditions. Addressing such questions may have important implications for dispersal, though note that we are working here on a spatially very restricted scale. To this end, we individually tracked butterflies of both sexes within an extended habitat patch and recorded weather conditions in parallel. As we used customary smartphones in combination with a tracking application, we additionally investigate whether such devices are suitable for investigating insect behaviour.

## Material and Methods

### Study Organism

The sooty copper *L. tityrus* is a widespread butterfly of the temperate zone, ranging from Western Europe to Central Asia (Ebert and Rennwald 1991). Central European low-altitude populations, including the one investigated here, are typically bivoltine with two distinct generations per year. *L. tityrus* inhabits different types of unimproved grass- and wetlands. The most important larval host plant is *Rumex acetosa*, but several congeneric plant species such as *R. acetosella* and *R. scutatus* are utilised as well (Ebert and Rennwald 1991; Tolman and Lewington 1998). Adults feed on a variety of composite (Compositae) and other nectar plants (Ebert and Rennwald 1991; Karl and Fischer 2009). For this study, individuals from a low-altitude population near the city of Greifswald (north-eastern Germany) were examined.

### Study Area

The study was conducted on an extended set-aside field near Greifswald (54°03′02”N, 13°26′26″E), harboring a large population of *L. tityrus*. Hence, the location is close to the Baltic Sea and thus the northern distribution limit of *L. tityrus* (GfS 2017). This part of Germany is characterized by a rather continental climate with an annual mean temperature of 8.0 °C and a precipitation of 566 mm per year (Müller 2006). The study area (ca. 20 ha) is situated 30–40 m above sea level, rather flat, and shows a relatively homogenous vegetation structure without shrubs or trees. The vegetation consists mainly of species indicative of rather nutrient-poor grassland. Host plants (*R. acetosa*, *R. acetosella*) occur in high density throughout the area. The lack of barriers and other disturbing structure renders this study area suitable for tracking individual butterflies.

### Field Methods and Data Analyses

We investigated the movement patterns of *L. tityrus* by tracking the flight paths of individual butterflies with a hand-held GPS device. As GPS device we used Android smartphones and the application “Geo Tracker – GPS tracker”. The following settings were used: accuracy 10 to 20 m, frequency of locating 1 per sec, minimal distance between two points 1 m, maximum distance between two points 500 m. To test for the accuracy of the GPS application and the smartphones used, tracks of a known distance were compared to measured GPS tracks (Online Resource Fig. 1), revealing a correlation coefficient of 0.995. Furthermore, repeatedly scoring the same position using Geo Tracker without moving revealed identical coordinates. Field work was conducted between mid-May and early June 2017, i.e. within the spring flight period of *L. tityrus*. Data were collected by 12 teams consisting of two persons each, which were consistent over the study period. One person concentrated on observing and tracking the butterfly while the other noted butterfly behavior, time periods, etc. (see further below).

To start a track, an individual of *L. tityrus* was located and its sex determined. Thereafter, the observation was started (to ease sex determination and avoid chasing butterflies, all tracks were started when butterflies were sitting). The observers kept a minimum distance of 2–3 m to the butterfly to minimize possible influences on the animal's behavior. Nevertheless, the actual flight path was tracked as closely as possible by avoiding any shortcuts. Tracking of a butterfly ended when the observer lost sight of the individual or after a maximum of 15 min (i.e. tracking was terminated in case an individual was still available after 15 min). Butterflies showing no flight activity within 15 min were omitted from further analyses.

The following parameters were recorded during tracking: date, sex, cloud cover on a scale between 1 and 8 (in n/8; thus 1/8 equals a cloud cover of one eighth of the sky and 7/8 cloudless), start and end time of tracking, the number of stops, the substrate at the place of alighting (either bare ground, host plant, nectar flower, or other vegetation). Thus, stops separated different flight steps, while crawling within the vegetation was not considered as movement. In total 196 tracks were taken, 106 from males and 90 from females, with each of the 12 observer teams contributing ≥10 tracks. The tracking application was used to extract the following data: time in motion, total track length, average movement speed, average movement speed in motion, and maximum movement speed. To assess whether a high activity may facilitate dispersal, we additionally measured the linear distance between the starting and end point of each track in Google Earth by exporting the tracks to a computer device. Step length was calculated as total track length divided by the number of stops. Data on temperature, wind speed, relative humidity, and precipitation during each individual track were obtained from the Deutscher Wetterdienst (DWD 2017) and are based on hourly means of the weather station closest to the study area (station Greifswald, distance 5.5 km, coordinates: 54°05′39”N, 13°24′20″E).

## Statistical Analyses

Considering the high density of *L. tityrus* and the large size of the study area, we deem it unlikely that a single individual was observed more than once, although we did not mark the individuals. Therefore, we consider our observations as independent samples representative of the butterfly behavior in this population. To analyze movement-related traits we used general linear mixed models with sex as fixed effect, observer team as random effect, and the covariates tracking time, cloud cover and temperature. Due to correlations with temperature, wind speed and relative humidity were excluded from further analyses. Additionally, precipitation was not considered as it showed essentially no variation, because field work was not carried out under rainy conditions (Online Resource Table 1 and Fig. 2). All statistical tests were performed with Statistica 12.0 (Tulsa, StatSoft, OK). All means are given ±1 SE.

## Results

Significant sex differences were found in track length, linear distance between start and end point, time in motion, average speed, average movement speed, and the number of stops on flowers and on host-plants, but not in step length, maximum speed, and the number of stops in total, on other vegetation or on bare ground (Table 1). On average, males compared with females exhibited longer track lengths (Fig. 1a) and distances between start and end point (22.3 ± 2.5 m vs. 14.5 ± 1.6 m), higher average speeds over the total observation period (0.78 ± 0.08 km/h vs. 0.22 ± 0.03 km/h) and also in motion (Fig. 1b), spent more time flying (Fig. 1c), and stopped more often on flowers (Fig. 1d) but less often on host-plants (Fig. 1e).

Regarding effects of environmental factors, only linear distance between start and end point, step length, and the number of stops on host-plants were significantly associated with cloud cover, indicating that increasing cloud cover increased distances (beta 0.17 ± 0.09, Online Resource Fig. 3) and step lengths (beta 0.18 ± 0.09) but decreased the number of stops on host-plants (beta −0.17 ± 0.08). Temperature exclusively affected the number of stops on bare ground, which increased with decreasing temperature (beta −0.36 ± 0.11). Track length (beta 0.17 ± 0.08), the total number of stops (beta 0.44 ± 0.07) and the number of stops on flowers (beta 0.23 ± 0.08), host-plants (beta 0.22 ± 0.08) and other vegetation (beta 0.32 ± 0.08) were all significantly positively related, whereas step length (beta −0.19 ± 0.09) and average speed (beta −0.36 ± 0.07) were negatively related to tracking time, while no significant association was found with any of the other dependent variables. Significant effects of observer team were found in all dependent variables except from step length and the number of stops on bare ground.

## Discussion

Our study revealed, as predicted, sex-specific differences in behavioral patterns of *L. tityrus*. Males spent more time flying and showed longer track lengths than females, in accordance with our expectation. We assume that the longer track lengths result from the males' higher overall activity (see also Kingsolver 1983). The males' higher activity is most likely due to spending much of their time locating mates including frequent inspection and patrolling flights as well as territorial disputes with rivalling males (Wickman 1985; Ebert and Rennwald 1991; Fischer et al. 1999). Females, in contrast, seem to generally spend less time flying and allocate more of their time to oviposition (Kingsolver 1983; Fischer et al. 1999). However, the fact that males also covered longer linear distances between the start and end points of observations is contrary to our expectation. For various reasons we expected females to cover longer distances owing to straighter flight trajectories, while males were supposed to stay within or at least close to their territories. Furthermore, the current data challenge earlier ones obtained from mark-recapture studies in related species, where males were found to be more stationary than females (Fischer et al. 1999; Fischer and Fiedler 2000b). We believe that our current results are biased due to the rather short observation periods (max. 15 min) compared to the mark-recapture studies in which butterflies were observed for several days. Thus, within this rather short period of time, the males'

**Table 1** General linear mixed models for the effects of sex (fixed), observer team (random), and the covariates tracking time, cloud cover and temperature on track length, linear distance between start and end point of track, step length, time in motion, maximum speed, average speed, average movement speed, total number of stops, the number of stops on flowers, the number of stops on host-plants (*Rumex* spec.), the number of stops on other vegetation, and the number of stops on bare ground in the butterfly *Lycaena tityrus*. Significant *p*-values are given in bold

| Track length | DF | MS | F | p |
|---|---|---|---|---|
| Sex | 1 | 55324 | 29.9 | **< 0.0001** |
| Observer team | 11 | 7336 | 4.0 | **< 0.0001** |
| Track time | 1 | 9653 | 5.2 | **0.0236** |
| Cloud Cover | 1 | 1943 | 1.5 | 0.3071 |
| Temperature | 1 | 205 | 0.1 | 0.7397 |
| Error | 179 | 1852 | | |
| | | | | |
| Linear distance | DF | MS | F | p |
| Sex | 1 | 2443 | 5.8 | **0.0173** |
| Observer team | 11 | 929 | 2.2 | **0.0165** |
| Track time | 1 | 6 | < 0.1 | 0.9077 |
| Cloud cover | 1 | 1677 | 4.0 | **0.0480** |
| Temperature | 1 | 549 | 1.3 | 0.2560 |
| Error | 177 | 423 | | |
| | | | | |
| Step length | DF | MS | F | p |
| Sex | 1 | 466 | 1.0 | 0.3170 |
| Observer team | 11 | 762 | 1.6 | 0.0890 |
| Track time | 1 | 2235 | 4.8 | **0.0292** |
| Cloud cover | 1 | 1852 | 4.0 | **0.0469** |
| Temperature | 1 | 53 | 0.1 | 0.7364 |
| Error | 179 | 462 | | |
| | | | | |
| Time in motion | DF | MS | F | p |
| Sex | 1 | 145652 | 26.3 | **< 0.0001** |
| Observer team | 11 | 18491 | 3.3 | **0.0003** |
| Track time | 1 | 8850 | 1.6 | 0.2077 |
| Cloud cover | 1 | 9056 | 1.6 | 0.2025 |
| Temperature | 1 | 11899 | 2.1 | 0.1444 |
| Error | 179 | 5536 | | |
| | | | | |
| Maximum speed | DF | MS | F | p |
| Sex | 1 | 20.8 | 2.6 | 0.1112 |
| Observer team | 11 | 27.8 | 3.4 | **0.0002** |
| Track time | 1 | 23.1 | 2.8 | 0.0936 |
| Cloud cover | 1 | 10.4 | 1.3 | 0.2595 |
| Temperature | 1 | 0.1 | < 0.1 | 0.9255 |
| Error | 179 | 8.1 | | |
| | | | | |
| Average speed | DF | MS | F | p |
| Sex | 1 | 4.5 | 14.1 | **0.0002** |

**Table 1** (continued)

| | | | | |
|---|---|---|---|---|
| Observer team | 11 | 1.5 | 4.7 | **< 0.0001** |
| Track time | 1 | 8.0 | 4.7 | **< 0.0001** |
| Cloud cover | 1 | 0.3 | 0.9 | 0.3342 |
| Temperature | 1 | < 0.1 | < 0.1 | 0.8840 |
| Error | 179 | 0.3 | | |
| Average movement speed | DF | MS | F | p |
| Sex | 1 | 39.6 | 6.5 | **0.0115** |
| Observer team | 11 | 25.2 | 4.2 | **0.0002** |
| Track time | 1 | 9.6 | 1.6 | 0.2104 |
| Cloud cover | 1 | 15.4 | 2.5 | 0.1129 |
| Temperature | 1 | 7.5 | 1.2 | 0.2687 |
| Error | 179 | 6.1 | | |
| Stops number | DF | MS | F | p |
| Sex | 1 | 13.8 | 0.7 | 0.3985 |
| Observer team | 11 | 64.1 | 3.3 | **0.0004** |
| Track time | 1 | 0.6 | 34.6 | **< 0.0001** |
| Cloud cover | 1 | 41.9 | 2.2 | 0.1423 |
| Temperature | 1 | 32.6 | 1.7 | 0.1954 |
| Error | 179 | 19.3 | | |
| Flower stops | DF | MS | F | p |
| Sex | 1 | 70.5 | 8.7 | **0.0035** |
| Observer team | 11 | 15.3 | 1.9 | **0.0420** |
| Track time | 1 | 59.7 | 7.4 | **0.0071** |
| Cloud cover | 1 | 0.4 | < 0.1 | 0.8276 |
| Temperature | 1 | 12.6 | 1.6 | 0.2124 |
| Error | 179 | 423.0 | | |
| *Rumex* stops | DF | MS | F | p |
| Sex | 1 | 62.4 | 17.6 | **< 0.0001** |
| Observer team | 11 | 8.2 | 2.3 | **0.0115** |
| Track time | 1 | 18.8 | 8.1 | **0.0049** |
| Cloud cover | 1 | 17.0 | 4.8 | **0.0300** |
| Temperature | 1 | 9.5 | 2.7 | 0.1037 |
| Error | 179 | 3.5 | | |
| Vegetation stops | DF | MS | F | p |
| Sex | 1 | 9.0 | 0.9 | 0.3382 |
| Observer team | 11 | 36.4 | 3.7 | **< 0.0001** |
| Track time | 1 | 157.1 | 16.0 | **< 0.0001** |

**Table 1** (continued)

| | | | | |
|---|---|---|---|---|
| Cloud cover | 1 | 3.1 | 0.3 | 0.5749 |
| Temperature | 1 | 2.6 | 0.3 | 0.6040 |
| Error | 179 | 9.8 | | |
| | | | | |
| Ground stops | DF | MS | F | p |
| Sex | 1 | < 0.1 | < 0.1 | 0.8934 |
| Observer team | 11 | 0.8 | 1.7 | 0.0744 |
| Track time | 1 | < 0.1 | < 0.1 | 0.8314 |
| Cloud cover | 1 | 0.6 | 1.3 | 0.2514 |
| Temperature | 1 | 5.1 | 11.0 | **0.0011** |
| Error | 179 | 0.5 | | |

higher activity may have caused longer linear distances. Note in this context the short absolute distances covered within the observation period. Additionally, males may have abandoned territoriality. Note that territorial behavior in *Lycaena* butterflies depends on context, and that males may switch to patrolling behavior during spells of beneficial weather conditions and at high densities of conspecifics (Fischer and Fiedler 2001), which was the case during the study period.

The finding that males achieved higher speeds than females has probably morphological and physiological reasons. Male (*Lycaena*) butterflies have a lower body mass and concomitantly wing loading, but a higher thorax-abdomen ratio, wing aspect ratio, and relative fat content compared with females (Karl et al. 2008; Saastamoinen et al. 2012). These traits are typically associated with increased flight ability and maneuverability (van Dyck et al. 1998; van Dyck and Wiklund 2002; Berwaerts et al. 2008),

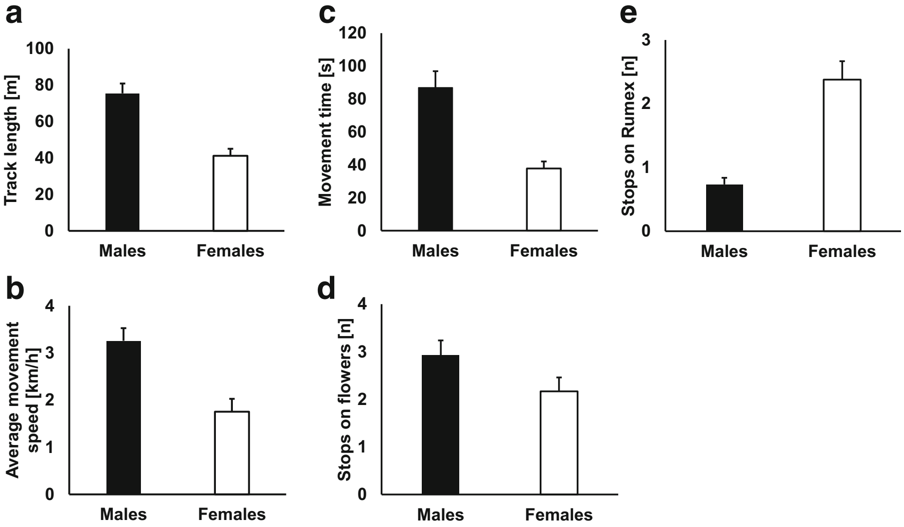

**Fig. 1** Sexual differences in *Lycaena tityrus* in track length (**a**), average movement speed (**b**), time in motion (**c**), and the number of stops on flowers (**d**) and *Rumex* host-plants (**e**)

likely of crucial importance for males to succeed in territorial contests and competition for mates. The fact that males alighted more often on flowers than females is presumably caused by the need for nectar to fuel their high flight activity, while the higher affinity of females to host-plants is certainly related to the search for oviposition plants (Fischer et al. 1999).

In contrast to the prevalent sexual differences in movement, effects of environmental factors were less pronounced. While cloud cover significantly affected three variables, temperature affected only one. The negative impact of cloud cover on the number of stops on host plants potentially reflects the high dependence of *L. tityrus* activity on solar radiation, being an extremely heliophilous butterfly (Wickman 2009). Thus, a lack of solar radiation may result in a reduced (egg-laying) activity. Typically, females try to spread their eggs over a wide range as a risk-spreading strategy (Hopper 1999). Contrary to our assumptions, the linear distance covered and step length were positively related to cloud cover, for which we have no straightforward explanation. Perhaps air temperature was still high enough to sustain flight activity. The more frequent stops on bare ground at cooler temperatures are probably related to thermoregulatory needs, thus alighting on relatively warm spots compared with the surrounding vegetation (Thomas and Lewington 2010; Pradel and Fischer 2011). Taken together, these findings lend at least some support to the notion that detrimental weather conditions may negatively affect flight activity and therefore dispersal in insects, as has been also found in other studies (Meyer and Sisk 2001; Dennis and Sparks 2006; Cormont et al. 2011; Kuussaari et al. 2016). Ultimately, this dependence rests on the high thorax temperature needed for flight activity (Pollard and Yates 1994), which cannot be maintained without solar radiation or at cool temperatures.

We additionally investigated the effects of tracking time and observer team. The positive relations between tracking time and several variables were expected, and simply reflect that increasing observation time increases track length, the number of stops, etc. The negative relation between tracking time and step length as well as average speed might indicate that it was easier for the observers to follow slow flying butterflies with short step lengths. Effects of observer team were also widespread, though our statistical approach effectively controlled for both sources of confounding effects.

## Conclusions

Our results show that customary smartphones can be suitable to reveal biologically significant and well interpretable behavioral patterns in insects. In particularly behavioral differences between the sexes could be readily determined. Similarly, earlier studies investigating butterfly flight using harmonic radar (Cant et al. 2005) but also GPS receivers (e.g. Breed and Severns 2015; Fernández et al. 2016) revealed solid data on butterfly flight behavior. More problematic than the technical device used seems to be the rather short observation period of 15 min at max. The principal problem here is that small flying insects are notoriously difficult to follow in the field (cf. Riley and Smith 2002; Cant et al. 2005). Accordingly, many tracks were even substantially shorter than 15 min. In that respect it is actually quite surprising that our study revealed robust data. We thus conclude that our approach was well appropriate to reveal sexual differences in and impacts of ambient weather on butterfly behaviour. However, tracking butterflies with handheld devices does not seem to be appropriate to estimate rates of dispersal and dispersal distances, such that any conclusions regarding insect dispersal need to be drawn with the greatest care.

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