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Animal Behaviour

Autumn southward migration of dragonflies along the Baltic coast and the influence of weather on flight behaviour

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Despite mass movements of insects being documented for decades, whether dragonflies migrate in Europe has not yet been experimentally tested. Similarly, little is known about the influence of weather on the movement decisions and intensity of dragonflies. Taking advantage of large movements of dragonflies along the Baltic Sea coast of Latvia, we investigated whether European dragonflies showed directed movements indicative of migratory behaviour and how weather influences their movements. First, we performed orientation tests with individual dragonflies of two commonly captured species, *Aeshna mixta* and *Sympetrum vulgatum*, to determine whether dragonflies showed directed flight and whether flight direction differed from wind direction. Both *A. mixta* and *S. vulgatum* displayed a uniform mean southward orientation, which differed from the prevailing overhead wind direction, indicating migratory behaviour. Second, we investigated the influence of weather conditions on the abundance of dragonflies captured. Differences in flight behaviour in relation to weather conditions were observed between *A. mixta* and the two smaller *Sympetrum* species (*S. vulgatum* and *S. sanguineum*). Generally, temperature, cloud cover and wind direction were the most important predictors for dragonfly abundance, with temperature positively, and cloud cover negatively, influencing abundance. *Aeshna mixta* appeared to select favourable tail winds (northerlies), whereas abundance of *Sympetrum* increased with more easterly winds. Our results provide important information on the influence of local weather conditions on the flight behaviour of dragonflies, as well as evidence of dragonfly migration along the Baltic coast.

Migration has evolved independently in a multitude of taxa within many of the major animal lineages (Alerstam, Hedenström, Åkesson, Hedenstrom, & Akesson, 2003; Bauer & Hoye, 2014; Dingle, 2014; Dingle & Drake, 2007). Insects are the most abundant and diverse group of terrestrial migrants (Chapman, Reynolds, & Wilson, 2015; Dingle & Drake, 2007; Holland, Wikelski, & Wilcove, 2006; Hu et al., 2016; Satterfield, Sillett, Chapman, Altizer, & Marra, 2020), yet migratory behaviour has only been well studied in relatively few insect taxa, often restricted to iconic species, such as the Monarch butterfly, *Danaus plexippus* (Flockhart et al., 2013), agricultural pests (Johnson, 1969; Drake & Reynolds, 2012; Chapman et al., 2015; Jones et al., 2019) or beneficial species (Gao et al., 2020; Wotton et al., 2019). Over the last 50 years,

new tools have been developed to study insect migration at a higher resolution, for example using vertical-looking radars (Chapman et al, 2003, 2011a; Drake & Reynolds, 2012) and radio-telemetry (Knight, Pitman, Flockhart, & Norris, 2019; Wikelski et al., 2006). Intrinsic markers such as stable isotopes have also been used to successfully track population-scale movements across the migratory cycle (Flockhart et al., 2013; Stefanescu et al., 2016; Hallworth, Marra, McFarland, Zahendra, & Studds, 2018; Hobson, Soto, Paulson, Wassenaar, & Matthews, 2012). These approaches have highlighted the importance of insect migration with respect to biomass movements and ecological impacts (Hu et al., 2016; Wotton et al., 2019) and have provided information regarding migratory routes and specific parameters such as migration height or flight speed (Chapman et al., 2015; Drake & Reynolds, 2012). Yet, insect migration is still largely unquantified, and the migratory behaviour and movements of many species remain elusive.

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Consequently, the use of more traditional methodology, such as flight interception traps and systematic counts, can provide critical baseline information for determining population trends, migratory phenology and behaviour in relation to local weather and topography (Brattström, Kjellén, Alerstam, & Åkesson, 2008; Krauel, Westbrook, & Mccracken, 2015).

Many insects are able to select suitable conditions for their migration (Brattström et al., 2008; Chapman, Klaassen, et al., 2011; Drake & Reynolds, 2012, Gao et al., 2020) and factors such as temperature and atmospheric pressure can influence movement behaviour, as well as provide cues for the initiation and termination of migration (Johnson, 1969; Wikelski et al., 2006; Brattström et al., 2008; Bauer & Klaassen, 2013). While many weak-flying smaller insects, for example aphids, have their migratory displacements dictated mostly by wind (Chapman, Drake, & Reynolds, 2011,b; Hu et al., 2016; Wainwright, Stepanian, Reynolds, & Reynolds, 2017; Huestis et al., 2019), larger insects such as moths, butterflies and dragonflies are, to a certain extent, able to control their direction relative to the ground by (partially) compensating for drift as well as exploiting tail winds (Chapman et al., 2008; Srygley, 2003). Some large, low-flying diurnal insects such as butterflies and dragonflies often migrate within their 'flight boundary layer', the zone extending up from the ground where the ambient wind speed is lower than the insect's airspeed (Srygley & Dudley, 2008). For these migrants, some proximate weather variables, for example air temperature, wind speed and direction or cloud cover, seem to be recurrent cues which initiate or maintain migratory movements (Brattström et al., 2008; Chapman et al., 2015; Wikelski et al., 2006). Furthermore, aerial migration of some insects often concentrates along topographic elements that may act as barriers or bottlenecks, funnelling migrating animals (Becciu et al., 2019). For example, large concentrations of migrating insects can be observed in areas such as mountain chains, alpine passes (Aubert 1962, 1964; Borisov, 2009; Lack & Lack, 1951; Thoma & Althaus, 2015) or coastlines (Brattström et al., 2008; Corbet, 1999; Russell, May, Soltesz, & Fitzpatrick, 1998).

While there have been numerous anecdotal reports of dragonfly movement and migration worldwide, beginning in 1494 (Calvert, 1893), few studies have systematically documented this phenomenon (Feng, Wu, Ni, Cheng, & Guo, 2006; May & Matthews, 2008; Hallworth et al., 2018; Shapoval & Buczyński, 2012), and relatively little is known about the detailed behaviour and ecology of dragonfly migration (Dumont & Hinnekint, 1973; Russell et al., 1998; Corbet, 1999; Parr 1996, 2010; May, 2013). Corbet (1999) provided a valuable baseline for dragonfly migration research by classifying different types of nontrivial flights. More recently, the use of radiotelemetry has provided insights into migratory behaviour on an individual level, with information on speed, direction and preferred weather conditions of migrating Anax junius in the United States (Knight et al., 2019; Wikelski et al., 2006). In the last decade, effort has been made to document the migratory routes and dynamics of the globally distributed Pantala flavescens (Anderson, 2009; Chapman et al., 2015) by using radar (Feng et al., 2006), stable isotopes (Hobson et al., 2012) and molecular tools (Troast, Suhling, Jinguji, Sahlén, & Ware, 2016). However, much of our knowledge of dragonfly migration is based on these two iconic species.

Large, annually recurring autumn movements of dragonflies have been reported along the Baltic Sea coast (von Rintelen 1997; Buczyński, Shapoval, & Bunczyńka, 2014). In this study, we investigated dragonfly phenology along the Baltic Sea coast in Latvia during autumn. To test whether the mass appearance of dragonflies can be attributed to migratory movements, we performed orientation experiments with individuals in the field. We hypothesized that at these northern latitudes some dragonfly species are migratory and, thus, show directional southward movement differing from the wind direction. Further, we investigated how local weather conditions influence the intensity of dragonfly occurrence and how movement phenology differs between species.

## METHODS

Study Site and Sampling

The study took place at the Pape ornithological station in southwestern Latvia (56°09′59″N, 21°01′03″E; Fig. 1a). The station is situated on the Baltic Sea coast with Pape Lake to the east. Pape Lake is situated parallel to the sea, possibly generating a bottleneck effect on migrating birds and insects (M. Briedis, personal communication), which often avoid flying over open waters (Alerstam & Christie, 1991; Becciu et al., 2019; Corbet, 1999), thereby funnelling the migrants along the strip of land between the lake and the sea (von Rintelen, 1997; Fig. 1a).

During summer and autumn, the station successively operates two funnel traps that open to the north (Fig. 1b), also called Heligoland or 'Rybachy' traps. These traps are primarily used to catch migrating birds and bats (Šuba, Petersons, & Rydell, 2012), but also trap a large number of migrating insects, in particular dragonflies (von Rintelen, 1997). The two traps are of different size and are situated at the same location. Dragonflies were caught between 13 August and 9 September 2016 using the large Heligoland trap (entrance size 15 m high × 35 m wide × 40 m long). From 11 September to 9 October, the larger trap was replaced by a smaller trap (entrance size 6 m high × 11.40 m wide × 28 m long). Trap replacement is the standard procedure of the ringing station in order to cope with the increase in capture rates of birds during autumn. The larger trap is adjustable in height to prevent weather damage to the structure. The height of the trap opening was noted every hour. The traps both have a mesh size of 2 × 2 cm and end in a box (100 × 40 cm and 40 cm high) from which animals can easily be collected. The box was emptied hourly between 0800 and 1800 hours (UTC+2) each day. At 1800, the rest of the trap was also searched, and the remaining dragonflies were removed and counted. The change from the larger to the smaller trap design caused a sharp reduction in the number of dragonflies captured (Appendix Fig. A1). Therefore, we excluded the data using the smaller trap from statistical analyses.

Dragonflies were identified to species level and sexed. Before release, they were marked on the upper side of the wings using waterproof, coloured paint markers (Edding 4000) with a week-specific colour code to determine the proportion of animals recaptured in the trap, and potentially provide insight into movements through resightings of marked individuals. Colour marking the wings of dragonflies is an effective method for mark−recapture studies and has been used for determining local movements and population dynamics (Borisov, 2009; Jacobs, 1955; Keller, Brodbeck, Flöss, Vonwil, & Holderegger, 2010; Kharitonov & Popova, 2011). The putative migratory status of the dragonfly species recorded was based on Corbet (1999) and Schröter (2011) (Table 1).

Orientation Tests

Flight orientation tests were carried out in the middle of an open field adjacent to the trap. The experimental site was located at least 40 m from the nearest visual cues (trees or bushes). We used a circular flight arena made of black mesh stretched by two metal rings (38 cm in diameter and 30 cm high, 1 cm mesh size), placed 45 cm above the ground on a stool of similar surface (Appendix Fig. A2). A video camera (Sony Handycam DCR-SR200, 4
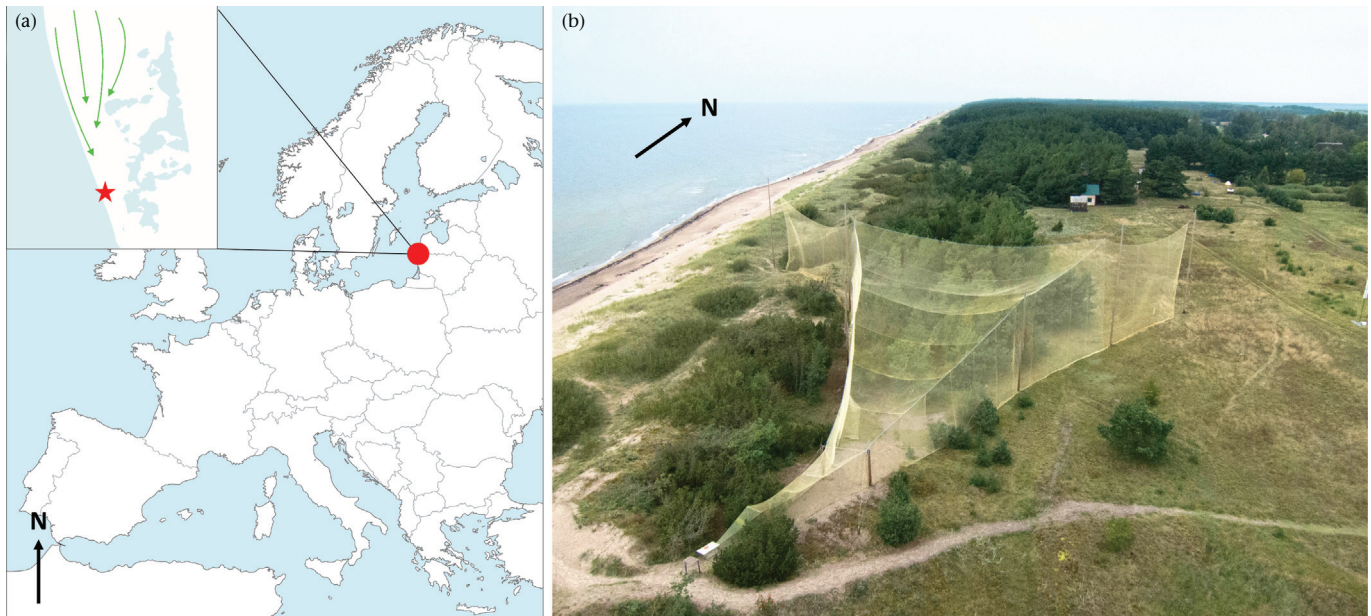
Figure 1. (a) Location of the Pape ornithological research station, Latvia. The red star indicates the position of the Heligoland trap. The green arrows represent the hypothetical flyways due to a bottleneck effect exerted on migrating dragonflies by the Baltic Sea and Pape Lake. (b) Photograph of the large Heligoland trap (Photo: Jasja Dekker).

MP, 60 fps) was positioned above the arena to record flight behaviour. Experiments were conducted with the two most commonly recorded species, *Aeshna mixta* and *Sympetrum vulgatum*. Both *A. mixta* and *S. vulgatum* are considered to be potential migrants (Dyatlova & Kalkman, 2008; Samraoui et al., 1998; Popova & Haritonov, 2014) and were captured in high numbers during the season (Table 1).

Dragonflies were released individually into the flight arena immediately after capture and filmed for 15 min (see Supplementary Video S1). The flight arena was rotated 90° between each experiment to randomize potential effects of the arena on flight direction. The videos were analysed using Solomon Coder software (version beta 16.06.26, Péter, 2011). The body orientation of the dragonfly was recorded every 1/20 s and estimated to the nearest 45°.

Supplementary video related to this article can be found at https://doi.org/10.1016/j.anbehav.2021.04.003

Weather Data

Hourly weather data (air temperature [°C], wind speed [km/h], wind direction [°], air pressure [bar] and humidity [%]) were obtained from a weather station (Davis Vantage Pro 2) situated 15 m above the ground, approximately 60 m from the trap and the orientation set-up. Additionally, cloud cover was recorded every hour on a 0–8 scale, 0 corresponding to no cloud and 8 to a completely overcast sky.

Statistical Analysis

The effect of weather on capture rate

All analyses were conducted in R (version 3.3.1., R Core Team 2016) unless otherwise specified. Initially, we performed a principal components analysis (PCA) to investigate whether the dragonfly species clustered based on their phenology. The PCA revealed that the four most common species (*Aeshna grandis, A. mixta, Sympetrum sanguineum, S. vulgatum*) were separated into two clear

clusters, with *A. mixta* and *A. grandis* forming one group, and *S. sanguineum* and *S. vulgatum* forming another (Appendix Fig. A3). Therefore, subsequent analyses of the influence of weather on abundance were performed based on this grouping. We also restricted our analysis to *A. mixta* and the two *Sympetrum* species, as these are considered to be migratory (Corbet, 1999; Schröter, 2011).

We used generalized linear mixed-effects models (GLMM) assuming a Poisson error distribution in the package 'lme4' (Bates, Mächler, Bolker, & Walker, 2015) to assess the influence of weather conditions (air temperature [°C], wind speed [km/h], wind direction [°], air pressure [bar], humidity [%] and cloud cover) on the number of dragonflies captured/h. As wind direction is circular, ranging from 0 to 360°, for better suitability for linear analysis, the sine and cosine of wind direction were calculated, with the sine corresponding to the east–west and cosine to the north–south components, respectively (Brattström et al., 2008). Trap height and number of days since the start of the sampling were also included in the models. Pairwise correlation between the explanatory variables was tested using Pearson correlation tests, with a correlation coefficient threshold of 0.7. Multicollinearity was investigated using variance inflation factors implemented in 'car' (Fox and Weisberg 2019). None of the variables were significantly correlated. Day number (expressed as ordinal date) was included as a random factor in the models to account for multiple samples per day. Continuous explanatory variables were scaled for the modelling by subtracting the mean and dividing by the standard deviation, using the 'scale' function in R. For all models, only dragonflies captured in the box at the end of the trap were used for the analysis.

Significance of the explanatory variables was determined by excluding the variable of interest and comparing the models with and without the variable, using ANOVA. Models were checked for overdispersion using the 'simulateResiduals' and 'testDispersion' functions implemented via 'DHARMa' (Hartig, 2020). If overdispersion was present, we included an observation level random effect (OLRE) in the model (Harrison, 2014). Models were compared using ANOVA and the OLRE was retained if it significantly improved

Table 1
Abundance and migratory status of dragonflies captured at Pape, Latvia

Species	Abundance	Migratory status
Migrant hawker, *Aeshna mixta*	662	Migrant
Vagrant darter, *Sympetrum vulgatum*	366	Migrant
Ruddy darter, *Sympetrum sanguineum*	231	Migrant
Brown hawker, *Aeshna grandis*	146	Unknown
Common hawker, *Aeshna juncea*	60	Unknown
Southern hawker, *Aeshna cyanea*	49	Unknown
Yellow-spotted emerald, *Somatochlora flavomaculata*	39	Unknown
Green hawker, *Aeshna viridis*	24	Unknown
Southern migrant hawker, *Aeshna affinis*	13	Migrant
Yellow-winged darter, *Sympetrum flaveolum*	7	Migrant
Brilliant emerald, *Somatochlora metallica*	5	Unknown
Common darter, *Sympetrum striolatum*	4	Migrant
Black darter, *Sympetrum danae*	3	Migrant
Black-tailed skimmer, *Orthetrum cancellatum*	3	Unknown
Lesser emperor, *Anax parthenope*	2	Migrant

Migrant as a status encompasses obligate, partial and facultative strategies, as in some cases status is not clear and prone to change depending on latitude, for example. Species with the status unknown are species for which no migration data was found in the literature (Corbet, 1999; Schröter, 2011). Data are from the box at the end of the larger trap (see Methods).

the model fit. Inclusion of an OLRE in the models improved the fit of the final model for both *A. mixta* and *Sympetrum*. As multiple hourly samples were taken per day, we tested for temporal autocorrelation in the model residuals using the 'testTemporalAutocorrelation' function in 'DHARMa', which conducts a Durbin−Watson test. There was no significant autocorrelation in the final models ($P > 0.05$). The marginal and conditional coefficients of determination (pseudo-R^2) were calculated for the final models using the 'r.squaredGLMM' function in the package 'MuMIn' (Barton, 2020). The marginal coefficient ($R^2{}_m$) is the proportion of variance explained by the fixed factors of the model, whereas the conditional coefficient ($R^2{}_c$) also includes the variance explained by the random factors (Nakagawa & Schielzeth, 2013).

Orientation tests

Analysis of the orientation tests was conducted using the software Oriana 4 (Kovach, 1994) and the circular statistics toolbox in Matlab (Berens, 2009). As the marking did not have any significant effect on flight direction (Hotelling's test: $F = 0$, $P < 0.001$), the data of the marked and unmarked dragonflies were pooled for further analyses. Uniformity of the distributions was tested using Moore's modified Rayleigh test, which determines the directedness of the mean vector ($R*$) based on the weighted mean directedness (vector length, r) of each individual (Moore, 1980). Sexes were pooled for the analyses. Multisample tests were performed to compare the orientation of the dragonflies with the overhead wind direction during the experiments. These analyses were carried out using a paired chi-square test in

which the classes with zero observations were dropped, more than 20% of the classes having expected frequencies less than five (Kovach, 2011). For this analysis, wind direction was converted into the direction towards which the wind blows to match the dragonfly flight direction.

Ethical Note

Fieldwork for this study was conducted under the permission of the Nature Conservation Agency of Latvia (permit Nr.14/2016-E). While there are no official ethical requirements when working with insects, care was taken when handling the dragonflies. All dragonflies were captured live in the Heligoland trap (as by-catch) and released following identification and marking. Dragonflies used in the orientation tests were not kept longer than necessary and were released following the experiments. Marked dragonflies did not behave differently than unmarked dragonflies in the orientation tests.

RESULTS

Phenology

In total, 1630 dragonflies were captured in the larger trap (1614 in the end box), of which 75.42% were males and 24.58% females. Overall, 15 species were captured, of which nine are considered to be migratory (Table 1). *Aeshna mixta* accounted for 39.7% of the individuals, followed by *S. vulgatum* (22.4%), *S. sanguineum* (14.4%)

Table 2
Results of generalized linear mixed models of hourly dragonfly abundance in relation to weather

Species	Variables	Estimate	SE	df	χ^2	P value	$R^2{}_m$	$R^2{}_c$
Aeshna	Intercept	−18.831	3.659				0.506	0.887
	Temperature	0.814	0.128	1	30.948	<0.001		
	Cloud cover	−0.117	0.050	1	5.293	0.021		
	Wind direction (cosine)	0.490	0.161	1	9.307	0.002		
	Humidity	0.046	0.021	1	4.666	0.031		
Sympetrum	Intercept	−17.844	2.991				0.465	0.949
	Temperature	0.947	0.155	1	52.657	<0.001		
	Cloud cover	−0.165	0.075	1	4.692	0.030		
	Wind direction (sine)	0.581	0.226	1	6.525	0.011		

Significance of variables was determined based on likelihood ratio tests using ANOVA. Only significant variables ($P < 0.05$) were retained in the final models presented here. Models investigating hourly abundance were fitted with a Poisson error distribution and included day number as a random factor. An observation level random factor was included in the models to account for overdispersion. Model estimates are based on unscaled variables. $R^2{}_m$ and $R^2{}_c$ are the marginal and conditional coefficients of determination for the model, respectively.

and *A. grandis* (9.3%). The other species each accounted for less than 4% of the total dragonflies captured. No damselflies (Zygoptera) were recorded within the trap box.

Of 2055 individuals marked during the study (147 individuals were caught in the small trap and 278 individuals opportunistically in the surrounds and marked), only 66 (3.2%) were recaptured in the trap (Table A1), with a single individual being reported elsewhere (2 km south of the trap; B. Gliwa, personal communication). Most of the recaptures (60.6%) took place in the same week the marking was done and the longest time interval between marking and recapture was approximatively 1 month.

Phenology differed between the four most commonly captured species. The median date of passage for *A. mixta* (26 August, interquartile range, IQR = 21 August − 28 August) and *A. grandis* (25 August, IQR = 22 August − 31 August) tended to be slightly earlier in the season than for the smaller *S. vulgatum* (1 September, IQR = 26 August − 8 September) and *S. sanguineum* (28 August, IQR = 26 August − 1 September; Appendix Fig. A1). Daily mean capture time was earlier for *A. mixta* (1307 ± 0251 SD) and *A. grandis* (1241 ± 0206 SD) compared to *S. vulgatum* (1436 ± 0200 SD) and *S. sanguineum* (1444 ± 0207 SD; Appendix Fig. A4).

The Effect of Weather on Capture Abundance

Hourly abundance of *A. mixta* was positively influenced by temperature (chi-square test: X^2_1 = 30.948, P < 0.001) and northerly winds (chi-square test: X^2_1 = 9.307, P = 0.002),

and negatively by cloud cover (chi-square test: X^2_1 = 5.293, P = 0.021), but was also positively influenced by humidity (chi-square test: X^2_1 = 4.666, P = 0.031, N = 251 h; Table 2, Fig. 2).

Similarly to *A. mixta*, hourly abundance of *Sympetrum* spp. was positively influenced by temperature (chi-square test: X^2_1 = 52.657, P < 0.001) and negatively by cloud cover (chi-square test: X^2_1 = 4.692, P = 0.030, N = 251 h; Table 2, Fig. 3). In contrast, hourly abundance of *Sympetrum* spp. increased with more easterly winds (sine of wind direction, chi-square test: X^2_1 = 6.525, P = 0.011).

Orientation Tests

Moore's modified Rayleigh tests rejected uniformity of distribution and showed significantly directed flight for both *A. mixta* (mean vector = 165.92°, Moore's modified Rayleigh test: R^* = 1.677, P < 0.001) and *S. vulgatum* (mean vector = 198.85°, R^* = 1.142, P < 0.025). Mean flight orientation (μ) for both species was significantly different from overhead wind direction during the experiments (*A. mixta*, chi-square test: X^2_1 = 27.259, P < 0.001; *S. vulgatum*, chi-square test: X^2_1 = 19.2, P = 0.008; Table 3, Fig. 4).

DISCUSSION

There is a growing body of evidence for seasonally directed autumn migratory movements in large and medium-sized insects,
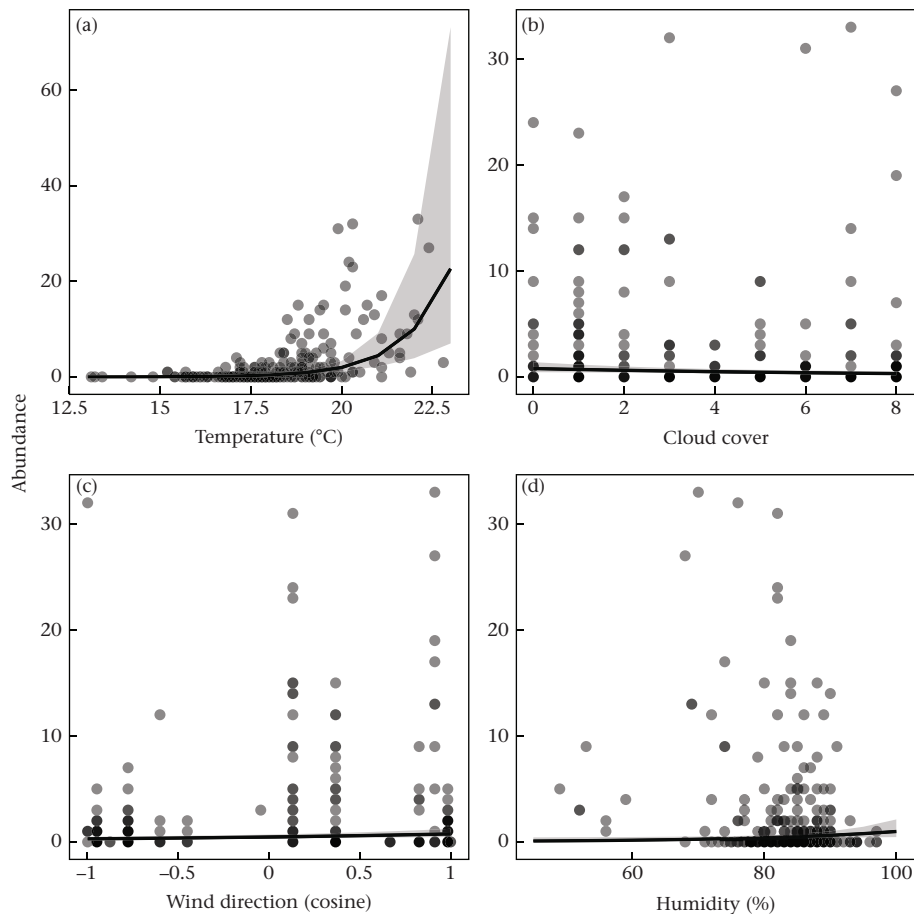
Figure 2. Relationship between the hourly abundance of *Aeshna mixta* and weather variables (a) temperature, (b) cloud cover, (c) wind direction (cosine) and (d) humidity. Results are based on a generalized linear mixed model with a Poisson distribution. The shaded areas represent 95% confidence intervals. For the cosine component of wind direction (−1) equals south and (+1) equals north.
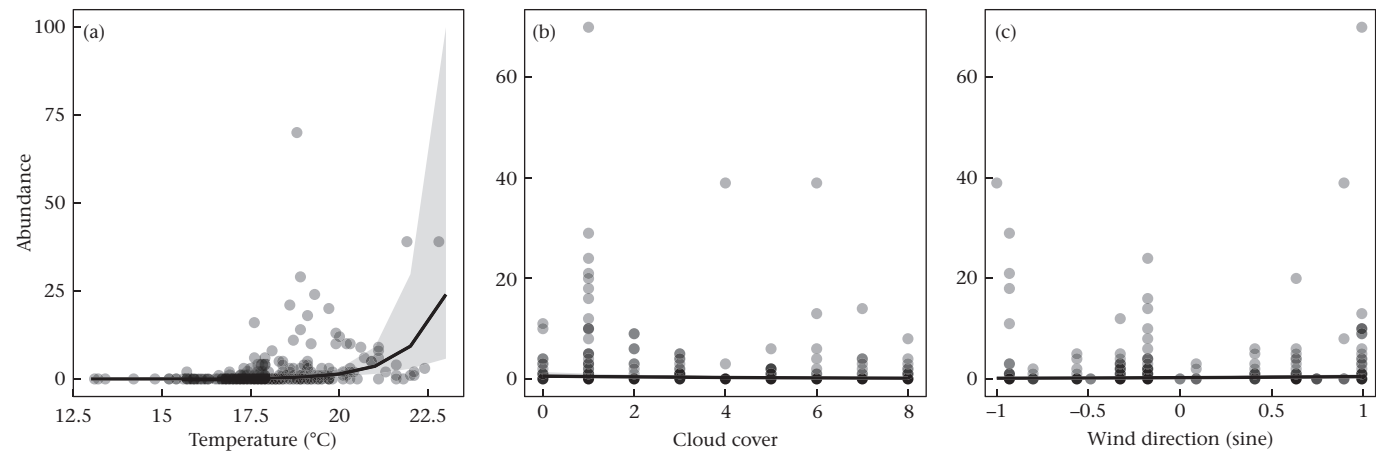
Figure 3. Relationship between the hourly abundance of *Sympetrum vulgatum* and *Sympetrum sanguineum* and weather variables (a) temperature, (b) cloud cover and (c) wind direction (sine). Results are based on a generalized linear mixed model with a Poisson distribution. The shaded areas represent 95% confidence intervals. For the sine component of wind direction (−1) equals west and (+1) equals east.

Table 3
Results of the flight orientation experiments for *A. mixta* and *S. vulgatum*

		A. mixta	*S. vulgatum*
One-sample tests	*N*	23	14
	Mean vector (μ)	166.67°	205.36°
	Length of μ	0.609	0.389
	SE of mean	12.32°	29.88°
	Grand mean vector (GM)	165.92°	198.85°
	Length of GM	0.412	0.334
	Moore's Rayleigh (*R**)	1.667	1.142
	Moore's Rayleigh (*P*)	<0.001	<0.025
Multisample tests	χ^2 pairwise	27.259	19.2
	χ^2 pairwise (*P*)	<0.001	0.008

Uniformity of direction was tested using Moore's modified Rayleigh tests, where *R** represents the directedness of the mean vector. Multisample tests were conducted to compare (μ) matched with the corresponding wind direction.
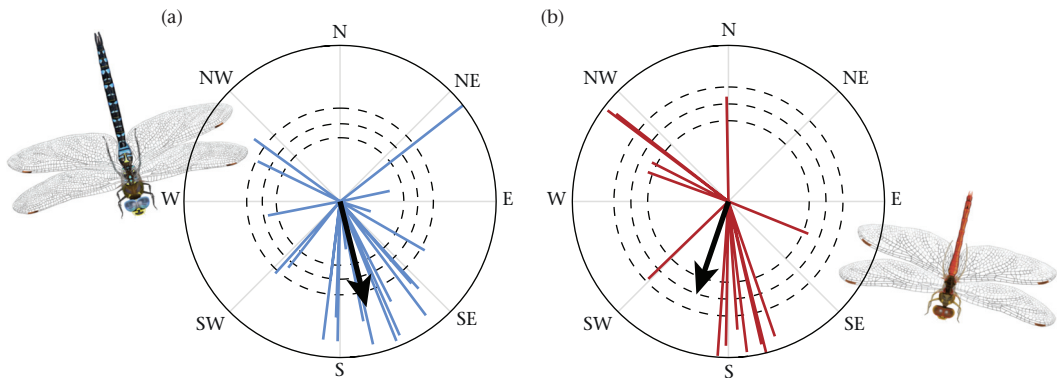
Figure 4. Results of the flight orientation tests. (a) and (b) represent the orientation direction of the dragonflies *A. mixta* (*N* = 23) and *S. vulgatum* (*N* = 14), respectively. The black arrows represent the weighted mean direction of the dragonflies as a group. The length of the black arrows represents the *R** value according to Moore's modified Rayleigh tests. The blue (a) and red (b) vectors (radial lines) represent the mean flight direction of the individual dragonflies. Directedness (*r*) for each dragonfly is represented by the length of each vector. The dashed circles indicate the significance levels of directional movement (Moore's modified Rayleigh test; from inner to outer dashed circle: *P* < 0.05; *P* < 0.01; *P* < 0.001).

including day-flying species (Chapman et al., 2015; Gao et al., 2020; Hu et al., 2016; Knight et al., 2019; Srygley & Dudley, 2008; Wotton et al., 2019). In dragonflies, directional autumn movements towards the south have been shown for long-distance migrant species such

as *A. junius* (Knight et al., 2019; Wikelski et al., 2006). However, relatively few systematic studies on migratory behaviour in dragonflies have been made in Europe (e.g. Shapoval & Buczyński, 2012). Our orientation tests revealed a strong unimodal flight

direction for *A. mixta and S. vulgatum* towards the south-southeast (166° and 199°, respectively) in autumn, which differed from the overhead wind direction.

In our models, temperature and cloud cover were the most important variables affecting hourly abundance of *A. mixta* and the two *Sympetrum* species tested. While temperature was positively correlated with hourly abundance, cloud cover negatively influenced dragonfly abundance. Both temperature and cloud cover are well-known predictors for insect migration rates (e.g. Brattström et al., 2008), and temperature has been shown to influence groundspeed of migrating *A. junius* (Knight et al., 2019). This general pattern regarding the influence of temperature and cloud cover is likely to be due to the effect of increased sunshine on flight activity in day-flying insects (Becciu et al., 2019).

Hourly abundance of *A. mixta* was higher in tail winds (in this case, northerlies). Given the predominant southerly flight direction of *A. mixta* revealed in our orientation tests, this pattern might be indicative of the ability to select favourable tail winds, which would facilitate migration. Many migratory insects such as dragonflies, moths and hoverflies have been shown to select favourable winds, possibly as an adaptation to maximize distance covered, optimize trajectories and reduce energy costs in their displacements (Alerstam et al., 2011; Anderson, 2009; Becciu et al., 2019; Gao et al., 2020; Knight et al., 2019). Across the study period, the prevailing winds from the southwest and west, coming from the Baltic sea, were the strongest and most frequent, while the less common winds from the east were of lower speed. The hourly abundance of *Sympetrum* increased with easterlies, which may indicate an adaptive response, flying lower to minimize drag and consequently drift due to a reduction in side-winds, or to avoid the possibility of being blown out to sea. Interestingly, an increase in *Sympetrum* in relation to easterly winds has been noted on the Curonian spit (Bertram & Haacks, 1999).

While many studies mention that dragonfly migration takes place predominantly in the flight boundary layer (Chapman, Drake, & Reynolds, 2011; Srygley & Dudley, 2008), high-altitude movements up to 1000 m above ground level have been documented for the migratory *P. flavescens* (Feng et al., 2006). We therefore cannot be sure whether the increase in passage intensity of *A. mixta* in tail winds (assuming a general southerly flight direction, based on the results of orientation tests) is limited to ground level or whether passage also intensifies at higher altitudes. In any case, at ringing stations where birds are captured during active migration, songbirds are usually captured in higher numbers when they are facing head winds (Komenda-Zehnder, Jenni, & Liechti, 2010), flying lower to minimize the effect of the wind, which is also the case at Pape (M. Briedis, personal communication). Birds tend to fly higher in tail winds to take advantage of directionally beneficial winds (Becciu et al., 2019; Komenda-Zehnder et al., 2010). Insects that are strong fliers, such as dragonflies, adopt similar strategies (Becciu et al., 2019; Chapman et al., 2015).

The differences observed in the abundance of *Aeshna* and *Sympetrum* throughout the day may be explained by physiological differences found between larger and smaller dragonfly species. Contrasting our results, the minimum temperature at which flight is possible has been shown to be positively correlated with body weight in dragonflies (May, 1976). However, differences in diel activity patterns may also arise because of inherent behavioural differences between species.

While the dragonflies captured in the trap may have been a mixture of migrating and local individuals, our results show that there were some differences in the way weather impacts flight behaviour of larger versus smaller dragonfly species. Generally, abundance, considered here as indicative of migration intensity, increased with temperature and decreased with cloud cover.

Moreover, based on the orientation tests, we have strong support that migration of *A. mixta* and some *Sympetrum* species does take place along the Baltic coast.

Investigation of migratory behaviour at altitude and the origin of individuals, which would provide further insight into migration routes and migratory behaviour, could be answered using a combination of techniques, such as radar (Chapman, Drake, & Reynolds, 2011; Drake & Reynolds, 2012), radiotelemetry (Knight et al., 2019; Wikelski et al., 2006) and stable isotope analysis of wing chitin (Hallworth et al., 2018; Hobson et al., 2012).

SUPPLEMENTARY MATERIAL

Supplementary material associated with this article can be found online at https://doi.org/10.1016/j.anbehav.2021.04.003.

References

Alerstam, T., Chapman, J. W., Backman, J., Smith, A. D., Karlsson, H., Nilsson, C., et al. (2011). Convergent patterns of long-distance nocturnal migration in noctuid moths and passerine birds. *Proceedings of the Royal Society B: Biological Sciences, 278*, 3074–3080.

Alerstam, T., & Christie, D. A. (1991). *Bird Migration*. Cambridge, U.K.: Cambridge University Press.

Alerstam, T., Hedenström, A., Åkesson, S., Hedenstrom, A., & Akesson, S. (2003). Long-distance migration: Evolution and determinants. *Oikos, 103*, 247–260.

Anderson, R. C. (2009). Do dragonflies migrate across the western Indian Ocean? *Journal of Tropical Ecology, 25*, 347–358.

Aubert, J. (1962). Observations sur les migrations d'insectes au col de Bretolet (Alpes valaisannes, 1923m.). Note préliminaire. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft, 35*, 130–138.

Aubert, J. (1964). L'activité entomologique de l'observatoire du col de Bretolet. *Bulletin de la Murithienne, 81*, 105–131.

Barton, K. (2020). *MuMIn: Multi-Model Inference*. R package version 1.43.17. https://cran.r-project.org/package=MuMIn.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-models using lme4. *Journal of Statistical Software, 67*, 1–48.

Bauer, S., & Hoye, B. J. (2014). Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science, 344*, 1242552.

Bauer, S., & Klaassen, M. (2013). Mechanistic models of animal migration behaviour—their diversity, structure and use. *Journal of Animal Ecology, 82*, 498–508.

Becciu, P., Menz, M. H. M., Aurbach, A., Cabrera-Cruz, S. A., Wainwright, C. E., Scacco, M., et al. (2019). Environmental effects on flying migrants revealed by radar. *Ecography, 42*, 942–955.

Berens, P. (2009). CircStat: A Matlab toolbox for circular statistics. *Journal of Statistical Software, 31*, 10.

Bertram, G., & Haacks, M. (1999). Beobachtungen von windverdrifteten Libellen auf der Kurischen Nehrung im September 1998. *Libellula, 18*, 89–94.

Borisov, S. N. (2009). Study of dragonfly (Odonata) migrations in the Western Tien Shan mountains using ornithological traps. *Entomological Review, 89*, 1025–1029.

Brattström, O., Kjellén, N., Alerstam, T., & Åkesson, S. (2008). Effects of wind and weather on red admiral, *Vanessa atalanta*, migration at a coastal site in southern Sweden. *Animal Behaviour, 76*, 335–344.

Buczyński, P., Shapoval, A., & Bunczyńka, E. (2014). Pantala flavescens at the coast of the Baltic sea (odonata: Libellulidae). *Odonatologica, 43*, 3–11.

Calvert, P. P. (1893). Catalogue of the Odonata (dragonflies) of the vicinity of Philadelphia , with an introduction to the study of this group of insects. *American Entomological Society, 20*, 153–272.

Chapman, J. W., Drake, V. A., & Reynolds, D. R. (2011). Recent insights from radar studies of insect flight. *Annual Review of Entomology, 56*, 337–356.

Chapman, J. W., Klaassen, R. H. G., Drake, V. A., Fossette, S., Hays, G. C., Metcalfe, J. D., et al. (2011). Animal orientation strategies for movement in flows. *Current Biology, 21*, 861–870.

Chapman, J. W., Reynolds, D. R., Mouritsen, H., Hill, J. K., Riley, J. R., Sivell, D., et al. (2008). Wind selection and drift compensation optimize migratory pathways in a high-flying moth. *Current Biology, 18*, 514–518.

Chapman, J. W., Reynolds, D. R., & Smith, A. D. (2003). Vertical-looking radar: A new tool for monitoring high-altitude insect migration. *BioScience, 53*, 503–511.

Chapman, J. W., Reynolds, D. R., & Wilson, K. (2015). Long-range seasonal migration in insects: Mechanisms, evolutionary drivers and ecological consequences. *Ecology Letters, 18*, 287–302.

Corbet, P. S. (1999). *Dragonflies: Behavior and Ecology of Odonata*. London, U.K.: Comstock.

Dingle, H. (2014). *Migration: The Biology of Life on the Move*. Oxford University Press.

Dingle, H., & Drake, V. A. (2007). What is migration? *BioScience, 57*, 113–121.

Drake, V. A., & Reynolds, D. (2012). *Radar Entomology: Observing Insect Flight and Migration*. Wallingford, U.K.: CABI.

Dumont, H. J., & Hinnekint, B. O. N. (1973). Mass migration in dragonflies, especially in *Libellula quadrimaculata* L.: A review, a new ecological approach and a new hypothesis. *Odonatologica, 2*, 1–20.

Dyatlova, E. S., & Kalkman, V. J. (2008). Massive migration of *Aeshna mixta* and *Sympetrum meridionale* in the Ukrainian danube delta (Odonata-Anisoptera: Aeschnidae, libellulidae). *Entomologische Berichten, 65*, 188–190.

Feng, H. Q., Wu, K. M., Ni, Y. X., Cheng, D. F., & Guo, Y. Y. (2006). Nocturnal migration of dragonflies over the Bohai Sea in northern China. *Ecological Entomology, 31*, 511–520.

Flockhart, D. T. T., Wassenaar, L. I., Martin, T. G., Hobson, K. A., Wunder, M. B., & Norris, D. R. (2013). Tracking multi-generational colonization of the breeding grounds by monarch butterflies in eastern North America. *Proceedings of the Royal Society B: Biological Sciences, 280*, 20131087.

Gao, B., Wotton, K. R., Hawkes, W. L. S., Menz, M. H. M., Reynolds, D. R., Zhai, B.-P., et al. (2020). Adaptive strategies of high-flying migratory hoverflies in response to wind currents. *Proceedings of the Royal Society B, 287*, 20200406.

Hallworth, M. T., Marra, P. P., McFarland, K. P., Zahendra, S., & Studds, C. E. (2018). Tracking dragons: Stable isotopes reveal the annual cycle of a long-distance migratory insect. *Biology Letters, 14*, 20180741.

Harrison, X. A. (2014). Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ, 2*, e616.

Hartig, F. (2020). *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models*. R package version 0.3.2.0. https://cran.r-project.org/package=DHARMa.

Hobson, K. A., Soto, D. X., Paulson, D. R., Wassenaar, L. I., & Matthews, J. H. (2012). A dragonfly (δ^2H) isoscape for north America: A new tool for determining natal origins of migratory aquatic emergent insects. *Methods in Ecology and Evolution, 3*, 766–772.

Holland, R. A., Wikelski, M., & Wilcove, D. S. (2006). How and why do insects migrate? *Science, 313*, 794–796.

Huestis, D. L., Dao, A., Diallo, M., Sanogo, Z. L., Samake, D., Yaro, A. S., et al. (2019). Windborne long-distance migration of malaria mosquitoes in the Sahel. *Nature, 574*, 404–408.

Hu, G., Lim, K. S., Horvitz, N., Clark, S. J., Reynolds, D. R., Sapir, N., et al. (2016). Mass seasonal bioflows of high-flying insect migrants. *Science, 354*, 1584–1587.

Jacobs, M. E. (1955). Studies on territorialism and sexual selection in dragonflies. *Ecology, 36*, 566–586.

Johnson, C. G. (1969). *Migration and Dispersal of Insects by Flight*. London, U.K.: Methuen.

Jones, C. M., Parry, H., Tay, W. T., Reynolds, D. R., & Chapman, W. J. (2019). Movement ecology of pest *Helicoverpa*: Implications for ongoing spread. *Annual Review of Entomology, 64*, 277–295.

Keller, D., Brodbeck, S., Flöss, I., Vonwil, G., & Holderegger, R. (2010). Ecological and genetic measurements of dispersal in a threatened dragonfly. *Biological Conservation, 143*, 2658–2663.

Kharitonov, A. Y., & Popova, O. N. (2011). Migrations of dragonflies (odonata) in the south of the west siberian plain. *Entomological Review, 91*, 411–419.

Knight, S. M., Pitman, G. M., Flockhart, D. T. T., & Norris, D. R. (2019). Radio-tracking reveals how wind and temperature influence the pace of daytime insect migration. *Biology Letters, 15*, 20190327.

Komenda-Zehnder, S., Jenni, L., & Liechti, F. (2010). Do bird captures reflect migration intensity?–Trapping numbers on an Alpine pass compared with radar counts. *Journal of Avian Biology, 41*, 434–444.

Kovach, W. L. (1994). *Oriana for windows, Version 4.0*. Wales, UK: Kovach computer services.

Kovach, W. L. (2011). *Oriana's user manual, Version 4.0*. Pentraeth, U,K: Kovach Computer Services.

Krauel, J. J., Westbrook, J. K., & Mccracken, G. F. (2015). Weather-driven dynamics in a dual-migrant system: Moths and bats. *Journal of Animal Ecology, 84*, 604–614.

Lack, D., & Lack, E. (1951). Migration of insects and birds through a pyrenean pass. *Journal of Animal Ecology, 20*, 63–67.

May, M. L. (1976). Thermoregulation and adaptation to temperature in dragonflies (Odonata: Anisoptera). *Ecological Monographs, 46*, 1–32.

May, M. L. (2013). A critical overview of progress in studies of migration of dragonflies (Odonata: Anisoptera), with emphasis on North America. *Journal of Insect Conservation, 17*, 1–15.

May, M. L., & Matthews, J. H. (2008). Migration in odonata: A case study of *Anax junius*. In A. Córdoba-Aguilar (Ed.), *Dragonflies, model organisms for ecological and evolutionary research* (pp. 63–77). Oxford, U.K.: Oxford University Press.

Moore, B. R. (1980). A modification of the Rayleigh test for vector data. *Biometrika, 67*, 175–180.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution, 4*, 133–142.

Parr, A. J. (1996). Dragonfly movement and migration in Britain and Ireland. *Journal of the British Dragonfly Society, 12*, 33–50.

Parr, A. (2010). Monitoring of Odonata in Britain and possible insights into climate change. *BioRisk, 5*, 127–139.

Péter, A. (2011). *Solomon coder (version beta 16.06.26): a simpler solution for behaviour coding*. https://solomon.andraspeter.com.

Popova, O. N., & Haritonov, A. Y. (2014). Mass reproductive wanderings of dragonflies of the genus Sympetrum (Odonata, Libellulidae). *Entomological Review, 94*, 21–28.

R Core Team. (2016). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

von Rintelen, T. (1997). Eine vogelreuse als libellenfalle: Beobachtungen in der Vogelwarte Pape, lettland. *Libellula, 16*, 61–64.

Russell, R. W., May, M. L., Soltesz, K. L., & Fitzpatrick, J. W. (1998). Massive swarm migrations of dragonflies (odonata) in eastern north America. *The American Midland Naturalist, 140*, 325–342.

Samraoui, B., Bouzid, S., Boulahbal, R., & Corbet, P. S. (1998). Postponed reproductive maturation in upland refuges maintains life-cycle continuity during the hot, dry season in algerian dragonflies (Anisoptera). *International Journal of Odonatology, 1*, 119–135.

Satterfield, D. A., Sillett, T. S., Chapman, J. W., Altizer, A., & Marra, P. P. (2020). Seasonal insect migrations: Massive, influential, and overlooked. *Frontiers in Ecology and the Environment, 18*, 335–344.

Schröter, A. (2011). A mass migration of *Aeshna affinis* in southern Kyrgyzstan: Attempt to provide a spatial and temporal reconstruction (odonata: Aeshnidae). *Libellula, 30*, 203–232.

Shapoval, A. P., & Buczyński, P. (2012). Remarkable odonata caught in ornithological traps on the courish spit, kaliningrad oblast, Russia. *Libellula, 31*, 97–109.

Srygley, R. B. (2003). Wind drift compensation in migrating dragonflies *Pantala* (Odonata: Libellulidae). *Journal of Insect Behavior, 16*, 217–232.

Srygley, R. B., & Dudley, R. (2008). Optimal strategies for insects migrating in the flight boundary layer: Mechanisms and consequences. *Integrative and Comparative Biology, 48*, 119–133.

Stefanescu, C., Soto, D. X., Talavera, G., Vila, R., & Hobson, K. A. (2016). Long-distance autumn migration across the Sahara by painted lady butterflies: exploiting resource pulses in the tropical savannah. *Biology letters, 12*(10), 20160561. https://doi.org/10.1098/rsbl.2016.0561

Šuba, J., Petersons, G., & Rydell, J. (2012). Fly-and-forage strategy in the bat *Pipistrellus nathusii* during autumn migration. *Acta Chiropterologica, 14*, 379–385.

Thoma, M., & Althaus, S. (2015). Beobachtungen von Libellen (Odonata) auf dem Col de Bretolet (VS). *Entomo Helvetica, 8*, 97–109.

Troast, D., Suhling, F., Jinguji, H., Sahlén, G., & Ware, J. (2016). A global population genetic study of *Pantala flavescens*. *PloS One, 11*, 1–13.

Wainwright, C. E., Stepanian, P. M., Reynolds, R. R., & Reynolds, A. M. (2017). The movement of small insects in the convective boundary layer: Linking patterns to processes. *Scientific Reports, 7*, 5438.

Wikelski, M., Moskowitz, D., Adelman, J. S., Cochran, J., Wilcove, D. S., & May, M. L. (2006). Simple rules guide dragonfly migration. *Biology Letters, 2*, 325–329.

Wotton, K. R., Gao, B., Menz, M. H. M., Morris, R. K. A., Ball, S. G., Lim, K. S., et al. (2019). Mass seasonal migrations of hoverflies provide extensive pollination and crop protection services. *Current Biology, 29*, 2167–2173.

Appendix

**Table A1**
Number of recaptured marked dragonflies per species

| Species	Number of recaptures
Aeshna mixta	30
Sympetrum vulgatum	12
Aeshna grandis	12
Sympetrum sanguineum	4
Aeshna cyanea	2
Aeshna juncea	2
Aeshna sp.	2
Aeshna viridis	1
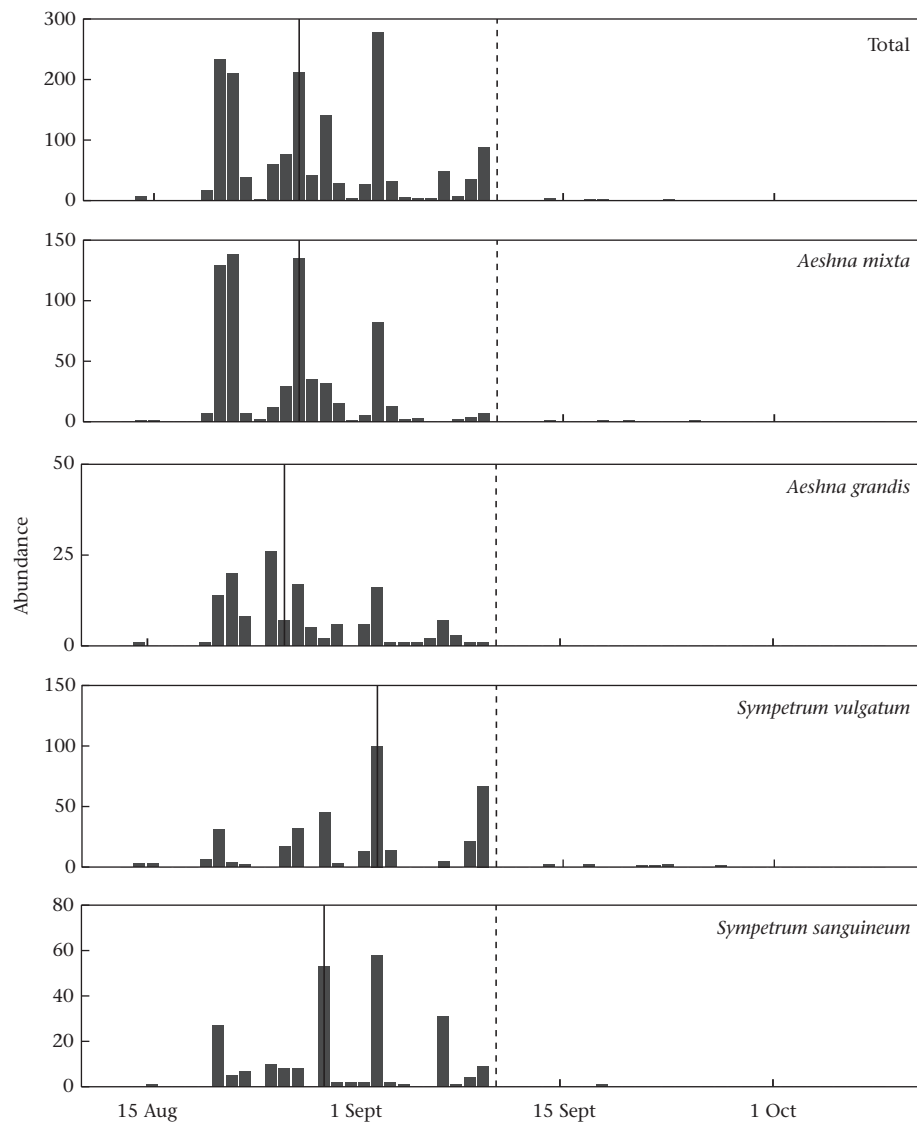
Figure A1. Phenology of dragonflies captured at Pape, Latvia during the study period (13 August to 9 October). The vertical dark line represents the median day of passage and the dotted line represents the date at which the large trap was taken down and replaced by the smaller trap.
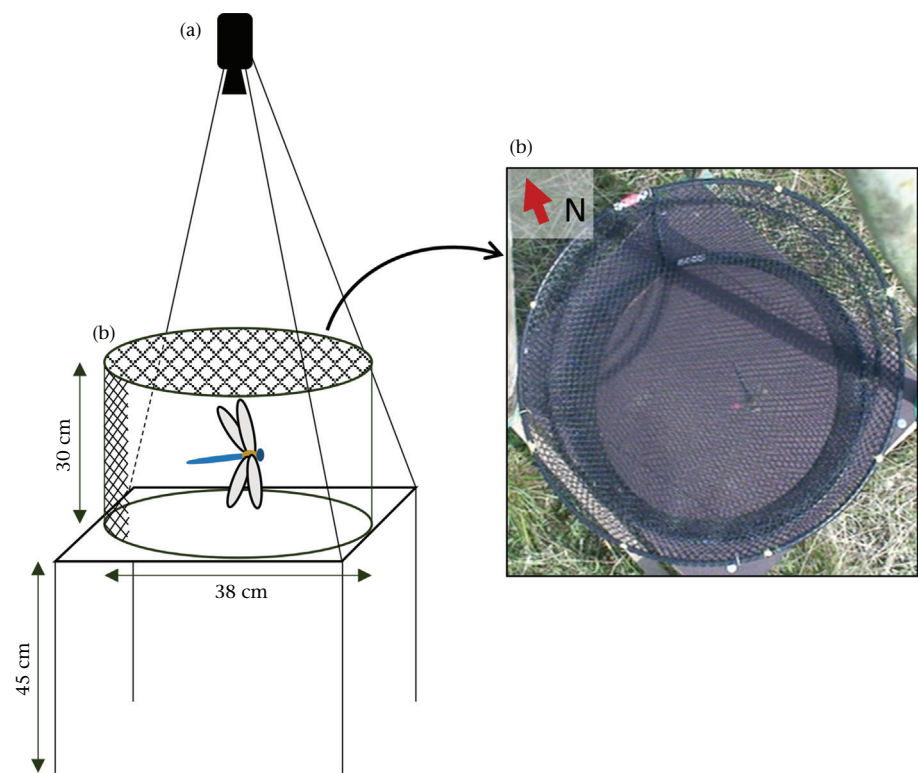
Figure A2. Set-up used for the orientation tests. A camera (a) was fixed above the flight arena (b) placed on a stool.
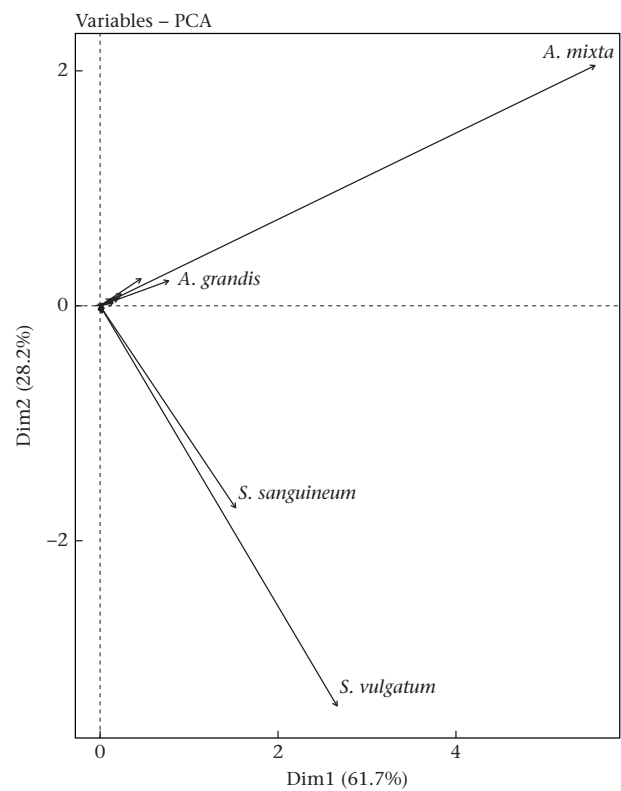
Figure A3. Principal components analysis of overall migration phenology. The first principal component (Dim1) explains 61.7% of the variance; 89.9% of the variance is accounted for in total by the two first components (Dim1 and Dim2). For better visibility only the four most commonly captured dragonfly species are labelled.
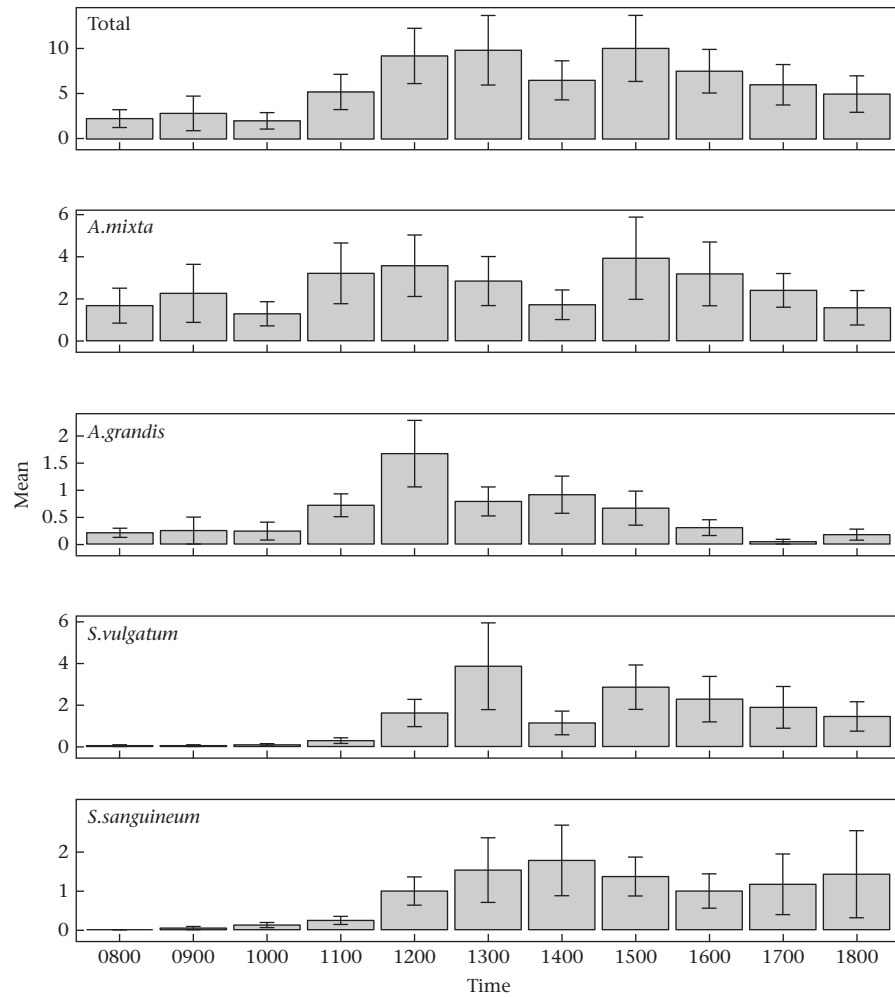
Figure A4. Daily phenology (mean ± SE) from the large trap (13 August to 9 September) of all captured species (Total) and of the four most commonly captured species.