1 **Influence of weather on dragonfly migration and flight behaviour along the Baltic**
2 **coast**

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14 Running title: Influence of weather on dragonfly migration.

15

16

17 **Abstract**

18 Despite mass movements of dragonflies being documented for decades, the influence of
19 weather on the movement decisions and movement intensity of dragonflies has rarely
20 been studied. Here, we investigate the influence of local weather conditions on flight
21 behaviour of dragonflies in Europe, taking advantage of large movements of dragonflies
22 occurring along the Baltic Sea coast of Latvia. Firstly, we performed orientation tests
23 with individual dragonflies of two commonly captured species, *Aeshna mixta* and
24 *Sympetrum vulgatum*, in order to determine if dragonflies showed directed flight and
25 whether flight direction was independent from wind direction. *Aeshna mixta* displayed a
26 uniform mean southward orientation (166.7°), independent from prevailing wind
27 directions, whereas *S. vulgatum* did not show a uniform orientation. Secondly, we
28 investigated the influence of weather conditions on the abundance of dragonflies
29 captured. Behavioural differences in relation to weather conditions were observed
30 between *A. mixta* and the two smaller *Sympetrum* species (*S. vulgatum* and *S.*
31 *sanguineum*). Generally, temperature, cloud cover and wind direction were the most
32 important predictors for migration intensity, with temperature positively influencing
33 abundance and cloud cover negatively influencing abundance. *Aeshna mixta* appeared to
34 select favourable tailwinds (northerlies), whereas hourly abundance of *Sympetrum*
35 increased with more easterly winds. Our results provide important information on the
36 influence of local weather conditions on the flight behaviour of dragonflies, as well as
37 evidence of migration for *A. mixta* and most likely some *Sympetrum* species along the
38 Baltic coast.

39
40 *Keywords:* *Aeshna*, flight behaviour, insect migration, orientation, *Sympetrum*, wind

41

42 INTRODUCTION

43 Migration has evolved independently in a multitude of taxa within many of the major
 44 animal lineages (Alerstam et al. 2003; Dingle and Drake 2007; Bauer and Hoyer 2014;
 45 Dingle 2014). Insects are the most abundant and diverse group of terrestrial migrants
 46 (Holland et al. 2006; Dingle and Drake 2007; Chapman et al. 2015; Hu et al. 2016;
 47 Satterfield et al. 2020), yet migratory behaviour has only been well studied in relatively
 48 few insect taxa, often restricted to iconic species, such as the Monarch butterfly, *Danaus*
 49 *plexippus* (Flockhart et al. 2013) or agricultural pests (Johnson 1969; Drake and Reynolds
 50 2012; Chapman et al. 2015; Jones et al. 2019) and beneficial species (Wotton et al. 2019;
 51 Gao et al. 2020). Over the last 50 years, new tools have been developed to study insect
 52 migration at a higher resolution, for example using vertical-looking radars (Chapman et
 53 al. 2003, 2011a; Drake and Reynolds 2012), and radio-telemetry (Wikelski et al. 2006;
 54 Knight et al. 2019). Intrinsic markers such as stable isotopes have also been used to
 55 successfully track population-scale movements across the migratory cycle (Hobson et al.
 56 2012; Flockhart et al. 2013; Stefanescu et al. 2016; Hallworth et al. 2018). These
 57 approaches have highlighted the importance of insect migration with respect to biomass
 58 movements and ecological impacts (Hu et al. 2016; Wotton et al. 2019) and have
 59 provided information regarding migratory routes and specific parameters such as
 60 migration height or flight speed (Drake and Reynolds 2012; Chapman et al. 2015). And
 61 yet, insect migration is still largely unquantified, and the migratory behaviour and
 62 movements of many species remains elusive. Consequently, the use of more traditional
 63 methodology, such as flight interception traps and systematic counts can provide critical
 64 baseline information for determining population trends, migratory phenology, and
 65 behaviour in relation to local weather and topography (Brattström et al. 2008; Krauel et
 66 al. 2015).

67

68 Many insects are able to select suitable conditions for their migration (Brattström et al.
69 2008; Chapman et al. 2011b; Drake and Reynolds 2012, Gao et al. 2020) and factors such
70 as temperature and pressure can influence movement behaviour, as well as provide cues
71 for the initiation and termination of migration (Johnson 1969; Wikelski et al. 2006;
72 Brattström et al. 2008; Bauer and Klaassen 2013). While many weak-flying smaller
73 insects, for example aphids, have their migratory displacements dictated mostly by wind
74 (Chapman et al. 2011a,b; Hu et al. 2016; Wainwright et al. 2017; Huestis et al. 2019),
75 larger insects such as moths, butterflies and dragonflies are, to a certain extent, able to
76 control their direction relative to the ground by (partially) compensating for drift as well
77 as exploiting tail-winds (Srygley 2003; Chapman et al. 2008). Some large, low-flying
78 diurnal insects – such as butterflies and dragonflies – often migrate within their ‘flight
79 boundary layer’ – the zone extending up from the ground where the ambient wind speed
80 is lower than the insect’s airspeed (Srygley and Dudley 2008). For these migrants, some
81 proximate weather variables, for example air temperature, wind speed and direction or
82 cloud cover, seem to be recurrent cues which initiate or maintain migratory movements
83 (Wikelski et al. 2006; Brattström et al. 2008; Chapman et al. 2015). Furthermore, aerial
84 migration of some insects often concentrates along topographic elements that may act as
85 barriers or bottlenecks, funnelling migrating animals (Becciu et al. 2019). For example,
86 large concentrations of migrating insects can be observed in areas such as mountain
87 chains, alpine passes (Lack and Lack 1951; Aubert 1962, 1964; Borisov 2009; Thoma
88 and Althaus 2015) or coastlines (Russell et al. 1998; Corbet 1999; Brattström et al. 2008).
89
90 While there have been numerous anecdotal reports of dragonfly movement and migration
91 worldwide, beginning in 1494 (Calvert 1893), few studies have systematically

documented this phenomenon (Feng et al. 2006; May and Matthews 2008; Shapoval and Buczyński 2012; Hallworth et al. 2018), and relatively little is known about the detailed behaviour and ecology of dragonfly migration (Dumont and Hineken 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 radio telemetry has provided insights into migration behaviour on an individual level, with information on speed, direction and preferred weather conditions of migrating *Anax junius* in the United States (Wikelski et al. 2006; Knight et al. 2019). 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) through the use of radar (Feng et al. 2006), stable isotopes (Hobson et al. 2012) and molecular tools (Troast et al. 2016). However, much of our knowledge of dragonfly migration is based on these two iconic species. Dragonflies impact both aquatic and terrestrial ecosystems (Van Buskirk 1988). Their role as natural enemies of pests, such as mosquitoes or aphids, as prey for birds and amphibians (Corbet 1999), but also as bioindicators of freshwater quality (Bulankova 1997, Smith et al. 2007, Da Silva Monteiro Júnior et al. 2015), makes understanding their dynamics and movements important for understanding ecosystem functioning.

By taking advantage of large, annually recurring autumn movements of dragonflies along the Baltic Sea coast, we investigated dragonfly orientation, flight phenology and behaviour, with respect to weather conditions, to provide evidence that the movements observed could be attributed to (long-distance) migration. Specifically, we (1) investigated if dragonflies showed directional flight, and if this is independent from wind direction, (2) investigated how weather conditions influence the strength of dragonfly

117 movement, and (3) explored how movement phenology in relation to weather conditions
118 varied between species.

119

120 **MATERIALS AND METHODS**

121 **Study site and sampling**

122 The study took place at the Pape ornithological station in south-western Latvia
123 (56°09'59"N, 21°01'03"E; Figure 1a). The station is situated on the Baltic Sea coast with
124 Pape Lake to the east. Pape Lake is situated parallel to the sea, possibly generating a
125 bottleneck effect on migrating birds and insects (M. Briedis pers. comm.), which often
126 avoid flying over open waters (Alerstam and Christie 1991; Corbet 1999; Becciu et al.
127 2019), thereby funnelling the migrants along the strip of land between the lake and the
128 sea (von Rintelen 1997; Figure 1a).

129

130 During summer and autumn, the station successively operates two funnel traps that open
131 to the North (Figure 1b) – also called Heligoland or “Rybachy” traps. These traps are
132 primarily used to catch migrating birds and bats (Šuba et al. 2012; Voigt et al. 2012), but
133 also trap a large number of migrating insects, in particular dragonflies (von Rintelen
134 1997). The two traps are of different size and are situated at the same location.

135 Dragonflies were caught between 13 August and 9 September 2016 using the large
136 Heligoland trap (entrance size 15 m high x 35 m wide x 40 m long). From 11 September
137 to 9 October, the larger trap was replaced by a smaller trap (entrance size 6 m high x
138 11.40 m wide x 28 m long). Trap replacement is the standard procedure of the ringing
139 station in order to cope with increase in capture rates of birds over the course of the
140 autumn season. The larger trap is adjustable in height to prevent weather damage to the
141 structure. The height of the trap opening was noted every hour. The traps both have a

142 mesh size of 2 x 2 cm and end in a box (100 x 40 x 40 cm) from which animals can easily
143 be collected. The box was emptied hourly between 08:00 and 18:00 hrs (UTC+2) each
144 day. At 18:00, the rest of the trap was also searched, and the remaining dragonflies were
145 removed and counted. The change from the larger to the smaller trap design caused a
146 sharp reduction of the number of dragonflies captured (Fig. S1). Therefore, we excluded
147 the data using the smaller trap from statistical analyses.

148

149 Dragonflies were identified to species level and sexed. Before release, dragonflies were
150 marked on the upper side of the wings using waterproof, coloured paint markers (Edding
151 4000) with a week-specific colour code to determine the proportion of animals recaptured
152 in the trap, and potentially provide insight into movements through re-sightings of
153 marked individuals. Colour-marking the wings of dragonflies is an effective method for
154 mark-recapture studies and has previously been used for determining local movements
155 and population dynamics (Jacobs 1955; Borisov 2009; Keller et al. 2010; Kharitonov and
156 Popova 2011). The putative migratory status of the dragonfly species recorded was based
157 on Corbet (1999), Jović et al. (2010) and Schröter (2011) (Table 1).

158

159 **Orientation tests**

160 Flight orientation tests were carried out in the middle of an open field adjacent to the trap.
161 The experimental site was located at least 40 m from the nearest visual cues (trees or
162 bushes). We used a circular flight arena made of black mesh (38 cm in diameter and 30
163 cm high), placed 45 cm above the ground. A video camera (Sony Handycam DCR-
164 SR200, 4 MP, 60 fps) was positioned above the arena to record flight behaviour.
165 Experiments were conducted with three of the most commonly recorded species, *Aeshna*
166 *mixta*, *Aeshna grandis* and *Sympetrum vulgatum*. Both *A. mixta* and *S. vulgatum* are

167 considered to be potential migrants (Dyatlova and Kalkman 2008; Samraoui et al. 2012;
168 Popova and Haritonov 2014) and were captured in high numbers during the season (Table
169 1).

170

171 Dragonflies were released individually into the flight arena immediately after capture and
172 filmed for 15 min. The flight arena was rotated 90° between each experiment in order to
173 randomise potential effects of the arena on flight direction. The videos were analysed
174 using Solomon Coder software (version beta 16.06.26, Péter 2011). The body orientation
175 of the dragonfly was recorded for each video frame and estimated to the nearest 45°.

176

177 *Weather data*

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

183

184 **Statistical analysis**

185 *Orientation tests*

186 Analysis of the orientation tests was conducted using the software Oriana 4 (Kovach
187 1994). As the marking did not have any significant effect on flight direction (Hotelling's
188 test: $F = 0$, $P < 0.001$), the data of the marked and unmarked dragonflies was pooled for
189 further analyses. Uniformity of the distributions was first tested using a Rayleigh test
190 (Ruxton 2017). We then performed a modified version of the Rayleigh test, also called a
191 V-test, to test for uniformity against a unimodal specified mean direction (μ). Mean

directions were set at 180°, as we hypothesised this to be the main direction during Autumn migration, and 160° which is the direction of the coast at the research station. Sexes were pooled for the analyses. *Aeshna grandis* was excluded from the analysis due to the relatively low number of individuals tested ($N = 5$). For dragonfly species where more than 10 individuals were tested (*A. mixta* and *S. vulgatum*), multi-sample tests were performed to compare their orientation with overhead wind direction during the experiments. These analyses were carried out using a paired χ^2 -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.

The effect of weather on capture rate

All analyses were conducted in R (version 3.3.1., R Core Team 2019) 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*, *Aeshna mixta*, *Sympetrum sanguineum*, *Sympetrum vulgatum*) were separated into two clear clusters, with *A. mixta* and *A. grandis* forming one group, and *S. sanguineum* and *S. vulgatum* forming another (Fig S2). Therefore, subsequent analyses of the influence of weather on abundance were performed based on this grouping. However, there being no mention of *A. grandis* showing migratory behaviour in the available literature, we excluded it from our models.

We used generalized linear mixed effects models in the package “lme4” (Bates et al. 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

217 number of dragonflies captured per hour. As wind direction is circular, ranging from
 218 0–360°, for better suitability for linear analysis, the sine and cosine of wind direction
 219 were calculated, with the sine corresponding to east-west and cosine corresponding to
 220 north-south (Brattström et al. 2008). Trap height and number of days since the start of the
 221 sampling were also included in the models. Day number (expressed as ordinal date) was
 222 included as a random factor in the models to account for multiple samples per day.
 223 Continuous explanatory variables were scaled for the modelling by subtracting the mean
 224 and dividing by the standard deviation, using the scale function in R. Models were fitted
 225 assuming a Poisson error distribution and checked for overdispersion using the package
 226 DHARMA (Hartig 2020). If overdispersion was present (>1.4), we included an
 227 observation-level random effect (OLRE) in the model (Harrison 2014). Models were
 228 compared using ANOVA and the OLRE was retained if it significantly improved the
 229 model fit.

230

231 Generalised linear models were used to investigate the influence of weather variables on
 232 daily captures, including the set of predictors as for the hourly models described above,
 233 as well as day since the beginning of the study. For each weather variable, we calculated
 234 the daily mean, between 08:00 and 18:00. We also included the lowest temperature and
 235 mean pressure registered on the preceding night (between 18:00 and 06:00 hours). As
 236 above, models were initially fitted assuming a Poisson error distribution and tested for
 237 overdispersion. If overdispersion was present, we applied a negative binomial model.

238

239 For all models, only dragonflies captured in the box at the end of the trap were used for
 240 the analysis. Significance of the variables was determined by excluding the variable of
 241 interest and comparing the models with and without the variable, using ANOVA. Model

fit was visually checked using quantile plots of the residuals. Correlation between the variables used in the models was tested using Pearson correlation tests, with a correlation coefficient threshold of 0.7. No variables were significantly correlated.

RESULTS

Orientation tests

The Rayleigh test rejected uniformity of distribution for *A. mixta* ($Z = 8.525$, $P < 0.001$). Mean flight orientation for the species was $166.67^\circ \pm 12.23$ (SE) and was significantly different from overhead wind direction during the experiments ($\chi^2 = 27.259$, $P < 0.001$, Table 3, Figure 2). *Sympetrum vulgatum* showed a mean flight orientation of $205.36^\circ \pm 29.88$. Uniformity of distribution could not be rejected based on the Rayleigh test, but flight orientation during the tests was significantly different to overhead wind direction ($\chi^2 = 19.2$, $P = 0.008$, Table 3, Figure 2).

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 *Sympetrum vulgatum* (22.4%), *Sympetrum sanguineum* (14.4%) and *Aeshna grandis* (9.3%). The other species each accounted for less than 4% of the total dragonflies captured. It is to be noted that no damselflies (Zygoptera) were recorded within the trap box.

Out of 2055 individuals marked during the study (147 individuals were caught in the small trap and 278 individuals were caught opportunistically in the surrounds and

marked), only 66 (3.2%) were recaptured in the trap (Table S1), with a single individual being reported elsewhere (2 km south of the trap; B. Gliwa, pers. 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 one month.

Phenology differed between the four most commonly captured species. The median date of passage for *A. mixta* (26 August, 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, Figure S3). Daily mean capture time was earlier for *A. mixta* (13:07 ± 02:51 SD) and *A. grandis* (12:41 ± 02:06 SD) compared to *S. vulgatum* (14:36 ± 02:00 SD) and *S. sanguineum* (14:44 ± 02:07 SD) (Figure S4).

The effect of weather on capture abundance

Daily abundance of *A. mixta* increased with temperature ($\chi^2 = 30.550$, df = 1, $P < 0.001$) and more northerly winds (cosine of wind direction, $\chi^2 = 3.930$, df = 1, $P = 0.047$), and decreased with cloud cover ($\chi^2 = 4.615$, df = 1, $P = 0.032$, $N = 25$ days, Table 3a, Figure 3). Similarly, hourly abundance of *A. mixta* was positively influenced by temperature ($\chi^2 = 30.948$, df = 1, $P < 0.001$) and northerly winds ($\chi^2 = 9.307$, df = 1, $P = 0.002$), and negatively by cloud cover ($\chi^2 = 5.293$, df = 1, $P = 0.021$), but was also positively influenced by humidity ($\chi^2 = 4.666$, df = 1, $P = 0.031$, $N = 251$ hours, Table 3b, Figure 4).

Daily abundance of *Sympetrum* spp. (*S. vulgatum* and *S. sanguineum*) was negatively influenced by cloud cover ($\chi^2 = 10.142$, $df = 1$, $P = 0.001$) and positively by trap height ($\chi^2 = 8.357$, $df = 1$, $P = 0.004$), with more individuals captured when the trap was fully open ($N = 25$ days, Table 3a, Figure 5). Hourly abundance of *Sympetrum* spp. was positively influenced by temperature ($\chi^2 = 52.657$, $df = 1$, $P < 0.001$) and negatively by cloud cover ($\chi^2 = 4.692$, $df = 1$, $P = 0.030$, $N = 251$ hours, Table 3b, Figure 6). In contrast to *A. mixta*, hourly abundance of *Sympetrum* spp. increased with more easterly winds (sine of wind direction, $\chi^2 = 6.525$, $df = 1$, $P = 0.011$).

DISCUSSION

There is a growing body of evidence for seasonally directed autumn migratory movements in large and medium-sized insects, including day-flying species (Srygley and Dudley 2008; Chapman et al. 2015; Hu et al. 2016; Knight et al. 2019; Wotton et al. 2019; Gao et al. 2020). In dragonflies, directional autumn movements towards the south have been shown for long distance migrant species such as *Anax junius* (Wikelski et al. 2006; Knight et al. 2019). However, to date, relatively few systematic studies on migratory behaviour in dragonflies have been made in Europe (eg. Shapoval and Buczyński 2012). Our orientation tests revealed a strong unimodal flight direction of *Aeshna mixta* towards the south-southeast (167°) in autumn, independent from overhead wind direction. Many insects are known to follow geographical cues on migration (Becciu et al., 2019), and the deviation from true south (180°) observed in *A. mixta*'s orientation could be due to animals following the coastline (160° at Pape). We did not find a significant uniform direction for *Sympetrum vulgatum*. Nonetheless, the mean direction of *S. vulgatum* indicated an orientation towards the south-southwest (205°) and differed from the prevailing overhead winds.

316

317 To date, the relationship between dragonfly movement decisions and weather factors has
 318 rarely been studied (but see Feng et al. 2006; Wikelski et al. 2016; Knight et al. 2019).
 319 We show that temperature and cloud cover were the most important variables affecting
 320 hourly and daily abundance of *Aeshna mixta* and the two *Sympetrum* species tested. Both,
 321 temperature and cloud cover are well-known predictors for insect migration rates (eg.
 322 Brattström et al., 2008), and temperature has been shown to influence groundspeed of
 323 migrating *Anax junius* (Knight et al. 2019). This general pattern regarding the influence
 324 of temperature and cloud cover is likely to be due to the effect of increased sunshine on
 325 flight activity in day-flying insects (Becciu et al. 2019).

326

327 Hourly and daily abundance of *A. mixta* was higher in tailwind conditions (in this case,
 328 northerlies). Given the predominant southerly flight direction of *A. mixta* revealed in our
 329 orientation tests, this pattern might be indicative of the ability to select favourable
 330 tailwinds, which would facilitate migration. Many migratory insects such as dragonflies,
 331 moths and hoverflies, have been shown to select for favourable winds, possibly as an
 332 adaptation to maximize distance covered, optimize trajectories and reduce energy costs in
 333 their displacements (Anderson 2009; Alerstam et al., 2011; Becciu et al. 2019; Knight et
 334 al. 2019; Gao et al. 2020). Across the study period, the prevailing winds from the SW and
 335 W – coming from the Baltic sea – were the strongest and most frequent, while the less
 336 common winds coming from the east were of lower speed. The hourly, but not daily
 337 abundance of *Sympetrum* increased with easterlies, which may indicate an adaptive
 338 response, flying lower to minimize drag and consequently drift due to a reduction in side
 339 winds, or to avoid the possibility of being blown out to sea.

340

341 While many studies mention that dragonfly migration takes place predominantly in the
 342 flight boundary layer (Srygley and Dudley 2008; Chapman et al. 2011a), high-altitude
 343 movements up to 1000 m above ground level have been documented for the migratory
 344 *Pantala flavescens* (Feng et al. 2006). We therefore cannot be sure whether the increase
 345 of passage intensity of *A. mixta* during tail-wind conditions (assuming a general southerly
 346 flight direction, based on the results of orientation tests) is limited to ground level or
 347 whether passage also intensifies at higher altitudes. In any case, at ringing stations where
 348 birds are captured during active migration, songbirds are usually captured in higher
 349 numbers when they are facing headwinds (Komenda-Zehnder et al. 2010), flying lower in
 350 order to minimize the effect of the wind, which is also the case at Pape (M. Briedis, pers.
 351 comm.). Birds tend to fly higher in tailwind conditions in order to take advantage of
 352 directionally beneficial winds (Komenda-Zehnder et al. 2010; Becciu et al. 2019). Insects
 353 that are strong fliers, such as dragonflies, also use similar mechanisms (Chapman et al.
 354 2015; Becciu et al. 2019). Change in the trap's height only affected the daily abundance
 355 of *Sympetrum* and did not seem to influence the abundance of *A. mixta*. Trap height
 356 affecting the capture of *Sympetrum* possibly indicates that either these species fly in a
 357 more defined altitudinal layer than the *Aeshna* species, or that they may generally fly
 358 higher above the ground. However, our results indicate that *A. mixta* may migrate
 359 relatively close to the ground, even in favourable tail-wind conditions, but this warrants
 360 further investigation.

361

362 The differences observed in the abundance of *Aeshna* and *Sympetrum* throughout the day
 363 may be explained by physiological differences found between larger and smaller
 364 dragonfly species. The minimum temperature at which flight is possible has been shown
 365 to be positively correlated with body weight in dragonflies (May 1976). Thus, for the

366 smaller *Sympetrum* species, the minimum required temperature for flight is higher and
367 hence later in the day.

368

369 While the dragonflies captured in the trap may have been a mixture of migrating and
370 local individuals, our results show that there were some differences in the way weather
371 impacts flight behaviour of larger versus smaller dragonfly species. Generally, migration
372 intensity increased with temperature and decreased with cloud cover. Moreover, based on
373 the orientation tests, we have strong support that migration of *A. mixta* and some
374 *Sympetrum* species does take place along the Baltic coast (Shapoval and Buczyński
375 2012).

376 Investigation of migration behaviour at altitude, and the origin of individuals – which
377 would provide further insight into migration routes and migratory behaviour – could be
378 answered using a combination of techniques, such as radar (Chapman, Drake, et al.,
379 2011a; Drake & Reynolds, 2012), radio-telemetry (Wikelski et al., 2006, Knight et al.
380 2019), and stable isotope analysis of wing chitin (Hobson, Soto, Paulson, Wassenaar, &
381 Matthews, 2012; Hallworth et al., 2018).

382

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395

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579 **Table 1**

580 Abundance and migratory status of dragonflies captured at Pape, Latvia. Migrant as a
581 status encompasses obligate, partial and facultative strategies, as in some cases status is
582 not clear and prone to change depending on latitude, for example. Non-migrant species
583 are species for which no migration data has been found in the literature (Corbet, 1999;
584 Jović et al., 2010; Schröter, 2011). Data are from the box at the end of the larger trap (see
585 Methods).

586

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

587

588 **Table 2**

589 Results of the flight orientation experiments for *Aeshna mixta* and *Sympetrum vulgatum*.

590 Uniformity of direction was tested using Rayleigh tests. *V*-tests were used to test for

591 uniformity of direction against a unimodal specified mean direction (μ) of 180°.

592

	<i>A. mixta</i>	<i>S. vulgatum</i>
<i>N</i>	23	14
Mean vector (μ)	166.67°	205.36°
Length of μ	0.609	0.389
SE of mean	12.32°	29.88°
<i>One sample tests</i>		
Rayleigh test (<i>Z</i>)	8.525	2.119
Rayleigh test (<i>P</i>)	< 0.001	0.12
<i>Multi-sample tests (matched with corresponding wind direction)</i>		
χ^2 pairwise	27.259	19.2
χ^2 pairwise (<i>P</i>)	< 0.001	0.008

593

594 **Table 3**

595 Results of the generalised linear models per dragonfly genus. a) Hourly abundance in
596 relation to weather. b) Daily abundance in relation to weather.

597

		Estimate	SE	df	χ^2	P value
b) <i>Aeshna</i>	Intercept	-16.697	2.739			
	Temperature	1.093	0.145	1	30.550	<0.001
	Cloud cover	-0.171	0.073	1	4.615	0.032
	Wind direction (cos)	0.758	0.392	1	3.930	0.047
<i>Sympetrum</i>	Intercept	0.766	1.217			
	Cloud cover	-0.396	0.092	1	10.142	0.001
	Trap height	3.997	1.175	1	8.357	0.004
a) <i>Aeshna</i>	Intercept	-18.831	3.659			
	Temperature	0.814	0.128	1	30.948	<0.001
	Cloud cover	-0.117	0.050	1	5.293	0.021
	Wind direction (cos)	0.490	0.161	1	9.307	0.002
	Humidity	0.046	0.021	1	4.666	0.031
<i>Sympetrum</i>	Intercept	-17.844	2.991			
	Temperature	0.947	0.155	1	52.657	<0.001
	Cloud cover	-0.165	0.075	1	4.692	0.030
	Wind direction (sin)	0.581	0.226	1	6.525	0.011

598

599 Significance of variables was determined based on likelihood-ratio tests using ANOVA.

600 Only significant or variables ($P < 0.05$) were retained in the final models presented here.

601 Models investigating hourly abundance were fitted with a Poisson error distribution and

602 included day number as a random factor. An observation-level random factor was
603 included to account for overdispersion. Models investigating daily abundance were fitted
604 with negative binomial models. Model estimates are based on unscaled variables.

605

606

607 **Figure 1**

608 (a) Location of the Pape ornithological research station, Latvia. The red star indicates the

609 position of the Heligoland trap. The green arrows represent the hypothetical flyways due

610 to a bottleneck effect exerted on migrating dragonflies by the Baltic Sea and Pape Lake.

611 (b) Photograph of the large Heligoland trap (Photo: Jasja Dekker).

612

613

614 **Figure 2**

615 Results of the flight orientation tests. The left column (green) represents the orientation

616 direction of the dragonflies (*A. mixta*, $N = 22$; *S. Vulgatum*, $N = 14$). The right column

617 (blue) represents the direction of the wind during these tests. The black arrow represents

618 the mean direction and the wedges the percentage of individuals having their mean

619 direction included in a given wedge. Note that the mean orientation direction for *S.*

620 *vulgatum* was not significant.

621

622

623 **Figure 3**

624 Relationship between weather variables and the daily abundance of *Aeshna mixta*.

625 Results are based on negative binomial regression. The shaded areas represent 95%

626 confidence intervals. For the cosine component of wind direction, (-1) equals south and

627 (+1) equals north.

628

629

630

631 **Figure 4**

632 Relationship between the hourly abundance of *Aeshna mixta*, and weather variables.

633 Results are based on a generalised linear mixed model with a Poisson distribution. The

634 shaded areas represent 95% confidence intervals. For the cosine component of wind

635 direction, (-1) equals south and (+1) equals north.

636

637

638 **Figure 5**

639 Relationship between weather variables and the daily abundance of *Sympetrum vulgatum*

640 and *Sympetrum sanguineum*. Results are based on negative binomial regression. The

641 shaded areas represent 95% confidence intervals.

642

643

644 **Figure 6**

645 Relationship between the hourly abundance of *Sympetrum* (*Sympetrum vulgatum* and

646 *Sympetrum sanguineum*) and weather variables. Results are based on a generalised linear

647 mixed model with a Poisson distribution. The shaded areas represent 95% confidence

648 intervals. For the sine component of wind direction, (-1) equals west and (+1) equals east.