Unravelling arthropod movement in natural landscapes: small-scale effects of body size and weather conditions

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Abstract

Movement is a crucial life history component and holds direct significance to population dynamics, thereby influencing population viability. For arthropods in general, larger species achieve greater dispersal distances and large-scale movements are influenced by weather conditions. However, many aspects of arthropod movement behaviour remain relatively unexplored, especially on small spatial scales. Studies on this topic are scarce and often limited to a few specific species or laboratory conditions. Consequently, it remains uncertain whether the effects of body size and weather conditions can be generalized across a wide range of arthropod species in natural environments. To help address this knowledge gap, we conducted a field study in two nature reserves in Belgium, focusing on both flying and cursorial arthropods. Over 200 different arthropod species were captured and released within a circular setup, allowing quantification of movement speed and direction. By analysing the relationship between these movement variables and morphological (body size) as well as environmental factors (temperature and wind), we aimed to gain insights into the mechanisms driving small-scale arthropod movement under natural conditions. For flying species, movement speed is positively correlated with both body size and (tail)wind speed. In contrast, movement speed of cursorial individuals was solely positively related with temperature. Notably, movement direction was biased towards the vegetated areas where the arthropods were originally caught, suggesting an internal drive to move towards suitable habitat. This tendency was particularly strong in larger flying individuals, in smaller cursorial species and under tailwind conditions. Furthermore, both flying and cursorial taxa were hindered from moving towards the habitat by strong upwind. Body size can be used as a useful proxy for not only movement speed, but orientation capacity as well. This movement-size correlation is, at least at small temporal scales, conditional to the prevailing wind conditions.

1. Background

Movement is a crucial component of the life history of many organisms. Across small and large spatial scales, it mitigates the finding of resources and mates, ultimately shaping species distributions and interactions (Gilbert, Gonzalez and Evans-Freke, 1998; McIntyre and Wiens, 1999; Bowler and Benton, 2005). Movement connects ecosystems by enabling long-distance dispersal, thereby bolstering genetic diversity and fortifying population viability (Leibold *et al.*, 2004; Blaum *et al.*, 2012). Despite this vital role of movement in shaping both biodiversity patterns and ecosystem functioning, arthropods are severely underrepresented in movement studies compared to vertebrates, even though they constitute a significantly larger portion of the global biodiversity (Clark and May, 2002; Kissling, Pattemore and Hagen, 2014). Admittedly, studying arthropod movement involves many inherent challenges, such as their small size and vast species diversity. Nevertheless, understanding the ecological dynamics of arthropods is crucial, as they play pivotal roles in ecosystem functioning through processes like pollination, nutrient cycling and trophic interactions (Yang and Gratton, 2014).

Motion and navigation constitute two fundamental processes of movement. “Motion” refers to the biomechanical properties enabling an individual’s movement, while “navigation” involves an individual’s orientation in time and space to make informed decisions about where to move (Nathan *et al.*, 2008). Both of these processes are influenced not only by the morphological and physiological state of the individual (“internal factors”, e.g. muscle volume, metabolic rates), but also by the environment through which it moves (“external factors”, e.g. habitat configuration, presence of predators) (Nathan *et al.*, 2008).

Body size stands out as one of the most relevant internal factors influencing arthropod movement, due to its association with various morphological, physiological and life-history traits (Woodward *et al.*, 2005; White *et al.*, 2007). Numerous arthropod taxa, ranging from cursorial groups (i.e. individuals running on the ground) like ants and beetles to flying taxa such as butterflies, bugs and dragonflies, seem to consequently exhibit an allometric relationship between body size and mobility (Hurlbert,

Ballantyne and Powell, 2008; Sekar, 2012; Kuussaari *et al.*, 2014; Hirt *et al.*, 2017; Wootton, 2020; Dingle, Blakley' and Miller, 2023). Larger arthropod individuals, both within and across species, generally display greater mobility, resulting in higher movement speeds and larger travelling distances. Additionally, the presence of functional wings also emerges as an important internal factor that significantly affects arthropod movement. In general, flying insects move faster and cover larger distances compared to wingless counterparts of the same or different species (Roff, 1986, 1990)

An organism's perceptual range is the distance at which sensory organs detect landscape features, which is often species-specific (Lima and Zollner, 1996). Navigation then results from the processing of various environmental stimuli within the animal's brain, ultimately shaping movement direction (Merckx *et al.*, 2003; Merckx and Van Dyck, 2007). For many taxa, including arthropods, perceptual range scales with body size (Baker, Kelty and Jakob, 2009; Pawar, Dell, and Van M. Savage, 2012; Schäpers *et al.*, 2015). Larger individuals, with a larger perceptual range, are thus expected to enhance their ability to make informed decisions regarding movement directions. Moreover, flying arthropods can more effectively survey the landscape during flight, potentially granting flying arthropods an advantage in environmental navigation.

Local weather conditions can significantly influence the movement of arthropods, in terms of both speed and direction. The impact of local weather conditions should be the clearest for small-scale movement bouts, because of the high variability of weather conditions at small temporal and spatial scales, either because of changing weather conditions or local microclimate. A first component of local weather conditions is the prevailing temperature. Higher ambient temperatures have been shown to positively impact the activity and running speed of invertebrate ectotherms, owing to improved oxygenation rates and enhanced kinetic properties of muscles (Hurlbert, Ballantyne and Powell, 2008; Frizzi, 2018). Moreover, arthropod species often adjust their movement behaviour according to the local thermal conditions, with some even requiring a minimum ambient temperature to initiate movement (Bonsignore and Bellamy, 2007; Frizzi, 2018; Knight *et al.*, 2019; González-Tokman *et al.*,

2020; Knoblauch, Thoma and Menz, 2021). However, movement responses to increased temperatures are also constrained by critical thermal upper-limits, leading to impaired movement capacity when temperatures exceed these thresholds (Heinrich, 1995; Dudley, 2000; Chown and Nicolson, 2004). A second component of local weather is wind. The direction and force of the wind exert considerable influence on movement distances and decisions, especially for flying insects undertaking long-distance dispersal (Knoblauch, Thoma and Menz, 2021). Many insects and spiders possess anemotactic reception, allowing them to accurately estimate the direction of prevailing winds by sensing air currents, and consequently, make informed choices regarding movement trajectories (Buehlmann, Mangan and Graham, 2020; Knoblauch, Thoma and Menz, 2021).

The relationship between an individual's body size and external weather conditions is intricate. Larger flying insects such as dragonflies, moths and butterflies tend to move in controlled directions related to their destination rather than following the wind, while smaller insects like aphids are more influenced by wind directions (Knoblauch, Thoma and Menz, 2021). Regarding body temperature, large arthropods are less constrained by prevailing thermal conditions, whereas smaller arthropods have body temperatures that are more closely tied to their immediate surroundings (Pincebourde, Dillon and Woods, 2021). Consequently, body size emerges as a central trait, linking internal and external factors that impact movement.

Current research on the biometeorological relationships in arthropod movement predominantly focuses on large-scale distances, and involves only a limited number of large and highly mobile species such as dragonflies and beetles (Frick *et al.*, 2013; Knight *et al.*, 2019; Knoblauch, Thoma and Menz, 2021). As a result, small-scale movement studies investigating the impact of weather on movement between and within habitat patches are scarce (Aikman and Hewitt, 1972; Eguagie, 1974; Merckx *et al.*, 2008). Traditional methods, such as capture-mark-recapture or tracking devices, have limitations in achieving large sample sizes, often leading to a narrow focus on individual species and hindering generalizations across taxa (Jonsen, Bourchier and Roland, 2001; Goodwin and Fahrig, 2002).

Moreover, concerns have been raised about the use of such tracking devices, as the impact of such tags on arthropods is often neglected, ultimately biasing data (Batsleer *et al.*, 2020). While some notable efforts have been made to study arthropod exploratory movement through image-based tracking under laboratory conditions, the applicability of these findings to natural field conditions remains uncertain (Hirt *et al.*, 2017; Terlau *et al.*, 2023).

This study aims to understand the interplay between movement, body size and weather conditions by investigating a diverse range of arthropod species on a small spatial scale in natural field conditions. The realised movement speed and direction of arthropods within the natural landscape—without relying on tracking devices—was measured and correlated with individual body size and prevailing weather conditions. More specifically, we applied release experiments which induce directional movements in arthropods. Such experiments are anticipated to represent dispersal behaviours in the matrix better than the tracking of routine behaviours in resource-rich habitat (Van Dyck and Baguette, 2005). We expect (i) a positive correlation between movement and body size, (ii) the strengthening of this effect under warmer temperatures and stronger tailwinds, (iii) an influence of wind conditions on the navigation of flying insects, and (iv) a biased navigation towards suitable environments due to the perception (correct interpretation by the individual) of the environment and avoidance of risks when crossing the hostile matrix.

2. Methods

2.1 Experimental field work

The field work for this study was conducted during the summer of 2021 at two distinct locations in Belgium. The first site was a coastal dune grassland in De Panne, while the second site encompassed both dry and wet heathland patches in Kalmthout (details in Appendix S.1). Within the vegetated areas at both sites, arthropod individuals from various species were randomly captured either by hand or by sweep netting. Each captured individual was assigned a unique ID and photographed in the field with a graph paper (1 mm squares) as background.

To assess the movement behaviour of these arthropods, separate set-ups were designed for flying and cursorial (i.e. running on the ground) individuals, as we anticipated different movement speeds and perceptual abilities. In a large area of open sand, two circular set-ups were demarcated by placing coloured flags at five different radii with uniform interval distances (2 metres for flying individuals and 20 centimetres for cursorial individuals). Movement speed was measured using a chronometer, whereby the movement time was recorded as the duration an individual took to traverse either 10 meters (for flying locomotion) or 1 meter (for cursorial locomotion), or when an individual came to stop at a specific distance. The directions of movement and wind were categorised using cardinal directions (N, NE, E, SE, S, SW, W or NW), and then converted into angles in degrees, with west serving as the zero degrees reference (see further). By comparing the movement and wind angles, we were able to determine whether the movement was aligned with the wind or not, and to differentiate between movement upwind and movement assisted by tailwinds. Specifically, we defined tailwind movements when the direction of movement deviated by a maximum of 45 degrees from the prevailing wind direction, while upwind movements deviated by at least 135 degrees from the prevailing wind direction (Figure 1). West was chosen as the zero degrees reference, as the vegetated areas where the arthropods were initially captured laid in this direction relative to the experimental set-up (Figure 1). This decision assumed that the arthropods would exhibit a preference for returning to the location where they were initially caught, since they were released in a hostile matrix with very few available resources. The surface area of the matrix was sufficiently large to assume that moving through it would bring a high energetic cost and uncertainty for the released arthropod. By adopting the orientation as shown in Figure 1, we aimed to gain insights in navigation behaviour, as movement patterns would likely reflect the tendency and ability to return to the habitat of origin. The experimental set-up at Kalmthout was surrounded by heathland on all sides (Appendix S.1), making it impossible to discern whether an arthropod moved towards habitat or not. Consequently, movement direction bias towards habitat is only considered for data from the site in De Panne.

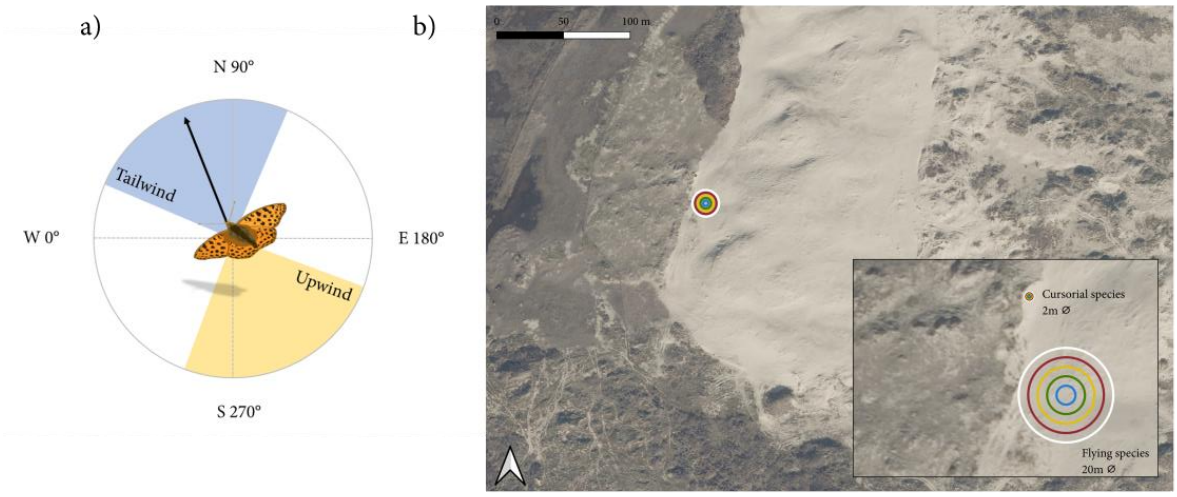


Figure 1: a) Schematic representation of how the cardinal directions were converted into angles. The black arrow indicates the direction of the movement. The blue area indicates all wind directions that can be classified as tailwind in this specific example, while the yellow area indicates upwind. b) Map of the experimental set-up at De Panne, with the vegetated areas to the west. Circular setups were drawn at a realistic scale.

During measurements, the captured arthropods were temporarily housed in cooling boxes to prevent thermal stress and minimize mortality, with each individual spending a maximum of thirty minutes in these boxes. Subsequently, the arthropods were taken out one by one and released in the open sand. To mitigate the likelihood of an escaping movement response and directional bias arising from the researchers' presence, cursorial animals were released at a distance of 1 meter from the observer, whereas flying animals were released above the observers' head. In total, 1355 arthropod individuals from 255 different species were tested. Among these individuals, 762 exhibited flying locomotion, while the remaining 593 displayed cursorial locomotion.

Every half-hour of the release experiments, wind direction, wind speed and temperature were recorded at an average height of 1.5 to 1.8 metres, using a weather station equipped with a built-in thermometer and anemometer. Wind speed was calculated as the average of the minimum and maximum values measured within a half-minute interval. Sampling days were carefully selected to ensure suitable weather conditions for representative arthropod movement: a cloud cover below 60% and temperatures between 15°C and 34°C.

182 Due to practical constraints, determining the dry weight of individual arthropods was not feasible.
183 Body length was used instead as an alternative proxy for body size (Ganihar, 1997; Martin, Proulx and
184 Magnan, 2014; Moretti *et al.*, 2017). The photos of the arthropods taken in the field were analysed
185 using ImageJ version 1.52a (Schneider, Rasband and Eliceiri, 2012). The grid pattern in the background
186 of the photos was used as reference to measure the length of each individual's body, starting from the
187 cephalon (excluding the antennae) and extending to the tip of the abdomen.

188 **2.2 Statistical analyses**

189 All data analyses were conducted using R version 4.2.2 (R Core Team, 2021). The "dplyr" package
190 (Wickham *et al.*, 2022) was used for general data manipulation and organization. All visuals were
191 created with the "ggplot2" (Wickham, 2016), "RColorBrewer" (Neuwirth, 2022) and "showtext" (Qiu,
192 2023) packages.

193

194 ***2.2.1 Movement speed***

195 As a first explorative analysis, Principal Component Analysis (PCA) was conducted, separately for flying
196 and cursorial species. The primary aim of this analysis was twofold: (1) to assess the extent to which
197 the internal (body size) and external (temperature and wind speed) variables contributed to explaining
198 the variation in the data, and (2) to explore whether arthropod species clustered together based on
199 their underlying phylogenetic position.

200 To confirm any observed relationships between movement speed, body size and weather conditions
201 in flying and cursorial arthropods, a distinct Bayesian Generalized Linear model was employed for each
202 group ("brms" package (Bürkner, 2021)). The dependent variable in these models was movement
203 speed, while the independent variables included body size, temperature and wind speed. The models
204 were fitted with a Gaussian distribution using 4 chains and 4000 iterations to ensure reliable results.
205 To address potential multicollinearity issues, the independent variables were rescaled. Non-

206 informative flat priors for the model parameters were used. As we expected wind speed to have
207 opposing effects depending on its orientation relative to an individual's movement, we constructed
208 additional models by splitting the dataset into individuals that moved either tail- or upwind, and ran
209 two separate models. This approach was used to test potential differences in responses and proved to
210 be more efficient than the incorporation of an interaction to the Bayesian models.

211 Since the models did not account for the potential influence of phylogenetic relationships between
212 species, additional models were constructed to address this issue. For this purpose, phylogenetic trees
213 were created by linking the species names to the Open Tree Taxonomy database, establishing a tree
214 based on the known phylogenetic relationships between species ("rotl" package (Michonneau, Brown
215 and Winter, 2016)). Branch lengths were calculated with the "ape" package (Paradis and Schliep, 2019)
216 using the "Grafen" method (Grafen, 1989), leading to the construction of a phylogenetic covariance
217 matrix ("geiger" package (Matthew *et al.*, 2014)). First of all, this tree was used to calculate Pagel's
218 lambda, a measure for the phylogenetic signal in a specific trait, for the movement speed of both flying
219 and cursorial species ("phytools" package (Revell, 2012)). Secondly, the phylogenetic distances
220 between species were incorporated into all Bayesian Generalized Linear models (similar to those
221 above) as blocking factors. By doing so, the models considered the phylogenetic relationships between
222 species when analyzing the correlation between movement speed and the other variables.

223 ***2.2.2 Movement direction***

224 The analysis of arthropod movement behaviour in different wind scenarios involved several circular
225 statistics tests ("circular" package (Agostinelli and Lund, 2022)). As mentioned before, only data
226 collected at the De Panne site were used for these analyses due to its clear separation between the
227 open sand and vegetated areas. After the removal of the data collected in Kalmthout, 976 observations
228 remained to be used in the following analyses.

229 To assess the correlation between wind direction and movement direction, the Jammalamadaka-
230 Sarma correlation coefficient (Jammalamadaka and Sarma, 1988) was calculated for both flying and

231 cursorial arthropods within different taxonomic orders, limited to orders represented by 8 or more
232 samples. Additionally, the Rayleigh's test of Uniformity (Pewsey, Neuhäuser and Ruxton, 2013) was
233 performed to examine whether there was a directional bias in arthropod movement. The Rayleigh test
234 was chosen specifically as it is suitable for detecting unimodal responses in the distribution of
235 movement directions. The significance of the results from these tests was evaluated by correcting for
236 multiple testing using the Benjamini-Hochberg method (Benjamini and Hochberg, 1995), addressing
237 potential issues of false positives.

238 Furthermore, several Bayesian Generalized Linear Models were fitted to explore the relationship
239 between an individual's body size and their movement direction. A binary value (0 or 1) was assigned
240 to indicate whether an individual had moved towards the habitat from where they were initially
241 caught. Deviations greater than 45 degrees from the zero-degree point (west) were considered as not
242 moving towards the habitat and were assigned a value of 0. Body size and wind speed were used as
243 independent variables, while this binary value was the dependent variable. Temperature was omitted
244 from these models because we considered it irrelevant in the context of navigation. Since the
245 dependent variable was binary, a binomial distribution with a logit link function was utilized. As with
246 movement speed, the datasets were again split to test whether different responses were present
247 under upwind or tailwind conditions. Each model was again corrected for phylogenetic relationships,
248 which involved constructing phylogenetic trees using Open Tree Taxonomy and incorporating
249 phylogenetic distances as blocking factors in the models.

250 # 3. Results

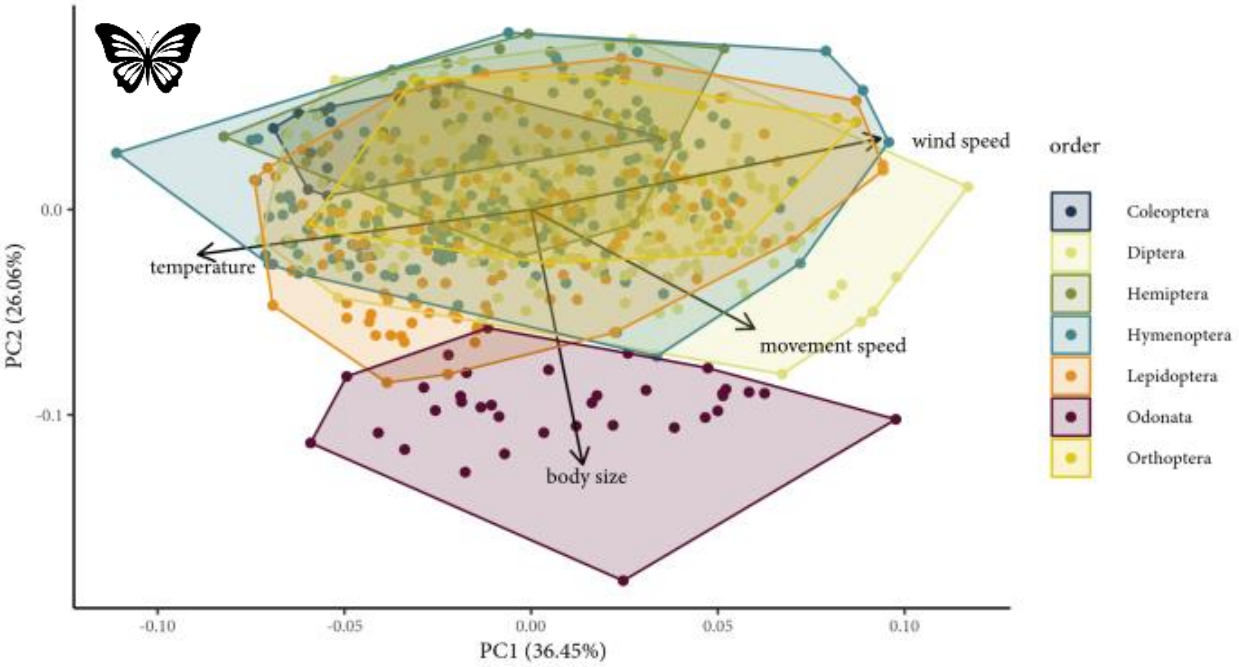
251 ### 3.1 Movement speed

252 The results of the PCA imply a positive correlation between movement speed of flying individuals and
253 both body size and wind speed (Figure 2, top). For these flying species, most clusters of taxonomic
254 groups overlap with each other (with Odonata as notable exception), indicating a limited effect of
255 phylogeny. Large flying individuals generally exhibited higher movement speeds compared to smaller

ones (Figure 3, left). However, this relationship appears to reach an optimal point around 15 mm body size, beyond which further increases in body size did not lead to higher movement speeds (Appendix S.2.2). The effect sizes and directions were clearly determined for the overall dataset (Figure 3, left). However, wind-movement speed correlation changed for flying arthropods according to the experienced wind: under tailwind (Figure 3, left), movement and wind speed were positively correlated, while under upwind (Figure 3, left), movement speed decreased with increasing wind speed (although the effect size is unclearly determined because of the wide posterior). For tailwind speed, the correlation also demonstrated a saturation point, which occurred around 3 m/s wind speed, beyond which movement speed did not increase further (Appendix S.2.1). The overall positive correlation between wind speed and movement speed is thus primarily driven by the correlations found under tailwind conditions (Figure 3). Temperature did not exhibit a clearly determined effect on the movement speed of flying individuals (Figure 3). Pagel's lambda was notably high (λ=0.733), indicating a strong phylogenetic signal. Nevertheless, as expected from the overlap among taxa in the PCA, phylogenetic corrections had no qualitative impact on the correlations (Figure 3).

In contrast, for cursorial individuals, the PCA showed that both body size and wind speed did not impact movement speed (Figure 2, bottom). Instead, temperature showed a positive correlation, indicating that cursorial species moved faster under warmer conditions (Figure 2, bottom; Figure 3, right). Like before, most taxonomic groups overlap, indicating a limited effect of phylogeny (with Orthoptera as a notable exception, being larger on average compared to other taxa). This positive correlation between movement speed and temperature was again supported by the Bayesian models (Figure 3), but this time Pagel's lambda was rather small (λ=0.357).

A) Flying individuals



B) Cursorial individuals

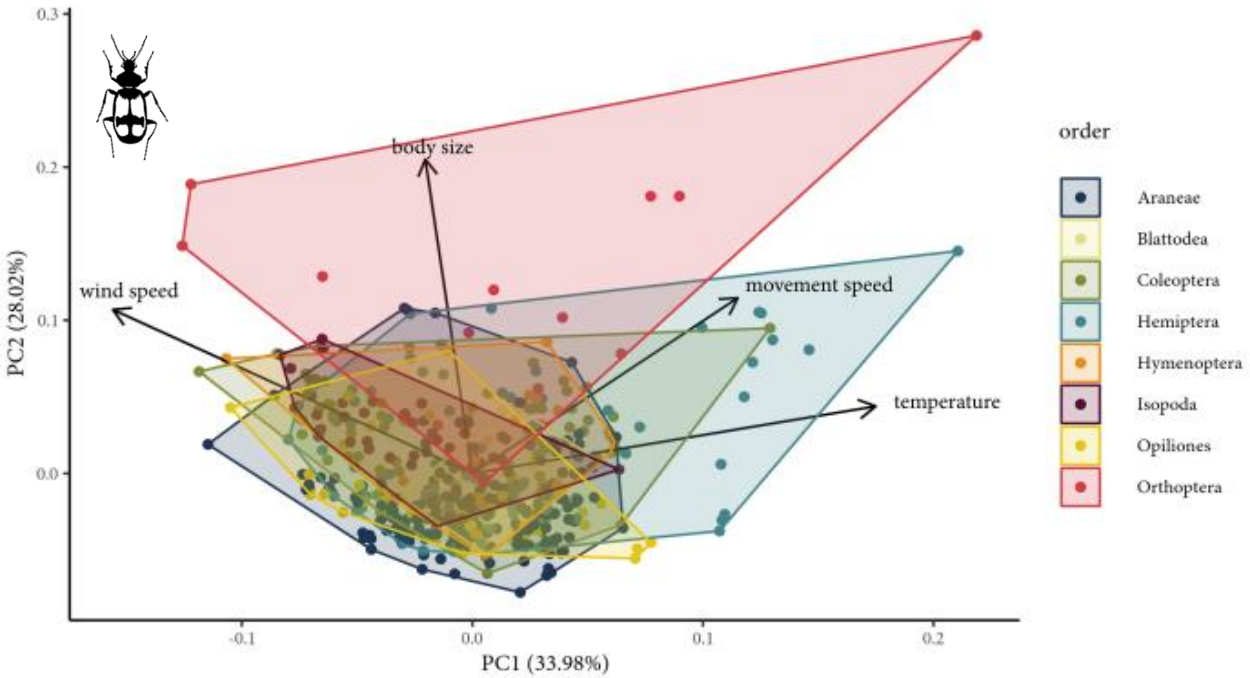


Figure 2: Results of the PCA analysis for a) flying and b) cursorial individuals. Dots representing individuals are colored according to their taxonomic order. Individuals of the same taxonomic order are clustered within a convex, by connecting the most extreme values.

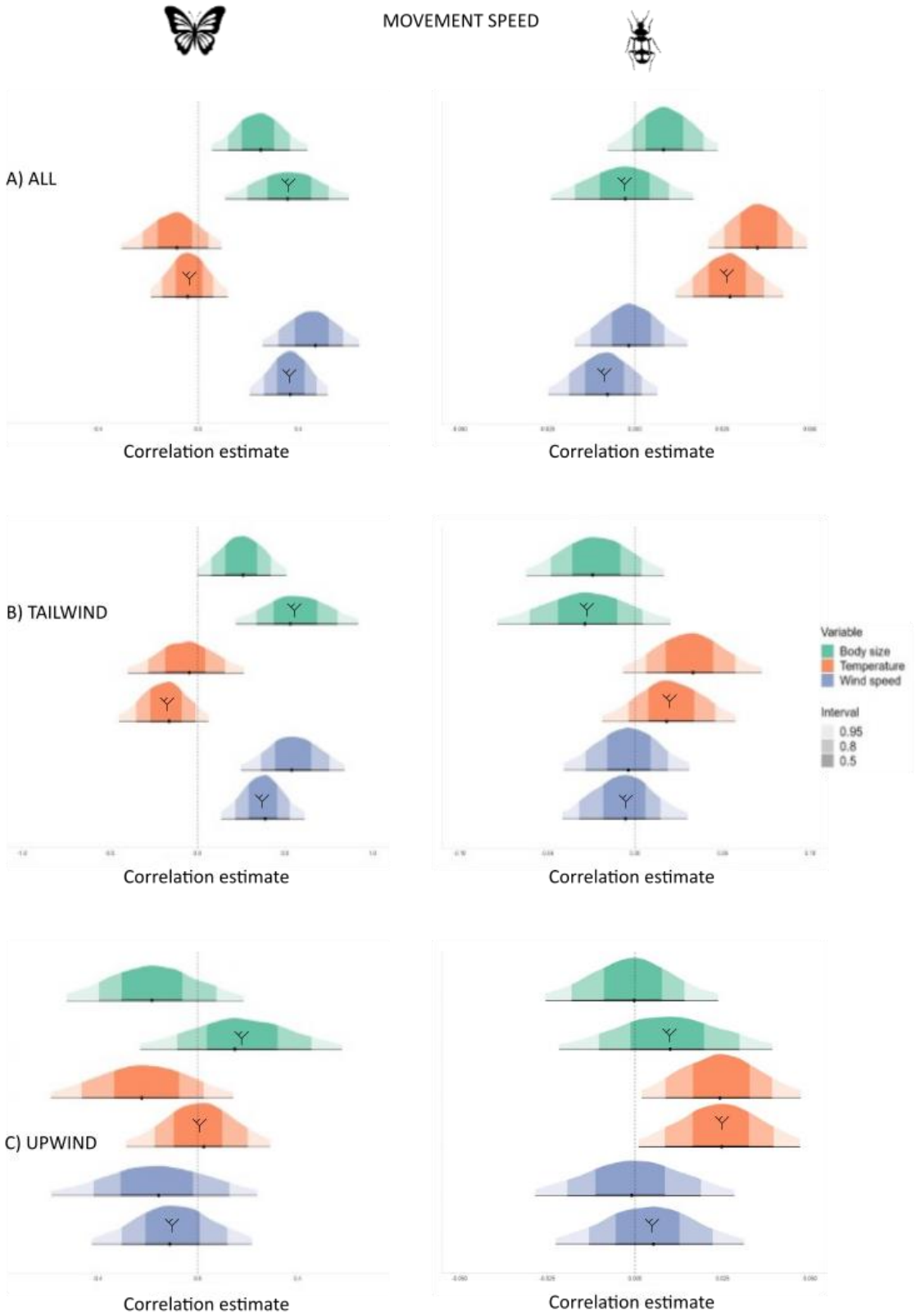


Figure 3: Estimates for the correlations between movement speed and body size, temperature and wind speed for a) all wind conditions, b) tailwind conditions (n=527) and c) upwind conditions (n=281). Posterior distributions that are marked with a phylogenetic tree resulted from the phylogenetically corrected models. Effect sizes were deemed clearly determined when 0 was not included in the 95% credibility intervals of the posteriors.

3.2 Movement direction

Arthropod movement at De Panne exhibited a noticeable directional bias, indicating that individuals did not move randomly (Figure 4). The R-values, representing concentration of movement and thus directional bias, were significant for most taxonomic orders except Orthoptera, Isopoda and Coleoptera (Appendix S.6). Both cursorial and flying taxa displayed similar degrees of bias, with flying individuals showing slightly higher directionality (R=0.30) compared to cursorial individuals (R=0.25). Interestingly, movement direction was mostly oriented towards habitat across all observations, independent of the prevailing wind direction. The lowest R-value was associated with a south-west wind, opposite to the habitat direction (R=0.19), while the highest R-value was linked to a south-east wind, largely aligned with the habitat direction (R=0.71). After correcting for multiple testing, all R-values, except for the SW model, remained significant. The results from the Jammalamadaka-Sarma correlations test supported these findings, indicating a generally weak correlation between wind direction and movement direction of individuals (Appendix S.7). However, the strength of this correlation varied strongly among orders, with Isopoda having the largest negative correlation (-0.27) and Araneae the largest positive correlation (0.34). In contrast, the Bayesian models showed that higher wind speeds reduce the tendency of flying individuals to move towards the habitat (Figure 5, left). After splitting the dataset based on the wind conditions, it was revealed that this effect was driven by individuals tested under upwind conditions. Similarly, cursorial species only showed a negative correlation between wind speed and movement direction under upwind conditions (Figure 5, right). This indicates that strong upwinds lower the propensity of both groups to navigate back to the habitat.

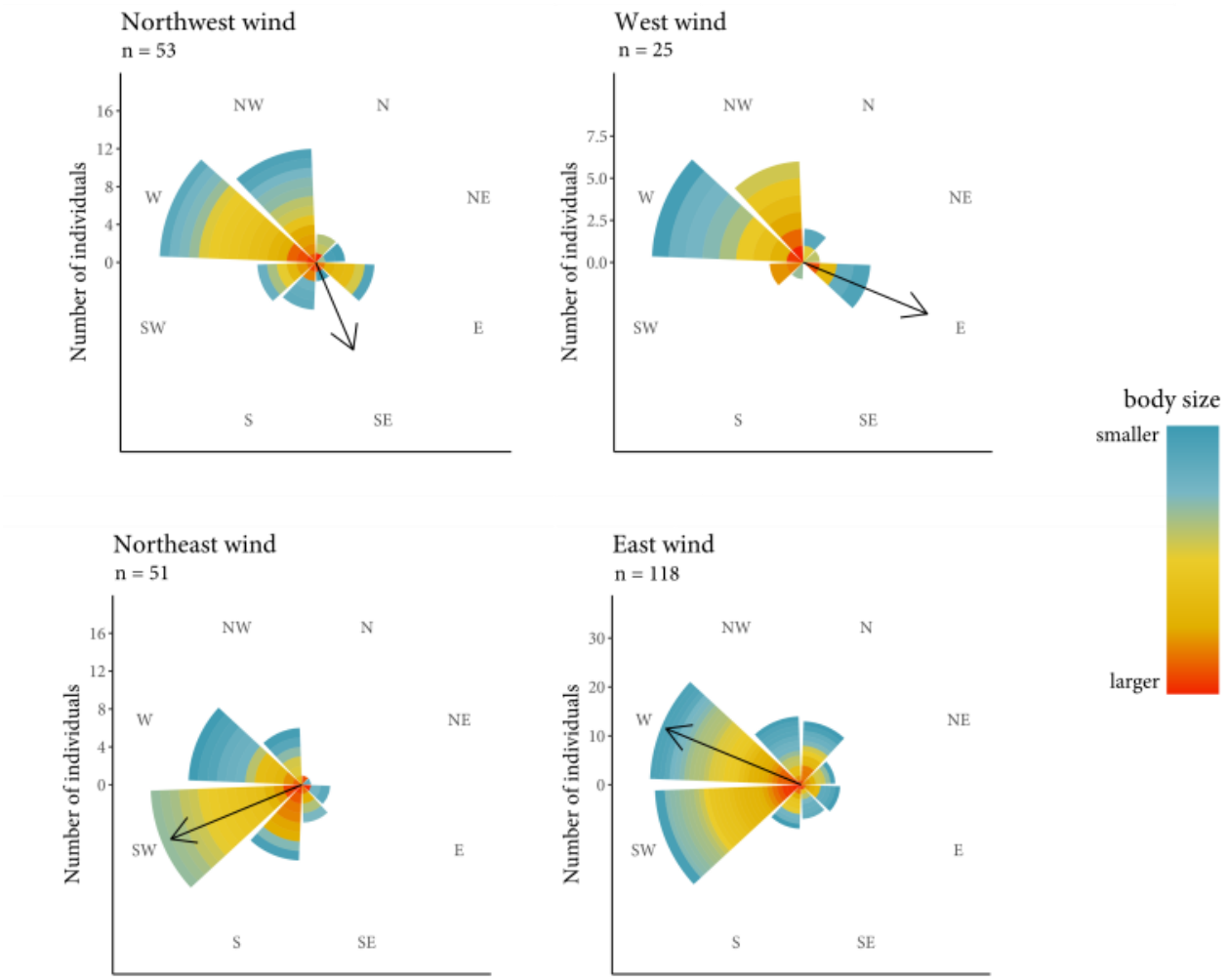


Figure 4: Circular bar plots of movement directions for flying species under 4 different wind scenarios. Each concentric slice on the bar represents an individual, and is colored according to its body size. The black arrows indicate the direction of the wind. Similar figures for cursorial species can be found in Appendix S.5.2.

307

Average movement directions also differed between both groups; flying species displayed an average direction of μ=-77.84 degrees, which corresponds to a direction between south and southwest. Cursorial individuals on the other hand showed a mean direction of μ=26.69 degrees, located between west and northwest. Additionally, body size significantly affects the direction of both flying and cursorial movement (Figure 5). However, the relationship is reversed for both groups: where larger flying individuals are more prone to move towards habitat, larger cursorial individuals are less prone. It has to be noted that the negative relationship between body size and successful navigation in cursorial species disappeared upon inclusion of phylogenetic relationships in the model, indicating that the correlation is largely driven by phylogeny (Figure 5). Additionally, the relationship becomes clearer when only individuals tested under upwind conditions were considered, suggesting an adverse effect of wind on the navigation of larger species.

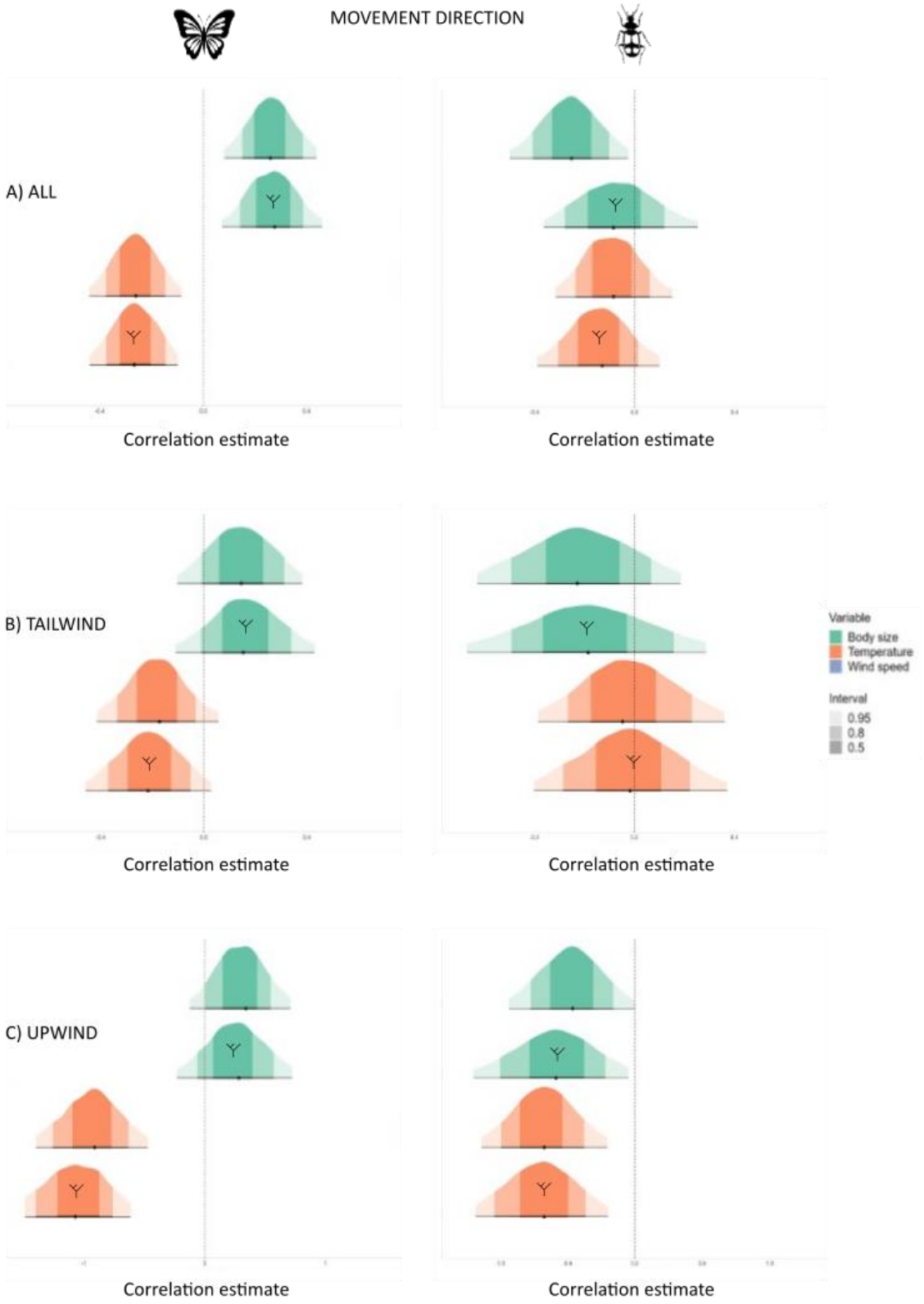


Figure 5: Estimates for the correlations between movement direction, body size and wind speed for a) all wind conditions, b) tailwind conditions (n=440) and c) upwind conditions (n=248). Posterior distributions that are marked with a phylogenetic tree resulted from the phylogenetically corrected models. Effect sizes were deemed clearly determined when 0 was not included in the 95% credibility intervals of the posteriors.

4. Discussion

Overall, our results highlight the influence of both internal and external factors on arthropod movement. Larger flying arthropods exhibited greater movement speed moved compared to their smaller counterparts, while the presence of strong tailwinds further increased their movement speed. In contrast, the movement speed of cursorial arthropods appeared unrelated to body size but displayed an increase in response to elevated temperatures. Notably, our observations revealed a clear directional bias towards habitat, indicating an internal drive among arthropods to move towards suitable environments. However, species showed varying levels of navigational proficiency, with larger flying and smaller cursorial arthropods displaying a greater tendency to move in the desired direction. Furthermore, our study identified strong upwinds as a hindrance to both groups, impeding the capacity for successful navigation.

The positive correlation between movement speed and body size in flying arthropods was in alignment with expectations. Previous studies already established that—within the same taxon—larger arthropods tend to move faster (Kuussaari *et al.*, 2014; Wootton, 2020; Dingle, Blakley' and Miller, 2023). Our study emphasizes that this effect remains consistent across multiple taxa. This positive correlation between body size and movement speed remained even after accounting for phylogenetic relationships, confirming its generality across taxonomic lineages and closely related species of flying species. The phylogenetic signal in the models for flying species was relatively large and mainly driven by Odonata, which were both larger and faster compared to many other species tested here. Thus, for example, larger bees are generally faster than smaller bees or smaller butterflies, but do not necessarily surpass the pace of a larger dragonfly.

In contrast, the absence of a correlation between movement speed and body size in cursorial arthropods contradicts previous studies demonstrating a positive relationship these two parameters (Hurlbert, Ballantyne and Powell, 2008; Foellmer, Marson and Moya-Laraño, 2011; Hirt *et al.*, 2017). A first possible explanation is that a relatively limited range of body sizes were tested, spanning from

350 1.21 mm to 21.31 mm, making it hard to detect a signal. Secondly, an alternative, more functionally
351 relevant measure of body size, such as dry weight, could potentially yield different outcomes. For
352 instance, harvestmen may appear small in our dataset due to their compact body length, but their long
353 legs could enable faster running compared to species with similar body length (Smith *et al.*, 2012;
354 Arnold, Cassey and White, 2017). The use of a relative measure does, however, not allow comparisons
355 across species and thus limits generality of the outcome. A third potential explanation is linked to the
356 interaction between the body mass of an individual and the texture of the surface on which it moves.
357 Sand is a porous substance, in which heavier objects might sink faster compared to smaller objects.
358 This could hamper movement of arthropods who do not have the morphological adjustments to move
359 supplely on coarse-grained surfaces.

360 In addition to body size, wind speed also positively influenced the movement speed of flying
361 individuals. Conversely, when individuals faced upwind, the effect reversed. This implies that inter-
362 habitat movement may be more pronounced during tailwind conditions towards the habitat, thereby
363 assisting arthropods in traversing the matrix (DiLeo *et al.*, 2022). However, under natural conditions,
364 the prospect of winds blowing arthropods out of their habitat might deter them from departing, as for
365 instance found in ballooning spiders (Bonte, Bossuyt and Lens, 2007). In this study, individuals were
366 forced to move, mimicking a flight reaction that poorly reflects the departure from a habitat, but is
367 more representative for the transfer phase of dispersal, i.e. the movement between habitats (Clobert
368 *et al.*, 2009; Bonte *et al.*, 2012).

369 Surprisingly, temperature did not significantly impact the movement speed of flying individuals. This
370 can potentially be attributed to the capacity of many flying arthropods to elevate their body
371 temperature through wing movement (Heinrich, 1974). Moreover, our dataset lacked extreme (hot or
372 cold) temperatures and we used an approximative measure for temperature, measured at the height
373 of the observer, not in the direct surroundings of the individuals. Both can potentially mask any trend
374 between temperature and movement of flying arthropods. In contrast, cursorial individuals

375 demonstrated the opposite pattern: temperature exerted a positive effect and wind did not. Given
376 that cursorial species remain in direct contact with the bare sand, they experience higher ambient
377 temperatures compared to flying species due to the fast and more extreme heating of sandy surface.
378 However they do not have specific mechanisms in order to increase body temperature (Maes *et al.*,
379 2006; Mutiibwa, Strachan and Albright, 2015) and it is thus expected that their movement is more
380 directly linked to ambient temperature. Our measurements reflect this, on condition that temperature
381 measured at observer height is directly related to surface temperature. Nevertheless, extremely high
382 temperatures can potentially even become detrimental when a certain thermal threshold is reached
383 (Heinrich, 1995).

384 Intriguingly, our findings reveal that on average, movement direction in cursorial species is more
385 closely correlated to the direction of the habitat in comparison to their flying counterparts, despite
386 showing a slightly more diffuse distribution in movement directions. First of all, both groups are
387 difficult to compare due to inherent differences in experiment set-up, since the cursorial individuals
388 were tested much closer to the habitat. Secondly, the elevated perspective of flying arthropods leads
389 to a more effective navigation, increasing opportunities to move in directions that may deviate from
390 the reference point but still lead to suitable habitat. In general, the movement direction of both flying
391 and cursorial species exhibited a clear bias towards habitat areas, indicating that the intention of
392 moving towards suitable environments is a more important driver for navigation than wind direction.
393 This was also recently observed in the migration patterns of a dragonfly species (Oelmann *et al.*, 2023).
394 Despite this, movement direction was not completely decoupled from wind conditions. For both flying
395 and cursorial species, strong upwind negatively impacted navigation, indicating the wind's ability to
396 divert individuals from their intended destination. Nonetheless, the preference for a specific direction
397 persisted despite wind resistance, implying that arthropods are willing to endure the energetic costs
398 associated with navigating towards hospitable environments. Similarly, tailwind assistance could
399 minimize energy expenditure during movement, which is in line with observations from migratory
400 species (Knight *et al.*, 2019; Knoblauch, Thoma and Menz, 2021). Only when winds were aligned with

401 the habitat direction, a clear-cut positive correlation between movement and wind direction was
402 observed, indicating that arthropods opportunistically harness winds to facilitate movement towards
403 their intended destinations.

404 Body size clearly influenced movement direction and navigation decisions. Flying arthropods show a
405 positive correlation between body size and navigation, which aligns with expectations, given the
406 advantages of larger body sizes in handling upwind movement (Kuenen and Cardé, 1993) and
407 potentially broader perceptual ranges (Pawar, Dell, and Van M. Savage, 2012). There was no clearly
408 determined correlation between body size and navigation for cursorial species in the phylogenetically
409 corrected models. However, the uncorrected models show a negative correlation, suggesting that
410 smaller taxa are more inclined to move towards habitat. This might imply that certain taxa with
411 generally small species, such as spiders, possess more extensive perceptual ranges, potentially because
412 they rely more on non-visual cues in order to navigate the environment (Foelix, 2011).

413 From a broader ecological perspective, our findings underscore that connectivity between habitat
414 patches is not random (Goicolea *et al.*, 2021). Instead, species tend to actively seek out their habitat
415 when they accidentally venture into the matrix. This suggests that movement between patches is
416 primarily an active decision rather than a random occurrence (Clobert *et al.*, 2009; Poethke, Gros and
417 Hovestadt, 2011; Bonte *et al.*, 2012). Nevertheless, the success of returning to a suitable habitat
418 depends heavily on both morphological attributes and prevailing weather conditions. Larger body sizes
419 and the ability to fly provide advantages for arthropods navigating through the matrix, enhancing their
420 efficiency and propensity to move in the desired direction. Moreover, ambient temperatures and wind
421 speeds can either augment or impede movement efficiency, depending on factors like wind direction
422 and thermal thresholds. The looming influence of climate change introduces another layer of
423 complexity, with expected potential changes in body sizes (Baar *et al.*, 2018; Davies, 2019; Polidori *et*
424 *al.*, 2020) and wind patterns (Greene, Morrissey and Johnson, 2010). This implies that changes in
425 weather conditions, associated with global warming, will not only influence population sizes by

increasing stress on a local scale, but might also exert a direct impact on small-scale movements by either increasing or decreasing the energetic costs of traversing the matrix. It is important to note that even though these results were interpreted in terms of connectivity, we measured flight responses rather than routine movements or long-distance dispersal. The findings from this study are thus relevant for the smaller "fundamental movement elements" (Getz and Saltz, 2008), but it remains to be explored how these small-scale spatiotemporal patterns eventually scale up to canonical and lifetime movement patterns. Such insights could potentially help to explain the weather dependence of dispersal, as measured by capture-mark-recapture studies (Cormont *et al.*, 2011; Delattre *et al.*, 2013; Kuussaari *et al.*, 2016) and gene flow across generations and populations (DiLeo *et al.*, 2022; Batsleer *et al.*, 2023).

Conclusion

In our small-scale release experiment under natural conditions, we observed that both body size and weather conditions play pivotal roles in shaping the movement of arthropods. Specifically, our study revealed that flying arthropods benefit from larger body sizes and the presence of strong tailwinds, facilitating their successful traversal and navigation through the matrix. In contrast, cursorial arthropods are mainly aided by higher ambient temperatures, with the smaller taxa having an navigational advantage. Remarkably, both groups show an inherent drive to move towards their preferred habitat, even when faced with adverse wind conditions. These insights were generated across multiple taxa and lay a basis for a trait-based predictive ecology on arthropod spatial dynamics.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and materials

The raw data is available via Zenodo at https://doi.org/10.5281/zenodo.8232574.

Competing interests

The authors declare that they have no competing interests.

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Author's contributions

GL, CT, FVH and DB designed the experiments. CT, FVH and GL conducted the practical work. GL and CT wrote the first draft of the manuscript. CT and GL analysed the data. All authors contributed substantially to the interpretation of the results and revision of the manuscript.

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References

Agostinelli, C. and Lund, U. (2022) 'R package "circular": Circular Statistics (version 0.4-95)'. Available at: https://r-forge.r-project.org/projects/circular/.

Aikman, D. and Hewitt, G. (1972) 'An Experimental Investigation of the Rate and Form of Dispersal in Grasshoppers', *The Journal of Applied Ecology*, 9(3), p. 807. Available at: https://doi.org/10.2307/2401906.

Arnold, P.A., Cassey, P. and White, C.R. (2017) 'Functional traits in red flour beetles: the dispersal phenotype is associated with leg length but not body size nor metabolic rate', *Functional Ecology*. Edited by E. Rezende, 31(3), pp. 653–661. Available at: https://doi.org/10.1111/1365-2435.12772.

Baar, Y. *et al.* (2018) 'Little effect of climate change on body size of herbivorous beetles: Climate change and beetle body size', *Insect Science*, 25(2), pp. 309–316. Available at: https://doi.org/10.1111/1744-7917.12420.

Baker, L., Kelty, E.C. and Jakob, E.M. (2009) 'The Effect of Visual Features on Jumping Spider Movements Across Gaps', *Journal of Insect Behavior*, 22(5), pp. 350–361. Available at: https://doi.org/10.1007/s10905-009-9177-0.

Batsleer, F. *et al.* (2020) 'The neglected impact of tracking devices on terrestrial arthropods', *Methods in Ecology and Evolution*. Edited by D.J. (Johan) Kotze, 11(3), pp. 350–361. Available at: https://doi.org/10.1111/2041-210X.13356.

Batsleer, F. *et al.* (2023) 'Asymmetrical gene flow between coastal and inland dunes in a threatened digger wasp', *Conservation Genetics* [Preprint]. Available at: https://doi.org/10.1007/s10592-023-01566-7.

Benjamini, Y. and Hochberg, Y. (1995) 'Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing', *Journal of the Royal Statistical Society: Series B (Methodological)*, 57(1), pp. 289–300. Available at: https://doi.org/10.1111/j.2517-6161.1995.tb02031.x.

Blaum, N. *et al.* (2012) 'Climate induced changes in matrix suitability explain gene flow in a fragmented landscape - the effect of interannual rainfall variability', *Ecography*, 35(7), pp. 650–660. Available at: https://doi.org/10.1111/j.1600-0587.2011.07154.x.

Bonsignore, C.P. and Bellamy, C. (2007) 'Daily activity and flight behaviour of adults of Capnodis tenebrionis (Coleoptera: Buprestidae)', *European Journal of Entomology*, 104(3), pp. 425–431. Available at: https://doi.org/10.14411/eje.2007.062.

Bonte, D. *et al.* (2012) 'Costs of dispersal', *Biological Reviews*, 87(2), pp. 290–312. Available at: https://doi.org/10.1111/j.1469-185X.2011.00201.x.

Bonte, D., Bossuyt, B. and Lens, L. (2007) 'Aerial dispersal plasticity under different wind velocities in a salt marsh wolf spider', *Behavioral Ecology*, 18(2), pp. 438–443. Available at: https://doi.org/10.1093/beheco/arl103.

Bowler, D.E. and Benton, T.G. (2005) 'Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics', *Biological Reviews*, 80(2), pp. 205–225. Available at: https://doi.org/10.1017/S1464793104006645.

Buehlmann, C., Mangan, M. and Graham, P. (2020) 'Multimodal interactions in insect navigation', *Animal Cognition*, 23(6), pp. 1129–1141. Available at: https://doi.org/10.1007/s10071-020-01383-2.

Bürkner, P.-C. (2021) 'Bayesian Item Response Modeling in R with brms and Stan', 100(5), pp. 1–54. Available at: https://doi.org/doi:10.18637/jss.v100.i05.

Chown, S.L. and Nicolson, S.W. (2004) *Insect phyisological ecology: Mechanisms and patterns*. Oxford: Oxford University Press.

Clark, J.A. and May, R.M. (2002) 'Taxonomic bias in conservation research', 297(5579), pp. 191–192.

Clobert, J. *et al.* (2009) 'Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations', *Ecology Letters*, 12(3), pp. 197–209. Available at: https://doi.org/10.1111/j.1461-0248.2008.01267.x.

Cormont, A. *et al.* (2011) 'Effect of local weather on butterfly flight behaviour, movement, and colonization: significance for dispersal under climate change', *Biodiversity and Conservation*, 20(3), pp. 483–503. Available at: https://doi.org/10.1007/s10531-010-9960-4.

Davies, W.J. (2019) 'Multiple temperature effects on phenology and body size in wild butterflies predict a complex response to climate change', *Ecology*, 100(4). Available at: https://doi.org/10.1002/ecy.2612.

Delattre, T. *et al.* (2013) 'Interactive effects of landscape and weather on dispersal', *Oikos*, 122(11), pp. 1576–1585. Available at: https://doi.org/10.1111/j.1600-0706.2013.00123.x.

DiLeo, M.F. *et al.* (2022) 'Effects of environment and genotype on dispersal differ across departure, transfer and settlement in a butterfly metapopulation', *Proceedings of the Royal Society B: Biological Sciences*, 289(1976), p. 20220322. Available at: https://doi.org/10.1098/rspb.2022.0322.

Dingle, H., Blakley', N.R. and Miller, E.R. (2023) 'Variation in Body Size and Flight Performance in Milkweed Bugs (Oncopeltus)'.

Dudley, R. (2000) *The biomechanics of insect flight - Form, function, evolution*. New York: Princeton University Press.

Eguagie, W.E. (1974) 'An Analysis of Movement of Adult Tingis ampliata H.-S. (Heteroptera: Tingidae) in a Natural Habitat', *The Journal of Animal Ecology*, 43(2), p. 521. Available at: https://doi.org/10.2307/3381.

Foelix, R.F. (2011) *Biology of Spiders*. 3rd edn. Oxford: Oxford University Press.

Foellmer, M.W., Marson, M. and Moya-Laraño, J. (2011) 'Running performance as a function of body size, leg length, and angle of incline in male orb-web spiders, Argiope aurantia', 13, pp. 513–526.

Frick, W.F. *et al.* (2013) 'Aeroecology', in R.A. Adams and S.C. Pedersen (eds) *Bat Evolution, Ecology, and Conservation*. New York, NY: Springer New York, pp. 149–167. Available at: https://doi.org/10.1007/978-1-4614-7397-8_8.

Frizzi, F. (2018) 'Complexity of searching movement in the European harvester ant Messor wasmanni: effect of temperature and body size', *Insectes Sociaux*, 65(2), pp. 263–273. Available at: https://doi.org/10.1007/s00040-018-0609-8.

Ganihar, S.R. (1997) 'Biomass estimates of terrestrial arthropods based on body length', *Journal of Biosciences*, 22(2), pp. 219–224. Available at: https://doi.org/10.1007/BF02704734.

Getz, W.M. and Saltz, D. (2008) 'A framework for generating and analyzing movement paths on ecological landscapes', *Proceedings of the National Academy of Sciences*, 105(49), pp. 19066–19071. Available at: https://doi.org/10.1073/pnas.0801732105.

Gilbert, F., Gonzalez, A. and Evans-Freke, I. (1998) 'Corridors maintain species richness in the fragmented landscapes of a microecosystem', *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 265(1396), pp. 577–582. Available at: https://doi.org/10.1098/rspb.1998.0333.

Goicolea, T. *et al.* (2021) 'Deterministic, random, or in between? Inferring the randomness level of wildlife movements', *Movement Ecology*, 9(1), p. 33. Available at: https://doi.org/10.1186/s40462-021-00273-7.

González-Tokman, D. *et al.* (2020) 'Insect responses to heat: physiological mechanisms, evolution and ecological implications in a warming world', 95, pp. 802–821. Available at: https://doi.org/10.1111/brv.12588.

Goodwin, B.J. and Fahrig, L. (2002) 'Effect of landscape structure on the movement behaviour of a specialized goldenrod beetle, *Trirhabda borealis*', *Canadian Journal of Zoology*, 80(1), pp. 24–35. Available at: https://doi.org/10.1139/z01-196.

Grafen, A. (1989) 'The phylogenetic regression', 326, pp. 119–157.

Greene, S., Morrissey, M. and Johnson, S.E. (2010) 'Wind Climatology, Climate Change, and Wind Energy: Wind climatology and wind energy', *Geography Compass*, 4(11), pp. 1592–1605. Available at: https://doi.org/10.1111/j.1749-8198.2010.00396.x.

Heinrich, B. (1974) 'Thermoregulation in Endothermic Insects: Body temperature is closely attuned to activity and energy supplies.', *Science*, 185(4153), pp. 747–756. Available at: https://doi.org/10.1126/science.185.4153.747.

Heinrich, B. (1995) 'Insect thermoregulation', 19(1), pp. 28–33. Available at: https://doi.org/10.1016/0160-9327(95)98891-I.

Hirt, M.R. *et al.* (2017) 'The little things that run: a general scaling of invertebrate exploratory speed with body mass', *Ecology*, 98(11), pp. 2751–2757. Available at: https://doi.org/10.1002/ecy.2006.

Hurlbert, A.H., Ballantyne, F. and Powell, S. (2008) 'Shaking a leg and hot to trot: the effects of body size and temperature on running speed in ants', *Ecological Entomology*, 33(1), pp. 144–154. Available at: https://doi.org/10.1111/j.1365-2311.2007.00962.x.

Jammalamadaka, S.R. and Sarma, Y.R. (1988) 'A correlation coefficient for angular variables', in *Statistical Theory and Data Analysis II*. North-Holland: Elsevier Science Publishers B. V., pp. 349–363.

Jonsen, I.D., Bourchier, R.S. and Roland, J. (2001) 'The influence of matrix habitat on Aphthona flea beetle immigration to leafy spurge patches', *Oecologia*, 127(2), pp. 287–294. Available at: https://doi.org/10.1007/s004420000589.

Kissling, W.D., Pattemore, D.E. and Hagen, M. (2014) 'Challenges and prospects in the telemetry of insects: Insect telemetry', *Biological Reviews*, 89(3), pp. 511–530. Available at: https://doi.org/10.1111/brv.12065.

Knight, S.M. *et al.* (2019) 'Radio-tracking reveals how wind and temperature influence the pace of daytime insect migration', *Biology Letters*, 15(7), p. 20190327. Available at: https://doi.org/10.1098/rsbl.2019.0327.

Knoblauch, A., Thoma, M. and Menz, M.H.M. (2021) 'Autumn southward migration of dragonflies along the Baltic coast and the influence of weather on flight behaviour', *Animal Behaviour*, 176, pp. 99–109. Available at: https://doi.org/10.1016/j.anbehav.2021.04.003.

Kuenen, L.P.S. and Cardé, R.T. (1993) 'Effects of moth size on velocity and steering during upwind flight toward a sex pheromone source by Lymantria dispar (Lepidoptera: Lymantriidae)', 6, pp. 177–193.

Kuussaari, M. *et al.* (2014) 'Higher mobility of butterflies than moths connected to habitat suitability and body size in a release experiment', *Ecology and Evolution*, 4(19), pp. 3800–3811. Available at: https://doi.org/10.1002/ece3.1187.

Kuussaari, M. *et al.* (2016) 'Weather explains high annual variation in butterfly dispersal', *Proceedings of the Royal Society B: Biological Sciences*, 283(1835), p. 20160413. Available at: https://doi.org/10.1098/rspb.2016.0413.

Leibold, M.A. *et al.* (2004) 'The metacommunity concept: a framework for multi-scale community ecology: The metacommunity concept', *Ecology Letters*, 7(7), pp. 601–613. Available at: https://doi.org/10.1111/j.1461-0248.2004.00608.x.

Lima, S.L. and Zollner, P.A. (1996) 'Towards a behavioral ecology of ecological landscapes', *Trends in Ecology & Evolution*, 11(3), pp. 131–135. Available at: https://doi.org/10.1016/0169-5347(96)81094-9.

Maes, D. *et al.* (2006) 'Habitat Use and Mobility of Two Threatened Coastal Dune Insects: Implications for Conservation', *Journal of Insect Conservation*, 10(2), pp. 105–115. Available at: https://doi.org/10.1007/s10841-006-6287-2.

Martin, C.A., Proulx, R. and Magnan, P. (2014) 'The biogeography of insects' length-dry mass relationships', *Insect Conservation and Diversity*. Edited by C. Dytham and J.M. Lobo, 7(5), pp. 413–419. Available at: https://doi.org/10.1111/icad.12063.

Matthew, P. *et al.* (2014) 'geiger v2.0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees', 30, pp. 2216–2218.

McIntyre, N.E. and Wiens, J.A. (1999) 'Interactions between landscape structure and animal behavior: the roles of heterogeneously distributed resources and food deprivation on movement patterns', 14, pp. 437–447.

Merckx, T. *et al.* (2003) 'The evolution of movements and behaviour at boundaries in different landscapes: a common arena experiment with butterflies', *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1526), pp. 1815–1821. Available at: https://doi.org/10.1098/rspb.2003.2459.

Merckx, T. *et al.* (2008) 'Thermal flight budget of a woodland butterfly in woodland versus agricultural landscapes: An experimental assessment', *Basic and Applied Ecology*, 9(4), pp. 433–442. Available at: https://doi.org/10.1016/j.baae.2007.03.009.

Merckx, T. and Van Dyck, H. (2007) 'Habitat fragmentation affects habitat-finding ability of the speckled wood butterfly, Pararge aegeria L.', *Animal Behaviour*, 74(4), pp. 1029–1037. Available at: https://doi.org/10.1016/j.anbehav.2006.12.020.

Michonneau, F., Brown, J.W. and Winter, D.J. (2016) 'rotl: an R package to interact with the Open Tree of Life data', 7(12), pp. 1476–1481. Available at: https://doi.org/doi:10.1111/2041-210X.12593.

Moretti, M. *et al.* (2017) 'Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits', *Functional Ecology*. Edited by C. Fox, 31(3), pp. 558–567. Available at: https://doi.org/10.1111/1365-2435.12776.

Mutiibwa, D., Strachan, S. and Albright, T. (2015) 'Land Surface Temperature and Surface Air Temperature in Complex Terrain', *IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing*, 8(10), pp. 4762–4774. Available at: https://doi.org/10.1109/JSTARS.2015.2468594.

Nathan, R. *et al.* (2008) 'A movement ecology paradigm for unifying organismal movement research', *Proceedings of the National Academy of Sciences*, 105(49), pp. 19052–19059. Available at: https://doi.org/10.1073/pnas.0800375105.

Neuwirth, E. (2022) 'RColorBrewer: ColorBrewer Palettes. R package version 1.1-3'. Available at: https://CRAN.R-project.org/package=RColorBrewer.

Oelmann, Y. *et al.* (2023) 'Autumn migration of the migrant hawker (Aeshna mixta) at the Baltic coast', *Movement Ecology*, 11(1), p. 52. Available at: https://doi.org/10.1186/s40462-023-00415-z.

Paradis, E. and Schliep, K. (2019) 'ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R', 35, pp. 526–528.

Pawar, S., Dell, A.I., and Van M. Savage (2012) 'Dimensionality of consumer search space drives trophic interaction strengths', *Nature*, 486(7404), pp. 485–489. Available at: https://doi.org/10.1038/nature11131.

Pewsey, A., Neuhäuser, M. and Ruxton, G.D. (2013) *Circular Statistics in R*. Oxford: Oxford University Press.

Pincebourde, S., Dillon, M.E. and Woods, H.A. (2021) 'Body size determines the thermal coupling between insects and plant surfaces', *Functional Ecology*, 35(7), pp. 1424–1436. Available at: https://doi.org/10.1111/1365-2435.13801.

Poethke, H.J., Gros, A. and Hovestadt, T. (2011) 'The ability of individuals to assess population density influences the evolution of emigration propensity and dispersal distance', *Journal of Theoretical Biology*, 282(1), pp. 93–99. Available at: https://doi.org/10.1016/j.jtbi.2011.05.012.

Polidori, C. *et al.* (2020) 'Climate change-driven body size shrinking in a social wasp', *Ecological Entomology*, 45(1), pp. 130–141. Available at: https://doi.org/10.1111/een.12781.

Qiu, Y. (2023) 'showtext: Using fonts more easily in R graphs. R package version 0.9-6'. Available at: https://CRAN.R-project.org/package=showtext.

R Core Team (2021) 'R: A language and environment for statistical computing'. Available at: https://www.r-project.org/.

Revell, L.J. (2012) 'phytools: An R package for phylogenetic comparative biology (and other things)', 3, pp. 217–223. Available at: https://doi.org/doi:10.1111/j.2041-210X.2011.00169.x.

Roff, D.A. (1986) 'The Evolution of Wing Dimorphism in Insects'.

Roff, D.A. (1990) 'The Evolution of Flightlessness in Insects', *Ecological Monographs*, 60(4), pp. 389–421. Available at: https://doi.org/10.2307/1943013.

Schäpers, A. *et al.* (2015) 'The Role of Olfactory Cues for the Search Behavior of a Specialist and Generalist Butterfly', *Journal of Insect Behavior*, 28(1), pp. 77–87. Available at: https://doi.org/10.1007/s10905-014-9482-0.

Schneider, C.A., Rasband, W.S. and Eliceiri, K.W. (2012) 'NIH Image to ImageJ: 25 years of image analysis', *Nature Methods*, 9(7), pp. 671–675. Available at: https://doi.org/10.1038/nmeth.2089.

Sekar, S. (2012) 'A meta-analysis of the traits affecting dispersal ability in butterflies: can wingspan be used as a proxy?: Factors affecting dispersal ability in butterflies', *Journal of Animal Ecology*, 81(1), pp. 174–184. Available at: https://doi.org/10.1111/j.1365-2656.2011.01909.x.

Smith, A.T. *et al.* (2012) 'Comparative study of walking and climbing speeds among Neotropical harvestmen from Costa Rica', *Journal of Arachnology*, 40(3), pp. 304–308. Available at: https://doi.org/10.1636/Hi10-103.1.

Terlau, J.F. *et al.* (2023) 'Predicting movement speed of beetles from body size and temperature', *Movement Ecology*, 11(1), p. 27. Available at: https://doi.org/10.1186/s40462-023-00389-y.

Van Dyck, H. and Baguette, M. (2005) 'Dispersal behaviour in fragmented landscapes: Routine or special movements?', *Basic and Applied Ecology*, 6(6), pp. 535–545. Available at: https://doi.org/10.1016/j.baae.2005.03.005.

White, E.P. *et al.* (2007) 'Relationships between body size and abundance in ecology', *Trends in Ecology & Evolution*, 22(6), pp. 323–330. Available at: https://doi.org/10.1016/j.tree.2007.03.007.

Wickham, H. (2016) 'ggplot2: Elegant Graphics for Data Analysis'. New York: Springer-Verlag.

Wickham, H. *et al.* (2022) 'dplyr: A Grammar of Data Manipulation. R package version 1.0.10'. Available at: https://CRAN.R-project.org/package=dplyr.

Woodward, G. *et al.* (2005) 'Body size in ecological networks', *Trends in Ecology & Evolution*, 20(7), pp. 402–409. Available at: https://doi.org/10.1016/j.tree.2005.04.005.

Wootton, R. (2020) 'Dragonfly flight: morphology, performance and behaviour', *International Journal of Odonatology*, 23(1), pp. 31–39. Available at: https://doi.org/10.1080/13887890.2019.1687991.

Yang, L.H. and Gratton, C. (2014) 'Insects as drivers of ecosystem processes', *Current Opinion in Insect Science*, 2, pp. 26–32. Available at: https://doi.org/10.1016/j.cois.2014.06.004.