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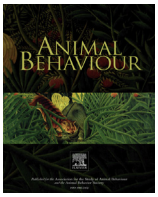

Effects of wind, ambient temperature and sun position on damselfly flight activity and perch orientation

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Many animals rely on movement for survival and reproduction. Directed movements incur metabolic costs, however, and animals adjust their behaviour to optimize energy expenditures in different abiotic conditions. Physical flows and solar radiation vary over time and space and influence animal behaviour at multiple spatiotemporal scales. Here, I quantify the effects of wind speed, wind direction, ambient temperature and sun position on the fine-scale movement ecology and perch orientation of a widespread damselfly, *Enallagma doubledayi*. Through field observations, I found that damselflies fly, forage and engage competitors in territorial interactions more often in calm rather than windy conditions. Furthermore, perched damselflies exhibit rheotaxis, in which individuals typically face into the wind, presumably to minimize biomechanical costs associated with drag and possibly to detect inbound prey on the water surface and in the air column. In contrast, ambient temperature and the position of the sun were largely unassociated with activity levels and damselfly orientation. At higher ambient temperatures, however, perched odonates faced the sun with increasing consistency, perhaps to thermoregulate by minimizing exposure to solar radiation. Taken together, these findings suggest that damselflies preferentially fly when the ratio of animal speed to wind speed is high and adjust their perch orientation to minimize energy loss. These findings strengthen conceptual links between activity budgets and perch orientation strategies among animals in variable abiotic conditions.

Movement is a fundamental behaviour of many animals. When animals perform directed movements, however, they incur a metabolic cost (Dickinson et al., 2000). Natural selection therefore optimizes movement-based behaviours to minimize energy expenditures and maximize fitness in different abiotic conditions (Dingle, 2014; Shepard et al., 2013). Physical flows, namely winds and aquatic currents, can dramatically affect animal activity levels and orientation strategies (Chapman et al., 2011; McLaren, Shamoun-Baranes, Dokter, Klaassen, & Bouten, 2014; Vogel, 1994). The direction and magnitude of water flow has pervasive impacts on animal activity in aquatic environments (Hart & Finelli, 1999; Liao, 2007; Poff & Zimmerman, 2010), while wind vectors similarly affect terrestrial organisms at multiple scales (Diehl, 2013; Kunz et al., 2007; Liechti & Bruderer, 1998). The majority of existing studies, however, have focused on animal responses to flows during long-distance movements, such as partial or full compensation for 'drift' during seasonal migration events (Aarestrup et al., 2009; Alerstam, Hedenström, & Åkesson, 2003; Chapman, Nesbit, & Burgin, 2010). Currents also influence short-distance movements, however, including mobile efforts involved with reproduction and foraging (Alma, Farji-Brener, & Elizalde, 2016; Bennetts, Fasola, Hafner, & Kayser, 2000; Conradt, Clutton-Brock, & Guinness, 2000).

Volant predators rely on rapid adjustments in flight speed and direction to capture prey, and often adjust their flight behaviour in response to wind (Alexander, 2002; Hedenström & Rosén, 2001; Moore & Biewener, 2015). Strong winds can impose biomechanical and energetic constraints (Elliott et al., 2014), but can also provide lift (Templin, 2000) or increase downwind velocities (Weimerskirch, Guionnet, Martin, Shaffer, & Costa, 2000). As a corollary, behavioural responses to wind vary among species and is often context dependent. Glaucous gulls, *Larus hyperboreus*, for example, increase predation rates on nesting thick-billed murre, *Uria lomvia*, at higher wind speeds (Gilchrist, Gaston, & Smith, 1998). In contrast, adult stoneflies are less active in strong winds (Briers, Cariss, & Gee, 2003), while wind speed does not influence flight activity among lesser kestrels, *Falco naumanni* (Hernández-Pliego, Rodríguez, & Bustamante, 2014). Additional studies on shags (Kogure, Sato, Watanuki, Wanless, & Daunt, 2016), aphids (Walters & Dixon, 1984) and blow flies (Digby, 1958) illustrate the

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wide variety of effects that wind can impose on animal activity levels.

Diel patterns in the position of the sun can also dramatically affect animal activity levels by altering ambient temperatures and the angle of incident sunlight (Angilletta, 2009). Animals may seek or avoid sunlight (Stevenson, 1985), alter their posture (Stelzner & Hausfater, 1986; Tracy, Tracy, & Dobkin, 1979) or change other aspects of their behaviour to thermoregulate (Angilletta, Niewiarowski, & Navas, 2002; Huey & Stevenson, 1979). Ectotherms, which rely on external sources of heat, generally become more active as the ambient temperature increases but may also decrease activity levels and alter their behaviour to prevent overheating at higher temperatures (Porter & Gates, 1969). While the influence of ambient temperature on ectotherm behaviour is well documented in many systems, fewer studies simultaneously consider the effects of both wind and ambient temperature on animal activity levels and orientation behaviour.

In addition to altering their activity levels, organisms can adjust their orientation in physical flows and relative to the position of the sun to optimize their energy balance. Orientation strategies involved in short-distance movements and resting orientations in physical flows can vary substantially among taxa and behaviour types. Organisms may face directly into flows to search for nearby food or mates (Cardé & Willis, 2008; Gardiner & Atema, 2010), compensate for drift on local scales (Krupczynski & Schuster, 2008; Riley, Reynolds, Smith, & Edwards, 1999) or leverage tail-winds while tracking resources over shorter distances (Sapir, Horvitz, Dechmann, Fahr, & Wikelski, 2014; Zavalaga, Benvenuti, & Dall'Antonia, 2008). The ability to initiate and/or maintain different orientation strategies depends on an organism's capacity for directed movement relative to the strength of the flow; higher ratios of animal speed to flow speed enable a wider array of potential orientations (Chapman et al., 2011). Individuals may face directly into flows to track chemical cues or locate resources that are displaced and transported by flows (Cardé & Willis, 2008; Farkas & Shorey, 1972). Orientation towards the incoming direction of flows, or rheotaxis, may therefore benefit small-bodied organisms that wish to remain stationary in flows by minimizing biomechanical stressors, or seek resources that are transported by flows when the ratio of animal airspeed to flow speed is favourable for movement.

Animals also alter their orientation to the sun to either increase or decrease the amount of surface area that is exposed to solar radiation. For example, many animals face either directly towards or away from the sun to minimize exposure at high ambient temperatures, including gulls (Luskick, Battersby, & Kelty, 1978), ground squirrels (Bennett, Huey, John-Alder, & Nagy, 1984) and spiders (Suter, 1981). In contrast, other organisms orient perpendicular to the sun to increase surface area exposed to solar radiation at low ambient temperatures (Waldschmidt, 1980). Thus, an organism's orientation relative to the sun often depends on the ambient temperature and their capacity for physiological or behavioural thermoregulation. While the effects of flow speed, flow direction and solar radiation have each been studied extensively on their own, the combined effects of flows and the position of the sun on the orientation strategies and short-distance movement ecology of many taxa remain unknown (Holyoak, Casagrandi, Nathan, Revilla, & Spiegel, 2008).

Odonates present a tractable system to study activity levels and orientation strategies in response to abiotic conditions. Adult odonates rely on visual cues to detect prey (Corbet, 1980) and rapid changes in flight speed and direction to feed on a wide variety of arthropods (Combes, Rundle, Iwasaki, & Crall, 2012). Here, I quantify the effects of wind speed, wind direction, ambient temperature and sun position on movement ecology and perch orientation behaviour of a widespread, ‘perching’ damselfly (Corbet, 1980; Corbet & May, 2008). By combining abiotic and observational data, I test multiple hypotheses regarding the flight and orientation behaviour of damselflies in different environmental conditions. First, I test whether damselflies change their flight-based activity levels in response to wind speed and ambient temperature. I predicted that damselflies would fly, forage and engage in territorial interactions more often at low wind speeds (Fig. 1a) and high ambient temperatures (Fig. 1d). This linear prediction with ambient temperature assumes that ambient temperatures will not exceed values that are too high for damselfly activity. I also tested whether resting damselflies exhibit a particular orientation strategy with respect to wind and sun position, and whether orientations are influenced by the strength of abiotic pressures. I predicted that individual damselflies would orient facing the wind when perched with decreasing variance as wind speed increases to minimize drag, conserve energy and visually scan for potential food items (Fig. 1b). With respect to sun position, I predicted that damselflies would orient broadside relative to the sun at low ambient temperatures to increase solar absorption and internal temperatures (Fig. 1c); in contrast, I predicted damselflies would face towards the sun at high ambient temperatures to decrease incident sunlight and prevent overheating (Fig. 1d).

METHODS

Study Area

I conducted this study at the Archbold Biological Station, Venus, FL, U.S.A. (27°8′6″N, 81°21′41″W). I observed damselflies at eight different sites separated by at least 10 m, each of which was a shallow, ephemeral pond filled with grassy vegetation. Each ephemeral pond hosted at least five individual damselflies. Field observations took place between 31 March 2016 and 2 April 2016.

Study Species

Bluets in the genus *Enallagma* (Odonata: Coenagrionidae) constitute a recent radiation of damselflies that has diversified rapidly across the Holarctic to inhabit littoral zones of various aquatic habitats (Brown, McPeek, & May, 2000; Callahan & McPeek, 2016; McPeek & Brown, 2000). Here, I focus on the flight and perching behaviour of the Atlantic bluet, *Enallagma doubledayi*, which is an abundant, widespread species that inhabits fish-free aquatic habitats, especially shallow, grassy, ephemeral ponds of the eastern United States (Paulson, 2012). I identified the focal taxon to species by examining abdominal segment patterning, the shape and size of blue dots on the dorsal side of the head and the length of the cerci (Dunkle, 1990). Bluets generally feed by perching near the water surface on projecting stems at the edge of open bodies of water; they feed on a wide variety of arthropods by gleaning prey off of the water surface or off of vegetation, or sometimes by taking prey on the wing.

Field Methods

At the beginning of each observational period, I estimated wind direction with a windsock and placed a Windflow WEATHERmeter (windflow.com; Scotts Valley, CA, U.S.A.) anemometer facing into the wind. I mounted the anemometer on a stake and placed it approximately 5 cm above the surface of the water in the centre of the ephemeral pond. The anemometer measured and averaged wind speed, wind gust speed and ambient temperature during each 5 min observational period.

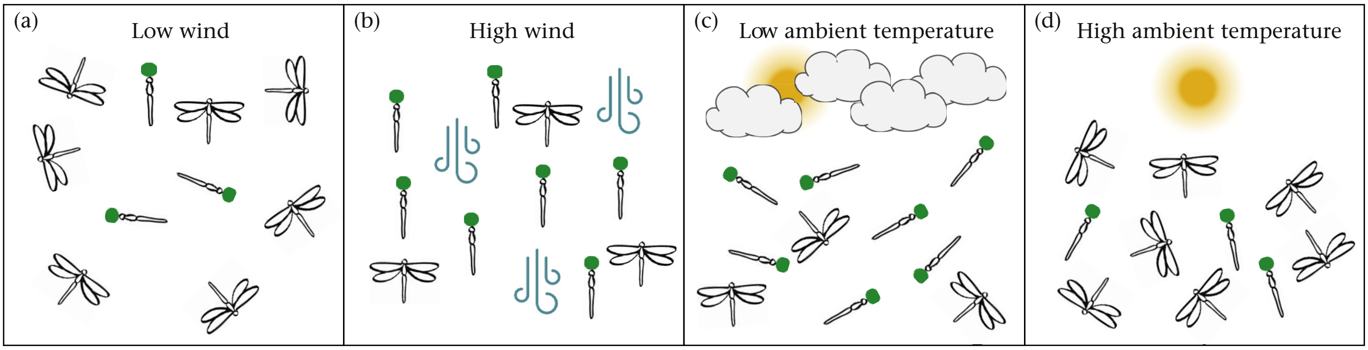

Figure 1. Predictions regarding the effects of wind conditions, ambient temperature and sun position on damselfly orientation and flight behaviour. In calm conditions (a), I predicted that damselflies would exhibit greater angular variance in perch orientation, fly more, forage more often and engage in more territorial interactions compared to windy conditions (b). At low ambient temperatures (c), I predicted that damselflies would be less active and would exhibit a mixture of orientations with respect to the sun while perched. At higher ambient temperatures (d), I predicted that damselflies would exhibit more flight activity and would face the sun when perched to minimize exposure to incident rays.

To quantify flight behaviour in different wind conditions, I haphazardly picked an individual damselfly from each ephemeral pond site and stood motionless for 1 min to allow the focal individual to acclimate to my presence. During each 5 min observational trial, I recorded the number and duration of flights, the number of foraging attempts and the number of territorial interactions. I defined foraging attempts as either successful or unsuccessful attempted air strikes at visible prey or exaggerated head motions to glean items off of the water surface or vegetation. I defined territorial interactions as aggressive, in-flight chases between conspecifics that involved the focal individual as either the pursuer or the pursued.

To quantify perch orientation, I located groups of at least five damselflies and stood motionless for 1 min to allow the damselflies to acclimate to my presence. During each 5 min observational trial, I estimated and recorded the angular orientation of each damselfly within eyesight using a compass. I measured the orientation of each individual that was perched at the beginning of the trial and each subsequent landing event. This sampling procedure implies that the unit of measurement is a perching or landing event rather than an individual. Therefore, an individual could have perched multiple times within an observational period, in which case the orientation of each perching event was treated as an independent observation. Raw data from these observational trials are available online through Dataverse (http://dx.doi.org/10.7910/DVN/LQNCBW).

Statistical Methods

To quantify the effect of wind speed on flight activity levels, I constructed a series of mixed effects generalized linear models (GLM) with log(wind speed) and ambient temperature as predictor variables within the R statistical environment (v.3.2.2; R Foundation for Statistical Computing, Vienna, Austria). I built a GLM with total flight time as a response variable under a Gaussian distribution of error. Because the remaining indices of flight activity were meristic (number of flights, number of foraging attempts, number of territorial interactions), I built all other GLMs with a Poisson distribution of error. For each GLM, I report the effect size (β) of both predictor variables and the corresponding P value.

I analysed damselfly perch orientation, wind direction and solar azimuthal position data with the ‘circular’ package (Agostinelli & Lund, 2013) within the R statistical programming environment (R Foundation for Statistical Computing). I acquired the azimuthal position of the sun for each observational period using the ‘oce’ package (Kelly & Richards, 2016) in R, which calculates the position of the sun based on a given time and location using algorithms first developed by Michalsky (1988). I converted all circular measurements (i.e. damselfly headings, wind direction, solar azimuth) into radians and calculated the mean direction of damselfly perches ($\bar{\theta}_{\text{damselfly}}$) to examine statistical associations with wind direction (θ_{wind}) and solar azimuth ($\theta_{\text{solar azimuth}}$). I tested for a correlation between $\bar{\theta}_{\text{damselfly}}$ and θ_{wind} by calculating a circular version of Pearson's product-moment correlation (ρ_{circ}; Jammalamadaka & SenGupta, 2001) and testing the null hypothesis that $\rho_{\text{circ}} = 0$. I similarly tested for a correlation between $\bar{\theta}_{\text{damselfly}}$ and $\theta_{\text{solar azimuth}}$. I also calculated the angular variance of odonate perching and landing events, which is a measure of dispersion among individuals' headings observed during observational trials. I tested whether angular variance is associated with wind speed and ambient temperature as predictor variables using a GLM with Gaussian error. Finally, I calculated the absolute difference between $\bar{\theta}_{\text{damselfly}}$ and θ_{wind}, which is hereafter annotated as $\left|\bar{\theta}_{\text{damselfly}} - \theta_{\text{wind}}\right|$, and the absolute difference between $\bar{\theta}_{\text{damselfly}}$ and $\theta_{\text{solar azimuth}}$, or $\left|\bar{\theta}_{\text{damselfly}} - \theta_{\text{solar azimuth}}\right|$. I subsequently tested whether $\left|\bar{\theta}_{\text{damselfly}} - \theta_{\text{wind}}\right|$ is correlated with wind speed and whether $\left|\bar{\theta}_{\text{damselfly}} - \theta_{\text{solar azimuth}}\right|$ is correlated with ambient temperature using a GLM with Gaussian error.

All R scripts used to process the raw data and conduct analyses are available online through Dataverse (http://dx.doi.org/10.7910/DVN/LQNCBW).

RESULTS

I conducted a total of 45 5-minute observational quantifications of individual damselfly flight behaviour, foraging and territoriality in addition to 55 5-minute observational quantifications of damselfly perch orientation. Individual damselflies varied in the amount of time spent flying (mean ± SD = 22.0 ± 22.44 s), the number of foraging attempts (mean ± SD = 2.73 ± 2.93) and the number of territorial interactions (mean ± SD = 0.98 ± 0.97). Wind speed (mean ± SD = 4.62 ± 3.33 km/h) and ambient temperature (mean ± SD = 27.90 ± 6.46 °C) also varied among the combined observational periods ($N = 100$).

Time spent flying was negatively correlated with wind speed ($\beta = -2.11$, $P = 7.65\text{e-}08$; Fig. 2a) and was uncorrelated with ambient temperature ($\beta = -0.031$, $P = 0.19$). The number of flights was negatively correlated with wind speed ($\beta = -0.97$, $P = 4.03\text{e-}06$; Fig. 2b) and uncorrelated with ambient temperature ($\beta = 0.011$, $P = 0.43$). The number of foraging attempts was negatively correlated with wind speed ($\beta = -1.876$, $P = 1.56\text{e-}12$; Fig. 2c) and

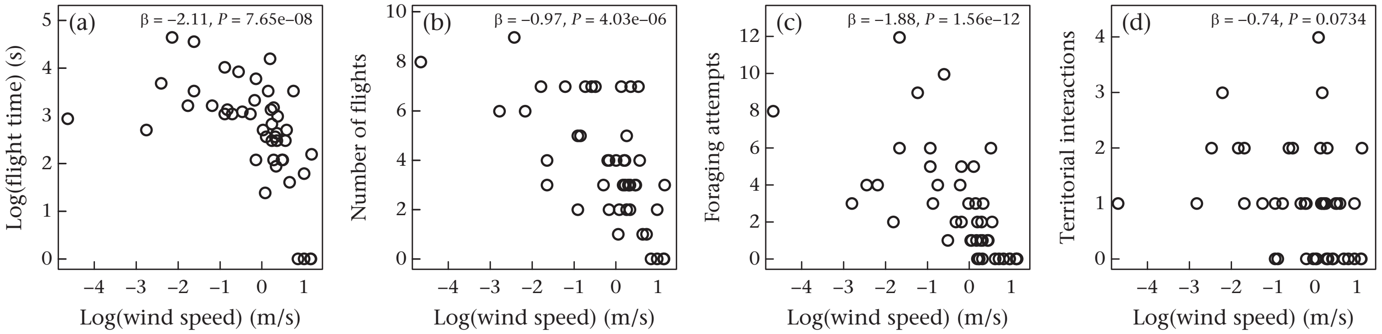

Figure 2. Effects of wind on damselfly flight behaviour: (a) flight time; (b) number of flights; (c) number of foraging attempts; (d) number of territorial interactions. Flight time and wind speed were log transformed to account for positive skew in the data and the residuals of the generalized linear model. Summary statistics, including the effect size (β) and the corresponding *P* value, are shown for each behaviour.

uncorrelated with ambient temperature ($\beta = -0.0003$, $P = 0.99$). The number of territorial interactions exhibited a marginally significant negative correlation with wind speed ($\beta = -0.743$, $P = 0.07$; Fig. 2d) and was uncorrelated with ambient temperature ($\beta = -0.006$, $P = 0.85$).

Damselfly orientation was positively correlated with wind direction ($\rho_{circ} = 0.85$, $P = 5.34\text{e-}08$; Fig. 3a, b, c) and uncorrelated with sun position ($\rho_{circ} = -0.25$, $P = 0.07$; Fig. 3d–f). I also observed that flying individuals generally faced into the wind during flight at lower wind speeds, although this in-flight orientation behaviour was not quantified. Angular variance among damselfly headings was negatively correlated with wind speed ($\beta = -1.06$, $P = 6.73\text{e-}09$; Fig. 4a) and uncorrelated with ambient temperature ($\beta = -0.01$; $P = 0.756$; Fig. 4c). Difference in the mean direction of perched damselflies and the wind direction ($\left|\bar{\theta}_{damselfly} - \theta_{wind}\right|$) was negatively correlated with wind speed ($\beta = -0.66$, $P = 8.95\text{e-}05$; Fig. 4b), while $\left|\bar{\theta}_{damselfly} - \theta_{solar\ azimuth}\right|$

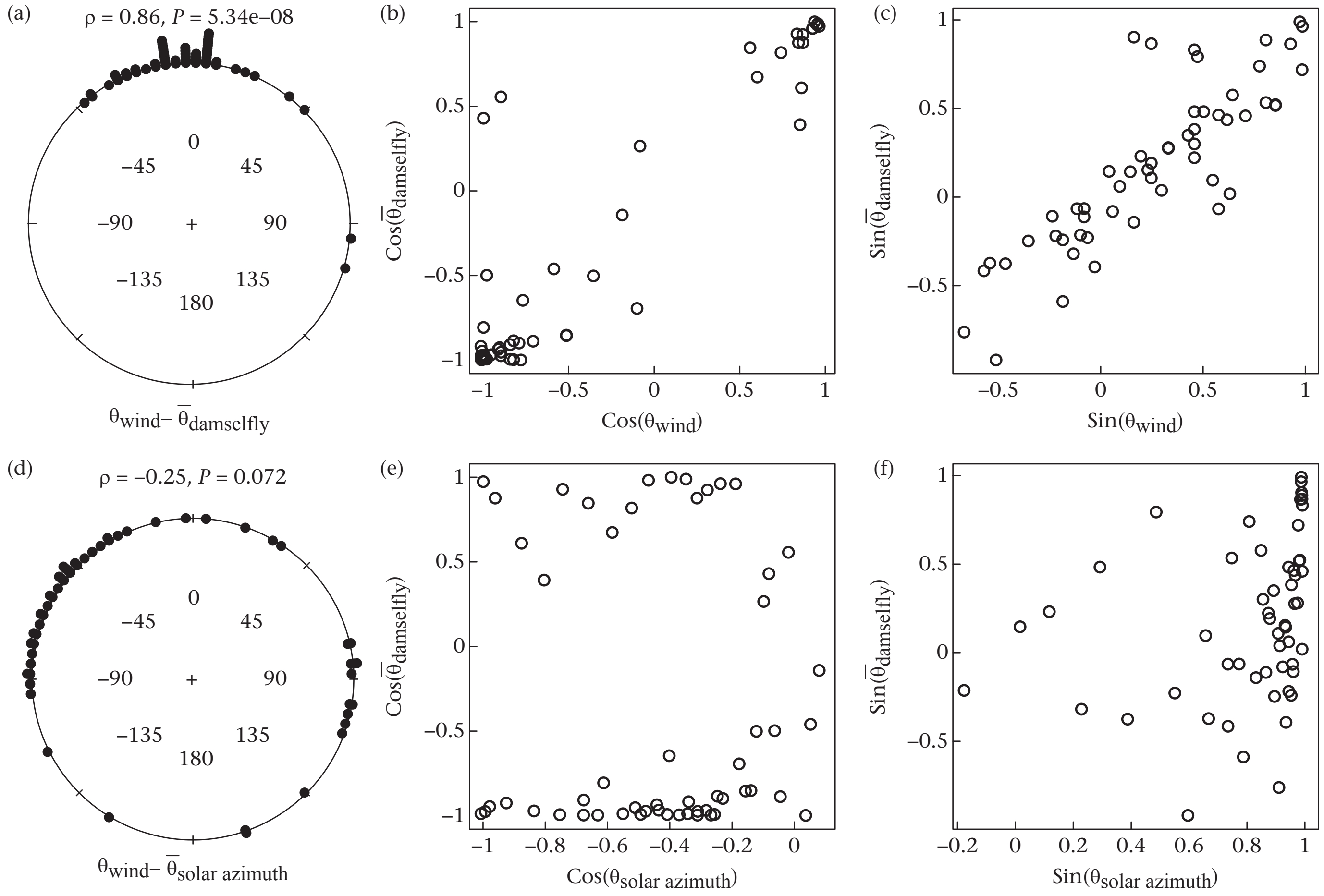

Figure 3. Circular plots show the difference between mean damselfly orientation for each observational period and (a) wind direction and (b) sun position. Scatterplots show the (b) cosine and (c) sine of the mean damselfly orientation and incoming wind and the (e) cosine and (f) sine of the mean damselfly orientation and solar azimuth for each observational trial.

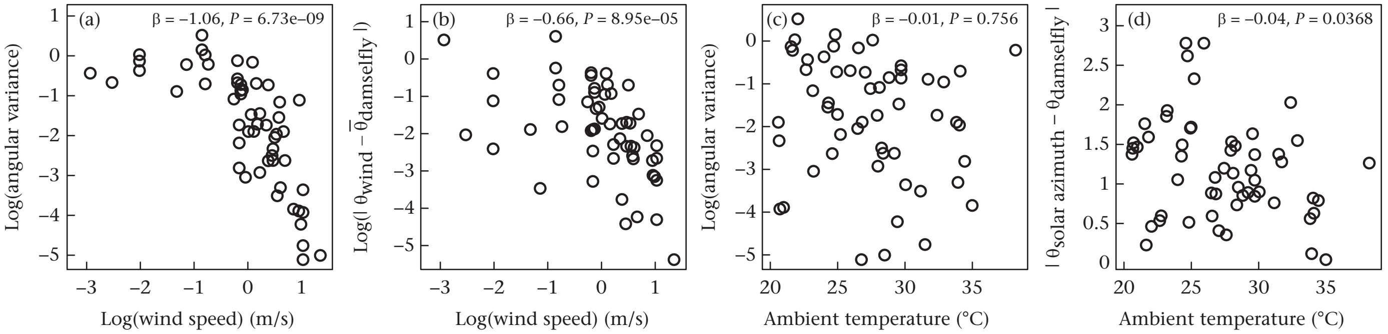

Figure 4. Relationship between wind speed and (a) angular variance in perch orientation and (b) angle of perch orientation in damselflies. Relationship between ambient temperature and (c) angular variance in perch orientation and (d) mean damselfly orientation and sun position. Summary statistics, including the Pearson's correlation coefficient (*r*) and the corresponding *P* value, are shown.

was negatively correlated with ambient temperature ($\beta = -0.041$, $P = 0.0368$; Fig. 4d).

DISCUSSION

Wind speed and direction imparted strong effects on the movement ecology and orientation behaviour of a small-bodied, perching damselfly that is widespread in eastern North America, the Atlantic bluet, *E. doubledayi*. Specifically, I found that at lower wind speeds, damselflies performed more flights (Fig. 2a), spent more time flying (Fig. 2b), foraged more often (Fig. 2c) and engaged in more territorial interactions (Fig. 2d). In contrast, damselfly activity levels were not associated with changes in ambient temperature. Furthermore, damselflies exhibited rheotaxis, in which perched and landing individuals faced into the wind (Fig. 3a), while wind speed was negatively correlated with both angular variance (Fig. 4a) and the absolute difference between the direction of incoming wind and mean damselfly perch orientation (Fig. 4b). Resting damselfly orientation was uncorrelated with sun position (Fig. 3d), and angular variance was uncorrelated with ambient temperature (Fig. 4c). At high ambient temperatures, however, the absolute difference between the position of the sun and damselfly perch orientations decreased (Fig. 4d). Together, these findings suggest that bluets respond to abiotic conditions by flying when wind speed is low or negligible, and that damselflies perch facing the wind and the sun with increasing consistency as wind speeds and ambient temperatures increase, respectively. These behavioural quantifications add to our growing knowledge of the organismal, biomechanical and thermoregulatory covariates of activity levels and orientation strategies of animals in flows (Chapman et al., 2011; Nathan et al., 2008).

Small-bodied, perching odonates, such as the bluets considered here, may preferentially fly at low wind speeds for multiple reasons. Foremost, perching damselflies rely on short ‘patrol’ flights to find and glean food off the water surface or nearby vegetation, which may require more energy in high wind conditions to compensate for drift and increased drag (Dickinson et al., 2000; Ellington, 1985). I observed more instances of gleaning than in-flight captures of prey, and high winds may impart stronger pressures on the ability to capture prey in flight rather than glean food off the water surface or plants. Furthermore, while the self-powered airspeed of the damselfly studied here is unknown, other odonates can achieve a maximum airspeed of 1.7 m/s (Wakeling & Ellington, 1997). Thus, when winds approach or exceed the airspeed of the damselflies, the damselflies may preferentially rest rather than fly and forage in windy conditions to conserve energy. Second, high winds reduce activity levels of other small arthropods (Hribar, DeMay, & Lund, 2010; Walters & Dixon, 1984), which is the sole food source for odonates (Corbet, 1980); there may therefore be less potential prey for odonates when wind speed is high. Finally, when wind speeds are very high, flying damselflies may be displaced from foraging grounds and blown far distances by strong winds, as documented in other damselflies (Mitchell, 1962). Corroborating this last point, multiple bluets were displaced from ephemeral ponds when winds exceeded 3 m/s (personal observation), and flying during stronger winds may cause long-distance displacement away from preferred habitat.

I observed that resting damselflies face incoming wind while perched. Facing the wind while perched reduces the surface area of the body exposed to physical flows, which conserves energy in maintaining position and prevents destabilization. Thus, the orientation behaviour documented here is most likely a response to biomechanical pressures imposed by wind. So-called rheotaxis is a common orientation strategy among organisms resting or maintaining position in flows and for short-distance, directed movements in many animals (Chapman et al., 2011). Because odonates use visual cues to detect and pursue prey (Combes, Salcedo, Pandit, & Iwasaki, 2013; Olberg, 2012), it may also be beneficial for bluets and other perching odonates to orient facing the wind to detect incoming prey pushed through the air or along the water surface. Certain regions of odonate eyes, namely the fovea on the dorsal side of the compound eye, are particularly sensitive to movement (Sauseng, Pabst, & Kral, 2003). Odonates may therefore adjust their body position and orientation to optimize their head position and vision. However, rheotaxis as a movement strategy for foraging loses efficiency at higher wind speeds: the metabolic and biomechanical capacity for bluets and other perched damselflies to fly into headwinds decreases as wind speeds increase. Maintaining rheotaxis at rest may enable damselflies to quickly take advantage of preferable abiotic conditions to initiate short foraging bouts when wind speeds are manageable.

I found that ambient temperature was uncorrelated with all indices of flight activity, suggesting that wind may impart a stronger selective pressure than ambient temperature on the activity budgets of the damselflies considered here. The apparent lack of an association between ambient temperature and activity levels was unexpected because odonates are ectotherms and rely on various thermoregulation strategies to achieve basal metabolic rates required for foraging (May, 1976); correspondingly, previous studies have found positive associations between ambient temperature and flight activity levels in odonates (Corbet & May, 2008; De Marco, Latini, & Resende, 2005). I found that damselfly orientation and sun position were uncorrelated; rather, damselflies exhibited a mixture of perpendicular and parallel orientations with respect to the sun. I also found that damselflies tend to face the sun at higher ambient temperatures, however, which could be an adaptation to minimize exposure to incident sunlight and avoid overheating, as seen in other animals (Luskick et al., 1978; Waldschmidt, 1980).

Taken together, this study presents novel findings that forge an empirical and conceptual link between flight behaviour and perch orientation strategies of a widespread odonate in different abiotic conditions. Future work could leverage a comparative framework to determine whether the strength of rheotaxis varies among odonate species that differ in foraging behaviour or body size. Experimental trials of damselfly flight behaviour and perch orientation in controlled settings, such as a wind tunnel, would facilitate more direct manipulations of flight speed and direction to observe how damselflies adjust their behaviour to abiotic conditions.

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