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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.