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BEHAVIOURAL RESPONSES OF *ENALLAGMA* TO CHANGES IN WEATHER (ZYGOPTERA: COENAGRIONIDAE)

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Odonates exhibit a variety of weather associated behaviours, including abandoning ponds just before storms begin. They may be able to detect changes in weather that alert them to approaching storms and allow them to escape the water's edge before it begins to rain. *E. annexum* and *E. boreale* were observed at a Colorado marsh (USA) to determine which weather factors contributed to the weather-induced behaviours they exhibit. They were observed for 191 five-minute periods and their flight activity quantified. Weather parameters were measured during each interval to account for rapid changes in conditions. Based on results from multiple regression analysis, it is clear that light intensity is the strongest weather parameter affecting zygopteran flight activity, but temperature, wind speed, and the presence of rain are also significant. The 2 spp. exhibited pond abandonment behaviour during storms. It is likely that storms are dangerous to zygopterans and their apparent ability to detect impending storms is a survival mechanism. Alternatively, pond abandonment behaviour may be triggered by the same factors necessary to trigger roosting and the zygopterans simply return to their roosting sites during storms.

INTRODUCTION

Weather is known to dramatically affect odonate behaviour (CORBET, 1999). Parameters such as temperature, light intensity, wind speed, and rain are known to impact odonate patrolling and diel patterns, posture, and prevalence of shade or sun seeking, among other behaviours (e.g. CORBET, 1962; BICK & BICK, 1963; MILLER, 1982; GONZALES-SORIANO, 1987). In one behaviour, called pond abandonment, odonates may be able to sense changes in the weather that

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prompt them to leave the water prior to the onset of storms (BICK & BICK, 1961; KIAUTA, 1964; OKAZAWA & UBUKATA, 1978). Indeed, few odonate species have been observed flying during rains (e.g. McVEY, 1988; GARRISON, 1989; KIAUTA & KIAUTA, 1994; CORBET, 1999), and those that do are usually strong fliers. For example, one of the strongest fliers is *Pantala flavescens*, a species able to fly both across oceans and during storms (SAMWAYS & CALDWELL, 1989; MOORE, 1993).

Despite the wealth of knowledge available regarding odonate behavioural responses to weather, few researchers have focused specifically on the role weather plays in odonate behaviour. Most of what is known has been culled from works focusing on other subjects, such as life history or diel patterns (e.g. DELL'ANNA et al, 1990; CORDOBA-AGUILAR, 1994). Responses to weather are often mentioned in the discussion as a possible explanation for aberrant data or unusual observed behaviours. Other researchers have left these data out (e.g. SWITZER & EASON, 2000; KIRKTON & SCHULTZ, 2001; STOKS, 2001), stating in the methods that data from days of inclement weather were not included in the analyses presented. Statements like these suggest that weather plays a major role in shaping odonate behaviour and that, by eliminating these data from analyses, we are left with an incomplete understanding of how odonates truly behave.

Few studies have focused specifically on the impacts of weather parameters on odonate behaviour (e.g. CALVERT, 1926; MITCHELL, 1962; MAY, 1976, 1978) and even fewer have studied more than one parameter simultaneously (e.g. BELYSHEV, 1967; LUTZ & PITTMAN, 1970). However, in most studies each parameter was analyzed independently of the others, making it impossible to determine how all of the parameters together affect odonate behaviour. A study by DE MARCO & PEIXOTO (2004) compared four weather factors in a multiple regression analysis, but such studies are rare.

Here I present data on the impacts of seven weather parameters (wind speed and direction, humidity, temperature, light intensity, barometric pressure, and presence of rain) on flight activity of a population of an *Enallagma* population (Zygoptera: Coenagrionidae) in a Colorado wetland. My objectives were to determine how the suite of weather parameters together impacted *Enallagma* flight activity levels and which parameters were most important in determining flight activity levels.

METHODS

The site was located in Fountain Creek Regional Park in Fountain, Colorado, USA (N 38° 42.95" W 104° 43.05", elevation 1,980 m). The area is a protected wetland containing several marshy ponds. All observations were made at a small, shallow pond (surface area = 1,060 m^2, maximum depth = 0.6 m) located near the northeastern boundary of the park. The pond was surrounded by cattails (*Typha* sp.) and other aquatic macrophytes. A representative 5.5 m^2 study area was selected that included 90% open water and 10% vegetation that was similar in plant composition and density to the remaining areas of the pond. All observations were made within this study area.

Observations were made on *Enallagma annexum* (Hagen) and *E. boreale* (Selys). Because they showed similar behavioural patterns in response to weather, both species were treated as a single group in the statistical analyses.

Observations were made on 18 days in June and July 1999 between 1600 and 1700 hours. Each observational period was divided into five-minute intervals for a total of 191 observations. During the first minute of each interval, the weather conditions were measured directly offshore: wind speed (m/s), wind direction (°), temperature (°C), light intensity (ft-c), relative humidity (%), barometric pressure (Pa), and the presence or absence of rain. A hand-held compass and digital anenometer oriented directly into the wind were used to determine wind direction and speed. A simple thermometer was used for temperature measurements. To measure light intensity, a hand-held light meter was pointed toward the water. A hygrometer was used to measure relative humidity and a barometric pressure gauge for barometric pressure. Presence of rain was noted visually.

The remaining 4 minutes of each time interval were spent counting the number of *Enallagma* flights within the study area. Flight was defined as any movement within the study area requiring the use of wings such that the damselfly was not in contact with a perch or substrate. All flights within the study area were counted for each time interval using a clicker counter. Individuals could be counted more than once and tandem pairs counted as two flights. *Enallagma* flying into the study area from outside were counted. At the end of 4 minutes, the total number of flights was recorded before starting the next 5 minute interval.

A multiple regression analysis was completed in JMP Version 6.0 (SAS Institute) using the seven weather variables as the explanatory variables and the number of flights per time interval as the response variable. Light intensity and the number of flights were log transformed to improve equality of variance. The presence of rain was indicated by coded numeric values with a 1 representing rain and a 0 the absence of rain.

RESULTS

Wind direction ($p = 0.12$), humidity ($p = 0.09$), and barometric pressure ($p = 0.16$) did not contribute significantly to flight activity after accounting for other variables and were removed from the final multiple regression analysis.

Temperature showed a positive relationship with flight activity (slope = 0.02 ± 0.009 SE, n =191, $p = 0.042$) (Fig. 1). The minimum temperature at which flights were observed was 24°C. Flight continued up to the maximum observed temperature of 37°C.

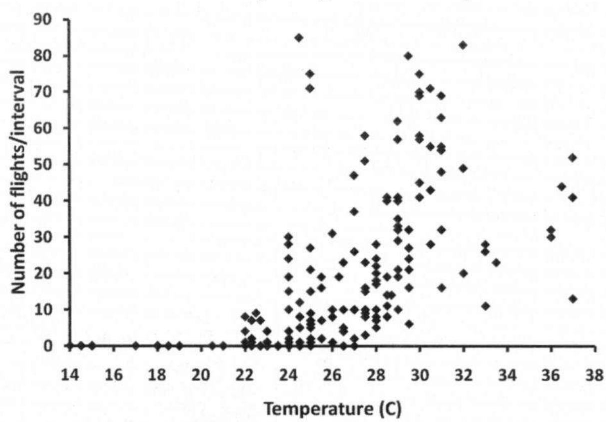

Fig. 1. Temperature and *Enallagma* flight activity.

An increase in wind speed was significant-

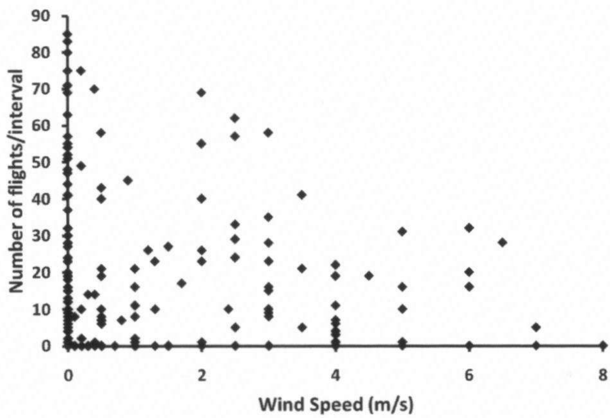

Fig. 2. Wind speed and *Enallagma* flight activity.

ly associated with a small decrease in flight activity (slope = -0.05 ± 0.012 SE, n =191, $p < 0.0001$) (Fig. 2). Wind speeds varied between 0 m/s and 8m/s throughout the study.

The number of flights increased with light intensity (slope = 0.94 ± 0.087 SE, n =191, $p < 0.0001$) (Fig. 3). The minimum light intensity recorded during the study was 25 ft-c and the maximum 950 ft-c.

Presence of rain significantly decreased the number of flights observed, with a slope estimated at –0.12 (± 0.029 SE, n = 191, p = 0.0003) (Fig. 4).

A predictive model was produced by the multiple regression analysis. The full model is:

μ {log(flights+1): temperature, wind speed, log light intensity, presence of rain} = -1.71 + 0.02 [temperature (°C)] – 0.05 [wind speed (m/s)] + 0.94 [log light intensity (ft-c)] – 0.12 [presence of rain]

The predicted number of flights can be obtained by entering measurements of the four weather factors within the range of values reported herein in the appropriate positions in the above model. Figure 5 represents the number of flights predicted by the model in poor, average, and good weather conditions, falling within the range of those conditions observed during this study.

The four weather factors included in the model explain about 80% of the variation in the data ($R^2 = 0.794$).

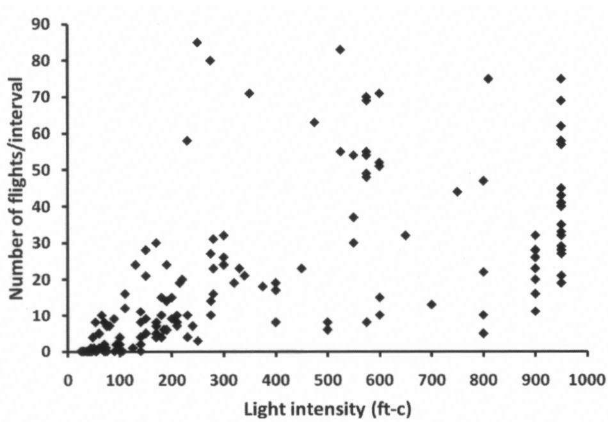

Fig. 3. Light intensity and *Enallagma* flight activity.

DISCUSSION

The positive relationship between flight activity and wind speed observed here is not surprising. Many insects are hindered by strong winds, and odonates are no exception. Hilfert (referenced in CORBET, 1999) suggests that Zygoptera rarely fly in winds above 3.5 m/s. WARINGER (1982) reported flight at a maximum wind speed of 8 m/s for *Coenagrion puella*, suggesting that some damselflies are capable of flying in wind speeds greater than 3.5 m/s. The *Enallagma* species I observed flew at speeds much greater than 3.5 m/s, up to 7 m/s, although there were no flights observed at the highest wind speed recorded (8 m/s).

Because zygopterans have large, broad wings and small, light bodies, wind likely severely impedes their flight and may even pose a threat if it reaches sufficient strength. Serious consequences may arise if an individual is blown into a perch, the ground, or the water, so they may not fly in strong winds to avoid these threats. Some studies have found that zygopterans do fly during high winds, but only in wind-protected areas (DUNKLE, 1976; CORBET, 1999). It is likely that most species do not fly in open areas during strong winds, as observed here and in other studies (BELYSHEV, 1967; WARINGER, 1982).

The relationship between temperature and flight activity is also no surprise. Odonates, like all arthropods, are exothermic and their body temperatures are close to ambient temperature. Below a certain temperature, odonates are unable to warm their flight musculature sufficiently to fly. This threshold appeared to be 24°C in the population I studied as no flights were observed below that temperature. Attempting to fly at low temperatures likely has similar consequences to flight in strong winds. A chilled zygopteran runs the risk of crashing into a perch or into the water, potentially damaging it or increasing its vulnerability to predation.

Light intensity has a strong impact on flight activity. Several researchers have examined the role light intensity plays in odonate behaviour (e.g. PINHEY, 1962; WILLIAMS, 1976; BOANO & ROLANDO, 2003) and it is clear that light is an important factor. LUTZ & PITTMAN (1970) found that light intensity had the largest impact on flight behaviour in the population they observed. My analysis corroborates their conclusion. Most of the decreases in light intensity

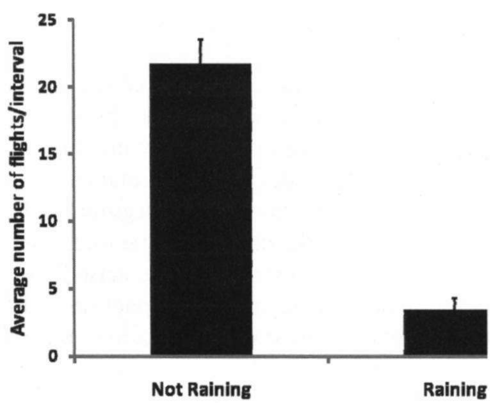

Fig. 4. Rain and *Enallagma* flight activity. Bars represent standard error.

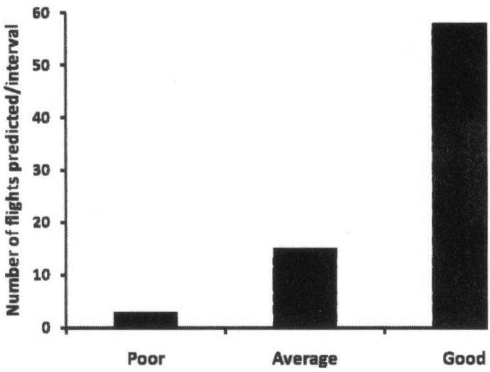

Fig. 5. Predicted number of *Enallagma* flights under various weather conditions. Poor conditions are defined as: temperature = 24°C, wind speed = 7m/s, light intensity = 200ft-c, and rain = 1; – Average conditions are defined as tempterature = 29.7°C, wind speed = 1.3m/s, light intensity = 344.0 ft-c, and rain = 0.2; – Good conditions are defined as temperature = 35°C, wind speed = 0.5m/s, light intensity = 950ft-c, and rain = 0.

during my observations were due to increases in cloud cover. At those times, it was possible to see a distinct decrease in activity with a decrease in light intensity through casual observation alone, before running any statistical tests.

In the *Enallagma* species observed, flight activity was greatly reduced in the presence of rain. It rained heavily one day in June and no zygopterans were observed in the study area at all. Although I did not attempt to quantify it, there was an obvious decrease in the number of individuals in the study area if the rains lasted more than a few minutes and they were apparently leaving the pond altogether during extended periods of rain. These observations agree with others who have observed pond abandonment behaviour preceding or during periods of rain (KIAUTA, 1964; BELYSHEV, 1967). While some anisopterans will remain flying during light rain (SAMWAYS & CALDWELL, 1989) or stop only in heavy or prolonged rain (MOORE, 1993), zygopterans are usually smaller than anisopterans and are much weaker fliers. It is likely that the former show far less activity during periods of rain than their larger relatives. In fact, during the course of this study I witnessed only one zygopteran flight in rain, and it was during an insignificant rain while the sun was shining. This observation is not perfectly reflected in Figure 4 as there are several flights indicated during rain, but it can easily be explained by my data collection method. Conditions could, and sometimes did, change dramatically during a 5-minute time interval such that it would be raining at the beginning of the interval and not at the end. Any flights recorded during these time intervals were recorded as flights during rain regardless of whether they were actually flying during rain. I suspect that rain has a much more significant impact on flight activity than my data suggests and more observations should be made to determine whether this is the case.

Light rain may not have a considerable damaging affect on Zygoptera, though it could increase the evaporative cooling rate of the insects and hinder their escape as conditions deteriorate. Moderate to heavy rains, however, are probably dangerous to them. These could cause direct physical damage and can potentially knock a resting individual from a perch onto the ground or into the water. The former could cause damage by direct physical contact, but the latter is probably particularly dangerous because the wings could easily become trapped in the surface film and expose the insect to drowning or predation.

If rain is in fact damaging, it is in a damselfly's best interest to leave the water in search of shelter before rain begins. In this case, it should be able to sense cues that storms are approaching and leave while conditions are still sufficiently acceptable to allow easy withdrawal from the pond. The use of cues to avoid damage by storms has been documented in other species (e.g. giant water bugs, LYTLE, 1999; hellgrammites, Carl Olsen, pers. comm.), so it is reasonable to suppose that zygopterans may employ a similar tactic toward the same end. The cues for pond abandonment are most likely the same weather factors that I measured during my study. In the area of Colorado where the study was undertaken, afternoon thunderstorms occur almost every day during the summer months. Storms usually approach and pass quickly, but can be incredibly violent. As a storm approaches, the light intensity decreases as the cloud cover becomes more extensive. The temperature begins to drop quickly and the wind usually becomes stronger. By the time rain begins, it is usually dark, cool, and windy, i.e. poor conditions for damselflies. As all four of these weather factors showed a significant association with their flight activity, changes in these factors likely act as cues for them, warning them of approaching storms. Indeed, as illustrated in Figure 5, the model predicts only about three *Enallagma* flights under poor conditions. Poor conditions in this figure represent typical rainy weather: low temperature, low light intensity, moderate wind, and rain. In contrast, much higher flight activity is predicted in good conditions (bright, warm, no wind or rain), suggesting that deteriorating weather conditions have a considerable impact on flight activity.

A drop in barometric pressure precedes the approach of storms and would act as an excellent advance warning system for odonates able to detect it. BELYSHEV (1967) suggests that barometric pressure affected the flight activity of *Leucorrhinia rubicunda*, so some odonates may use pressure as an abandonment cue. The *Enallagma* I studied did not. Because barometric pressure drops long before rain begins, damselflies using pressure as an abandonment cue may leave the pond too soon. An increase in mating activity has been observed in *Enallagma* immediately preceding or just after the start of storms (WHITE-CROSS, 1984), so leaving the pond before it becomes necessary would limit an odonate's chances to mate and may decrease its fitness.

While odonates appear to use abandonment cues to avoid approaching storms, it is possible that they do not abandon ponds as a protective measure. During the storms I witnessed, it became quite dark and cool before the rains began. This drop in light intensity and temperature may have prompted the odonates to seek their evening roosts. They are visual animals, using their remarkable vision to hunt, assess oviposition sites, protect their territories, and find mates (CORBET, 1999).

They are also known to use light and temperature to regulate their diel patterns (LUTZ & PITTMAN, 1970; WARINGER, 1982) and during pond abandonment (MILLER, 1964, 1983; BICK & BICK, 1961; OKAZAWA & UBUKATA, 1978). Studies of roosting behaviour in Anisoptera have found that roosting is closely correlated with light intensity (PARR & PARR, 1974; HASSAN, 1976; MILLER, 1989). Similar pond abandonment behaviours have been documented in response to solar eclipses (MITRA, 1996; KIAUTA & KIAUTA, 1999), suggesting that odonates may abandon ponds in response to drops in light intensity regardless of whether a storm follows or not. It is likely that a zygopteran returns to its roost before a storm simply because the conditions are similar to those that prompt a return to the roost at night. This is a simpler explanation of pond abandonment behaviour than the use of cues to avoid storms, though the data presented here do not lend credence to either hypothesis. Further studies are necessary to tease apart these two hypotheses and to determine whether light intensity and/or temperature are sufficient triggers for roosting and whether damselflies are able to detect changes in their environment to use cues to avoid storms.

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