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FACTORS AFFECTING INTERACTION RATES IN *PLATHEMIS LYDIA* (DRURY) (ANISOPTERA: LIBELLULIDAE)

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Interspecific interaction rates and space use were observed for *P. lydia* at 3 ponds in north-central Texas from June to August 2007. Aggressive interactions of marked individuals were tallied for each interacting sp. by which individual was the aggressor or target and which sp. won or lost. The space used was also mapped. These data were also collected for one individual each of the libellulids *Pachydiplax longipennis* and *Tramea lacerata* and compared to *P. lydia*. Interaction rates were different depending on the category of interacting odon. (perching or flying), supporting the hypothesis that the thermoregulatory categories of perching and flying aid in habitat partitioning among spp.

INTRODUCTION

Aggressive behavior in Odonata is due to territorial competition (aggressive defense of a unit of space) and encounter competition (interactions between mobile organisms that cause injury or loss of energy or time) (SCHOENER, 1983). These two types of competition can apply both intra- and inter-specifically. Competition usually does not affect the overall species assemblage at a pond (MOORE, 1964, 1991), but the aggressive interactions can affect local spatial distribution of species. For example, HUTCHINSON (1977) observed two species of *Epitheca* (Corduliidae), similar in flight pattern and appearance, flying together at territories along a river. One species excluded the other from the river shore. In the absence of the more aggressive species, the second species could fly along the shore. Additionally, TYNKKYNEN, et al. (2006) discussed two *Calopteryx* (Ca-

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lopterygidae) species where experimental removal of one species allowed members of the other species to expand their territories.

Changes in space use can be caused by interspecific interactions. REHFELDT & HADRYS (1988) found spatial partitioning promoted by aggressive interactions between two *Sympetrum* (Libellulidae) species. The presence of heterospecifics changed perching heights and interaction times for both species. This spatial separation has the potential to reduce conflict between interacting species, such as the aforementioned *Epitheca* and *Calopteryx*. For example, MICHIELS & DHONDT (1987) noted that habitat separation occurred between three *Sympetrum* species, but they did not determine if separation was due to current or past interspecific interactions.

There are differences in space use related to other aspects of life history, such as the dragonfly being a perching or flying species. CORBET (2004) defines fliers as the odonates that "typically remain on the wing when active" and perchers as those that "spend most of their time on a perch from which they make short flights." Some species do not fit neatly into a single category (PARR, 1983) and may change behavior depending on temperature (MAY, 1977). Although the dichotomy is based on thermoregulation, it could also prevent conflict because the dragonflies use different spaces at the pond.

This study examines the connection between space use (the perching/flying dichotomy and patterns of territory use) and interspecific interaction rates in *Plathemis lydia*, with tentative data on two sympatric libellulids, *Pachydiplax longipennis* and *Tramea lacerata.*

METHODS

STUDY SITES – The three study ponds were located in northeastern Wise county in the Cross Timbers and Prairies ecoregion of north-central Texas (DIGGS, et al., 2000; Fig. 1). Of these ponds, two were located on the Lyndon B. Johnson National Grasslands (grasslands units 67 and 71). The remaining pond, named the pit, was located on private property near Greenwood, Wise county, Texas. All three sites had few to no trees immediately surrounding the ponds. These were simple in shape (basically round with no long inlets of water). The two grasslands ponds were similar in being somewhat round stock tanks with clay-lined bottoms. The pit was an abandoned drilling mud pond lined with clay and bentonite; it was rectangular with a peninsula in the middle. Unit 71 was visited by cattle and was stocked with fish; the other two ponds (Unit 67 and the pit) lacked fish and were not visited by cattle.

A grid of 2×2m squares was marked around each pond, similar to McMILLAN (2000), which used 1×1m observation grids. The Unit 67 pond was enclosed completely by the grid (1024 m^2), whereas smaller portions of the pit (about half of the pit; grid area 1120 m^2) and Unit 71 had a grid (360 m^2). The grid areas on Unit 67 and Unit 71 were small enough to be completely visible from outside the grid. McMILLAN (2000) similarly used small ponds so the observation areas would be completely visible from the bank. The pit's surface was also visible from all angles until cattails grew up at one end of the grid. Each pond was visited for data collection and marking one or two times per week.

STUDY SPECIES – *Plathemis lydia* is considered a perching species based on field observations in this study; it tended to perch in a core area. However, it is an intermediate percher since individuals spent anywhere from 0% (one observation) to over 75% of the time perching. *Pachydiplax longipennis* was also studied but only one observation under comparable weather conditions to the *P. lydia* observations occurred. Additional species were captured and marked, but observations were made on only one *Tramea lacerata*. Categories of perching and flying were defined for each interacting species based on the field observations and descriptions of behavior in ABBOTT (2005).

MARKING – Each captured individual was painted on the abdomen with 1-3 stripes of colored acrylic paint. Numbers were written on the wing using a black permanent Sharpie © marker. Re-sighted individuals were identified by the unique color combination and number.

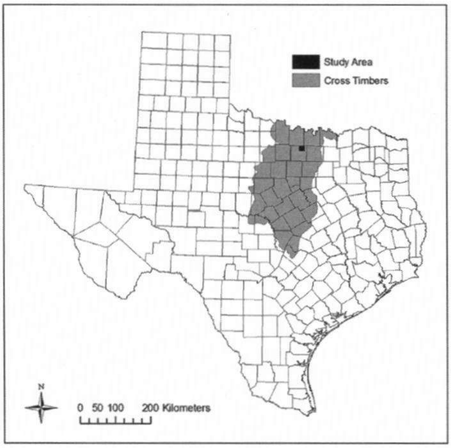

Fig. 1. Location of study area in Texas and Cross Timbers ecoregion. Sources of data layers: county layer: GLO (no date given); – ecoregion layer: ACKERSON (2007)'s digitized version of GOULD, F.W., 1975. *Texas plants: a checklist and ecological summary*. Texas agric. exp. stn, Publ. 585.

OBSERVATIONS – Observations of interactions were made on re-sighted individuals from June to August 2007; observation periods varied with how long the odonate was visible. Weather data were recorded at the end of each observation period. Observations were made with the observer sitting outside the grid or at least 2-4m from the odonate's flight area. Amount of time spent perching in the grid, flying in the grid, perching outside the grid, flying outside the grid, and time not visible were recorded. The starting and ending times for the observation were also recorded.

For each interacting species (including intraspecifics), status in interactions was recorded as aggressor or target and win or lose for both the observed and interacting individuals. Aggressor/target was based on the observed individual; if the observed individual attacked another odonate, that individual was considered the aggressor.

The observed individual was defined as winning the interaction if

When the aggressor,

- It caused the other individual to change flight path
- It caused a perching odonate to leave its perch and not return immediately
- When interacting with an intraspecific female, it caught the female

When the target,

- It was not forced to leave its perch by the interacting odonate
- It was not forced to change flight path by the interacting odonate

The observed individual lost if

When the aggressor,

- It failed to cause the other individual to change flight path
- It failed to cause a perching odonate to leave its perch and not return immediately

When the target,

- It was forced to leave its perch by the interacting odonate
- It was forced to change flight path by the interacting odonate
- When interacting with an intraspecific female, it failed to catch the female

Space use was mapped for each observed individual on a map of the pond and grid. The map showed major features of the pond, such as trees, cattails, areas of sedge, and the shape of the pond to allow flight paths and perches to be drawn on the map. Examples of maps (with data for *P. lydia, P. longipennis*, and *T. lacerata*) are found in Figure 4.

DATA ANALYSIS – Interaction rates were calculated from the number of interactions divided by time visible (in minutes). Interaction rates (interactions per minute) can be calculated from the data for each interacting species, category, or other characteristics of interacting species. Alternately, the interaction rates for each observed individual can be summed for an overall interaction rate for the observation period. Area used was calculated by multiplying the number of grid squares time the area in each grid ($4m^2$)

Analysis was performed on observations made under standard conditions (>11:00am, cloud cover < 70%, maximum wind speed ≤7KT, and time visible <60 min) to reduce variations in interaction rates from weather conditions, time of day, and observer effort. Graphs were created in Sigmaplot 9.01 (SysStat Software, Inc., 2004).

RESULTS

INTERACTION RATES

All data are for *Plathemis lydia* except where noted. Interactions with flying species decrease with more time spent perching (Fig. 2A), while interactions with perching species stay approximately the same (Fig. 2B). When interaction rates with flying species were examined by status in interaction and proportion of time spent perching, each status category decreased with increased time perching (Fig. 3). The interaction rates with the observed individual as a target were higher than the individual as aggressor. *P. lydia* is targeted by flying species at reduced interaction rates when it spends more time perching (r^2=0.36, p=0.011, n=17). Interaction rate as aggressor decreases with more time perching (less likely to encounter fliers while perching), but the trend is not statistically significant (r^2=0.16, p=0.14, n=15). Perching species as aggressor (linear regression: negative correlation, r^2=0.0024, p=0.86, n=16) and target (linear regression: positive correlation, r^2=0.034, p=0.66, n=8) showed no such correlation.

When averaged over all perching times, the interspecific interaction rate for *P. lydia* was higher with flying species than with perching species (ANOVA: p=0.0049, flying n=19, perching n=17). When this is analyzed by status in interaction, there are slightly more interactions with flying as a target (ANOVA: p=0.040, aggressor n=15, target n=17). Interaction rate with perching species is approximately the same for each interaction status (ANOVA: p=0.90, aggressor n=16, target n=8).

SPACE USE

Tramea lacerata flew around the pond and through the middle, with no focal territory or perches (Fig. 4A). *Plathemis lydia* had a core territory (a main patrol or perching area) as shown in Figure 4B, instead of the whole-pond use shown by the one *T. lacerata* mapped. Finally, use of the pond by *Pachydiplax longipen-*

nis was centered over multiple perches consisting of debris and sedges in Unit 67, which had a low water level at the time (Fig. 4C).

Additionally, each species spent different amounts of time perching (ANOVA, p=0.091). *P. longipennis* spent more time perching (82.61%, n=1) than *P. lydia*

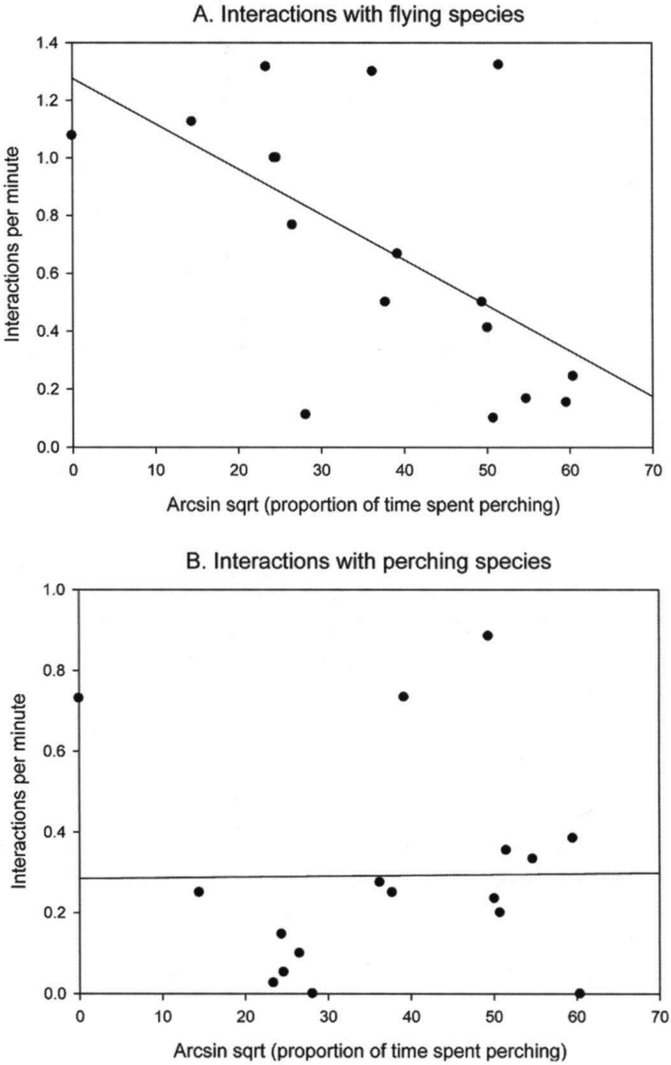

Fig. 2. Interspecific interactions per minute of *Plathemis lydia* by category as a function of proportion of time spent perching (arcsine square-root transformed). (A) flying r^2=0.36, p=0.010, n=17; – (B) perching r^2=0.011, p=0.69, n=17.

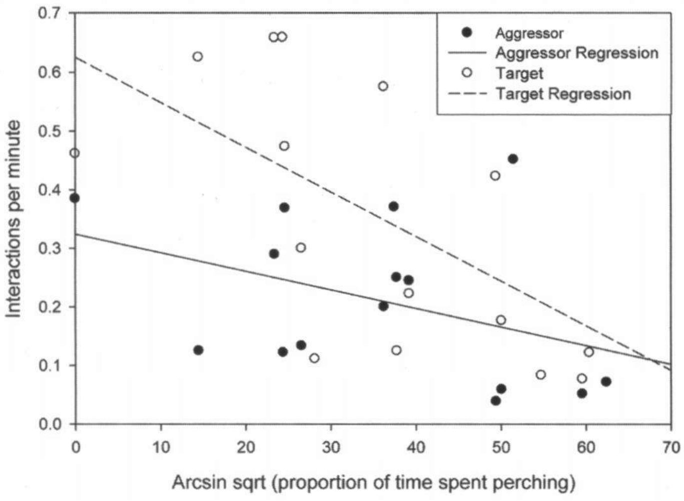

Fig. 3. Interaction rate of *Plathemis lydia* with flying species (interspecific) as a function of proportion of time spent perching (arcsine square-root transformed), with status in interaction: aggressor ($r^2=0.16$, p=0.14, n=15) and target ($r^2=0.36$, p=0.011, n=17).

(39.16±24.72%, n=17), while *T. lacerata* (0%, n=1) did not perch during the observation.

Interspecific interaction rates for each species are shown in Table 1. *P. longipennis* tended to interact more with other perchers, while *T. lacerata* mainly interacted with flying species. *P. lydia*, although classified as a percher, had a statistically significant higher interspecific interaction rate with flying species (ANOVA: p=0.0049, flying n=19, perching n=17) consistent with its intermediate amount of time spent perching.

The higher rate of flying interactions for *P. lydia*, a perching species, is due to attacks by *Libellula luctuosa*. The latter species contributed an average of over 30% of the flying species interactions with *P. lydia*, over 70% of flying species interactions with *T. lacerata*, and was the only flying species to interact with *P. longipennis* (*L. luctuosa* was the aggressor). When *L. luctuosa* is excluded from analysis, *T. lacerata* still has a higher interaction rate with flying species (0.61 interactions per minute) than with perching species (0.13 interactions per minute). For *P. lydia*, however, the difference between perching and flying interactions becomes insignificant (ANOVA: p=0.37, flying n=19, perching n=17) when *L. luctuosa* is excluded.

DISCUSSION

The prediction of this study was that interspecific encounter competition should cause perching species and flying species to affect each other less because they are using different spaces and are thus less likely to have time- and energy-consuming aggressive encounters. The interaction rate data supported this prediction with variation in interaction with flying species being dependent on the percent time spent perching (i.e., the amount of overlap in space use) for *Plathemis lydia*. The interaction rates and space use diagrams for *Pachydiplax longipennis* and *Tramea lacerata* tentatively support this conclusion as well.

The interspecific interaction rate divided by category (Fig. 2) shows that interactions with flying species decrease with more time spent perching, while interactions with other perching species stay the same. For interactions with heterospecific perchers, no trends are statistically significant, but it appears that *P. lydia*

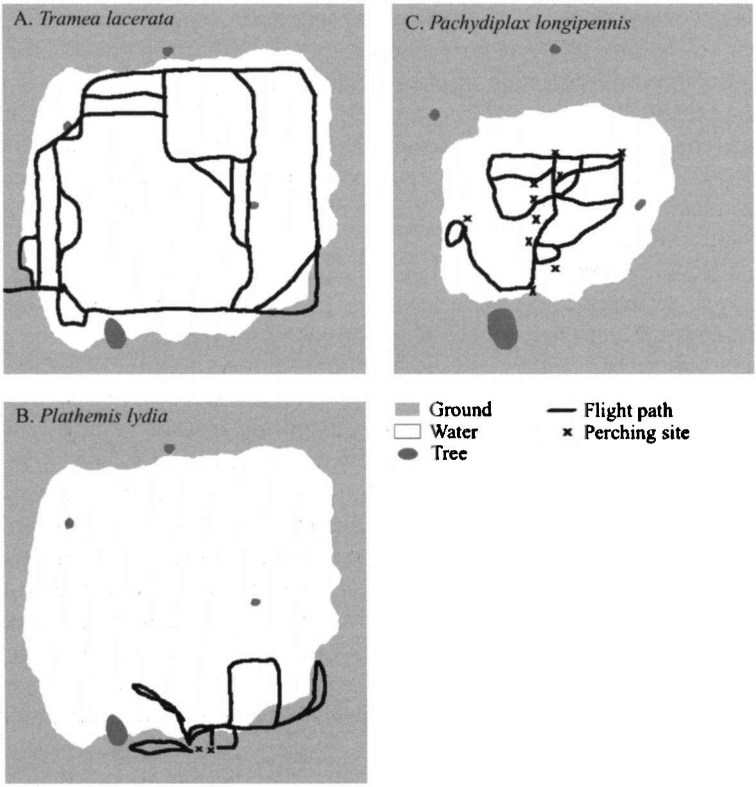

Fig. 4. Map of typical territories for: (A) *Tramea lacerata* (11 June 2007, Unit 67, visible for 25 minutes); – (B) *Plathemis lydia* (2 July 2007, Unit 67, visible for approximately 30 minutes); – (C) *Pachydiplax longipennis* (17 August 2007, Unit 67, visible for approximately 25 minutes).

Table I
Interspecific interaction rates (interactions per minute) by category for *Pachydiplax longipennis*, *Plathemis lydia* (average ± 1 S.D.; flying interaction is significantly different, ANOVA: p=0.0049, flying n=19, perching n=17), and *Tramea lacerata*

Species	Interaction rate with perching species	Interaction rate with flying species
P. longipennis (n=1)	0.48	0.043
P. lydia (n=19)	0.30±0.25 (n=17)	0.68±0.46 (n=19)
T. lacerata (n=1)	0.13	2.09

interacts with other perchers at similar rates regardless of status in interaction or percent of time perching. These data indicate that changes in time spent perching (which is a change in space use) can change the interaction rates by category of interacting odonates.

When solely looking at category, interaction rate with flying species is on average higher than with perching species (excluding intraspecifics). *P. lydia* is more often a target than an aggressor in interactions with fliers and is targeted less when perching more (Fig. 3). No differences are apparent for its interactions with perching species. This could be due to the potential tendancy of flying species to attack any airborne odonate. *P. lydia* appears to mainly concentrate on chasing conspecifics while in flight.

Because data was collected mainly for *P. lydia*, a comparison of territory space use between different categories is tentative. The lone *T. lacerata* datum did show a different pattern of territory use, flying extensively around the pond instead of having a core territory like *P. lydia*. Additionally, it showed a different pattern of interaction rates, mainly interacting with other flying species. *P. longipennis*, a perching species that spent more time perching than *P. lydia*, mainly interacted with perching species and used several different perches, of which many were available due to low water in the pond. These data for *P. longipennis* and *T. lacerata* are useful despite the small sample size because they follow the trend observed in *P. lydia*. They suggest that the perching and flying species will tend to interact with other species in the same category. However, another factor that could be affecting the interaction rates is the degree of overlap between each species' preferred perching sites and flight heights within each category. For example, *P. longipennis* and *P. lydia*, both perchers, had different flight patterns and sometimes perched at different locations in the pond, which probably reduced their interaction rate in spite of both being perchers.

Categories of perching and flying are regarded as thermal adaptations (CORBET, 2004) but they could aid in segregating species and preventing unnecessary conflicts. The data in the current study supports this supposition, but more data are needed. Other studies have looked at how interspecific interactions affect perching heights (REHFELDT & HADRYS, 1988), habitat (MICHIELS & DHONDT, 1987), and space use (HUTCHINSON, 1977; TYNKKYNEN, et al., 2006), but this is the first study to examine how the perching/flying dichotomy might partition the environment.

The species composition of the ponds would have to be altered or ponds with more species similar in appearance would be needed to see if this effect acts on *P. lydia*. Some of the differences noted could be due to the presence of highly aggressive species such as *L. luctuosa*. Comparisons of different species' interactions could shed light on exactly why certain species tend to attack others. Is it only a coincidence of shared space for non-similar species or does it depend more on the aggressiveness of the interacting species, such as with the highly aggressive *L. luctuosa*? This hypothesis needs further examination in areas with different species in each category to determine the effect of species composition on category interaction rates. If it is the perching/flying dichotomy, then species composition should only make a slight difference depending on aggressiveness of the species present.

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