

Differences in perch height and response to intruders for territorial and non-territorial *Calopteryx maculata* (Odonata: Calopterygidae)

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Research Article



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All relevant data are within the paper and its [Supporting Information files](#).

Abstract. In the damselfly *Calopteryx maculata*, territorial males court potential mates and guard ovipositing females near the surface of the water. We conducted a survey and an experiment to determine whether there was a relationship between territoriality (site fidelity and agonistic behavior) and perch height. In the survey, males were captured, numbered, and released, and their perch height and location along a stream was noted for two weeks. Mean perch height was positively correlated with total distance travelled and negatively correlated with the number and percentage of times observed at the same site. Males that travelled less than 4 m had a significantly lower mean perch height than males that travelled more than 4 m. We conclude that males with greater site fidelity perch lower than males that travel widely. To test for a relationship between agonistic behavior and perch height, live male and female decoys, and a stick control, were run along a 20 m zip-line at two heights (25 cm and 75 cm), and the responses of resident males were recorded. Resident males that perched low (< 1 m high) approached decoys more often than resident males that perched high, and low-flying decoys were approached more than high-flying decoys. We conclude that territorial males—identified by greater site fidelity and agonistic behavior—perch lower than other males and are particularly responsive to low flying intruders. The benefits and costs of perching low and responding to low-flying intruders are discussed.

Key words. Dragonfly, alternative reproductive tactics, territoriality

Introduction

In many odonate species, males exhibit different behaviors for acquiring mates. These “alternative reproductive tactics and strategies” (ARTS) arise as consequences of intra-sexual selection (Lozano & Ros, 2022; Taborsky et al., 2008). In territorial odonates, for example, males that cannot acquire or hold a territory resort to other methods of mate acquisition. They may remain within or near a dominant male’s territory as a ‘subordinate’ or ‘satellite’ male and attempt to ‘sneak’ a mating, or they may ‘wander’ or ‘float’ through the habitat and may intercept females away from established territories or ‘poach’ females from territorial males (Corbet, 1999: pp. 465–460). For a given individual, these ARTS may be permanent or ephemeral, reversible or irreversible (Lozano & Ros, 2022), and they may be associated with: (1) distinct morphologies (Contreras-Garduño et al., 2006; Rivas-Torres et al., 2019; Romo-Beltrán et al., 2009); (2) physical/physiological attributes like body size (Samejima & Tsubaki, 2009), fat reserves (Romo-Beltrán et al., 2009), hormone levels (Córdoba-Aguilar & Munguia-Steyer, 2015), body temperature (Samejima & Tsubaki, 2009), immunocompetence (Lozano & Ros, 2022), or parasite loads (Marden & Cobb, 2004); and (3) environmental/populational characteristics like male density and aggressiveness (Poethke & Kaiser, 1987; Tsubaki & Ono, 1986), perch availability (Waltz & Wolf, 1988), light levels (Larison, 2007) or

the density (Larison, 2007) or behavior (Khelifa, 2019) of ovipositing females. In short, male mating behaviors in territorial odonates vary, and are determined by the morphological and physiological state of the organism and the environmental context.

Not surprisingly, male odonates exhibiting different tactics often select different microhabitats—presumably maximizing the adaptive value of their behavior. Territorial males usually defend oviposition sites and mate with incoming females, and so they typically select microhabitats along banks of waterbodies, on emergent vegetation close to oviposition sites, or on the oviposition site, itself.

Subordinate/satellite/wandering/floater males (hereafter: “non-territorial” males) may be restricted to microhabitats farther from water to avoid confrontation with territorial males (Irusta & Araújo, 2007). Microhabitat selection can influence the cost/benefit ratios associated with territoriality. Although territorial males benefit from increased mating frequency (Waage, 1973) and increased reproductive success (Forsyth & Montgomerie, 1987; Waage, 1979a, 1979b), there are several costs of territoriality (Ord, 2021; Suhonen et al., 2008): (1) the energetic costs of battling other males to acquire, hold, advertise, and patrol a territory; (2) the risk of injury from these contests or from predators attracted by these activities; and (3) the opportunity cost of time that could have been spent foraging, courting, and mating. So, perching near oviposition sites over open water might reduce the length and energetic expenditures of defensive patrols and courtship flights, but it might increase apparency to predators.

Since the foundational papers by Waage (1973, 1975, 1979a, 1979b, 1983, 1984) that described the complex courtship behavior, sperm removal, and mate-guarding in the damselfly, *Calopteryx maculata* (Beauvois, 1807), this species has become a model system for studies in territoriality, ARTS, sexual selection, and speciation. In general, younger mature males with larger fat reserves are more likely to acquire and hold territories (Marden & Rollins, 1994; Marden & Waage, 1990), while older displaced males maintain some level of reproductive success as non-territorial males (Forsyth & Montgomerie, 1987). The ability of female *C. maculata* to reject mating attempts suggests that mating in this species is largely driven by apparent or cryptic female choice rather than male coercion (Fincke, 1997), perhaps related to a male’s genetic integrity and/or energetic reserves. Since genetic integrity and energetic reserves could be indicated by the ability to defend and hold territories with high quality oviposition sites (Alcock, 1987a; Beck & Pruett-Jones, 2002), many studies have compared territorial and non-territorial *C. maculata* males with respect to potential male fitness indicators like body symmetry (Beck & Pruett-Jones, 2002) and body size or color (Fitzstephens & Getty, 2000; Sarfaty & Pruett-Jones, 2010). In other damselflies, display duration (Fincke, 1997), and copulation duration (Andrés & Cordero-Rivera, 2000) vary with territorial role. Few

studies, however, have examined how microhabitat selection varies between territorial and non-territorial males of *C. maculata* (but see Kirkton & Shultz, 2001, for differences in habitat use based on age.)

Flight is an energetically expensive behavior that can also increase an organism’s apparency to predators and prey (Grether, 1997; Grether & Grey, 1996). If selection favors repertoires that minimize these costs, then territorial *C. maculata* males should perch close to oviposition sites on the surface of the water and should limit revealing patrol flights to intruders representing likely territorial threats (if male), and limit revealing courtship flights and displays to situations with legitimate mating opportunities (if female). Perching close to oviposition sites might also have direct reproductive benefits beside energy conservation, by providing more direct access to incoming females, better oversight of ovipositing females, and a stronger association with the oviposition site for choosy females. This investigation was conducted to determine: (1) if territorial *C. maculata* males perch lower than non-territorial males; and (2) if the frequency that perched males approach intruders is affected by intruder sex, intruder flight height, and the territorial status of the perched male. The costs and benefits of these behaviors is discussed.

Materials and methods

A perch location survey was conducted from June 7–22, 2022, on Little Creek (34.921456° N, 82.434827° W) on the campus of Furman University, Greenville, SC, USA, to test the hypothesis that territorial males of *Calopteryx maculata* perch lower than non-territorial males. Twenty-six points were established along a 125 m section of Little Creek at 5 m intervals. Morning (09:30–11:00) and afternoon (14:00–15:30) surveys were conducted Monday–Friday, by walking the transect once during each interval and recording the position of as many dragonflies as possible. The locations of 155 perching males were described by recording: (1) the distance and direction (upstream or downstream) from the closest point; (2) the side of the creek used; and (3) the height of the perch above the waterline. Individuals were collected by aerial net, marked on the left hind wing with a unique number, and released. Total distance travelled was calculated by summing distances between observations. The creek was 5 m wide, so we added 5 m of flight distance when an individual moved from one side to the other. Average distance travelled per day was computed by dividing total distance travelled by the total number of days between the first and last observation. The time between morning and afternoon observations was considered 0.5 days. Only the 51 individuals observed at least twice, more than 0.5 days apart, were included in the analyses.

The degree of site fidelity, which is an important component of territoriality, was assessed by: (1) the number of observations, made at least one day apart,

in which an individual was within 4 m of the same location; (2) the percentage of observations an individual was at the same location; and (3) traveling a cumulative distance of 4 meters or less across all observations. This distance was chosen because territorial males usually perch within 2 m of the oviposition site (Waage, 1973), but they could select different perches within the territory upstream or downstream from the oviposition site.

The relationship between site fidelity and perch height in male *C. maculata* was described by correlating mean perch height with distance travelled (both total distance travelled and mean distance travelled/day) and site fidelity (both number of times observed at a particular site and percentage of total times observed at a particular site). Spearman rank correlations were used because distance and fidelity metrics were not normally distributed (Kolmogorov-Smirnov tests, $p < 0.05$). One-tailed Spearman correlations were used because the hypotheses predicted a particular directionality to the relationships: if territorial males perch lower than satellite males, then perch height should be positively correlated to distance travelled and negatively correlated with site fidelity. In addition, the perch height of males with a cumulative distance travelled of 4 m or less was compared to the perch height of males with a cumulative distance travelled of more than 4 m, using a Student's t-test for independent samples. All statistical tests were conducted using SPSS v. 28.0.0.0 (IBM, 2021).

An experiment was conducted from 25 July – 4 August, 2022, to determine whether the response of *C. maculata* males is affected by the sex and flight height of territorial intruders, and by the perching position of the territorial males. A stretch of Little Creek was selected that typically had 2–4 territorial males. Vertical rebar bars were driven into the streambed 20 m apart and a fishing reel was supported on each vertical support. The fishing lines were connected by a clasp, creating a “zip-line” that could be reeled back and forth (similar to that used by Worthen & Phillips, 2014). A loop was made in the center of a 20 cm piece of fishing line, and the loop was gently positioned and tightened around the thorax of a live *C. maculata* ‘decoy’, between the fore and hind wings. The top of the line was attached to the clasp on the zip-line with a paper clip, and the bottom received a small fishing weight so that the dragonfly was suspended below the zip-line (Fig. 1). The dragonfly was reeled along the zip-line at approximately 1 m sec^{-1} (video: Supplemental file ‘Mekhi.mp4’). Decoys were numbered and released after their ten runs and were not used again.

Male and female decoys were run on the zip-line. The zip-line was raised and lowered on the vertical supports, so the decoy traversed the stream either 25 cm (‘low’) or 75 cm (‘high’) above the water. For each experimental replicate, a male decoy and a female decoy were run at both heights, for five consecutive runs at each height. The order of the heights (high runs first or second) and the order of the decoys was random-

ized. In this way, both male and female decoys were presented at both heights to roughly the same group of focal males during each experimental replicate. There were 10 replicates of the experiment conducted over the 10-day period, usually once/day (but twice—in the morning and afternoon—on two occasions). In five of the ten replicates, a stick was run on the zip-line as a control—at both heights for five runs each, randomized with the male and female decoys.

Many of the focal males could be identified by the numbers received during the perch-height investigation. Others were captured after a replicate was complete and were numbered and released so they could be identified in later replicates. The perch height of all focal males was categorized as either ‘low’ (< 1 m) or ‘high’ (> 1 m), and their distance from the water were categorized as either ‘edge’ (< 20 cm from the water or over the water) or ‘bank’ (more than 20 cm away from the water). On each run, we recorded whether each focal male left his perch and approached the moving decoy. The responses of focal males were considered independent events, as interactions between focal males was very rare (less than 5 throughout the course of the experiment)—probably because territorial limits had already been established.

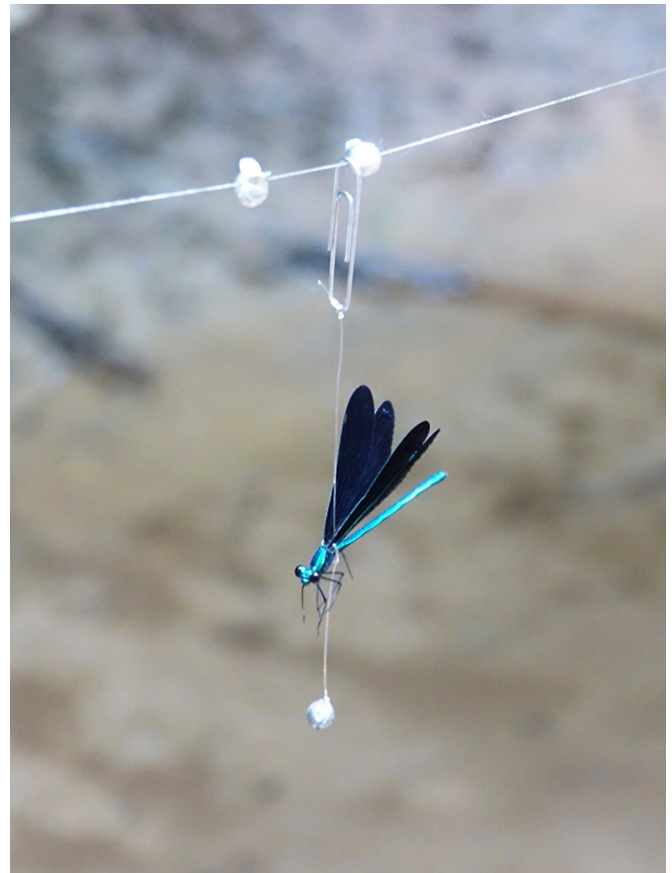


Figure 1. A photograph of the decoy assembly. A loop of fishing line holds the live decoy, which was numbered, photographed, and released alive after 10 runs. The silver balls are fishing weights to keep tension on the loop and maintain the position of the decoy on the zip-line as it was reeled.

There were two-minute pauses between runs and five-minute pauses between treatment changes to allow focal males to resettle on their perches. Nonetheless, because males came and went from the study site throughout the experimental period, the number of focal males varied between runs. So, although the experimental design was ‘balanced’ with respect to the number of runs at each height with each decoy, the number of sampling units (individual males recorded) varied among the treatment combinations.

The effects of decoy type, decoy flight-height, focal perch height, and focal position (proximity to the bank) on the response rate of territorial males were assessed with a general linear model (binary logistic) that included all main effects and 2-way interactions. Post-hoc Chi-Square tests were used to describe differences among treatments for effects that were significant ($p < 0.05$) in the model. Since control sticks were approached only once, the analyses were performed with and without the stick treatments included; only those without the stick treatment are presented.

Results

Perch height and travel of territorial and non-territorial males

Males used perches that averaged 0.83 ± 0.48 m ($\bar{x} \pm 1$ sd, $N = 155$) in height and ranged from 0–1.80 m. Travel distances between observations were strongly skewed, averaging 7.2 ± 14.52 m ($\bar{x} \pm 1$ sd, $N = 93$) and ranging from 0–85 m. As predicted, mean male perch height was positively correlated with total travel distance ($r = 0.247$, $p = 0.040$, $N = 51$); males that travelled less tended to perch lower than males that travelled farther. In addition, males with greater site fidelity (perching repeatedly at a particular site) tended to perch lower than other males—in an absolute sense (times observed at a particular site, $r = -0.286$, $p = 0.021$, $N = 51$) and a relative sense (percentage of observations where they were at a particular site, $r = -0.333$, $p = 0.008$, $N = 51$). However, mean male perch height was not significantly correlated with mean travel distance/day ($r = 0.154$, $p = 0.14$, $N = 51$). Lastly, the mean perch height of males that travelled 4 m or less ($\bar{x} \pm 1$ sd = 72.0 ± 34.7 cm, $n = 21$) was significantly lower than the mean perch height of males that travelled more than 4 m ($\bar{x} \pm 1$ sd = 94.4 ± 28.1 cm, $n = 30$; $t = 2.54$, $p = 0.007$, $df = 49$).

Responses to decoys

In the zip-line experiment, the control stick was only approached once in 111 opportunities (0.9%); significantly less than approaches to male decoys (12.6%; $X^2 = 12.93$, $df = 1$, $p < 0.001$) and female decoys (11.6%; $X^2 = 11.42$, $df = 1$, $p < 0.001$), which did not differ from one another in the rates they were approached ($X^2 = 0.13$, $df = 1$, $p > 0.05$). As such, the stick treatment was de-

Table 1. Results from a General Linear Model (binary logistic) analyzing the effects of decoy flight height (‘Decoy ht’), decoys sex (‘Decoy sex’), focal male perch height (‘Focal ht’) and focal male position (‘Focal pos’) on the frequency that focal males approached decoys. Decoys were run at 25 cm (‘low’) or 75 cm (‘high’), focal height was characterized as ‘low’ (< 1.0 m) or high (> 1.0 m), and focal position was characterized as within 20 cm of the water (‘edge’) or beyond (‘bank’). $df = 1$; boldface = statistically significant effects ($p < 0.05$).

Source	Type III Wald X^2	p
Intercept	65.751	0.001
Decoy ht	2.143	0.143
Decoy sex	1.671	0.196
Focal ht	0.327	0.568
Focal pos	1.437	0.231
Decoy ht × Decoy sex	4.148	0.042
Decoy ht × Focal ht	3.939	0.047
Decoy ht × Focal pos	0.182	0.670
Decoy sex × Focal ht	0.153	0.696
Decoy sex × Focal pos	0.608	0.436
Focal ht × Focal pos	0.053	0.817

leted from further analyses to focus on differences in responses to male and female decoys.

Focal male responses depended on the interactive effects between decoy sex, decoy flight height, and focal height (Table 1). Male decoys were approached significantly more often when flying low than when flying high (Fig. 2a; $X^2 = 26.49$, $p < 0.001$). Female decoys were also approached more often when flying low (Fig. 2a), but the difference was less pronounced than for male decoys ($X^2 = 3.68$, $p = 0.06$), accounting for the significant ‘decoy height × decoy sex’ interaction (Table 1).

Focal males that perched high were generally unresponsive to decoys (Fig. 2b), and there was no difference in their response to decoys flying high or low (Fig. 2b; $X^2 = 0.215$, $p > 0.643$). Focal males that perched lower, however, were affected by the flight height of the decoy, with significantly more responses to low flying decoys (Fig. 2b; $X^2 = 30.24$, $p < 0.001$). This accounts for the significant ‘decoy height × focal height’ interaction (Table 1). For these low-perching focals, approaches to low-flying decoys were significantly greater than approaches to high-flying decoys for both female decoys (Fig. 3; $X^2 = 7.00$, $p = 0.008$) and male decoys (Fig. 3; $X^2 = 24.48$, $p < 0.001$). Though again, the effect of decoy height was more dramatic for male decoys than for female decoys.

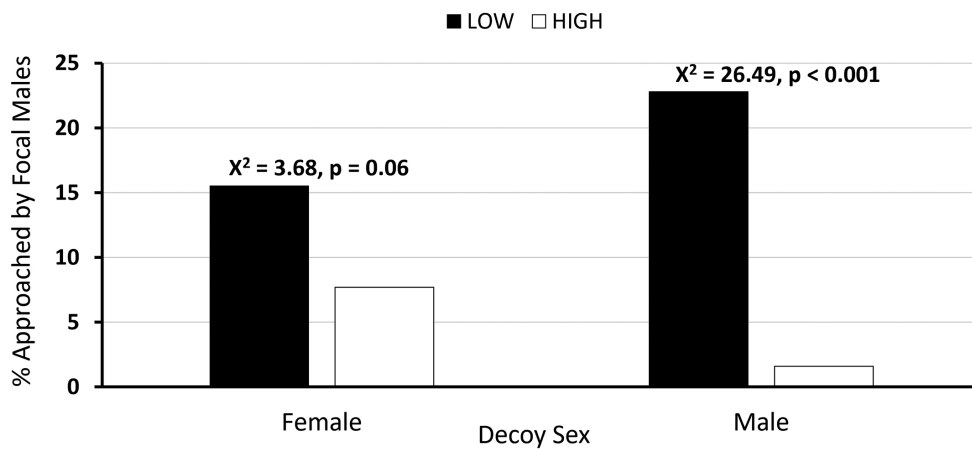
Discussion

The purpose of this investigation was to determine whether territorial males of *C. maculata* perch lower than non-territorial males, and to determine whether investigative sorties are affected by the territorial status

of the male and the sex and flight height of territorial visitors. Miller (2009) defined territoriality as “the exclusive use of fixed space, which entails obtaining, defending, or advertising occupancy of the space”. In our

dispersal survey, males that travelled less and showed greater site fidelity perched lower than other males. In our zip-line experiments, the focal males that approached intruders most perched lower than less re-

A. Approaches to females and male decoys by focal males



B. Approaches to decoys by focal males perching at different heights

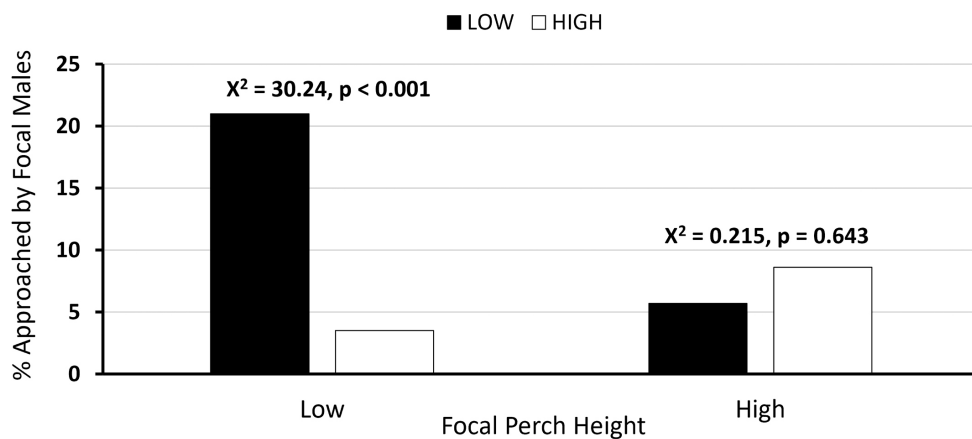


Figure 2. The percentage of opportunities in which focal male *Calopteryx maculata* approached *C. maculata* decoys propelled on a zip-line 25 cm (“LOW”) and 75 cm (“HIGH”) above the water. Comparisons based on: A – decoy sex, and B – focal perch height (“Low” = < 1 m, “High” = > 1 m). Chi-square values compare approach frequencies to low and high decoys in each treatment category.

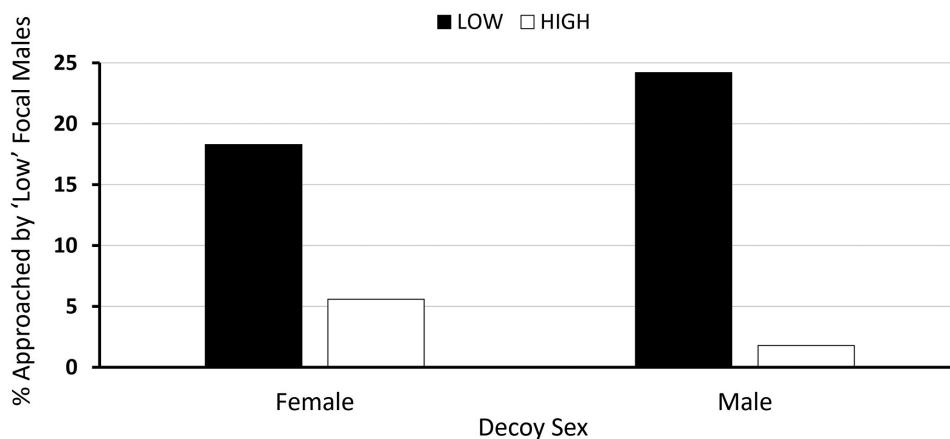


Figure 3. The percentage of opportunities in which low-perching focal *Calopteryx maculata* males approached male and female *C. maculata* decoys, propelled on a zip-line 25 cm (“LOW”) and 75 cm (“HIGH”) above the water. Low decoys were approached significantly more often than high decoys for both females ($\chi^2 = 7.00, p = 0.008$) and males ($\chi^2 = 24.48, p < 0.001$).

sponsive males. So, defined by site fidelity and agonistic behavior, territorial males perched lower than non-territorial males.

The response by territorial males in the zip-line experiment also depended on the flight height of the decoy. Territorial males approached low-flying male and female decoys significantly more often than they approached high-flying intruders. This is consistent with our hypothesis that, for a variety of possible reasons, low flying intruders should be perceived as more serious threats (if male) or mating opportunities (if female) and should be approached and engaged more often than high-flying intruders.

Territorial males may perch low and may respond differentially to intruders for several reasons, including direct reproductive benefits, energetic cost/benefit considerations, predator/prey considerations, and habitat constraints. By perching low, territorial males are closer to oviposition sites on the surface of the water. This might confer direct reproductive benefits by increasing the likelihood of seeing a female coming to oviposit and being associated with the oviposition site (Martens, 2001). Females may not select males directly; rather, they may select the oviposition site and mate with the nearest male—so proximity to the oviposition site could have direct reproductive advantages. Likewise, if low-flying females are coming to oviposit while high-flying females are just passing through, then preferentially approaching and courting sexually-receptive low-flying females should increase a territorial male's reproductive success.

However, the reproductive biology of territorial species is complicated by the costs of territory acquisition and defense, the risk of injury from territorial battles or predators, and reduced energy intake from reduced time foraging or more wary prey (Ord, 2021; Suhonen et al., 2008). For example, many behaviors in *C. maculata*—such as the duration of territorial disputes (Waage, 1988), selection of oviposition sites (Waage, 1987), and courtship decisions (Alcock, 1983)—have been explained in the context of energetic efficiencies of reducing flight costs. Most territorial disputes among males are resolved by short, energetically thrifty bouts that last only a few seconds (Forsyth & Montgomerie, 1987; Waage, 1988). Longer dogfights lasting hours may be 'wars of attrition' that may select for males with larger fat reserves (Marden & Waage, 1990) and may result from overlapping male territories (Waage, 1988). Also, to some degree, *C. maculata* males seem to recognize females with whom they have previously mated; these females are not courted like novel females when they re-enter the territory (Alcock, 1983; but see Waage, 1979a), which also saves energy. Females are attracted to larger oviposition sites with more resources that require less travel and have other ovipositing females defended by males, allowing for efficient undisturbed oviposition (Waage, 1973, 1987). As predicted for sites with more females, males at these sites defend smaller territories, and spend more time courting and defend-

ing to maintain the same mating frequency in the face of higher male densities (Alcock, 1983; Meek & Herman, 1990). So, by perching low and limiting investigative flights to low-flying intruders, territorial males may limit costs to flights with the greatest value for territorial defense or mating.

Although low-flying decoys of both sexes were approached significantly more than high-flying decoys, the effect was more dramatic for male decoys. This difference may also be explained in the context of energetic/reproductive costs and benefits. Approaching a high-flying male that does not represent a threat is a costly waste of energy with little possible benefit. However, approaching a high-flying female might result in some—albeit lower—probability of a successful courtship. As such, there might be some reproductive value to approaching a high-flying female, too, especially if she is only travelling 75 cm above the oviposition sites. This may explain the greater frequency of approaches to high-flying females and the smaller effect of female decoy height.

Also, there may be complex conflicts between aporency to conspecifics and vulnerability to predators, involving both morphology and behavior. Although perching in the open near oviposition sites might deter encroachment by other males and might increase a territorial male's likelihood of selection by an incoming female, it also increases a male's visibility to predators. In addition, swirling territorial combats and fluttering courtship routines should attract the attention of visual predators, even more (Suhonen et al., 2008). Indeed, even just the act of flying increases the likelihood of being caught in a spider's web (Rehfeldt, 1992). Interestingly, territorial males may have higher survivorship than non-territorials in spite of costly behaviors or sexually-selected ornamentations (Grethier, 1997; Pena-Firme & Guillermo-Ferreira, 2020), perhaps as a consequence of their superior physical condition (Palacino-Rodríguez et al., 2016). The fact that immature males of *Mnesarete pudica* are colored like cryptic females, which may reduce both aggression from mature males and predation (Cezário et al., 2021) is further evidence of the complex selective pressures on territorial odonate species.

Lastly, *C. maculata* males may prefer to perch low because of the environmental constraints of the small woodland streams they inhabit. In open areas, perching high may confer an advantage by providing a larger field of view with longer sight lines. This might explain why many organisms exhibit "hilltopping" behavior for lek formation or mating rendezvous, where they congregate on isolated trees on ridgetops in open country (Alcock, 1984, 1987b). Likewise, the size-dependent competitive hierarchy exhibited by libellulid species on open ponds and lakes—where large species use tall perches and displace and relegate smaller species to shorter perches (Worthen, 2017, 2018; Worthen & Jones, 2006, 2007)—would also suggest that tall perches are preferred in these open habitats. However, in the

shaded understory of a forest stream, perching low provides longer sight lines along the stream course than higher perches where sight lines are blocked by overhanging vegetation.

Additional experiments will be necessary to confirm the patterns we found and to define the costs and benefits of perch behavior by *C. maculata*. There were several attributes of this survey and experiment that should be improved or studied more explicitly. This study was limited to one site, with gently sloping banks and numerous perch and oviposition sites. It is possible that a denuded cut bank that provides few perch opportunities, or a stream in an open habitat with longer sight-lines, could change perch height patterns. Likewise, limiting the experiment to one location where several males were sampled repeatedly compromised the generalizability of this study and created problems of pseudo-replication and the possibility that males were changing their behavior from one trial to the next. Indeed, the rapid sequential presentation of decoys, with only two minutes between runs, probably exceeds the natural rate of visitation and may have caused attenuation or sensitization in focal males. And lastly, more explicit treatment groups would allow for a more refined understanding of these behaviors. Frankly, we were surprised that the very coarse treatment levels used in this study (25 vs. 75 cm intruder height; focal categorization of > or < 1 m; 20 cm delineation of “bank position”) elicited different biologically interesting patterns. Accepting these shortcomings, this study provides a tantalizing foundation for subsequent studies looking at the costs and benefits of perch-site selection. Surveys and experiments on predation rates on territorial and non-territorial dragonflies may be of particular value.

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Supplementary material

Supplementary material 1. Video clip of the zip-line apparatus in use, and the response of a focal male.