Target species affects the duration of competitive interactions in the Neotropical dragonfly, *Micrathyria atra* (Odonata: Libellulidae)

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Abstract. Dragonflies often engage in aggressive interactions over access to mates, food, or other resources. We should expect species to have behavioral adaptations for minimizing such interactions with other species because they are not competing with them for mates and often require different resources. We conducted observational trials in natural water pools that provide new evidence for one such adaptation in the Neotropical dragonfly, *Micrathyria atra*: males in this species have shorter interactions with individuals of other species than with conspecifics.

Further key words. Dragonfly, Anisoptera, Black dasher, mistaken-identity hypothesis, species recognition, insect behavior

Introduction

Odonates frequently engage in aggressive interactions with both individuals of the same species (intraspecific interactions) and individuals of different species (interspecific interactions). These interactions may determine access to mates, food, shelter, or other resources (Baird & May 2003). Therefore, winning contests can be very beneficial for an individual, despite the energetic cost and risk of bodily damage associated with such interactions (reviewed by Suhonen et al. 2008).

Because conspecifics (members of the same species) compete for mates and the same resources, while heterospecifics (members of different species) do not compete for mates and often require different resources, individuals may have less to gain from interspecific contests. For this reason, selection should favor behavioral adaptations to avoid interspecific interactions (*e.g.* Baird & May 2003; Schultz & Switzer 2001), such as approaching heterospecific intruders less frequently than conspecific ones (Fitzpatrick & Wellington 1983). Previous studies have shown, however, that dragonflies frequently make mistakes in identifying the species of potential competitors from a distance (Schultz & Switzer 2001). Another potential

strategy to minimize costs could be to shorten the length of interspecific interactions (*e.g.* Baird & May 2003). This would reduce costs because longer interactions require more energy (Marden & Waage 1990) and likely have a higher risk of injury (Rüppell & Hilfert-Rüppell 2013). Under this strategy, territorial males might approach intruders to identify them, and then terminate the interaction if the intruder is a heterospecific.

In this study, we investigate the competitive interactions of the Neotropical dragonfly, *Micrathyria atra* (Martin, 1897). Recently, Worthen (2017) showed that *M. atra* males attacked conspecific males more often than was expected by their relative abundance, providing evidence for the first strategy described above for reducing the costs of interspecific interactions. Here, we test for evidence of the second strategy, predicting that *M. atra* males would spend less time in interspecific interactions than intraspecific ones.

Methods

Study site

We performed our study at Cantarrana swamp (10°25'47" N, 84°00'21" W) at La Selva Biological Station in Heredia Province, Costa Rica, in July 2016. Cantarrana swamp is an approximately 80 m by 30 m wetland located within tropical wet forest and is a designated reserve area where collecting and manipulative experiments are prohibited.

Study design

We conducted 63 observational trials of 15 minutes in Cantarrana swamp. We selected 10 small pools (*i.e.*, open water areas in the swamp) and conducted focal behavioral observations using binoculars from a boardwalk above the swamp. For each trial, we chose a focal male that was perched on a grass blade or twig directly overlooking the pool. The observational trials were spread throughout the day (ranging from 08:00 a.m. to 04:00 p.m.; CST; UTC -6 h), encompassing most of the activity period of *M. atra* (May 1977). During each trial, we measured the frequency of interactions – defined as a focal male leaving its perch and approaching another individual – and recorded the identity (conspecific or heterospecific) of each individual approached. In 49 of these trials, we also measured the duration of each interaction, from the time the focal individual left its perch to the time it began to return to its perch. We recorded interaction duration as either "short" (< 5 seconds) or "long" (> 5 seconds). This classification was similar to the classification used by Singer (1989) and made it more logistically feasible to measure duration than measuring the exact duration. Singer (1989) used a threshold of two seconds, we extended this threshold to five seconds to be more conservative with what we classified as a "long" interaction. From personal observations, trials that we classified as "short" typically lasted only a few seconds while "long" trials typically lasted longer than 15 seconds. Because this study is not focused on mating behavior, all interactions with conspecific females were removed from analyses (N = 4).

Table 1. Contingency table of interaction length and interaction type. The proportion of interactions that were classified as long significantly differed by the type of interaction (Fisher's Exact test, $P < 0.001$).

	Intraspecific	Interspecific	Total
Short	16	48	64
Long	45	4	49
Total	62	52	113

Results

During the 63 fifteen-minute trials, we observed a total of 176 interactions (112 intraspecific and 64 interspecific). Interactions occurred in 53 of the 63 trials. On average, focal males pursued conspecifics more often than heterospecifics (Fig. 1). However, the difference between the means was only marginally significant (Wilcoxon signed-ranked test, $V = 525.5$, $P = 0.057$) and no consideration was given to the relative abundances of species in the environment.

Interaction type (intraspecific or interspecific) significantly affected the duration of interactions (Table 1, Fisher's Exact test, $P < 0.001$). In agreement with our prediction, intraspecific interactions were more likely to be classified as long: 45 out of 61 intraspecific interactions were classified as long (74.2 %), while only four out of 52 interspecific interactions were (7.7 %; Table 1).

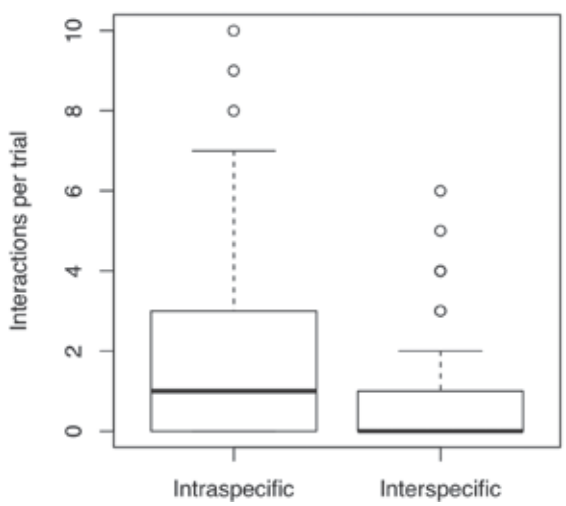

Figure 1. The frequency of intraspecific and interspecific interactions by males of *Micrathyria atra* during 15-minute observational trials. We defined an interaction as a focal male approaching another individual. Intraspecific interactions occurred more frequently but the difference was only marginally significant (Wilcoxon signed-ranked test, $V = 525.5$, $P = 0.057$).

Discussion

Our observations support the hypothesis that *M. atra* males have behavioral adaptations to minimize interactions with heterospecific species. In agreement with Worthen (2017), we found that intraspecific interactions were more frequent than interspecific ones, although we did not account for relative abundance, so less insight can be drawn from our conclusions. More interestingly, interspecific interactions were shorter than intraspecific ones, supporting the hypothesis that this species has behavioral adaptations for reducing the length of interspecific interactions. These results, in combination with those of Worthen (2017), suggest males of *M. atra* invest more in intraspecific interactions than interspecific ones, consistent with predictions of maximizing fitness.

Males of *M. atra* can distinguish between conspecifics and heterospecifics, probably by using visual cues for species recognition (Svensson et al. 2007). Future studies should examine if individuals are identifying conspecifics by morphological or behavioral characteristics such as flight pattern, and whether this depends on the other species present in the environment.

Our results also shed some light on the long-standing question of why territorial males pursue heterospecifics, even though they are not competing with them for mates (Fitzpatrick & Wellington 1983). Behavioral adaptations to minimize the duration of interspecific interactions, such as we observed in *M. atra*, would reduce the costs of heterospecific pursuits and thus the selective pressure to eliminate them. Furthermore, the ability of dragonflies to visually recognize conspecifics is constrained by distance, angle of approach, and background (Switzer & Eason 2000), therefore investigatory approaches may be necessary for the identification of morphologically similar competitors. If heterospecific pursuits are mainly investigatory, we would expect interspecific interactions to be short, as we observed in this study. Baird & May (2003) observed a similar pattern in *Pachydiplax longipennis* guarding feeding territories. However, neither their study nor ours explicitly looked for this pattern in the context of guarding mating territories. We hope that future studies will do so in order to advance our understanding of territoriality in odonates.

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