

Differences in male-male tandem formation in two species of *Micrathyria* (Odonata: Libellulidae)

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Abstract. Male-male tandem formation in odonates is typically described as a mistaken sexual advance by one male on another. If so, male-male tandem formation should be less frequent in more sexually dimorphic species. In a small experiment designed to describe patterns of intra- and interspecific aggression by *Micrathyria atra* and *M. mengeri*, I placed live tethered male decoys of these species in the territories of territorial males. In the less sexually dimorphic *M. mengeri*, nine of 21 intraspecific interactions by three different males resulted in male-male tandem attempts. In the more sexually dimorphic *M. atra*, only one of 25 intraspecific interactions resulted in a male-male tandem attempt. The higher incidence of male-male tandem formation in *M. mengeri* may reflect a greater mistake rate by males in this less dimorphic species.

Further key words. Dragonfly, Anisoptera, sexual polychromatism, Costa Rica

Introduction

Copulation in odonates is preceded by the formation of a ‘tandem’, in which the male grasps the female with his anal appendages, either engaging the female’s mesostigmal plates or clasping her behind the head (CORBET 1999: 483 ff.). Males of some species often grasp conspecific males and members of other species, particularly at roost sites when targets may be immobilized by cool temperatures (REHFELDT 1993). Morphological and behavioral differences between species have probably evolved, in part, as species recognition cues to reduce the fitness costs of unproductive heterospecific couplings and heterospecific aggression (WAAGE 1975; SVENSSON et al. 2007; TYNKKYNEN et al. 2008; IYENGAR et al. 2014; GREYER et al. 2015).

Within species, sexual dichromatism (difference in color rather than difference in size) also serves as a sex recognition cue that can reduce the frequency of males courting and coupling with males (CORDERO & ANDRÉS 1996; SHERRATT & FORBES 2001; BEATTY et al. 2015). There are other selective pressures, however, that also favor developmental or genetically fixed sexual dichromatism. Female choice can drive male coloration and patterning in some species (FINCKE 1997), where females accept tandem formation and complete copulation more frequently with males that are more pigmented (MOORE 1990; SIVA-JOTHY 1999; CÓRDOBA-AGUILAR 2002). In some territorial species, sexual dichromatism is driven by male-male competition: males with more pigmentation have better fighting ability (CONTRERAS-GARDUÑO et al. 2006; SAMWAYS 2006; MOORE & MARTIN 2016), and are more successful at acquiring and holding prime territories than less pigmented males, giving

them greater access to females (GRETHER 1996; GUILLERMO-FERREIRA et al. 2015; MOORE & MARTIN 2016). Apparently, pigmentation is a true signal of competitive ability in these species, as more pigmented males are attacked less by other males (GUILLERMO-FERREIRA et al. 2015).

These benefits can be undermined by selective pressures favoring males and females that ‘cheat’, resulting in polychromatism within one or both sexes that may affect the frequency of male tandem formation. Gynochromic or ‘sneaker’ males can enter territories of dominant males and mate surreptitiously, or simply mate with females outside of defended territories (PLAISTOW & TSUBAKI 2000; ROMO-BELTRÁN et al. 2009). Gynochromic males may experience reduced agonism from territorial males, but more sexual harassment and tandem attempts (GRETHER et al. 2015). Androchromic females may gain a fitness advantage through reduced harassment from courting males and reduced time spent in supernumerary copulations (ROBERTSON 1985). Female polychromatism can also increase the frequency of male-male tandems by selecting for males that maintain behavioral flexibility in mate recognition and grab any conspecific they can, rather than forfeit an opportunity to reproduce (VAN GOSSUM et al. 2005).

So, although male-male tandem formation is usually interpreted as a mistaken sexual advance, it may be adaptive under some circumstances. Indeed, in some cases, it may be purposeful. SWITZER & SCHULTZ (2000) suggest that territorial males may clasp conspecific males as a rare, hyper-aggressive, mate-guarding strategy – physically prohibiting an intruding male from mating with a female ovipositing in the territory.

The causes and fitness consequences of male-male tandem formation are complex and require further study. The first step is to document the frequency of these events in species with different reproductive ecologies and different levels of sexual dichromatism. Here, I describe observations of male-male tandem formation in two sympatric species of *Micrathyria* Kirby, 1889 that differ dramatically in the level of sexual dichromatism. I found that the more sexually dichromatic species had a significantly lower frequency of male-male tandem formation than the less dichromatic species.

Study site and methods

I observed male-male tandem formation by *Micrathyria atra* (Martin, 1897) and *M. mengeri* Ris, 1919 at the La Selva Biological Station of the Organization for Tropical Studies (OTS), in Heredia Province, Costa Rica (10.43248 N, 84.008070 W). In *M. atra*, females and immature males have a striped thorax and a striking red abdomen; these areas darken to black as males mature (Figs 1a–c). In contrast, the sexes of *M. mengeri* have more similar thoracic and abdominal coloration, though females and immature males have light latero-dorsal stripes on the abdomen and the male abdomen darkens more with age (Figs 1d–f).

Observations were made from 06-vi- through 16-vi-2017, while conducting an experiment on the effects of perch height on intra- and interspecific interactions

along the Teska Elevated Boardwalk. To begin the experiment, I captured a male of one of these species and gently taped its legs to the end of a wooden dowel (0.7 × 20 cm). I taped this dowel to another, positioning the decoy 50 or 100 cm above the waterline and approximately 2 m from a territorial male of either species. I recorded

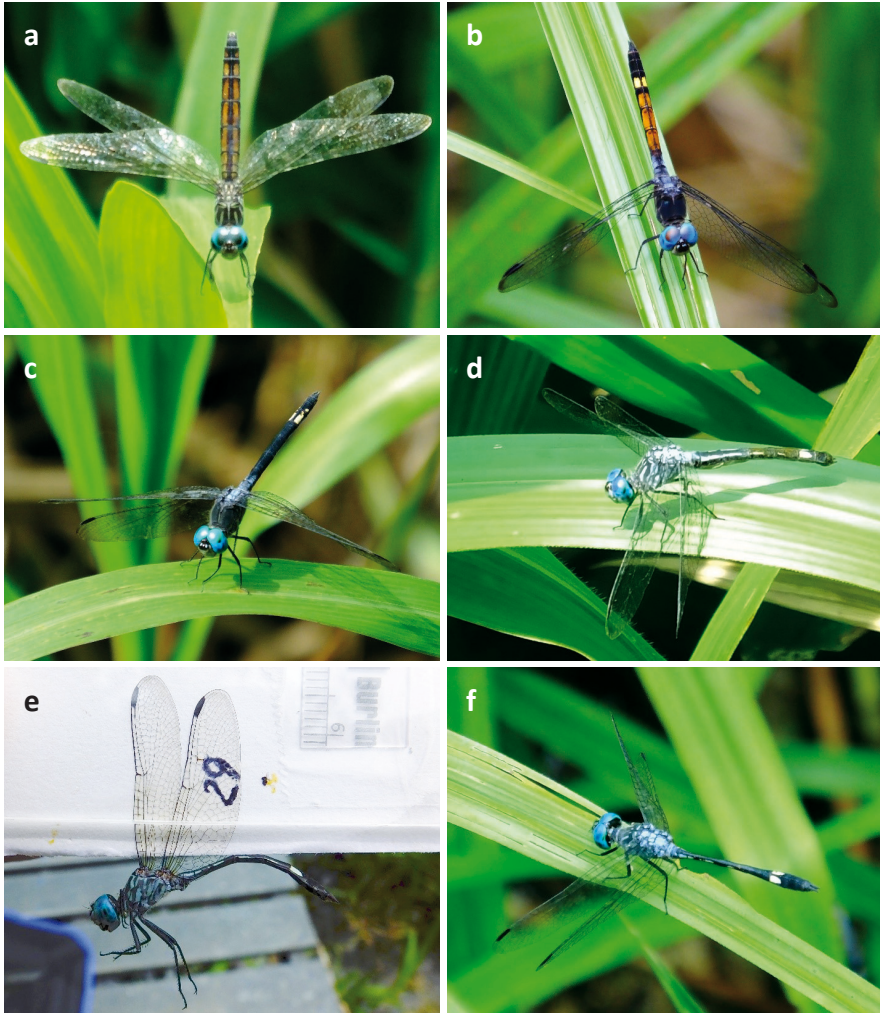


Fig. 1. Sexual dimorphism in *Micrathyrta atra* and *Micrathyrta mengeri*: a) *Micrathyrta atra* female; b) *M. atra* immature male; c) *M. atra* mature male; d) *Micrathyrta mengeri* female; e) *M. mengeri* immature male; f) *M. mengeri* mature male. Note that the brownish color on the abdomen of the *M. mengeri* female (d) is caked mud from underwater oviposition. Photographs: WW

the number of times the territorial male attacked or attempted tandem formation with the decoy in five minutes. An attempted tandem was recorded if the territorial male landed on the decoy and attempted to grasp the decoy behind the head with his terminal appendages (Fig. 2). After five minutes, the decoy was placed in another territory at another height. I released each decoy after 3–4 trials, and captured another male to continue the experiment. One *M. mengeri* decoy was killed while taping, and so was pinned to the dowel for experimental trials. There were no interspecific male-male tandems, so only intraspecific interactions were considered for this analysis. There were 19 replicates of *M. atra* decoys placed in *M. atra* territories, and nine replicates of *M. mengeri* decoys placed in *M. mengeri* territories. Attacks and attempted tandem formations were pooled across replicates and across perch heights for this analysis.

Results

Three of the nine territorial *M. mengeri* males attacked conspecific decoys, and each of these males attempted to tandem with the decoy (Figs 2a–b), for a total of nine tandem attempts in 21 (42.8%) interactions. (Two of these tandem attempts, and

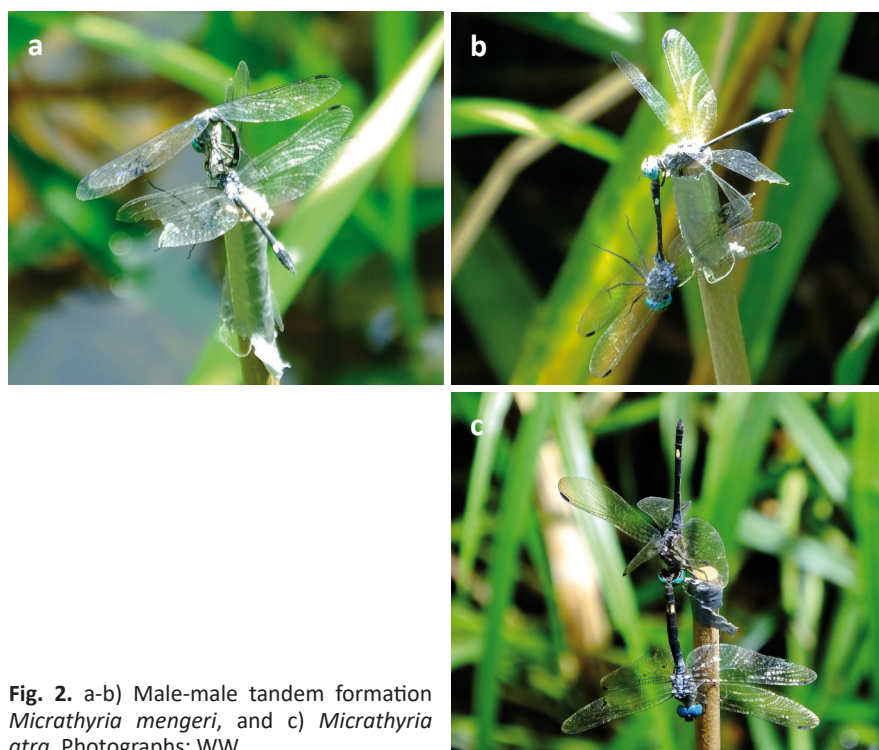


Fig. 2. a-b) Male-male tandem formation *Micrathyrta mengeri*, and c) *Micrathyrta atra*. Photographs: WW

five attacks, were made by one male on the dead decoy.) Six of the 19 territorial *M. atra* males attacked conspecific decoys a total of 25 times, but there was only 1 attempt to form a tandem (1 in 25 interactions = 4.0%; Fig. 2c). Pooling across individuals, the rate of attempted tandem formation was significantly higher in *M. mengeri* than in *M. atra* ($\chi^2 = 10.11$, $df = 1$, $p < 0.005$).

Discussion

Sexual dichromatism is probably a critical variable in sexual recognition in odonates, and it should reduce the frequency of unproductive tandem formation between males. The results of this study are consistent with this hypothesis; the sexually dichromatic *Micrathyria atra* had a lower rate of male tandem formation than the less dichromatic *M. mengeri*, probably because *M. atra* males could more easily identify the sex of the decoy.

It is possible, however, that these behaviors were induced by the tethering procedure, itself. In a contemporaneous study on intra- and interspecific interactions between these and other species, I did not observe any male-male tandems in 93 interactions between free-flying *M. atra* males or 30 interactions between free-flying *M. mengeri* males. As such, tethering affected tandem formation to some degree, increasing the likelihood that a territorial male could catch another dragonfly that enters his territory. Nonetheless, the probability of catching the decoy was equal between species, and yet *M. mengeri* males proceeded to the next step – attempting tandem formation – more than *M. atra*. Given the morphological similarity of *M. mengeri* males and females, perhaps territorial *M. mengeri* males attempt tandem formation with any conspecific they can catch (as suggested by VAN GOSSUM et al. 2005), and tethering provided that opportunity. Under natural conditions, males probably fight or flee when approached, while receptive females allow themselves to be captured.

In sexually dichromatic libellulids like *M. atra*, both sexes are usually fairly similar as immatures; females maintain this color pattern (or change slightly) while males acquire a different color pattern as they mature. This transition can take many days to complete, and males may be sexually active while still sporting an immature, gynochromic morphology. For example, McVEY (1985) identified 17 morphological stages in the developmental trajectory of male *Erythemis simplicicollis* (Say, 1839), from green gynochromic immatures to fully pruinose blue mature males. Although it could take 2–3 weeks for males to complete this sequence, some males arrived at breeding ponds to mate at stage 3, while still mostly green (McVEY 1985). Although these developmental changes in male morphology can be delayed by low food intake or low temperatures (McVEY 1985), it is also possible that selection might favor a delayed color change in species where males transition from satellite males when young to territorial males when mature – a pattern that might occur if the acquisition of a territory correlates with developmental increases in fat reserves

that can determine competitive outcomes (SUHONEN et al. 2008). The dramatic color change of male *M. atra* opens this possibility.

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