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# THE MALE-MALE TANDEM: A NOVEL FORM OF MATE GUARDING IN *PERITHEMIS TENERA* (SAY) (ANISOPTERA: LIBELLULIDAE)

P.V. SWITZER* and J.K. SCHULTZ
Department of Biological Sciences, Eastern Illinois University, Charleston, IL 61920, United States
*Fax: (217) 581-7141; – e-mail: cfpvs@eiu.edu

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Observations on male-male tandems are reported; these tandems occur at very low frequency during mate guarding sequences. When initiating a tandem, a male territory resident grabs an intruding male behind the head and flies with him. This behavior is similar to the tandem formation more usually associated with male-female pairs. Because the male-male tandems occurred during mate-guarding and because tandems do not follow courtship of the intruder by the resident, this rare behavior is interpreted as a form of mate guarding rather than misdirected mating behavior.

## INTRODUCTION

Odonates are frequent research subjects for studies of sexual behavior and mating systems (see reviews in CORBET, 1962; PARR, 1983; THORNHILL & ALCOCK, 1983; WAAGE, 1984). One reason for their popularity is that dragonflies and damselflies exhibit a wide variety of sexual behavior. For example, some odonates do not mate guard, some species guard while flying near the female and other species guard while remaining in physical contact with the female (CORBET, 1962; UÉDA, 1979; PARR, 1983; WAAGE, 1984). In addition, while many odonate species are territorial, other species do not defend specific areas (CORBET, 1962). Such behavioral variety within one taxon provides an excellent basis for conducting comparative studies (e.g. CORBET, 1962; PARR, 1983; ALCOCK, 1987).

One aspect of odonate sexual behavior that has rarely been the subject of comparative studies is the type of interactions that occur during territorial aggression. Two components of aggressive behavior appear to vary among odonates. First, species differ in whether discrete stages or behaviors exist within territorial contests. Contests of some species have relatively simple structure: residents simply chase

other males away from their territory (e.g. DEBANO, 1993). Other species, however, have distinct types of interactions that occur within a contest (e.g. JACOBS, 1955; PAJUNEN, 1964, 1966; WAAGE, 1988). Second, species differ in whether direct physical contact occurs within a territorial contest. Some species have "physical battles", with participants occasionally coming into direct contact with each other (e.g. MOORE, 1952; PAJUNEN, 1964; PEZALLA, 1979; CAMPANELLA, 1975). The physical contact is rarely extended in these species; although the interactions may include biting and grasping (PAJUNEN, 1964), contact is more usually reported as a clattering of wings as the two males fly against each other. Other odonates have "energetic battles", with participants rarely coming into contact and instead having contests with chases and hovers (e.g. JACOBS, 1955; JOHNSON, 1962; NAKAMUTA et al., 1983; WAAGE, 1988). However, even for those species in which contact does not usually occur, occasional physical contact between males may be observed. For such species, investigating the contexts under which the contact occurred may give us useful insights into the general role of aggressive interactions in the species' sexual behavior. Here, we report a rare but repeatedly observed case of contact between males of *Perithemis tenera*, a species which otherwise has territorial contests in which males do not contact each other.

## GENERAL *PERITHEMIS TENERA* BEHAVIOR

Male *P. tenera* defend small territories around oviposition sites on bodies of still or slow moving water (JACOBS, 1955; SWITZER, 1997a). Males detected by the territory resident are immediately chased (SWITZER & WALTERS, 1999; SWITZER & EASON, 2000). If the intruding male persists, the contest between the resident and intruder has several distinct stages, corresponding to different levels of escalation of the fight (JACOBS, 1955; SWITZER, 1995). Males do not typically come into contact during any part of these contests, with the occasional exception being when one of the males perches on the territory and is detected by the other male; the other male may then slightly "bounce" on the back of the perching male, presumably in an attempt to get it to leave the area.

Females arrive periodically at the breeding area; when a male detects a female he flies out to her and leads her back to his oviposition site (JACOBS, 1955; SWITZER, 1997b). The female may either reject the male and leave his territory or mate with the male. Prior to mating, the female will slow her flying and/or perch, making it easier for the male to grab her. After mating, the male leads the female back to the oviposition site and hovers or perches nearby. Any males detected by this guarding male are immediately and vigorously chased (see also JACOBS, 1955).

## MALE-MALE TANDEMS AND THEIR CONTEXT

We recorded the following observations opportunistically while conducting other observational and experimental studies on *P. tenera*. On 13 occasions (10 at a small pond in east-central Kansas, USA and 3 at small ponds in east-central Illinois, USA; see SWITZER, 1995; SWITZER & WALTERS, 1999; SWITZER & EASON, 2000, for descriptions of the study sites), a male *P. tenera* was observed flying in tandem with another male. The leading male was attached to the back of the head

of the trailing male in a manner that appeared identical to the usual male-female connection that occurs prior to assuming the wheel position while mating. The tandem males never landed; rather, the males slowly flew around within a few meters of the resident's oviposition site (i.e., within his territory). The durations of the tandems were not measured, but the connection was maintained for well over 1 minute in some cases.

On 10 of the 13 occasions, a female was observed to be within the immediate vicinity of the tandem (usually ovipositing). On all 5 occasions in which we were able to distinguish the resident from the intruder, the resident was the leading male in the tandem. On 4 of the 13 occasions, the attachment process was observed by one of us. In each case, the resident was hover guarding the ovipositing female when another male entered the territory and was very close to the female. The resident pounced upon the back of the intruding male, grabbed him behind the head and began flying with him. On 5 of the 6 occasions when the males' behavior following the tandem were recorded, a pursuit flight ensued (i.e. the most escalated form of male-male interaction; JACOBS, 1955).

## INTERPRETATION OF MALE-MALE TANDEMS

Two possible explanations exist for the male-male tandems: misdirected mating attempts and mate guarding. First, residents may be mistaking the intruding male for a female and attempting to mate with him. During courtship, male *P. tenera* have occasionally been observed attempting to copulate with either the wrong areas of a female or with other nearby objects (e.g. flowers of *Potamogeton*); males have also been observed trying (and sometimes succeeding) to grab "unwilling" females (e.g. those that had not slowed down their flying or perched) and attempting to mate with them (JACOBS, 1955; SWITZER, 1995). However, we feel that attempted mating is unlikely to be the explanation for the tandems we observed. The males initiating the tandems were the territory residents and a territory resident exhibits courtship behavior prior to trying to mate, even if another female is already ovipositing at his site (see also JACOBS, 1955). We never observed such courtship behavior prior to a male-male tandem. Furthermore, the lead male did not initiate any behaviors subsequent to grabbing the other male that indicated he was trying to continue the mating process (e.g. landing, etc.). Following a tandem, the pair of males often immediately had an escalated fight, suggesting that the resident was treating the other individual as a male.

Given our observations, the second and more likely explanation for tandems in *P. tenera* is that they represent an opportunistic and potentially escalated form of mate guarding. Thus, the resident is grabbing an intruder that is likely to disturb his female and physically keeping the intruder away from her. The benefit of the tandem to the resident is clear; however, the tandems are also likely to be costly. Even the ordinary mate guarding contests are energetically costly to the resident,

as they tend to occur immediately at the most escalated levels of contest behavior (i.e. pursuit flights), rather than the more incremental escalation that occurs in the absence of a female (SWITZER, 1995). However, residents may incur even more costs from male-male tandems. In a male-male tandem the risk of injury may be greater due to the physical contact with the intruder. Also, the risk of being preyed upon may be greater due to the fact that the males in tandem are very visible and flying relatively slowly. And finally, the risk of losing the female to other males may be greater because residents are probably less able to chase away additional intruders due to being in a tandem. In support of this latter possibility, on one occasion, a third male was observed guarding an ovipositing female while two males were in a tandem, suggesting that the third male had mated with the female while the first two were in tandem. However, the observation of this particular tandem was made too far along in the behavioral sequence to confirm or refute this speculation.

The potentially large risks, in combination with the potential rarity of the appropriate opportunities (e.g. position of the intruder, successfully grabbing the intruder, the female not immediately leaving upon being disturbed by the intruder, etc.), may lead to the rarity of the male-male tandems. Between us, we have conducted well over one thousand hours of observations of *P. tenera* and have only observed this behavior 13 times. However, because we have observed these male--male tandems multiple times and in geographically separated areas, we suggest that under certain conditions, male-male tandems may be an integral component of the aggressive behavior of male *P. tenera*.

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