

# Male-Male Agonistic Behavior and Ant-Mimicry in a Neotropical Richardiid (Diptera: Richardiidae)

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## Abstract

The Richardiidae are acalyptrate dipterans about which very little is known. Here we describe male-male agonistic interactions and test a hypothesis of ant-mimicry in a new richardiid species in the genus *Sepsisoma*. Males of *Sepsisoma* sp. show several ritualized agonistic behaviors, with a clear escalation from simpler to more elaborate displays, which are described here in detail. We could distinguish four (not clearly discrete) behavioral stages during the escalation: Chase, Orientation, Leg display and Body raising. As the displays shifted from simpler to more elaborate, there was also a decrease in their relative frequency. Curiously, small males were by far the most aggressive, and most of their agonisms were directed to large males. The *Sepsisoma* flies in this study show a clear ant-like appearance, particularly resembling the formicine ant *Camponotus crassus*. We conducted laboratory experiments which support this hypothesis, providing the first experimental evidence that ant-like dipterans may deceive a potential predator.

**Keywords:** Richardiidae, lekking behavior, mimicry, myrmecomorphism, *Camponotus*.

The Richardiidae are acalyptrate dipterans about which very little is known (Ferrar, 1987; Steyskal, 1987; Borror et al., 1991). Pie (1998) discovered that the mating strategy of the richardiid *Setellia* sp. is a genuine case of lek polygyny, providing the first detailed behavioral account for the entire family. Here we describe for a new richardiid species in the genus *Sepsisoma* the male-male agonistic interactions and test a hypothesis of ant-mimicry. The species studied here is new and a formal description will be published elsewhere. Voucher specimens have been deposited in the Museu de História Natural of the Universidade Estadual de Campinas, Brazil and in the Museu da Biodiversidade do Cerrado of the

Universidade Federal de Uberlândia, Brazil. The animals used in this study were collected in the cerrado reserve of the 'Clube de Caça e Pesca Itororó de Uberlândia' park in the Municipality of Uberlândia, state of Minas Gerais, Brazil (48°13' W, 18°52'S). This site has a savanna-like vegetation corresponding to the cerrado *sensu stricto* of Goodland (1971). This vegetation is dominated by plants that bear extrafloral nectaries (EFNs), a structure often associated with protective ant-plant mutualisms (see Oliveira & Pie, 1998 for review). Even though ants are by far the most common visitors to EFNs, other animals may also feed on them, such as wasps and flies (see Keeler, 1989; Del-Claro et al., 1996). Indeed, several richardiid fly species may feed on the extrafloral nectar of a variety of plant species (K. Del-Claro & M.R. Pie personal observations).

In November 1998, we encountered several *Sepsisoma* sp. males on a single *Qualea multiflora* shrub (Vochysiaceae). A thorough survey of neighbouring plants, with an emphasis on other *Q. multiflora* shrubs in an area of approximately 50m<sup>2</sup> revealed the following distribution: 9 males were found on the same *Qualea multiflora* shrub, 3 on other neighbouring *Q. multiflora* plants and 1 male on a *Tabebuia aurea* (Bignoniaceae) at 2m from the first *Q. multiflora*. The observation of such a high density of these rare flies in a very limited space, as well as the extreme male-biased sex ratio at the site, led us to hypothesise the existence of a lek mating system in this species. If true, we would expect elaborate and ritualised displays and agonisms during male-male encounters, as occurs in all dipteran lekkingers (see Höglund & Alatalo, 1995 for review).

These animals were brought to the laboratory, where we conducted several experimental tests of these predictions. In each experiment we placed 4 males in an arena built with two glass plates held parallel by a wooden frame (30 cm high,

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30 cm high wide, 10 cm deep). Since we had observed extensive size variation amongst the males (wing length range = 2–5.1 mm,  $\bar{x}$  = 3.6 mm, SD = 1.06), we placed two small males (wing length < 3.1 mm) and two large males (wing length > 3.8 mm) each time. Following a 5 min initiation period, we noted all behaviors performed by the flies ('all occurrence sample,' *sensu* Altmann, 1974) for up to 2 h. The experiments were repeated with different males and each experiment lasted up to 2 h of continual observation.

Consistent with our predictions, males of *Sepsisoma* sp. showed several ritualised agonistic behaviors, with a clear escalation from simpler to more elaborate displays, which are described here in detail. We could distinguish four (not clearly discrete) behavioral stages during the escalation:

*Chase*: this was the simplest agonistic interaction. One male approaches another male – either walking or flying – and then stalks.

*Orientation*: in this stage one or both males stop for a few seconds and orient head-to-head with the opponent, which soon afterward may be stalked or simply walk or fly away.

*Leg display*: after the orientation one or both males begin to extend their first pair of legs (one or both) toward the opponent, and wave them downwards, sometimes touching the opponent male. Also, one male may stalk the opponent or simply fly away.

*Body raising*: the leg display may escalate this elaborate display, where one or both males raise the anterior part of the body, lower the tip of the abdomen, while continuing to wave the front legs. In this stage the wings may be brought backwards.

The body and the wings could assume several different positions, but those behaviors were so variable that it was not clear whether and in which ways they actually played a part in the contest. During all these stages it was common to observe self-grooming. As the displays shifted from the simpler to the more elaborated ones, there was also a decrease in their relative frequency (Fig. 1). Curiously, the small males were by far the most aggressive ones (Fig. 2), performing 38 (80.8%) of the 47 observed interactions. Moreover, most of their agonism was directed at large males (32 out of 38 observed interactions – 84.2%). Furthermore, even though this behavior was not systematically quantified, the small males were clearly more active than the large ones.

The *Sepsisoma* flies in this study show a clear ant-like appearance (myrmecomorphy), particularly in relation to *Camponotus crassus*, an ant species very common in plants bearing EFNs (Fig. 3) (Oliveira & Brandão, 1991). We tested the hypothesis of Batesian ant mimicry by conducting the following experiments: In the same arena described above we placed simultaneously one *Sepsisoma* fly, one *C. crassus* worker, one *Musca domestica* and one salticid spider. We repeated this experiment 5 times without replacement, and each experiment lasted 20 minutes. The spiders consistently avoided contact with the *Sepsisoma* fly in a way similar to

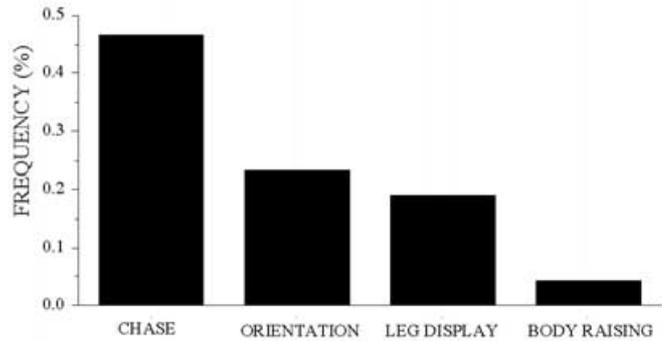


Fig. 1. Relative frequencies of escalation stages during male-male agonistic interactions in *Sepsisoma* sp. (N = 49 observations). See text for more detailed descriptions of the escalation stages.

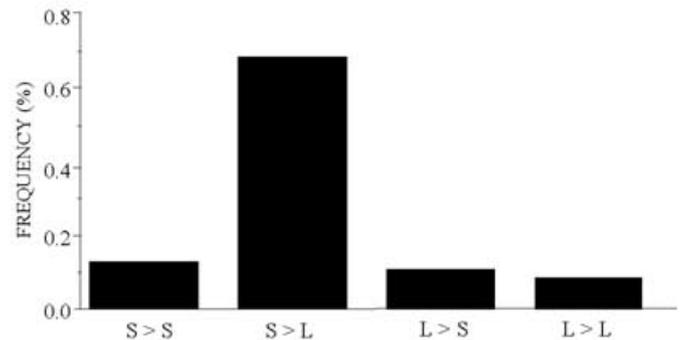


Fig. 2. Frequency of observed agonistic interactions in which (s > s) small males attacked other small males; (s > l) small males attacked large males; (l > s) large males attacked small males; (l > l) large males attacked large males (N = 47 observations).

when they are faced with ants, always avoiding close contact. On the other hand, the spiders attacked and promptly ate the *M. domestica* in four of these experiments. In the remaining experiment the spider pounced on the richardiid, but immediately released it, and did not feed on it later on. When faced either with the spider or the ant, the richardiid constantly moved in such a way that its body was presented in a head-on view, a behavior that was frequently observed in the field.

Myrmecomorphy is considered to be a widespread phenomenon (McIver & Stonedahl, 1993), but most studies on myrmecomorphy (particularly on dipterans) are anecdotal (see McAlpine, 1988; 1990; 1995). The present study provides the first experimental evidence that ant-like dipterans may deceive a potential predator.

Lek behavior is a mating strategy in which: (1) males do not provide any parental care, (2) only a limited portion of the habitat is used as mating encounter site, and (3) males defend exhibition territories, which lack any essential resource to the females (Bradbury, 1985; Thornhill & Alcock, 1983). By this definition, the mating strategy employed by *Sepsisoma* sp. would traditionally be classified not as a lek, but rather as an instance of resource defence polygyny. In fact, *Sepsisoma* sp. adults not only feed on extrafloral nectar, but their larvae do

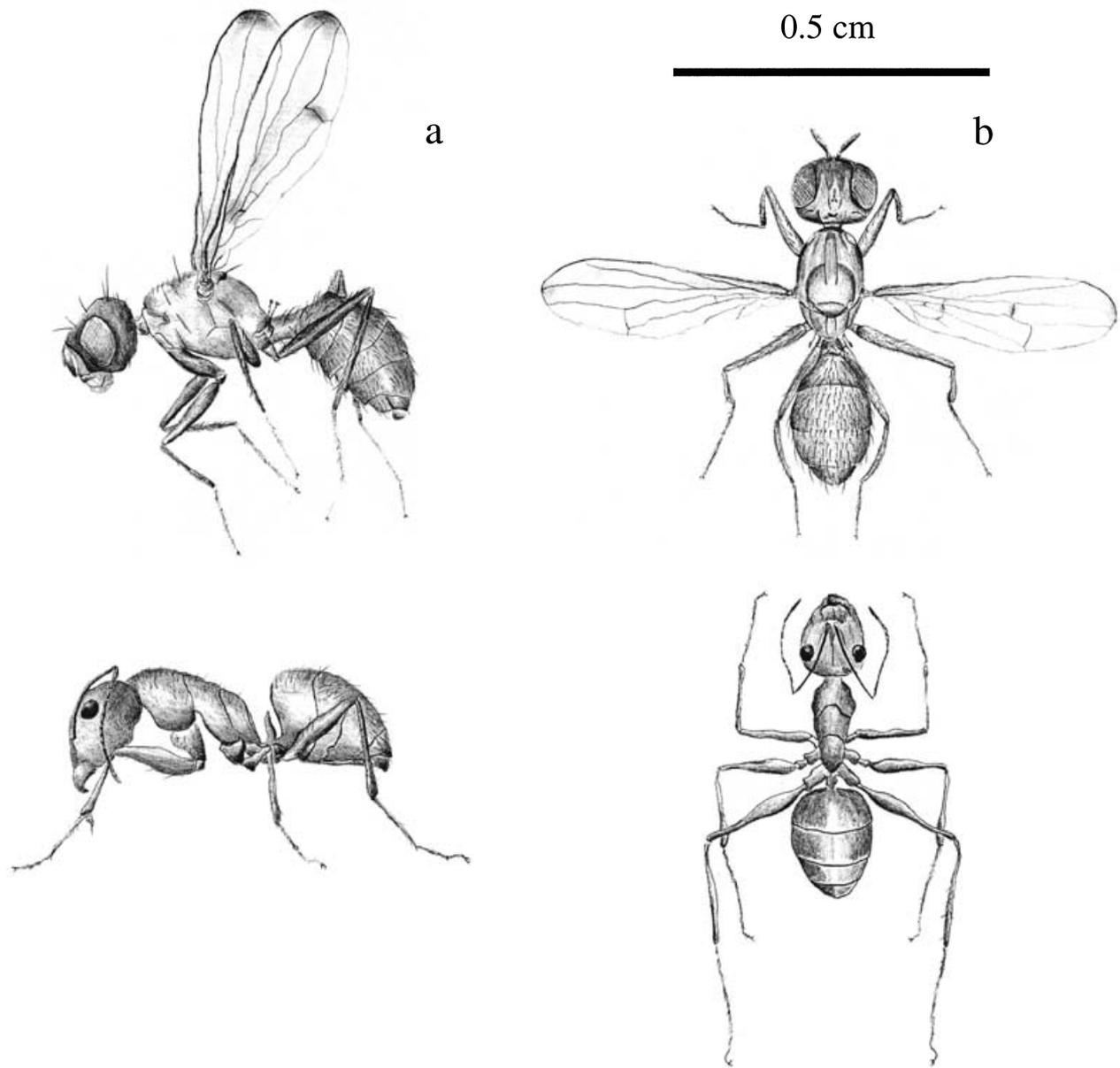


Fig. 3. A male of *Sepsisoma* sp. (A) and its possible model, *Camponotus crassus* (B).

so as well, building a shelter over the EFN with plant material, which may protect larvae against ant attack (Prado, Pie & Del-Claro, pers. observation). Plants bearing EFNs are very common and diverse in the Brazilian cerrados (Oliveira & Brandão, 1991). In fact, 43% of the individual plants in our study area are EFN-bearing plants (Oliveira, 1994). This suggests that extra-floral nectar and nectaries are not themselves a limiting resource for these flies, and in this case the mating system could be classified as lek polygyny (Bradbury, 1985). However, another possibility remains. The distribution of the Batesian model ant, *Camponotus crassus*, is much more restricted spatially than plants bearing EFNs, and therefore plants with *C. crassus* visiting ants could occur in spatially defensible resource patches. Future studies are needed to clarify these hypotheses. If this scenario is true, this richardiid

species has a quite unusual form of complex interaction, involving both ant-plant mutualism and sexual selection.

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