Sexual selection in *Hetaerina titia* males: a possible key species to understand the evolution of pigmentation in calopterygid damselflies (Odonata: Zygoptera)

Alex Córdoba-Aguilar\(^1,2\), Ana C. Lesher-Treviño\(^1\) & Christopher N. Anderson\(^3\)

\(^1\) Departamento de Ecología Evolutiva, Instituto de Ecología, Universidad Nacional Autónoma de México, Circuito Exterior s/n, Apdo. Postal 70-275, México, D.F. 04510, México; \(^3\) University of California at Los Angeles, 621 Charles E. Young Drive, Box 951606, Los Angeles, CA 90095-1606, USA

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**Summary**

*Hetaerina titia* males bear wing pigmentation patterns similar to *Hetaerina* and *Calopteryx* (a derived sister genus of *Hetaerina*) species: black (typical of *Calopteryx*) and red (typical of *Hetaerina*). Sexual selection has operated on red (via male-male competition) and black (via male-male competition and female choice) in *Hetaerina* and *Calopteryx*, respectively. We investigated sexual behavior and pigmentation in *H. titia* to understand their evolution in both genera using *H. titia* as a possible evolutionary transitional stage. Similar to *Calopteryx*, the black pigmentation correlated with five male quality aspects: defending a territory, survival, immune ability, parasite resistance and fat reserves. We hypothesize that black pigmentation, but not red, may be used to signal energetic condition when males compete for a territory.

The red pigmentation, despite indicating male quality in *Hetaerina* species, did not correlate with quality but showed a positive relation with parasite burden. These results suggest that the red lost its function which was gained by the black pigmentation, possibly via intrasexual competition, in the absence of female choice (as *H. titia* does not show male pre-copulatory courtship as in *Calopteryx*, during which females choose males based on black pigmentation). It is unknown why the red pigmentation was retained.

**Keywords:** *Hetaerina titia*, pigmentation, fat reserves, immunity, parasites, Calopterygidae.
Introduction

Sexual selection theory has been extensively applied to calopterygid damselflies in recent years (reviewed by Córdoba-Aguilar & Cordero Rivera, 2005). Males usually compete for the possession of riverine territories which may (e.g., *Calopteryx*; Waage, 1987) or may not (e.g., *Hetaerina*; Alcock, 1987) contain oviposition resources. The defense of a territory is a prerequisite for copulation by females (e.g., Waage, 1973; Conrad & Herman, 1987) although in the *Hetaerina* genus, non-territorial males (i.e., males not able to acquire and/or defend a territory) also gain some copulations (Serrano-Meneses et al., 2007). Territorial competition takes place via ritualized contests in which both contestants face each other in spiralling flights of ascending and descending trajectories (e.g., Waage, 1973; Lefevre & Muehler, 2004). These contests may last from a few seconds to hours and those males that have more muscular thoracic fat are more likely to win (Marden & Waage, 1990; Plaistow & Siva-Jothy, 1996; Koskimäki et al., 2004; Contreras-Garduño et al., 2006; Serrano-Meneses et al., 2007). Another variable that has been shown to be related with contest success is male pigmentation. In most calopterygids, males have wings covered with pigmentation of inter- and intra-specifically variable patterns which at the age of sexual maturation, becomes fixed and does not change anymore (Córdoba-Aguilar & Cordero Rivera, 2005). Studies in the genera *Calopteryx* and *Hetaerina* show that those males with more pigmentation are more likely to win contests or defend a territory (Grether, 1996; Siva-Jothy, 1999; Córdoba-Aguilar, 2002; Contreras-Garduño et al., 2006; Serrano-Meneses et al., 2007). Pigmentation and fat reserves in *H. americana* are, in fact, closely correlated (Contreras-Garduño et al., 2006; Serrano-Meneses et al., 2007). Due to this, wing pigmentation has been hypothesized to communicate the energetic condition to conspecific males during male-male competition (Contreras-Garduño et al., 2006).

Male pigmentation is also inter-sexually selected in this family. In the genus *Calopteryx*, males perform a courtship display in front of the female prior to copulation. During this courtship, the male flutters in front of the female and keeps his posterior wings motionless while the anterior wings sustain flight (e.g., Pajunen, 1966; Heymer, 1973; Waage, 1973; Kumar & Prasad, 1977; Higashi, 1981; Conrad & Herman, 1987; Siva-Jothy, 1999; Córdoba-Aguilar, 2000). Not all courtship events lead to copulation (Waage,