Female Mating History Influences Copulation Behavior but Not Sperm Release in the Orb-Weaving Spider *Tetragnatha versicolor* (Araneae, Tetragnathidae)

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We examined the influence of female mating history on copulation behavior and sperm release in the haplogyne spider Tetragnatha versicolor. Despite significant behavioral differences during mating, males released equivalent amounts of sperm to virgin and non-virgin females. When mating with non-virgin females, males showed twice as many pedipalp insertions and half the copulation duration as compared to virgin females; however, males were as likely to mate with non-virgin as virgin females. Even with these overt behavioral differences, males released half of the sperm contained within their pedipalps during mating, regardless of female mating history. With respect to male mating order, first or second, we suggest the numbers of sperm released would lead to an expectation of unbiased paternity. In this species, sperm release is not directly proportional to total copulation duration.

**KEY WORDS:** sperm competition; sexual selection; arthropod; arachnid.

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INTRODUCTION

For most species, we know little about the relationship between copulation duration and sperm release. Depending on the underlying mechanism of sperm competition, a male’s fertilization success will generally increase as the number of his sperm stored within a female is increased, relative to those of other males (Parker, 1970; Parker et al., 1990). When sperm release is proportional to copulation duration, males that copulate longer have higher fertilization success (Birkhead and Moller, 1998; Simmons, 2001). Yet, copulation may serve functions in addition to the release of sperm, such as courtship (Eberhard, 1996) and implementation of sperm competition avoidance mechanisms (Birkhead and Moller, 1998; Simmons, 2001). Studies that examine the relationship between natural variation in copulation behavior and numbers of sperm released via direct counts are relatively rare (but see Pitnick and Markow, 1994; Cook and Gage, 1995; Markow, 1996; Bukowski and Christenson, 1997; De Jong et al., 1998; Wedell and Cook, 1999; LaMunyon, 2000; Snook and Markow, 2001) and yet quite useful in interpreting the mechanisms underlying paternity patterns (Cook et al., 1997; Simmons and Siva-Jothy, 1998).

We examined copulation duration and male sperm release directly by quantifying the amount of sperm released to virgin and mated females in the orb-weaving spider Tetragnatha versicolor (Walckenaer Tetragnathidae). Spiders are unusual in that they exhibit indirect sperm transfer such that all sperm available for transfer during mating are readily quantifiable. Some species exhibit first-male advantage in paternity, a pattern rarely found in other arthropod taxa, while others exhibit last-male advantage (Lewis and Austad, 1990; Elgar, 1998). Austad (1984) noted that the paternity pattern (first- or last-male priority) is associated with a particular type of female reproductive morphology. Female spiders have sperm storage organs that can be divided into two morphological categories, entelegyne and haplogyne, although not all taxa conform to these types sensu stricto (Wiehle, 1967; Uhl and Vollrath, 1998). Entelegyne taxa typically show first-male advantage (reviewed in Elgar, 1998; Elgar et al., 2000; Schneider et al., 2000; but see Watson, 1990), whereas haplogyne taxa often show last-male advantage (Kaster and Jakob, 1997; Yoward, 1998; West and Toft, 1999; Schafer and Uhl, 2002; but see Eberhard et al., 1993). Austad (1984) proposed that these differences were due to ejaculate stratification within the reproductive tract. Yet, evidence is mounting that, in entelegyne spiders, the relative numbers of sperm released by two males to mate with a female appear to be a primary factor determining the paternity patterns (Christenson, 1990; Suter, 1990; Masumoto, 1993; Andrade, 1996; Bukowski and Christenson, 1997; Elgar et al., 2000; Schneider et al., 2000; Bukowski et al., 2001; but...