



Artificial insemination unveils a first-male fertilization advantage in the guppy



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Several factors are involved in determining the outcome of sperm competition. In addition to sperm number, sperm quality and male phenotype, insemination order is often associated with skewed paternity share. Patterns of sperm precedence can be produced by the mechanics of sperm storage and fertilization, or by active processes under male or female control. However, as males and females always interact during copulation, it is difficult to identify the mechanism responsible. The Trinidadian guppy, *Poecilia reticulata*, is a polyandric species characterized by last-male sperm precedence in natural matings. During such matings, females allow attractive males to inseminate more sperm by controlling copulation duration. We used artificial insemination to clarify the extent to which female control of sperm transfer influences the observed pattern of sperm precedence in this species. This technique allowed us to experimentally manipulate the number of sperm transferred and the timing of insemination. We found a significant first-male fertilization advantage. This advantage, however, declined as the time between insemination and parturition increased. Presumably, the anatomy and the physiology of the female genital tract favour egg fertilization by the first ejaculate inseminated, whereas sperm mixing is likely to be responsible for the reduction in first-male advantage associated with longer insemination–parturition intervals. Our results suggest that the last-male precedence detected after two consecutive natural matings is caused by cryptic female preference for attractive males associated with a female trading-up strategy (i.e. the second male is more frequently more attractive than the first male), rather than by insemination order per se. As the pattern of sperm precedence has important consequences for male reproductive strategies (for example mate guarding and male mate choice copying), unravelling its dynamic represents an important contribution to understanding the sexual behaviour of this model species.

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Sperm competition occurs when a female mates with more than one male during the same reproductive cycle (Parker, 1970). Many factors related to male attractiveness, ejaculate characteristics and male–female genetic compatibility are known to affect paternity patterns under sperm competition (Fitzpatrick & Lüpold, 2014). Studies covering several animal groups with internal fertilization have shown that insemination order is often involved as well, with fertilization success biased in favour of either the first or the last mate (Birkhead & Hunter, 1990). Such patterns of sperm precedence

(SP) have important implications for male postcopulatory success, as they influence, in turn, both male and female precopulatory strategies for increasing reproductive success and avoiding the costs of mating (Birkhead & Hunter, 1990). For example, last-male precedence (LMP) is usually associated with mate guarding and prolonged copulation (Parker, 1970), whereas first-male precedence (FMP) can lead to the evolution of a strong male preference for virgin females (Eberhard, Guzmán-Gómez, & Catley, 1993) and eventually to extreme male strategies such as traumatic inseminations observed in bed bugs, *Cimex lectularius* (Stutt & Siva-Jothy, 2001) and patrolling for about-to-emerge females in Dawson's burrowing bees, *Amegilla dawsoni* (Houston, 1991). In polyandrous species, SP is therefore crucial to understand the adaptive value of mating system dynamics in the two sexes.

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LMP is observed in most insects and birds (Birkhead, 1987; Danielsson, 1998; Parker, 1970; Simmons, 2001). In contrast, FMP is less widespread (e.g. Birkhead & Pringle, 1986; Elagoze, Poirie, & Periquet, 1995; Jones, Adams, & Arnold, 2002), but seems extremely common in spiders (Austad, 1984; Uhl, 2002). In other taxa, such as mammals, where sperm usually remain viable in female reproductive tracts for a very short time (Ginsberg & Huck, 1989), there are no general sperm precedence patterns and male fertilization success therefore largely results from the interaction between mating time/order and timing of ovulation (Birkhead & Hunter, 1990). The influence of insemination order on paternity shares is a subject that has been largely neglected in internal fertilizing fishes, with the only exception of guppies, *Poecilia reticulata* (Evans & Magurran, 2001; Neff & Wahl, 2004; Pitcher, Neff, Rodd, & Rowe, 2003).

Patterns of SP, related to insemination order, can result from different mechanisms, often interacting with one another to produce the fertilization outcome. The patterns of SP are determined by the interaction between the ejaculate and the female reproductive tracts and sperm storage organs (Walker, 1980), and are often linked to female anatomy. For example, FMP can be produced by mechanical constraints when one male's ejaculate serves as a physical impediment and limits sperm transfer by subsequent males, or when the ejaculates stratify and the first sperm to enter are in a more advantageous position for subsequent fertilizations ('first in, first out'; Austad, 1982; Uhl, 2002). Alternatively, first males can also bias paternity in their favour by placing mating plugs in the female genital openings and thus preventing or limiting the efficiency of subsequent inseminations (Masumoto, 1993; Parker, 1970). Finally, first-male advantage can result from active processes under female control, when females get most of their sperm stores from the first mate, and then 'top off' their storage organs with smaller quantities of sperm from additional mates (Jones et al., 2002). Similarly, LMP may result from different processes. LMP is typically observed when ejaculates form layers within the female sperm storage organs and the uppermost layer, derived from the last copulation, is in a favoured position to fertilize eggs ('last in, first out'; Birkhead & Hunter, 1990). In this case, last-male advantage may decrease with the time elapsed between insemination and fertilization, as a result of sperm mixing. LMP may also derive from the gradual loss of sperm from the female reproductive tract over time ('passive sperm loss'). Because of such loss, the proportion of the initial number of sperm stored after a copulation will progressively decrease with time and, if males transfer ejaculates of similar size, the first male will be disadvantaged (Lessells & Birkhead, 1990). In this case, last-male advantage will increase with the time elapsed since the previous copulations. 'Sperm senescence' can produce the same pattern: when successive inseminations occur, sperm from the first male will be older than those from subsequent copulations and may thus have reduced competitive fertilizing potential (Snook & Hosken, 2004; Tsubaki & Yamagishi, 1991; Winge, 1937). It has also been proposed that last males may take advantage of the prior 'buffering' of the hostile environment of the female reproductive tract by previous males' ejaculates, which could reduce their sperm mortality (Hodgson & Hosken, 2006). Alternatively, sperm can be displaced from the female reproductive tract by the 'flushing out' of one ejaculate by a subsequent one, or through an active removal operated by the last male during copulation (Birkhead & Hunter, 1990). Indeed, males of several species have evolved copulatory organs provided with specialized structures to scoop or brush out previously stored sperm (Cordero-Rivera, 2016; Waage, 1979; Wada, Takegaki, Mori, & Natsukari, 2005). LMP may also derive from the incapacitation of competitor's sperm when the seminal fluid from the most recent copulation interferes with the survival or fertilization capability of

previously stored sperm (den Boer, Baer, & Boomsma, 2010). Finally, cryptic choice allows females to influence the outcome of sperm competition by favouring one male's sperm over another's both through differential discharge (Pizzari & Birkhead, 2000; Snook & Hosken, 2004) and transport to storage and fertilization sites (Bloch Qazi, Aprille, & Lewis, 1998; Tregenza & Wedell, 2002; and for recent reviews on cryptic female choice mechanisms see Firman, Gasparini, Manier, & Pizzari, 2017; Peretti & Aisenberg, 2015). When cryptic female choice is concordant with mate choice (i.e. it favours attractive males also at the postmating level, Pizzari & Birkhead, 2000), it may obscure otherwise expected sperm precedence patterns, for example by masking the effect of passive sperm loss from the female sperm storage organs or the senescence of stored sperm, or may itself generate a sperm precedence pattern, for example when matings with the most attractive males occur more frequently in a given order (Pitcher et al., 2003).

Understanding which mechanisms are responsible for the pattern of sperm precedence observed in a species is not straightforward: recognizing interactions of the ejaculate with the female reproductive tract or discriminating between male and female influence is complicated by the fact that they interact during copulation and several mechanisms often occur simultaneously (Manier et al., 2013). The use of artificial insemination can represent a useful tool to overcome this issue: by excluding male–female behavioural interactions before and during copulation, it has the power to highlight processes related to the mechanics of storage and fertilization. Furthermore, it allows the experimental manipulation of the number of sperm transferred and the temporal pattern of insemination (Bonnier & Trulsson, 1939), thus controlling for adjustments of male sperm allocation and female ejaculate manipulation influenced, for example, by male phenotype or the sociosexual context (Ala-Honkola & Manier, 2016; Kelly & Jennions, 2011; Pizzari & Birkhead, 2000). Successfully performed for the first time in the late 1700s on a bitch by Lazzaro Spallanzani (Foote, 2002), artificial insemination has been largely developed for the animal breeding industry first (bees, Watson, 1928; cattle, Salisbury & VanDemark, 1961; poultry, Bonnier & Trulsson, 1939; Lake & Stewart, 1978) and for conservation biology later (e.g. peregrine falcon, *Falco peregrinus*, Blanco, Wildt, Hofle, Voelker, & Donoghue, 2009; giant panda, *Ailuropoda melanoleuca*, Masui et al., 1989; chimpanzee, *Pan troglodytes*, Matsubayashi, Kumazaki, & Kamanaka, 1985), and is now performed on species as different as insects (Baer & Schmid-Hempel, 2000; Davis, 1965), garter snakes, *Thamnophis marcianus* (Quinn, Blasedel, & Platz, 1989), skates, *Raja eglanteria* (Luer, Walsh, Bodine, & Wyffels, 2007) and hamsters, *Mesocricetus auratus* (Smith, Koyanagi, & Yanagimachi, 1987). Artificial insemination has also been used to study sperm competition, for example in mice (Musialek, 1969), birds (Bonnier & Trulsson, 1939; Brillard & Bakst, 1990) and poeciliid fishes (Clark, 1950; Evans, Zane, Francescato, & Pilastro, 2003; Gasparini, Simmons, Beveridge, & Evans, 2010; Lodi, 1981), and it has been decisive in understanding the effect of insemination order on competitive fertilization success, in the domestic fowl, *Gallus gallus* (Birkhead, Wishart, & Biggins, 1995; Compton, Van Krey, & Siegel, 1978), the mallard, *Anas platyrhynchos* (Cheng, Burns, & McKinney, 1983), and the honeybee, *Apis mellifera* (Moritz, 1986). In these species, artificial insemination has produced the same patterns of sperm precedence as those from natural copulations, suggesting that they are determined by mechanics of sperm storage and fertilization rather than female behaviours.

Guppies are small, freshwater, live-bearing, internally fertilizing fish native to Venezuela and Trinidad (Magurran, 2005). Females show a mating preference for males with high courtship display rates and large areas of orange coloration (Houde, 1997). Female

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