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Short communication

Experimental manipulation of male behaviour during copulation in *Stenomacra marginella* (Heteroptera: Largidae): Effect on copula duration, female remating and oviposition

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Abstract

Apparently stimulatory male copulatory behaviour (MCB) is widespread among arthropods and it could help males to increase their fitness by inducing favourable behavioural and physiological changes in females. The empirical study of female responses to MCB is hindered because its experimental manipulation is difficult. We have developed a technique for reducing, with minimal disturbance, the frequency of MCB in the true bug *Stenomacra marginella*. Here, we test the idea that, in a polygamous species like *S. marginella*, sexual selection favours males whose MCB induces females to increase copula duration (thereby increasing the amount of sperm and accessory substances transferred), reduce their sexual receptivity to additional males and increase their rate of oviposition. Males prevented from performing MCB increased their rate of attempts to perform MCB. Copulations with previously mated females were of longer duration than those with virgin females, probably as a male adaptation for sperm competition, and MCB could have played a role in inducing this effect. Partial or total experimental reduction of MCB frequency had no effect on remating rates, because most females accepted remating at the first opportunity (1 day after their first copula). The probability of egg laying was reduced in females whose first mate was partially prevented from performing copulatory courtship, but not in females whose first mate was completely prevented from performing copulatory courtship. This is an intriguing result and further experiments are needed to understand its causes. We hypothesize that MCB evolved as a result of sexual selection.

Keywords: Antagonistic seduction; Copula duration; Copulatory courtship; Cryptic choice; Female receptivity; Oviposition

1. Introduction

Males of many species perform stereotyped, repetitive behaviours during copulation that appear to be designed to stimulate females (we called this behaviour "apparently stimulatory male copulatory behaviour" or MCB). There are two evolutionary explanations for this type of behaviour. According to the first hypothesis, MCB is "copulatory courtship" evolved in response to post-copulatory ("cryptic") female choice (Eberhard, 1991, 1994, 1996). This hypothesis proposes that females assess males through their copulatory courtship performance and use this information to adaptively allocate paternity among males through differential physiological (e.g., rate of egg maturation and oviposition) and behavioural (e.g., remating rate) responses (Eberhard, 1996; Tallamy et al., 2003). The alternative interpretation of MCB is derived from the chase-away model of sexual selection (Holland and Rice, 1998). According to this hypothesis, MCB is a form of "antagonistic seduction" used by males to manipulate the reproductive physiology and behaviour of females to the benefit of the males themselves and to the detriment of the females. According to this explanation, the allocation of offspring among males (achieved also through differential physiological and behavioural responses) is not adaptive from the female point of view and entails direct fitness costs. Both explanations assume female polyandry and, therefore, sperm competition.

Despite their fundamental differences (Cordero and Eberhard, 2003; Pizzari and Snook, 2003), both hypotheses are based on the idea that female physiology and behaviour are affected by MCB. Although there is abundant indirect evi-

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Fig. 1. *Stenomacra marginella* copulatory behaviour. (a) Pair in the "tail to tail" mating position (male to the left). (b) The male is turning to the right previous to an MCB (male behaviour during copulation apparently aimed to stimulate the female) act; the white arrow indicates the (out of focus) right rear leg raised, typical of this situation (male to the right). (c) Male embracing the female in a MCB act during which he rubs her whole body with his legs and antenna (male to the right).

dence supporting this assumption (Eberhard, 1996; Shuker et al., 2002), in few species MCB has been manipulated and female responses measured (Córdoba-Aguilar, 2000; Edvarsson and Arnqvist, 2000, 2005; Hoikkala et al., 2000; Tallamy et al., 2003; King and Fischer, 2005). This scarcity of studies probably results from the fact that experimental manipulation of MCB is usually very difficult.

In the true bug *Stenomacra marginella*, males perform behaviours during copulation that fulfill the criteria for putative copulatory courtship proposed by (Eberhard, 1991, 1994, 1996); we suggest that similar criteria also apply to male behaviours designed for antagonistic seduction. Sometimes during copulation, when the couple is in the typical "tail to tail" mating position (Fig. 1a), the male raises one of his rear legs and begins to turn towards the female (Fig. 1b). When the male reaches the female, during several seconds he rubs the dorsal and lateral parts of her body and head with his legs, antenna and sometimes the ventral part of his body (Fig. 1c), and then returns to the "tail to tail" mating position. Males perform this behaviour a variable number of times during copulation (see "Control" in Table 1). In

Table 1
Variables measured in experimental females; median [$Q_{25\%}$–$Q_{75\%}$] (sample size) are given in each cell

	"Control"	"Partial Interruption of MCB"	"No MCB"
Duration of first copula (s)	5739.5 [3587–9277.5] (n = 12)	5555.5 [4737–6088] (n = 10)	4728.0 [4127–5969] (n = 13)
Duration of second copula (s)	13950.0 [9988–16333] (n = 9)	15937.0 [12204–24334] (n = 7)	8140.0 [5490–22004] (n = 11)
Days between second copula and oviposition	10.5 [6.5–16] (n = 8)	–	7 [5–10] (n = 6)
Number of eggs laid	30.5 [24–42.5] (n = 8)	0 (n = 8)	32.5 [22–39] (n = 6)
Percentage of eggs hatching	89.5 [79.6–100] (n = 8)	–	96.2 [63.6–100] (n = 6)
Number of MCB acts in first copula	18.5 [12–32.5] (n = 12)	18.5 [14–28] (n = 10)	–
Number of MCB acts in second copula	29 [17–30] (n = 9)	36.5 [13.5–58.5] (n = 8)	19 [11–32] (n = 11)

MCB, apparently stimulatory male copulatory behaviour; "Control" group, females whose first mate was allowed to perform MCB ad libitum; "Partial Interruption of MCB" treatment, females whose first mate's MCB was partially prevented; "No MCB" treatment, females whose first mate's MCB was totally prevented. None of the "Partial Interruption of MCB" females laid eggs.