



Effect of mating history on gender preference in the hermaphroditic snail *Physa acuta*

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Several internally fertilizing hermaphroditic animals can only perform one sexual role at a time. In such species, two individuals that engage in a copulation may have different interests in acting as male or female. A gender choice must be made which, if both individuals have the same preference, may give rise to a severe sexual conflict. Here we tested the hypothesis that gender choice could be influenced by mating history, using the freshwater snail, *Physa acuta*. We recorded the copulatory behaviour of 240 pairs composed of a focal individual and a partner, each either short- or long-isolated. We found that the time to the first copulation was unaffected by isolation status, suggesting that first contacts in this species are random processes. In contrast, the duration of copulations and the frequency of rejection behaviours suggested that individual gender preference switches from male biased to female biased as isolation increases. In addition, snails rejected copulations more frequently when presented to a partner with the same isolation status. Reciprocity, measured as the rate of gender swapping between the first and second copulations, was high irrespective of gender status. We suggest possible evolutionary causes for this gender preference switch and discuss its potential importance in natural population as well as its consequences for the maintenance of hermaphroditism.

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Hermaphroditic animals have long been considered as unaffected by sexual selection (Anderson 1994). Initially, these organisms were thought to have too low perceptual and cognitive abilities to show proper sexual preferences (Darwin 1871). More recently, it has been argued that the occurrence of both sexes within each individual may limit sexual selection for traits involved in mate choice (Greeff & Michiels 1999). However, hermaphroditic animals with internal fertilization show an impressive variety of sexual traits and behaviours such as penis chewing in *Ariolimax* (Leonard et al. 2002) or dart shooting in some

terrestrial snails (Pomiankowski & Reguera 2001; Schilthuisen 2005). These numerous and diverse reproductive features suggest that sexual selection does play a key role in the evolution of hermaphroditic mating systems (Schilthuisen 2005; Leonard 2006).

In species with separate sexes, sexual selection is driven by the conflicting interests of males and females. Gender role being fixed, it is not a source of conflict in these species. In contrast, when two hermaphroditic animals engage in a copulation, each of them may have an interest in acting as a male (donate autosperm), as a female (receive allosperm) or both. A gender choice must thus be made (Wethington & Dillon 1996). Models of sexual conflicts in hermaphrodites predict that there should be a preferred gender role (Bateman 1948; Charnov 1979; Michiels 1998). Because the male function (producing sperm) is thought to be energetically cheaper than the female one (producing ovules) (Locher & Baur 2000), the preferred gender should be male (Bateman's principle, Bateman 1948; Charnov 1979). In a theoretical paper,

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however, Greeff & Michiels (1999) have recently emphasized that acting as a female is not necessarily more costly than acting as a male notably in species with multiple mating and sperm digestion. Moreover, because of sperm competition and cryptic sperm selection, the variance in reproductive success is lower in females than in males. The preferred gender role may thus be female in a number of species (Gillespie's principle, Leonard & Lukowiak 1991; Leonard 1999). Although reaching opposite conclusions, these theories agree that in a given hermaphroditic species, one gender role should consistently be preferred over the other, thereby providing frequent opportunities for sexual conflict.

Recent empirical studies, however, suggest that there is not a consistently preferred gender role. Gender preference may even change within an individual during the course of a mating session as shown in *Navanax inermis* (Michiels et al. 2003). Various factors may affect the preferred gender role. First is body size (DeWitt 1991; Gianguzza et al. 2004; Ohbayashi-Hodoki et al. 2004), where bigger individuals usually prefer being female (Petersen & Fischer 1996; Angeloni & Bradbury 1999; Schärer & Wedekind 2001). Partner availability has also been shown to generate biases in gender allocation (Trouvé et al. 1999; Tan et al. 2004; Schärer et al. 2005; Schleicherova et al. 2006). There is also growing evidence that the time between two copulations (hereafter isolation time) may influence gender preference (Van Duivenboden & Ter Maat 1985; Wethington & Dillon 1996). It is commonly argued that the probability of initiating a copulation as a male increases with isolation time presumably because of the subsequent increase in stored autosperm (Van Duivenboden & Ter Maat 1985; Wethington & Dillon 1996; De Boer et al. 1997; Locher & Baur 1999; Michiels et al. 2003). Because females may pay minimal energetic costs during copulations and may benefit from sperm and seminal fluid digestion (Greeff & Michiels 1999), they are thought to be always receptive (Van Duivenboden & Ter Maat 1985; Wethington & Dillon 1996). These results were, however, obtained over short-isolation periods (a few days). It is questionable whether autosperm levels continue to increase with time over longer periods (Wethington & Dillon 1996). Moreover, in species where inbreeding depression is strong (and thus self-fertilization should be avoided), female receptivity is expected to be negatively correlated with isolation time (Wethington & Dillon 1996; Tan et al. 2004). Individuals isolated for long enough to lack allosperm should thus prefer the female role, until their allosperm store is replenished.

In the present paper, we study the hypothesis that isolation time influences gender preferences over long periods using the hermaphroditic snail, *Physa acuta*. We experimentally test the two predictions of this 'isolation-time' hypothesis. (1) As suggested by previous studies, individuals isolated for a few days should prefer the male role since their store of allosperm is not yet depleted and their store of autosperm should have been replenished. In contrast, individuals isolated for longer, should lack allosperm and thus prefer the female role. (2) If gender preference correlates with isolation time, then two individuals

that experienced the same isolation time should share the same gender preference. Conflicts should therefore be more intense between two individuals that have experienced the same isolation time than between two individuals with different isolation times.

METHODS

Species Studied

Physa acuta is a simultaneous and internally fertilizing hermaphroditic freshwater snail (Basommatophora) with a sperm storage organ (Paraense & Pointier 2003). Although self-fertilization is possible, it prefers outcrossing with selfing rates generally lower than 0.1 in natural populations (Jarne et al. 2000; Bousset et al. 2004). Large self-fertilization depression was detected in laboratory conditions (up to 0.9 over a full life cycle, Jarne et al. 2000). As in all Basommatophoran pulmonates, only one gender role can be performed at a time (Wethington & Dillon 1996). Gender roles can easily be distinguished. As in other closely related species (Van Duivenboden & Ter Maat 1985; DeWitt 1991), a typical copulation involves (1) approach and climbing onto the shell of an intended female by a male role snail, (2) crawling to the 'female' gonophore, (3) preputium eversion for intromission (copulations may last up to 30 min), and (4) dismounting (Wethington & Dillon 1996; Ohbayashi-Hodoki et al. 2004; Facon et al. 2006). Moreover, when acting as females, individuals can display rejection behaviours such as shell swinging and phallus biting (Wethington & Dillon 1996; Ohbayashi-Hodoki et al. 2004; Facon et al. 2006).

Rearing Protocol

Twenty mature individuals (G_0) were sampled in an irrigation canal in Ecublens (46°31'N, 6°32'E; Switzerland), brought back to the laboratory, and isolated in 75-ml plastic boxes filled with water. As body size and age may influence the mating behaviour of *P. acuta* (Ohbayashi-Hodoki et al. 2004), we collected clutches only during the first 2 days in the lab to obtain G_1 offspring similar with respect to age and size. Two weeks later, 24 G_1 offspring per G_0 individuals (20 families) were each isolated in 75-ml plastic boxes for 5 more weeks. After this period, individuals were allowed to mate freely as males and females, so as to avoid any bias due to reproductive history. To this purpose, G_1 juveniles from different families were mixed in boxes of 20 individuals (one individual per family) during 2 weeks, after being marked with gouache paint previously shown to be harmless (Henry et al. 2003). *Physa acuta* reaches female maturity around 5 weeks (Tsitrone et al. 2003) after passing a short male stage ('slight protandry'; Wethington & Dillon 1993). Since individuals in this experiment are 9 weeks old, they should have received allosperm from one or more partners. The 24 G_1 juveniles of each family were then randomly assigned to one of the two treatments (Fig. 1): (1) 30 days of complete isolation (LI for long-isolation; 12 individuals/family), and (2) 24 days during

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