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Male penile propulsion into spiraled spermathecal ducts of female chrysomelid beetles: A numerical simulation approach

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HIGHLIGHTS

- Penial propulsion velocity and energy depend on female ducts shapes.
- The velocity dependence on the female duct spirals radius has a sigmoidal shape.
- The smaller the radius of the spiral, the lower the penile propulsion velocity.
- Reversal turns of the female duct results in higher penial propulsion velocity.
- But propagation on the reversals requires higher energy expenditure by males.

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ABSTRACT

Genital diversification in animals is an interesting evolutionary phenomenon. Sexual selection is the main driving force behind the diversification. However, evolutionary mechanisms that have established and maintained variations in genitalia shape parameters observed in related species are not well understood. Here, for the first time, we used numerical simulations to test the hypothesis that variations in female spermathecal duct shapes among related beetle species mechanically interfere with penile propulsion in varying ways. Our numerical simulations showed that high curvature of the spiraled spermathecal ducts of the female have effects with a threshold-based interaction on male penile insertion. The relative size of spirals observed in the beetle, *Cassida rubiginosa*, studied here is not small enough to interfere with penile propulsion. But the model revealed that propulsion is impeded by the presence of reverse turns in spermathecal ducts. This type of morphology leads to an increase in the velocity of the propulsion but also to an increase in the propulsion energy cost for males. Our results showed that quantitative differences in spermathecal duct shape can mediate qualitative differences in penile motion. This explains, in part, the mechanism behind origin and maintenance of genital divergence among closely related species in general.

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1. Introduction

Morphology of male genitalia in animals is extremely diverse, and much research has been devoted to understanding evolutionary reasons behind this phenomenon (e.g., Eberhard, 1985, 1996, 2010; Schapiro and Porter, 1989; Arnqvist et al., 1997; Eberhard et al., 1998; Hosken and Stockley, 2004; Joly and Schmitt, 2010; Simmons, 2014; Dougherty et al., 2015). In contrast to male genitalia, the shape of female genitalia had generally been regarded as more conservative and their role in the process of sexual selection is largely ignored (Ah-King et al., 2014). However, the

female genitalia is now regarded as more diverse than previously thought and co-evolutionary patterns or responses between male and female genitalia have recently been reported in many animals (e.g., Ilango and Lane, 2000; Rodriguez et al., 2004; Brennan et al., 2007; Evans et al., 2011; Macagno et al., 2011; Simmons and Garcia-Gonzalez, 2011; Burns et al., 2013; Matsumura et al., 2014).

Several comprehensive comparative approaches have shown that sexual selection is the primary driving force behind the structural diversification of genitalia (Eberhard, 1985; Arnqvist, 1998). Empirical studies, mainly performed on insects, have shown that genital shape variation within species is related to male reproductive success or reduced female reproductive costs (e.g., Arnqvist and Rowe, 1995; Rodriguez, 1995a; Arnqvist and Danielsson, 1999; Cordoba-Aguilar, 2005; Holwell et al., 2009;

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Simmons et al., 2009; Lieshout and Elgar, 2010; Sakurai et al., 2012; Simmons, 2014). However, the reasons for how remarkable quantitative differences in the genital shape have evolved and been maintained in related species are unclear. Moreover, the mechanisms of how these differences affect mating strategy in each sex is unknown as the information on functional morphology and biomechanics of genital variations is very limited.

Leaf beetles in the subfamily Cassidinae (Fig. 1a) are an appropriate model organism for studying genital evolution. Because genitalia of both sexes are highly sclerotized and have relatively simple morphology, morphological variations between sexes in their presumably co-diverged structures (Rodriguez et al., 2004) can easily be quantified. Females have a spiraled, well-sclerotized spermathecal duct that connects the vagina (bursa copulatrix) to the female sperm receptacle organ (spermatheca) (Fig. 1b–d). In the spiral duct, reverse turns (herein referred to as knots) are present. Males have a narrow, hyper-elongated flagellum (part of the intromittent organs), which is inserted into the female spermathecal duct during mating to transfer sperm (Rodriguez et al., 2004). Co-evolution of the male flagellum and female duct lengths has been suggested based on comparative morphological data (Rodriguez et al., 2004). Considerable quantitative variability in spiral features (such as its diameter, length and the number and size of coiled reverse turns) has been used as a

distinguishing characteristic in taxonomic studies (Bordy and Doguet, 1987; Borowiec and Skuza, 2004; Chaboo, 2007; Borowiec and Pomorska, 2009; Rodriguez et al., 2004; Suenaga, 2013). Moreover, empirical data have recently demonstrated that female genital spirals in a waterfowl that do not match the chirality of the spiraled penis interfere with penile propulsion (Brennan et al., 2010). Based on this information, we hypothesized that the structural diversity of female genitalia reflects strategic differences in male–female interference mechanisms during mating.

Testing this hypothesis requires evaluation of functional and mechanical differences in female genital shape and their effects on copulation, which is very difficult or even impossible to assess experimentally. For this reason numerical modeling of mechanical interactions between male penis and female genitalia was used in the present study. To compare with the beetles, we also assessed genital features of the cassidine beetle species, *Cassida rubiginosa*. To evaluate whether variations of female spiral shapes affect male penile propulsion, the propulsion “velocity and energy spent by the male” were used as measures of effectivity in penile insertion. The following questions were addressed. (1) Do spermathecal duct spirals and/or their knots influence propulsion of male flagellum? (2) Do quantitative differences in the morphology of female spirals have different functional effects?



Fig. 1. Variability of the spermathecal duct structure in representatives of Cassidinae and Lamprosomatinae. (a–d) *Cassida rubiginosa* (Cassidinae); (e) *Cassidavirvex* (Cassidinae); (f) *Oomorphoides cupreatus* (Lamprosomatinae). (a) a pair of *C. rubiginosa*; (b, e, f) spermatheca; (c, d) spermathecal duct from different individuals. BC: bursa copulatrix; SpC: spermathecal capsule; SpD: spermathecal duct; SpGI: spermathecal gland; SpM: spermathecal muscles. Scales: b, e, f: 500 μ m; c, d: 200 μ m.

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