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Plasticity of male mating behaviour in a marine bioluminescent ostracod in both time and space

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Spectacular and abundant light displays consisting of highly complex and repeated vertical trains of secreted bioluminescent pulses are ejected into the water column above shallow grass beds in the western Caribbean about an hour after the sun sets if there is no moon present. These are male courtship displays produced by upwardly swimming male *Photeros* (formerly *Vargula*) *annecohenae*, small (<2 mm) myodocopid ostracod crustaceans, attempting to attract females, which approach males while remaining photically quiescent. Observations in both the laboratory and the field revealed different behaviours by males during the courtship period. Using infrared videography in the laboratory to track individuals, we observed distinct male mating behaviours from multiple males in a single tank. Each participating male is capable of (1) 'initiating' a luminescent display train (~leaders), (2) 'entraining' on another displaying male in loose luminescent synchrony (~followers), and (3) 'sneaking' silently on a luminescing male. Males can switch among these three tactics even during a single, 10–19 pulse display train (ca. 12 s). The alternative mating tactic chosen by a male is highly predicted by the orientation and distance of the responding male to the initial courtship display at the start of that tactic. Thus, the complex interplay of these different tactics among a group of males even during a single display train is highly choreographed in both time and space. The mating tactics of *P. annecohenae* are an extreme example of plastic, neuronally controlled courtship behaviour and provide rich new avenues for investigations into understanding communal sexual displays and sexual selection.

Mating systems in animals are diverse and often highly complex. Analyses of these diverse systems have provided significant understanding of the underlying mechanisms. The standard paradigm posits that mating systems that involve any kind of precopulatory behavioural interactions will involve sexual selection that should lead to male–male competition and female choice (Andersson 1994; Shuster & Wade 2003). Male–male competition has been demonstrated to have generated a wide variety of alternative mating tactics among males including, morphological and/or behavioural differences between males. Communal sexual displays, which are shown by many animals, provide a rich arena for examining both proximate and ultimate drivers of mate choice and sexual selection (Bradbury & Vehrencamp 1998; Greenfield 2005). There is a substantial literature that particularly focuses on insects, anurans and fireflies (Greenfield 2002; Lewis & Cratsley 2008; Schwartz & Freeberg 2008).

In addition to these well-studied systems, there is a species-rich clade of ostracod crustaceans from the Caribbean that produce communal, species-specific luminescent courtship displays. While detailed experiments on male–female and male–male interactions are only beginning, they promise to be an excellent system for answering basic sexual selection questions. Although numerous studies have been published on the basic signalling patterns, systematics, phylogeny, morphology and ecology of this group of ostracods (Morin 1986; Morin & Cohen 1991; Cohen & Morin 1993, 2003; Gerrish et al. 2009; and references therein), the present paper is the second in a series that begins to tease apart the details of the signal patterns and their intra- and intersexual interactions (see also Rivers 2007; Rivers & Morin 2008).

Phenotypic plasticity describes the ability of an organism to adapt to changing environments within its lifetime. Although most associate this term in the physical or structural sense (such as change in shell morphology as a function of wave action in a coastal shoreline; e.g. Etter 1989), it is equally applicable to behavioural changes. Rapid switching between discrete behavioural phenotypes is expected when the environment is highly variable within an individual organism's lifetime, with different situations favouring different behaviours (Levins 1968; Shuster & Wade 2003). In mating systems where both female choice is possible and male–male

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competition is high, alternative mating behavioural tactics are common (Andersson 1994; Gross 1996; Shuster & Wade 2003). Here, we define 'tactics' as behaviours that can potentially be shown by all males in a population (i.e. are plastic and may vary depending on the circumstances), while 'strategies' are considered immutable for the individual and show distinct genetic conditions (i.e. a particular trait) (for discussion, see Gross 1996; Shuster & Wade 2003). The reversibility between alternative tactics is hypothesized to be highest when these tactics are under neuronal control, rather than hormonal or developmental control, as has been described in a variety of mating systems including scorpionflies, frogs and toads (Thornhill 1981; Sullivan 1983; Howard 1984; see Shuster & Wade 2003). Alternative male mating tactics can include sneaking, satellites on territorial individuals, competing calls (such as synchronizing with or alternating on an already displaying male) and female mimicry (Gross 1996; Shuster & Wade 2003). In addition to neuronal control, one would expect a high rate of plasticity when the male's condition or competitive situation varies on short timescales (Shuster & Wade 2003). The timescale of most previously described mating systems where males 'rapidly' switch between tactics is usually on the order of minutes, hours or days (Perrill et al. 1978; Hadad 1991; Höbel & Gerhardt 2007). Alternatively, in situations where all males are actively participating in calling or displaying, individual tactic changes may involve a follower (an individual that starts displaying only after another individual initiates a display) becoming a leader (an individual that initiates a display before other nearby males) in subsequent bouts (Greenfield 2005), or the dominant/calling male being temporarily or permanently removed from the courtship setting (such as by successfully mating with a receptive female or being eaten), thus opening up the opportunity for a previous sneaker or satellite male to start calling, such as in green treefrogs (Perrill et al. 1978, 1982).

The marine ostracod *Photeros annecohenae* (Crustacea: Ostracoda, Myodocopa, Cypridinidae) is found in great abundance in shallow sea grass beds of Belize (note: *Photeros annecohenae* was formerly known as *Vargula annecohenae*; see Cohen & Morin, in press). Individuals are tiny (males ca. 1.6 mm, females ca. 2.0 mm) and nocturnally active. Males produce highly visible luminescent courtship displays in repeated, predictable and complex patterns in the water column during times of near darkness above the sea grass beds (Torres & Morin 2007; Rivers & Morin 2008; Gerrish et al. 2009). Their complex, multipulse displays start about 45 min after sunset (during astronomical twilight) or after moonset, whichever occurs last (Morin 1986; Morin & Cohen 1991; Gerrish et al. 2009), when males leave the benthos of the grass bed and enter the water column to secrete packets of luminescence, via nozzles on their upper lips, as a precise vertical array of light pulses. Each approximately 12 s display consists of two phases: a bright, 'stationary' phase of three to four pulses, which we hypothesize acts in species identification and to attract the attention of both females and competing males, and a somewhat dimmer, predictable 'helical phase' of up to 16 pulses, which we hypothesize allows conspecifics to orient to, track and intercept the displaying male (Rivers & Morin 2008) (Fig. 1). We have observed and recorded both females and

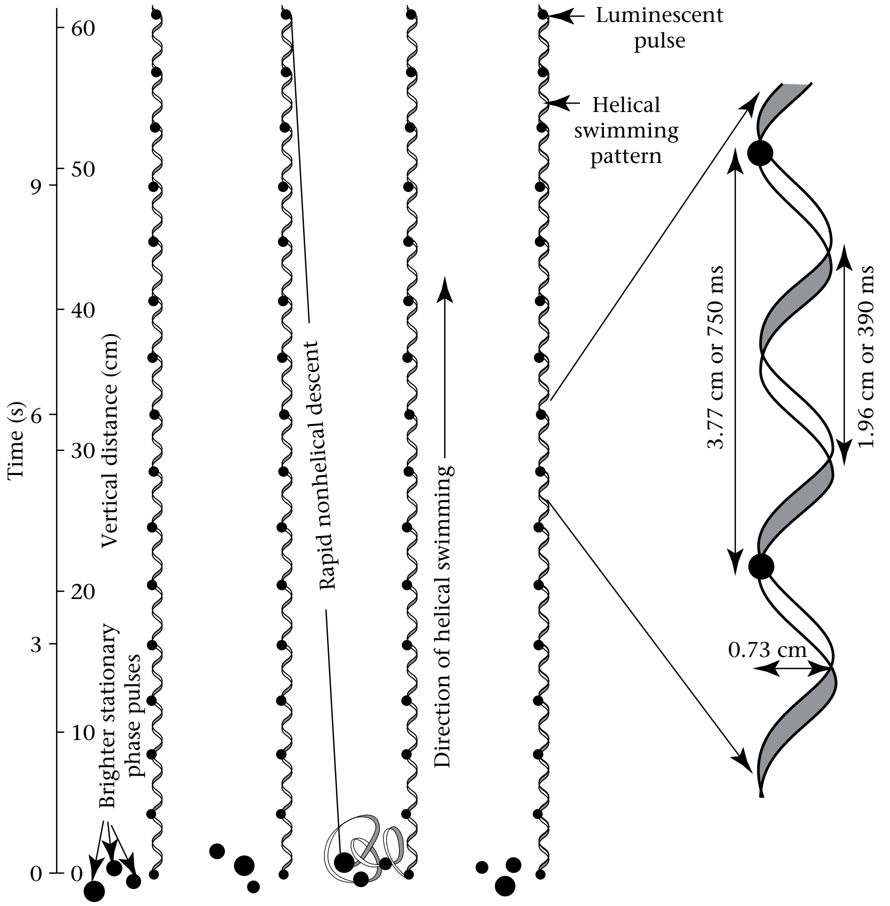

Figure 1. Model of a single male producing four successive displays (adapted from Rivers & Morin 2008 with permission from the Company of Biologists Ltd), based on interpulse intervals, interpulse distances, pulse intensities and swimming patterns of males displaying in the laboratory. Black dots are the location of the pulses, and their size corresponds to relative intensity; light ribbons indicate swimming pattern. The first three pulses are in the stationary phase; the remaining pulses are in the helical phase. Only the third display train shows the swimming pattern of a typical stationary phase. A male reaches the top of the helical phase, descends directly down, and then commences displaying again.