



The curse of being single: both male and female *Gammarus pulex* benefit energetically from precopulatory mate guarding



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Precopulatory mate guarding (PCMG) is frequently presented as a classic case of sexual conflict between partners. For instance, long-lasting PCMG is regarded as an adaptive male strategy to secure a female in a context of strong intrasexual competition, while females guarded for a long time are assumed to bear many costs. This assumption has been derived from guarding systems where females obviously resist males' attempts to initiate early guarding. However, females of some species such as the freshwater amphipod *Gammarus pulex* do not seem to possess adaptations to reduce PCMG duration, which remains to be explained from an evolutionary perspective. In this model organism for sexual conflict research, a male grasps a female several days before her sexual receptivity. Here we tested the hypothesis that *G. pulex* females might benefit from being passively transported by their partner during PCMG, whereas the male alone bears the costs of swimming while carrying his mate. We therefore compared the energetic states of paired and single individuals and found that, after 5 days of PCMG in controlled conditions, paired individuals contained more protein, lipid and glycogen reserves than single individuals in both sexes. Our results suggest that PCMG might be energetically beneficial not only to the female, but also to the male. We discuss overall fitness consequences of PCMG for both partners given the mutual benefits we highlighted here. We plead for a more precise estimation of the cost/benefit ratio for each sex to improve our understanding of how sexual conflict shapes guarding patterns.

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In arthropods as well as vertebrates, reproduction may involve precopulatory mate guarding (PCMG, also called amplexus or precopula), during which a male monopolizes a female until copulation (Bowcock, Brown, & Shine, 2009; Jormalainen, 1998). PCMG is particularly widespread when the number of sexually active males exceeds the number of females available for reproduction (Parker, 1974). In many species (especially among crustacean taxa such as amphipods and isopods), the male-biased operational sex ratio results from the short period of sexual receptivity of females, which typically lasts a few hours after their reproductive moult (Jormalainen, 1998; Parker, 1974). Consequently, receptive females are rare at any time, whereas almost all mature males are sexually active.

The evolutionarily stable strategy in response to such male–male competition is to precociously pair with a female long before her sexual receptivity (Grafen & Ridley, 1983; Jormalainen & Merilaita, 1993; Jormalainen, 1998). In that context, PCMG is defined as the time a male is willing to spend guarding a female before copulation instead of searching for another one (Yamamura & Jormalainen, 1996). It was theoretically shown that a male able to rely on slightly longer PCMG than his competitors will access a larger number of unguarded females, hence improving his chance to secure reproduction (Grafen & Ridley, 1983). Males are thus expected to irreversibly increase PCMG duration (Jormalainen, 1998; Jormalainen, Tuomi, & Yamamura, 1994; Yamamura & Jormalainen, 1996). However, the male optimal guarding duration is also constrained by associated costs, such as loss of other opportunities of reproduction (Parker, 1974) or decreased food intakes (Robinson & Doyle, 1985). Guarded females are, on the other hand, expected to receive no benefits and rather only incur costs from such a male-competitive strategy. Several studies have put forward higher energetic expenditure as a prominent cost for guarded

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females, for instance due to the transport of a passive male during PCMG in the water strider *Aquarius remigis* (Watson, Stallmann, & Arnqvist, 1998). Additionally, energetic depletion could result from reduced food intake documented for females and hermaphrodites engaged with a male in PCMG (Benvenuto & Weeks, 2012; Bowcock et al., 2009). Other costs endured by guarded females include increased vulnerability to some predators, as shown in the amphipod *Hyalella* sp. (Cothran, 2004) or reduced locomotor efficiency, as shown in the cane toad, *Bufo marinus* (Bowcock et al., 2009). These costs increase proportionally with the guarding duration. Optimal guarding duration is thus predicted to be shorter in females than in males (Jormalainen, 1998; Jormalainen et al., 1994; Yamamura & Jormalainen, 1996).

Because of this asymmetry between partners in the costs and benefits associated with PCMG, the duration of PCMG is now widely accepted to result from the conflicting interests of both partners. In other words, it can be considered as an example of intersexual conflict (Jormalainen, Merilaita, & Härdling, 2000; Plaistow, Bollache, & Cézilly, 2003; Yamamura & Jormalainen, 1996). This contrasts with early approaches considering PCMG as a purely male decision-making problem (Parker, 1974). Progress in the conceptual framework dealing with the evolution of PCMG can be achieved with additional information concerning females' gains resulting from this reproductive behaviour. A precise evaluation of the relative costs and benefits of PCMG for both partners is therefore needed to estimate more accurately the intensity of sexual conflict and how it acts as a selective pressure shaping the evolution of mate-guarding strategies (Chapman, Arnqvist, Bangham, & Rowe, 2003; Cothran, Chapman, Stiff, & Relyea, 2012; Karlsson Green & Madjidian, 2011). Recently, there has been mounting evidence that females' gains associated with PCMG could be more common than initially supposed. For instance, females experiencing long-lasting PCMG show reduced predation risks in the wild cricket *Gryllus campestris* (Rodríguez-Muñoz, Bretman, & Tregenza, 2011), but also increased reproductive rates in the freshwater amphipod *Gammarus pulex* (Galipaud, Dechaume-Moncharmont, Oughadou, & Bollache, 2011). As these latter authors argued, assessments of the effect of PCMG on the energetic budget should help researchers to understand more deeply the fitness consequences for both partners, especially for the female's reproductive output.

Gammarus pulex is a model organism for the study of sexual conflict (Galipaud et al., 2011; Plaistow et al., 2003). In this freshwater amphipod, males start initiating guarding when females are undergoing vitellogenesis (e.g. egg biosynthesis). Females can be inseminated within the 12 h following their reproductive moult, after which eggs are moved to a ventral brood pouch where they are fertilized and incubated until hatching (Jormalainen, 1998; Sutcliffe, 1992). For three main reasons, this species is a good candidate to put forward the link between benefits for guarded females, intensity of sexual conflict and the evolution of the related mating strategies. First, PCMG duration is much longer in *G. pulex* than in most other related taxa exhibiting PCMG (Jormalainen, 1998). In laboratory conditions, *G. pulex* amplexus last 217 h at 10 °C (up to 600 h at 1 °C). This remains relatively longer than closely related isopod species (*Idotea baltica*: 34–46 h; *Asellus aquaticus*: 104 h; *Lirceus fontinalis*: a few days) and amphipod species (*Gammarus zaddachi*: 100 h; *Gammarus lawrencianus*: 91 h; *Hyalella azteca*: 26–115 h; Jormalainen, 1998). From field observations, Birkhead and Clarkson (1980) reported that PCMG in *G. pulex* could even last up to 20 days, which remains to be explained from an evolutionary perspective. Second, *Gammarus* females lack the behavioural adaptations (female resistance behaviour in response to male pairing attempts) observed in other crustacean taxa to shorten PCMG duration, which seems to contradict the classic

evolutionary outcomes of a sexual conflict (Birkhead & Clarkson, 1980; Jormalainen & Merilaita, 1995; Yamamura & Jormalainen, 1996). Third, paired females of this species are passive and transported by the male during PCMG. Indeed, it has been shown that the swimming performance of the pair is positively related to the size of the male relative to the size of the female. This implies that only the male contributes to the locomotion effort of the pair, the female being just a load when the pair swims (Adams & Greenwood, 1983). We therefore hypothesized a sex-specific energetic cost arising from the pair locomotion in *G. pulex*: the female should suffer lower energetic losses than the male. The female could even benefit from being carried during PCMG through energetic savings. Surprisingly, only one study has examined the energetic consequences of PCMG in this species, and focused only on males, revealing absolute energetic losses for those that were guarding, attributed to pair formation (Plaistow et al., 2003). However, this study did not compare the energetic reserves of single and paired individuals. Such a comparison is now needed to explore more deeply the energetic consequences of PCMG in this species.

Here, we investigated the impact of PCMG on the energetic states of both sexes in *G. pulex* by comparing single and paired individuals. Owing to their passive transport by males, we expected guarded females to save energy compared to single females. This should translate into higher lipid and protein contents, as these metabolites are stored during vitellogenesis, the crucial stage of egg production (Sutcliffe, 1992). On the other hand, paired males actively transporting their partners are thought to bear alone the energetic costs of the pair's locomotion, affecting glycogen and soluble carbohydrates, which are known to fuel short-term activities such as locomotion (Plaistow et al., 2003).

METHODS

Ethical Note

This work followed the ASAB/ABS guidelines for the treatment of animals in behavioural research. Information about individuals' origin, collection, housing conditions and killing are described below. Transport between sampling site and laboratory, as well as daily monitoring of experimental units, were devised to reduce stress and maximize animals' welfare.

Biochemical Assays

Precopula pairs of *G. pulex* were collected on May 2016 in the River Suzon (Burgundy, France). As energy reserves of females may vary with their reproductive status, we visually selected only pairs whose females were undergoing vitellogenesis, with black dorso-lateral ovaries (Sutcliffe, 1992). Each pair was gently split and the resulting single individuals were randomly placed under controlled conditions (14 °C, 12:12 h light:dark cycle), either alone (40 males or 40 females) or with their former partner (240 pairs) in glass crystallizers (diameter = 6 cm, height = 4.5 cm) filled with 70 ml of water coming from the sampling site. No food was provided to avoid the potential compensation of PCMG costs through energy intakes. The pairing status of each individual was monitored four times a day for 5 days. This duration was determined by preliminary experiments: it was sufficiently long to observe an effect of the pairing status on energy budgets of both sexes, but sufficiently short to limit the risk of missing data due to pairs splitting after copulation. Individuals that did not pair within the first 30 min of the experiments ($N = 44$) or that split before the end of the 5 days ($N = 135$) were excluded from molecular analyses. We also excluded individuals that moulted ($N = 46$ pairs and one single

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