



## Assortative mating by size without a size-based preference: the female-sooner norm as a mate-guarding criterion

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The study of size-assortative mating, or homogamy, is of great importance in speciation and sexual selection. However, the proximate mechanisms that lead to such patterns are poorly understood. Homogamy is often thought to come from a directional preference for larger mates. However, many constraints affect mating preferences and understanding the causes of size assortment requires a precise evaluation of the pair formation mechanism. Mate-guarding crustaceans are a model group for the study of homogamy. Males guard females until moult and reproduction. They are also unable to hold a female during their own moult and tend to pair with females closer to moulting than them. Using a theoretical approach, we tested the potential for size-assortative mating to arise from such a state-dependent male decision rule. Consistent with previous experimental observations, we found a pattern of size assortment that strengthened with male–male competition over females. This decision rule, which we call the female-sooner norm, may be a major cause of homogamy in mate-guarding crustaceans. This highlights the potential for size assortment to arise from preferences not based on body size. It emphasizes the importance of considering pair formation processes when studying the link between preference and pattern in order to avoid inferential fallacies.

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Mating partners are often found to resemble each other in various traits, such as colour, age or body size (Ridley 1983). This pattern, called positive assortative mating or homogamy, is particularly widespread in nature. Size-assortative mating, defined as a positive correlation between male and female size among couples in a population, has been well described in several taxa, including birds (Helfenstein et al. 2004), reptiles (Shine et al. 2001, 2003), fishes (Baldauf et al. 2009) and humans (Courtiol et al. 2010). Most notably, it is a very common mating pattern in insects (Arnqvist et al. 1996) and crustaceans (Bollache & Cézilly 2004a).

Because it restricts gene flow within populations, homogamy can have major effects on sexual selection and speciation and is the subject of intense research (Kirkpatrick 2000; de Cara et al. 2008). Beyond its evolutionary consequences, the causes of homogamy remain largely unknown. However, the link between the behavioural traits and the resulting mating pattern is rarely straightforward. For a full understanding of the evolution of these traits, we need to consider not only the consequences of a particular mating pattern on gene flow but also the underlying mechanisms by which

they lead to such a pattern. That is why the mechanisms leading to size-assortative mating have been a major research topic over the past three decades (Parker 1983; Ridley 1983; Venner et al. 2010). Crespi (1989) proposed that size-assortative mating results from three nonexclusive mechanisms. First, physical constraints can prevent mismatched pairs from achieving mating. For example, a male could be physically unable to pair with a female too large or too small compared with his own size, therefore making mismatched pairs less frequent than size-assorted pairs (e.g. Han et al. 2010). Second, if same-sized mates co-occur in time or space, mating should be size-assortative. Individuals of different sizes sometimes have different periods of receptivity for pairing (Miyashita 1994) or are found in different habitats (Bollache et al. 2000). Third, size-assortative mating can be observed in a population in which one or both sexes are exerting directional preference towards larger mates (Johnstone 1997). When each male prefers large mates, size-assortative mating arises if larger males also outcompete smaller males for access to preferred females, leaving them to pair with smaller females (e.g. Fawcett & Johnstone 2003; Härdling & Kokko 2005; Venner et al. 2010). When females also prefer larger males, smaller individuals of both sexes are rejected by larger mates and size-assortative mating should occur (Parker 1983). Directional mate preference for large partners has been extensively explored since Crespi (1989). It remains, by far, the

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most commonly invoked process to explain size-assortative mating in nature (e.g. Elwood et al. 1987; Brown 1990; Rowe & Arnqvist 1996; Beeching & Hopp 1999; Shine et al. 2001; Baldauf et al. 2009; but see Taborsky et al. 2009).

However, studying the link between a mating preference and a mating pattern is highly challenging (Wagner 1998; Widemo & Sæther 1999). A mating pattern results from the interaction between individuals' preferences and internal or external constraints that may act on these preferences (Cotton et al. 2006). For instance, scramble competition (i.e. in which individuals' access to mates is solely constrained by the pairing success of competing individuals) is likely to constrain strongly the availability of potential partners, therefore limiting access to preferred mates. In that context, observations of individual preferences in the absence of competition, as reported in several experimental studies, do not necessarily account for a particular mating pattern (Wagner 1998). Reciprocally, an observed pattern of size-assortative mating is not sufficient to identify the traits targeted by the underlying preference, nor it is enough to infer either the shape of the preference function or the decision rule used to discriminate mates. Individuals may base their preferences on a variety of traits other than body size that reflect the quality of their potential partners. Also, apart from directional preference for larger mates, preference functions may sometimes depend on an individual's own quality (Alpern & Reyniers 1999). They could either prefer to mate with like (i.e. homotypic preference; Burley 1983; Cézilly 2004) or discriminate between potential mates according to a state-dependent threshold (Riebel et al. 2010). Homotypic or state-dependent preferences have rarely been invoked to explain assortment by size (but see Kalick & Hamilton 1986), nor have been mating preferences based on traits other than size.

Size-assortative mating is usually reported when pairs are conspicuous and easily identified. This is the case in species in which mating partners share parental investment or display pre- or postcopulatory mate guarding. It is probably why size-assortative mating in mate-guarding crustaceans has been the subject of an extensive literature (e.g. Birkhead & Clarkson 1980; Adams & Greenwood 1983; Elwood et al. 1987; Iribarne et al. 1996; Bollache & Cézilly 2004a, b; Franceschi et al. 2010), although its proximate mechanisms are still poorly understood (Sutherland et al. 2007). In mate-guarding crustaceans, individuals grow continuously throughout their lives after each moult. An individual's intermoult duration (the time between two successive moults) increases with body size. Females are only receptive for copulation for a short period of time, as their eggs can be fertilized for only a few hours after their moult. The strong male–male competition for access to receptive females favoured the evolution of long-lasting precopulatory mate guarding, as guarding a female earlier in her intermoult period provides the male with a competitive advantage (Parker 1974; Grafen & Ridley 1983; Jormalainen 1998). Perhaps owing to this close link between precopulatory mate guarding and sexual selection, size assortment in this mating system has often been considered to result from a directional male mating preference for larger, more fecund females combined with a size bias in male competitive ability (e.g. Elwood et al. 1987; Elwood & Dick 1990; Bollache & Cézilly 2004a; Sutherland et al. 2007). Larger males are commonly expected to have a competitive advantage over smaller ones in gaining access to a preferred female. They can usurp larger females from other males after take-overs (Ward 1983) or invest more energy in mate guarding than smaller males (Elwood & Dick 1990).

Surprisingly, other areas of the biology of mate-guarding crustaceans have been overlooked in explanations of size assortment. In amphipod crustaceans for instance, Males have been described as unable to guard a female during their own moult (Ward 1984).

Because mating is only ensured if a male holds a female at the time of her moult (i.e. female sexual receptivity), males should decide to pair with females that moult before they do (Thomas et al. 1998; Bollache & Cézilly 2004b). Although mating preference based on time left to moult as been studied in amphipods (e.g. Birkhead & Clarkson 1980; Ward 1984; Elwood et al. 1987; Galipaud et al. 2011), its potential role in leading to size assortment has almost never been investigated.

In this study, we tested the overlooked hypothesis that a state-dependent decision rule based on time left to moult is sufficient to lead to size-assorted pairs. Using an individual-based model, we studied pair formation when males decided to pair with females that moulted before themselves and we observed the resulting mating pattern. Unlike other hypotheses, we did not consider any interference between males or any effect of female behaviour. However, we explicitly took scramble competition into account and we never assumed any preference function or decision rule based on body size.

## THE MODEL

We parameterized the model in reference to the biology of *Gammarus pulex*, a well-studied species of amphipod crustacean, but we kept it as general as possible in order to fit the biology of most species of crustaceans with continuous growth. All individuals were sexually mature. Each individual was defined by its sex, mating status (unpaired or paired) and its size,  $S$  (usually measured in millimetres in *G. pulex*). Male and female sizes were drawn from normal distributions with means  $\mu_m$  and  $\mu_f$ , respectively, and standard deviation  $\sigma$ . By default, we used  $\mu_m = 2.75$  mm and  $\mu_f = 2$  mm, as these are the mean sizes of the fourth coxal plate (used as a proxy of body size) measured in natural populations of *G. pulex* (Bollache & Cézilly 2004a). Sexual size dimorphism (SSD) was represented as the ratio  $\mu_m/\mu_f$ . As default value, we chose  $SSD = 1.375$ , which roughly corresponds to the SSD found in natural populations of *G. pulex*. The length of an individual's moulting cycle  $M_{max}$  (in days) was assumed to increase linearly with its body size ( $M_{max} = 14.83 \times S + 6.75$ ; Fig. 1; e.g. in *G. pulex*, Galipaud et al. 2011; L. Bollache, unpublished data). The time left to the next moult,  $M$  (in days; Fig. 1), equalled  $M_{max}$  immediately after a moult, but declined by one unit each day in between moults. After each moult, individuals grew in size by a factor  $g$ , the relative growth rate (by default  $g = 1.1$ ). When a paired female moulted, she became receptive for copulation, after which the couple separated. When a paired male moulted, he could not hold his female anymore, so the couple separated (Ward 1984). Every day, each individual had a probability  $d$  of dying ( $d = 0.012$  by default). Individuals thus had a life expectancy of 83.3 days and 99% of them died before reaching 380 days. This is consistent with the life span observed in natural populations of *G. pulex* (Sutcliffe 1993). Every dead individual was replaced by a mature individual of the same sex and of a size chosen from the normal distributions described above. This ensured that population size and sex ratio were constant. If an individual died while paired, its partner immediately became available for re-pairing.

The population was composed of  $N$  individuals of both sexes. The numbers of males and females depended on the sex ratio  $SR$ , defined as the proportion of males. To simulate reproductive asynchrony, individuals entered the population with a value of  $M$  chosen randomly from the distribution of all possible values between 0 and  $M_{max}$  (Fig. 1). Pairings occurred through male mate choice only. Males only paired with females that would moult sooner than themselves, thereby preventing premature pair separation caused by their own moult (this assumption is relaxed in latter analysis, leaving the possibility for males to make errors).

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