Contents lists available at SciVerse ScienceDirect

Animal Behaviour

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

Matthias Galipaud*, Loïc Bollache, François-Xavier Dechaume-Moncharmont

UMR CNRS 6282 Biogéosciences, Université de Bourgogne, Dijon, France

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.

© 2012 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

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

* Correspondence: M. Galipaud, UMR CNRS 6282 Biogéosciences, Université de Bourgogne, 6 Boulevard Gabriel, 21000 Dijon, France.
E-mail address: matthias.galipaud@u-bourgogne.fr (M. Galipaud).

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 μ_m and μ_f, respectively, and standard deviation σ. 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 μ_m/μ_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).
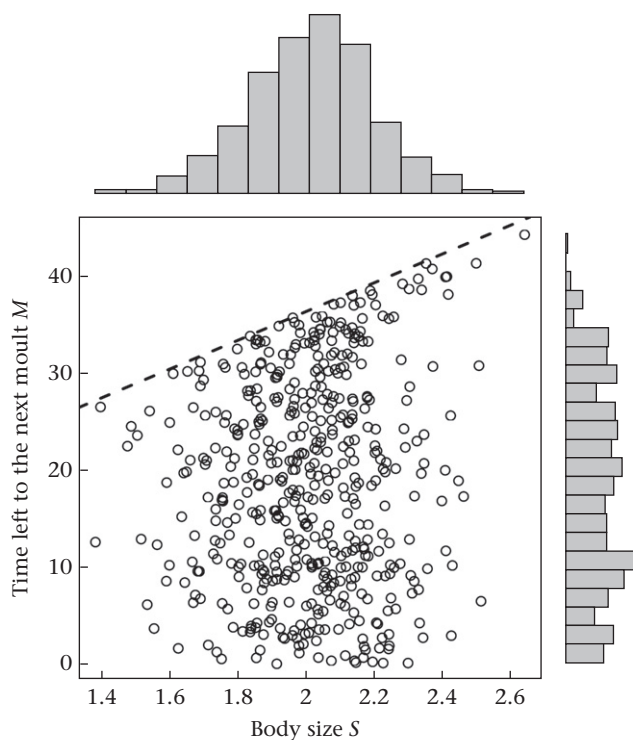
Figure 1. Time left to the next moult as a function of body size. The dashed line represents the correlation between body size and maximum time left to moult. As moulting was not synchronous, at the beginning of the simulation individuals ($N = 1000$) entered the population with a time left to moult randomly chosen among values between 0 and M_{max}. This resulted in a distribution of M almost uniform in a population, although individual body size S followed a normal distribution. Corresponding distribution frequencies are represented as side histograms.

Each time step t of the simulation represented 1 day for individuals. At each t, we ordered the unpaired males randomly and then gave each one in turn the opportunity to pair. For a given male, a mate was randomly chosen from the remaining unpaired females that met his guarding criterion ($M_f < M_m$), if any. After being assigned to a particular male, a female was not available for pairing with other males before she was released by her current partner. Pairs remained together until the female moulted or one of the two partners died. After separation, males and females were immediately available for pairing with a new mate. The model was written in R language (R Development Core Team 2012).

Simulations

We allowed cycles of guarding and mating to continue until the pattern of size-assortative mating had reached an equilibrium, which always happened within 1000 time steps (t_{max}). We assessed the degree of size assortment between mating partners with the Pearson coefficient of the correlation between male and female size in pairs (Arnqvist et al. 1996). Pairing sequence may be subject to variations between replicates of a given simulation. To make sure that we could draw conclusions from the observed pattern, we ran r replicates of the same simulation (i.e. with exactly the same set of parameter values) and considered the mean response for interpretation. Because the availability of partners influences mating patterns, we first assessed the effect of the sex ratio SR on size-assortative mating. Second, we considered the effects of g, d and SSD on homogamy for size.

At t_{max}, we also looked at the size of unpaired and paired individuals within each sex. To guarantee independence between observations, we randomly sampled one individual at t_{max} for each repetition of the simulation among unpaired (for 500 repetitions of the simulation) and paired individuals (for a separate set of 500 repetitions). We then assessed the strength of the disparity in size between unpaired and paired individuals, calculating the Cliff's δ as a measure of effect size (Nakagawa & Cuthill 2007). Following the same procedure, we measured the time that paired males spent in precopula with a particular female by looking at the M_f of their current partner at t_{max}. We tested for an effect of male body size on precopula duration with a linear regression model.

Individual's Error in Choice

In nature, males are unlikely to be able to assess perfectly a female's time left to moult relative to their own before engaging in precopula. We therefore added errors in male's decision making in our simulations (McNamara et al. 1997). When encountering a female, a male had a probability P of accepting her, given by:

$$P = \frac{1}{1 + e^{-\lambda(M_m - M_f)}},$$

where λ controls the accuracy of male choice. The greater the value of λ, the better the male can assess the female's time left to moult. When $M_m >> M_f$, $P \approx 1$ whereas when $M_m << M_f$, $P \approx 0$.

RESULTS

All simulations led to positive size-assortative mating. The strength of homogamy varied according to the sex ratio (Fig. 2). One important mechanism in creating the mating pattern was a disadvantage of small males with relatively short M_m in getting access to large females with long M_f. However, this mechanism only led to size assortment under particular conditions of male–male scramble competition for pairing.

There were two ways for pairs to split up. Separations were either caused by the death of one of the two partners or, in the vast majority of cases, by the female's moult. Under low SR, females were abundant in the population, male–male scramble competition was low and size-assortative mating was weak (Fig. 2). Newly
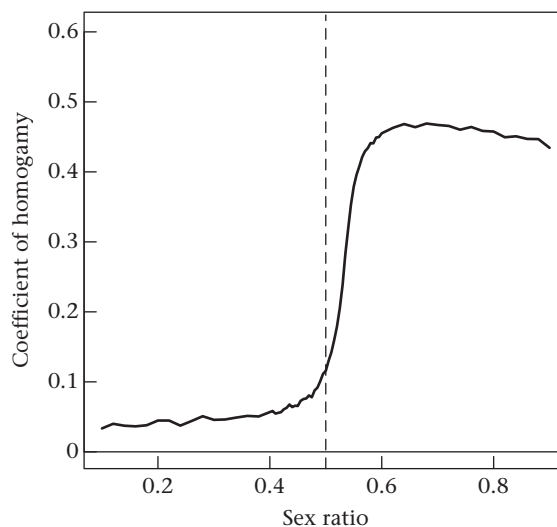

Figure 2. Coefficient of homogamy (measured as the mean Pearson coefficient of the correlation between male and female body size in pairs over 500 simulations) as a function of sex ratio. The vertical dashed line indicates an even sex ratio (0.5). Parameters: $N = 1000$, $d = 0.012$, $g = 1.1$, SSD $= 1.375$.

released females did not always immediately find a new male with which to form precopula. To do so, they had to wait for a few days, bringing them closer to the moult. Because both large and small females sometimes did not pair until close to their moult, this resulted in a weak correlation between female size and M_f. Unpaired males were thus likely to pair with females of any size whatever their own M_m. That is why we observed only weak size-assortative mating for low values of SR (Fig. 2). When SR reached higher values, male–male scramble competition increased and size-assortative mating was stronger (Fig. 2). Each male that secured a female strongly affected the pairing success of other males. After their moult, females rapidly entered into precopula with a new male. Newly released males were close to their moult and were therefore unable to find a female meeting their guarding criterion. In order to pair with a new female, they had to wait until their own moult and the beginning of a new moulting cycle. Size and M_m were therefore correlated in males that were able to pair. In a nutshell, with increasing male–male competition, there was a strong correlation between size and time left to moult in the population of unpaired individuals that were able to pair. Under these circumstances, small males had a disadvantage in access to large females with $M_f > M_m$, which resulted in more frequent assorted pairs (Fig. 2). This also explains why large females were less likely than smaller females to be found in precopula and why unpaired males were smaller than paired males (Table 1). In addition, large males tended to be passively trapped for a long time with females, therefore spending more time in precopula than smaller males (SR = 0.4: $t_{198} = 1.29$, $P = 0.2$, slope = 1.75, CI from −0.91 to 4.41; SR = 0.5: $t_{198} = 1.02$, $P = 0.3$, slope = 1.24, CI from −1.14 to 3.63; SR = 0.6: $t_{198} = 6.13$, $P < 0.0001$, slope = 7.93, CI from 5.40 to 10.47). Thus, at any time, large males were more likely to be paired than small males. This also accounts for the size difference between paired and unpaired males we observed (Table 1) and is consistent with previous experimental studies (Rowe & Arnqvist 1996). By segregating individuals according to their size, this passive accumulation of large males with large females resulted in even stronger size-assortative mating. However, passive accumulation alone is not sufficient to explain size assortment. Without a state-dependent decision rule, size-assortative mating was no longer found. To sum up, when male–male scramble competition increased, this strengthened the correlation between size and time left to moult among males and females that formed precopula. Small males were unable to pair with large females far from moult, therefore creating size-assortative mating at a population level. The necessary component for homogamy to arise was the positive correlation between S and M. Without this correlation, no size-assortative mating was observed.

It is worth pointing out that at SR = 0.5, some newly released unpaired males were close to moulting and were unable to find a mate meeting their guarding criterion, owing to the long M_f of unpaired females (i.e. females that just began a new moulting cycle). Despite there being an equal number of males and females in the population as a whole, the actual number of unpaired males

able to pair (i.e. with a large M_m) was still lower than the number of available unpaired females. The operational sex ratio (OSR; here defined as the relative number of males and females available for pairing, not for mating; Lemaître et al. 2009) was thus female-biased and the strength of male–male competition was still low. This accounts for the relatively low size-assortative mating we observed at SR = 0.5, before it rapidly increased as the OSR became biased towards males (Fig. 2).

Size assortment was also sensitive to individual relative growth rates and the probability of dying. For these parameters, the default values we chose led to a weaker pattern of size assortment than expected under slightly different conditions. Mates were more strongly assorted by size when they were less susceptible to individual mortality (Fig. 3a) or when they grew more at each moult (Fig. 3b). Size-assortative mating also increased when males and females tended to be similar in size (Fig. 4). Under low SSD, males and females tended to be more similar in their M_{max}. Several females had their M_{max} greater than small males' M_{max}. The size bias in pairing success among males was therefore strengthened because small males were even less likely to encounter a large female meeting their guarding criterion. Size-assortative mating
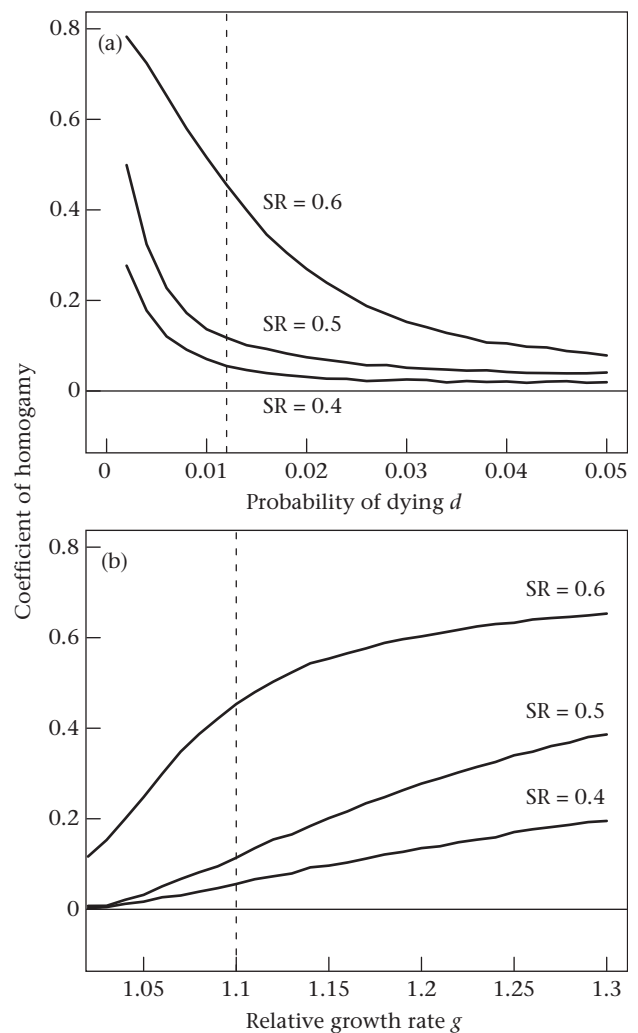

Figure 3. Effect of (a) probability of dying d and (b) relative growth rate g on size-assortative mating, for three values of the sex ratio (SR = 0.4, SR = 0.5 and SR = 0.6). In both graphs, dashed lines indicate the default values of (a) d and (b) g. Parameters: $N = 1000$, SSD = 1.375.

Table 1
Size disparity between unpaired and paired individuals within each sex

Sex ratio	Male		Female	
	Cliff's δ	95% Confidence interval	Cliff's δ	95% Confidence interval
0.4	−0.15	−0.21 to −0.07	0.06	−0.01 to 0.14
0.5	−0.08	−0.15 to −0.01	0.19	0.12 to 0.26
0.6	−0.19	−0.26 to −0.12	0.99	0.96 to 1.00

Negative values of Cliff's δ indicated that paired individuals were larger than unpaired individuals while positive values indicated the opposite.
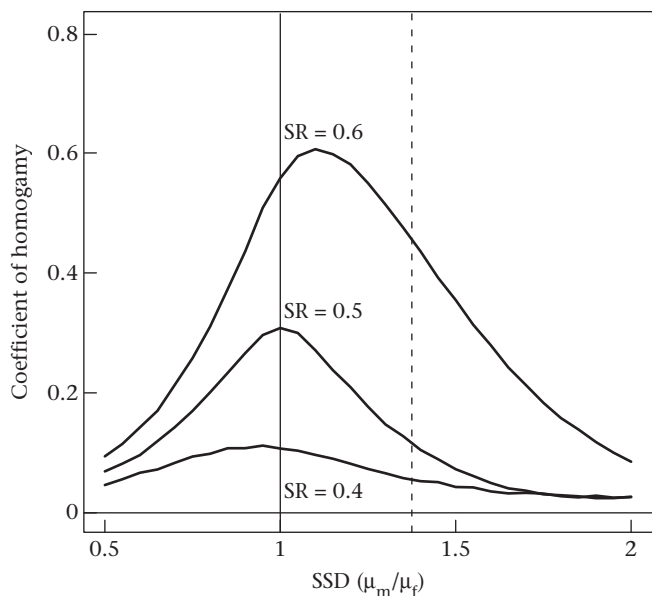
Figure 4. Effect of sexual size dimorphism on size-assortative mating for three values of the sex ratio. At SSD = 0 (solid line) the male and female size distributions are identical ($\mu_m = \mu_f = 2$; $\sigma = 0.2$). The dotted line indicates the default value of SSD. Parameters: $N = 1000$, $d = 0.012$, $g = 1.1$.

was resistant to errors in male assessment of female time left to moult (Fig. 5).

DISCUSSION

We showed that it is possible to find size-assortative mating without assuming either a preference function or a decision rule based on body size. This contrasts with previous work on amphipods, which considered male mating preference for larger, more fecund females as the main mechanism leading to homogamy (Elwood et al. 1987; Bollache & Cézilly 2004a; Sutherland et al. 2007). One could argue that our result is only a by-product of the weak correlation between size and time left to moult we found in the simulations. A preference based on time left to moult would then actually be a preference for body size. If so, males would presumably prefer, and most likely pair with, larger, more fecund females that also happen to be far from moult. This is precisely the opposite of the pattern reached in the model, with males tending to pair with smaller females rather close to moult, leaving larger females unpaired (e.g. Hatcher & Dunn 1997). The mate-guarding criterion we modelled based on time left to moult did not act as a directional mating preference for large females.

The state-dependent male decision rule we assumed is comparable to the male-taller norm in human mating (Gillis & Avis 1980). Human females are described as preferring to consort with males that are exclusively taller than them. This human mating strategy has also been shown to lead to size-assortative mating (Courtiol et al. 2010). Similarly, in our model, we considered that males would pair exclusively with females closer to moult than they are (Bollache & Cézilly 2004b). This female-sooner norm represents a novel hypothesis to explain size-assortative mating in crustaceans.

The effect of variation in mate-guarding duration has previously been invoked to explain size assortment. Some authors have argued that in reproductive systems where larger individuals have longer-lasting breeding periods, larger males would tend to accumulate passively with larger females, hence leading to size assortment (McCauley & Wade 1978). However, according to our results, this 'passive accumulation' alone is not a sufficient mechanism to explain the pattern of size assortment. Another previous hypothesis, called the 'timing hypothesis' (Elwood & Dick 1990) also suggested that, because males incur an energy cost in precopula, there should be a size bias towards males' ability to guard females. Large males, with more energy, should be more successful in guarding females over a long period of time compared with smaller males. According to this hypothesis, every male prefers larger females also further from moult than smaller females. Large males are better able to overcome the costs of guarding them, hence leading to size assortment. Our hypothesis differs on two points from the 'timing hypothesis'. First, the female-sooner norm we proposed does not consider costly precopulas for males. Even without consideration of size or energetic reserves, males close to moult were less likely to find a female meeting their guarding criterion. Under strong male–male competition, small males tended to be closer to moult than large males. This resulted in a size bias in male access to unpaired females and eventually to size-assortative mating. Second, the 'timing hypothesis' predicts that males should trade female size against time left to moult to choose partners in order
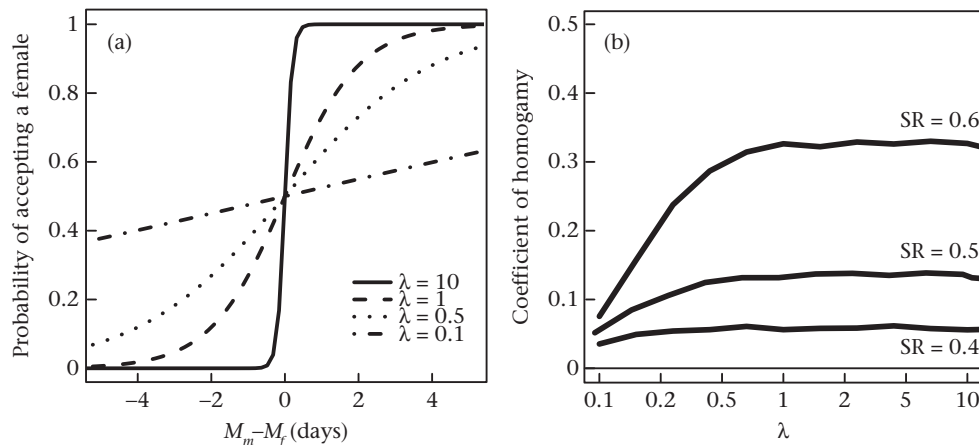

Figure 5. Male errors in mate choice. (a) When males are capable of perfect assessment of female M_f relative to their own M_m ($\lambda \geq 10$), male mate choice occurs without mistakes and males pair with females only if the difference $M_m - M_f$ is positive. When λ decreases, the male probability of making an error and accepting a female further from moult than himself increases. The effect of λ on the coefficient of homogamy is represented in (b) for three values of the sex ratio (SR = 0.4, SR = 0.5 and SR = 0.6). Parameters: $N = 1000$, $d = 0.012$, $g = 1.1$, SSD = 1.375.

to maximize the number of offspring they sire per guarding event (Elwood et al. 1987). In our study, males based their choice solely on female time left to moult, which led to size-assortative mating even under rather strong errors in assessment. In that sense, we suggest a parsimonious alternative to explain homogamy in mate-guarding crustaceans.

In our model, male–male scramble competition for access to females is the main mechanism to explain size-assortative mating. Size-assortative mating strongly increased with a more male-biased sex ratio. This is highly consistent with previous observations of homogamy in crustaceans (Bollache et al. 2000; Bollache & Cézilly 2004a). We also found that paired males tended to be larger than unpaired males. This has also been observed in previous studies (Birkhead & Clarkson 1980; Ward 1986). Yet, authors often erroneously interpret this pattern as evidence for large males having priority of access to larger, preferred females. Here we have shown that it is possible to obtain these patterns without any size bias in male capacity to undergo precopula or to dislodge competitors from preferred females (e.g. take-over). Because mating patterns potentially arise from several processes, direct explanations of mating patterns at the population level from observed preferences or biases in mating success only represent inferential fallacies (Burley 1983; Mueller 1995; Rowe & Arnqvist 1996).

It is also worth noting that the very same decision rule can lead to wide variation in the level of homogamy according to environmental conditions. Death rates, relative growth rates and sexual size dimorphism all affected the strength of size assortment in our model. Populations under different conditions of predation, food availability or selection pressure on growth may therefore vary widely regarding the strength of size assortment between mating partners, even if the main mechanism it results from remains the same. This could partly account for the strong intraspecific variation in size-assortative mating observed between different natural populations (e.g. Ward 1986; Arnqvist et al. 1996; Bollache et al. 2000; L. Bollache, unpublished data).

Conclusion

The female-sooner norm represents a novel hypothesis to explain size-assortative mating. It is embedded in the biology of mate-guarding crustaceans, a particularly well-studied group when it comes to homogamy. Unlike previous hypotheses, this one considers size assortment to result from a decision rule not based on body size. Males tended to pair with females that moulted sooner than themselves. State-dependent preferences are not as restrictive as a directional preference, so males still found plenty of potential mates meeting their criterion. Competition among males is presumably relaxed under such a preference, making its maintenance easier to explain within natural populations (Barry & Kokko 2010). This highlights the fact that there is not necessarily a direct relationship between preferences and mating patterns. There are likely to be many constraints on pairing processes resulting from a particular mating preference under natural conditions. Its observation under controlled environments using specific experimental procedures is not sufficient to infer a mating pattern at the level of the population. There is a need for a better understanding of pairing processes leading to mating patterns in order to link preference functions and decision rules to actual reproduction, and thus evolution.

Acknowledgments

References

Adams, J. & Greenwood, P. J. 1983. Why are males bigger than females in pre-copula pairs of *Gammarus pulex*? *Behavioral Ecology and Sociobiology*, **13**, 239–241.

Alpern, S. & Reyniers, D. 1999. Strategic mating with homotypic preferences. *Journal of Theoretical Biology*, **198**, 71–88.

Arnqvist, G., Rowe, L., Krupa, J. J. & Sih, A. 1996. Assortative mating by size: patterns in water striders a meta-analysis of mating. *Evolutionary Ecology*, **10**, 265–284.

Baldauf, S. A., Kullmann, H., Schroth, S. H., Thünken, T. & Bakker, T. C. M. 2009. You can't always get what you want: size assortative mating by mutual mate choice as a resolution of sexual conflict. *BMC Evolutionary Biology*, **9**, 129.

Barry, K. L. & Kokko, H. 2010. Male mate choice: why sequential choice can make its evolution difficult? *Animal Behaviour*, **80**, 163–169.

Beeching, S. C. & Hopp, A. B. 1999. Male mate preference and size-assortative pairing in the convict cichlid. *Journal of Fish Biology*, **55**, 1001–1008.

Birkhead, T. R. & Clarkson, K. 1980. Mate selection and precopulatory guarding in *Gammarus pulex*. *Zeitschrift für Tierpsychologie*, **52**, 365–380.

Bollache, L. & Cézilly, F. 2004a. Sexual selection on male body size and assortative pairing in *Gammarus pulex* (Crustacea: Amphipoda): field surveys and laboratory experiments. *Journal of Zoology*, **264**, 135–141.

Bollache, L. & Cézilly, F. 2004b. State-dependent pairing behaviour in male *Gammarus pulex* (L.) (Crustacea, Amphipoda): effects of time left to moult and prior pairing status. *Behavioural Processes*, **66**, 131–137.

Bollache, L., Gambade, G. & Cézilly, F. 2000. The influence of micro-habitat segregation on size assortative pairing in *Gammarus pulex* (L.) (Crustacea, Amphipoda). *Archiv für Hydrobiologie*, **147**, 547–558.

Brown, W. D. 1990. Size-assortative mating in the blister beetle *Lytta magister* (Coleoptera: Meloidae) is due to male and female preference for larger mates. *Animal Behaviour*, **40**, 901–909.

Burley, N. 1983. The meaning of assortative mating. *Ethology and Sociobiology*, **4**, 191–203.

de Cara, M. A. R., Barton, N. H. & Kirkpatrick, M. 2008. A model for the evolution of assortative mating. *American Naturalist*, **171**, 580–596.

Cézilly, F. 2004. Assortative mating. In: *Encyclopedia of Animal Behavior* (Ed. by M. Bekoff), pp. 876–881. Westport, Connecticut: Greenwood Press.

Cotton, S., Small, J. & Pomiankowski, A. 2006. Sexual selection and condition-dependent mate preferences. *Current Biology*, **16**, R755–R765.

Courtiol, A., Raymond, M., Godelle, B. & Ferdy, J.-B. 2010. Mate choice and human stature: homogamy as a unified framework for understanding mating preferences. *Evolution*, **64**, 2189–2203.

Crespi, B. J. 1989. Causes of assortative mating in arthropods. *Animal Behaviour*, **38**, 980–1000.

Elwood, R. W. & Dick, J. T. A. 1990. The amorous *Gammarus*: the relationship between precopula duration and size-assortative mating in *G. pulex*. *Animal Behaviour*, **39**, 828–833.

Elwood, R. W., Gibson, J. & Neil, S. 1987. The amorous *Gammarus*: size assortative mating in *G. pulex*. *Animal Behaviour*, **35**, 1–6.

Fawcett, T. W. & Johnstone, R. A. 2003. Mate choice in the face of costly competition. *Behavioral Ecology*, **14**, 771–779.

Franceschi, N., Lemaître, J.-F., Cézilly, F. & Bollache, L. 2010. Size-assortative pairing in *Gammarus pulex* (Crustacea: Amphipoda): a test of the prudent choice hypothesis. *Animal Behaviour*, **79**, 911–916.

Galipaud, M., Dechaume-Moncharmont, F.-X., Oughadou, A. & Bollache, L. 2011. Does foreplay matter? *Gammarus pulex* females may benefit from long-lasting precopulatory mate guarding. *Biology Letters*, **7**, 333–335, http://dx.doi.org/10.1098/rsbl.2010.0924.

Gillis, J. S. & Avis, W. E. 1980. The male-taller norm in mate selection. *Personality and Social Psychology Bulletin*, **6**, 396–401.

Grafen, A. & Ridley, M. 1983. A model of mate guarding. *Journal of Theoretical Biology*, **102**, 549–567.

Han, C. S., Jablonski, P. G., Kim, B. & Park, F. C. 2010. Size-assortative mating and sexual size dimorphism are predictable from simple mechanics of mate grasping behavior. *BMC Evolutionary Biology*, **10**, 359.

Härdling, R. & Kokko, H. 2005. The evolution of prudent choice. *Evolutionary Ecology Research*, **7**, 697–715.

Hatcher, M. J. & Dunn, A. M. 1997. Size and pairing success in *Gammarus duebeni*: can females be too big? *Animal Behaviour*, **54**, 1301–1308.

Helfenstein, F., Danchin, E. & Wagner, R. H. 2004. Assortative mating and sexual size dimorphism in black-legged kittiwakes. *Waterbirds*, **27**, 350–354.

Iribarne, O., Fernandez, M. & Armstrong, D. 1996. Mate choice in the amphipod *Eogammarus oclairi* Bousfield: the role of current velocity, random assortment, habitat heterogeneity and male's behavior. *Marine and Freshwater Behaviour and Physiology*, **27**, 223–237.

Johnstone, R. A. 1997. The tactics of mutual mate choice and competitive search. *Behavioral Ecology and Sociobiology*, **40**, 51–59.

Jormalainen, V. 1998. Precopulatory mate guarding in crustaceans: male competitive strategy and intersexual conflict. *Quarterly Review of Biology*, **73**, 275–304.

Kalick, S. M. & Hamilton, T. E. 1986. The matching hypothesis reexamined. *Journal of Personality and Social Psychology*, **51**, 673–682.

Kirkpatrick, M. 2000. Reinforcement and divergence under assortative mating. *Proceedings of the Royal Society B*, **267**, 1649–1655.

Lemaître, J.-F., Rigaud, T., Cornet, S. & Bollache, L. 2009. Sperm depletion, male mating behaviour and reproductive 'time-out' in *Gammarus pulex* (Crustacea, Amphipoda). *Animal Behaviour*, **77**, 49–54.

McCauley, D. E. & Wade, M. J. 1978. Female choice and the mating structure of a natural population of the soldier beetle, *Chauliognathus pennsylvanicus*. *Evolution*, **32**, 771–775.

McNamara, J. M., Webb, J. N., Collins, E. J., Székely, T. & Houston, A. I. 1997. A general technique for computing evolutionarily stable strategies based on errors in decision-making. *Journal of Theoretical Biology*, **189**, 211–225.

Miyashita, T. 1994. Size-related mating and mate guarding in the orb-web spider *Nephila clavata* (Araneae, Araneidae). *Journal of Insect Behavior*, **7**, 289–296.

Mueller, H. C. 1995. Correlation coefficients as evidence of female preference for size of mate. *The Condor*, **97**, 284.

Nakagawa, S. & Cuthill, I. C. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews of the Cambridge Philosophical Society*, **82**, 591–605.

Parker, G. A. 1974. Courtship persistence and female-guarding as male time-investment strategies. *Behaviour*, **48**, 157–184.

Parker, G. A. 1983. Mate quality and mating decisions. In: *Mate Choice* (Ed. by P. Bateson), pp. 141–166. Cambridge: Cambridge University Press.

R Development Core Team. 2012. *R: a Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Ridley, M. 1983. *The Explanation of Organic Diversity: the Comparative Method and Adaptations for Mating*. Oxford: Clarendon Press.

Riebel, K., Holveck, M.-J. J., Verhulst, S. & Fawcett, T. W. 2010. Are high-quality mates always attractive? State-dependent mate preferences in birds and humans. *Communicative and Integrative Biology*, **3**, 271–273.

Rowe, L. & Arnqvist, G. 1996. Analysis of the causal components of assortative mating in water striders. *Behavioral Ecology and Sociobiology*, **38**, 279–286.

Shine, R., O'Connor, D., LeMaster, M. P. & Mason, R. T. 2001. Pick on someone your own size: ontogenetic shifts in mate choice by male garter snakes result in size-assortative mating. *Animal Behaviour*, **61**, 1133–1141.

Shine, R., Phillips, B., Waye, H., LeMaster, M. & Mason, R. T. 2003. The lexicon of love: what cues cause size-assortative courtship by male garter snakes? *Behavioral Ecology and Sociobiology*, **53**, 234–237.

Sutcliffe, D. W. 1993. Reproduction in *Gammarus* (Crustacea Amphipoda): female strategies. *Freshwater Forum*, **3**, 26–65.

Sutherland, D. L., Hogg, I. D. & Waas, J. R. 2007. Is size assortative mating in *Paracalliope fluviatilis* (Crustacea: Amphipoda) explained by male–male competition or female choice? *Biological Journal of the Linnean Society*, **92**, 173–181.

Taborsky, B., Guyer, L. & Taborsky, M. 2009. Size-assortative mating in the absence of mate choice. *Animal Behaviour*, **77**, 439–448.

Thomas, F., Liautard, C., Cézilly, F. & Renaud, F. 1998. A finite time horizon influences sequential mate choice in male *Gammarus aequicauda* (Amphipoda). *Canadian Journal of Zoology*, **76**, 400–404.

Venner, S., Bernstein, C., Dray, S. & Bel-Venner, M. 2010. Make love not war: when should less competitive males choose low-quality but defendable females? *American Naturalist*, **175**, 650–661.

Wagner, W. E. 1998. Measuring female mating preferences. *Animal Behaviour*, **55**, 1029–1042.

Ward, P. I. 1983. Advantages and a disadvantage of large size for male *Gammarus pulex* (Crustacea: Amphipoda). *Behavioral Ecology and Sociobiology*, **14**, 69–76.

Ward, P. I. 1984. *Gammarus pulex* control their moult timing to secure mates. *Animal Behaviour*, **32**, 927.

Ward, P. I. 1986. A comparative field study of the breeding behaviour of a stream and a pond population of *Gammarus pulex* (Amphipoda). *Oikos*, **46**, 29–36.

Widemo, F. & Sæther, S. 1999. Beauty is in the eye of the beholder: causes and consequences of variation in mating preferences. *Trends in Ecology & Evolution*, **14**, 26–31.