Original Article

Males do not always switch females when presented with a better reproductive option

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Paired individuals are expected to leave their current partner for newly encountered ones of higher quality. In such cases, animals should therefore be able to compare the quality of their current partner to the quality of a new prospective mate next to the couple. We tested this prediction in *Gammarus pulex*, an amphipod species where paired males have been described to switch females before copulation. Contrary to expectations, a majority of males remained paired to their current female when presented to an unpaired female of higher quality. In fact, males did not seem to compare the quality of the 2 females before switching. They rather based their decision on the quality of their current female only, switching when it was of low quality. We suggest that mate switching functions as a male mate choice strategy under strong competition for female access in *G. pulex*. Unpaired males may first randomly pair with a female to gather information about its quality as a mate before switching for a new female when the expected quality of unpaired females in the population exceeds that of their current partner.

Key words: **amphipod, discounted quality, mate choice, mate switching, precopulatory mate guarding, sampling rule.**

INTRODUCTION

Mate switching is a mate choice strategy according to which paired individuals leave their current partner to consort with a new unpaired mate. It occurs in species with long lasting pair bonding either before or after copulation, such as in monogamous species or in species with temporary pairing due to pre- or post-copulatory guarding. For example, in several species of birds (where it is called divorce), individual switch mates either between reproductive seasons (i.e., when previously paired partners do not pair again the next reproductive season, Choudhury 1995 for a review) or within reproductive seasons (i.e., when a pair breaks up before the onset of reproduction, e.g., Cézilly and Johnson 1995; Black 1996; Jacot et al. 2010). Mate switching has also been described in mammals (Lardy et al. 2011), in fishes (Triefenbach and Itzkowitz 1998; Kvarnemo et al. 2000), and in invertebrates, especially crustaceans (Dick 1992; Wada et al. 2011).

Causes for adaptive mate switching have mostly been inferred from observations of mating patterns and their fitness consequences for both females and males (e.g., Choudhury 1995; Heg et al. 2003; Poirier et al. 2003; Jeschke et al. 2007; Lardy et al. 2011; but see Maness and Anderson 2008; Pérez-Staples et al. 2013). Depending on whether

divorcing benefits 1 or both partners, different hypotheses have been put forward to explain it (Choudhury 1995; Dhondt 2002). Mating associations sometimes eventually result in poor reproductive success due to low compatibility between mates. In that case, it has been suggested that both partners should benefit from divorcing to find more compatible mates (Coulson 1972). Switching can also result from the behavior of only 1 of the 2 partners, which benefits from divorcing at the expense of the other partner. In particular, individuals terminate parings to correct initial errors in mate choice and/or to pair up with a partner of higher quality (Ens et al. 1993; Choudhury 1995). This so-called "better option hypothesis" has often been put forward to account for mate switching (e.g., Otter and Ratcliffe 1996; Catry et al. 1997; Triefenbach and Itzkowitz 1998; Ramsay et al. 2000; Poirier et al. 2003). However, studies lack assessments of proximal behaviors by which individual exert their choice. Understanding mechanisms on which individual base their decision is yet utterly important because they influence the subsequent choice pattern observed at the population level (Burley 1983; Gimelfarb 1988; Jennions and Petrie 1997; Galipaud et al. 2013). Under the better option hypothesis, paired individuals are expected to possess sampling and choice behaviors that enable them to compare the quality of unpaired partners with the quality of their current partner before deciding to switch or not.

In mate guarding crustaceans, reproduction is tightly linked to females' molting cycle. Females are receptive for copulation shortly

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after molting and only for a few hours. After copulation, they begin a new molting cycle, which can last several days up to several weeks depending of the species (Ridley 1983; Jormalainen 1998). Females molt several times during their lives and therefore experience several reproductive events. Females do not store sperm (Sutcliffe 1992) and only 1 male usually sires most of the eggs females produce at each reproductive event (Birkhead and Pringle 1986). From a male's perspective, a female's quality as a mate strongly depends on its proximity to molting. In fact, when presented to 2 unpaired females at different time in their molting cycle, unpaired males tend to pair with the female closest to molting and reproduction (e.g., Birkhead and Clarkson 1980; Thompson and Manning 1981; Dunn 1998; Sparkes et al. 2000; Lemaître et al. 2009). The quality of a female also depends on its body size, as larger females produce more eggs than smaller ones (Sutcliffe 1992). Accordingly, when given the opportunity, unpaired males have been described to prefer larger females over smaller ones (e.g., Elwood et al. 1987; Reading and Backwell 2007; Franceschi et al. 2010; Wada et al. 2011). In mate guarding crustaceans, female quality assessment seems possible only by direct physical contact (Borowsky 1991). Water-borne pheromones have only been shown to carry information about the sex and the species of individuals, but not about their body size or their time left to molt (TLM, Dahl et al. 1970; Borowsky 1991). Also, it is unclear whether females can choose mates. In certain species, females can resist pairing attempts made by males, hence exerting an indirect mate choice if male's ability to overcome resistance depends on its phenotype (Cothran 2008a). In other species, especially gammarids, resistance is rare and, if ever, is mostly displayed by large females (Ward 1984).

At any time, females receptive for copulation are scarce and scramble competition for their access is strong among unpaired males. Males are therefore likely to encounter females sequentially rather than simultaneously. Contrary to what is found in male mate choice experiments with simultaneous encounter of females, unpaired males have been shown to discriminate very little between sequentially encountered unpaired females, even though they prefer large females close to molting when competition is relaxed (Dick and Elwood 1989). To ensure their access to reproduction, it pays them to pair with females rather far from molting (Grafen and Ridley 1983; Yamamura 1987; Härdling et al. 2004), thereby engaging into long-lasting precopulatory mate guarding (also called precopula or amplexus). Males grab their female with their claws for a few hours up to several days before female's molt (Jormalainen 1998). Despite this substantial time between initial pairing and reproduction, males have often been assumed to be resolute in their choice, holding on tightly to their female against competitors (Parker 1974). On the other hand, little is known about mate switching as an adaptive mate choice strategy in mate guarding crustaceans. Males have yet been observed to switch females, releasing their current female to grab a new one at close proximity (Dick and Elwood 1989; Dick 1992; Iribarne et al. 1996; Wada et al. 2011). But these studies, which were not primarily investigating mate switching strategies only reported a few mate change, for example, 4 out of 75 trials in the amphipod *Gammarus pulex* (Dick and Elwood 1989) or 2 out of 21 trials in the hermit crab *Pagurus middendorffi* (Wada et al. 2011), which limits investigations about its causes.

We investigated the behavioral causes of mate switching in the mate guarding amphipod *G. pulex* in which male mate choice has been largely studied (Birkhead and Clarkson 1980; Elwood et al. 1987; Bollache and Cézilly 2004; Franceschi et al. 2010). As in other mate guarding crustaceans, female quality assessment in *G. pulex* is mainly based on 2 cues: the female's TLM and the female's body size (Elwood et al. 1987; Dick and Elwood 1989). In fact, it has been suggested that males could combine information received from both cues in order to assess the female's discounted quality (i.e., female's fecundity weighted by the time they need to be held before copulation) and pair with sampled females associated with greater fecundity to guarding time ratio (Thompson and Manning 1981; Elwood et al. 1987; Dick and Elwood 1989). By investigating which modalities of female quality were involved in mate switching in *G. pulex*, our aims were 2-fold. First, contrary to studies on mate switching conducted by observing mating patterns in the field, we wanted to look at the choice behaviors of paired males that could allow them to switch for better quality females when given a chance in an experimental set up. Second, we generally aimed at understanding adaptive mate choice strategies under sequential encounters resulting from competition for access to receptive mates.

MATERIALS AND METHODS

We collected amphipods in a tributary of the river Suzon (Burgundy, France, N: 47°24′215″; E: 4°52′974″) using the kick sampling method (Hynes 1954). This consists of gently moving the rocks of the river bottom with 1 foot while placing a hand net downstream to collect the dislodged amphipods. Individuals were immediately brought back to the laboratory and housed in a large tank filled with well aerated water at 15 °C that had been previously filtered and UV treated for pathogens. For experiments, we directly collected pairs of amphipods from the stock tank. They were first gently separated from their current partner before being housed in individual glass cups (of 6 cm diameter) also filled with UV-treated water. Using individuals already found paired in the field ensured that both females and males were sexually mature and showed willingness to pair. This last condition is important considering that female resistance to males' pairing attempts occurring too early in their molting cycle, albeit rare in gammarids (Birkhead and Clarkson 1980; Jormalainen and Merilaita 1993; Hatcher and Dunn 1997), has been observed in mate guarding crustaceans (Jormalainen 1998). Every individual used in experiments spent less than a week in the laboratory under a 12:12-h light:dark photoperiod.

We presented paired males with unpaired females of equal or better quality than their current females in an attempt to favor situations of mate switching. Males were first isolated in glass cups for 24 h and fed with elm leaves ad libitum for acclimatization. After 24 h, the leaves were removed and a female chosen from the previously paired females was added to the cup to allow precopula formation (hereafter called the current female). Once the couple formed, which typically took a few minutes, we waited 20 min before adding a second single female (hereafter called the new female) also chosen from the previously paired females. The 3 amphipods were then left to interact for 24 h, after which we determined whether or not the male had changed partners. The male was then removed from the cup. We estimated its body size using the length of its fourth coxal plate (Bollache and Cézilly 2004) by placing it under a stereoscopic microscope (Nikon SMZ 1500) and using the Lucia G 4.81 software. This procedure allowed us to control for the potential effect of male body size on their decision to pair with females (Fawcett and Johnstone 2003; Härdling and Kokko 2005).

Females in each trial were of different quality. Before adding them to the cups, we roughly assessed their body size and their TLM. The 2 females were considered differing in body size when

we could observe a size difference with the naked eye. We estimated their TLM thanks to the maturity of embryos in their brood pouch (Geffard et al. 2010). Female were considered close to molt when carrying bright orange young and far from molt otherwise. Such an estimation of female quality also enabled us to discriminate between the 2 females in each trial. Once the trial was completed, we precisely assessed the quality of each female. Females remaining unpaired have been shown to have longer molting cycles than paired ones (Galipaud et al. 2011). Because we wanted to assess TLM as if the female had remained paired with a male to avoid biases related to female plasticity in molting time when unpaired, we individually housed females with a new male until their molt (Galipaud et al. 2011). We then measured their body size following the same procedure as the one used for males (see above).

From the initial 122 trials, 112 males started precopula with the first female (i.e., the current female). This represents 8% of male's mate rejection when both males and females were unpaired. In 19 of the 112 remaining trials, 1 of the 2 females died or was eaten by a male during the experiment. The remaining 93 trials covered a wide spectrum of situations, where the new female was either of better quality according to both cues, of better quality only according to size, of better quality only according to TLM, of same quality, or in a few cases, of worst quality according to both cues. The mean size (±standard deviation) of current females' fourth coxal plate was 1.87 ± 0.22 mm and that of new females was 2.09 ± 0.25 mm. The Cohen's d of the difference between estimated body size of current females and new females was therefore 0.93, 95% confidence interval (CI) [0.89, 0.98]. The mean TLM of current females was 10.17 days, 95% CI [1, 38.5] and that of new females was 3.96 days, 95% CI [1, 17.4]. The Cliff's δ (Cliff and Keats 2002) of the difference between mean TLM of current females and new females was 0.5, 95% CI [0.34, 0.63].

Using new individuals originating from the same tributary of the river Suzon, we also allowed 53 males to form precopula with randomly chosen females. However, we did not add a new female to the cup. We recorded the number of split couples after 24 h. This allowed us to control for possible effects of laboratory conditions, in particular the isolation of couples in individual cups, on the rate of couple separation.

Data analysis

Male could base their switching decision on either an absolute or comparative assessment of females' qualities. We therefore considered 3 types of predictor variables. First, we considered the simple variables TLM_c, S_c and TLM_n, S_n as the values of TLM and body size of the current and the new female, respectively. Second, we considered the composite variables DQ_c and DQ_n as the ratio of size over TLM for each female. The composite variables thus represented the discounted quality of females (Thompson and Manning 1981; Elwood et al. 1987). Third, we considered the comparative variables, which included the values of differences in TLM ($D_{tlm} = TLM_c - TLM_n$), body size ($D_s = S_n - S_c$) and discounted quality ($DDQ = DQ_c - DQ_n$) between the current and the new female. We did not have a priori knowledge about the relative importance of these different variables in explaining mate switching. Inferences about male mate choice behavior thus depended on a wide range of alternative models (i.e., representing alternative hypotheses to explain male mate switching behavior). The probability of switching was studied by comparing logistic regression models with male propensity to switch as the response variable. For analyses, we first considered a set of candidate models including the set of predictor variables presented above and chosen based on our expertise on amphipod biology (as suggested by Burnham and Anderson 2002). We did not include interactions between predictor variables within the model set for 2 reasons. First, in a statistical sense, considering ratio variables DQ_c and DQ_n is similar to considering interactions between body size and TLM for the current and the new female. However, composite ratio variables carry useful information about the discounted quality of females (i.e., the ratio of body size over TLM), which is not included in interaction terms (i.e., the product of body size and TLM). Second, including predictor variables alongside their interaction terms in candidate models severely impairs interpretation about variable's importance in model averaging (Galipaud et al. 2014). The model selection procedure was based on models' AIC_c value, that is, Akaike information criterion for small samples size (Burnham and Anderson 2002; Symonds and Moussalli 2011). In order to avoid problems related to collinearity, we conducted distinct AIC_c model selection procedures for model sets that included simple, composite, or comparative variables (Freckleton 2011). A measure of the difference in AIC_c between the model with the smallest AIC_c value (i.e., the best ranked model) and alternative models i was given by Δ_i. For each alternative model, we also calculated its pseudo R^2 (based on the formula proposed by Nagelkerke 1991) and its Akaike weights w_i as a measure of the weight of evidence that i is the best model to describe male's behavior. Unless w_i of the best ranked model is very high, it is recommended that interpretations should be based on a set of equally supported models instead of 1 single model (Burnham and Anderson 2002). Following each model selection, we therefore performed model-averaging procedures on sets of models for which their cumulative weights was equal to 0.95. For each predictor variable, this allowed calculation of averaged parameter estimates β. We estimated variables' influence on switching behavior by summing the weights of each model where the variable appears, hence calculating variable's sum of Akaike weights Σw_i (Burnham and Anderson 2002; Garamszegi et al. 2009). We also performed 500 independent permutations of the response variable (i.e., the male propensity to switch) in the data set and we calculated Σw_i for each predictor variable in each permuted data set. The resulting baseline sums of weights distribution represented, for each predictor variable, the range of Σw_i values expected when the considered variable has no influence on the response variable (Burnham and Anderson 2002; Galipaud et al. 2014). Baseline Σw_i can take a wide range of possible values and unless the Σw_i calculated for the predictor variable is very large (close or equal to 1), the interpretation about its support is limited (Galipaud et al. 2014). For every predictor variable, 95% of baseline Σw_i values ranged from 0.25 to 0.83. To be conservative, we thus only interpreted predictor variables with $\Sigma w_i = 1$ as having an influence on mate switching. Model selection and averaging procedures were conducted using the MuMIn 1.10.0 package (Bartoń 2014) for R 3.1 (R Development Core Team 2014).

RESULTS

No female molted during the experiment. Accordingly, we did not observe any copulated female in trials (easily observable by the presence of newly laid black eggs in the female's brood pouch). Of the 93 trials, 89 involved a new female of better quality compared with males' current female. This confirms the reliability of our initial estimation of females' quality with the naked eye. In the 89 situations where switching presumably involved greater reproductive

success, only 26 males switched females. Of the 47 males, 13 switched mates when the new female was of better quality than the current female according to both cues. Of the 19 males, 9 switched females when the new female was of better quality according to size only. Of the 23 males, 4 switched females when the new female was of better quality according to TLM only. In the 4 situations involving a new female of lower quality on both cues compared with the current female, males never switched mates. In trials involving only 1 male paired with 1 female, couples only split up 3 out of 53 times.

Results of model selection analyses are presented in Table 1. In the analysis considering simple variables, best ranked models (i.e., models with lowest AIC_c values) always included variables related to the characteristics of the current female (TLM_c and S_c). This suggests that mate switching was mainly influenced by the quality of the male's current female. Similarly, in the composite variables analysis, the best ranked model only included DQ_c (Table 1). Models including comparative variables generally had greater AIC_c values than models including simple and composite variables, suggesting that the difference in quality between the current and the new female had a lower influence on mate switching than absolute females' quality (Table 1). Note that models including simple and composite variables explained about 30% of the total variance in male behavior (as showed by the pseudo R^2 values for best ranked models, Table 1). This confirms that the female characteristics we measured in our experiments are likely involved in mate switching behavior.

Consistent with model selection findings, DQ_c likely influenced mate switching, as suggested by its high averaged parameter estimate and sum of weights in model-averaging analyses (Table 2).

Males switched mates when their current female was of low discounted quality, that is, females' ratio of size over TLM was low (Figure 1b). Model averaging also pointed out the influence of TLM_c and the difference D_{tlm} on mate switching (Table 2). Males seemed to switch females with a greater probability when their current female was far from molting (Figure 1a) or when the difference in females TLM was high. However, as models containing comparative variables showed lower support than models containing simple and composite variables (Table 1), it is likely that the high Σw_i value for D_{tlm} actually resulted from the high Σw_i of TLM_c alone. Current female size alone did not seem to influence mate switching and characteristics of the male or the new female alone were also of little explanatory power for switching behavior (Table 2). According to our multimodel analysis, males thus seemed to switch mates when their current female was small and far from molt and reproduction (Figure 1).

DISCUSSION

When given a choice, the majority of males remained with their current female. Doing so, they neglected females associated with discounted fitness payoffs potentially greater than their current females. Thus, contrary to expectations, once paired, male decision rule for mate choice did not always provide them with access to the best available female. In the next paragraphs, we propose possible explanations for this apparently suboptimal behavior.

At first glance, males seemed to behave like they preferred their own female over the best available female. But mate switching occurred independently of the characteristics of the new unpaired female. This does not necessarily suggest that males preferred the

Table 1

Set of candidate logistic regression models testing the male propensity to switch females as a function of females' quality. For each model, we calculated its AIC_c value, its weight w_i, its pseudo R^2, and its difference Δ_i in AIC_c with the best ranked model, that is, the model with the greatest weight

Type of variables	Models				k	AIC_c	Δ_i	w_i	Pseudo R^2
Simple									
		S_c		TLM_c	3	94.45	0.00	0.18	0.30
		S_c		TLM_c	TLM_n	4	95.02	0.58	0.14	0.32
		S_c	S_n	TLM_c	4	95.47	1.02	0.11	0.32
				TLM_c	TLM_n	3	95.84	1.39	0.09	0.29
				TLM_c	2	95.96	1.51	0.09	0.26
		S_c	S_n	TLM_c	TLM_n	5	96.55	2.10	0.06	0.33
	S_{male}		S_n	TLM_c	4	96.63	2.18	0.06	0.30
			S_n	TLM_c	3	96.78	2.33	0.06	0.27
	S_{male}	S_c		TLM_c	TLM_n	5	97.08	2.63	0.05	0.32
			S_n	TLM_c	TLM_n	4	97.20	2.76	0.05	0.30
	S_{male}	S_c	S_n	TLM_c	5	97.61	3.16	0.04	0.32
	S_{male}			TLM_c	TLM_n	4	97.69	3.24	0.04	0.29
	S_{male}			TLM_c	3	98.06	3.62	0.03	0.26
Composite									
		DQ_c			2	90.63	0.00	0.59	0.32
		DQ_c	DQ_n		3	92.72	2.09	0.21	0.32
	S_{male}	DQ_c			3	92.76	2.13	0.20	0.32
Comparative									
			D_{tlm}		2	101.94	0.00	0.58	0.18
		D_s	D_{tlm}		3	103.95	2.00	0.21	0.18
	S_{male}		D_{tlm}		3	104.08	2.14	0.20	0.18
			DDQ		2	111.14	0.00	0.52	0.05
					1	112.26	1.12	0.30	0
	S_{male}		DDQ		3	113.27	2.13	0.18	0.05

S_{male}, size of male; S_c, size of the current female; TLM_c, TLM of the current female; S_n, size of the new female; TLM_n, TLM of the new female; DQ_c, ratio of size over TLM for the current female; DQ_n, ratio of size over TLM for the new female; D_{tlm}, difference in TLM between the 2 females; D_s, difference in size between the 2 females; DDQ, difference in ratio of size over TLM between the 2 females.

Table 2

Model-averaged estimates for predictor variables. For each variable, we considered its Σw_i and its averaged parameter estimate β (with its 95% CI)

Type of variables	Variables	Averaged β	95% CI for β	Σw_i
Simple	S_{male}	−0.30	−2.34, 1.74	0.22
	S_c	2.29	−0.33, 4.92	0.65
	S_n	1.12	−1.11, 3.35	0.32
	TLM_c	0.10	0.05, 0.15	1
	TLM_n	0.07	−0.03, 0.16	0.43
	Intercept	−5.63	−12.90, 1.64	
Composite	S_{male}	−0.07	−2.02, 1.88	0.20
	DQ_c	−6.00	−9.47, −2.55	1
	DQ_n	−0.11	−1.19, 0.96	0.21
	Intercept	0.87	−1.62, 3.35	
Comparative	S_{male}	0	−1.89, 1.87	0.20
	D_s	−0.27	−1.75, 1.21	0.21
	D_{tlm}	0.07	0.03, 0.12	1
	Intercept	−1.50	−3.76, 0.76	
	S_{male}	−0.09	−1.87, 1.70	0.18
	DDQ	−0.70	−1.50, 0.10	0.70
	Intercept	−1.12	−3.18, 0.93	

S_{male}, size of male; S_c, size of the current female; TLM_c, TLM of the current female; S_n size of the new female; TLM_n, TLM of the new female; DQ_c, ratio of size over TLM for the current female; DQ_n, ratio of size over TLM for the new female; D_{tlm}, difference in TLM between the 2 females; D_s, difference in size between the 2 females; DDQ, difference in ratio of size over TLM between the 2 females.

worst of the 2 females in terms of expected fitness payoffs. It could be that our own estimation of the quality of females differed from the 1 performed by males. They could have based their quality assessment of the new female on a cue that we did not measure. However, except for mate discrimination based on female parasitic status (acanthocephalan parasites, Bollache et al. 2002; but see Poulton and Thompson 1987), studies reporting male mate choice based on female cues other than body size or TLM are scarce. In our study, none of the animals were infected by acanthocephalan parasites, but we cannot rule out the possibility that other, undescribed cues played a role in female quality assessment. Alternatively, males may have simply not compared the quality of the 2 females, hence basing their decision of switching on the quality of their current female only. Such a behavior may be adaptive if quality comparison between possible mates is too much costly or too difficult to achieve without errors in quality assessment. In *G. pulex*, males have been described to assess mate quality over a complex behavioral sequence during which they touch the female's body with their antennae for several minutes (Dick and Elwood 1989). This may be difficult to perform when males are already paired to a female, hence limiting the accuracy of quality assessments of an unpaired female. In addition, unpaired males repeatedly engage in contests with paired males to dislodge them from their females (Birkhead and Clarkson 1980; Ward 1983; Elwood et al. 1987; Cothran 2008b). Males have been shown to be able to manipulate simultaneously 2 females at the same time, presumably for quality assessment (Dick 1992). During these manipulations, paired males have looser grips for each female (when holding 2 females at the same time, males only use 1 claw instead of 2 to grab each female, personal observation) and they may be particularly vulnerable to interferences with rival males.

Based on the above hypothesis, males must know the absolute value of their own female before deciding to switch or not. However, it has been suggested that quality estimations based on absolute scalar measures are rare if not absent in nature (Bateson and Healy 2005; Ariely and Norton 2008; Vlaev et al. 2011). In *G. pulex*, we indeed cannot rule out the possibility that paired males based their mate choice on a relative rather than absolute

estimation of female quality. Instead of comparing the quality of their current female to the quality of an unpaired female at proximity, it is possible that males valued their current female relatively to the quality of other females they mated or sampled during past reproductive experiences (Luttbeg 1996; McNamara et al. 2006; Fawcett and Bleay 2009; Bleu et al. 2012). Hunte et al. (1985) have suggested that males of the closely related amphipod species *Gammarus lawrencianus* use prior estimate of the quality distribution of unpaired females for mate choice. Males can thereby compare the quality of encountered females with the expected quality distribution of females still available for pairing in the population. A similar assessment strategy is consistent with our results. Males could have decided to switch when the quality of their current female was lower than the average expected quality of unpaired females in the population. In our experiment, males only switched when their female was rather small and far from molting leading to several situations of apparent suboptimal choice. However, the point to appreciate is that precopulatory mate guarding by males depletes the amount of unpaired females close to molting in populations so that these females may be very rarely found. Unpaired females we proposed to males may have been of higher quality than the quality normally expected by males under natural conditions of competition, leading them to remain paired with their current female. Basing mate switching decision on the quality of their current female may be suboptimal in rare situations where paired males could encounter unpaired females of relatively greater quality than their current female (like in our experiment), but it is a rule of thumb that presumably performs well in natural populations under strong competition for receptive females and where unpaired females close to molting are scarce (Hutchinson and Gigerenzer 2005).

Prior estimations of unpaired females' quality distribution may not be straightforward. Putting aside the fact that thresholds of current female's quality for switching decision could be fixed, males may achieve better estimation of unpaired females' quality distribution with experience allowing them to flexibly adjust their switching decision rule. Previous mating events as well as successive switching and guarding of new females should influence males' future mate
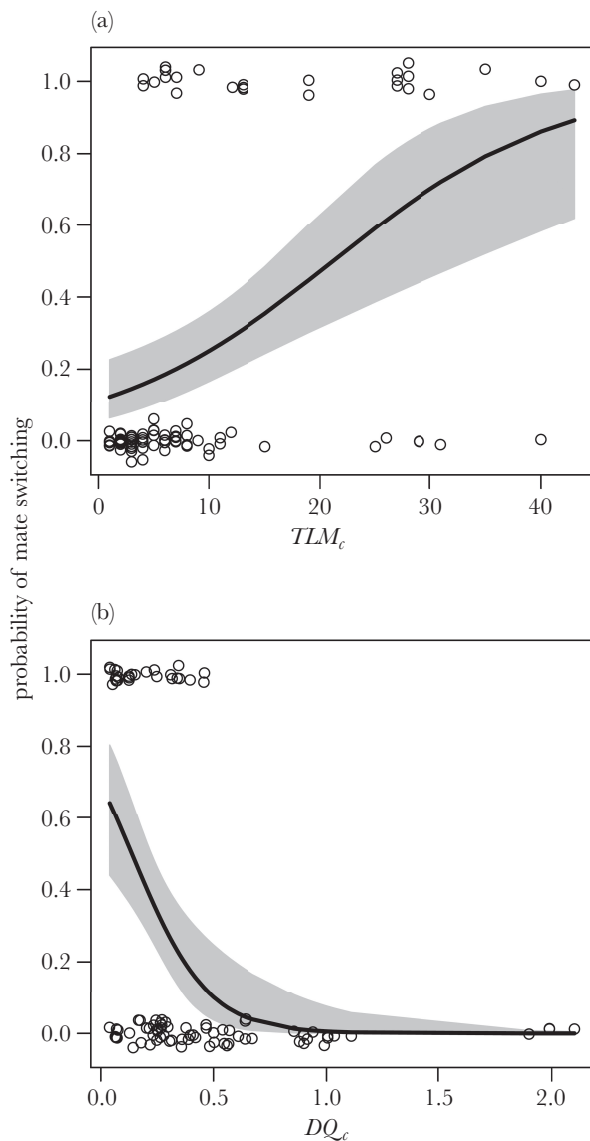
Figure 1
Male probability of mate switching as a function of (a) the TLM_c and (b) the current female ratio of size over TLM (DQ_c). Low values of TLM_c and high values of DQ_c were associated with greater female quality. We added a jitter on the *y*-axis values for representation purposes. This does not account for the real values, which only take 0 when the male stayed with its current female or 1 when it switched females. Solid curves and gray areas represent respectively the estimated logistic regression and its 95% CI, based on a generalized linear model with a logit link function.

choice decisions. Note also that the level of competition for female access experienced by males should indirectly inform them about the quality of females remaining unpaired in the population (i.e., with increasing competition, unpaired females should be rather far from molting). Such a prior estimation is implicit in most theoretical models of precopulatory mate guarding evolution (Grafen and Ridley 1983; Yamamura 1987; Härdling et al. 2004) and decreased choosiness has been observed experimentally in males kept in highly competitive environments (Dunham and Hurshman 1990; Jormalainen 1998).

Male mate choice in amphipods may proceed as guarding-switching sequences. A male may first pair with the first encountered female without discrimination and gather information about the female's quality while guarding (Hunte et al. 1985; Goshima et al. 1998). This is in accordance with our results and previous findings on *G. pulex* (Dick and Elwood 1989; Franceschi et al. 2010). Most males rapidly paired with the first female we presented them to. This also seems to be a general mate choice pattern in several other species when mates are encountered sequentially (Dougherty and Shuker 2014). If unpaired females are available, the paired male can then decide to switch females based on its knowledge of its current mate's quality and the average quality of unpaired females in the population. This is of particular interest considering that precopulatory mate guarding has almost only been considered as a male competitive strategy (Grafen and Ridley 1983; Jormalainen 1998; Härdling et al. 2004; Harts and Kokko 2013), but never as a mate sampling strategy. Besides, such a decision rule may be particularly effective under strong competition between males for access to receptive females. Because the sampling process occurs while males are already paired, males will eventually have access to reproduction even if they do not find a better partner, thereby limiting the cost of losing reproductive opportunities when searching for good quality mates. Finally, the female quality below which a male decides to leave its current partner represents its threshold of mating preference expressed under competitive situation (as the male's estimation of expected female quality in the population depends on the quality distribution of unpaired females). On a methodological perspective, studying mate choice under a mate switching context therefore provides an estimation of individual choosiness under competition for mate access (see also Wagner 1998).

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