

Male courtship repeatability and potential indirect genetic benefits in a wolf spider

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Indirect benefits derived by females that mate with males that express preferred traits are important to our understanding of 'good genes' models of sexual selection. However, few studies have explored male courtship behaviours with potential indirect benefits conferred to females in order to ascertain whether these behaviours serve as honest indicators of male quality. Using a common species of wolf spider, *Pardosa milvina*, we addressed the honesty of male courtship behaviours in two laboratory experiments. In our first experiment, we quantified the repeatability of courtship rate in adult males that were manipulated to be in high or low condition and were sequentially presented with adult virgin females that similarly differed in body condition. In our second experiment, we explored the effect of male courtship rate on several measures of fitness: number of offspring produced, days until offspring emerged and offspring viability measured as offspring survival. Our experiments show that male courtship rate is statistically significantly repeatable except when males in high condition have repeated encounters with females in low condition. Our results also reveal that females have the potential to gain indirect genetic benefits by mating with males that naturally court at high rates: females produced more offspring that emerged from eggsacs sooner and survived starvation better compared to females that mated with males that naturally courted at low rates. Our study provides additional support that male courtship rate is an honest indicator of quality, and it makes the novel finding that the repeatability of courtship rate is context sensitive.

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The roles of elaborate male sexual traits such as ornaments, courtship behaviours, calls and other signals in sexual selection have received intensive study over a period of decades (Andersson 1982, 1994). Although alternative explanations abound, two contrasting hypotheses have emerged as primary explanations for female choice for male sexual traits: one suggests that male secondary sexual characters are arbitrary yet aesthetically attractive to females, an idea originally envisaged by Fisher (1930), and the other claims that they are honest indicators of underlying genetic quality (Zahavi 1975). The latter posits that females gain an advantage through the success of their offspring (an indirect benefit) because offspring sired by these males have above-average attractiveness and/or viability (Zahavi 1975, 1977; Iwasa et al. 1991; Andersson 1994). Although there have been surprisingly few empirical studies demonstrating female-choice-derived fitness benefits (Kokko et al. 2003), most have provided at least partial

support for this hypothesis (Simmons 1987; Ryan et al. 1990; Alatalo et al. 1998). For example, the sons of highly successful male field crickets, *Gryllus bimaculatus*, mate more frequently as adults than do sons of less successful males (Wedell & Tregenza 1999), yet it remains unclear whether females derive indirect benefits via mate choice per se. Watson (1998), working with sierra dome spiders, *Neriene litigiosa*, showed that females that mated with males superior in male–male competition had faster growing offspring in the early instars, a life stage entailing a severe survival bottleneck. This is a rare study in that Watson (1998) controlled for female multimale mating and several maternal effects on offspring fitness. Because few studies have demonstrated female preferences for genetic benefits, additional information is needed about the honesty of male sexual traits that females prefer and whether these traits translate into improved offspring performance to better understand the evolution of sexual communication (Rivero et al. 2000; Fuller et al. 2005).

One potentially honest measure of the genetic basis of male sexual traits is the repeatability of courtship behaviours. A trait can be an honest indicator of genetic quality if it is reliable, and if it is not repeatable in a given context, then it may be unreliable. However, one of the chief tasks of a choosy mate is to analyse

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whether the context in which the signal of an individual is being sent is one that makes the signal reliable. The repeatability of male mating behaviours has been used in quantitative genetics to explore the genetic contribution underlying behaviour by relating the proportion of variance in a character that occurs among rather than within individuals, or its heritability (Falconer 1960; Lessells & Boag 1987; Hoikkala & Isoherranen 1997; Aragaki & Meffert 1998; Reinhold et al. 2002; Sattman & Cocroft 2003; Holveck & Riebel 2007; Bell et al. 2009). Consistent or repeatable differences between courting males, which tie behaviour to genetic constitution, can be an important prerequisite for the evolution of female choice, and if a trait, like courtship rate, is manifested with high fidelity within individuals and differs between individuals, it can respond to selection (Boake 1989; Aragaki & Meffert 1998). A highly repeatable male courtship behaviour can only be useful to females if it reveals honest information about the genetic quality of a male. Courtship behaviours with low repeatabilities can be unimportant to females because of the inconsistency of the signals (Rivero et al. 2000) and, therefore, may not be targets of sexual selection, unless females can track the contexts that affect the quality of the signal's information content and adjust their responses accordingly. Thus, attempts to tease apart the factors that affect the repeatability of male courtship signals would shed valuable insight into the reliability of information available to females, especially if those signals are honest indicators of the fitness benefits that may accrue by mating with particular males.

Wolf spiders (Araneae: Lycosidae) are well suited for studies of male courtship repeatability and the potential indirect benefits derived by female choice, since they are among the most intensively studied invertebrate taxa in modern investigations of sexual communication (Mappes et al. 1996; Kotiaho et al. 1999; Rypstra et al. 2003; Hebets 2005; Taylor et al. 2005, 2006; Roberts & Uetz 2005; Lynam et al. 2006; Delaney et al. 2007; Uetz & Norton 2007; Gibson & Uetz 2008). The wolf spider *Pardosa milvina* is an active cursorial predator that lives in agricultural and early successional habitats throughout much of the midwestern United States, often reaching high densities (Marshall & Rypstra 1999; Marshall et al. 2000, 2002; Persons et al. 2002). When in the presence of adult females or pheromone-laden female silk, adult male *P. milvina* engage in conspicuous courtship displays that include repeated front leg raises (Rypstra et al. 2003; Hoefler et al. 2008). Although virgin females are less choosy than mated females, both show preferences for males that engage in more vigorous courtship as evidenced by a high rate of leg raises (and body shakes) (Rypstra et al. 2003). This result suggests that courtship rate reveals something to females about male quality and, if it is an honest indicator, it should be repeatable within a given context. Underlying this female preference may be the relationship that courtship rate has with male condition and viability: compared to males that court at low rates, males that court at high rates are in relatively good phenotypic condition, a measure of the resources available to improve fitness (Lorch et al. 2003), and are more likely to escape predation (Hoefler et al. 2008). However, it is unknown whether male *P. milvina* courtship rates are genetic, or repeatable, or whether females gain indirect fitness benefits by mating with males that court at high rates.

We conducted two experiments to explore context-dependent repeatability of male courtship and its potential to indicate male quality that would benefit the offspring of a female. Firstly, we calculated the context-dependent repeatability of male courtship rate by determining how the body condition of both males and females affected the frequency of leg raises. Secondly, we tested whether or not laboratory-mated females use male courtship rate as an indicator of male genetic quality by quantifying a number of direct and indirect fitness components.

METHODS

Acquisition and Maintenance of Spiders

All *P. milvina* used were collected as juveniles from Miami University's Ecology Research Center (Oxford, Butler County, OH, U.S.A.) during the summer and autumn of 2007 and reared to adulthood in the laboratory. We maintained spiders individually in clear cylindrical plastic containers (5.5 cm high, 5.5 cm diameter), adding a 2 cm layer of a moistened mixture of peat moss and potting soil (1:1) as a substrate to minimize risks of desiccation. Spiders were fed two domestic crickets (2 mm; *Acheta domesticus*) twice per week unless they were assigned to experimental feeding regimes (see below), and peat moss substrates were watered regularly. All containers with spiders were housed in an environmentally controlled chamber with approximately 70% RH, on a 13:11 h light:dark cycle and at a temperature of approximately 25 °C.

Experiment 1: Male Courtship Repeatability

We determined the repeatability of male courtship in *P. milvina* using pairs of males and females that had been maintained on feeding regimes that are known to affect body condition (Hoefler et al. 2008). After males and females matured, we randomly assigned 60 adult males and 60 adult females to one of two condition groups: a low condition group ($N = 30$ males, 30 females) and a high condition group ($N = 30$ males, 30 females). Spiders assigned to the low condition group were fed one 2 mm cricket twice per week, and spiders assigned to the high condition group were fed four 2 mm crickets twice per week. We maintained all spiders on their respective diet regimes for 3 weeks, as this feeding regime protocol produces statistically significant differences in body condition in *P. milvina* (see Hoefler et al. 2008). We subsequently randomly paired males and females in a completely crossed design such that we had four categories of paired spiders: high condition male paired with high condition female ($N = 15$), high condition male paired with low condition female ($N = 15$), low condition male paired with high condition female ($N = 15$) and low condition male paired with low condition female ($N = 15$).

To conduct a trial, we placed a virgin female of a pair of spiders in an arena (described below) and allowed her to deposit cues (silk, excreta and associated pheromones) on a filter paper substrate for 1 h before the trial began. Substrate-borne cues are known to elicit male courtship behaviours including front leg raises (Rypstra et al. 2003). After 1 h of cue deposition, we corralled the female in the centre of the arena under an overturned glass vial (8 cm high, 2 cm diameter) and introduced the virgin male. Male *P. milvina* could thus respond to both visual and chemotactile cues from females, but they could not physically interact. Each male was allowed to court the same female for 5 min on three consecutive days with 24 h between each trial so that we were able to record three courtship rates for each male.

Arenas used in trials were constructed from cylindrical plastic containers (7.75 cm high, 19 cm diameter), and in each arena, we poured 250 ml of DAP® Plaster of Paris (DAP Products Inc., Baltimore, MD, U.S.A.) to create a smooth, level floor. Before trials began, we placed a piece of Whatman® Filter Paper (Whatman International Ltd, Kent, ME14 2LE, U.K.) on the plaster floor to serve as a substrate. Before and after each use, we washed reused arena containers thoroughly in warm soapy water and rinsed them with 95% ethanol to remove residual chemical cues from spiders. We placed arenas in an isolated booth under a Panasonic WV-CP470 video camera located in an environmentally controlled room. The camera was connected to a GOVIDEO R6740 DVD recorder located

in a nearby laboratory room. We videorecorded all trials and later scored them by recording the number of male *P. milvina* leg raises that occurred during the 5 min trial period as well as courtship rate (=leg raises/min).

To calculate the repeatabilities of male courtship rate, we followed the methods of Lessells & Boag (1987) using intraclass correlation coefficients, which were based on variance components derived from analyses of variance (Table 1). We also conducted a repeated measures ANOVA to examine the effect that treatment (=male/female pairing category) and time had on male courtship rate. All statistical analyses were conducted using JMP™ 7.0 statistical software (SAS, Cary, NC, U.S.A.).

Experiment 2: Male Courtship Rate and Indirect Benefits

We explored the possible indirect benefits accrued by females that mated with males that courted at particular rates using a separate group of adult virgin *P. milvina*. All of these animals were fed two 2 mm crickets twice per week to minimize diet effects on male courtship rate, which allowed us to assume that any differences in courtship were due, at least in part, to genetic differences. We used a pretrial to categorize males into high and low courtship groups. A pretrial involved placing an adult virgin female in an arena, allowing her to deposit cues for 1 h, corralling her under a glass vial and allowing a male to court her for 5 min. We counted the number of front leg raises performed by all males from videorecordings and separated males using the upper and lower quartile ranges. Males that courted at high rates were those with courtship rates in the upper quartile range ($\bar{X} + SE = 5.9 + 0.48$ leg raises/min, $N = 21$) and those in the low courtship rate group were those with courtship rates in the lowest quartile range ($3.04 + 0.11$ leg raises/min, $N = 36$). During test trials, we used the same basic protocol except that after the 5 min period during which the male courted the sequestered female, the vial was removed and the pair was allowed to interact for an additional hour or until mating ended. For each mated female, we recorded several components of fitness: days until an eggsac was produced, days until spiderlings hatched, the number of spiderlings that emerged and spiderling survival. To measure spiderling survival, we separated them individually into empty clear plastic containers (5.5 cm high, 5.5 cm diameter) at emergence and checked them once a day until they died. Spiderlings were not fed or offered water, and they were maintained in an environmentally controlled chamber with approximately 70% RH.

We compared the courtship rates of males assigned to the high courtship rate and low courtship rate groups during trials using a two-sample *t* test. The frequency of mating between treatments (high court versus low court males) was compared using a contingency test. To compare differences in fitness components of females that mated with males that courted at high versus low rates, we conducted Mann–Whitney *U* tests for days until eggsac production and for days until spiderling emergence, because data were not normally distributed. We also conducted a two-sample *t* test for number of emerged spiderlings and a Kaplan–Meier survival regression analysis to compare survival distributions of spiderlings.

RESULTS

Experiment 1: Male Courtship Repeatability

Male courtship rate (front leg raises) showed significant repeatability for trials involving high condition males paired with high condition females ($r = 0.461$, $N = 15$, $P = 0.0017$), low condition males paired with high condition females ($r = 0.324$, $N = 15$, $P = 0.02$) and low condition males paired with low condition females ($r = 0.444$, $N = 15$, $P = 0.002$). Male courtship rate did not

Table 1

Courtship rate repeatabilities (r) and one-way ANOVA of courtship rate for male wolf spiders, *Pardosa milvina*, based on measures from the three consecutive encounters with adult females

Pair	r	Courtship rate	
		$F_{14,30}$	P
HC _m –HC _f	0.461	3.57	0.0017
HC _m –LC _f	0.031	1.09	0.4
LC _m –HC _f	0.324	2.44	0.02
LC _m –LC _f	0.444	3.39	0.002

HC: high condition; LC: low condition; m: males; f: females.

show significant repeatability for trials involving pairs of high condition males and low condition females ($r = 0.031$, $N = 15$, $P = 0.4$; Table 1). A repeated measures ANOVA revealed a significant effect of treatment on courtship rate ($F_{3,56} = 6.95$, $P < 0.0001$) as well as an effect of time on courtship rate, with courtship rate declining over trials with high condition males paired with low condition females ($F_{2,55} = 6.28$, $P = 0.0035$; Fig. 1).

Experiment 2: Male Courtship Rate and Indirect Benefits

Of the 21 trials involving males that courted at high rates, 14 (67%) resulted in mating, whereas only 14 of 36 (39%) trials involving males that courted at low rates resulted in successful copulation, and the difference between these two was statistically significant (contingency test: $\chi^2_1 = 4.15$, $N = 57$, $P = 0.04$). The males that we singled out as courting at a high rate in pretrials courted at significantly higher rates than males assigned to the low courtship rate group (paired *t* ratio test: $t_1 = 10.1$, $N = 28$, $P < 0.001$). The number of days that elapsed before females produced eggsacs did not depend upon whether a female mated with a male that courted at a high rate versus a low rate (Mann–Whitney *U* test: tied $Z = 1.06$, $N_1 = N_2 = 14$, $P = 0.29$). Spiderlings sired by males that courted at high rates emerged from eggsacs significantly earlier than spiderlings sired by males that courted at low rates (Mann–Whitney *U* test: tied $Z = 2.85$, $N_1 = N_2 = 14$, $P = 0.004$;

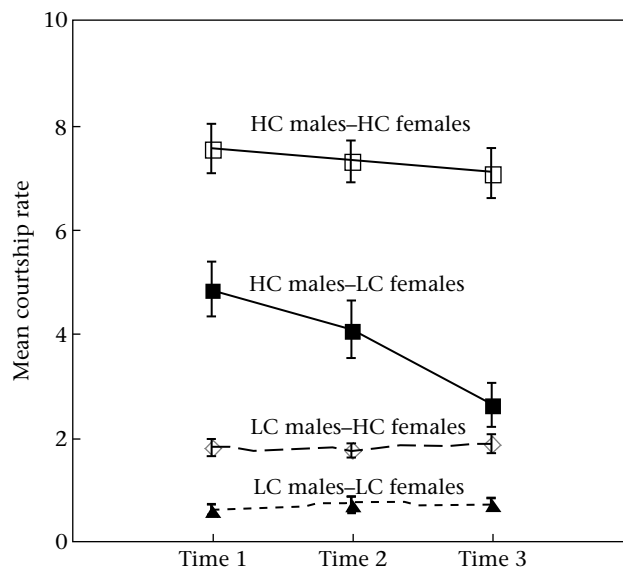


Figure 1. Mean \pm SE male *P. milvina* courtship rate over three successive encounters with the same female: high condition (HC) males paired with high condition females, high condition males paired with low condition (LC) females, low condition males paired with high condition females, and low condition males paired with low condition females.

Fig. 2). Females that mated with high courtship males produced significantly more spiderlings than females that mated with low courtship males (t ratio test: $t_{26} = 4.75$, $N = 28$, $P < 0.0001$; Fig. 3). Spiderlings sired by males that courted at high rates had significantly greater survivorship ($\bar{X} = 2.32$ days, maximum = 4 days) than spiderlings sired by low courtship males ($\bar{X} = 1.86$ days, maximum = 3 days) (Mantel–Cox test: $\chi^2_1 = 126.5$, $N = 945$, $P < 0.0001$).

DISCUSSION

Although male *P. milvina* courtship rate, or at least the frequency of front leg raises, varied depending on both male and female condition, it was highly repeatable in three of the four scenarios that we tested. This result indicates that the ability to retain constancy in courtship rate varies not with male or female condition alone but with context, namely a specific permutation of male/female pairs that varied in body condition. Specifically, in all circumstances where a male had an opportunity to court a female whose condition was equivalent to or exceeded his, courtship was repeatable. Only when males in high condition were paired with females in low condition was courtship not repeatable; it declined steadily with each exposure (Fig. 1). Overall, mating was more likely to occur when males courted at high rates, and females that mated with high courtship males produced more offspring that emerged from eggsacs sooner and survived longer than did females that mated with low courtship males. Taken together, these results are consistent with the hypothesis that courtship is a genetic trait that varies by condition and context, and that courtship rate is an honest indicator of male quality. Our results call into question the notion that conventional repeatability studies reveal whether a signal is honest or whether the underlying fitness qualities on which the quality of the signal depends are heritable. In addition, our results suggest that studies of repeatability that do not take into account reasons why individuals should not always engage in a behaviour at the same rate will probably underestimate repeatabilities.

Repeatability can be used to examine the consistency of male courtship signals in addition to providing an indication of the potential utility of the signal as an honest indicator of quality. For example, the ‘hisses’ or acoustic signals produced by male Madagascar hissing cockroaches, *Gromphadorhina portentosa*, are

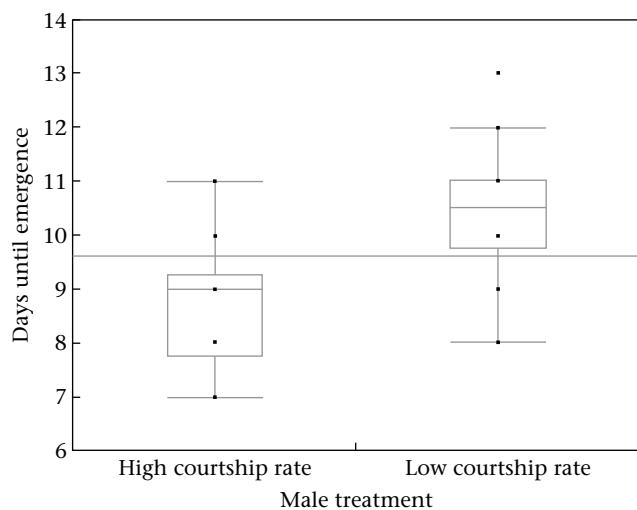


Figure 2. Days until emergence from eggsacs by *P. milvina* spiderlings sired by males that courted at high versus low rates. Box plots show lower and upper quartiles, lines across boxes identify the median sample value, and points are unjittered data.

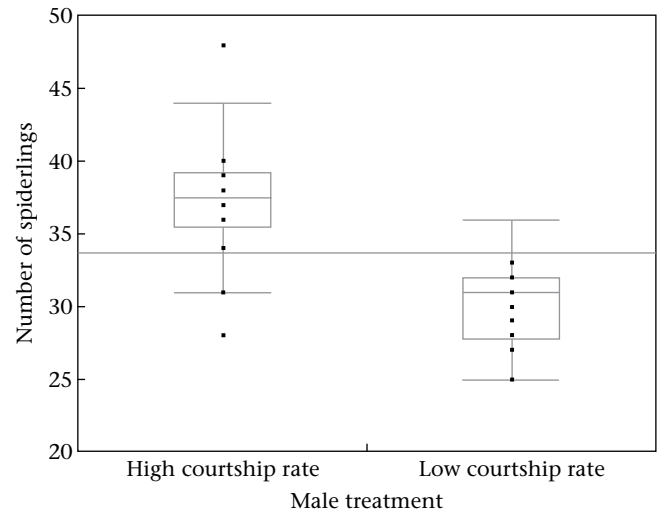


Figure 3. Number of *P. milvina* spiderlings that emerged from eggsacs sired by males that courted at high versus low rates. Box plots show lower and upper quartiles, lines across boxes identify the median sample value, and points are unjittered data.

repeatable, and larger, dominant males hiss significantly more often and for longer durations than subordinate males (Clark & Moore 1995). *Pardosa milvina* male courtship rate is dependent on condition, males in high condition court at significantly higher rates than males in low condition (Hoefler et al. 2008) and courtship rate is repeatable in all situations where males have an opportunity to mate with a female in average or above-average condition. Thus, males appear to be setting a consistent courtship level for prospective mates that are in similar or better condition, but not in poorer condition. When a high-quality male was exposed successively to the same low-quality female, he lowered his courtship intensity with each exposure. This finding suggests that the male gathered information during each exposure that the female was unresponsive and/or was not worth maximum courtship effort. Because of the growing body of evidence revealing that courtship and mating behaviours are sensitive to context and condition and are more flexible than previously perceived (Dugatkin 1996; Owens et al. 1999; White 2004; Dukas 2006), one intriguing hypothesis that may offer a starting point for further investigation involves condition- and experience-mediated learning. Learning or imprinting of particular phenotypes occurs in other wolf spiders (Hebets 2003), and in *P. milvina*, males reduce courtship intensity towards previously mated females (Rypstra et al. 2003).

The inconsistent courtship rate of high condition male *P. milvina* paired with low condition females may be a product of an effect of condition acting in tandem with experience. Several studies of experience effects on mating behaviours strongly suggest that learning is critical, which may have important and yet underappreciated implications for sexual selection (Gibson & Langen 1996; Lachlan & Servadio 2004). For example, male garter snakes, *Thamnophis sirtalis*, exposed to females of different sizes causes them to alter their courtship criteria (Shine et al. 2006). Learning effects can also be mediated by condition. For example, song learning in passerines can be modulated by nutritional stress on neural development (Nowicki et al. 1998), and high body condition indirectly promotes learning in meerkats, *Suricata suricatta* (Thornton 2008). In our study, only male *P. milvina* in high body condition significantly reduced their rates of courtship over time towards females in low condition, which explains the lack of repeatability. This finding is consistent with the idea that, in

contrast to males in low condition, males in high condition gain information via learning about a prospective mate or about the mean quality of local females and adjust their courtship rates accordingly. This may be fitness enhancing if the threshold of the female's acceptance rate is low and contingent upon detectable cues, since high courtship rates in wolf spiders have evolutionarily meaningful costs, including energetic (Kotiaho 2000) and predation (Lindström et al. 2006; Hoefler et al. 2008) costs.

Mutual mate choice (Owens & Thompson 1994; Johnstone et al. 1996; Bonduriansky 2001; Kokko & Johnstone 2002), perhaps operating in concert with learning, may also be crucial for explaining context-sensitive repeatability of male *P. milvina* courtship rates. In arthropods and other taxa, mounting evidence suggests that the assessment of detectable cues revealing information about species identity and condition is important to mate choice in both sexes (Bonduriansky 2001; Rypstra et al. 2003; McNamara et al. 2004; Sato & Goshima 2007; Aquiloni & Gherardi 2008a). Males and females may also be expected to respond to different cues and/or to use different sensory modalities to enhance fitness. For example, in *P. milvina*, visual and possibly vibratory cues are critical for female choice, whereas chemotactile cues are critical for the assessment of females by males (Rypstra et al. 2003). Quantities or qualities of silk and pheromonal cues used by female *P. milvina* to attract males may also be condition dependent, and thus, males in high condition may be more sensitive to these cues and their responses may be mediated by learning to a greater degree than are responses of males in low condition. Males in high condition did court females in low condition, albeit inconsistently and less over time, which suggests that females in low condition still have potential reproductive value and/or that some components of male courtship signalling are important for species recognition. It may be especially important for an adult male to be correctly recognized as a potential mate by a female in low condition, as this state may increase risks of precopulatory cannibalism (Andrade 1998). Furthermore, males in high condition may have more to lose (e.g. greater future reproductive success) when courting a potentially cannibalistic female (i.e. one in low condition), although males in better body condition may also be more adept at fending off aggressive females (e.g. Persons & Uetz 2005). Finally, females may also incur costs, especially if they are in low condition, from mating with aggressive males in high condition. Females may show reluctance to mate in these situations. If so, then it would be important for males to temper their courtship displays, and this may also help explain the reduced courtship of low condition females by high condition males.

In our second experiment, we controlled the male phenotype to the extent possible by selecting animals that courted at a high or low rate in a pretrial. This set-up allowed us to demonstrate that choosing to mate with a male that courted at a high rate may have conferred indirect benefits to the female. High courtship rates led to faster emergence of spiderlings, more offspring and higher survival of those offspring. Thus, in spite of the contextual effects that we observed on repeatability in experiment 1, high courtship rate appears to be an indicator of high-quality genes, and females mating with these males are able to pass beneficial qualities to their offspring (Hunt et al. 2005). The mechanism by which these traits influence offspring is unclear; although males that courted at high and low rates were maintained on the same diet, males that courted at high rates may have produced more nutritive seminal products that could have provided benefits to offspring (Eberhard & Cordero 1995). Alternatively, females may be manipulating some of these measures of fitness. In other taxa, females produce larger eggs (e.g. Aquiloni & Gherardi 2008b) or more eggs after mating with preferred males, which can affect offspring quality (but see Gowaty et al. 2007) but may not be directly related to the overall

genetic quality of the male. A future avenue of inquiry that would help resolve this would include investigations of the heritability of male courtship rate.

Female *P. milvina* prefer males that court at high rates, because they are more likely to mate with them (Brautigam & Persons 2003; Rypstra et al. 2003; Taylor et al. 2005; Lynam et al. 2006; this study). High courtship males produce more offspring, and their offspring develop more quickly prior to emergence from eggsacs and have higher survivorship. Another critical assumption of sexual selection models involving indirect benefits is that male sexual signals are heritable. In our second experiment, the variation in courtship rate between males might have been caused either by environmental influences during development or by heritable differences between males. Final resolution will come from more sophisticated studies that aim to determine whether female choice of male courtship rate can evolve as a correlated response to selection acting on genes coding for male quality.

In conclusion, male *P. milvina* courtship rate is repeatable and not affected by body condition alone, yet is sensitive to context, which may be driven by condition-mediated learning and/or effects of mutual mate assessment. This finding provides additional support for the notion that male courtship rate provides some indication of male quality. Adult females preferred to mate with males that courted at high rates, and this preference may have evolved because of indirect benefits manifested as offspring that develop quickly and have high survivorship. To better understand the underlying reasons why preferences for high courtship rates may have evolved, it would be valuable to study the heritability of male courtship rate as well as female preferences for male courtship rate.

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References

- Alatalo, R. V., Kotiaho, J., Mappes, J. & Parri, S. 1998. Mate choice for offspring performance: major benefits or minor costs? *Proceedings of the Royal Society of London, Series B*, **265**, 2297–2301.
- Andersson, M. 1982. Sexual selection, natural selection and quality advertisement. *Biological Journal of the Linnean Society*, **17**, 375–393.
- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Andrade, M. C. B. 1998. Female hunger can explain variation in cannibalistic behavior despite male sacrifice in redback spiders. *Behavioral Ecology*, **9**, 33–42.
- Aquiloni, L. & Gherardi, F. 2008a. Mutual mate choice in crayfish: large body size is selected by both sexes, virginity by males only. *Journal of Zoology*, **274**, 171–179.
- Aquiloni, L. & Gherardi, F. 2008b. Evidence of female cryptic choice in crayfish. *Biology Letters*, **4**, 163–165.
- Aragaki, D. L. R. & Meffert, L. M. 1998. A test of how well repeatability of courtship predicts its heritability. *Animal Behaviour*, **55**, 1141–1150.
- Bell, A. M., Hankison, S. J. & Laskowski, K. L. 2009. The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, **77**, 771–783, doi:10.1016/j.anbehav.2008.12.022.
- Boake, C. R. B. 1989. Repeatability: its role in evolutionary studies of mating behavior. *Evolutionary Ecology*, **3**, 173–182.
- Bonduriansky, R. 2001. The evolution of male mate choice in insects: a synthesis of ideas and evidence. *Biological Reviews*, **76**, 305–339.
- Brautigam, S. E. & Persons, M. H. 2003. The effect of limb loss on the courtship and mating behavior of the wolf spider *Pardosa milvina* (Araneae: Lycosidae). *Journal of Insect Behavior*, **16**, 571–587.
- Clark, D. C. & Moore, A. 1995. Variation and repeatability of male agonistic hiss characteristics and their relationship to social rank in *Gromphadorhina portentosa*. *Animal Behaviour*, **50**, 719–729.

- Delaney, K. J., Roberts, J. A. & Uetz, G. W. 2007. Male signaling behavior and sexual selection in a wolf spider (Araneae: Lycosidae): a test for dual functions. *Behavioral Ecology and Sociobiology*, **62**, 67–75.
- Dugatkin, L. A. 1996. Copying and mate choice. In: *Social Learning in Animals: the Roots of Culture* (Ed. by C. M. Heyes & B.G. Galef Jr), pp. 85–106. San Diego: Academic Press.
- Dukas, R. 2006. Learning in the context of sexual behavior in insects. *Animal Biology*, **56**, 125–141.
- Eberhard, W. G. & Cordero, C. 1995. Sexual selection by cryptic female choice on male seminal products: a new bridge between sexual selection and reproductive physiology. *Trends in Ecology & Evolution*, **10**, 493–496.
- Falconer, D. S. 1960. *Introduction to Quantitative Genetics*. London: Longman.
- Fisher, R. A. 1930. *The Genetical Theory of Natural Selection*. Oxford: Clarendon.
- Fuller, R. C., Houle, D. & Travis, J. 2005. Sensory bias as an explanation for the evolution of mate preferences. *American Naturalist*, **166**, 437–446.
- Gibson, R. M. & Langen, T. A. 1996. How do animals choose their mates? *Trends in Ecology & Evolution*, **11**, 468–470.
- Gibson, J. S. & Uetz, G. W. 2008. Seismic communication and mate choice in wolf spiders: components of male seismic signals and mating success. *Animal Behaviour*, **75**, 1253–1262.
- Gowaty, P. A., Anderson, W. W., Bluhm, C. K., Drickamer, L. C., Kim, Y.-K. & Moore, A. J. 2007. The hypothesis of reproductive compensation and its assumptions about mate preferences and offspring viability. *Proceedings of the National Academy of Sciences, U.S.A.*, **104**, 15023–15027.
- Hebets, E. A. 2003. Sub-adult experience influences adult mate choice in an arthropod: exposed female wolf spiders prefer males of a familiar phenotype. *Proceedings of the National Academy of Sciences, U.S.A.*, **100**, 13390–13395.
- Hebets, E. A. 2005. Attention-altering signal interactions in the multimodal courtship display of the wolf spider *Schizocosa uetzi*. *Behavioral Ecology*, **16**, 75–82.
- Hoefler, C. D., Persons, M. H. & Rypstra, A. L. 2008. Evolutionarily costly courtship displays in a wolf spider: a test of viability indicator theory. *Behavioral Ecology*, **19**, 974–979.
- Hoikkala, A. & Isoherranen, E. 1997. Variation and repeatability of courtship song characters among wild-caught and laboratory-reared *Drosophila montana* and *D. littoralis* males (Diptera: Drosophilidae). *Journal of Insect Behavior*, **10**, 193–202.
- Holveck, M. J. & Riebel, K. 2007. Preferred songs predict preferred males: consistency and repeatability of zebra finch females across three test contexts. *Animal Behaviour*, **74**, 297–309.
- Hunt, J., Brooks, R. & Jennions, M. D. 2005. Female mate choice as a condition-dependent life-history trait. *American Naturalist*, **166**, 79–92.
- Iwasa, Y., Pomiankowski, A. & Nee, S. 1991. The evolution of costly mate preferences. II. The 'handicap' principle. *Evolution*, **45**, 1431–1442.
- Johnstone, R. A., Reynolds, J. D. & Deutsch, J. C. 1996. Mutual mate choice and sex differences in choosiness. *Evolution*, **50**, 1382–1391.
- Kokko, H. & Johnstone, R. A. 2002. Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signaling. *Philosophical Transactions of the Royal Society of London, Series B*, **357**, 319–330.
- Kokko, H., Brooks, R., Jennions, M. D. & Morley, J. 2003. The evolution of mate choice and mating biases. *Proceedings of the Royal Society of London, Series B*, **270**, 653–664.
- Kotiaho, J. S. 2000. Testing the assumptions of conditional handicap theory: costs and condition dependence of a sexually selected trait. *Behavioral Ecology and Sociobiology*, **48**, 188–194.
- Kotiaho, J. S., Alatalo, R. V., Mappes, J. & Parri, S. 1999. Sexual signalling and viability in a wolf spider (*Hygrolycosa rubrofasciata*): measurements under laboratory and field conditions. *Behavioral Ecology and Sociobiology*, **46**, 123–128.
- Lachlan, R. F. & Servedio, M. R. 2004. Song learning accelerates allopatric speciation. *Evolution*, **58**, 2049–2063.
- Lessells, C. M. & Boag, P. T. 1987. Unrepeatable repeatabilities: a common mistake. *Auk*, **104**, 116–121.
- Lindström, L., Ahtiainen, J. J., Mappes, J., Kotiaho, J. S., Lyytinen, A. & Alatalo, R. V. 2006. Negatively condition dependent predation cost of a positively condition dependent sexual signaling. *Journal of Evolutionary Biology*, **19**, 649–656.
- Lorch, P. D., Proulx, S., Rowe, L. & Day, T. 2003. Condition-dependent sexual selection can accelerate adaptation. *Evolutionary Ecology Research*, **5**, 867–881.
- Lynam, E. C., Owens, J. C. & Persons, M. H. 2006. The influence of pedipalp autotomy on the courtship and mating behavior of *Pardosa milvina* (Araneae: Lycosidae). *Journal of Insect Behavior*, **19**, 63–75.
- McNamara, K. B., Jones, T. M. & Elgar, M. A. 2004. Female reproductive status and mate choice in the hide beetle, *Dermestes maculatus*. *Journal of Insect Biology*, **17**, 337–352.
- Mappes, J., Alatalo, R. V., Kotiaho, J. & Parri, S. 1996. Viability costs of condition-dependent sexual male display in a drumming wolf spider. *Proceedings of the Royal Society of London, Series B*, **263**, 785–789.
- Marshall, S. D. & Rypstra, A. L. 1999. Patterns in the distribution of two wolf spiders. *Environmental Entomology*, **28**, 1052–1059.
- Marshall, S. D., Walker, S. E. & Rypstra, A. L. 2000. A test for differential colonization and competitive ability in two generalist predators. *Ecology*, **81**, 3341–3349.
- Marshall, S. D., Pavuk, D. M. & Rypstra, A. L. 2002. A comparative study of phenology and daily activity patterns in the wolf spiders *Pardosa milvina* and *Hogna helluo* in soybean agroecosystems in southwestern Ohio (Araneae, Lycosidae). *Journal of Arachnology*, **30**, 503–510.
- Nowicki, S., Peters, S. & Podos, J. 1998. Song learning, early nutrition and sexual selection in songbirds. *American Zoologist*, **38**, 179–190.
- Owens, I. P. F. & Thompson, D. B. A. 1994. Sex differences, sex ratios and sex roles. *Proceedings of the Royal Society of London, Series B*, **258**, 93–99.
- Owens, I. P. F., Rowe, C. & Thomas, A. L. R. 1999. Sexual selection, speciation and imprinting: separating the sheep from the goats. *Trends in Ecology & Evolution*, **14**, 131–132.
- Persons, M. H. & Uetz, G. W. 2005. Sexual cannibalism and mate choice decisions in wolf spiders: influence of male size and secondary sexual characters. *Animal Behaviour*, **69**, 83–94.
- Persons, M. H., Walker, S. E. & Rypstra, A. L. 2002. Costs and benefits of chemotactile mediated antipredator behavior in the wolf spider *Pardosa milvina* (Araneae: Lycosidae). *Behavioral Ecology*, **13**, 386–392.
- Reinhold, K., Reinhold, K. & Jacoby, K. J. 2002. Dissecting the repeatability of female choice in the grasshopper *Chorthippus biguttulus*. *Animal Behaviour*, **64**, 245–250.
- Rivero, A., Alatalo, R. V., Kotiaho, J. S., Mappes, J. & Parri, S. 2000. Acoustic signalling in a wolf spider: can signal characteristics predict male quality? *Animal Behaviour*, **60**, 187–194.
- Roberts, J. A. & Uetz, G. W. 2005. Discrimination of female reproductive state from chemical cues in silk by males of the wolf spider, *Schizocosa ocreata* (Araneae, Lycosidae). *Animal Behaviour*, **70**, 217–223.
- Ryan, M. J., Hews, D. K. & Wagner Jr, W. E. 1990. Sexual selection on alleles that determine body size in the swordtail *Xiphophorus nigrensis*. *Behavioral Ecology and Sociobiology*, **26**, 231–237.
- Rypstra, A. L., Wieg, C., Walker, S. E. & Persons, M. H. 2003. Mutual mate assessment in wolf spiders: differences in the cues used by males and females. *Ethology*, **109**, 315–325.
- Sato, T. & Goshima, S. 2007. Female choice in response to risk of sperm limitation by the stone crab, *Haplogaster dentata*. *Animal Behaviour*, **73**, 331–338.
- Sattman, D. A. & Coccoft, R. B. 2003. Phenotypic plasticity and repeatability in the mating signals of *Enchenopa* treehoppers, with implications for reduced gene flow among host-shifted populations. *Ethology*, **109**, 981–994.
- Shine, R., Webb, J. K., Lane, A. & Mason, R. T. 2006. Flexible mate choice: a male snake's preference for larger females is modified by the sizes of females encountered. *Animal Behaviour*, **71**, 203–209.
- Simmons, L. W. 1987. Female choice contributes to offspring fitness in the field cricket, *Gryllus bimaculatus* (de Geer). *Behavioral Ecology and Sociobiology*, **21**, 313–321.
- Taylor, P. W., Roberts, J. A. & Uetz, G. W. 2005. Flexibility in the multi-modal courtship of a wolf spider, *Schizocosa ocreata*. *Journal of Ethology*, **23**, 71–75.
- Taylor, P. W., Roberts, J. A. & Uetz, G. W. 2006. Mating in the absence of visual cues by *Schizocosa ocreata* (Hentz 1844) wolf spiders (Araneae, Lycosidae). *Journal of Arachnology*, **34**, 501–505.
- Thornton, A. 2008. Early body condition, time budgets and the acquisition of foraging skills in meerkats. *Animal Behaviour*, **75**, 951–962.
- Uetz, G. W. & Norton, S. 2007. Preference for male traits in female wolf spiders varies with the choice of available males, female age and reproductive state. *Behavioral Ecology and Sociobiology*, **61**, 631–641.
- Watson, P. J. 1998. Multi-male mating and female choice increase offspring growth in the spider *Neriene litigiosa* (Linyphiidae). *Animal Behaviour*, **55**, 403–403.
- Wedell, N. & Tregenza, T. 1999. Successful fathers sire successful sons. *Evolution*, **53**, 620–625.
- White, D. J. 2004. Influences of social learning on mate-choice decisions. *Learning & Behavior*, **32**, 105–113.
- Zahavi, A. 1975. Mate selection: a selection for a handicap. *Journal of Theoretical Biology*, **53**, 205–214.
- Zahavi, A. 1977. The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology*, **67**, 603–605.