

Consistent patterns of male mate preference in the laboratory and field

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Abstract

Mate preference by males is a widely observed phenomenon; however, it is not well understood how these preferences are expressed in wild populations. Most studies that describe the expression of male mate preference in the wild tend to observe assortative mating, where higher quality males express a strong preference for high quality females while low quality males express either no preference or a preference for low quality females. We examined male mate preference in *Bolitotherus cornutus*, the forked fungus beetle, a system that exhibits male–male combat and protracted male courtship. We conducted no-choice trials in the laboratory and monitored male courtship in a wild population. In the laboratory, we found a strong preference for larger, more fecund females across all sizes of males. Results from the field were similar to those in the lab; larger females were courted more often, and there was no relationship between the size of a male and the mean size of females he courted (i.e., no assortative mating). This study documents an unusual pattern of expression of male mate preference in the wild and suggests that mate preference by males may be underappreciated in species with intense male–male competition and non-assortative mating.

Significance statement

While males of many species express a preference for high-quality females, their preferences can change in complex

social situations such as those in wild populations, often resulting in pairing for quality. However, recent mathematical theory suggests that male preference could evolve in a variety of social contexts. We studied the mate preferences of male forked fungus beetles in the laboratory and a wild population. In the lab, males of all sizes preferred larger females. In the complex social environment of a wild population, males still preferred larger females even though there was a strong male–male competition. There was no pairing for quality as often observed in other species. These results suggest that male mate preferences may evolve in a variety of systems not just those with flexible preferences and pairing for quality.

Keywords Male mate preference · Courtship · No-choice experiments · Non-assortative mating

Introduction

Mate preference by males has recently been recognized as a widely exhibited phenomenon, occurring in a diversity of mating systems and taxa (Bonduriansky 2001; Clutton-Brock 2007; Edward and Chapman 2011). However, the expression of male mate preference in wild populations is not well understood, especially in systems without sex role reversal. When females vary in quality, especially in fecundity, it may be advantageous for males to seek high quality mates rather than courting indiscriminately (Andersson 1994; Kvarnemo and Simmons 1999). Male mate choice is hypothesized to evolve when mating behaviors are costly to males (Bonduriansky 2001; Edward and Chapman 2011). If (1) the costs of sperm production (Wedell et al. 2002; Hardling et al. 2008), courtship (Kokko and Monaghan 2001), copulation (Roberts and Uetz 2005), mate guarding (Alcock 1994), or parental care (Trivers 1972) to males are high; (2) there is variance in

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female quality; and (3) the costs of mate searching and choosing are low, then we expect males to preferentially court high quality females (Bonduriansky 2001).

While an underlying male preference for high quality females may be exhibited when males are assayed in simple social environments (e.g., just the male and one or two females), the expression of male mate preference may be altered when it occurs in different social contexts (Jennions and Petrie 1997; Fawcett and Johnstone 2003; Hardling and Kokko 2005; Callander et al. 2012). There are several factors that are hypothesized to contribute to the evolution of condition- or context-dependent expression including the level of aggression in a population; the outcome of combat, sex ratio, and density of males; and the difficulty in finding mates (Hardling and Kokko 2005). One approach to examining this context dependence is to change one social variable in a controlled laboratory setting and measure changes in the expression of male mate preference. These controlled laboratory experiments have been successful at understanding how specific mechanisms affect the expression of male mate preference (Amundsen and Forsgren 2003; Ng and Williams 2014). However, under natural conditions in complex social environments, the expression of male mate preference may be influenced by several social and extrinsic factors simultaneously that could interact to have non-intuitive effects on mating patterns (Hardling and Kokko 2005). It is the final expression of male mate preference in natural social environments upon which selection acts, therefore, if we are to understand the conditions under which male mate preference has evolved, both laboratory experiments and observations of natural patterns of male mate preference are needed.

The expression of male mate choice in the presence of a natural and complex social environment often results in assortative mating, even in systems with an underlying male mate preference across all qualities of males, because lower quality males either change their preference (toward lower quality females) or are excluded from mating with high quality females (Crespi 1989; Kokko and Johnstone 2002; Callander et al. 2012). While many field studies of male mate preference tend to examine systems with assortative mating for quality (e.g., Shine et al. 2001; Amundsen and Forsgren 2003; Bel-Venner et al. 2008; Candolin and Salesto 2009) game theory models do find evolutionary stable scenarios that could result in the evolution of male mating preference with other mating patterns (i.e., disassortative mating or no correlation for mate quality; Hardling and Kokko 2005), suggesting that male mate preference may exist in a variety of mating systems, not just those with context dependence and assortative mating. Understanding what patterns of male mate preference are expressed in wild populations may help us to understand the conditions in which male mate preference can evolve.

Several characteristics of *Bolitotherus cornutus* (the forked fungus beetle) make it an excellent system in which to document

male mate preference in the wild: clear variance in male quality based on body size, intense male competition and combat (Conner 1988, 1989), prolonged and easily observable courtship behavior (Brown and Bartalon 1986), and most importantly, there is an observable division between male preference (courtship) and female mating (copulation) decisions (Brown et al. 1985). *B. cornutus* is a tenebrionid beetle species and a classic example of density-dependent sexual selection through male combat (Conner 1988, 1989; Formica et al. 2011). Male competition in the wild results in larger males obtaining more copulations and is a clear indication of varying quality of males based on body size (Conner 1988, 1989; Formica et al. 2011). The mating behavior of *B. cornutus* makes it an especially useful system to study the expression of male mate preference because males seem to have complete control over a protracted courtship (Brown and Siegfried 1983; Brown et al. 1985; Brown and Bartalon 1986). The courtship can last for over 12 h (Brown et al. 1985), which enables us to capture most mating attempts by males with scan sampling. The courtship behavior does not include any transfer of sperm or nuptial gifts and females appear to maintain control over copulation via an anal sternite that blocks access to genitalia (Conner 1987; Conner 1988). Previous work suggests there is no female choice for male horn or body size (Brown et al. 1985; Brown and Bartalon 1986).

Identifying patterns of male mate preference in the wild, while unable to identify the specific mechanisms for individual behaviors, allows us to generate specific hypotheses about what social factors may be influencing the expression of mate choice under natural conditions. The first goal of this study was to determine if there was male mate preference for larger females in *B. cornutus* in the absence of a complex social environment and if there were differences in the expression of this preference among males of varying size. The males of many species of insects prefer larger females because larger females tend to be more fecund (Bonduriansky 2001). To address this goal, we conducted no-choice laboratory experiments. The second goal was to determine if these preferences were also expressed in the complex social environment of a natural population. To this end, we conducted an observational study of male mate preference in a large, wild population by examining naturally occurring courtship pairs.

Methods

Study species

Bolitotherus cornutus live on trees infected with polypore shelf fungi, primarily of the genera *Ganoderma* and *Fomes*, and associated dead trees (Pace 1967; Brown and Bartalon 1986; Conner 1988). The fungus brackets of these species serve as the courtship and combat arenas as well as a food source (Liles 1956; Conner 1988). Males typically encounter

females either singly or in small groups on or near fungal brackets (VF, personal observation). While the sex ratio in our meta-population is slightly female biased, it is unclear whether this translates to a biased operational sex ratio.

The mating behavior of *B. cornutus* makes it a useful system to study male preference—it appears that males largely initiate courtship as there is no observable signal from females and it often begins while females are eating or laying eggs (Conner 1987; Conner 1988). The courtship behavior consists of the males climbing onto the backs of females in the direction of his head to her abdomen (Brown et al. 1985; Brown and Bartalon 1986). The males then shake from side to side and front to back. Males have also been observed courting dead females for protracted periods of time, anecdotally suggesting that female participation is not required for initiation or continuation of courtship (VF, personal observation). Therefore, we regarded male courtship largely as an indicator of male preference. After successful copulation, males guard females by facing head to head for several hours (Brown et al. 1985; Conner 1987; Conner 1988). The guarding posture is a reliable indicator of successful spermatophore transfer (Conner 1988). There is no parental care from either sex as single eggs are laid on the surface of the fungus and larvae burrow into brackets after hatching (Weiss and West 1920; Liles 1956).

B. cornutus are holometabolous insects and so their size does not change after they eclose. *B. cornutus* are sexually dimorphic for horns and the males have a continuous distribution of horn length (Brown and Siegfried 1983). Males compete by using their horns to prevent other males from accessing females, often dislodging males that are holding onto females or throwing competitors off the bracket (Conner 1987; Conner 1988, 1989). Larger males are more likely to win fights (unpublished data) and have stronger grip strength than smaller males that should enable them to resist a takeover in the courtship or mate guarding stage (Benowitz et al. 2012). Therefore, we consider larger males to be of higher quality in this system. Previous studies have demonstrated that populations of this species experience strong sexual and social selection for larger horns/body size in males, although the magnitude of this selection gradient is larger in low-density populations than in high-density populations (Conner 1988, 1989; Formica et al. 2011). The greater copulation success by larger males is hypothesized to be due to male–male competition for access to females (Conner 1988, 1989; Formica et al. 2011) and not due to female choice for larger males (Brown and Siegfried 1983; Brown et al. 1985; Brown and Bartalon 1986).

Laboratory methods

To determine if there was male preference for female body size, we conducted mate choice trials in the laboratory in which wild-caught males and females were randomly paired with

respect to size. In systems with sequential mate choice, results from simultaneous tests may lead toward a bias in detecting choice (Barry and Kokko 2010). Because *B. cornutus* males tend to encounter females in small groups or alone in a mostly sequential fashion (VF, personal observation), we used a no-choice test. Isolating pairs in the lab also allowed us to prevent male–male competition. We used the number of unique courtship events and the total time spent courting as indicators of male preference; these are commonly used measures of pre-copulatory male preference in many taxa (Olsson 1993; Bonduriansky 2001; Couldrige 2001). Two hundred and thirty-nine *B. cornutus* were collected from 29 populations located near Mountain Lake Biological Station in Giles County, VA (37.375613, –80.523176). The state of Virginia does not require permits to collect *B. cornutus* for scientific study. Populations of *B. cornutus* are typically defined as a single log or dead standing tree that is infected with fungus and is more than 3 m from another such log (sensu Heatwole and Heatwole 1968; Conner 1987; Formica et al. 2011). Scans of the beetles' dorsal, ventral, and right sides were made using an Epson Perfection V600 Photo scanner. ImageJ software (Abramoff et al. 2004) was used to measure body size (elytra length) in both sexes. All individuals were housed individually in an incubator at 21 °C with an 18:6 light:dark cycle with small piece of moist fungus ad libitum. Individuals were isolated for at least 10 days before mating experiments began. Experiments took place in a temperature-controlled room kept at 21 °C and 60 % humidity, with the same light cycle as the incubator. A dim red light was used to aid observation during the six dark hours without disturbing the beetles.

Pairs of *B. cornutus* were placed in small plastic trays (9 cm² with 11 cm tall walls) with moist filter paper and a piece of *Ganoderma tsugae* (6 cm²) for food and substrate. Behavioral observations were taken manually every 20 min for 24 h for each mating trial, and pairs were scored as touching, courting, attempting copulation, guarding, or none of the above. A courtship event was defined as an uninterrupted series of observations consisting of only courting or copulation attempts, but not guarding. Three rounds of mating trials were conducted, with novel pairings for each trial ($N = 326$ pairings with 120 males and 119 females). Males were randomly assigned to new females for each trial, except that beetles from the same wild population were not paired to avoid using beetles that might have been familiar with each other. Beetles were separated for 2 days between each mating trial. Observers were blind to the body size measurements of individuals; however, individuals on the tails of the size distribution are noticeable. At the conclusion of the experiment, all individuals were kept in captivity as part of a larger breeding colony until they died of natural causes. All procedures were in accordance with the ethical standards of the Swarthmore College and Mountain Lake Biological Station, where the studies were conducted.

To determine the effect of the body size of both partners on courtship behavior in the lab, we used a linear mixed model. The total time spent courting was included as the dependent variable while male elytra length and female elytra length were included as independent variables; male ID and female ID were included as random effects; the trial order (1, 2, or 3) for each male was also included as a random effect to control for changes in courtship effort across trials. The population of origin for each male was also included as a random effect, to account for any differences in social environment males may have experienced before capture. Interactions between male and female elytra length were initially included and were removed when found to be non-significant ($P > 0.05$). The same model with the number of courtship events as the dependent variable was run, except that we used a Poisson distribution; this model was not overdispersed. P values were obtained using type III Wald chi-square tests. Statistical analysis was conducted using R statistical software (R Core Team 2014) with the lme4 (Bates et al. 2014) and blme4 (Korner-Nievergelt et al. 2015) packages.

Field methods

Observational scan sampling of beetles in the field was made on a single population near Mountain Lake Biological Station, in Giles County, VA to document expressed male mate preference under natural environmental and social conditions. At the beginning of the field season, all beetles from the population were collected, scanned, and labeled with fluorescent three-letter labels using Tuffleye light-cured acrylic (Wet-a-Hook Technologies®, San Antonio, TX). Body size was measured as described above, and all individuals were returned to their location of capture within 36 h.

Field observations were made four times a day throughout June and July 2011 at approximately 04:30, 10:30, 16:30, and 22:30. A scan observation consisted of two trained assistants searching the surface and undersides of all fungal brackets and recording the location of all beetles present. We also recorded whether each beetle was involved in courtship, attempted copulation, guarding, or if they were not engaged in mating behavior. At night, dark red light was used to aid observation without disturbing beetle behavior. We defined a single courtship event as any uninterrupted series of scan observation periods in which a pair was engaged in courtship. It was not possible to conduct blind observations because we recorded behaviors of marked individuals in their natural environment; however, observers were blind to the actual sizes of the courting pairs. Additionally, most of the observers were unaware of the questions regarding male mate preference, and no observer knew the findings of the laboratory experiment during field data collection as the two studies were

done simultaneously and the data not analyzed until both studies were concluded.

To determine the effect of body size on courtship behavior under natural conditions, we conducted a generalized linear regression with the number of unique courting events as the dependent variable and elytra length as the independent variable. Because larger *B. cornutus* tend to be more active (Formica et al. 2011; Formica et al. 2012), we included the number of days a beetle was observed in the model as a covariate to control for activity level. This analysis was done separately for males and females. For all analyses involving count data, we used the following approach. Each model was initially run with a Poisson distribution; if the model was overdispersed (Zuur et al. 2009), it was rerun with a negative binomial distribution with a zero-inflation correction (Bolker 2008). However, there were no qualitative differences in patterns of significance when using the negative binomial or Poisson distributions, or if the models were adjusted for zero inflation. Statistical analysis was conducted using R statistical software (R Core Team 2014) with the lme4 (Bates et al. 2014), AER (Kleiber and Zeileis 2008), and glmmADMB packages (Skaug et al. 2015).

To test for size assortative mating, we ran a linear regression with male elytra length and the mean of all of his female mating partners' elytra lengths as the dependent variable. The number of days he was active and the number of females he courted were included as covariates in the model. While examining similar trends (male mate preference across size ranges of males), it is important to note that these analyses are not identical to the laboratory results as the laboratory analyses were between pairs of confined beetles using the number and duration of courtship results. In the field analysis, the unit of observation was the individual and the dependent variable was the number of unique times beetles were seen courting (or being courted) via scan sampling. All regression coefficients (β) are unstandardized (remain in the units of the variables) except for the standardized selection gradients described below.

Competition is one of the many social factors that have been shown to affect the expression of male mate preference (e.g., Fawcett and Johnstone 2003; Shine et al. 2004; Candolin and Salesto 2009). To quantify the level of competition in our natural population, we conducted a selection analysis (Lande and Arnold 1983; Conner 1988, 1989; Brodie et al. 1995; Formica et al. 2011). The number of times a male was observed mate guarding has been shown to be a reliable indicator of insemination success (Conner 1988) and was regressed on male elytra size and the number of days active; this was done with a generalized linear model with a Poisson distribution to determine significance. Standardized selection gradients (β) were calculated with a general linear regression with relative

fitness and all traits were standardized (Lande and Arnold 1983; Brodie et al. 1995).

Post hoc fecundity analysis

After the analysis of the above data, we ran an additional (post hoc) analysis to examine a possible correlation between fecundity and elytra size in female *B. cornutus*. We used data from a previous breeding study (Donald et al. 2012) in which the elytra size and the number of eggs laid over a 2-month period were collected in the laboratory. The methods of this analysis are described in detail in Donald et al. (2012), but are briefly described here as well. Forty wild-caught male and forty wild-caught female *B. cornutus* were randomly paired and kept in small plastic containers and fed dried *Ganoderma tsugae ad libitum*. While this study was designed to evaluate the effects of a DNA sampling technique, Donald et al. (2012) found no effect of the procedure on fecundity and so 77 pairs were used in the current analysis (in three pairs, at least one individual died or escaped and so were excluded). The body sizes of individuals were measured as described above. During the 2 months of this study, the number of eggs laid was recorded for each pair. To test for a relationship between female size and fecundity, we used a generalized linear model with a Poisson distribution; the number of eggs laid per pair was the dependent variable and female elytra size was the independent variable. Statistical analysis was conducted using R statistical software (R Core Team 2014) with the glmmADMB packages (Skaug et al. 2015).

Results

Laboratory results

In laboratory trials, in the absence of a complex social environment, females with larger elytra lengths were courted significantly more often (Fig. 1a; $\chi^2_{df=1} = 4.08$, $P = 0.04$, $\beta_{\text{female size}} = 0.22$) and for longer (Fig. 1b; $\chi^2_{df=1} = 16.82$, $P < 0.001$, $\beta_{\text{female size}} = 81.99$). Male elytra length was not significantly associated with the number of times he courted the female in his container ($\chi^2_{df=1} < 0.01$, $P = 0.97$, $\beta_{\text{male size}} = 0.008$) or the time he spent courting ($\chi^2_{df=1} = 0.01$, $P = 0.93$, $\beta_{\text{male size}} = -3.68$). There was no significant interaction between male and female body size on the number of courtship events ($\chi^2_{df=1} = 0.05$, $P = 0.82$, $\beta_{\text{female size} \times \text{male size}} = -0.058$) or time spent courting ($\chi^2_{df=1} = 0.04$, $P = 0.84$, $\beta_{\text{female size} \times \text{male size}} = -0.41$), suggesting that a male's size does not influence his preference for female size; all males courted larger females more often and for longer than they courted smaller females. For unknown reasons, females did not copulate during the trials (no copulations or guarding was observed); while this did not allow us to observe female choice, it does mean that

our measurements of courtship number and duration are not confounded by successful completion of the courtship process.

Field results

In our survey of the wild population, we captured and marked 67 males and 81 females. Using the number of guarded females (successful inseminations) as our fitness component, we detected strong and significant sexual selection for male body size and the number of days a male was observed ($\beta_{\text{std. male size}} = 0.34$, $\chi^2_{1,75} = 5.20$, $P = 0.023$; $\beta_{\text{std. days obs}} = 1.28$, $\chi^2_{1,75} = 82.10$, $P < 0.001$) confirming the presence of male competition in our focal population. We recorded and analyzed a total of 351 unique courtship events involving 49 males and 68 females. The sex ratio of the adult population was 0.45 (males/total).

There was a significant, positive relationship between the size of a female and the number of times she was courted over the course of the breeding season ($\chi^2_{1,73} = 6.08$, $P = 0.014$, $\beta_{\text{female size}} = 0.23$; Fig. 2), matching the laboratory result that larger females are courted more often and for longer. We included the number of days a female was observed (activity) as a covariate in the model, and it too predicted the number of times females were courted ($\chi^2_{1,73} = 192.30$, $P < 0.0001$, $\beta_{\text{days obs. (female)}} = 0.05$). While active males initiated courtships more often ($\chi^2_{1,58} = 86.55$, $P < 0.0001$, $\beta_{\text{days obs. (male)}} = 0.06$), there was no significant relationship between the size of a male and how many times he was observed courting females ($\chi^2_{1,58} = 0.81$, $P = 0.37$, $\beta_{\text{male size}} = 0.16$). This matches the non-significant result between male body size and courtship effort we observed in the laboratory trials.

There was no relationship between the size of a male and the mean size of the females he courted (i.e., no assortative mating; $F_{2,46} = 1.19$, $P = 0.28$, $\beta_{\text{male size}} = -0.21$) nor were either of the covariates significant (days observed: $F_{2,46} = 0.07$, $P = 0.78$, $\beta_{\text{days obs. (male)}} < 0.01$; number of courted females: $F_{2,46} = 1.09$, $P = 0.30$, $\beta_{\text{days obs. (female)}} = -0.01$). This result matches the lack of a significant interaction between male and female body size with courtship effort that we observed in the laboratory trials.

Female body size is often correlated with fecundity in insect systems (Bonduriansky 2001)—in order to confirm this trend in *B. cornutus* we conducted a post hoc analysis on a data set from a captive breeding population (Donald et al. 2012). The results revealed that there was indeed a significant positive relationship between the elytra size of the female and the number of eggs she produced ($\chi^2_{1,73} = 12.73$; $P < 0.001$; mean \pm SD = 6.78 ± 0.45 eggs, $\beta_{\text{female size}} = 0.66$). Each additional millimeter of female elytra size resulted in ~ 0.7 more eggs produced. Male and female size were uncorrelated in this experiment ($F_{1,75} = 0.68$; $P = 0.41$).

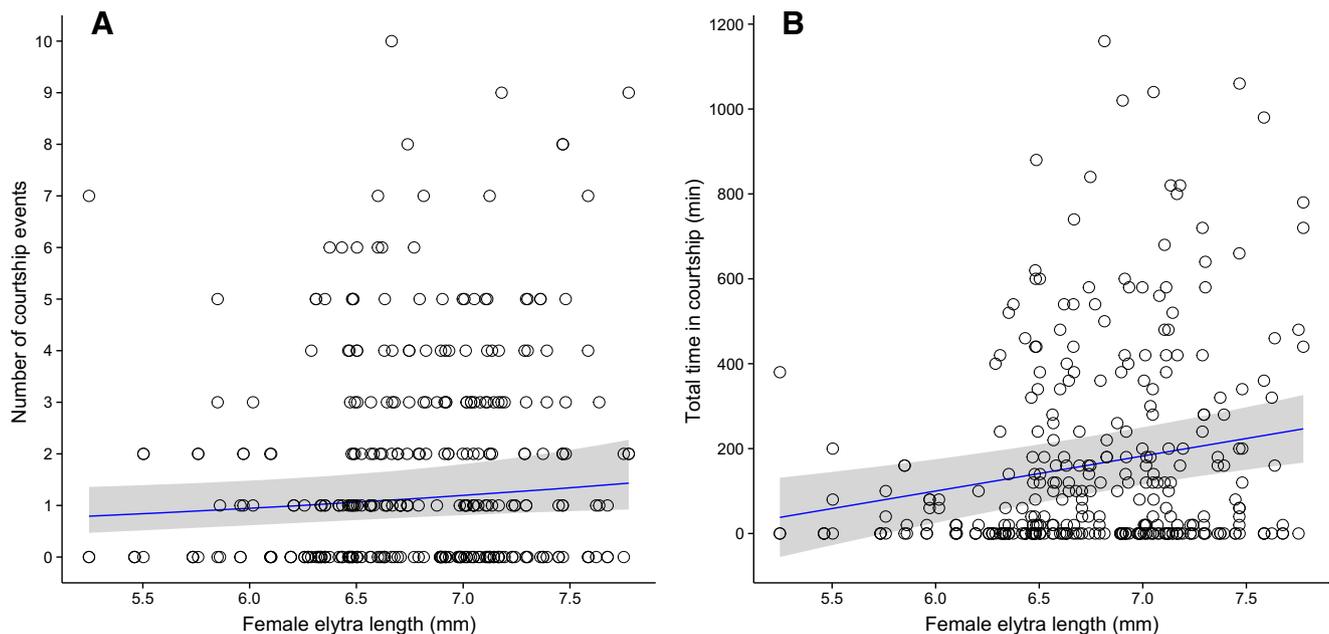


Fig. 1 The number of times females were courted (**a**) and the time males spent courting a female (**b**). Males paired with larger females courted females with more courtship events and for longer periods of time

Discussion

We observed a clear preference for larger females by male *B. cornutus* in our no-choice experiment in the laboratory in the absence of a complex social environment. Males courted larger females more often and for longer periods of time

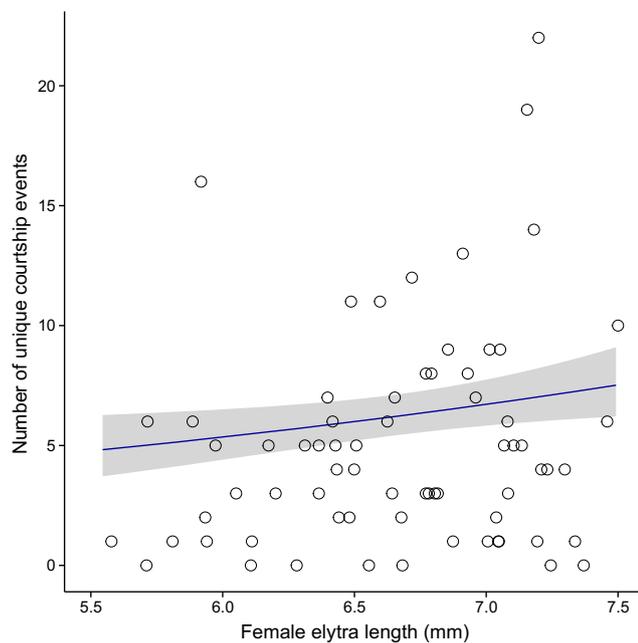


Fig. 2 Courtship patterns in a wild population of *B. cornutus*. Larger females are courted significantly more often than smaller females. The regression line and the 95 % confidence intervals (were generated from the complete model and were back transformed from the GLMM

regardless of the focal male's body size. The regression line and 95 % CI shaded region are back transformed from the original models described in the text

regardless of their own size. Larger *B. cornutus* females seem to be more valuable as mates as they are more fecund than smaller females. The results from the wild population matched those we observed in the lab—larger females were also courted more often. The body size of a male did not predict the mean size of the females he courted.

These findings add another example of a strong male mating preference for larger, more fecund females (Bonduriansky 2001). In the laboratory, where social interactions were limited to a single male and female, we detected a significant, positive relationship between female-partner body size and courtship effort (number of events and duration; Fig. 2). Because the males of this species initiate courtship, this result suggests an underlying male mate preference for larger females in *B. cornutus*. Large females are more fecund, the largest of which can produce two more offspring on average than the smallest females, indicative of a clear fitness benefit to males that mate with large females.

Investment of resources by males in finding, courting, or securing a female is hypothesized to contribute to the evolution of male mate preference because the cost of investment may be high enough to out-weigh the potential loss of fitness associated with mate rejection (Bonduriansky 2001). *B. cornutus* have complex and long lasting courtship behavior that can last for several hours (Brown et al. 1985). In the lab component of our study, one male courted the female for 19 of the 24 h. Additionally, during copulation, male *B. cornutus* fill their spermatophore with liquid until it fills the female's entire reproductive tract (VF, personal observation), presumably an energetically costly process (*sensu* Wedell et al. 2002). After a

successful copulation, males also mate guard females for several hours (Brown et al. 1985; Brown and Bartalon 1986; Conner 1988). All of these costs associated with mating may contribute to selection for male *B. cornutus* to court high quality females instead of courting indiscriminately.

The wild population that we observed for the field component of this study exhibited high levels of male competition, as measured by the strong, positive sexual selection gradient for larger males ($\beta_{\text{std. male size}} = 0.34$); however, the patterns of male mate preference observed in the lab were still expressed in the wild; larger females were still courted more often (Fig. 2). Unlike most other studies of male mate choice in the field, we also did not observe assortative mating (Fig. 3). Despite the strong positive relationship between male body size and successful copulation, small males still courted females of similar size to the females courted by larger males (Fig. 3). This result combined with the no significant interactions between male and female body size, and male courtship effort in the laboratory, suggests that small male *B. cornutus* are not drastically altering their courtship preferences in this wild population. In other words, despite the competitive environment, we measured in the wild population, we did not observe a strong signal of condition-dependent male mate preference as often observed in other systems with male-male competition (e.g., Shine et al. 2001; Amundsen and Forsgren 2003; Bel-Venner et al. 2008; Candolin and Salesto 2009).

Our results from the field do not match any of the evolutionary stable strategies described by game theory models of male mate choice developed by Hardling and Kokko (2005). These models predict that, in the face of strong competition,

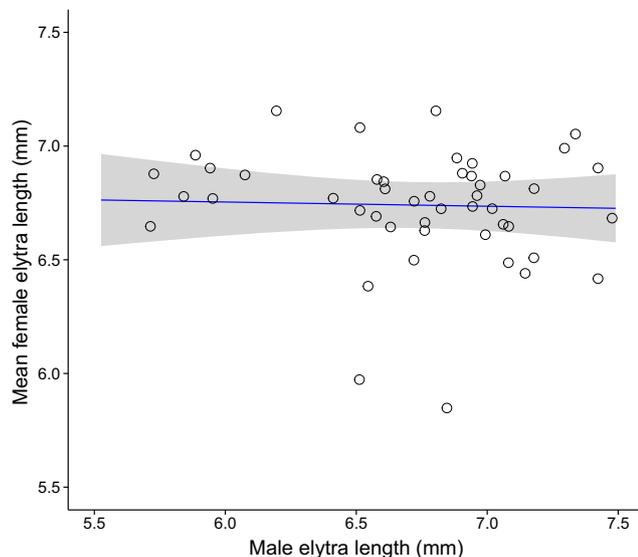


Fig. 3 Male body size and the mean body sizes of females courted in the field. There was no assortative courtship pattern between the body sizes (elytra) of males and the mean body size of the females they courted. The regression lines and all 95 % CIs were generated from the complete model that includes the number of days observed and the number of females courted for each male

systems with male mate choice should evolve “prudent choice”, where low quality males change their preference from high quality females to low quality females while high quality males continue to prefer high quality females and reject low quality females (Fawcett and Johnstone 2003; Hardling and Kokko 2005). Prudent choice should result in strong positive-assortative mating. Interestingly, many empirical studies that quantify population-level patterns of male mate preference in the wild tend to be in systems with assortative mating (e.g., Olsson 1993; Shine et al. 2001; Shine et al. 2004; Bel-Venner et al. 2008). Even when Hardling and Kokko (2005) relaxed the assumptions of their game theory model, the evolutionary stable strategies they uncovered resulted in one group (low or high quality males) mating indiscriminately with regards to female quality, which should result in detectable positive or negative assortative mating. Lastly, Hardling and Kokko (2005) also found an evolutionary stable strategy that results in all males mating indiscriminately (no male mate preference). However, in this study, we detected no correlation (positive or negative) between male and female quality in courtship pairs (Fig. 3) and it is unlikely that all males matedx indiscriminately since larger females were courted more often in the wild (Fig. 2).

If our findings from this population are representative of *B. cornutus*, this species could be an exception to the more commonly observed patterns of assortative and context-dependent prudent choice. Our findings suggest that even in systems with strong sexual selection, competition among males, and no assortative mating, there may be underappreciated male mate preference that affects mating patterns in the wild.

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