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Forced copulation as a conditional alternative strategy in camel crickets

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Abstract In the animal kingdom, males typically acquire reproductive access to females through courtship, nuptial gifts, or combat. In many species, small or poor-condition males that are unable to produce an attractive display, proffer an adequate mating gift, or dominate in male–male competition may resort to forced copulation. Forced copulation has been previously demonstrated in the camel cricket *Pristoceuthophilus marmoratus* and is uniquely facilitated by male hind leg weaponry that functions in both intrasexual competition and sexual coercion. Because male leg armaments are positively allometric, the largest males would seem best equipped to force-copulate, although they might be the most attractive to females, and so least likely to adopt a forced copulation strategy. In order to resolve this potential paradox and determine which males are in fact most likely to force-copulate, we manipulated male body size using diet and performed mating trials. Results showed that (1) male size increased with diet quality, (2) females appear to prefer larger males, and (3) smaller males were more likely to attempt forced copulation. Our results thus suggest that forced copulation is a condition-dependent alternative mating tactic used by small males unattractive to females.

Keywords Forced copulation · Alternative mating strategy · *Pristoceuthophilus marmoratus*

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Introduction

Male combat, courtship displays, and nuptial gifts often come with substantial costs and risks that may be minimized by alternative mating strategies such as satellite and forcing behaviors. The use of these alternative mating strategies is usually contingent on a male's condition (Alcock 2009). Satellite males, commonly found in acoustically displaying species, are often small individuals that cannot front the expense of producing a high-quality song attractive to females (Cade 1980). Such males wait near calling males and intercept females homing in on a calling male. In contrast, forcing behaviors do not necessarily occur near a displaying male. Male guppies (*Poecilia reticulata*) can reduce predation risk by forgoing their mating display, a conspicuous dance that emphasizes their color spots, and simply swimming toward females and thrusting their intromittent organ into a female's gonopore (Evans et al. 2003). In sagebrush crickets (*Cyphoderris strepitans*), males lacking the fleshy hind wings that serve as nuptial gifts use a specialized abdominal pinching structure, or "gin trap," to restrain females and force copulation (Sakaluk et al. 1995). Forced copulation is also common in waterfowl, where it is employed by unpaired, territory-less, and presumably unattractive males (Cheng et al. 1982; McKinney et al. 1983).

Alternative explanations for forced copulation exist. Early non-evolutionary hypotheses include satisfaction of male sexual urges or simply abnormal male behavior (McKinney et al. 1983). The former could be a byproduct of male over-eagerness, while the latter could stem from genetic abnormalities. However, both of these hypotheses suggest that the use of forced copulation would be random, which is generally not the case (Clutton-Brock and Parker 1995). Allen and Simmons (1996) posited that females assess male vigor while being subdued prior to forced copulation, implicating female choice. However, other studies show that females being forced to copulate suffer reduced fecundity and longevity (Thornhill 1980; McLain and Pratt 1999), implying a lack of female choice. Kokko (2005) suggested a twist on Fisherian selection in that females should prefer coercive males in order to produce coercive sons. However, given that forced copulation is typically employed by only a minority of males in a population as an alternative mating strategy (McLain and Pratt 1999; Evans et al. 2003), Kokko's hypothesis seems likely to apply only to those species in which coercion is commonplace, e.g., bed bugs (Stutt and Siva-Jothy 2001), water striders (Arnqvist and Rowe 2002), and *Anonconotus* bushcrickets (Vahed 2002; Vahed and Carron 2008).

The camel cricket *Pristoceuthophilus marmoratus* (Orthoptera, Rhaphidophoridae) presents a potentially paradoxical situation with regard to male quality and forced copulation. In this species, males possess highly modified hind legs, with two large ventral spines on an enlarged femur and a markedly bent tibia. Males use these modified hind legs to fight with other males (Haley and Gray 2012). However, Haley and Gray (2012) showed that males sometimes also use their hind legs to trap females and subsequently force them to mate. In a forced copulation, a male grabs and holds a female in the crook of one hind leg and then forces his genitalia into her genital opening. The forced copulation position looks very different from the voluntary copulation stance, where the female climbs up onto the male's back. Videos of the mating interactions can be viewed as supporting information for Haley and Gray (2012) [http://onlinelibrary.wiley.com/doi/10.1111/j.1439-0310.2011.01985.x/suppinfo]. Females often struggle against hind leg submission by males and sometimes escape before genital coupling occurs. Like other forms of armament, the male hind leg modifications in *P. marmoratus* (femoral spines, thickened femur, and tibial bend) are positively allometric (Haley and Gray 2012), meaning that they are expressed to a disproportionate degree in large individuals and nearly unnoticeable in small individuals. The allometry of these armaments creates a situation in which the largest and presumably most attractive males are best equipped to coerce females to mate.

Although Haley and Gray (2012) noted that non-virgin females were more likely to be forced to mate than virgin females, they did not investigate which males were most likely to be forcers. The goals of the present study were to: (1) test the condition dependence of male body size and leg armaments by manipulating diet, (2) in a subsequent study of un-manipulated adults, determine if male size and/or condition is a predictor of forced copulation, and (3) evaluate if female preference is correlated with male quality. We hypothesized that low-quality males will be most likely to be forcers, despite having relatively inferior coercive structures.

Experiment 1: condition dependence of male traits

Rationale

Diet manipulations were performed to test the condition dependence of somatic and sexually selected traits. Males on a high-quality diet were expected to grow larger and express sexually selected traits to a greater degree than males on a low-quality diet.

Methods

Collection and rearing

In early July 2012, young nymphs (undifferentiated by sex) of *P. marmoratus* were collected from Malibu Creek State Park (Los Angeles County, California, USA; 34.10°N, 118.73°W, elev. 200 m). Collection was accomplished by placing oatmeal piles along the dry bed of Malibu Creek approximately 1 h before sunset and returning to the piles half an hour after sunset. Captured nymphs were returned to the lab and randomly placed on one of two diet treatments, a high-quality (HQ) diet and a low-quality (LQ) diet. The diets were taken from a study by Patton (1967) on house crickets (*Acheta domesticus*). The LQ diet contained equal parts by mass of soybean meal and wheat chaff, while the HQ diet contained dried milk (15 %), liver powder (5 %), cornmeal (35 %), brewer's yeast (5 %), soybean meal (10 %), and wheat chaff (30 %). In Patton's study, the diets promoted similar survivorship but large differences in growth and mass increases. Individuals assigned to the diet treatments did not differ in pre-diet initial mass (HQ, 13.08±0.76 mg; LQ, 13.29±0.76 mg; $t=-0.20$, $df=140$, $p=0.84$).

Individuals were reared in a 27 °C growth room on a 12:12-h dark/light reversed photoperiod. Each individual was housed in a 500-mL plastic tub with cotton-plugged water vial, ad libitum food, and egg carton pieces for shelter. Eclosion to adulthood began in early October 2012 and ended in late December.

Measurements of condition and armature investment (Experiments 1 and 2)

Adult males were weighed to the nearest 0.1 mg and then preserved in ethanol so that their pronotum and hind legs could be measured. Pronotum length was measured with digital calipers to 0.01 mm. Male condition was determined by taking the residuals from a linear regression of mass on pronotum length ($r^2=0.82$, $p<0.001$). Male hind legs were removed and then photographed against a standard white background incorporating a millimeter ruler scale; ImageJ was then used to measure three armament traits: length of proximal femoral spine, femur area, and angle of tibial deflection (calculated as 180° minus the angle of the tibial bend). Each pronotum and hind leg trait was measured twice, and the average of the two values was used. Measures of allometric slopes were made by log–log regression of the three armament traits on pronotum length via reduced major axis (RMA) regression using Bohonak and van der Linde's (2004) online software (http://www.kimvdline.com/professional/rma.html), and after square root-transforming femur area and arcsine square root-transforming the angle of tibial deflection to linearize these measures.

Results

Condition dependence of somatic and armament traits

Males on the high-quality diet (HQ) were significantly heavier ($t=3.03$, $df=27$, $p_{\text{1-tailed}}=0.003$), larger ($t=2.07$, $df=27$, $p_{\text{1-tailed}}=0.024$), and in better condition ($t=2.27$, $df=27$, $p_{\text{1-tailed}}=0.016$) than males on the low-quality diet (LQ) (Fig. 1). There was no difference in development time (time to adulthood since the start of the diet manipulation) between diet treatments ($t=0.72$, $df=27$, $p_{\text{1-tailed}}=0.24$). One-tailed tests were used because males on the high-quality diet were expected to be superior to males on the low-quality diet.

Hind leg armaments were also condition-dependent (Table 1). Armaments were defined as traits with allometric slopes significantly greater than 1. Not only did HQ males have absolutely larger femoral spines ($t=3.07$, $df=27$, $p_{\text{1-tailed}}=0.002$) and thicker femurs ($t=3.20$, $df=27$, $p_{\text{1-tailed}}=0.002$; Fig. 2a, c), but they also invested relatively more in armaments when controlling for body size (relative spine length, $t=2.86$, $df=27$, $p_{\text{1-tailed}}=0.004$; relative femur area, $t=3.29$, $df=27$, $p_{\text{1-tailed}}=0.001$; Fig. 2d, f). Only the angle of tibial deflection trait was not affected by diet (absolute angle, $t=0.24$, $df=27$, $p_{\text{1-tailed}}=0.41$; relative angle, $t=-0.23$, $df=27$, $p_{\text{1-tailed}}=0.42$; Fig. 2b, e).

Experiment 2: female preference and predictors of forced copulation

Rationale

In order to identify factors that predict forced copulation, we compared traits of males at three key points in the typical mating behavior sequence of *P. marmoratus* (Haley and Gray 2012). After a mating invitation from a male, in which the male spreads his hind legs and pushes his abdomen back toward the female, the female can either voluntarily mount the male or not (Fig. 3, Branch point 1). After this point, a rejected male can either attempt forced copulation by grabbing a female with a hind leg or not (Fig. 3, Branch point 2); those that attempt forced copulation can either be successful or not if the female escapes (Fig. 3, Branch point 3). Any differences between males at any branch points will shed light on which males force copulation.

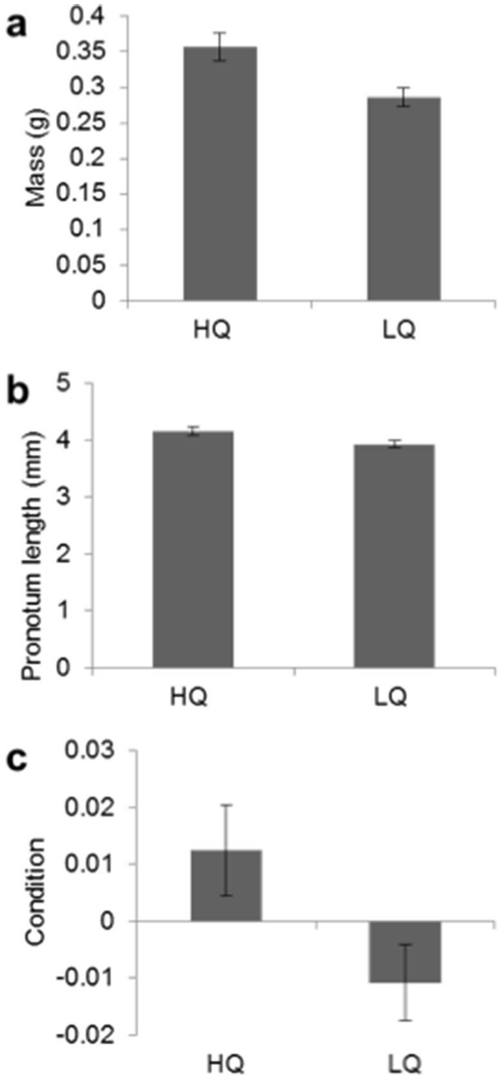


Fig. 1 Males on the high-quality (HQ) diet ($n=13$) were heavier (**a**), bigger (**b**), and in better condition (**c**) than males on the low-quality (LQ) diet ($n=15$). Means ± SE are shown (as in all subsequent graphs)

Additionally, we evaluated female preference for male traits by offering females two males consecutively (no-choice trials) and comparing female willingness to remate as a function of the difference between the first and second males.

Note that crickets used in this experiment were not the individuals from the diet manipulation in Experiment 1.

Methods

Collection and housing

In early October 2013, adult *P. marmoratus* males and females of unknown mating history were collected as described

Table 1 RMA regressions of hind leg traits on male body size for n=28 males from the diet manipulation experiment (Experiment 1)

Trait	RMA slope ± SE	r^2	*P* value	Allometry
Spine length	5.24±0.81	0.38	<0.01	Positive
Asin sqrt (tib. deflection)	3.12±0.51	0.31	<0.01	Postive
Sqrt (femur area)	1.08±0.11	0.72	0.47	Weakly positive[a]

Traits with RMA slopes significantly different from 1 are allometric; here, the listed p values indicate significance of a test of whether the slope=1 (isometry), not whether the slope=0. Variables were log-transformed

Sqrt square root, *asin* arcsine

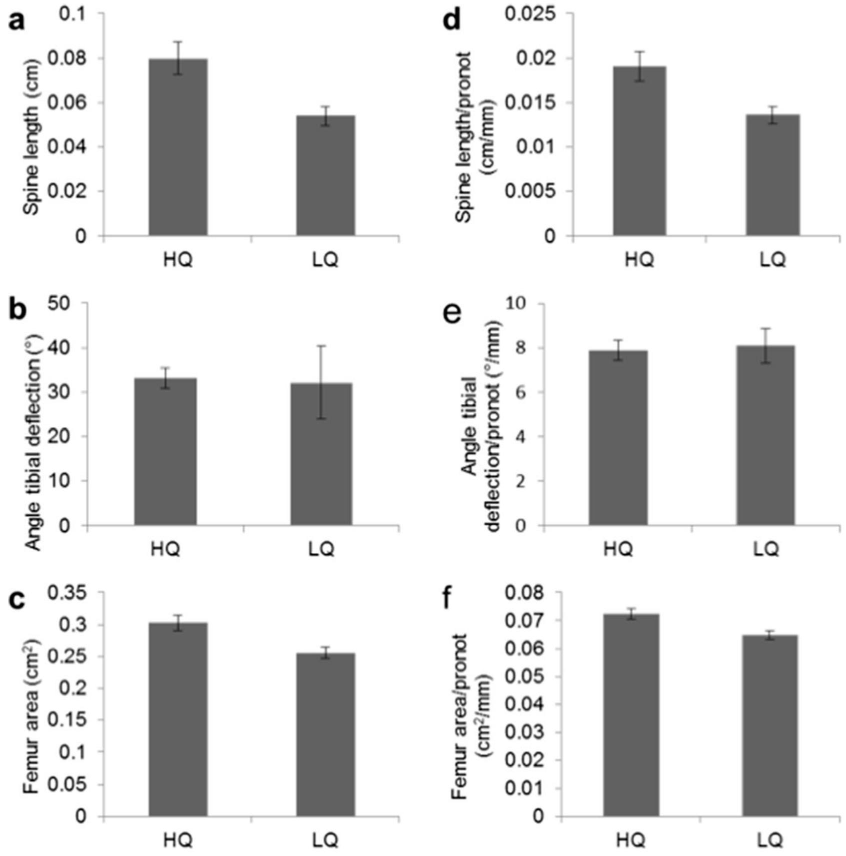
[a] Although the RMA slope for sqrt femur area was not significantly different from 1 in this data set, Haley and Gray (2012) showed this trait to be positively allometric (RMA slope 1.16±0.08, n=23). Additional data with larger sample size also show positive allometry for this trait (slope 1.06±0.03, n=101; see Table 2). For this reason, femur area is considered weakly positively allometric and is included in subsequent comparisons of armaments of HQ and LQ males

previously. After collection, individuals were isolated in 500-mL plastic tubs with water vials, cat food, and egg cartons. Post-capture isolation was at least 2 weeks to ensure complete sexual maturity and to eliminate individuals that were harboring tachinid larvae. Individuals were housed in a 27 °C room on a 12:12-h dark/light reversed photoperiod.

Male–female mating trials

Adult males and females were randomly paired for mating trials to determine whether male condition (residual mass), body size (pronotum length), and/or "armature score" (from principal components analysis, see below) influence the likelihood of using forced copulation. Each male was only used once, but females were used in two trials each to determine if they prefer any male traits (no-choice trials). There were at least 2 days between each female's first and second trials, and no oviposition took place in the interim (indeed, no oviposition ever took place in our laboratory setting; see "Discussion"). Mating trials were conducted during the dark portion of the crickets' photoperiod at 22 °C, which simulated autumn nighttime temperatures. Each trial was preceded by a

Fig. 2 Condition dependence of hind leg armature traits. Males on the HQ diet (n=13) not only had larger femoral spines (**a**) and greater femoral area (**c**) than LQ males (n=15); they also invested more in femoral spines and femoral area when controlling for body size (**d** and **f**). Diet did not affect either the absolute or body size-controlled angle of tibial deflection (**b** and **e**)



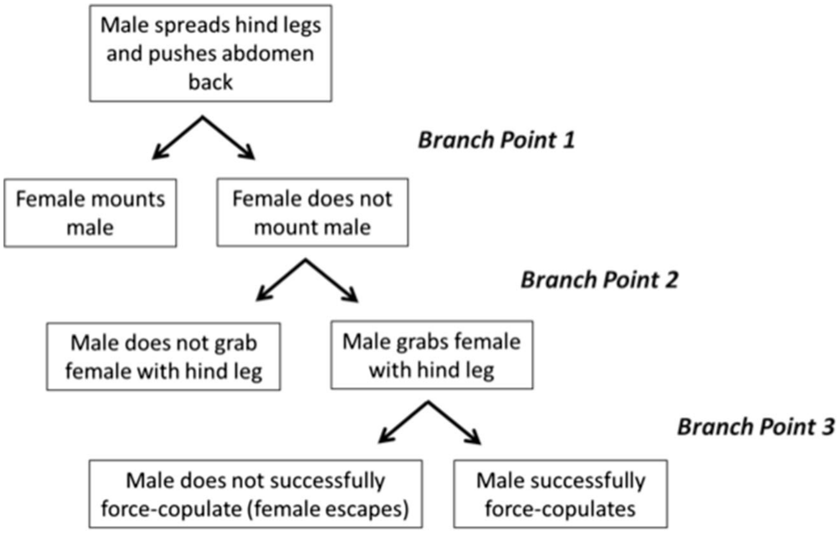


Fig. 3 Mating sequence of *P. marmoratus,* showing the path to successful forced copulation. Differences between males at each branch point will be analyzed in order to determine which males are most likely to force-copulate

30-min acclimation period, then each male–female pair was placed in a $14\times8\times10$ cm plastic tub under a red light, to minimize light disturbance.

Each trial was 3 h long, but up to six trials (in six tubs) were conducted simultaneously. We noted the crickets' behavior while minimizing movement and noise and recorded the following outcomes: no copulation attempted by the male, successful voluntary copulation, unsuccessful forced copulation (where the male grabbed the female with one or both hind legs but the female struggled and escaped before genital coupling), or successful forced copulation (where the male restrained the female with one or both hind legs while the female was on the ground or on her side during genital coupling). A total of 101 mating trials were performed.

Results

Male–female mating trials

Of the 101 males in the mating trials, 14 obtained voluntary copulations. Of the remaining 87 trials where voluntary mating did not occur, 19 males attempted to force copulation. Of these 19 males, four were successful. The remaining 68 males neither voluntarily copulated nor attempted to force copulation. All males, however, did attempt voluntary copulation by spreading their hind legs and presenting their abdomens to females.

Using the typical mating sequence of *P. marmoratus* (Fig. 3), we analyzed whether there were differences between males at different points along the path. Analysis was done with binomial generalized linear models (GLMs). To account for the fact that females were used in two trials each, we included female trial status (either Trial 1 or Trial 2) as a factor in the GLMs; thus each model contained two independent variables (female trial status and male trait) and one dependent variable (behavior outcome at a given Branch point). If female trial status was not significant, it was dropped from the model; however, if female trial status was significant, then the data could not be pooled for analysis and were analyzed separately. The male traits analyzed were body size, condition, and armature score of males at each node. Armature score was determined by combining three positively allometric armament traits (Table 2) into one trait (Factor 1 in a principal components analysis; eigenvalue=2.648, 88.3 % of variance explained; component loadings, spine length=0.96, femur area=0.93, angle of tibial deflection=0.93).

Female trial status was non-significant at Branch points 1 and 3 (all p values>0.05) and trial status was thus dropped from GLMs at these Branch points. However, female trial status was significant at Branch point 2 (p values<0.05), indicating a non-random distribution of male phenotypes among females in their first trial versus females in their second trial (despite our assignment of males to females randomly). Therefore, for each male trait at Branch point 2, data were analyzed separately.

Statistical results from the mating trials are given in Table 3. There were no differences in body size, condition, or armature score between males that obtained a voluntary copulation ($n=14$) versus those that did not ($n=87$) (Branch point 1). However, when unsuccessful males could either attempt a forced copulation ($n=6$ for males paired with first trial females, $n=13$ for males paired with second trial females) or not ($n=43$ for males paired with first trial females, $n=25$ for males paired with second trial females) (Branch point 2), forcers were significantly smaller (Fig. 4a) and had smaller armaments (Fig. 4b) than non-forcers (but this was only true for males paired with second trial females). There was no difference in male "condition" (measured as residual mass)

Table 2 RMA regressions of hind leg traits on body size for *P. marmoratus* males (n=101)

Trait	RMA slope ± SE	r^2	*P* value	Allometry
Spine length	4.67±0.29	0.71	<0.01	Positive
Asin sqrt (tib. deflection)	2.35±0.13	0.76	<0.01	Positive
Sqrt (femur area)	1.06±0.03	0.94	0.05	Weakly positive

Traits with RMA slopes significantly different from 1 are allometric; here, the listed p values indicate significance of a test of whether the slope=1 (isometry), not whether the slope=0. Variables were log-transformed

Sqrt square root, *asin* arcsine

between forcers and non-forcers for either type of female trial. At the last point in the path (Branch point 3), there were no differences between successful forcers (n=4) and unsuccessful forcers (n=15).

Female preference

Each female was used in two mating trials to determine if female preferences for male traits exist. Only females that survived to the second trial (n=44) produced analyzable comparisons. The observed outcomes for each female are shown in Table 4. Of the observed outcomes, only "first trial voluntary copulation, second trial no voluntary copulation" had both sufficient sample size (n=10 females) and biological relevance. Females that did not re-mate after their first mating can be considered unwilling to trade their first mate's sperm for another's.

Paired t tests were used to compare each female's first and second trial males. When females mated with the first male but not the second male, the first male was significantly heavier than the second male (t=2.41, df=9, one-tailed $p_{1\text{-tailed}}$=0.02) (Fig. 5a). (One-tailed p values were used because accepted first males were expected to be superior to rejected second trial males.) There were non-significant but collectively suggestive trends indicating the same pattern with respect to male body size (t=1.50, df=9, $p_{1\text{-tailed}}$=0.086), condition (t=1.56, df=9, $p_{1\text{-tailed}}$=0.078), and armature score (t=1.16, df=9, $p_{1\text{-tailed}}$=0.14) (Fig. 5b, c, d).

Binomial sign tests were also performed to compute the probabilities of the observed differences (+/−) between the first trial males and the second trial males. When females mated with the first male, but not with the second, the first trial males were significantly heavier (p= 0.011) and marginally significantly bigger (p=0.055) and more heavily armed (p=0.055) than the second trial

Table 3 Parameter estimates for male traits as predictors of mating behavior at three branch points in the mating pathway

Comparison[a]	Variable	Parameter estimate ± SE	Z	ρ^2	*P* value
Branch point 1	Body size	0.03±0.7	−0.05	<0.01	0.481
	Condition	6.83±9.8	−0.70	<0.01	0.243
	Armature score	0.68±0.8	−0.83	<0.01	0.204
Branch point 2	Body size (female trial 1)	−3.82±15.0	−0.26	<0.01	0.400
	Body size (female trial 2)	1.88±1.0	1.97	0.10	0.024
	Condition (female trial 1)	−3.82±15.0	−0.26	<0.01	0.400
	Condition (female trial 2)	9.32±11.3	0.83	0.01	0.204
	Armature score (female trial 1)	−0.38±0.5	−0.77	0.02	0.220
	Armature score (female trial 2)	0.73±0.4	1.83	0.08	0.034
Branch point 3	Body size	0.01±1.5	−0.01	<0.01	0.498
	Condition	1.55±21	−0.08	<0.01	0.470
	Armature score	−0.21±1.5	−0.14	0.01	0.444

Z = Wald statistic, ρ^2 = McFadden's Rho-Squared; one-tailed p values are given due to *a priori* predictions

[a] Branch point 1 = males that obtained voluntary copulation (n=14) versus males that did not (n=87); Branch point 2 = males that attempted forced copulation (n=19) versus males that did not (n=68); Branch point 3 = males that successfully forced copulation (n=4) versus males that were unsuccessful (n=15)

[b] For Branch points 1 and 3, female trial status was not significant and so was not included in the final model, whereas, at Branch point 2, female trial status was significant, therefore, data from the two trial types were analyzed separately (see text); for males that were paired with females in their first trial, n=49 (6 forcers, 43 non-forcers). For males that were paired with females in their second trial, n=38 (13 forcers, 25 non-forcers)

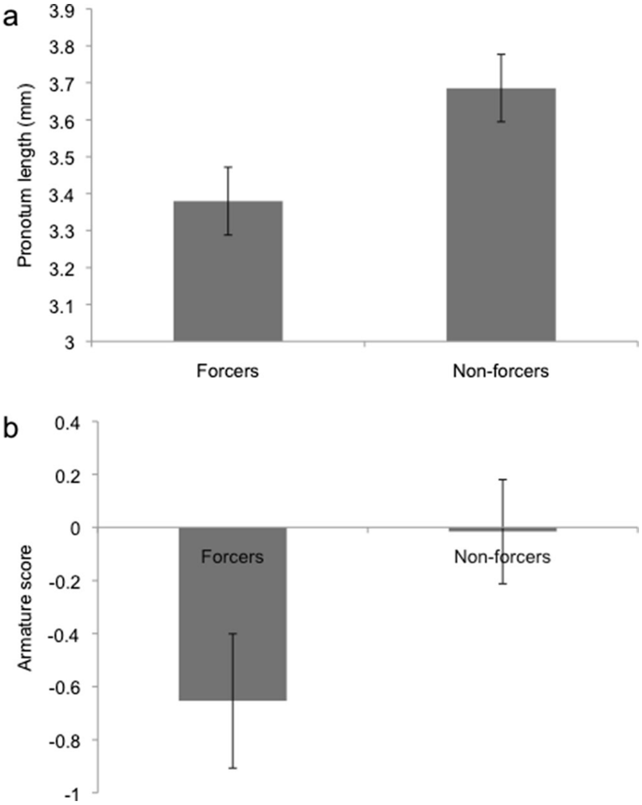


Fig. 4 When males were paired with second trial females, males that attempted to force copulation (n=13) were smaller (**a**) and with a lesser degree of armature (**b**) than males that did not attempt to force copulation (n=25)

males; male condition as residual mass was not significantly different, p=0.38. Taken as a whole, these trends indicate that females were unwilling to trade down after mating with a comparatively larger male.

Table 4 Frequencies of observed outcomes of each female's first and second mating trials

Female's first trial	Female's second trial	Frequency (no. of females)
No cop	No cop	16
Vol cop	Vol cop	1
Att. forced cop	Att. forced cop	1
Forced cop/att. forced cop	No cop	2
No cop	Forced cop/att. forced cop	10
No cop	Vol cop	4
Vol cop	No cop[a]	7
Vol cop	Forced cop/att. forced cop[a]	3

[a] Females that mated with their first trial male but whose second trial either resulted in no copulation or forced copulation/attempted forced copulation (first trial vol cop, second trial no vol cop) were considered females unwilling to trade down from their first mate (n=10). This is the only biologically meaningful category that can be analyzed to indicate female preference

Discussion

Forced copulation as a conditional alternative mating strategy

This study helps to elucidate the nature of an alternative mating strategy in *P. marmoratus*. Experiment 1 demonstrated that male somatic traits, such a body size, and sexually selected armaments are positively condition-dependent. Experiment 2 showed (1) that forced copulation is employed by males with small bodies and small armaments, and (2) that females appear to prefer larger males as mates; we interpret these results to suggest that forced copulation is a negatively condition-dependent alternative mating strategy. These findings are in accord with the body of literature on alternative mating strategies (Cade 1980; Dawkins 1980; Cheng et al. 1983; McKinney et al. 1983; Andersson 1994; Clutton-Brock and Parker 1995; Alcock 2009) and countless examples of female preference for larger males (Andersson 1994).

By comparing traits of males at each branch point in the typical mating sequence of *P. marmoratus* in Experiment 2, it is possible to determine the conditions under which forced copulation is likely to happen. There were no differences between males that were able to attain a voluntary copulation and those that were not (Branch point 1). However, males could decide to try to force a copulation or not (Branch point 2), when paired with second trial females forcers had significantly smaller bodies and armaments (both of which are condition-dependent traits) compared with non-forcers. It is interesting that males paired with first trial females did not show this effect; possible reasons include less statistical power in the first trial female analysis (6 forcers compared with 13 forcers in the second trial female analysis), or a bias because of the non-random distribution of male phenotypes among female trial types. Male condition, measured as residual mass, was not a significant predictor of forced copulation, but Gray and Eckhardt (2001) showed that residual mass is not always the best measure of actual male condition (in their study, measured as male fat reserve).

We interpret the differences between males at Branch point 2 as follows: Smaller males, whose mating invitations were rebuffed, were "making the best of a bad job" (Dawkins 1980) and seizing their only possible mating opportunity. There are several possible reasons why larger males chose not to force at this same branch point. Potential fitness differences (number of offspring fathered) between forcing and voluntarily copulating could discourage large males from pursuing forced copulation (see Thornhill 1980; McLain and Pratt 1999). These attractive males could have decided to simply wait for another mating opportunity with a different female in the future instead of spending the energy to chase and subdue an unwilling female for a low payoff (females do struggle and try to resist forced copulation attempts). Another explanation

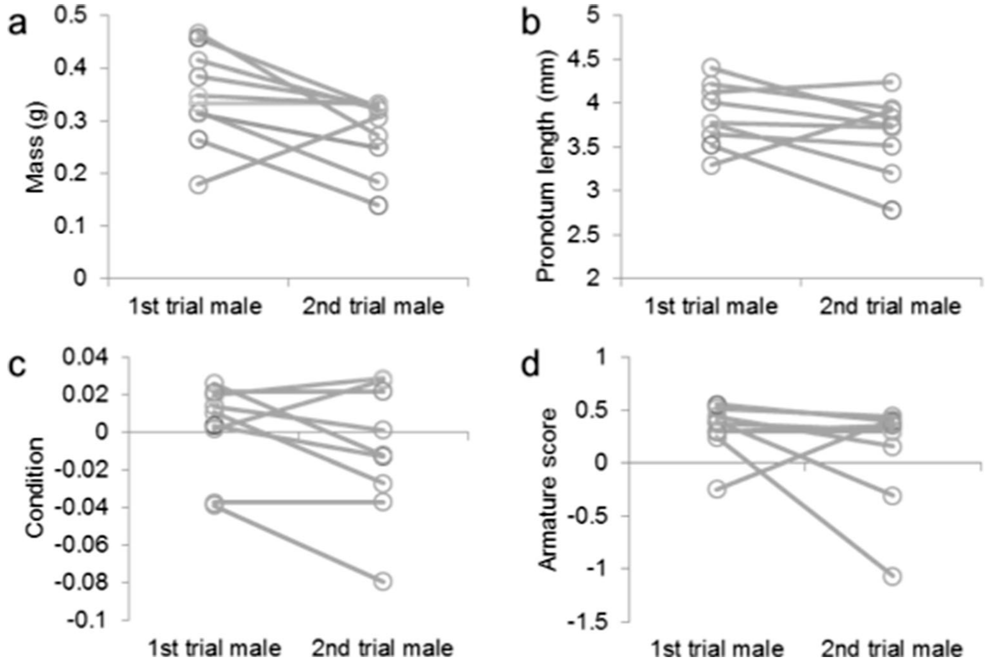


Fig. 5 Paired *t* tests comparing first and second trial males that were matched with females ($n=10$) that mated with the first male and did not mate with the second male. First trial males were significantly heavier (**a**) than second trial males. This trend was non-significant but collectively suggestive for body size (**b**), condition (**c**), and armature score (**d**)

could be that these males might have been reluctant to antagonize a female (in the trial) that might later consent to copulation. In either case, larger males were most plausibly banking on future reproduction, whereas for smaller males, the chances of future reproduction were probably minimal. Because of this, smaller males' best chance of reproducing would be by forcing any female at hand (or at leg, as it were).

There were no differences between males at Branch point 3 (whether an attempted forced copulation is successful or not). This lack of a difference was likely due to the very small sample size of the successful forcers ($n=4$). It might be expected that larger forcers would be more successful than smaller forcers because they would be better at catching and subduing a female.

The results of the female preference analysis dovetail with the finding that smaller males are forcers. Females significantly refused to trade down to a lighter male after mating with a heavier male. This trend was non-significant but suggestively repeated for male body size, condition, and armament score. Female unresponsiveness to smaller males after mating with larger males provides a selective pressure that would favor small males that try to force copulation.

Disadvantages of forced copulation for males

When conditionally used, forced copulation is an alternative mating strategy because it often results in lower fitness compared with voluntary copulation (Thornhill 1980; McLain and Pratt 1999). Thornhill showed (1980) showed that only half of forced copulations resulted in sperm transfer in *Panorpa* scorpionflies, while all voluntary copulations led to sperm transfer. In the Heteropteran insect *Neacoryphus bicrucis*, sexual coercion lowered female fecundity (number of eggs laid; McLain and Pratt 1999). McLain and Pratt hypothesized that the energetic costs of female fleeing and resisting behavior could have reduced their fecundity. They also suggested that female cryptic choice (sensu Eberhard 1996) could have lowered female investment in the progeny of coercive males.

Females of *P. marmoratus* have so far been unwilling to oviposit in a laboratory setting, despite being offered a variety of egg-laying substrates. Because of this, we have been unable to investigate whether males that force copulation have fewer offspring than males that attained voluntary copulation. However, the rate of successful completion of voluntary versus forced copulation (14 VC versus 4 FC) and the fact that forced copulation is employed by small males suggest that forced copulation is not the most desirable strategy.

Despite its relatively lower fitness payoff, forced copulation is still a viable option for low-quality males. These males would likely have no offspring otherwise. For this reason, forced copulation persists in numerous taxa as a conditional alternative strategy.

Forced copulation in a gift-less and display-less species

According to Thornhill (1980), forced copulation should be most likely in species where males provide direct benefits, such as nuptial gifts, territories, or nesting sites. In such species, not all males are able to provide these benefits and thus have nothing to offer a female in exchange for a voluntary copulation. In Thornhill's 1980 study of scorpionflies, males that could not acquire a dead insect or produce a salivary mass for females to eat during mating were likely to force copulation (by grasping females with a specialized abdominal structure). In many waterfowl, forced copulation is an alternative mating strategy employed by unpaired males that do not defend territories (Cheng et al. 1983; McKinney et al. 1983). Forced copulation also occurs in species whose mating displays are highly conspicuous to predators (Evans et al. 2003).

Unlike these gift-providing and display-producing species, *P. marmoratus* males do not offer any direct benefits or signal conspicuously (at least not conspicuously to humans; see next paragraph). While many other male Ensiferans provide their mates with large, externally attached spermatophores (sperm ampulla + an edible spermatophylax) (Vahed 1997; Lehmann and Lehmann 2000), copulation in *P. marmoratus* consists of insertion of eversible male genitalia without any nuptial feeding. Although *P. marmoratus* in this population are often parasitized by a tachinid parasitoid fly *Dichocera lyrata* Williston (O'Hara and Gray 2004), the fly does not home in on any male song (camel crickets do not chirp) and parasitizes juveniles, females, and adult males indiscriminately (L. P. Conroy, E. L. Haley, and D. A. Gray, unpublished data). Courtship invitations by males consist of them spreading their legs and pushing their abdomen toward the female, actions that occur at close range and are hardly noticeable from afar.

The way(s) in which females assess male quality in this species are currently unknown. Visual inspection of male size seems unlikely in this nocturnal species, although perhaps antennation is sufficient for females to evaluate male physique. Haley and Gray (2013) showed preliminary evidence that females are attracted to the cuticular pheromones produced by structures called tubercles on the males' abdomens. While pheromones have the potential to indicate a male's genotypic quality in this species, other morphologically similar *Pristoceuthophilus* lack tubercles altogether. Future research should involve further pheromone analyses (gas chromatography) and perhaps experimental manipulation of females' antennae, in order to tease apart female assessment in a species where differences in male quality are enough to generate an alternative mating strategy.

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