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Mating Behavior and Dual-Purpose Armaments in a Camel Cricket

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Abstract

Sexual selection has often been dichotomized into intersexual and intrasexual components of selection, favoring ornaments and weapons, respectively. Here, we show that a weapon used in male–male combat is sometimes also used in a functionally similar manner for grasping females during mating. The hind legs of adult males of some species of *Pristoceuthophilus* camel crickets have strongly bent tibia and stout femora with two large conspicuous spines. Here, we show that (1) leg armature is positively allometric, (2) males use these leg modifications when fighting other males, (3) males sometimes use the same leg modifications in the same functional manner for grabbing and holding females for mating, (4) virgin females show more interest in males than do non-virgin females, and (5) males are more likely to use their leg modifications to grab and hold females when paired with non-virgin females than when paired with virgin females. We interpret these results as suggesting that males employ an alternative coercive mating strategy when paired with unreceptive females; alternative explanations are also discussed.

Introduction

Ever since Darwin (1871), most work on sexual selection has included a distinction between male–male competition and female choice. Male–male competition favors not only traits such as overt weapons used to fight other males (Darwin 1871; Andersson 1994) but also less overt traits such as enhanced locomotor or sensory capability favored in scramble competitions (Able 1999; Bertin & Cézilly 2005; Kelly et al. 2008), ejaculate and sperm traits favored in sperm competition (Birkhead 2000; Simmons 2001; Birkhead et al. 2009), and alternative male reproductive strategies (Oliveira et al. 2008). Female choice may favor overt morphological, acoustical, chemical, or behavioral displays in males (Andersson 1994; Gerhardt & Huber 2002; Byers et al. 2010), as well as more cryptic features of mating behavior and morphology (Eberhard 1996). There is widespread recognition that male weapons may also serve as signals of male vigor and that such signals may be used both in fighting assessment by males and in mate assessment by females (Kodric-Brown & Brown 1984; Berglund et al. 1996). Male weapons could also be used in male–female interactions, perhaps to intimidate females and force copulation. However, other than general features such as size and strength, we are not aware of any examples of specialized male weapons being used to coerce females to mate.

Coercive mating is an alternative reproductive tactic used by males to mate with unreceptive females. A mating behavior can be ‘coercive’ even if it imposes little or no ultimate net fitness cost on females; some have even argued that coerced females may receive indirect fitness benefits via the production of sons that are good at coercing other females to mate (for discussion, see Cordero & Eberhard 2003). Coercion in mammals and birds often includes direct physical force (McKinney et al. 1983; Mitani 1985); in several species of live-bearing fish, coercion involves unsolicited male thrusting of the intromittent organ toward the female genital opening (Bisazza et al. 2001). In arthropods, coercion typically involves specialized grasping or clamping structures to hold females. For example, male scorpionflies, *Panorpa vulgaris*, use the notal organ to hold females (Thornhill & Sauer 1991), male sagebrush crickets, *Cyphoderris strepitans*, use a specialized structure on their dorsum to hold females (Sakaluk et al. 1995), modified cerci are used by several species of *Anonconotus* bushcrickets to grasp and hold females (Vahed 2002; Vahed & Carron 2008), male dung flies, *Sepsis cynipsea*, used modified forelegs to hold onto females' wings (Allen & Simmons 1996), and in several species of *Gerris* waterstriders males hold females using abdominal claspers to which females have evolved varying degrees of resistance (Arnqvist & Rowe 1995, 2002). Non-grasping structures are also sometimes used to coerce female mating, for example, male *Schizocosa ocreata* spiders employ their fangs during mating with unreceptive females and actually puncture the female resulting in injury (Johns et al. 2009). None of these male traits are thought to have evolved in the context of male–male competition however.

Here, we present data on the mating behavior of the camel cricket *Pristoceuthophilus marmoratus* Rehn (Orthoptera, Raphidophoridae). Adult male *P. marmoratus* have enlarged hind femora with two fixed prominent spines and strongly bent hind tibia (Fig. 1). *Pristoceuthophilus* mating behavior has never been studied, nor has the function of this peculiar leg modification ever been demonstrated, although a function in male–male combat has long been suspected (T. J. Cohn, pers. comm.). We show that this leg morphology is indeed a key element of the fighting repertoire of males, that it functions like a 'nutcracker' by grasping an opponent between the tibia and femur such that closure of the tibia forces the opponent against the femoral spines, that hind leg size in adult males is positively allometric, and that males also sometimes use the modified hind legs to grasp females unwilling to mate and force copulation.

Methods

Collections and Rearing

All our collections were from the understory of coast live oak, *Quercus agrifolia*, forest in the Santa Monica Mountains, Los Angeles Co., California, USA (34.1°N, 118.7°W; Elev. approx. 200 m). To examine male hind leg allometry, we collected nine adult males in Oct. and Nov. 2003 and supplemented those data with 14 additional adult males collected as juveniles in 2009 following their use in behavioral trials. For laboratory behavioral trials, we collected juveniles from July to Oct. 2009. Juveniles were reared to adulthood in the laboratory at 24°C with a 12:12 h photoperiod on an *ad libitum* diet of rolled oats, ground dry cat food (Purina), and flake fish food (TetraMenu); cardboard egg carton was provided as shelters, and water was continuously available in cotton-plugged vials. At later instars, individuals were isolated in 500-ml individual containers with food and water to ensure virginity of males and females. A subset of these individuals were paired and allowed to mate to generate a set of previously mated non-virgin females; we expected non-virgin females to be less willing to mate than virgin females, potentially inducing male coercive mating strategy. Individuals were only used once each in behavioral trials.

Leg Allometry

Measurements were made on 23 dead adult male specimens. To measure body size, we measured

Fig. 1: Legs of adult *Pristoceuthophilus marmoratus* camel crickets. (a) An adult female and an adult male leg. (b) A close-up of the male femoral spines.

pronotal length to the nearest 0.01 mm using digital calipers. For leg measurements, the left hind leg was separated from the body, placed flat on a white background next to a millimeter ruler, and photographed with a digital camera. Digital photographs were analyzed using NIH ImageJ software (Abramoff et al. 2004). We measured femur length, femur area, the length of the larger of the two spines, and the angle of tibial bend across the dorsal side. All measurements were made twice and repeatability calculated following Lessells & Boag (1987); we then used the average of the two measurements in reduced major axis (RMA) regression of ln transformed data (McArdle 1988).

Videotaped Trials

We conducted three different sets of videotaped trials: two males with a single virgin female (male–male combat trials), a single male with a single virgin female (virgin female trials), and a single male with a previously mated female (non-virgin female trials). All video trials used the same basic setup: individuals were removed from their 500-ml individual containers and placed together in a 10 × 15 cm clear plastic arena. The arena was covered with white paper on all sides except the front camera side. Crickets were videotaped under red light in an otherwise dark room during the dark portion of their photoperiod. A high-definition HDMI video camera (Canon Vixia HV30, Canon USA, Lake Success, NY, USA) was used to record interactions on a 64-min high-definition tape. The arena was washed after each trial.

Video and Data Analysis

Videotapes of male–male combat were watched to verify the long suspected role of male legs in combat, but individual behaviors were not quantified formally. Videotapes of male–female pairs were analyzed using JWatcher Video v.1.0 (http://www.jwatcher.ucla.edu/) to quantify formally male–female mating interactions and allow statistical comparison between interactions of males with virgin females and males with non-virgin females. Behavioral codes with corresponding definitions are given in Table 1. We conducted a sequential analysis in JWatcher to determine which behaviors followed other behaviors more often than expected by chance. Sequential analysis reports the number of transitions between each pair of events found within an entire behavioral sequence (Blumstein & Daniel 2007). Kinematic diagrams showing only the statistically significant transition probabilities were created for sexual behaviors. The sexual behavior category included: antennation conspecific, leg up, body vibration, push back, leg mount, unforced copulation, and forced copulation. To summarize male forceful behavior, we combined one and two leg holding with leg mount as a single behavior as they are functionally equivalent.

Results

Male Hind Leg Allometry

All measurements were highly repeatable (repeatability = 0.93 for pronotal length measured with calipers, repeatability >0.97 for all other traits analyzed

Table 1: Description of male and female behaviors scored during video analysis

Behavior	Description
Depart (D)	Female moves away from male
Mount (M)	Female moves up onto male's abdomen
Unforced copulation (C)	Female mounts the male and remains on top, resulting in spermatophore transfer
Follow (F)	Male follows female
Leg mount (L)[a]	Male grasps female between hind tibia and femur and holds her while extending abdomen
Leg up (U)	Male raises one or both hind legs toward female
One leg hold (O)[a]	Male holds female with one hind leg
Two leg hold (T)[a]	Males holds female with both hind legs
Push back (B)	Male pushes backwards and extends abdomen toward female
Forced copulation (c)	Male grabs female via leg mount and holds during spermatophore transfer
Antennation (A)	Cricket moves antennae, but not toward conspecific
Antennation conspecific (a)	Cricket moves antennae into contact with the other cricket
Escape (E)	Cricket attempts to climb walls, or otherwise escape container
Grooming (G)	Cricket grooms self with mouthparts
Pause (P)	Cricket remains immobile for at least 10 s
Body vibration (V)	Cricket spreads hind legs and rocks body side to side or back and forth

[a] Leg mounts, one leg holds, and two legs holds were scored separately but combined in analysis.

via image analysis, all $p < 0.0001$). Hind femur length was isometric with pronotal length (RMA slope ± SE = 0.96 ± 0.08, $r_{21} = 0.92$, $p < 0.001$), whereas all other hind leg modifications were positively allometric (square-root femur area RMA slope ± SE = 1.16 ± 0.08, $r_{21} = 0.94$, $p < 0.001$; femoral spine length RMA slope ± SE = 3.47 ± 0.42, $r_{21} = 0.84$, $p < 0.001$; angle of tibial deflection RMA slope ± SE = 2.01 ± 0.32, $r_{21} = 0.69$, $p < 0.001$). Figure 2 shows hind legs of a large and a small male.

Male–Male Combat

Of 20 male pairs, 12 fought. Initially, males made antennal contact, and if neither male retreated, they turned around and faced away from each other and used their hind legs to grab and hold one another. If the contest escalated, males interlocked their legs and wrestled until one eventually retreated or until one male grabbed and pinned the other male and his legs (see Video S1).

Mating Behavior

Virgin females (n = 26) showed more interest in males than did non-virgin females (n = 24) as measured by the numbers of times they antennated males (Fig. 3, Kruskal–Wallis nonparametric ANOVA $k_1 = 5.901$, $p = 0.015$); however, males did not differ in numbers of antennations of virgin and non-virgin females, although the difference was nearly significant (Fig. 3, Kruskal–Wallis nonparametric ANOVA $k_1 = 3.558$, $p = 0.059$).

Figure 4 shows kinematic diagrams of male sexual behaviors when paired with virgin females (Fig. 4a, n = 26 male–female pairs) and with non-virgin females (Fig. 4b, n = 24 male–female pairs). Only statistically significant transitions are shown; the same behavioral transitions were statistically significant in both cases; therefore, the diagrams overall appear very similar. Both show that approx. 95% of the time after a male antennates a female, the next behavior he performs is to raise a hind leg (96% and 95% of the time when paired with virgin and non-virgin females, respectively); raising a hind leg was the only behavior that followed antennation more than expected by chance. Both also show that after raising a hind leg, the next behavior that the male performs is to either antennate the female again (approx. 50% of the time) or push his abdomen back toward the female (32% and 34% of the time); no other behaviors significantly followed leg raising. After males pushed back toward females, each of three behaviors occurred more than was expected by chance: (1) the female might mount the male and copulate (unforced copulation), (2) males might vibrate their body and then often once again push their abdomen back toward the female, or (3) the male might grab the female with his hind leg(s) and force copulation (forced copulation); see Videos S2 and S3.

Fig. 2: Comparison of male hind legs from a large and a small male; leg modifications, but not femur length, are positively allometric.

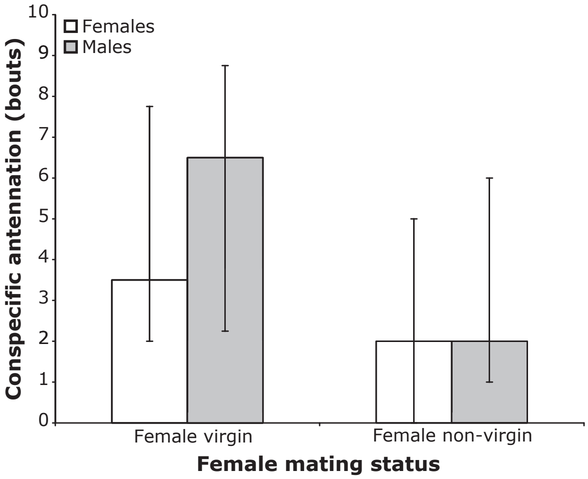

Fig. 3: Median and interquartile ranges for numbers of times male and female *Pristoceuthophilus marmoratus* antennated each other in videotaped trials as a function of female mating status.

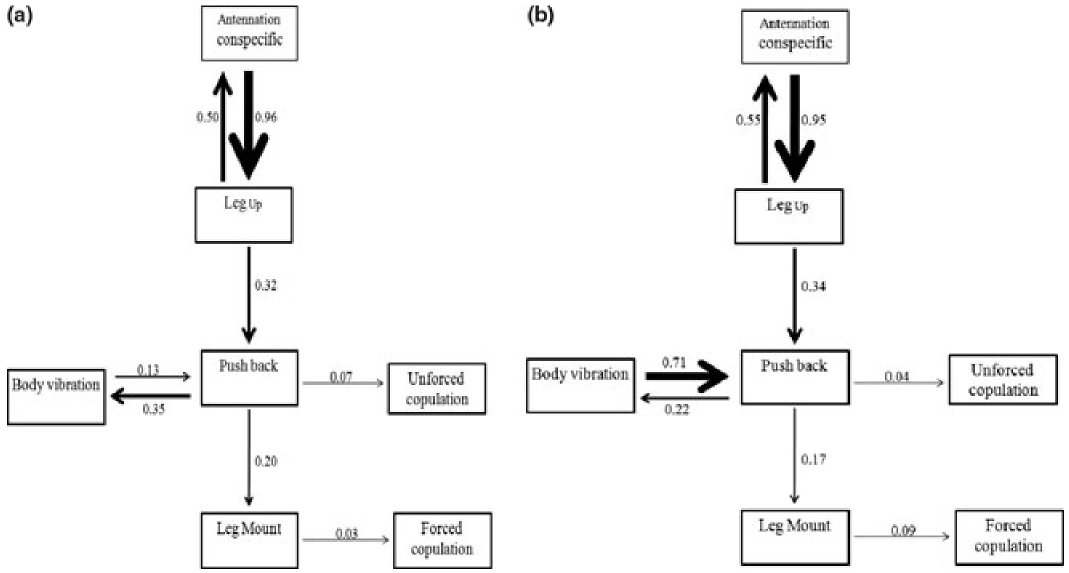

Fig. 4: Kinematic diagram showing male mating behaviors when paired with either virgin (a) or non-virgin (b) females. Only behaviors that followed one another with probability greater than expected by chance are shown. Numbers and line thicknesses correspond to transition probabilities from one behavior to the next.

Despite the overall similarity of the males' behavioral sequences, there was a statistically significant difference between the males paired with virgin and non-virgin females. Thirteen percent of males with virgin females went from leg mount to forced copulation and 87% went from leg mount to a behavior other than forced copulation, whereas 50% of males with non-virgin females went from leg mount to forced copulation and 50% went from leg mount to a behavior other than forced copulation ($G^2 = 5.45$, df = 1, p = 0.02).

Behavioral sequences for female sexual behaviors are shown in Fig. 5 (A: virgin females, B: non-virgin females); as in Fig. 4, only statistically significant behavioral transitions are shown. Upon antennating a male, females typically paused (83% and 82% of the time) and then antennated the male again (91% and 86% of the time). Following antennation, females sometimes mounted the male voluntarily (14% and 11% of the time) and then copulated (27% and 11% of the time). While paused, females were occasionally grabbed by males and forced to copulate (4% and 16% of the time). There was only one significant difference between the sequences of virgin and non-virgin female behaviors. Four percent of virgin females went from paused to forced copulation and 96% went from paused to a behavior other than forced copulation, whereas 16% of mated females went from paused to forced copulation and 84% went from paused to a behavior other than forced copulation ($G^2 = 6.75$, df = 1, p = 0.009). This suggests that non-virgin females were more likely to be forced to copulate. We tested this by comparing mating of virgin and non-virgin females: virgin and non-virgin females did not differ in their likelihood of mating during a trial (38% virgin females and 32% non-virgin females, $G^2 = 0.233$, df = 1, p = 0.629); however, virgin females that did mate during a trial were less likely to be forced to copulate than were non-virgin females (Fig. 6, four of ten virgin females that mated during a trial were forced, whereas seven of eight non-virgin females that mated during a trial were forced, $G^2 = 4.57$, df = 1, p = 0.03). Forced and unforced copulations did not differ in duration ($\bar{x} \pm$ SD duration forced copulations 28.4 ± 16.5 min, n = 11; unforced copulations 28.1 ± 25.1 min, n = 7; ANOVA; $F_{1,16} < 0.001$, p = 0.97).

Discussion

Male *P. marmoratus* use their modified hind legs for both fighting and for what we interpret as coercive mating. The hind leg modifications, but not hind femur length, show positive allometry as is common with both ornaments and weapons (Green 1992; Bonduriansky & Day 2003; Bonduriansky 2007). Positive allometry of ornaments and weapons reflects greater fitness payoff for investment in weapon/ornament elaboration relative to payoff for further somatic investment (Kodric-Brown et al. 2006). The leg modifications function as a

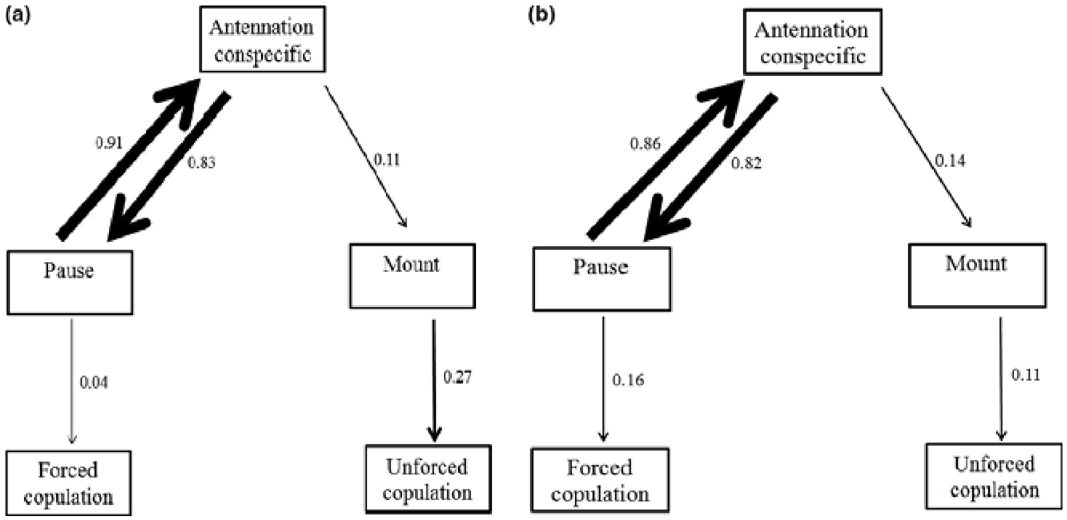

Fig. 5: Kinematic diagram showing mating behaviors of virgin (a) or non-virgin (b) females when paired with males. Only behaviors that followed one another with probability greater than expected by chance are shown. Numbers and line thicknesses correspond to transition probabilities from one behavior to the next.

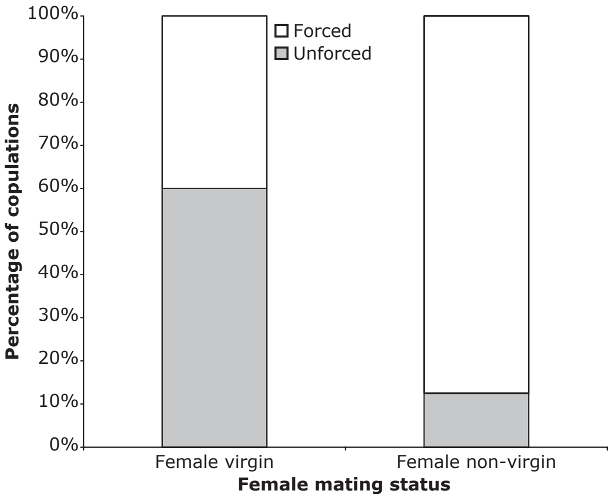

Fig. 6: Virgin and non-virgin females differed in their likelihood of being subjected to forced copulation.

'nutcracker' that closes upon either an opponent or a female. To our knowledge, this is the first demonstration of a specialized male trait functioning in the same way for both fighting other males and during mating. One amazing feature of our results was the consistency with which males utilized their legs in mating interactions: approx. 95% of the time after antennating a female, the next behavior males performed was to raise a hind leg toward her. This suggests that the leg modifications play a major role in camel cricket interactions and that their use is routine rather than an occasional anomaly.

We interpret this male behavior as 'coercive' because it circumvents female choice and was employed more commonly against non-virgin females who, as a group, exhibited less interest in males. If this interpretation is correct, then an interesting feature about this alternate male strategy is that the largest males have disproportionately larger legs. Therefore, the greatest expression of the coercive structures is associated with males in (presumably) good condition rather than with small males in (presumably) poor condition. This is unusual in animals as most conditional alternate strategies are employed by males in poor condition that are 'making the best of a bad job' (Dawkins 1980; Gross 1996; Oliveira et al. 2008), although at least one study has found that larger males in better condition were more likely to employ an apparently coercive strategy (Wilgers et al. 2009).

Is 'coercion' the right terminology? Some colleagues have suggested an alternate explanation of male–female mating behavior: perhaps grasping of females serves as a test of male size and/or strength. Virgin females may willingly mate to obtain sperm, but then later as non-virgins mate only with large strong males with modified legs large enough to force copulation. That is, a coercive mating system may have advantages to females indirectly via enhanced genetic sperm quality and/or via production of coercive sons (Cordero & Eberhard 2003); whether those potential benefits offset potential costs is unknown. In our view, the ultimate cost/benefit balance to females is a separate question from whether or not this behavior is 'coercive'. Direct costs in terms of the extent of female injury from forced copulation, if any, are unknown and may be negligible without changing our interpretation of this behavior as 'coercive'. Male coercion of females via the threat of injury is effective because compliance minimizes costs; the costs of non-compliance may be high, but never realized by females (or measured by scientists) if females comply so as to avoid those costs. In every instance we observed, females ceased to struggle immediately upon capture by a male. This may minimize damage to the female; no visible injuries were ever apparent to us. As sexual conflict should favor counter-adaptations in females, not just coercive adaptations in males (Tregenza et al. 2006), we are curious if female passivity once captured is adaptive at least in the sense of avoiding injury. Future studies, particularly comparative study across the genus to address female costs and potential benefits, as well as condition dependence of male leg modifications and the relative success at courting, fighting, and coercive mating as a function of leg size, will be very informative.

Virtually nothing else is known of the mating behavior of these camel crickets or their congeners. Camel crickets (Raphidophoridae) do not produce acoustic signals such as are important in true crickets (Gryllidae), katydids (Tettigoniidae), and some other ensiferan families. How males and females encounter one another in the field is unknown; however, our field observations suggest that they are often at fairly high density (often >1 per 5 m^2 in suitable habitat). Chemical communication is likely important, but as of yet has not been described in the literature. We currently have no way of knowing the relative importance of selection in the context of fighting vs. selection in the context of coercion that has favored the development of elaborated male legs. We speculate that the fighting function evolved first and was co-opted for mating; testing this will require comparative study across the genus in a phylogenetic context. The geographic range of the 13 named species of *Pristoceuthophilus* is restricted to western North America, primarily British Columbia, Washington, Montana, Oregon, California, Arizona, and south to the southwestern states of Mexico. Of these, only a subset have similarly modified male hind legs (*Pristoceuthophilus arizonae*, *P. marmoratus*, *Pristoceuthophilus pacificus*, and *Pristoceuthophilus unispinosus*). Unfortunately, there is no phylogeny available, and there are likely to exist a number of currently undescribed species (T. J. Cohn, pers. comm.). Nonetheless, this system seems likely to produce valuable insights into sexual conflict and mating behavior. Because the apparently coercive leg structure is also a key feature of male–male competitive interactions, male hind leg evolution in a mating context may be constrained by the legs functional role in male combat. As this is the first example of a dual-purpose armament used in combat and coercion, the evolutionary trade-offs will be especially novel to explore within this system.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Video S1: Male–Male.avi shows two adult *Pristoceuthophilus marmoratus* males fighting in the presence of an apparently uninterested female.

Video S2: Unforced.avi shows an adult virgin female *Pristoceuthophilus marmoratus* mounting an adult male.

Video S3: Forced.avi shows an adult male *Pristoceuthophilus marmoratus* capturing an apparently uninterested previously mated female.