

## RESEARCH ARTICLE

# Bite force, body size, and octopamine mediate mating interactions in the house cricket (*Acheta domesticus*)

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**Abstract**

Mating interactions are rife with conflict because the evolutionary interests of males and females seldom coincide. Intersexual conflict affects sexual selection, yet the proximate factors underlying male coercive ability and female resistance are poorly understood. Male combat outcomes are often influenced by bite force, with superior biters being more likely to achieve victory over poorer biters in a range of species, including crickets. If good performers also achieve mating success through sexual coercion, then bite force might play a role in intersexual conflict as well. We tested the capacity of bite force to influence mating interactions in house crickets both directly by measuring bite forces of males and females and by altering male bite capacity through neuropharmacological manipulation. In addition, the invertebrate neurotransmitter octopamine both mediates aggression and underlies motivation to bite in male house crickets. By blocking octopamine receptors through the application of an antagonist, epinastine, we tested the effects of reduced bite force on male mating success. Our results show that male bite capacity, in combination with body size, influences both the likelihood and the outcomes of mating interactions, whereas treatment of males with epinastine eliminates motivation to mate. Our results suggest a functional role for bite force in affecting both sexual conflict and sexual selection and expand our knowledge of the influence of biogenic amines on reproductive behaviour.

**KEYWORDS**
*Acheta domesticus*, female choice, performance, sexual conflict

## 1 | INTRODUCTION

Reproductive interactions between males and females can give rise to conflict if the evolutionary interests of the sexes are incompatible. In mating systems that are dominated by female choice, males may attempt to subvert female mating preferences, often resulting in females mating with non-preferred males (Arnqvist & Rowe, 2005; Parker, 1979). Although the evolutionary consequences of this interlocus sexual conflict have received a great deal of attention (Bonduriansky, 2011; Edward et al., 2014; Hall et al., 2010; Lailvaux et al., 2010), we currently lack a general understanding of the proximate mechanisms by which males are able to coerce matings from uncooperative females. Understanding these mechanisms is necessary

if we wish to gain insight into whether selection commonly acts on similar mechanisms in females to resist unwanted matings or if female resistance and male coercion are functionally distinct.

Performance is relevant to both male–male combat (Hall et al., 2010; Lailvaux & Irschick, 2007; McLean et al., 2020) and female competition (Bywater et al., 2008); in that better performers tend to be victorious over poorer performers in aggressive intraspecific interactions with other individuals of the same sex (reviewed in Husak & Fox, 2008; Lailvaux & Irschick, 2006). For example, in crickets, maximum bite force has been positively associated with the likelihood of winning male–male fights both by itself (Condon & Lailvaux, 2016) and in combination with other performance traits, such as jumping ability (Hall et al., 2010). However, those performance traits that are

associated with success in male combat situations are typically not the same traits that are preferred by females (Lailvaux et al., 2010; McCullough & Simmons, 2016; Okada et al., 2014), and consequently, the utility of performance traits might be sex-specific and thus subject to conflict over either their expression or use in males and females (reviewed in Husak & Lailvaux, 2014; e.g. Tarka et al., 2014). If performance also mediates reproductive conflicts between males and females during mating, then whole-organism performance capacities could be targets of selection within the contexts of male coercion or female resistance, or both.

In addition to measuring performance of individuals involved in reproductive interactions, insight into the effect of performance capacities on reproductive outcomes might be gained via performance manipulation. Octopamine and its precursor tyramine are the invertebrate analogs of adrenergic neurotransmitters (Farooqui, 2007). Octopamine affects arthropod movement, including muscle performance and respiration, activity, and aggressive behaviours in males along with the fight or flight response and motivation (Hoyer et al., 2008; Roeder, 2005). In addition, octopamine can also affect the expression of whole-organism performance traits. For example, male, *Achaeta domestica* crickets treated with a synthetic octopamine antagonist, epinastine, exhibit a significant decrease in maximum bite force expression compared to control animals (Bubak et al., 2022). A similar neuropharmacological intervention affects courtship call structure in this same species (Adeola et al., 2022). Furthermore, in crickets levels of octopamine increase in the hemolymph after courtship, fight encounters, and flying (Adamo et al., 1995; Rillich et al., 2019). Despite the role of the biogenic amines in affecting aggression and male combat (Palavicino-Maggio & Sengupta, 2022; Rillich et al., 2019), previous studies administering octopamine antagonists have shown that octopamine does not affect courtship behaviours in those insects studied thus far, including the cricket *Gryllus bimaculatus* (Rillich et al., 2019; Zhou et al., 2008). Collectively, these findings suggest that octopamine is a promising candidate for modifying bite force expression and thus for experimentally testing the role of bite force in mediating male-female conflict during mating interactions.

The unfettered expression of female mating preferences is associated with higher female fitness in a variety of species and contexts (e.g. Havens et al., 2011; Iyengar & Eisner, 1999), despite the costs incurred by choosiness (Forstmeier et al., 2021; Vitousek et al., 2007). However, when female choice is subverted by males, females commonly suffer a variety of additional costs associated not only with the act and consequences of mating (Morrow & Innocenti, 2012) but also with the evolution of resistance to unwanted matings, particularly in low-resource environments (Rostant et al., 2020). Males can potentially thwart female mating preferences in a variety of ways. In crickets, for example, sexual conflict occurs over the attachment of the male spermatophore to the female reproductive tract. Unattractive males might take longer to solicit matings from females (i.e. exhibit longer latency to mate) and may also attempt to override female mating preferences by coercing her into allowing attachment of the spermatophore during mating, altering overall mating time. Once

attached, the female can attempt to remove the spermatophore, and unattractive males might harass her to prevent her from doing so, thus ensuring that more ejaculate is transferred than she might like due to longer attachment times. Although these behaviours are well-characterized, relatively little attention has been paid to the role of physical, functional traits such as whole-organism performance capacities (defined as the ability to perform dynamic, physically challenging and ecologically relevant tasks such as jumping, running, or biting) (Irschick et al., 2008; Lailvaux & Irschick, 2006) underlying those behaviours in facilitating either male harassment and coercion or female resistance to unwanted matings (Husak & Lailvaux, 2014; Watson et al., 1998).

To test the hypothesis that bite force mediates reproductive interactions in *A. domestica* house crickets, we measured maximum bite force both before and after trials and estimated the utility of bite force to predict mating outcomes and to affect the time course of mating interactions. Specifically, we predicted that differences in bite force and body size between males and females will affect not only the probability of successfully mating but also the latency to mate, time it takes to mate, and the attachment times of the spermatophore packets. We then tested the secondary hypothesis that altering octopamine levels through oral supplementation of epinastine prior to mating trials affects both bite force expression and consequently the timing and outcomes of mating interactions. We predict that treatment groups will differ in these same four variables, namely mating success, latency to mate, mate time, and spermatophore attachment time.

## 2 | MATERIALS AND METHODS

The *A. domestica* crickets used for this experiment were laboratory descendants of 1000 count cricket stocks originating from Fluker's Cricket Farm, Baton Rouge, Louisiana. The experiment was conducted at the University of New Orleans from January 2018–September 2019. We stored crickets, at similar densities, in 66-quart storage containers with mesh nets in the lid for ventilation. We monitored food and water provisions bi-weekly, similar to previous studies (e.g. Adeola et al., 2022; Condon & Lailvaux, 2016). Once crickets reached maturity, distinguishable by eclosure where the final moult results in wings, we randomly allocated 300 male and female crickets to either control ( $n=200$ ) or treatment ( $n=100$ ) groups. We separated males used in the experiment into 66-quart storage containers at 5 weeks in age prior to eclosure to ensure virginity before the start of the trials, but we kept females in 66-quart storage containers with other females and non-experimental males. Therefore, females had the option to mate before the start of the trial, so that when paired they would not mate due to lack of options as females engage in polyandry in this species (Mautz & Sakaluk, 2008; Rillich et al., 2009). Between 5 and 7 days of crickets within each group eclosing, we separated adult crickets into separate  $8 \times 8 \text{ cm}^3$  containers. The males used in the trials were pulled from the male-only storage containers once they were adults. The

females used in the trial were pulled from the container with both females and non-experimental males.

We fed males in the treatment group a pureed sweet corn and epinastine mixture at a concentration of 15 mg/mL (as in Adeola et al., 2022; Bubak et al., 2013, 2022). Control males were fed similar amounts of pureed sweetcorn without epinastine. We allowed males 2 h to feed and returned them to the  $8 \times 8 \text{ cm}^3$  containers, after which we measured the bite force of each isolated cricket using standard methods with the Tekscan FlexiForce™ standard model A201 Sensor (Tekscan Inc.) (see Freeman & Lemen, 2008 for detailed description; Hall et al. (2010), Lailvaux et al. (2011), Kelly (2014), and Bubak et al. (2022) for previous studies that have used this equipment to measure bite force in orthopterans) with a Windows XP in lab desktop computer. The sensors were calibrated over the range from 0 N to 1.5 N, encompassing all recorded bite force measures, using weights of known mass mounted on angled tweezers to simulate the area and point of contact of the cricket mandibles (Suzuki & Okanoya, 2021). Briefly, we encouraged crickets to bite down on an Economical Load and Force System printed circuit strip calibrated in Newtons. This circuit is very thin relative to the crickets, and consequently, every organism was able to fit their mandibles around the sensor and interact with the force-sensitive area at a similar angle regardless of the size of the animal. Because we were interested in the maximum bite force capacities of each individual, and to deal with issues of variation in measured performance capacity (see Losos et al., 2002 for general discussion of maximum locomotor performance), we measured bite force three times per cricket and used the maximum value obtained for each individual in subsequent analyses (Bubak et al., 2022; Condon & Lailvaux, 2016; Hall et al., 2010; Lailvaux et al., 2011). Different sensors were used for males and females to avoid female ingestion of trace amounts of neurotransmitters from possible regurgitation of sweet corn blends. The sensors were .203 mm in thickness with a 9.53 mm diameter sensing area. To measure maximum bite force, we held each cricket firm to the container wall ( $8 \times 8 \text{ cm}^3$ ) with their head and pronotum free above the container. While crickets were held in place, we vertically inserted the sensors between the horizontally opening crickets' mandibles until they bit. We restarted the sensor frequently to account for any sensor drift, which was in any case minimal. Because orientation of the animal and sensors can affect measured bite force in crickets (Weihmann et al., 2015), as in other species (see Lappin and Jones (2014) for discussion of similar issues with bite force in lizards), we measured bite forces using this standardized protocol, consistent with earlier studies.

For mating interactions, the numbers assigned to the crickets were placed in an array and randomly permuted to choose pairings. We placed cricket pairs in  $17 \times 11.5 \times 6 \text{ cm}^3$  containers with clear lids and damp paper towels at the base of the containers to provide favourable mating conditions (Adeola et al., 2022; Hall et al., 2008). We allowed the pairs an average of approximately 2.5 h to initiate mating. We defined the latency to mate as the time in seconds from when males and females were placed in the same container to the initial start of mating where backwards slipping of males under the

female occurs to engage in copulation. We defined mate time as the time the male took to attach the spermatophore packet once back slipping under the female began. If the mating attempt was successful (i.e. a spermatophore packet was produced and attached to a female during copulation), the bite force for both sexes was measured. We defined attachment time as the time the spermatophore packet was attached to the female post-copulation till the time it was discarded from the female external genitalia. If unsuccessful, the same pairs were re-mated within 48 h with their same partner. The bite force of males and females was measured before and after trials regardless of outcome as long as they were alive. Of the 100 control pairs, 11 mated successfully on the first pairing, and 12 mated only on the second pairing. There were 45 pairs of crickets in the epinastine group; however, none of them mated. Before re-mating, male crickets were additionally supplemented with treatment dosages. Once re-mated we again measured the bite forces.

### 3 | STATISTICAL ANALYSIS

We conducted all analyses using R version 4.0.4 (R Development Core Team, <http://www.R-project.org>).

We tested the influence of bite force on mating interactions by measuring the difference between the maximum bite forces of the male and female that constitute a given mating pair. We also measured thorax size differences between males and females to account for allometric effects of body size on bite force. Within the control trials, we tested the influence of size and bite force on the probability of mating by fitting a logistic mixed model using binomial errors and Adaptive Gaussian Quadrature (Pinheiro & Bates, 1995) to the binomial mating outcomes. Because cricket pairs that did not mate on the first pairing were given a second opportunity to do so the next day, we coded grouping as a random effect to control for any associated variance and included this in our probability of mating mixed model. Fixed effects in this model were the differences between both bite force and thorax size between the male and female involved in each interaction, as well as the interaction between size and bite force differences. We fit this logistic mixed model using the GLMMadaptive package.

For latency to mate, mate time, and attachment time, we fit separate generalized linear models to test for effects of thorax size differences and bite force differences between males and females on the respective dependent variables. We used Poisson distributions to model the amount of time seconds it took for crickets paired in their containers to start mating (i.e. latency to mate); the amount of time in seconds it took crickets to mate (i.e. mate time); and the amount of time the spermatophore packet was attached to each female (i.e. spermatophore attachment time) (Dobson & Barnett, 2008). In addition to testing for effects of size and bite differences and the interaction between them, we also fit a nonlinear term for bite force difference in all of the saturated models to all for the possibility that such differences might disproportionately affect the timing of these key events depending on their relative

magnitudes. In all cases, we used log-likelihood ratio reduction tests to find the minimum adequate model for each dependent variable (i.e. the simplest model explaining the greatest amount of variation for each instance) (Crawley, 1993). We note that we did not conduct any statistical analyses on the epinastine-treated crickets because, out of the 45 pairs of epinastine-treated crickets, none successfully mated, and including these data in the mixed model logistic regression skewed the dataset and introduced singularity errors which prevented model convergence.

## 4 | RESULTS

Males within the control group of this study had a greater mating success rate when their recorded maximum bite force measurements were stronger than the paired female (Table 1; Figure 1). The minimum adequate models retained significant interactions between thorax size differences and bite force differences for mating success, latency to mate, mate time, and spermatophore attachment time. Males in the epinastine group did not mate;

| Mate success generalized linear mixed effects model |          |        |           |            |
|---|----------|--------|-----------|------------|
| Fixed effects                                       | Estimate | SE     | Conf. low | Conf. high |
| (Intercept)   | -1.7244  | 0.3161 | -2.344    | -1.1048    |
| bitediff  | 4.2070   | 2.0021 | 0.283     | 8.1310     |
| thoraxdiff  | -0.7565  | 0.7617 | -2.249    | 0.7363     |
| bitediff:thoraxdiff                                 | 6.8016   | 5.5277 | -4.033    | 17.6357    |
| ...   |          |        |           |            |

TABLE 1 Generalized linear models explaining mate time with interactions between bite force and differences in thorax size between males and females.

Note: The method used was the adaptive Gauss-Hermite quadrature rule.

### Mating success ratios

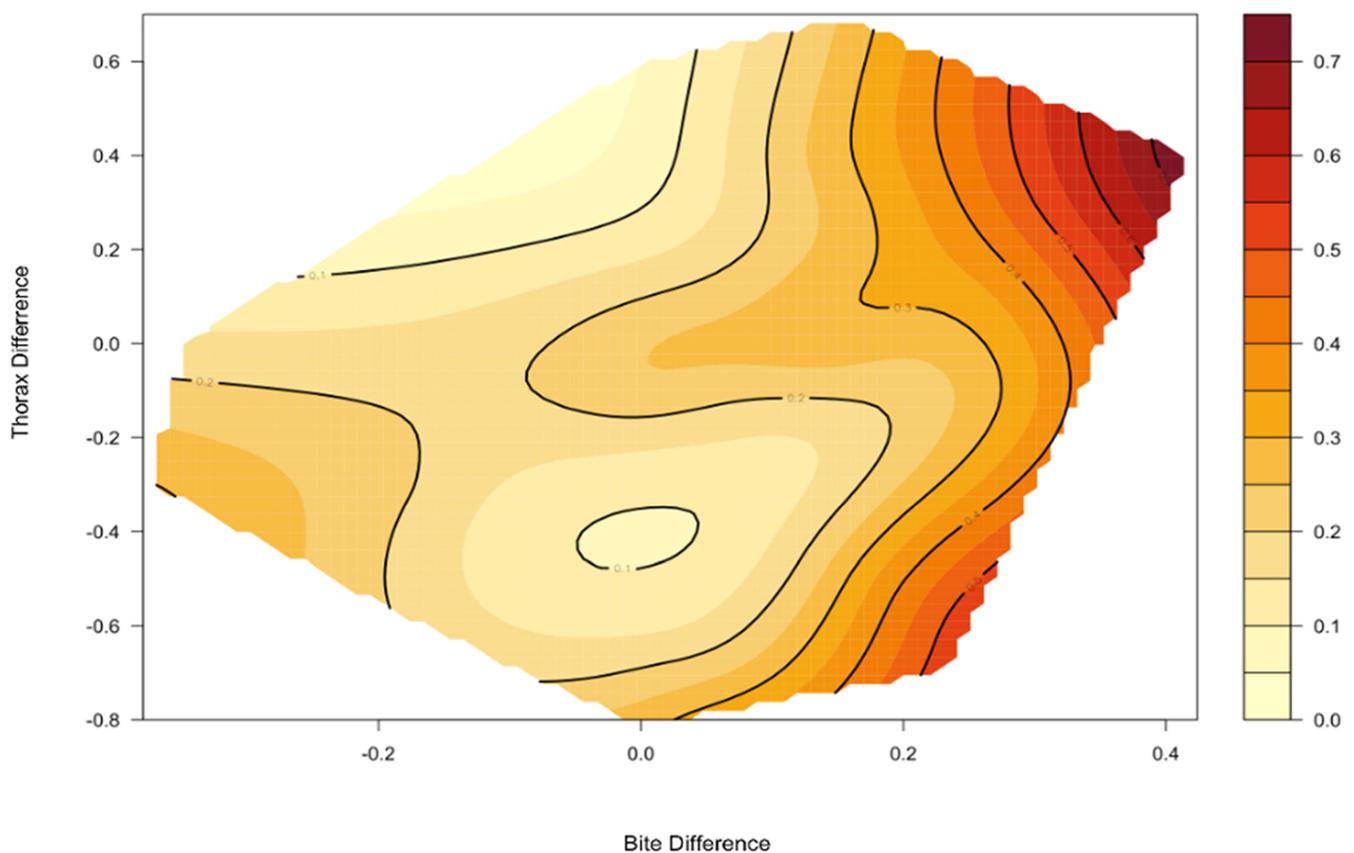


FIGURE 1 Males within the control group of this study enjoyed greater mating success when they were both larger and exhibited higher maximum bite forces than the specific females they were paired with, whether they mated on the first or second pairing. Males in the epinastine group did not mate.

consequently, all of the subsequent analyses pertain to the 100 control mating pairs.

Within the control group, larger males that bit harder than the females with which they were paired were more likely to successfully mate, even after accounting for mating group (i.e. whether pairs mated on the first or second attempt) (Table 1; Figure 1). Our model for mate time showed males who had weaker bite forces than females and were smaller in thorax width took a longer time to initiate mating (i.e. latency to mate) compared to males that were larger and stronger biters than the paired female (Table 2a; Figure 2). Larger crickets that bit harder were also more likely to have both shorter mating times and longer spermatophore attachment times (Table 2b,c; Figures 3 and 4). Mating times were also prolonged in cases where females were larger, but males had bite force differences of greater than  $-0.15\text{N}$ . (Figure 3).

For all three of these variables, the minimum adequate model was the saturated model, retaining not only interactions between size differences and bite force differences but also nonlinear effects

TABLE 2 Generalized linear models explaining initiation time (a); mate time (b); and attachment time (c).

| (a) Latency to mate generalized linear mixed effects model |           |          |         |
|--|-----------|----------|---------|
| Fixed effects  | Estimate  | SE       | Z value |
| (Intercept)  | 8.373455  | 0.004442 | 1884.90 |
| thoraxdiff   | -0.800833 | 0.011149 | -71.83  |
| bitediff   | -0.610972 | 0.026005 | -23.49  |
| l(bitediff^2)  | -7.145587 | 0.088831 | -80.44  |
| thoraxdiff:bitediff  | 5.062986  | 0.086031 | 58.85   |
| ...  |           |          |         |
| (b) Table: Mating time                                     |           |          |         |
| Coefficients   | Estimate  | SE       | Z value |
| (Intercept)  | 4.93716   | 0.02162  | 228.313 |
| thoraxdiff   | 0.51133   | 0.06080  | 8.411   |
| bitediff   | -2.39595  | 0.13279  | -18.043 |
| l(bitediff^2)  | 5.99539   | 0.37984  | 15.784  |
| bitediff:thoraxdiff  | 7.74370   | 0.42169  | -18.364 |
| ...  |           |          |         |
| (c) Table: Attachment time                                 |           |          |         |
| Coefficients   | Estimate  | SE       | Z value |
| (Intercept)  | 7.958917  | 0.005518 | 1442.33 |
| thoraxdiff   | -0.591354 | 0.016365 | -36.13  |
| bitediff   | 2.031494  | 0.028259 | 71.89   |
| l(bitediff^2)  | 2.597051  | 0.095966 | 27.06   |
| thoraxdiff:bitediff  | 2.594166  | 0.085568 | 30.32   |
| ...  |           |          |         |

Note: All models retained interactions between bite force and thorax size differences between males and females, as well as a nonlinear effect of bite force difference in each case, as indicated by log-likelihood ratio tests.

of bite force differences on all of the time variables (Table 2). These results indicate that not only are latency to mate, mate time, and spermatophore attachment time significantly affected by both size and bite force differences between males and females but also the effects of bite force become ever more pronounced as the differences between male and female biting become larger. The nonlinearity is particularly manifest in the case of overall mate time, in the sense that the surface for mate time shows two distinct peaks, with mate times being especially prolonged in both males with both weak and strong bite forces relative to females, depending on the specific combination of bite force and size differences (Figure 3).

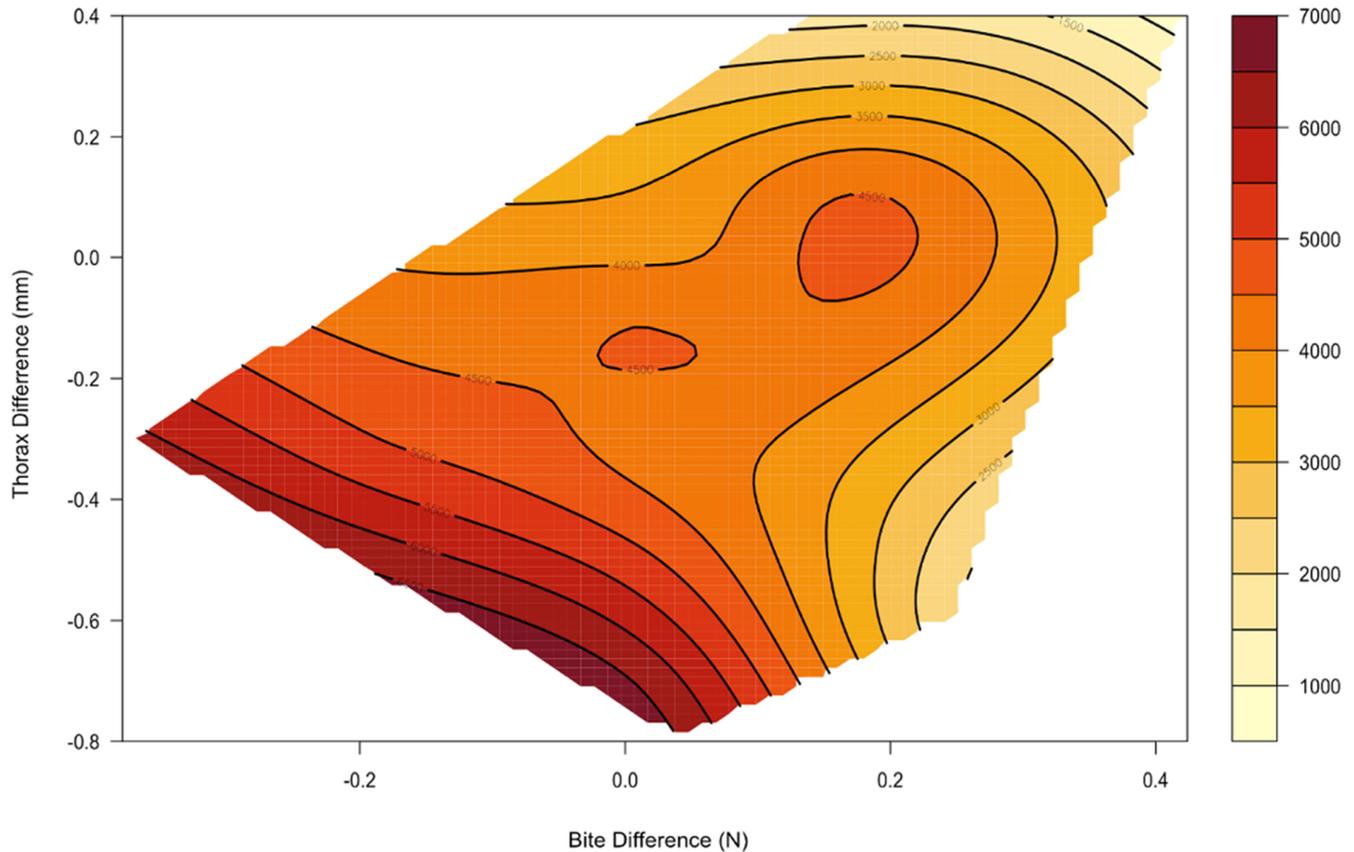
## 5 | DISCUSSION

Whole-organism performance abilities such as the ability to exert forceful bites affect male combat outcomes in a variety of vertebrate (Husak, 2006; Lailvaux et al., 2004) and invertebrate taxa (Condon & Lailvaux, 2016; Hall et al., 2010). However, the functional factors bolstering males' coercive abilities are not as well understood from a performance perspective. We measured maximum bite force for both males and females to determine the potential for bite force to mediate conflict between the sexes, and to test the hypothesis that reducing bite force via octopamine manipulation would affect reproductive interactions.

The difference in bite force and thorax size between males and females engaging in reproductive interactions consistently predicted both the outcomes and the time course of those interactions. Where males that were able to successfully mate with females at all depended significantly on both the difference in body size as indicated by the size of the thorax and the difference in bite force between males and females in a given interaction. Because bite force has an interaction with thorax size, we cannot independently determine the likelihood of mating success based on thorax size difference or bite force difference alone (see Engqvist, 2005), but only in combination with each other, such that males who were both larger and stronger biters than their respective females exhibited higher mating success. The mechanism by which bite force influences the probability of successfully mating is not apparent from our current dataset, but could be determined via more detailed behavioural observations than we employed here. However, our results are consistent with the interpretation that sexual conflict in this species has a functional basis that involves biting as a means of either coercion or resistance to unwanted matings (Watson et al., 1998).

We define success in this context as males that were able to successfully attach a spermatophore packet to females (Figure 1) (Richmond, 2014). It is of note that only  $>25\%$  of mating interactions in our control group resulted in successful matings on either the first or second mating trials. But more marked even than this was the effect of epinastine administration on the likelihood of mating. We had expected that treatment of males with an octopamine inhibitor would reduce bite force, thus affecting the time course of each of the mating variables of interest; what we found instead is that not even a single male in the epinastine treatment group mated successfully. Thus,

## Latency to mate in seconds



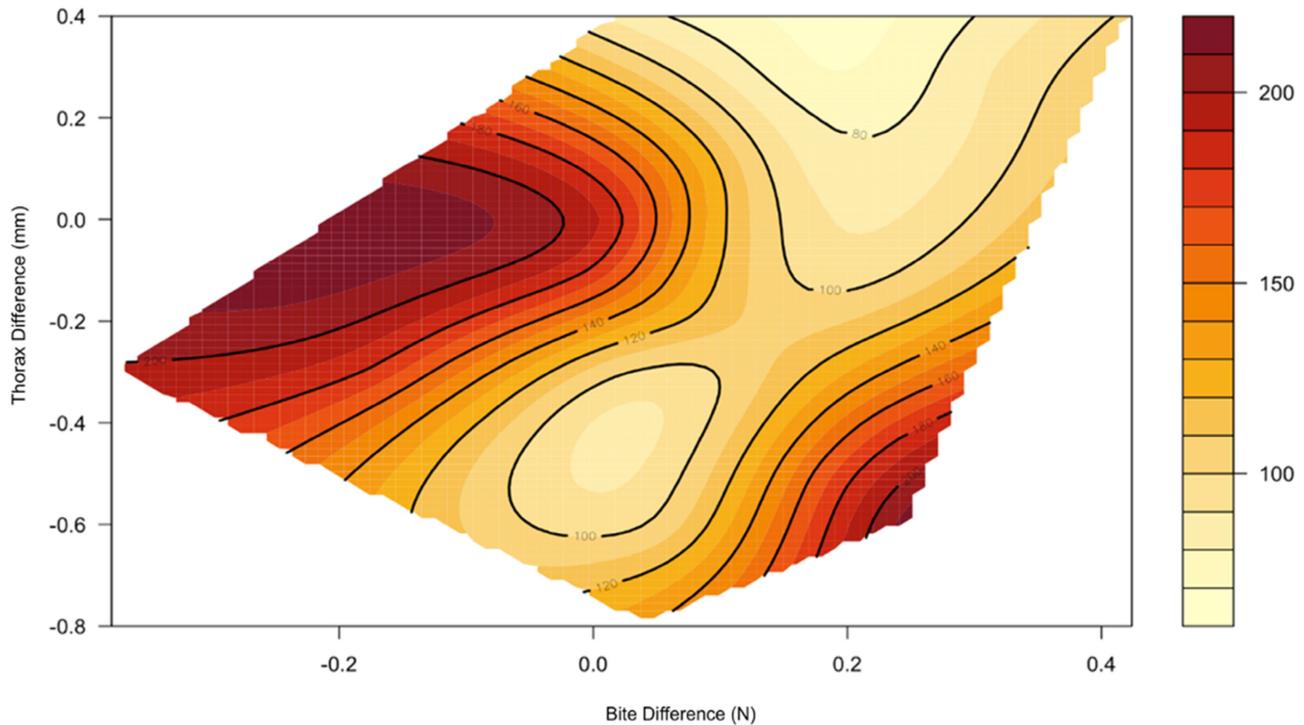
**FIGURE 2** The minimum adequate model for latency to mate retained a significant interaction between thorax size differences and bite force difference in males and females, such that these times (seconds) were longer when male crickets were smaller and exhibited weaker bite forces than females.

epinastine treatment eliminated mating entirely in this experiment, and indeed during mating trials treatment males seldom moved or engaged with the females. Previous behavioural work on octopamine and its antagonists has demonstrated a key role for octopamine in moderating male aggressive behaviour in insects (Bubak et al., 2014; Hoyer et al., 2008), but no effects on courtship or mating success. For example, octopamine depletion reduces the intensity of aggressive behaviour and reduces the likelihood of male contest escalation in *Gryllus bimaculatus* crickets (Stevenson et al., 2000, 2005). But although Zhou et al. (2008) found that mutant *Drosophila* flies lacking octopamine entirely were nonetheless able to express normal courtship behaviours, and Rillich et al. (2019) found that epinastine did not significantly affect key aspects of male courtship in *G. bimaculatus*, our results show a drastic effect of blocking octopamine receptors on male courtship. These results point to some potential differences in the octopaminergic systems of these different cricket species. For example, Rillich et al. (2019) also found that treatment with epinastine did not affect courtship call production in *G. bimaculatus*, yet courtship call structure is significantly altered by epinastine in *A. domesticus* (Adeola et al., 2022). The cause of these differences is not apparent from our current dataset, although it could be the case that certain traits are affected differently by the various biogenic amines in different species, as both courtship behaviour and courtship calls are affected by

dopamine and serotonin in *G. bimaculatus* (Rillich et al., 2019). However, it could also be the case that these differences stem from the epinastine treatment protocol we employed. Specifically, we administered epinastine orally at a concentration of 15 mg/mL (as in Adeola et al., 2022; Bubak et al., 2013, 2022), whereas other studies have used injections of various concentrations of saline and epinastine, particularly to test aggressive encounters in male crickets (Rillich et al., 2011, 2019; Stevenson & Rillich, 2012). It could be that bulk administration of epinastine as in this study entirely saturates the octopamine receptors, resulting in differences in behaviour that are not observed in studies using more fine-grained epinastine manipulation.

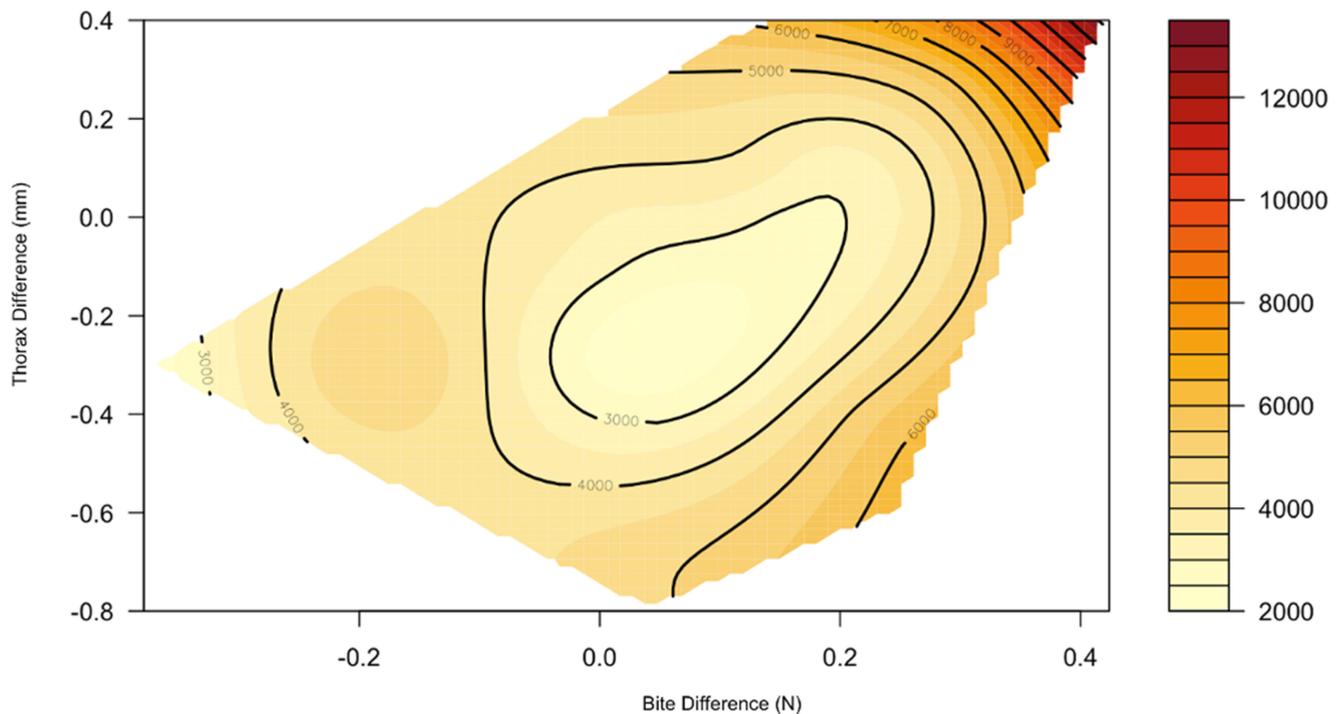
The results of our epinastine treatment notwithstanding, our results demonstrate clear effects of bite force on all stages of the *A. domesticus* mating interactions. However, it is important to note that these effects are, in all cases, significant in combination with that of overall body size. In interactions where males were both larger and bit harder than females, males were able to initiate mating more quickly. The spermatophores also remained attached for longer in such pairings, implying potential fitness benefits to the males in these interactions because longer attachment times allow for more sperm to be transferred to the females in cricket species such as *Teleogryllus commodus* (Bussière et al., 2006; Hall et al., 2010). Although previous studies have pointed to aggressive harassment and mate-guarding behaviours on the part of the male as instrumental in

### Mating time differences in seconds



**FIGURE 3** The minimum adequate model for mate time retained a significant interaction between thorax size differences and bite force difference between male and female mating pairs such that mate time (seconds) was the longest both when females mated with larger males with weak bite forces and when females mated with smaller males with stronger bite forces.

### Attachment time differences in seconds



**FIGURE 4** The minimum adequate model for spermatophore attachment time (seconds) shows that females were slowest to remove attached spermatophores of males that were both larger and bite harder than females. The nonlinear nature of these effects is manifest as the marked peak for such males as these differences become ever larger.

prolonging spermatophore attachment (Bussière et al., 2006), our results strongly imply, but do not directly demonstrate, a role for bite force in enabling harassment behaviour as well. This suggests a common role for functional capacities such as bite force in enabling male aggression towards both males and females, but also raises the possibility that the failure of males who are smaller and bite less forcefully than females are less successful in manipulating mating interactions to their advantage at least in part because of their relatively poorer functional abilities. Indeed, the inclusion of the nonlinear term for bite force differences in all of our models suggests that such differences become even more important as the gap in male and female functional capacities increases, such that males with especially strong bite force relative to female mating partners should have enhanced capacity to manipulate mating outcomes. Future studies that combine performance measurement with detailed behavioural studies of male–female mating interactions, in the same way that researchers have previously done to test the role of performance in male combat, would be useful for understanding exactly how these capacities are used to affect the outcomes of those interactions.

Studies of interlocus sexual conflict have demonstrated the importance of both pre- and postcopulatory male–female interactions in driving and altering evolutionary trajectories in crickets (e.g. Hall et al., 2013). Our results extend previous findings of this phenomenon in two important ways. First, we show that octopamine is necessary for successful mating in *A. domesticus* in a way that does not appear to be the case for other cricket species studied so far. Second, we show that the relative performance capacities of males and females, in combination with their respective differences in body size, exert a strong influence on the timing, latency to mate, and outcomes of mating interactions in this same species. These findings demonstrate that animal functional capacities are relevant to sexual conflict, just as they are to sexual selection, and suggest that selection might act on such capacities in both males and females in *A. domesticus*, not only males.

#### AUTHOR CONTRIBUTIONS

**Fadeke Adeola:** formal analysis; investigation; methodology; visualization; writing; review and editing. **Simon Lailvaux:** formal analysis; review and editing; writing.

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#### CONFLICT OF INTEREST STATEMENT

The authors declares no conflicts of interest.

#### PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/jeb.14226>.

#### DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available on Dryad <https://doi.org/10.5061/dryad.bg79cnpngs>.

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