



## Contest interactions and outcomes: relative body size and aggression independently predict contest status

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In species with pronounced male armaments, body and weapon size often determine success in agonistic interactions. However, the behavioural components of interactions also play a significant role in determining outcomes and individuals that win agonistic interactions may not be the ones that start contests. In this study, we used dyadic, intrasexual assays to characterize agonistic behaviours and determine whether body size and/or the propensity to start interactions influences contest outcome. We characterized agonistic interactions from start to end in the sexually dimorphic forked fungus beetle, *Bolitotherus cornutus*. Males of the species are known to use their thoracic horns in intrasexual combat, but other aspects of male–male behaviour are undescribed. We created an ethogram that described transitions between behaviours and categorized actions as aggressive, nonaggressive and mounting. Individual aggressive and nonaggressive behaviours were highly repeatable between trials while mounting behaviours were not repeatable. The initiation of nonaggressive and mounting behaviours was not predictive of contest outcome. Relative body size and absolute aggression independently predicted contest outcome. Our results indicate that traits important for establishing contest outcome are not always correlated. Considering either aggression or body size alone may be misleading when determining competitor abilities.

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In sexually dimorphic species, larger body size and armaments are selected for through male agonistic interactions (Berglund, Bisazza, & Pilastro, 1996; Emlen, 2008; Hoem, Melis, Linnell, & Andersen, 2007), female choice (Bonduriansky & Rowe, 2003; Oliveira & Custódio, 1998) and mate coercion (Arnqvist & Rowe, 2002; Haley & Gray, 2012). Males use armaments in a variety of behaviours during agonistic competitions over resources and mates, usually resulting in the male with the largest armament winning the interaction (reviewed in Emlen, 2008). Agonistic competitions consist of both aggressive and nonaggressive behaviours; however, aggressive behaviours are often the determinants of contest outcome (McGhee & Travis, 2010; Sih, Chang, & Wey, 2014; Wilson, Gelin, Perron, & Réale, 2009; Wilson, Grimmer, & Rosenthal, 2013). Because aggression is an important behaviour used during agonistic interactions, it is easy to assume that larger

males are more aggressive, but this assumption is hardly ever tested. Instead, many studies examine how morphological traits correspond with contest outcome (Bonduriansky & Rowe, 2003; Okada, Miyanoshita, & Miyatake, 2006; Okada & Miyatake, 2004; Schuett, 1997), and not whether morphological variation is correlated with important combat behaviours. Additionally, studies on male–male competition focus on the effects of aggression on contest outcome, but rarely consider the other suites of behaviours performed during intrasexual interactions (but see Bertram, Rook, Fitzsimmons, & Fitzsimmons, 2011; McGinley, Prenter, & Taylor, 2015). The totality of a male–male interaction from start to finish must be characterized to determine how the combined effects of morphology and intrasexual behaviours influence contest outcome.

Behaviours that seem unremarkable may be essential for the progression of an interaction or lead to contest outcome. Some species use ritualized transitions of approaches and touching to assess their competitor (Chen, Lee, Bowens, Huber, & Kravitz, 2002; Jang, Gerhardt, & Choe, 2008), allowing contest outcome to be determined in the absence of overt aggressive behaviours (Cooper, 1987; Enquist, 1983; Jaeger, 1981; López & Martín, 2001). For

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example, males may avoid costly aggressive interactions by assessing their competitors using nonaggressive means (Berglund et al., 1996; Holekamp & Strauss, 2016; Jenssen, Decourcy, & Congdon, 2005). To understand what determines contest outcomes, we must understand the totality of agonistic interactions because of the importance of these complex suites of behaviours (Bertram et al., 2011; Chen et al., 2002; Jang et al., 2008; Oliveira, Silva, & Simões, 2011).

Attributing specific agonistic behaviours to an individual is difficult because social behaviour inherently involves input from a competitor. The identity of a competitor may cause individual behaviours to vary from one interaction to the next. However, some proportion of an individual's behaviour will remain consistent and repeatable across social contexts (Bell, Hankison, & Laskowski, 2009; Brooks & Endler, 2001; Dochtermann & Nelson, 2014; McGhee & Travis, 2010; Schuster, Carl, & Foerster, 2017). Repeatability, or the proportion of variance that can be explained by differences among individuals, varies depending on the behaviour and species in question (Bell et al., 2009). Despite the expected importance of social context, agonistic behaviours exhibit especially high repeatability. Across all behaviours, repeatability averages 0.37 across taxa, whereas repeatability of agonistic behaviours averages 0.5 (Bell et al., 2009).

In this paper, we characterized male–male interactions in forked fungus beetles, *Bolitotherus cornutus*, to test the assumption that body size is correlated with aggression and determine whether agonistic behaviours and/or body size influence contest outcome. *Bolitotherus cornutus* are sexually dimorphic and promiscuous tenebrionid beetles that live on and consume polypore shelf fungus that grows on dead wood. Females mate multiply within a season and lay one egg per laying event (Pace, 1967). Males in the wild are observed mounting females in a head-to-abdomen position, engaging in a suite of courting behaviours, then transitioning to a head-to-head position for copulation (Brown & Bartalon, 1986). Males remain in a head-to-head mounting position for several hours to ensure insemination (Conner, 1988, 1989). Rival males can engage the mating male in agonistic contests at any point in this interaction. Longer head-to-head 'mate guarding' is suggested to increase insemination (Conner, 1995), so the ability of a rival male to remove a guarding male from the back of a female should decrease the likelihood of insemination for the first male and increase mating opportunities for the rival male.

Male *B. cornutus* perform suites of agonistic behaviours using two sets of horns (clypeal and thoracic) (Benowitz, Brodie, & Formica, 2012; Conner, 1988). Horn size is a sexually selected trait that is tightly correlated with body size and assumed to correlate with aggression (Conner, 1988, 1989; Formica et al., 2011). Males engage in agonistic interactions both in the absence and presence of females (Conner, 1988), suggesting that interactions may be important for obtaining both mating and food resources. Male beetles are often observed touching other males in the wild without escalating to fighting or chasing and a few instances of male–male mounting similar to male–female mating behaviours have been observed. However, the consequences of these behaviours are unknown. Nonaggression and male–male mounting behaviours may be performed to establish a dominance hierarchy and could be indicative of contest outcome (Holekamp & Strauss, 2016; López & Martín, 2001; McGinley et al., 2015).

## METHODS

### *Beetle Collection, Husbandry and Ethical Note*

We collected beetles from a large metapopulation near Mountain Lake Biological Station in Pembroke, Virginia, U.S.A., in May

2016. A total of 130 male beetles were housed individually in small, plastic containers (5 × 2.5 × 5 cm) containing a thin layer of plaster to retain moisture, mulch, and a piece of their host fungus *Ganoderma tsugae* as a food resource. Water was administered as needed to beetle containers via a small, squeeze wash bottle. Beetles were housed in natural light conditions with room temperature held constant at 20 ± 1.5 °C. We isolated beetles for about 1 month before beginning trials.

Behavioural assays were performed in July 2016. Before interaction trials, we photographed each beetle using an Epson scanner, then measured elytra length using the photographs in ImageJ (Abramoff, Magalhães, & Ram, 2004). Elytra length is a known indicator of body size in most coleopterans. The elytra of every beetle was then painted with a black or white stripe to allow us to identify them in dyadic trials. We used nontoxic, acrylic paint for these stripes. Beetles physically interacted with competitors, but there were no signs of harm after trials. Beetles were housed in the small, plastic containers following the trials until the end of their natural lives.

### *Interaction Trials*

A total of 48 unique beetles were randomly paired in different combinations in three trials for a total of 72 trials. Beetles were paired with a different male competitor in each trial and allowed to interact freely. Half of the beetles ( $N = 24$ ) were designated as 'focals' in each trial. Behaviours were assayed in 10 × 10 cm plastic containers filled approximately 2 cm deep with plaster. A 5 × 5 cm square piece of *G. tsugae* fungus was set in plaster in the middle of the arena as a resource for the beetles to fight over. We differentiated between beetles in each trial by painting either black or white stripes on their elytra. We randomly paired beetles with respect to body size. Beetles were paired with competitors collected from different wild populations. Beetles experienced no previous interactions with any of their trial competitors.

Trials started with each male placed on an opposite side of the *G. tsugae* bracket and ended after 4 h of recording. We returned beetles to their husbandry chambers after each trial and waited 2 days before placing them in another trial. Between trials, the plaster and fungus were replaced and the plastic containers were washed. The beetles painted black were arbitrarily designated as focal beetles after the trials, and only observations of these focal beetles were included in analyses of ethograms and contest outcomes to avoid pseudoreplication.

*Bolitotherus cornutus* are most active in low-light periods of the day (e.g. night and early morning), so we recorded trials in a dark, temperature-controlled room using Canon PowerShot G1 X digital camera on infrared setting placed 1 m above interaction arenas. We attached infrared lights to each camera to enhance visibility. Cameras recorded beetle activity by taking a picture every 5 s using a Neewer© LCD digital shutter release remote control. We then stitched images into a video using FFmpeg software (version be1d324).

We recorded the initiation and duration of the following behaviours using Inqscribe® (version 2.2.4): touch, bump, head, mount, flip, chase, grapple, fungus patrolling, end. See Table 1 for description of behaviours. Mounting is typically a behaviour performed during male–female courtship and mating (Conner, 1988). Mounting in a male–male context may be interpreted as adaptive or nonadaptive (Bailey & Zuk, 2009). Males may be establishing dominance by mounting (Lane, Haughan, Evans, Tregenza, & House, 2016). Alternatively, males may be more likely to perform mounting behaviours on other males as a by-product of high activity (Bailey, Hoskins, Green, & Ritchie, 2013; Boutin, Harrison, Fitzsimmons, McAuley, & Bertram, 2016). Therefore, we used

mounting as its own suite of behaviours that is sometimes followed by courting and copulation. Male–male courting and copulation attempts were observed on rare occasions in our trials. We scored whether a beetle initiated each behaviour and the duration of that behaviour. We assigned initiation of a behaviour to the individual that approached its competitor and progressed physically into the behaviour. The end of an interaction was assigned to the individual that left the area before its competitor.

### Creating Ethograms

We constructed a matrix of transitions between behaviours in the first trial ( $N = 24$ ). The behaviours of each beetle were considered for this analysis, so the transition matrices are properties of the trial, not the individual. The transition matrix included the following behaviours: bump, touch, head, mount, chase, flip, grapple and end. Fungus patrolling is a behaviour conducted by only one individual (not an interaction), so we did not include it in the creation of our ethogram. We combined the transition matrices for dyadic trials for a total count of the number of times every behaviour was followed by a subsequent behaviour. We conducted three trials for every beetle with 2 days in between trials, and all beetles experienced the same trial on the same day. We created an ethogram using only the first trial to avoid pseudoreplication. We then performed a contingency analysis to determine which transitions occurred at a greater likelihood than expected (Bertram et al., 2011; Chen et al., 2002). Using this matrix, we performed a Markov-chain analysis to construct an ethogram of nonrandom transitions from one behaviour to the next in a string of interactions (Bertram et al., 2011; Chen et al., 2002). Ethograms were constructed using the 'markovchain' package in R.

### Characterizing Winners and Losers

We counted the number of behaviours that the focal beetle (black) initiated. From the clustering of behaviours in the ethogram analysis, we used the following behavioural categories (see below) in the analysis of winning/losing status: aggressive, nonaggressive and mounting. We classified a male as losing the entire trial if it ended more interactions than its competitor. We chose the proportion of ends as a conservative measure because the time required to establish dominance in *B. cornutus* is unknown. We alternatively could have designated losers as the beetle who ended the final interaction of the 4 h trial. These two metrics of contest outcome were highly correlated ( $r = 0.61$ ,  $P < 0.001$ ). Results of analyses were qualitatively similar regardless of the metric used in the models. Trials that ended inconclusively because both males ended an equal number of interactions were not included in the analysis. Using the 'lmer' package in R (Bates, Machler, & Bolker, 2015), we assessed the effect of the number of initiated behaviours in a trial on winning/losing status with a generalized linear

mixed model using a binomial distribution: winning/losing status ~ aggressive behaviours + nonaggressive behaviours + mounting behaviours + size difference (focal elytra length – competitor elytra length) + trial date. Winning/losing status was coded as 1 for winning and as 0 for losing. We included focal beetle identity (ID) and competitor beetle ID as random effects. We assessed the components of this model with a type III Wald  $\chi^2$  test using the 'car' package in R.

### Repeatability and Correlations

To calculate repeatability for each behaviour category (aggression, nonaggression, mounting), we obtained measures of within- and between-individual variance and covariance using univariate generalized linear mixed models (Dingemanse & Dochtermann, 2013). Our models included behaviour as the dependent variable and focal and competitor identity as random effects. We used the 'MCMCglmm' package in R for our analyses (Hadfield, 2010). MCMC chains used 500 000 iterations, a burn-in rate of 5000 and thinning intervals of 100. We assumed a Poisson error model because many individuals performed zero or one behaviour in each category. The described behaviours have not been quantified before in *B. cornutus*, so we used noninformative priors with an assumed Poisson distribution in our MCMC models. Noninformative priors make no assumptions about how we would expect the variances to be structured. We calculated repeatability from model outputs of variance using methods described in Nakagawa and Schielzeth (2010). We calculated correlations using Pearson's correlation test between number of initiated behaviours within individuals and between focal males and competitor males. We adjusted for multiple comparisons using Bonferroni adjustment for 28 tests (alpha of 0.002).

## RESULTS

### Male–Male Interaction Behaviours

To reduce the number of behavioural variables used in our subsequent analyses, we used our ethogram to group behaviours into categories of related interactions. We designated male–male interactive behaviours into three categories: aggressive, nonaggressive and mounting (Fig. 1). Following Holekamp and Strauss's (2016) definition of aggression, we categorized aggressiveness as the suite of behaviours that most often led to one beetle ending the interaction. Nonaggressive behaviours were more likely to transition to other behaviours than to end an interaction. In the case of 'head' behaviour, no nonrandom transitions occurred to or from this behaviour in the ethogram. Thus, beetles that initiated a 'head' interaction had to transition to another behaviour with random probability.

**Table 1**  
Behaviours observed in male–male interaction trials

Behaviour	Description
Bump	Head of one beetle comes into contact with any part of the body of the second beetle
Touch	Any physical contact that is not characterized by another behaviour
Head	Both beetles touch head to head
Mount	One beetle crawls onto the back of the second beetle
Chase	One beetle rapidly follows the second beetle
Flip	One beetle flips the second beetle onto its back
Grapple	Both beetles are in full contact and tumbling over each other
Fungus patrolling	One beetle moves around the perimeter of the provided fungus square
End	One or both beetles leave an interaction

In the first trial, focal beetles interacted with their competitors for an average of 10.3% of the 4 h trial (range 0.0–86.6%). A total of 19% of interactions consisted of males coming into proximity of one another, then immediately ending the interaction. During the proportion of time that beetles spent interacting with their competitor, focal males were most frequently seen mounting their competitor. We frequently observed males cycling through bouts of touching and mounting. Males spent 57.3% of their total interaction time mounting their competitor. Males initiated more nonaggressive behaviours (301 of 415 total initiated behaviours) than other behaviours, but the actual duration of nonaggressive behaviours accounted for only 16.5% of the time spent interacting. Males conducted a total of 48 aggressive behaviours, which accounted for 26.2% of trial duration. In both focal and competitor beetles, individuals that performed more aggressive behaviours also performed more nonaggression and mounting behaviours (Table 2).

### Repeatability

The number of initiated aggressive and nonaggressive behaviours were highly repeatable across the three trials. Aggression had an estimated repeatability of 0.79 (95% CI: 0.46, 0.99). Nonaggressive behaviours had an estimated repeatability of 0.39 (95% CI: 0.06, 0.68). The number of initiated mounting behaviours that an individual conducted in a trial were not repeatable (0.00, 95% CI: 0.00, 0.65).

### Contest Outcomes

The majority of trials resulted in conclusive winning/losing status (one beetle ended more interactions than the other). Only six (of 72) trials resulted in a 'draw' between both beetles; five of those inconclusive trials resulted when beetles performed no interactions during the 4 h trial. A total of 37 trials resulted in the focal beetle winning and 28 trials resulted in the focal beetle losing. Nine of the

48 focal beetles emerged as winners in all three of their trials. Four emerged as losers in all three of their trials.

The size difference between competitors and the number of initiated aggressive behaviours predicted winning status (Table 3). Larger males who initiated more interactions were more likely to emerge as winners. Difference in competitor body size was not correlated with the number of initiated aggressive behaviours (Table 2). Nonaggressive behaviours, mounting behaviours and trial date had no significant effect on winning status (Table 3). The focal male's winning status was also predicted by the number of aggressive behaviours initiated by its competitor. Losing focal males had highly aggressive competitors (Table 2).

## DISCUSSION

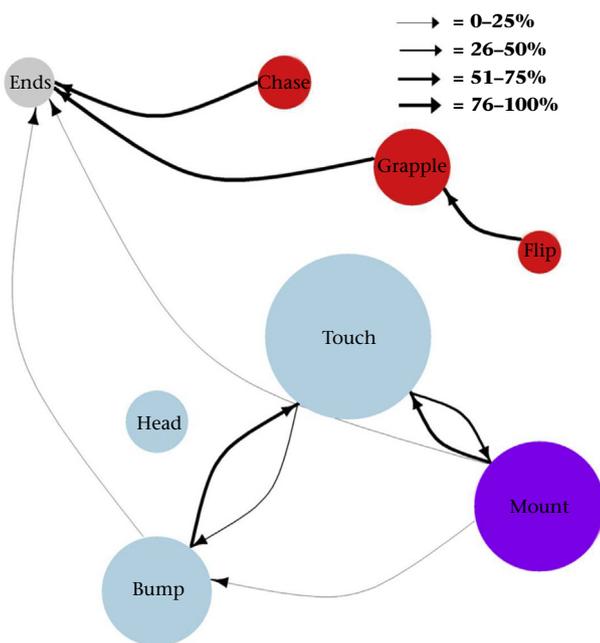
Behaviours exhibited by *B. cornutus* during agonistic interactions were classifiable into three suites of related actions (aggressive, nonaggressive and sexual) that identify important transitions for contest outcome (Fig. 1). We found that (1) males often cycled through bouts of touching and mounting, (2) sexual behaviours did not lead to aggressive behaviours and (3) nonaggressive behaviours precluded aggression. Most of the interaction time consisted of one male mounting the other. The numbers of aggressive and nonaggressive behaviours initiated were significantly repeatable across trials.

Relative body size and the number of initiated aggressive behaviours independently predicted trial outcome. Difference in competitor body size and number of initiated aggressive behaviours were not significantly correlated. Larger beetles were not necessarily more aggressive, which challenges previous assumptions of the link between male morphological traits and contest behaviours. It is unknown whether contest outcome results in access to more resources; however, we can infer that contest winners will gain more access to females. Because aggression and relative body size independently predicted contest status, we would expect both larger and more aggressive individuals to mate frequently with females.

*Bolitotherus cornutus* males initiated a similar number of aggressive behaviours regardless of competitor identity (Table 3). Although nonaggressive and mounting behaviour did not predict contest outcome, these behaviours were tightly correlated with aggression (Table 2). We observed a few instances of nonaggressive behaviours transitioning to the initiation of aggressive behaviours in our trials. However, these transitions were not significantly different from random in our contingency analysis. The suite of nonaggressive behaviours may be used for establishing male–male relationships without escalating to aggression, which could explain the high correlation of aggressive and nonaggressive behaviours (López & Martín, 2001; Maynard Smith & Parker, 1976).

Competitor assessment may explain why *B. cornutus* males in the wild are frequently observed engaging in nonaggressive behaviours compared to aggressive behaviours. In asymmetric contests, males with different body and horn size must assess whether the cost of aggression is worth the resource benefit (Maynard Smith & Parker, 1976; McGinley et al., 2015). Nonaggression is used by many species as a form of competitor assessment, where smaller males with less competitive abilities can determine the costs and benefits of fighting versus fleeing during an interaction (Jenssen et al., 2005; McGinley et al., 2015). Observations of wild *B. cornutus* males engaging in nonaggressive touches and bumps could be a similar form of contest assessment where males assess the probability of winning and the associated benefits of a resource compared to the costs of aggression.

Differences in aggression within a population may be due to intrinsic individual phenotypes that are highly repeatable



**Figure 1.** Markov-chain diagram for male–male interactions. Circle diameter indicates the number of times that a behaviour occurred across all trials. Arrow width indicates the probability that one behaviour transitioned to the following behaviour. Blue = nonaggressive states; purple = mounting states; red = aggressive states; grey = terminal state.

**Table 2**

Within-individual and between-competitor correlation matrices

Correlations	Winning status	Aggression	Nonaggression	Mounting
<b>Within individuals</b>				
Winning status				
Aggression	<b>0.391</b>			
Nonaggression	0.241	<b>0.770</b>		
Mounting	0.286	<b>0.797</b>	<b>0.800</b>	
<b>Between competitors</b>				
Winning status				
Aggression	<b>-0.418</b>	-0.171		
Nonaggression	-0.369	-0.139	-0.045	
Mount	-0.341	-0.180	-0.146	
Relative size	<b>0.417</b>	0.259	0.0431	0.104

Winning status was designated as the proportion of times a beetle 'ended' interactions within a trial, where losing beetles ended more interactions compared to their competitor. Behaviours (aggression, nonaggression and mounting) are the total number of initiated behaviours for each individual beetle within a trial. Within-individual correlations were quantified using focal, black-painted beetles. Between-competitor correlations were quantified by comparing focal, black-painted beetles to the behaviours of their three competitors. Bolded values indicate statistically significant correlations Bonferroni adjusted for multiple comparisons (alpha of 0.002) as determined by Pearson's correlation test.

regardless of social context or plasticity of aggression that depends on the characteristics of an individual's social partners (Bell et al., 2009; Matessi, Matos, Peake, McGregor, & Dabelsteen, 2010; Santostefano, Wilson, Araya-Ajoy, & Dingemans, 2016; Wilson et al., 2009). If aggressiveness is dependent on social context, an individual's behaviour will depend on its partner's morphology and competitive ability (McGlothlin, Moore, Wolf, & Brodie, 2010; Moore, Brodie, & Wolf, 1997; Santostefano et al., 2016; Wilson et al., 2009). Alternatively, if aggression itself is important for contest outcome, individuals should maintain their level of aggressiveness regardless of their competitor's characteristics. In our study, males retained their level of aggressiveness regardless of the identity of their competitor, supporting the latter explanation.

One surprising finding of our study was the frequency and duration of same-sex mounting behaviours. Mounting behaviours in *B. cornutus* have been observed only infrequently in wild populations (L. D. Mitchem, personal observation) and yet, in our trials, mounting behaviours accounted for just over half of total activity time. Differences between observations in the wild and in our laboratory study may be due to the inherent nature of observing these behaviours while they are occurring, or it could be an artefact of the spatially constrained dyadic contest arenas used in our laboratory study. However, if same-sex mounting behaviours do occur in natural settings, they may have important consequences. Same-sex mounting behaviours are hypothesized to provide a variety of functions in other taxa (Bailey et al., 2013; Bailey & Zuk, 2009). Same-sex mounting behaviours can function as a means of establishing dominance, therefore limiting the cost of aggression, or as a way of demonstrating sexual prowess to a broad audience of viewers (Bailey et al., 2013; Dukas, 2010; Lane et al., 2016). In

insects, studies have found that same-sex mounting behaviours are a result of repeatable personality traits performed regardless of social context (Boutin et al., 2016; Levan, Fedina, & Lewis, 2009). Individuals perform mounting behaviours in a variety of social situations, regardless of whether or not that behaviour is adaptive (Duckworth, 2006; Levan et al., 2009; Wey, Chang, Fogarty, & Sih, 2014).

High correlations between behavioural traits may indicate the presence of behavioural syndromes, or correlations among repeatable behaviours across social contexts (Brommer & Class, 2017; Sih, Bell, & Johnson, 2004). Male aggressive, nonaggressive and mounting behaviours were all highly correlated in our study. Nonaggressive and mounting behaviour used in other social contexts (mating or mate defence) are also expressed during male–male interactions despite having no effect on contest outcome. If aggression is correlated with nonaggression and mounting in mating contexts, then highly aggressive males may incur a fitness loss when initiating aggression towards potential mates (Dingemans, Dochtermann, & Nakagawa, 2012; Duckworth, 2006; Réale, Reader, Sol, McDougall, & Dingemans, 2007; Wey et al., 2014). The fitness loss of aggression towards mates may, however, be counteracted by frequently mounting mates (Sih, Bell, Johnson, & Ziemba, 2004). Less aggressive phenotypes would also incur a potential fitness loss in mating contexts due to initiation of fewer mounting behaviours (Sih, Bell, Johnson, et al., 2004). The actual costs and consequences of aggression in *B. cornutus* are largely unknown. Future studies should examine aggression across multiple fitness contexts and its correlation with other social behaviours to determine the potential constraints of aggressive personality on behavioural plasticity.

**Table 3**GLMM describing winning/losing status of focal male in each male–male trial using type III analysis of variance (Wald  $\chi^2$  test)

Model term	Coefficient	SE	$\chi^2$	P
<b>Winning/losing status</b>				
No. of focal-initiated aggressive behaviours	1.32	0.65	4.13	0.04*
No. of focal-initiated nonaggressive behaviours	-0.13	0.08	2.55	0.11
No. of focal-initiated mounting behaviours	0.19	0.29	0.41	0.52
No. of competitor-initiated aggressive behaviours	-0.78	0.38	4.28	0.04*
No. of competitor-initiated nonaggressive behaviours	-0.04	0.09	0.16	0.68
No. of competitor-initiated mounting behaviours	0.36	0.38	0.93	0.34
Elytra size difference (focal size – competitor size)	9.76	4.62	4.47	0.03*
Trial date	-0.05	0.49	0.01	0.91

Model includes 65 trials with unique pairs and 26 focal individuals. The number of initiated behaviours is the number of times a focal individual initiated a specific behaviour towards their competitor. Trials where both focal and competitor beetles performed equally, resulting in an undetermined trial status, were excluded from the model. \* $P < 0.05$ .

Male–male interactions rarely resulted in physical aggression. In our trials, only 16.6% of all initiated behaviours were characterized as aggressive. Instead, male–male interactions were largely nonaggressive (67.9%). Two nonexclusive explanations may underlie this result. First, individuals may be avoiding costly aggressive behaviours by assessing their competitors using nonaggressive means (Berglund et al., 1996; Coleman & Wilson, 1998; Unrug, Tomkins, & Radwan, 2004). Second, our experimental context may not have reflected a limiting resource for our population of *B. cornutus*. In our trials, males were given a piece of fungus as a food resource to fight over, but individuals may not assess this context as one needing aggression. Male beetles in the wild use aggression in a variety of scenarios. Fighting occurs either between two males, in groups of many males, as well as during mating and courtship. Whether or not *B. cornutus* males are territorial remains unknown. Future studies should measure male–male interactions in scenarios that vary in resource value (i.e. food, mates, etc.) to further examine how context affects the proportion of aggressive versus nonaggressive behaviours. Future studies should also explore the repeatability of correlated behaviours across multiple social contexts (i.e. male–female interactions versus contests over food or mates).

Both size and aggression are important in establishing contest outcome, but these traits are not correlated in this species. Our study does not support the assumption that body size is correlated with aggression in sexually dimorphic species. Overall, we conclude that (1) difference in competitor body size is correlated with contest outcome, (2) difference in competitor body size and number of initiated aggressive behaviours are independently predictive of contest outcome, (3) aggressive and nonaggressive behaviours are highly repeatable and (4) male–male interactions over food resources are mostly nonaggressive. Considering body size or aggression alone may be misleading in predicting contest outcome.

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