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## Original Article

# Selection on male physical performance during male–male competition and female choice

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Male contest competition and female choice are key features of the mating systems of many species, and whole-organism performance may be targeted by both mechanisms given the dynamic body movements required during fighting and courtship displays. Using the dimorphic horned dung beetle *Onthophagus taurus* as a model system, we tested whether physical performance was important in determining a male's victory in fights, and whether successful fighters were preferred by females as mates. We found that physical strength, horn length, and body mass were significant predictors of male fighting success, but males that won fights were not more attractive to females. Rather, females preferred males that delivered a high courtship rate, which was not correlated with strength, horn length, or body mass, but previously has been shown to be genetically correlated with body condition. The fact that there was no relationship between fighting success and mating success suggests that selection on traits favored by male–male competition and female choice can act relatively independently in this species, although both mechanisms appear to favor traits (strength and courtship, respectively) that are linked to a male's ability to acquire and allocate resources for mass gain. Future work is needed to determine the relative contributions of these processes to the total strength of sexual selection acting on male phenotypes.

**Key words:** dung beetle, female choice, male–male competition, *Onthophagus taurus*, whole-organism performance.

## INTRODUCTION

Male–male competition and female choice are the primary selective forces driving the evolution of male secondary sexual characters, with male–male competition resulting in the evolution of weapons, and female choice favoring the evolution of ornaments and courtship displays (Darwin 1871; Andersson 1994). Although the evolution of weapons and ornaments is traditionally envisioned as occurring via one or the other of these 2 processes, this dichotomy is likely to be overly simplistic in most taxa because the same male trait can be important in determining the outcome of both male contests and mate choice (Berglund et al. 1996; Qvarnström and Forsgren 1998; Wong and Candolin 2005; Hunt et al. 2009).

For example, many traits that are used by males to signal fighting ability and intimidate rivals are also used to attract females (see Berglund et al. 1996 for review). Male–male competition and female choice can therefore reinforce each other to enhance the total strength of selection acting on the male sexual trait. In other taxa, however, males that are successful in contest competition are

not necessarily preferred by females as mates (Qvarnström and Forsgren 1998; Wong and Candolin 2005), so male–male competition and female choice can also act in opposition to diminish net selection on male sexual traits. Because of the numerous ways by which male–male competition and female choice can interact, studies need to evaluate the relative importance of both processes in order to gain an accurate view of how sexual selection operates (Qvarnström and Forsgren 1998; Hunt et al. 2009).

In addition to selection on ornaments and weapons, male–male competition and female choice are expected to favor correlated changes in general morphology, physiology, and performance capabilities that allow males to wield their weapons and perform their courtship displays more effectively (Tomkins et al. 2005; Lailvaux and Irschick 2006; Byers et al. 2010). Indeed, the outcome of male contests and female preference are often largely determined by physical performance capabilities, or how well an organism performs an ecologically relevant task (Lailvaux and Irschick 2006; Irschick et al. 2007). For example, males with greater energy reserves, speed, and/or endurance are typically more likely to win aggressive encounters with rival males (reviewed in Lailvaux and Irschick 2006), and females often choose mates based on their ability to execute energetically demanding and complex courtship

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displays (reviewed in Byers et al. 2010). These observations suggest that whole-organism performance itself (e.g., strength, endurance, agility) is an important target of sexual selection (Lailvaux and Irschick 2006; Irschick et al. 2007). However, little is still known about whether the same aspects of performance are favored by both male–male competition and female choice, or how these 2 mechanisms interact to determine net selection on performance capabilities.

We examined the interactions between male–male competition, female choice, and physical performance in the horned dung beetle *Onthophagus taurus*. Horned dung beetles are an ideal system for studying interactions between male–male competition and female choice because both processes are known to impose selection on males (Emlen 1997; Moczek and Emlen 2000; Kotiaho et al. 2001; Kotiaho 2002). Females dig tunnels beneath fresh dung pads where they mate and build brood masses in which to lay their eggs (Halfiter and Edmonds 1982). Mating occurs inside these tunnels, so a male's ability to control access to tunnels is critical to his reproductive success. Males are dimorphic, with those above a critical body size developing a pair of long, curved head horns, and those below this threshold developing no horns or only rudimentary horns (Hunt and Simmons 1997; Moczek and Emlen 1999). Large males use their horns as weapons in fights with rival males over ownership of breeding tunnels containing females, whereas small hornless males rely on sneaking behaviors and dig intercepting side-tunnels to gain matings inside the tunnels guarded by horned males (Emlen 1997; Moczek and Emlen 2000). Specifically, horned males engage in aggressive head-to-head contests to push opponents out of tunnels, and larger horned males appear to have competitive advantage over smaller males (Moczek and Emlen 2000) that translates into greater reproductive success (Hunt and Simmons 2001).

Females, however, cannot be forced to mate, so a male that gains access to a breeding tunnel must also court the resident female and persuade her to open her genitalia before copulation can occur (Werner and Simmons 2008). Males court females by vigorously tapping on the female's back with their antennae, head, and fore-legs in bouts that last several seconds, and females are more likely to mate with males that deliver higher courtship rates, regardless of their body size or horn length (Kotiaho et al. 2001; Kotiaho 2002).

Because both fighting and courting require dynamic, coordinated body movements, and because females prefer the most actively courting males as mates, we hypothesized that whole-body physiological performance would be favored by both male–male competition and female choice. We tested this hypothesis by measuring the physical strength of males, and evaluating whether stronger males were more likely to win in male–male contests and to be selected by females as mates.

## METHODS

Beetles were collected from a dairy farm in southwest Western Australia and bred in the laboratory following published protocols (Simmons and Kotiaho 2002). Newly emerged, first-generation adults were kept in single-sex populations and fed fresh cow dung ad libitum for 2 weeks prior to experiments to ensure that they were sexually mature and unmated. Because tunneling behavior naturally occurs in darkness, we conducted all observations in a dark room under dim, red-filtered light.

To measure male courtship, we placed 1 male and 1 randomly chosen female in an artificial tunnel of clear vinyl tubing (13-mm internal diameter), and observed the pair for 60 min, or until the

beetles mated. We checked pairs every 2 min and noted whether the male was courting or mating. Courtship rate was calculated as the number of observations in which the male was courting, divided by the total duration of the trial (60 min for unmated pairs or time until copulation for mated pairs) (Simmons and Holley 2011). Only males that engaged in courtship were included in the fighting and strength trials (see below) because we could not infer an outcome of female choice without any male courtship.

We measured male fighting success by staging contests between 2 males over ownership of an artificial tunnel (Emlen 1997; Moczek and Emlen 2000; Pomfret and Knell 2006). The observation chambers consisted of a 12-cm-long tunnel of clear vinyl tubing that was fitted beneath a small plastic arena (8 × 8 × 5 cm) filled with moist sand. We glued sand onto the inside of the tunnel wall to give beetles a rough surface to grip as they moved up and down the tunnel. The bottom of the tube was covered with nylon mesh and then plugged with another piece of tubing filled with fresh cow dung to mimic the brood balls built by females at the blind end of tunnels (Emlen 1997; Moczek 1998), and to lure males to the bottom of the tunnel.

To stage a fight, we placed one male into the tunnel and allowed him to adjust to the chamber for 3 min. We then added a second male to the tunnel and observed the pair continuously until one male was evicted from the tunnel or for 60 min. Because beetles always ran down toward the dung after being added to the tunnel, the new male quickly encountered the resident male, which typically resulted in an immediate head-to-head fight (Moczek and Emlen 2000). Fights usually lasted only a few minutes, with one male being pushed out of the tunnel, and the other male remaining inside the tunnel or guarding the entrance (see Supplementary Video). The male that was evicted was scored as the loser, and the male that remained in the tunnel was scored as the winner. If both males exited the tunnel, or if both remained in the tunnel at the end of the 60-min trial, the interaction was scored as a tie. We marked the intruding male with a small dot of white correction fluid to differentiate between the 2 males.

To analyze male fighting success, we selected the intruding male from each contest as the focal male, and scored the interaction as 0 if the focal male was the loser, 1 if the focal male was the winner, and 0.5 if the focal male tied. Intruders were no more likely to win fights than residents ( $\chi^2 = 0.22$ , degrees of freedom [df] = 2,  $P = 0.90$ ), so our results should not be biased by selecting the intruder as the focal male. We calculated the difference in body mass, horn length, and strength (see below) between each focal male and his opponent, and used these measurements as the independent variables in our analyses.

We measured strength as the amount of force required to pull a male out of an artificial tunnel (Lailvaux et al. 2005; Knell and Simmons 2010). Trials were conducted in a horizontal tunnel of clear vinyl tubing with interior walls that had been roughened with sand. A loop of thread was superglued to a male's elytron and attached on the other end to a Pesola spring scale. The beetle was encouraged to fully enter the tunnel, and then the thread was pulled gently to stimulate the beetle to brace its legs against the tunnel walls as it would in a typical fight (Moczek and Emlen 2000). We then measured the beetle's strength by slowly pulling on the spring scale until the beetle was dislodged from the tunnel. Strength was measured 3 times for each individual (repeatability = 0.78; 95% confidence interval = [0.74, 0.83];  $P < 0.001$ ), and the maximum force from these trials was used in the statistical analyses (Losos et al. 2002; McCullough 2014). Strength measurements were square-root transformed to control for heteroskedasticity.

Prior to experiments, body mass was measured to the nearest 0.1 mg on a digital balance, and body size (pronotum width) was measured to the nearest 0.01 mm with digital calipers. At the end of the strength trials, the beetles were frozen, and a digital photograph of each male's head was taken for horn measurements. Horn length was measured in ImageJ as the length of the horn curve from the lowest point on the top of the head to the center of the horn tip (Measurement 4 in Tomkins et al. 2006). We conducted all analyses on log-transformed measurements (hereafter simply referred to as body mass, body size, and horn length).

We determined male morph by fitting a switch-point regression between horn length and body size width using the *segmented* package in R (Muggeo 2003; Knell 2009). This regression gave a switch-point at a log pronotum width of 0.664 (standard error = 0.006). Males with a log pronotum width greater than or equal to this switch-point were classified as majors, and the remaining males were classified as minors.

Because body mass, body size, horn length, and morph are strongly correlated, it was not appropriate to include all of these traits, and their interactions as explanatory variables in our analyses. To minimize the problem of multicollinearity, we fit a general linear model for strength with all 4 potential explanatory variables and second-order interactions, and calculated the variance inflation factors (VIFs) of each variable using the *vif* function in the *car* package in R (Fox and Weisberg 2011). We then sequentially removed the variable with the highest VIF and recalculated the VIFs for the reduced model until all VIFs were less than 10 (Zuur et al. 2010). Body size and the second-order interactions had very high VIFs, and therefore were removed from the analyses. Conditioning plots showed no evidence of the presence of interactions, so our results should not be biased by excluding these second-order interactions from the models.

We used general linear models to identify the most important predictors of male strength and courtship, and a generalized linear model with binomial errors and a logit link function to identify the most important predictors of mating success (mated = 1, unmated = 0). Models were initially fit with all potential explanatory variables, and then simplified to the minimum adequate model by sequentially removing nonsignificant terms on the basis of deletion tests (Crawley 2007). We report Nagelkerke's  $R^2$  for the generalized linear model to aid in the assessment of model goodness of fit (Nagelkerke 1991).

We analyzed the fighting outcome data in 2 ways. First, we fitted a generalized linear model with binomial errors and a logit link function to identify the most important predictors of definitive fighting success (winner = 1, loser = 0). Our data did not meet the proportional odds assumption, so we were unable to use ordinal logistic regression to identify the strongest determinants of all 3 possible outcomes (wins, ties, and losses). Interactions that resulted in a tie were excluded from these analyses ( $n = 19/112$  total contests), but our results are qualitatively the same if we classified males that tied as winners. The full model included the differences in the quantitative measures of mass, horn length, and strength, and focal male morph as dependent variables, and was simplified to the minimum adequate model on the basis of deletion tests (Crawley 2007). Second, we used a multivariate analysis of variance (MANOVA) to test whether the differences in mass, horn length, and strength between a focal male and his opponent differed among fights that resulted in a win, tie, or loss, and used post hoc Student's  $t$ -tests to evaluate whether these differences were significantly different from zero.

## RESULTS

There was a strong positive relationship between maximum strength and both body mass ( $R^2 = 0.60$ ,  $F_{1,213} = 319.6$ ,  $P < 0.001$ ) and horn length ( $R^2 = 0.54$ ,  $F_{1,213} = 254.4$ ,  $P < 0.001$ ), but body mass was the only predictor that remained in the minimum adequate model (Table 1). Post hoc examination of the data found that a quadratic model described the relationship between body mass and strength better than a linear model ( $F_{2,213} = 6.00$ ,  $P = 0.02$ ). The final model therefore included both body mass and squared body mass, and explained 61% of the variation in male strength (Figure 1;  $R^2 = 0.61$ ,  $F_{2,212} = 166.6$ ,  $P < 0.001$ ).

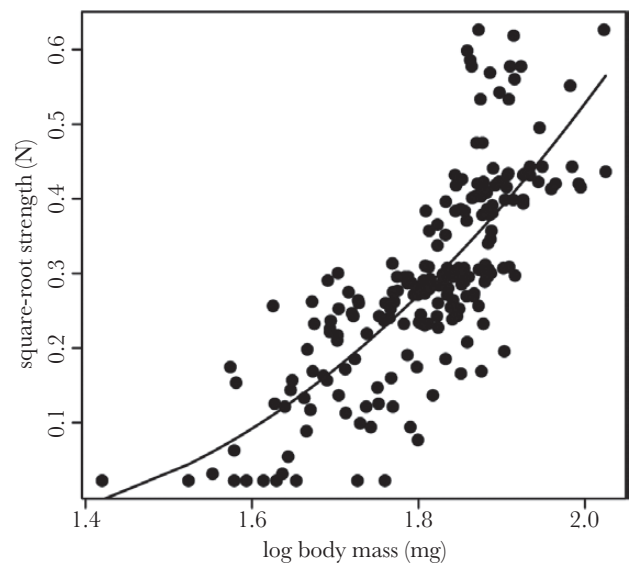
Morph was a weak, but significant predictor of courtship rate ( $R^2 = 0.022$ ,  $F_{1,213} = 6.9$ ,  $P = 0.03$ ). Courtship rate was higher for minor males ( $0.16 \pm 0.15$  bouts per min, mean  $\pm$  standard deviation) than major males ( $0.12 \pm 0.12$  bouts per min), but morph only explained 2% of the variation in courtship rate. Similarly, there was a trend for a negative association between courtship rate and body mass ( $R^2 = 0.02$ ,  $F_{1,213} = 3.3$ ,  $P = 0.07$ ), but this relationship was not statistically significant. There were no significant relationships between courtship rate and either horn length ( $R^2 = 0.008$ ,  $F_{1,213} = 1.7$ ,  $P = 0.20$ ) or strength ( $R^2 = 0.008$ ,  $F_{1,213} = 1.8$ ,  $P = 0.18$ ). Morph was the only explanatory variable that remained in the minimum adequate model (Table 2).

**Table 1**

**Explanatory variables retained and removed (shown in *italics*) for the general linear model predicting maximum strength**

Explanatory variable	Coefficient	SE	<i>F</i>	<i>P</i>
Intercept	-1.57	0.10		
Log body mass	1.03	0.06	319.6	<0.001
<i>Log horn length</i>			3.87	0.05
<i>Morph</i>			1.94	0.17

The  $F$ -statistics and  $P$  values are from partial  $F$ -tests comparing the goodness of fit between models with and without the explanatory variable in question when less significant terms have been removed. SE, standard error.



**Figure 1**

Relationship between log body mass and the square root of strength ( $R^2 = 0.61$ ,  $F_{2,212} = 166.6$ ,  $P < 0.001$ ; strength =  $1.44 - 2.38 \times \text{body mass} + 0.96 \times \text{body mass}^2$ ).

Courtship rate was the only significant predictor of mating success (Table 3). There was a significant positive relationship between courtship rate and mating success (Figure 2;  $\chi^2 = 7.2$ ,  $df = 1$ ,  $P = 0.007$ ); courtship rates were significantly higher among males that mated ( $0.16 \pm 0.15$  bouts per min) than males that did not mate ( $0.11 \pm 0.10$  bouts per min). However, the minimum adequate model only explained 5% of the observed variation in mating success (Nagelkerke's  $R^2 = 0.048$ ). Our conclusions were the same if we used latency to mating instead of mating success as a measure of female mating preference (Shackleton et al. 2005; Simmons and Kotiaho 2007): Courtship rate was the only significant predictor of a female's latency to mate, but it explained only a small portion of the variation in female preference ( $R^2 = 0.03$ ,  $F_{1,213} = 6.9$ ,  $P = 0.009$ ).

Males that won fights were significantly heavier ( $t = 9.41$ ,  $df = 98.1$ ,  $P < 0.001$ ), had longer horns ( $t = 7.98$ ,  $df = 183.7$ ,  $P < 0.001$ ), and were stronger ( $t = 8.97$ ,  $df = 103.6$ ,  $P < 0.001$ ) than their opponents. Males that won fights were also more likely to be majors than minors ( $\chi^2 = 6.91$ ,  $df = 1$ ,  $P = 0.009$ ). However, body mass, horn length, strength, and morph are all positively correlated, and the difference in body mass between a focal male and his opponent was the only predictor that remained in the minimum adequate model (Table 4; Figure 3;  $\chi^2 = 13.5$ ,  $df = 1$ ,  $P < 0.001$ ). The difference in body mass explained 24% of the variation in the outcome of fights (Nagelkerke's  $R^2 = 0.238$ ), and 66% of fights were won by males that were heavier than their opponent. In contrast, the difference in horn length explained just 15% of the variation in the outcome of fights (Nagelkerke's  $R^2 = 0.146$ ), and the difference in strength explained 19% (Nagelkerke's  $R^2 = 0.190$ ).

**Table 2**

**Explanatory variables retained and removed (shown in *italics*) for the general linear model predicting courtship rate**

Explanatory variable	Coefficient	SE	<i>F</i>	<i>P</i>
Intercept	0.12	0.01		
Morph	0.04	0.02	4.73	0.03
<i>Horn length</i>			0.18	0.67
<i>Body mass</i>			0.92	0.34
<i>Strength</i>			0.01	0.91

The *F*-statistics and *P* values are from partial *F*-tests comparing the goodness of fit between models with and without the explanatory variable in question when less significant terms have been removed. SE, standard error.

**Table 3**

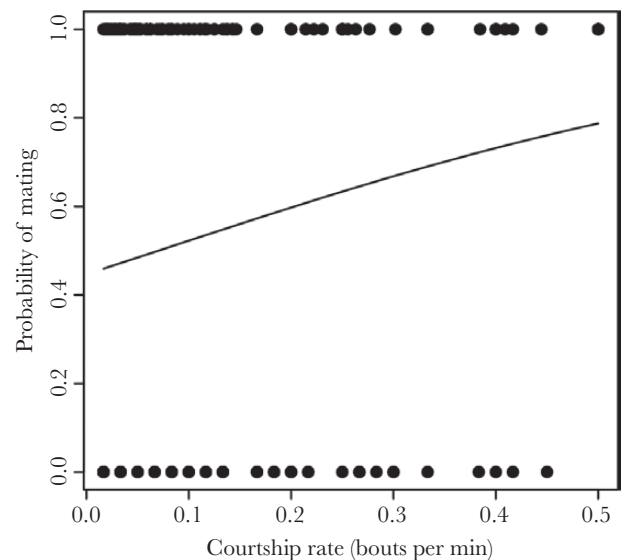
**Explanatory variables retained and removed (shown in *italics*) for the generalized linear model with binomial errors and a logit link predicting male mating success**

Explanatory variable	Coefficient	SE	Deviance	<i>P</i> ( $>\chi^2$ , 1 df)
Intercept	-0.21	0.20		
Courtship rate	3.04	1.13	7.88	0.005
<i>Horn length</i>			2.20	0.14
<i>Body mass</i>			1.41	0.23
<i>Strength</i>			1.55	0.21
<i>Morph</i>			0.13	0.72

The changes in deviance and *P* values are from chi-square tests comparing the goodness of fit between models with and without the explanatory variable in question when less significant terms have been removed. SE, standard error.

The differences in body mass, horn length, and strength were significantly different among fights that resulted in wins, ties, and losses (Figure 4; MANOVA: Pillai's trace = 0.19,  $F_{3,108} = 8.30$ ,  $P < 0.001$ ). Specifically, the difference in strength was marginally greater than zero among focal males that won ( $t = 2.19$ ,  $P = 0.03$ ), significantly less than zero among focal males that lost ( $t = -3.39$ ,  $P < 0.001$ ), and not significantly different from zero among focal males that tied ( $t = 0.46$ ,  $P = 0.65$ ). The difference in body mass was marginally greater than zero among focal males that tied ( $t = 2.16$ ,  $P = 0.04$ ), significantly less than zero among focal males that lost ( $t = -4.87$ ,  $P < 0.001$ ), and not significantly different from zero among focal males that won ( $t = 1.32$ ,  $P = 0.20$ ). The difference in horn length was significantly less than zero among focal males that lost ( $t = -3.81$ ,  $P = 0.001$ ), but not significantly different from zero among focal males that either won ( $t = 0.78$ ,  $P = 0.44$ ) or tied ( $t = 1.06$ ,  $P = 0.30$ ).

There was no relationship between fighting success and mating success ( $\chi^2 = 0.52$ ,  $df = 2$ ,  $P = 0.77$ ), or between fighting success and a female's latency to mate ( $F_{1,213} = 0.07$ ,  $P = 0.79$ ). Considering only the fights among major males, there also was no relationship between fighting success and mating success ( $\chi^2 = 0.21$ ,  $df = 2$ ,  $P = 0.90$ ), or between fighting success and a female's latency

**Figure 2**

Relationship between courtship rate and mating success (Nagelkerke's  $R^2 = 0.05$ ,  $\chi^2 = 7.2$ ,  $df = 1$ ,  $P = 0.007$ ).

**Table 4**

**Explanatory variables retained and removed (shown in *italics*) for the generalized linear model with binomial errors and a logit link predicting fighting success between 2 males**

Explanatory variable	Coefficient	SE	Deviance	<i>P</i> ( $>\chi^2$ , 1 df)
Intercept	0.14	0.24		
Difference in body mass	11.54	3.15	18.28	<0.001
<i>Difference in strength</i>			2.36	0.12
<i>Morph</i>			1.68	0.20
<i>Difference in horn length</i>			0.83	0.36

The changes in deviance and *P* values are from chi-square tests comparing the goodness of fit between models with and without the explanatory variable in question when less significant terms have been removed. SE, standard error.



to mate ( $F_{1, 128} = 0.49, P = 0.48$ ). Finally, there was no difference in courtship rate between males that won or lost fights ( $t = 0.65, df = 169.4, P = 0.52$ ).

### DISCUSSION

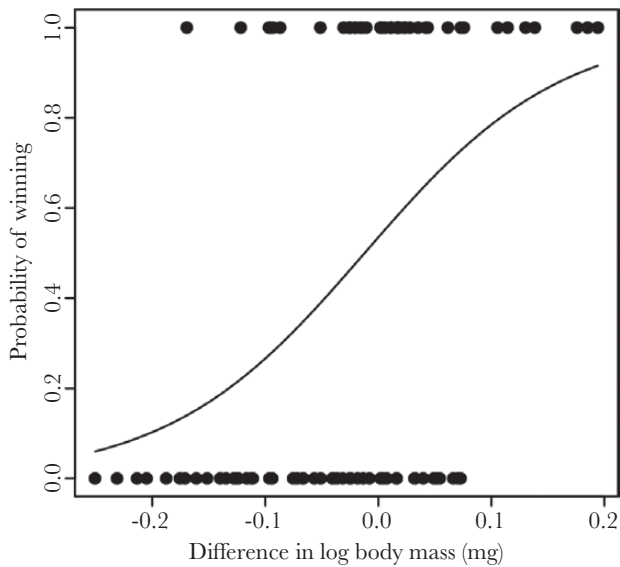
Both male–male competition and female choice are known to be important in determining male mating success in the horned dung beetle *O. taurus* (Moczek and Emlen 2000; Kotiaho et al. 2001), and whole-organism physical performance might be targeted by both mechanisms given the importance of dynamic muscular movements during fights and courtship displays (Lailvaux and Irschick 2006). Physical strength, horn length, and body mass were significant predictors of a male’s victory in fights, but males that won

in fights were not more likely to be preferred by females as mates. Instead, females preferred to mate with males that delivered high courtship rates, which were not correlated with strength, horn length, or body mass. Our results therefore suggest that the traits favored by male–male competition are different from those favored by female choice and that the evolution of male fighting behavior and courtship displays may proceed relatively independently in this species. Future studies, however, are needed to assess the genetic correlations underlying these traits (Lailvaux and Kasumovic 2011).

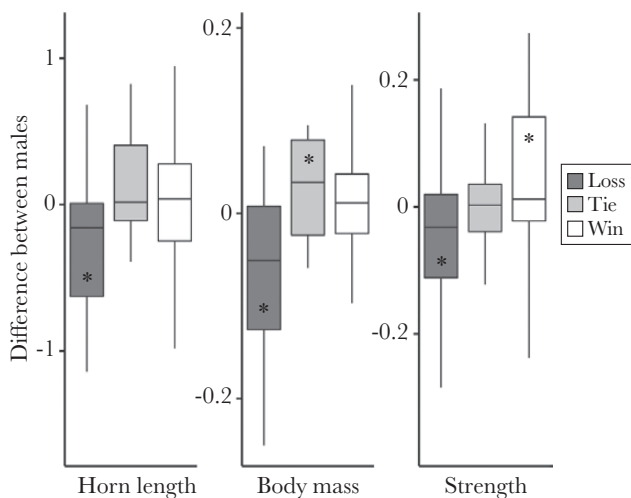
Males that won fights were significantly heavier, had longer horns, and were stronger than their opponents, which suggests that all 3 traits are favored by male–male competition. However, body mass, horn length, and strength were tightly correlated, and model comparison found that body mass alone was the strongest predictor of a male’s victory in fights. The fact that body mass, but not morph, remained in the final model is particularly interesting because it suggests that mass is more important in determining fighting outcome than size, as major and minor morphs were separated on the basis of a threshold body size. Unfortunately, because our study was correlational, we were unable to partition the separate effects of body mass, body size, horn length, and strength on male fighting success. However, previous experimental studies that staged fights between size-matched males have shown that males with longer horns are more likely to win (Emlen 1997; Moczek and Emlen 2000), which indicates that horn size has an independent effect on the outcome of fights. It was not feasible to pair rival males of equal mass in this study because we had to first screen males for courtship before conducting any fighting trials, and therefore were restricted in the number of potential competitors. However, the fact that the contests that resulted in ties occurred between males that differed in body mass, but were closely matched in horn length and strength, provides further evidence that all 3 traits are indeed important in resolving fights. Of course, future studies that stage contests between males that are matched for body mass and/or strength are needed to fully tease apart these relationships.

In addition to being the most significant determinant of fighting success, body mass was the most important predictor of a male’s physical strength. These patterns suggest that the connection between body mass and fighting success is mediated by differences in physical performance, and provides a mechanism for why larger males win fights: Larger males have the physical capacity to out-compete rivals (Sneddon et al. 2000; Lailvaux et al. 2004; Lailvaux et al. 2005). We measured physical strength as the amount of force required to pull a male out of a tunnel. This capacity is expected to be important in the context of fights because males that can resist more force will be better at defending ownership of breeding tunnels. In support of this hypothesis, we found that intruding males that were stronger than their opponents definitively won fights; intruding males that were weaker than their opponents definitively lost fights; and intruding males that were equal in strength with their opponents were unable to resolve fights. We note, however, that strength is just one measure of whole-organism performance (Lailvaux and Irschick 2006), and other physical capabilities, such as endurance or speed, may also play a role in determining fighting success (Marden and Waage 1990; Briffa and Elwood 2001; Briffa and Elwood 2004; Lailvaux et al. 2005).

Our finding that body mass was the best predictor of male strength is consistent with previous findings that *O. taurus* major males, who directly compete with other males for access to mates, allocate more resources toward residual body mass when they are exposed to rivals during the period of sexual maturation following



**Figure 3** Relationship between the difference in log body mass between competing males and the probability of winning a fight (Nagelkerke’s  $R^2 = 0.24, \chi^2 = 13.5, df = 1, P < 0.001$ ).



**Figure 4** Boxplots showing the differences in log horn length, log body mass, and square-root strength between an intruding male and his opponent for contests that resulted in a loss (dark gray bar), tie (light gray bar), or win (open bar). Asterisks inside the bars denote means that are significantly different from zero ( $P < 0.05, 2$ -tailed  $t$ -test).

adult emergence (Simmons and Buzatto 2014). That is, when males develop in competitive environments, major males invest more resources to increase mass gain, which should improve their physical strength, and likelihood of winning in male–male fights. In fact, a recent study using path analysis in the dung beetle *Euoniticellus intermedius* found that there was a direct link between weight gain following adult emergence and male strength, which suggests that the resources assimilated during this period of “maturation feeding” are allocated directly to the musculature that improves fighting performance (Reaney and Knell 2015). However, in contrast with our findings for *O. taurus*, body size and horn length were equally important in predicting male strength in *E. intermedius* (Lailvaux et al. 2005). These results suggest that the degree to which horns are used to signal competitive ability to opponents, and thus the relative importance of strength, body size, body mass, and horn length in resolving fights, can differ among species (Emlen 2008). In particular, we note that *O. taurus* is male dimorphic whereas *E. intermedius* is not, and the patterns of selection on mass allocation may be very different for dimorphic versus monomorphic species.

We found no evidence that males who won fights were more attractive to females. These results are consistent with previous studies that also found no effect of either body or horn size on a male’s mating success (Kotiaho et al. 2001; Kotiaho 2002). Our findings are nevertheless interesting because females should benefit from preferentially mating with large males. Large *O. taurus* males help females provision dung during brood mass construction (Hunt and Simmons 1998; Hunt and Simmons 2000), which reduces the costs of maternal care (Hunt et al. 2002), and results in the production of significantly heavier brood masses (Hunt and Simmons 1998; Hunt and Simmons 2000). Because brood size determines larval development and final adult size (Emlen 1994; Moczek 1998), and because large adult body size improves both male and female fitness (Hunt and Simmons 2001; Hunt et al. 2002), females should benefit from producing larger offspring. So why do not females choose to mate with larger males?

One possibility for why females do not prefer large males is that adult body size is strongly affected by variation in the larval food environment (Emlen 1994; Hunt and Simmons 1997), such that offspring size cannot be reliably predicted from the paternal phenotype (Moczek and Emlen 1999; but see Hunt and Simmons 2000). As a result, females may benefit from choosing mates based on traits that are more closely linked with male genetic quality. Females appear to prefer males that deliver high courtship rates, and this preference may help females gain indirect benefits for their offspring (Kotiaho et al. 2001; Kotiaho 2002; Simmons and Holley 2011). Indeed, because courtship rate is heritable and genetically correlated with body condition (Kotiaho et al. 2001; Kotiaho 2002), females benefit from mating with males displaying higher courtship rates by producing sons that achieve higher mating success (Kotiaho et al. 2001), and offspring with greater viability (García-González and Simmons 2011; Simmons and Holley 2011). Importantly, these studies measured body condition as residual body mass, which suggests that male–male competition and female choice both favor traits (fighting ability and courtship rate, respectively) that are linked to a male’s ability to acquire and allocate resources for mass gain. The fact that we found no relationship between fighting success and mating success is intriguing, but highlights the fact that condition is a complex, multivariate phenomenon (see Wilson and Nussey 2010; Lailvaux and Kasumovic 2011 for reviews), and there may not be a single axis of among-individual heterogeneity that best explains variation in individual fitness under all selective

contexts (Bonduriansky and Rowe 2003; Lailvaux et al. 2010; Lailvaux and Kasumovic 2011).

We also note at least 2 possibilities of how our experimental design could have influenced our ability to detect a relationship between fighting success and mating success. First, we measured male attractiveness using no-choice tests by presenting females with a single male and scoring whether (and how quickly) he was accepted as a mate. Mating preferences are generally stronger when measured using choice tests, in which 2 or more males are presented simultaneously, so our measure of male attractiveness may have been affected by our experimental design (Dougherty and Shuker 2015). Unfortunately, we do not know how many males a female encounters at a given time inside natural breeding tunnels, so it is unclear whether choice or no-choice tests will yield the most ecologically relevant estimates of female preference in this species. Second, we measured fighting success by scoring a male’s ability to evict a rival male from an artificial tunnel, and the outcome of these contests is obviously highly dependent on the relative qualities of the males in each dyad. As a result, a male that is classified as a winner may not, in fact, be a good fighter in comparison with the majority of males in the population, and even if females prefer males that are good fighters, they may not chose winners more often than losers. To explore this issue further, we examined the outcome of fights that involved just major males, which are likely to be competitively superior to minor males. Among these large males, there was no relationship between fighting success and mating success, which is consistent with the hypothesis that the traits that affect fighting success are not correlated with those that affect male attractiveness.

Future work is needed to determine the relative contributions of male–male competition and female choice to the total strength of sexual selection under natural conditions (Hunt et al. 2009). Because *O. taurus* mates exclusively within underground tunnels, a male’s ability to win fights and gain access to breeding tunnels is likely to be critical to his reproductive success (Emlen 1997; Moczek and Emlen 2000). In particular, large horned males that are able to defend ownership of breeding tunnels should have a reproductive advantage over small hornless males, and previous studies have confirmed that large males do enjoy higher mating (Emlen 1997) and fertilization (Hunt and Simmons 2001) success. However, fights with rival males and subsequent turnovers in tunnel ownership are common, and tunnels are often intercepted by side-tunnels that are excavated and used by hornless males to sneak copulations (Emlen 1997; Moczek and Emlen 2000). Females may therefore encounter several different males inside tunnels and may be able to assess and preferentially mate with attractive males (i.e., those delivering the highest courtship rates; Kotiaho et al. 2001; Kotiaho 2002).

Females may also exert cryptic, postcopulatory preferences by biasing the use of sperm from attractive males to fertilize their eggs (i.e., cryptic female choice; Eberhard 1991), and sperm from different males may also compete within a female’s reproductive tract for access to her eggs (i.e., sperm competition; Parker 1970; Simmons 2001). In *O. taurus*, these selective episodes are likely to act synergistically. Females preferentially use shorter sperm to fertilize eggs; males with larger testes gain higher fertilization success; and both short sperm and large testes are genetically correlated with residual body mass or body condition (reviewed in Simmons 2011). Intriguingly, these results suggest that a male’s ability to allocate resources to weight gain is favored by all 4 episodes of sexual selection (i.e., male–male competition, female choice, sperm competition, and cryptic female choice), and experimental evolution

studies have shown that sexual selection acts to increase male condition (Simmons and García-González 2008) and purge deleterious mutations that affect male strength (Almbro and Simmons 2014). Studies that examine how these mechanisms interact are needed to fully understand net selection on male condition and the patterns of resource allocation to different fitness-enhancing traits (e.g., testes, muscle, and energy reserves).

More generally, this study adds to a small but growing number of studies that find that male–male competition and female choice can act in opposition or target different traits (e.g., insects: Moore AJ and Moore PJ 1999; Sih et al. 2002; Candolin 2004; Bonduriansky and Rowe 2003; Shackleton et al. 2005; Okada et al. 2014; birds: Pryke et al. 2001; Andersson et al. 2002; fish: Forsgren 1997; Wong 2004; Casalini et al. 2009; lizards: López et al. 2002). Thus, males that are successful fighters are not always preferred as mates (Qvarnström and Forsgren 1998; Hunt et al. 2009). The challenge now is to determine how these selective episodes play out under natural conditions in order to gain an accurate view of the overall strength of sexual selection on male phenotypes.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>

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