Intralocus tactical conflict: genetic correlations between fighters and sneakers of the dung beetle *Onthophagus taurus*

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Abstract

Males and females differ in their phenotypic optima for many traits, and since the majority of genes are expressed in both sexes, some alleles can be beneficial to one sex but harmful to the other (intralocus sexual conflict; ISC). ISC theory has recently been extended to intrasexual dimorphisms, where certain alleles may have opposite effects on the fitness of males of different morphs that employ alternative reproductive tactics (intralocus tactical conflict; ITC). Here we use a half-sib breeding design to investigate the genetic basis for ISC and ITC in the dung beetle *Onthophagus taurus*. We found positive heritabilities and intersexual genetic correlations for almost all traits investigated. Next, we calculated the intrasexual genetic correlation between males of different morphs for horn length, a sexually selected trait, and compared it to intrasexual correlations for naturally selected traits in both sexes. Intrasexual genetic correlations did not differ significantly between the sexes or between naturally and sexually selected traits, failing to support the hypothesis that horns present a reduction of intrasexual genetic correlations due to ITC. We discuss the implications for the idea of developmental reprogramming between male morphs, and emphasize the importance of genetic correlations as constraints for the evolution of dimorphisms.
Keywords: Alternative reproductive tactics, conditional strategy, intrasexual dimorphism, male dimorphism, phenotypic plasticity, polyphenism, quantitative genetics.

Introduction

Conspecific males and females are usually under different selective pressures, which can result from different life histories, for example when females have different physiological demands (due to egg production), diets, or even habitats than males (Shine, 1989). In extreme cases, like some species of fig wasps and deep-sea anglerfish, males do not forage as adults, are ephemeral and have rudimentary feeding and dispersal traits, whereas conspecific females forage normally, live longer, and have fully developed traits for flying/swimming (Weiblen, 2002; Pietsch, 2005). The different phenotypic optima between the sexes is also evident when sexual selection for weapons and ornaments drives exaggerated phenotypes in only one of the sexes, generally males ( Andersson, 1994). Since most genes are expressed in both sexes, intersexual genetic correlations (Falconer, 1952; Falconer & Mackay, 1996) might be present even in traits that have very different phenotypic optima between the sexes. This constitutes the basis for intralocus sexual conflict (ISC, Lande, 1980), where an allele is beneficial to one sex but harmful to the other (sexually antagonistic allele, Rice, 1984; Rice & Chippindale, 2001). ISC can impose significant costs to male and female fitness, and set constraints to the evolution of morphology, physiology and behavior. Such costs select for mechanisms that suppress intersexual genetic correlations (Bonduriansky & Chenoweth, 2009), and ISC can be partially or completely resolved depending on the degree of sexual dimorphism that evolves and allows both sexes to be closer to their phenotypic optima.
Although intralocus sexual conflict has been known for at least 30 years (Rice, 1984), it is only very recently that this theory has been extended to dimorphisms within a sex. Intrasexual dimorphism is usually the result of alternative reproductive tactics among males (Oliveira et al., 2008), but is also well documented in the body coloration of female Odonata (Fincke et al., 2005; Svensson et al., 2009) and body size and flight related traits in ant queens (Heinze & Keller, 2000). These dimorphisms indicate that the different morphs within a sex have divergent phenotypic optima for the same trait, analogous to the different phenotypic optima that may occur between the sexes under ISC. Moreover, here it is even more evident that genes can affect the same trait in individuals of different morphs, since they belong to the same species and sex, and will share alleles on autosomes and sex chromosomes. As a consequence, intrasexual genetic correlations for these male (or female) dimorphic traits would be the genetic basis for intralocus tactical conflict (ITC, Morris et al., 2013), where the word ‘tactical’ is used to refer to the alternative reproductive tactics that are normally employed by dimorphic males (Oliveira et al., 2008).

The same criteria are required for both ISC and ITC to occur (Morris et al., 2013). Firstly, the two types of conflict will affect a trait when males and females (or males of different morphs) have different phenotypic optima for the same trait, as discussed above. A formal demonstration of this requires artificial selection experiments or estimating selection differentials in natural populations (Arnqvist & Tuda, 2010; Berg & Maklakov, 2012). Secondly, ISC and ITC can only occur if the different sexes and morphs are not at their respective optima, otherwise the conflicts would be resolved (Morris et al., 2013). Demonstrating this second element can also be achieved through artificial selection. This approach has been used to detect ISC in the broad-horned flour beetles, where the evolution of mandible size in males is constrained by female fitness, as selection for an increase in the...
former caused a decrease in the latter (Harano et al., 2010). For ITC, studies in dung beetles have demonstrated that head horns are under positive selection in large fighting males (henceforth ‘majors’, Moczek & Emlen, 2000; Hunt & Simmons, 2001), however behavioral experiments suggest that in small sneaker males (henceforth ‘minors’) horns may reduce speed and maneuverability, potentially decreasing the efficiency of their sneaking tactic (Moczek & Emlen, 2000; Madewell & Moczek, 2006). Consequently, the presence of rudimentary horns in small sneaker males of these species implies that these males are not at their phenotypic optimum, suggesting ITC.

The third and last essential element of intralocus conflict is a shared genetic architecture between the sexes (for ISC), or between the morphs (for ITC), for the trait in question. This shared genetic architecture cannot be assumed, nor can it be inferred from the functions of the traits of males and females, or males of different morphs. However, as we argued above, genetic correlations between the sexes (and especially between morphs within a sex) are probably prevalent, and would be the most straightforward way to investigate the third element of ISC and ITC (Morris et al., 2013).

Here we investigate intersexual and intrasexual genetic correlations for a variety of naturally and sexually selected traits in the dung beetle Onthophagus taurus. Major male O. taurus bear a pair of head horns which are used in fights for access to the subterranean tunnels where females lay their eggs. Meanwhile, minor males only bear very short rudimentary horns (or lack horns altogether), and their mating tactic is based on sneaking into tunnels and furtively mating with females guarded by the major males (Hunt & Simmons, 1997; Moczek & Emlen, 2000). This dimorphism is conditional on the environment, as the amount of dung provided by the parents to an individual male larva is positively correlated with the probability that it will develop as a major male in the future (Hunt &
Simmons, 1997; 2000). Our main goal was to ask whether intrasexual genetic correlations between majors and minors constrain the evolution of horn length. ITC is likely to be present in *O. taurus*, since only majors benefit from having horns, and yet minors express rudimentary horns that seem to be detrimental for their mating tactic (Moczek & Emlen, 2000; Madewell & Moczek, 2006). Consequently, the first two criteria for detecting ITC are visibly met in this species, but the shared genetic architecture between male morphs is still poorly known.

Despite our focus being mainly on the evolution of male dimorphism in horns, we nevertheless included females (which lack horns) in this study, and we also analyzed naturally selected traits (body size measured as pronotum width, elytra length, and rear and front femur lengths), in order to compare the genetic correlations within and between the sexes for these traits with those for horn length. We predicted that body size and general shape traits (pronotum width, elytra length, and rear and front femur lengths) would not have strikingly different phenotypic optima between the sexes and male morphs, and therefore would present positive intersexual and intrasexual genetic correlations. On the other hand, since horn length is sexually selected in majors only, this trait is expected to have different phenotypic optima between male morphs, and should present a reduction or complete breakdown of intrasexual genetic correlations as a result of ITC (Morris et al., 2013). In summary, we expected significant and positive intersexual genetic correlations for all traits, with the obvious exception of horn length, which is not expressed in females. For the intrasexual genetic correlations, we expected them to be significant and positive for all traits in females, but only for naturally selected traits in males. Regarding male horn length, the presence of positive intrasexual genetic correlations would be consistent with current ITC, whereas a partial resolution of this conflict would result from reduced genetic correlations.
(when compared to other male traits), and a complete resolution of ITC would result from a lack of any intrasexual correlation for horn length.

**Materials and methods**

**Model organism**

Adult dung beetles were collected from cow dung in Margaret River (Western Australia), and maintained in the laboratory at 25°C for one week with access to cow dung *ad libitum*. Females were then established in individual chambers (PVC piping: 25 cm length, 6 cm diameter) for one week. Chambers were three-quarters filled with moist sand, and 250 ml of cow dung was added to each. After the breeding period, chambers were sieved, and brood masses retrieved and incubated in moist sand until adults started to emerge, approximately three weeks later. Emerging adults were housed in single sex populations with access to cow dung *ad libitum* for two weeks.

**Breeding design and morphological measurements**

In order to establish a half-sibling breeding design (Falconer & Mackay, 1996), 75 male *O. taurus* were collected from field populations, and each paired with four laboratory-reared virgin females. These mating groups were kept separately in plastic boxes (7 cm x 7 cm base, 5 cm height) for five days with moist sand and constant access to fresh dung. Females were then established in individual breeding chambers for seven days (as described above). Females were re-established in fresh breeding chambers with new cow dung every 7 days until death. Brood masses were incubated in moist sand at 25°C until the emergence of adults, which were preserved immediately in alcohol. Pronotum width, elytra length, front...
femur length, and rear femur length were measured with digital calipers to the nearest 0.01 mm. For the horn length (males only), measurements were made to the nearest 0.1 mm using a binocular microscope.

Genetic analyses

We performed the genetic analysis of elytra length, front femur length, and rear femur length both on the absolute values of these traits (without controlling for body size), and on their relative sizes (controlling for body size by adding pronotum width as a covariate in the models). Male horn length was analyzed directly and using the residuals from a Richards’ growth function that best describes the sigmoid allometry of horn length and pronotum width in *O. taurus* (Buzatto *et al.*, 2012). The analysis of pronotum width was performed directly on the measurements of the trait, which is itself a widely used proxy for body size in the species (Moczek & Emlen, 2000; Hunt & Simmons, 2001). Importantly, the weight of brood masses produced by females transmit a strong maternal effect on offspring body size (Hunt & Simmons, 2000), which can inflate estimates of heritability and genetic correlations involving absolute measures of size when males affect maternal investment (Kotiaho *et al.*, 2003). However, maternal effects and these potential indirect paternal effects are controlled for in our analyses using residuals or including body size as a covariate.

To estimate the heritability of each trait separately for each sex, we fitted a univariate animal model (Henderson, 1950; Kruuk, 2004) with the trait mean as a fixed effect and the additive genetic effect of each individual as a random effect. We fitted this mixed effects model in R version 3.0.2 (R Core Team, 2013), using the library ASReml-R (Butler, 2009). By providing the model in ASReml-R with a pedigree file, it is possible to calculate the inverse of the numerator relationship matrix (A-matrix), and then fit the random effects that
represent the additive genetic effect of individuals for all members of the pedigree, taking into account the A-matrix. We chose this approach because our data-set was unbalanced due to variation in the number of male and female offspring produced by each female. ASReml-R uses restricted maximum likelihood (REML), which is more appropriate than least squares ANOVA for unbalanced designs (Lynch & Walsh, 1998). We measured heritability as the proportion of total phenotypic variance \( V_P \) that is explained by the additive genetic effect of individuals \( V_A \), as estimated by the random effect in the above model. Therefore, \( h^2 = \frac{V_A}{V_P} \), where \( V_P = V_A + V_R \) and \( V_R \) is the residual variance.

For the intersexual genetic correlations, we fitted a bivariate animal model with the trait mean and its interaction with sex as fixed factors, and the additive genetic effect of each individual as a random effect. The data file for this type of analysis was organised so that each trait was coded as two different traits depending on which sex it is being expressed in, and each individual contained a missing value for the expression of the trait in the opposite sex. The genetic correlation was then estimated as the covariance between the male trait and the female trait divided by the square root of the product of the variance components for the male and the female trait. In order to estimate the significance of these correlations, we created models with the covariance term fixed to zero, and compared them with the original models through log-likelihood ratio tests (cf. Butler et al., 2009). Additionally, we also estimated intersexual genetic correlations by regressing the mean trait of paternal half sibling males on the mean trait of paternal half sibling females (sire family mean correlation), using weighted least-squares with families being weighted according to the number of offspring. Sire family mean correlations were used here instead of full-sibling mean correlations because the former are not inflated by non-genetic maternal effects in a half-sibling breeding design. These sire family mean correlations for relative elytra length, relative front femur

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length, and relative rear femur length were done using the residuals from the linear relationships of these traits with body size, measured as pronotum width. These analyses were also performed in R version 3.0.2 (R Core Team, 2013). Family means usually underestimate the magnitude of genetic correlations (Via, 1984), but can be used when the goal is to test for their direction, rather than to provide accurate estimates of their magnitude (Astles et al., 2006). We included family means analyses here because our estimates of genetic correlations through animal models in ASReml-R sometimes converged on the boundary of parameter space, resulting in non-informative estimates.

We employed the same approach for intrasexual genetic correlations, but this time using morph instead of sex in the model. In both sexes, we split individuals into two morphs at the body size value of 4.92 mm, which has been estimated as the switchpoint between majors and minors of the dung beetle *O. taurus* (Hunt & Simmons, 2001). This method can misclassify some of the males (Kotiaho & Tomkins, 2001), however it has the advantage that we can use the same body size split in females (artificially splitting them in two ‘pseudo-morphs’), and therefore investigate whether intrasexual genetic correlations found between male morphs are also found between small and large females.

Finally, we calculated the genetic correlation (through the family means method) for relative horn length within majors, as ITC should cause this correlation to be weaker between morphs than within a morph. In order to calculate this ‘within-morph genetic correlation’, we randomly assigned each major to one of two groups, and calculated the correlation between sire family means for these two groups, a procedure that was repeated 10,000 times. We could not apply this method in minors or females due to small sample sizes, since this approach can only be applied with families that have at least two males of each morph.
In order to compare heritabilities and genetic correlations across traits and sexes, we calculated 84% confidence intervals around all estimates so that significance at the 0.05 level could be visually detected based on whether the intervals of two estimates overlap. Generally, 95% confidence intervals are used to compare estimates with a fixed expectation (0 or 1, for instance), but in order to use the non-overlap criteria, the intervals must be adjusted to 1.39 times the standard error, which equals 84% (following Goldstein & Healy, 1995). For estimates derived from the animal model in ASReml-R, we calculated the 84% confidence intervals by multiplying the standard error of the heritability estimate by 1.39, and then adding or subtracting the result to the heritability estimate to find the upper and lower confidence limits, respectively. For estimates obtained through correlations of sire family means, we calculated the 84% confidence intervals with the function CIr() from the library ‘psychometric’ (Fletcher, 2010) in R version 3.0.2 (R Core Team, 2013).

Results and Discussion

The main goal of this study was to investigate the role of genetic correlations as potential constraints for the evolution of male dimorphism in *O. taurus*. We analyzed the heritabilities of, as well as the intersexual and intrasexual genetic correlations in pronotum width — a proxy for body size in this species (Moczek & Emlen, 2000; Hunt & Simmons, 2001) — and three traits that were both analyzed directly and analyzed through their relative size when compared to pronotum width; in the case of horn length by using the residuals of a Richard’s growth function fitted to the sigmoid relationship between body size and horn length, and in the case of other traits by adding body size as a covariate in the linear models. Analyses of the relative sizes of traits are expected to be free of indirect paternal influences on maternal effects.
We found highly significant heritabilities in all traits analyzed, ranging from 0.17 for male relative femur length to as high as 0.81 for male pronotum width (Table 1). In general, heritabilities estimated for the direct measurements of each trait were higher (mean of 0.69) than those estimated for the relative sizes of traits (mean of 0.32; Welch Two Sample t-test, \( t_{9.76} = 6.78, P < 0.0001 \)). Therefore, our results show that the phenotypic traits measured present significant heritabilities in both sexes, and the only sex differences in heritability (non-overlapping 84% confidence intervals in Table 1) were found for relative rear and front femur length, which both had higher heritability estimates in females than in males (Table 1). This means that relative leg length has a greater environmental component in males, which could be related to the alternative fighting and sneaking male phenotypes, whose expression is greatly affected by nutrition (Hunt & Simmons, 2000; 2004). Indeed, a previous study found that relative horn length is developmentally integrated with the relative length of the forelegs in male *O. taurus* (Tomkins et al., 2005a), which could explain why relative horn length and relative front and rear femur lengths in males were the least heritable traits here. Nonetheless, for the purposes of our study, significant heritabilities in both sexes are important because they are necessary for intra- and intersexual genetic correlations between and within these traits, since genetic correlations are theoretically undefined for traits without any additive genetic variance (Roff, 2006).

All the intersexual genetic correlations we estimated were also significant and positive (Table 2), and were underestimated by the sire family means method when compared to the animal model method (Fig. 1), which is expected for traits under the influence of maternal effects (Astles et al., 2006). The correlations between male and female traits in *O. taurus* were as high as 0.92, five of them being above 0.80 and one of them not significantly different from 1. This is an interesting result, as any genetic variation for sexual dimorphism would require that the correlation between the effects of genes in males and females is less than one.
(Robertson, 1959; Lynch & Walsh, 1998). Consequently, our results indicate almost no variance for sexual dimorphism across several traits, such that even if selection did favor different optima for each sex, there would be little genetic variation on which selection could operate. This agrees with the lack of sexual dimorphism in these traits. Similarly, the strength of intersexual correlations has been found to be negatively correlated with the degree of sexual dimorphism across traits of a waltzing fly (Bonduriansky & Rowe, 2005).

Since genetic correlations reflect the degree to which traits have genes in common (Roff, 1996a), a simple interpretation of these positive intersexual genetic correlations is that they result from alleles having similar effects on the same trait in males and females. Nonetheless, the presence of strong and positive intersexual genetic correlations that we found for all traits but horn length (females do not express horns) does not necessarily indicate intralocus sexual conflict (ISC), as male and female O. taurus could share the same phenotypic optimum for these traits. In the case of horn length, if female O. taurus ever expressed head horns in the evolutionary history of this species, ISC would have selected for the suppression of horns in that sex, and the evolution of complete sexual dimorphism for this trait resolved the conflict.

If a positive intersexual genetic correlation indicates a similar action of an allele on males and females, a positive intrasexual genetic correlation should point to a similar action of an allele on siblings of the same sex but different body sizes — majors and minors in the dimorphic O. taurus males, or small and large females (Fig. 2). We expected such correlations to be even stronger than the ones between the sexes, since they result from genes affecting the same trait in individuals of the same sex that might therefore share alleles on autosomes and sex chromosomes. Surprisingly, however, we only found one significant intrasexual genetic correlation, for relative elytra length between majors and minors (Table 3). It is

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important to emphasize that the estimates we present for such correlations were derived from sire family means, as the majority of our estimates of intrasexual genetic correlations using ASReml-R converged on the boundary of parameter space (not shown), rendering them meaningless. As we argued for the intersexual correlations, the method of family means usually underestimates the magnitude of genetic correlations (Astles et al., 2006).

However, our family mean estimates of intersexual genetic correlations were always significant, and the mean of these estimates (0.39) was significantly higher than the mean of the estimates of intrasexual genetic correlations (mean pooled from both sexes: 0.175; Welch Two Sample t-test, $t_{19.48} = 5.27, P < 0.0001$).

We acknowledge that a simple interpretation for the lack of significant intrasexual genetic correlations in our study is that our sample sizes were not adequate to detect such correlations. This might seem unlikely, since we analyzed a total of 1,054 males and 887 females from 71 different families. However, only subsets of this large dataset were available for each of our analyses, and intrasexual analyses only use half the data that is available for the intersexual analyses. For instance, estimates of intersexual correlations were only possible with families that had both male and female offspring (66 families). Moreover, estimates of intrasexual correlations were only possible with families that had both major and minor male offspring (for the correlations between the two male morphs), or female offspring with pronotum widths smaller and larger than 4.92mm (for the correlations between small and large females). Therefore, the number of families used for the estimation of intrasexual correlations ranged from 27 to 40 (mean ~ 34). Calculating the power of correlation tests using the package ‘pwr’ (Champely, 2012) in R version 3.0.2 (R Core Team, 2013), we found that our power to detect the significance of intrasexual genetic correlations was under 30% for weak correlations ($r \leq 0.25$), but up to 87% for moderate correlations ($0.25 < r \leq 0.5$), and higher than 97% for correlations with $r > 0.6$. 

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Regardless of their statistical significance, however, the magnitude of the estimates of intrasexual genetic correlations in males and females can be compared, in a way that sheds some light on our hypotheses. Intrasexual genetic correlations did not differ significantly between the sexes (Welch Two Sample t-test, \( t_{10.81} = 1.63, P = 0.133 \)), and their mean in males (0.22) was actually higher than that for females (mean of 0.12), a difference in the opposite direction to which we originally predicted. Therefore, we found no evidence for the effects of ITC reducing the intrasexual genetic correlations between males of different morphs.

Another important comparison can be made between the magnitude of the intrasexual correlations in male horn length and in remaining traits. Here again, we predicted that horn length would be the male trait under the strongest ITC (if not the only trait targeted by selection from ITC), and should present a weaker intrasexual genetic correlation, when compared to other male traits. The mean of these correlations for the naturally selected male traits (pronotum width, elytra length, rear and front femur lengths, relative elytra length, and relative rear and front femur lengths) was 0.23, which did not differ significantly from the correlations for horn length and relative horn length (respectively 0.10 and 0.24; Welch Two Sample t-test, \( t_{1.73} = 0.78, P = 0.528 \)). Once again, we found no evidence that horn length is under a stronger ITC than any of the other morphological traits studied. Finally, after calculating the genetic correlation for relative horn length within majors, we found no significant difference between the within majors correlation (0.37; 84% confidence interval: 0.16—0.55) and the between morphs correlation for relative horn length (0.24; 84% confidence interval: 0.01—0.44; Table 3). This further supports our interpretation that horns in dung beetles do not present a reduction of intrasexual genetic correlations as a result of ITC.

It is tempting to interpret the general lack of statistical significance for the intrasexual genetic correlations between male morphs (Table 3) as evidence for the developmental
reprograming hypothesis. This hypothesis states that alternative phenotypes go through a reprograming event that switches the developmental path of the animal (Emlen & Nijhout, 1999; Nijhout, 1999; 2003), decoupling the genetic architecture of alternative phenotypes and allowing them to respond to selection independently and achieve dramatically divergent phenotypes (Emlen & Nijhout, 2000; West-Eberhard, 2003; Moczek, 2010; Snell-Rood et al., 2010). However, we found no evidence that intrasexual correlations in male horns are smaller in magnitude than the correlations in other male traits, or in females. Although we would not conclude that our results refute the developmental reprogramming hypotheses, they are more consistent with the positive allometry hypothesis which argues that alternative phenotypes are generated when there is a steep positive allometry between the dimorphic trait and body size, and that limitation on trait growth for the largest males produces the asymptote in the curve (Tomkins et al., 2005b). Under this hypothesis, there is no developmental dissociation between alternative phenotypes, which are hence unable to respond to selection independently (Tomkins et al., 2005b; Tomkins & Moczek, 2009).

Another recent study supports the view that these alternative phenotypes do not have completely decoupled developmental routes (Snell-Rood et al., 2010).

Finally, the fact that intersexual correlations were stronger than intrasexual correlations, even in females, was an unexpected result of our study, as there is no biological reason to expect this result. We believe that there is a great need for more empirical studies on intrasexual genetic correlations between individuals of different size classes or morphs, in order to investigate whether this is a general pattern. The genetic basis for intrasexual genetic correlations, as well as the methods to detect them, certainly deserve more attention from evolutionary biologists. These overlooked correlations are especially important to test hypotheses related to the new and exciting topic of intralocus tactical conflict (Morris et al., 2013), and its interaction with intralocus sexual conflict (Bielak et al., 2014), both types of
conflict being potentially important to all kinds of within-sex polyphenisms. The coexistence of two alternative phenotypes within the same sex is a widespread morphological (Roff, 1994; 1996b; Brockmann, 2001), behavioral (Moczek & Emlen, 2000) and physiological (Mousseau & Roff, 1989) trait, making ITC a promising topic in evolutionary biology.

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### Table 1

Summary statistics and heritabilities (estimated with an animal model in ASReml-R) for all traits analyzed through a half-sibling breeding design in the dung beetle *Onthophagus taurus*.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Female trait (mm)</th>
<th>Male trait (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Descriptive statistics</strong></td>
<td>n° offspring / n° sires</td>
<td>mean / SE</td>
</tr>
<tr>
<td>Pronotum width</td>
<td>887 / 71</td>
<td>5.25 / 0.008</td>
</tr>
<tr>
<td>Elytra length</td>
<td>851 / 71</td>
<td>3.56 / 0.005</td>
</tr>
<tr>
<td>Rear femur length</td>
<td>845 / 71</td>
<td>2.80 / 0.004</td>
</tr>
<tr>
<td>Front femur length</td>
<td>859 / 71</td>
<td>2.44 / 0.003</td>
</tr>
<tr>
<td>Relative elytra length</td>
<td>851 / 71</td>
<td>-</td>
</tr>
<tr>
<td>Relative rear femur length</td>
<td>845 / 71</td>
<td>-</td>
</tr>
<tr>
<td>Relative front femur length</td>
<td>859 / 71</td>
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</tr>
</tbody>
</table>

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<table>
<thead>
<tr>
<th>Trait</th>
<th>Sample Size</th>
<th>Mean ± SE</th>
<th>84% CI</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elytra length</td>
<td>852 / 70</td>
<td>3.47 / 0.005</td>
<td>0.61 / 0.49–0.74 (&lt;0.0001)</td>
<td></td>
</tr>
<tr>
<td>Rear femur length</td>
<td>783 / 70</td>
<td>2.78 / 0.005</td>
<td>0.64 / 0.52–0.77 (&lt;0.0001)</td>
<td></td>
</tr>
<tr>
<td>Front femur length</td>
<td>909 / 70</td>
<td>2.55 / 0.005</td>
<td>0.66 / 0.54–0.79 (&lt;0.0001)</td>
<td></td>
</tr>
<tr>
<td>Horn length</td>
<td>1054 / 70</td>
<td>2.44 / 0.033</td>
<td>0.79 / 0.68–0.90 (&lt;0.0001)</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Relative trait length</th>
<th>Sample Size</th>
<th>Mean ± SE</th>
<th>84% CI</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Relative elytra length</td>
<td>852 / 70</td>
<td>-</td>
<td>0.31 / 0.21–0.42 (&lt;0.0001)</td>
<td></td>
</tr>
<tr>
<td>Relative rear femur length</td>
<td>783 / 70</td>
<td>-</td>
<td>0.22 / 0.13–0.31 (0.0007)</td>
<td></td>
</tr>
<tr>
<td>Relative front femur length</td>
<td>909 / 70</td>
<td>-</td>
<td>0.17 / 0.10–0.25 (0.0015)</td>
<td></td>
</tr>
<tr>
<td>Relative horn length*</td>
<td>1054 / 70</td>
<td>-</td>
<td>0.21 / 0.14–0.28 (0.0001)</td>
<td></td>
</tr>
</tbody>
</table>

†P < 0.05 that are in bold indicate values significantly greater than 0 at the table-wide α level after sequential Bonferroni correction (Rice, 1989), which was done separately for the direct analyses of traits (non-shaded rows) and for the analyses of relative trait sizes (shaded rows). Estimates and their 84% confidence intervals are in bold when they are significantly different between the sexes. *Relative horn length was analyzed using the residuals from a Richards’ growth function that best describes the sigmoidal allometry of horn length and pronotum width in O. taurus (see Materials & methods).
Table 2 Summary of intersexual genetic correlations (estimated with an animal model in ASReml-R and through correlations between sire family means) for all traits analyzed through a half-sibling breeding design in the dung beetle Onthophagus taurus.

<table>
<thead>
<tr>
<th>traits</th>
<th>Animal model (ASReml-R)</th>
<th>Sire family means</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$r_A / 84%CI (P)^\dagger$</td>
<td>$r / 84%CI (P)^\dagger$</td>
</tr>
<tr>
<td>Pronotum width</td>
<td>0.92 / 0.86—0.98 (&lt; 0.0001)</td>
<td>0.45 / 0.30—0.58 (0.0002)</td>
</tr>
<tr>
<td>Elytra length</td>
<td>0.85 / 0.75—0.94 (&lt; 0.0001)</td>
<td>0.40 / 0.24—0.54 (0.0009)</td>
</tr>
<tr>
<td>Rear femur length</td>
<td>0.87 / 0.79—0.96 (&lt; 0.0001)</td>
<td>0.31 / 0.14—0.46 (0.0120)</td>
</tr>
<tr>
<td>Front femur length</td>
<td>0.88 / 0.81—0.96 (&lt; 0.0001)</td>
<td>0.40 / 0.24—0.54 (0.0008)</td>
</tr>
<tr>
<td>Relative elytra length</td>
<td>0.47 / 0.24—0.70 (0.0051)</td>
<td>0.35 / 0.19—0.50 (0.0045)</td>
</tr>
<tr>
<td>Relative rear femur length</td>
<td>0.90 / 0.72—1.08 (&lt; 0.0001)</td>
<td>0.50 / 0.36—0.62 (&lt; 0.0001)</td>
</tr>
<tr>
<td>Relative front femur length</td>
<td>0.34 / 0.09—0.60 (0.0423)</td>
<td>0.32 / 0.15—0.47 (0.0099)</td>
</tr>
</tbody>
</table>

$^\dagger P < 0.05$ that are in bold indicate values significantly greater than 0 at the table-wide $\alpha$ level after sequential Bonferroni correction (Rice, 1989), which was done separately for the direct analyses of traits (non-shaded rows) and for the analyses of relative trait sizes (shaded rows).
Table 3 Summary of intrasexual genetic correlations (estimated through correlations between sire family means) for all traits analyzed through a half-sibling breeding design in the dung beetle *Onthophagus taurus*.

<table>
<thead>
<tr>
<th>traits</th>
<th>Intrasexual genetic correlations (as paternal half sibling family means)</th>
<th>Males</th>
<th>Females</th>
<th>Number of families</th>
<th>Number of families</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>r / 84%CI (P)†</td>
<td>Number of families</td>
<td>r / 84%CI (P)†</td>
<td>Number of families</td>
</tr>
<tr>
<td>Pronotum width</td>
<td></td>
<td>0.29 / 0.08—0.49 (0.070)</td>
<td>40</td>
<td>-0.06 / -0.31—0.19 (0.735)</td>
<td>33</td>
</tr>
<tr>
<td>Elytra length</td>
<td></td>
<td>0.23 / 0.00—0.44 (0.168)</td>
<td>38</td>
<td>0.19 / -0.09—0.45 (0.341)</td>
<td>27</td>
</tr>
<tr>
<td>Rear femur length</td>
<td></td>
<td>0.23 / -0.02—0.45 (0.199)</td>
<td>34</td>
<td>-0.05 / -0.33—0.23 (0.825)</td>
<td>27</td>
</tr>
<tr>
<td>Front femur length</td>
<td></td>
<td>0.08 / -0.16—0.31 (0.634)</td>
<td>38</td>
<td>0.14 / -0.14—0.40 (0.473)</td>
<td>28</td>
</tr>
<tr>
<td>Horn length</td>
<td></td>
<td>0.10 / -0.13—0.32 (0.556)</td>
<td>40</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Relative elytra length</td>
<td></td>
<td>0.42 / 0.21—0.60 (0.008)</td>
<td>38</td>
<td>0.09 / -0.19—0.36 (0.662)</td>
<td>27</td>
</tr>
<tr>
<td>Relative rear femur length</td>
<td></td>
<td>0.22 / -0.03—0.44 (0.210)</td>
<td>34</td>
<td>0.31 / 0.03—0.54 (0.117)</td>
<td>27</td>
</tr>
<tr>
<td>Relative front femur length</td>
<td></td>
<td>0.16 / -0.08—0.38 (0.345)</td>
<td>38</td>
<td>0.21 / -0.07—0.46 (0.279)</td>
<td>28</td>
</tr>
<tr>
<td>Relative horn length*</td>
<td></td>
<td>0.24 / 0.01—0.44 (0.137)</td>
<td>40</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

†P < 0.05 that are in bold indicate values significantly greater than 0 at the table-wide α level after sequential Bonferroni correction (Rice, 1989), which was done separately for the direct analyses of traits.
traits (non-shaded rows) and for the analyses of relative trait sizes (shaded rows). Relative horn length was analyzed using the residuals from a Richards’ growth function that best describes the sigmoid allometry of horn length and pronotum width in O. taurus (see Materials & methods).

**Fig. 1** Intersexual genetic correlations for all traits analyzed through a half-sibling breeding design in the dung beetle *Onthophagus taurus*. Estimates derived from correlations between sire family means were plotted against estimates derived from an animal model in ASReml-R. The figure shows that, despite there being a positive correlation (one-tailed Spearman’s correlation; \( \rho = 0.72, S_\alpha = 15.6, P = 0.034 \)), the method of sire family means underestimates the magnitude of genetic correlations, which was specially true for rear femur length.

**Fig. 2** An illustration of the idea that positive correlations in family means should be expected between the traits of minors and majors of the dung-beetle *Onthophagus taurus*, indicating a positive intrasexual genetic correlation. The same rationale applies for female siblings of different size classes. The gray distribution in (a) represents a family with a trait mean lower than the trait mean of the family represented in (b) by the black distribution. In both (a) and (b), a fictitious threshold is used to split males into minor and major morphs (or to split females into small and large classes; in our data this split was done at the body size value of 4.92 mm; see Materials and methods). Continuous arrows and full circles represent the mean trait value for majors (or large females) in both families, whereas dashed arrows and open circles represent the mean trait value for minors (or small females). (c) The result is a hypothetical correlation between the family means for males of different morphs or females of different size classes.