


Morph-specific investment in testes mass in a trimorphic beetle, *Proagoderus watanabei*

J. M. Parrett^{1,2}, E. M. Slade³ & R. J. Knell² 

¹Evolutionary Biology Group, Faculty of Biology, Adam Mickiewicz University, Poznań, Poland

²School of Biological and Behavioural Sciences, Queen Mary, University of London, London, UK

³Asian School of the Environment, Nanyang Technological University, Singapore City, Singapore

Keywords

alternative tactics; dung beetle; horned beetle; intrasexual competition; polymorphism; polyphenism; reproductive tactics; sperm competition.

Correspondence

Robert J. Knell, School of Biological and Behavioural Sciences, Queen Mary, University of London, London, UK.

Email: R.Knell@qmul.ac.uk

Editor: Gabriele Uhl

Received 9 May 2021; revised 18 August 2021; accepted 27 October 2021

doi:10.1111/jzo.12941

Abstract

When competition between males for mates is intense, it is common to find that some males will adopt alternative tactics for acquiring fertilizations, often involving the use of 'sneak' tactics whereby males avoid precopulatory contests. These alternative tactics are sometimes associated with discrete differences in male morphology, with sneak males investing less in weaponry but more in traits such as testes which may give an advantage in sperm competition. In some cases, it appears that males develop into more than two morphs, with a number of examples of tri- and even tetramorphic arthropod species being described. Here, we analyse the scaling relations of the dung beetle species *Proagoderus watanabei*, which expresses two distinct weapon traits: paired head horns and a pronotal horn. We find that males of this species are trimorphic, with alpha males expressing long head horns and a pronotal horn, beta males with long head horns but no pronotal horn and gamma males with short head horns only. We also find that alpha males invest relatively less in testes than do beta or gamma males, indicating that beta and gamma males in this species probably experience higher risks of sperm competition than do alphas.

Introduction

Strong intraspecific competition between males for mates is often associated with the use of alternative tactics by males of different status (Gross, 1996; Taborsky et al., 2008). In taxa as diverse as mites, fish, crickets, frogs and bovids (Oliveira et al., 2008), some males in a population will avoid aggressive precopulatory contests with more dominant males, instead attempting to acquire matings by other means and therefore shifting male–male competition to the postcopulatory arena. In many cases, these alternative tactics are themselves associated with distinct morphological differences between males. In the insects, these differences are common in the Coleoptera and especially in the superfamily Scarabaeoidea, where male dimorphism is frequently found in the Lucanidae (Matsumoto & Knell, 2017), the Dynastinae (McCullough et al., 2015) and the Scarabaeinae (Emlen et al., 2005; Simmons et al., 2007). In these animals, one morph, usually called the 'major' morph, typically invests heavily in weaponry such as horns or enlarged mandibles while the other, the 'minor' morph bears reduced or no weaponry, leading to non-linear scaling relationships between weapon size and body size (Knell, 2009; McCullough et al., 2015).

One of the best studied consequences of alternative reproductive tactics was first pointed out by Parker (1990): when

males adopt two different tactics, sneak and guard, then, in general it is expected that the sneak males should invest more into traits associated with performance under sperm competition such as testes size (Kustra & Alonzo, 2020). This arises because the risks of sperm competition are greater for sneaks, who will usually be exposed to it whenever mating, than for guards, who will prevent other males from mating with females and so experience lower risks. The degree of difference in risk between sneaks and guards will itself depend on the frequency of sneaks in the population: when there are many sneaks the risk of sperm competition experienced by guards will be higher and so the differential between guards and sneaks is predicted to be lower (Gage et al., 1995; Parker, 1990; Simmons et al., 2007). Testes size in species with alternative reproductive tactics has been studied in a variety of animals, especially fish (Kustra & Alonzo, 2020), but also Onthophagine dung beetles (Knell & Simmons, 2010; Simmons et al., 1999, 2007) where these predictions have been found broadly to be supported.

In recent years, a number of examples of arthropods which have more than two male morphs, and therefore presumably exhibit more than two types of alternative tactics, have been described. Three different male morphs have been found in some species of *Philotrypesis* fig wasp (Jousselin et al., 2004), a number of dung beetle species (Rowland & Emlen, 2009),

stag beetles (Iguchi, 2013; Matsumoto & Knell, 2017; Rowland & Emlen, 2009), a weta (Kelly & Adams, 2010), a weevil (Rowland & Emlen, 2009) and two species of harvestman (Painting et al., 2015; Powell et al., 2020). In two lucanid species, there is even evidence for four separate male morphs (Matsumoto & Knell, 2017).

Here, we analyse morphological data from males of a common Southeast Asian Onthophagine dung beetle, *Proagoderus watanabei* (Ochi & Kon, 2002), and find evidence to support a trimorphic model of male morphology in this species. We then examine the relationship between testes mass and somatic mass in the different morphs to test whether patterns of investment in traits associated with sperm competition success vary between the different morphs in a similar way to the males of dimorphic dung beetles.

Materials and methods

Both sexes of *P. watanabei* express paired head horns although these are considerably shorter even in the largest females than those of most males, many of whom bear striking long, curved horns. Both sexes also have considerable pronotal sculpting, which, in some males, develops into a single pronotal horn. In the original species description, Ochi and Kon, (2002) described the males as occurring in three types, on the basis of the size of the head and pronotal horns but made no quantitative analysis of this. Moczek et al., (2004) analysed the allometric relationship between horn length and body size in both males and females of this species with a focus on comparing the scaling relationship of the head and pronotal horns but did not focus on the degree of polymorphism shown by the males.

Male *P. watanabei* were sampled and measured as part of a community-wide study (Parrett et al., 2019). In brief, trapping was performed at the SAFE project (Ewers et al., 2011) in Sabah, Malaysian Borneo in both 2011 and 2015. Pitfall traps baited with human dung were set across a habitat gradient, ranging from undisturbed and logged tropical forests to oil palm plantations. In 2015, live trapping was performed over 24 hours to gain measurements of testes mass, whereas, in 2011, beetles were killed during trapping and stored in ethanol, with traps being left out for roughly 48 hours. In 2015, beetles were housed in plastic containers with damp tissue paper prior to processing. All individuals were processed within 72 hrs of trapping. Individuals were killed by freezing, their total body mass taken, and then their testes were dissected out immediately and weighed to the nearest 0.1 mg using a Sartorius BP2215 balance. A calibration weight was used before each measurement. A total of 182 males were measured in 2011 and 122 in 2015.

The testes dissection was carried out by firstly pinning a freshly killed animal to a wax block through the gap between the pronotum and elytra. The elytra, wings, the membrane on top of the abdomen and the guts were removed, leaving the testes and aedeagus exposed. The testes were then simply lifted out with fine forceps and placed in a weighing dish. This method is sufficiently quick that there is no need to dissect the testes into something like insect saline: the period from them initially being exposed to being weighed is usually of the order of 15–20 seconds. In all cases, beetles were photographed

from above and the side using a USB microscope and their pronotum width and horn length were measured using ImageJ v1.47 (Schneider et al., 2012).

As with all trapping methodologies, there is some potential for sampling bias here if, for example, one male morph is more likely to be trapped than another. We have no information on whether that is likely to happen in this case, but since we are not especially concerned with the numbers in each morph but rather the morphology and other traits of individual beetles, we do not regard this as a particular concern.

Statistical analysis

For the analysis of male morphology, we followed the procedure outlined in Knell (2009). After initial inspection of scatterplots of horn length vs. body size (pronotal width), we looked for evidence of bimodalism in frequency distributions of the ratios of horn length to body length. On the basis of potential morph allocations derived from these initial data explorations, we analysed the scaling relationship of head horn length to body size in log-log space by comparing the AIC score for a series of candidate models with and without the various potential morph allocations as factors, plus a sigmoidal model as used in Moczek et al., (2002). These data were collected from a number of replicate trapping stations so we used mixed effects models with replicate included as a random factor to control for the non-independence this introduces. We also fitted a breakpoint linear regression (Knell, 2009) without a random factor since methods for fitting mixed effects breakpoint models are not well developed, and a model which included year as a factor to check for temporal effects.

Testes mass data were only available for beetles collected in 2015 and were analysed by fitting a series of candidate models with and without morph as an explanatory factor. The effect of size was controlled for by including somatic mass, calculated as total mass minus testes mass, as an explanatory factor in the model. Because of multicollinearity issues, we only used somatic mass as an explanatory variable and not pronotum width, with somatic mass chosen because it is probably a more reliable indication of investment in body parts other than testes than is pronotum width. Initial exploratory analysis indicated the possibility of a curved relationship between testes mass and somatic mass so a quadratic term was included in one candidate model.

All analyses were carried out in R v4.03 (R Development Core Team, 2021) and mixed effects models were fitted using the lme4 package (Bates et al., 2015). The breakpoint regression was fitted using the Segmented package (Muggeo & Muggeo, 2017). Data visualization was done using ggplot2 (Wickham, 2016). Full code and results for the analysis and data visualization are included in the Appendix S1.

Results

Analysis of male morphology

The relationship between head horn length and body size is non-linear, and the histogram for the ratio of head horn length

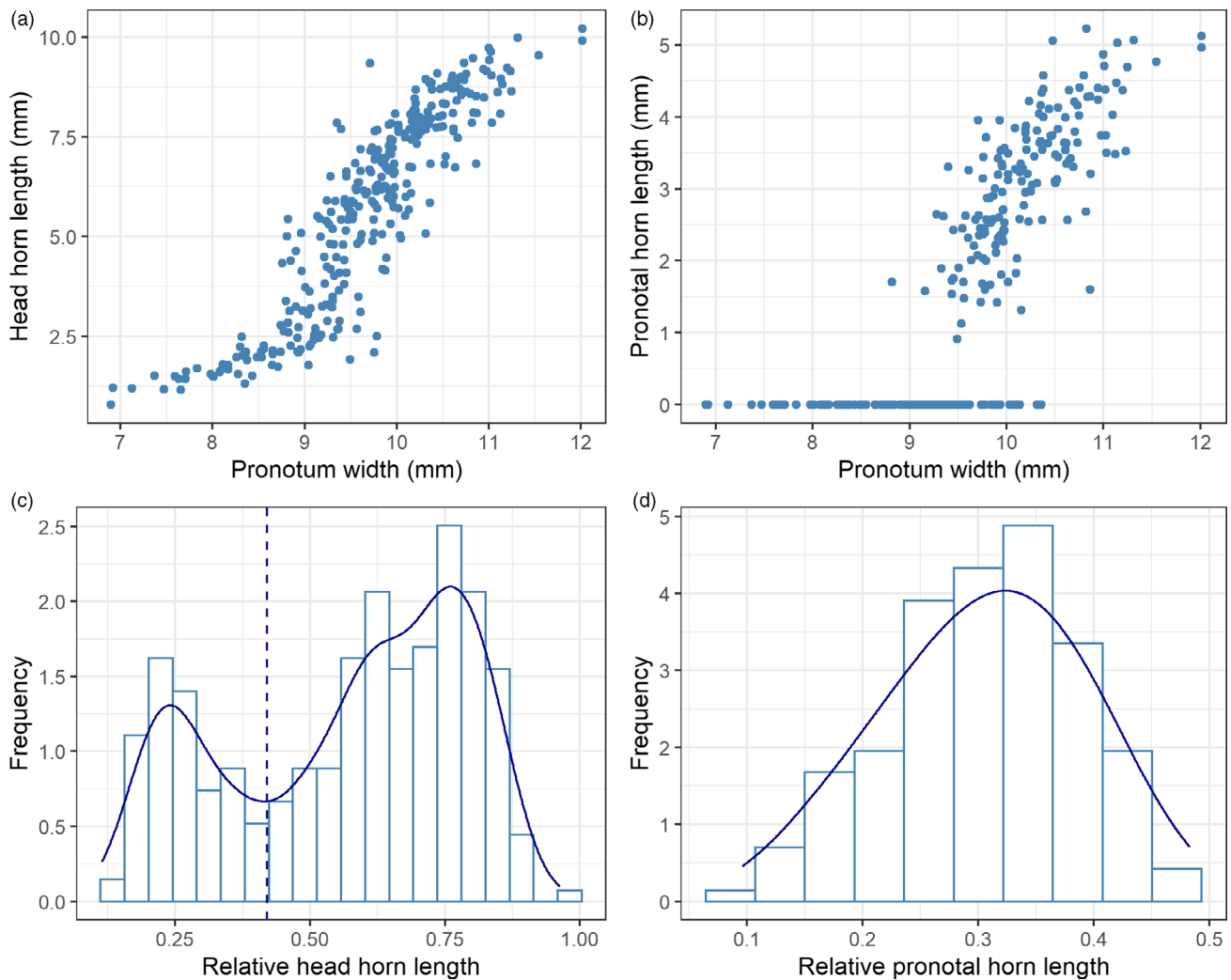


Figure 1 Horn lengths and ratios of horn length to body size (pronotum width) in *Proagoderus watanabei*. (a) Head horn length plotted against pronotum width. (b) Pronotal horn length against pronotum width. (c) Frequency distribution of the ratio of head horn length to pronotum width. The solid line shows a kernel density estimator, and the vertical dashed line shows the minimum between the two peaks at a ratio of 0.42. (d) Frequency histogram of the ratio of pronotal horn length to pronotum width, with a kernel density estimator shown as for (c).

to pronotum width is bimodal with a minimum between the two peaks at 0.42 (Fig. 1). Many beetles (45%) have no pronotal horn, and there appears to be a qualitative difference between those with and those without horns: there is only one animal in the data set with a pronotal horn which is less than 1mm long. The histogram for the ratio of pronotal horn length to pronotum width is unimodal when those animals with no pronotal horn at all are excluded. On this basis, we can divide these male beetles into three groups (Fig. 2): beetles with small head horns and no pronotal horn (*gamma* morphs), beetles with large head horns and no pronotal horn (*beta* morphs) and beetles with large head horns and a pronotal horn (*alpha* morphs).

Of our candidate set of models, the model with a discontinuous relationship split into the three morphs outlined above

has by far the lowest AIC score. The model including year only has a small Δ AIC but the top model is nested within it and so we disregard the model with year on the basis of the nesting rule (Harrison et al., 2017), making the former our preferred model for *P. watanabei* – note that including morph allocation based on the pronotal horn makes a considerable improvement to the model's goodness of fit when explaining the patterns in the head horns (Fig. 3, Table 1).

Analysis of testes mass

Out of our candidate set of models for testes mass, the AIC scores indicate the strongest support for the model with the quadratic term (T4). The two models which did not include morph (T1 & T2) were not well supported with Δ AIC scores

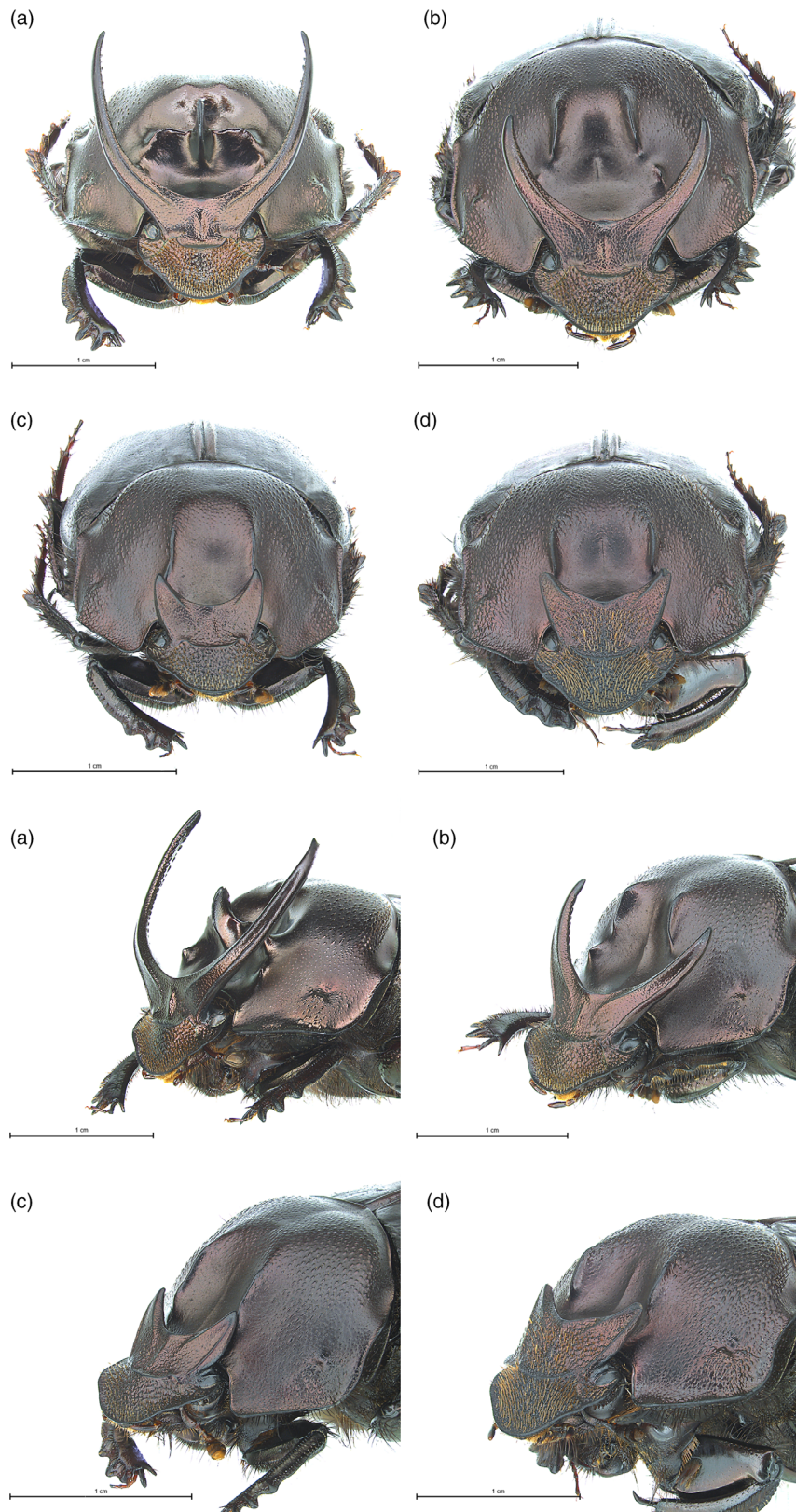


Figure 2 Frontal (top four panels) and angled (lower four panels) views of (a) an alpha male morph, (b) a beta male morph, (c) a gamma male morph and (d) a female of *Proagoderus watanabei*. Image credit Xin Rui Ong, TEE Lab, NTU Singapore.

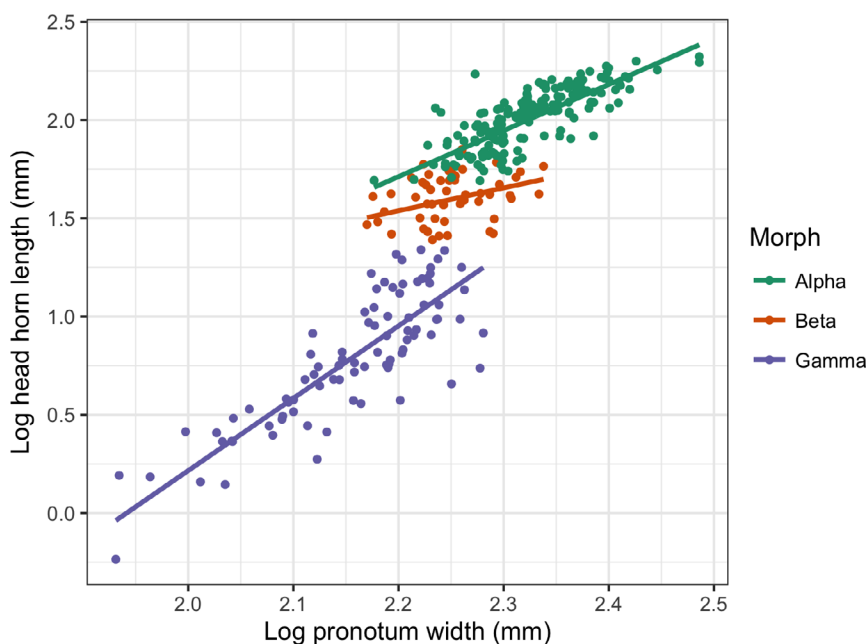


Figure 3 Scaling relationship between head horn length and pronotum width in *Proagoderus watanabei* plotted on a log-log scale. Colours indicate morph allocations. Lines show the predicted values from the fixed effects in the fitted statistical model.

Table 1 Candidate models to describe the scaling relationship between log head horn length and log pronotum width and their AIC and Δ AIC scores

Candidate Model	AIC	Δ AIC
M1: simple linear regression	-12.0	368.9
M2: polynomial regression with a quadratic term	-19.48	361.4
M3: breakpoint linear regression fitted with the Segmented R package (Muggeo & Muggeo, 2017)	-6.56	374.3
M4: four-parameter non-linear sigmoid model as used by (Moczek et al., 2002)	-102.41	278.5
M5: linear model with 'morph' as a factor and pronotum width as a continuous predictor variable, where 'morph' is a two-level factor based on head horn length.	-291.7	89.2
M6: linear model with 'morph' as a factor and pronotum width as a continuous predictor variable, where 'morph' is a two-level factor based on the presence or absence of a pronotal horn.	-153.1	227.8
M7: linear model with 'morph' as a factor and pronotum width as a continuous predictor variable, where 'morph' is a three-level factor dividing the males into three morphs on the basis of both head horn length and the presence or absence of a pronotal horn.	-380.9	0
M8: as M7 but with 'year' added as a factor.	-380.1	0.8

All models except M3 were fitted as mixed effects models with replicate as a random factor.

Table 2 Candidate models to describe the relationship between testes mass, somatic mass and morph, with their AIC and Δ AIC scores

Candidate Model	AIC	Δ AIC
T1: testes mass explained by somatic mass only	-1348.9	13.6
T2: testes mass explained by somatic mass plus a quadratic term for somatic mass.	-1349.5	13.03
T3: testes mass explained by main effects of morph and somatic mass	-1356.0	6.58
T4: testes mass explained by main effects and interaction of morph and somatic mass	-1355.9	6.65
T5: testes mass explained by main effects of morph and somatic mass plus a quadratic term for somatic mass.	-1362.6	0

of >13 in both cases. Models with morph as an explanatory variable but without the quadratic term (T3 and T4) have weak support with a Δ AIC of about 6.6 in both cases (Table 2). The nesting rule (Harrison et al., 2017) suggests that we should discount model T4, so we conclude that there is strong support for an effect of both morph and somatic mass on testes mass, slightly weaker support for a quadratic effect of somatic mass and little support for an interaction between morph and somatic mass.

Figure 4 shows testes mass plotted against somatic mass for the three morphs. In all morphs, testes mass increases with

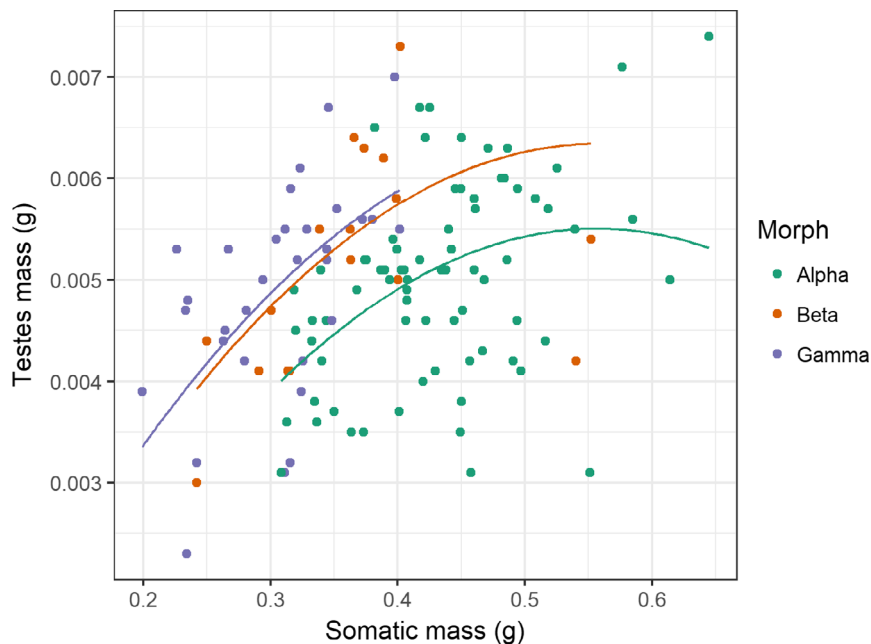


Figure 4 The relationship between somatic mass and testes mass for the three different morphs. Somatic mass is calculated as total body mass minus testes mass. The lines represent predicted values from the fixed effects component of the best supported fitted model.

somatic mass but this increase declines as the animals get larger, with the slope of the relationship approximating to zero for the largest males. Beta and gamma morphs seem to be investing in a similar way in testes, whereas alpha morphs have testes that are roughly 0.8-1mg lighter for any given body size, meaning that the larger beta and gamma individuals tend to have testes that are as large, or larger than those of alpha males, despite the latter often being substantially larger overall.

Discussion

On the basis of the scaling relationships of weapons and body size, we find that *P. watanabei* males group into three separate morphs, and that those males with large head horns and pronotal horns, the alpha morph, invest relatively less in testes mass than do either the beta males (large head horns but no pronotal horn) or the gamma males (small head horns and no pronotal horn). Previous studies of trimorphic arthropod males have analysed differences in the scaling relationships of single weapon traits only (Matsumoto & Knell, 2017; Painting et al., 2015; Powell et al., 2020; Rowland & Emlen, 2009). The males of many beetle species carry horns on both their heads and their pronota (Emlen, 2008; Emlen et al., 2005; Knell, 2011), and we suggest that further study of some of these might reveal similar complex polymorphisms to the one described here.

Our finding of complex scaling relations for the head horns and trimorphic males in *P. watanabei* contrasts with the previous investigation of male horn scaling in *P. watanabei* which concluded that the scaling relationship for the head horns was

best described by a linear model and that males are essentially monomorphic (Moczek et al., 2004). There are also similarities between both data sets: for example, Moczek et al., (2004) also noted a clear binary difference between males which do or do not express prothoracic horns and that the allometry of head horns was best described by a non-linear relationship. By using our considerably larger data set (304 compared to 71), we were able to detect a discontinuous relationship between head horn length and pronotum width, and by assigning a binary value for prothoracic horn expression, we were able to allocate males to a third ‘intermediate’ morph (i.e. beta males), confirming the qualitative description of three male morphs in this beetle suggested by Ochi and Kon (2002).

Genetically based trimorphisms have been described from a number of lizard species (Sinervo et al., 2007; Sinervo & Lively, 1996), from one bird species (the Ruff, *Philomachus pugnax*, (Küpper et al., 2016) and the isopod *Paracerceis sculpta* (Shuster & Wade, 1991). The recently described arthropod trimorphisms are, however, likely to be conditional strategies rather than genetic polymorphisms (Rowland et al., 2017), but to date, we know little of their biology beyond the fact of their existence. The three morphs of male *Phylotrypesis* fig wasps appear from their morphology to have clear roles as large, aggressive male, small sneak male and winged disperser (Jousselin et al., 2004), but the roles played by the different morphs in other examples are less clear. Painting et al., (2015) described morph-specific behaviour during contests in the harvestman *Pantopsalis cheliferoideis* but we know little further regarding questions like whether the different morphs in these animals behave differently. This makes interpretation of the

data described here somewhat difficult, but nonetheless, we can refer to what we know of dimorphic species to help us understand these patterns.

The aggressive tactics adopted by large, well-armed beetles and the sneak tactics used by small, unarmed males are well known from dimorphic species, and it is likely that the alpha and gamma males of *P. watanabei* behave in similar ways. But what of the beta males? One possibility is that they might adjust their reproductive behaviours plastically depending on context: using their horns and adopting aggressive behaviours to monopolize females in the presence of gamma males, and using sneak tactics in the presence of alpha males. The function of the prothoracic horn is not known but based on the pronotum shape of males which do not express a prothoracic horn (Fig. 2), it seems likely that it acts as a signal to other males, conveying information on overall body size.

The mass of insect testes is determined by a complex suite of factors including, for example, adult nutrition (Reaney & Knell, 2015) and recent mating history (Greenway et al., 2020), but the relationship between overall testes size and the risk of sperm competition is probably the strongest such pattern (Simmons, 2001). Horned beetles are known to trade-off horn size against testes mass (Simmons & Emlen, 2006), and so, the relative amount of resource invested in these traits is therefore likely to reflect the relative selective benefits of traits which increase success in contests and traits which increase sperm competitiveness. Previous work on scarab species with dimorphic males has found that major males tend to have smaller testes for their body size than minor males (Simmons et al., 1999, 2007). This is seen as an adaptation to different degrees of risk of sperm competition among these morphs, and it is likely that the patterns found here reflect this as well. It seems, therefore, that in this species, the alpha males are at reduced risk of sperm competition than the beta and gamma males, with increased investment in weaponry bringing greater selective benefits for these animals. On this basis, we can speculate that alpha males, as with major males in dimorphic species, are able to defend females against most rivals thereby reducing the risk of sperm competition.

Beta males of *P. watanabei* invest in traits that function in both physical contests (horns) and in sperm competition (testes). If they are less able to defend females than alphas, then their risk of sperm competition will be increased since they will more often be ousted by rival males who will then mate with the female that they were defending. The gamma males, with reduced horns, are likely to be sneak mating specialists and so will also experience high levels of sperm competition. Why there is no difference between beta and gamma males is not currently clear, and it must be remembered that testes mass is not the only variable that is important in determining the outcome of sperm competition, with many males adjusting their ejaculate depending on circumstances (Simmons, 2001). It is possible that, overall, there is no difference because the balance of costs (resources used) and benefits (better outcomes when exposed to sperm competition) is the same for both morphs. The alternative is that because of a type II error (i.e. a 'false negative'), we have failed to detect an existing small difference. There is obvious potential here for further research to determine what behavioural

differences exist between male morphs and to describe the function of different horn types in *P. watanabei*.

Acknowledgements

We are grateful to the Land use Options for Maintaining Biodiversity and eKosystem functions (LOMBOK) Project research assistants for their assistance in the field. We thank Marx Lim and Xin Rui Ong, TEE lab., for the photographs in Figure 2 and Arthur Chung, Glen Reynolds and SEARRP, The SAFE Project, The Maliau Basin Management Committee, and the Sabah Biodiversity Council, Malaysia, for their support in obtaining permits and research permissions. Samples were collected under SaBC access licence number JKM/MBS.1000-2/2 (381) to EMS and JMP. EMS was supported by a UK Natural Environment Research Council grant (NE/K016407/1), and NTU start-up grant. JMP was supported by a QMUL postgraduate studentship and funding from QMPGRF.

References

- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, Articles*, **67**, 1–48.
- Emlen, D. J. (2008). The evolution of animal weapons. *Annual Review of Ecology and Systematics*, **39**, 387–413.
- Emlen, D. J., Marangelo, J., Ball, B., & Cunningham, C. W. (2005). Diversity in the weapons of sexual selection: horn evolution in the beetle genus *Onthophagus* (Coleoptera: Scarabaeidae). *Evolution*, **59**, 1060–1084.
- Ewers, R. M., Didham, R. K., Fahrig, L., Ferraz, G., Hector, A., Holt, R. D., Kapos, V., Reynolds, G., Sinun, W., Snaddon, J. L., & Turner, E. C. (2011). A large-scale forest fragmentation experiment: The Stability of Altered Forest Ecosystems Project. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**, 3292–3302.
- Gage, M. J. G., Stockley, P., & Parker, G. A. (1995). Effects of alternative male mating strategies on characteristics of sperm production in the Atlantic salmon (*Salmo salar*): Theoretical and empirical investigations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **350**, 391–399.
- Greenway, E. V. G., Cirino, L. A., Wilner, D., Somjee, U., Anagnostou, M.-E., Hepple, R. T., & Miller, C. W. (2020). Extreme variation in testes size in an insect is linked to recent mating activity. *Journal of Evolutionary Biology*, **33**, 142–150.
- Gross, M. R. (1996). Alternative reproductive strategies and tactics: Diversity within sexes. *Trends in Ecology & Evolution*, **11**, 92–98.
- Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C., Robinson, B., Hodgson, D. J., & Inger, R. (2017). Best practice in mixed effects modelling and multi-model inference in ecology. *PeerJ*, **6**, e4794.
- Iguchi, Y. (2013). Male mandible trimorphism in the stag beetle *Dorcus rectus* (Coleoptera: Lucanidae). *European Journal of Entomology*, **110**, 159–163.

- Jousselin, E., van Noort, S., & Greeff, J. M. (2004). Labile male morphology and intraspecific male polymorphism in the *Philotrypesis* fig wasps. *Molecular Phylogenetics and Evolution*, **33**, 706–718.
- Kelly, C. D., & Adams, D. C. (2010). Sexual Selection, Ontogenetic Acceleration, and Hypermorphosis Generates Male Trimorphism in Wellington Tree Weta. *Evolutionary Biology*, **37**, 200–209.
- Knell, R. J. (2009). On the analysis of non-linear allometries. *Ecological Entomology*, **34**, 1–11.
- Knell, R. (2011). Male contest competition and the evolution of weapons. In L. W. Simmons & T. Ridsdill-Smith (Eds.), *Ecology and evolution of dung beetles* (pp. 47–64). John Wiley & Sons, Ltd.
- Knell, R. J., & Simmons, L. W. (2010). Mating tactics determine patterns of condition dependence in a dimorphic horned beetle. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 2347–2353.
- Küpper, C., Stocks, M., Risse, J. E., Dos Remedios, N., Farrell, L. L., McRae, S. B., Morgan, T. C., Karlionova, N., Pinchuk, P., Verkuil, Y. I., Kitaysky, A. S., Wingfield, J. C., Piersma, T., Zeng, K., Slate, J., Blaxter, M., Lank, D. B., & Burke, T. (2016). A supergene determines highly divergent male reproductive morphs in the ruff. *Nature Genetics*, **48**, 79–83.
- Kustra, M. C., & Alonzo, S. H. (2020). Sperm and alternative reproductive tactics: A review of existing theory and empirical data. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **375**, 20200075.
- Matsumoto, K., & Knell, R. J. (2017). Diverse and complex male polymorphisms in *Odontolabis* stag beetles (Coleoptera: Lucanidae). *Scientific Reports*, **7**, 16733.
- McCullough, E. L., Ledger, K. J., O'Brien, D. M., & Emlen, D. J. (2015). Variation in the allometry of exaggerated rhinoceros beetle horns. *Animal Behavior*, **109**, 133–140.
- Moczek, A. P., Brühl, C. A., & Krell, F.-T. (2004). Linear and threshold-dependent expression of secondary sexual traits in the same individual: insights from a horned beetle (Coleoptera: Scarabaeidae). *Biological Journal of the Linnean Society*, **83**, 473–480.
- Moczek, A. P., Hunt, J., Emlen, D. J., & Simmons, L. W. (2002). Threshold evolution in exotic populations of a polyphenic beetle. *Evolutionary Ecology Research*, **4**, 587–601.
- Muggeo, V. M. R., & Muggeo, M. V. M. R. (2017). Package 'segmented'. *Biometrika*, **58**, 516.
- Ochi, T., & Kon, M. (2002). *A new horned species of the genus Onthophagus (Coleoptera, Scarabaeidae) from Sabah, Borneo. Spec. Bull. Jpn. Soc. Coleopterol.*
- Oliveira, R. F., Taborsky, M., & Brockmann, J. H. (2008). *Alternative reproductive tactics: An integrative approach*. Cambridge University Press.
- Painting, C. J., Probert, A. F., Townsend, D. J., & Holwell, G. I. (2015). Multiple exaggerated weapon morphs: A novel form of male polymorphism in harvestmen. *Scientific Reports*, **5**, 16368.
- Parker, G. A. (1990). Sperm competition games: sneaks and extra-pair copulations. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **242**, 127–133.
- Parrett, J. M., Mann, D. J., Chung, A. Y. C., Slade, E. M., & Knell, R. J. (2019). Sexual selection predicts the persistence of populations within altered environments. *Ecology Letters*, **83**, 238.
- Powell, E. C., Painting, C. J., Hickey, A. J., & Holwell, G. I. (2020). Defining an intrasexual male weapon polymorphism in a New Zealand harvestman (Opiliones: Neopilionidae) using traditional and geometric morphometrics. *Biological Journal of the Linnean Society*, **130**(2), 395–409.
- R Development Core Team (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Reaney, L. T., & Knell, R. J. (2015). Building a beetle: How larval environment leads to adult performance in a horned beetle. *PLoS One*, **10**, e0134399.
- Rowland, J. M., & Emlen, D. J. (2009). Two thresholds, three male forms result in facultative male trimorphism in beetles. *Science*, **323**, 773–776.
- Rowland, J. M., Qualls, C. R., & Buzatto, B. A. (2017). A model for conditional male trimorphisms. *Journal of Theoretical Biology*, **419**, 184–192.
- Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, **9**, 671–675.
- Shuster, S. M., & Wade, M. J. (1991). Equal mating success among male reproductive strategies in a marine isopod. *Nature*, **350**, 608–610.
- Simmons, L. W. (2001). *Sperm competition and its evolutionary consequences in the insects*. Princeton University Press.
- Simmons, L. W., & Emlen, D. J. (2006). Evolutionary trade-off between weapons and testes. *Proceedings of the National Academy of Sciences*, **103**, 16346–16351.
- Simmons, L. W., Emlen, D. J., & Tomkins, J. L. (2007). Sperm competition games between sneaks and guards: a comparative analysis using dimorphic male beetles. *Evolution*, **61**, 2684–2692.
- Simmons, L. W., Tomkins, J. L., & Hunt, J. (1999). Sperm competition games played by dimorphic male beetles. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **266**, 145–150.
- Sinervo, B., Heulin, B., Surget-Groba, Y., Clobert, J., Miles, D. B., Corl, A., Chaine, A., & Davis, A. (2007). Models of density-dependent genic selection and a new rock-paper-scissors social system. *American Naturalist*, **170**, 663–680.
- Sinervo, B., & Lively, C. M. (1996). The rock–paper–scissors game and the evolution of alternative male strategies. *Nature*, **380**, 240–243.
- Taborsky, M., Oliveira, R. F., & Brockmann, H. J. (2008). The evolution of alternative reproductive tactics: concepts and questions. *Alternative Reproductive Tactics: An Integrative Approach*, **1**, 21.

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*.

Supplementary Material: Code for downloading data from the SAFE project data repository and for all of the analyses carried out for this manuscript.

Supporting Information

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