

Research



Cite this article: Graham ZA, Garde E, Heide-Jørgensen MP, Palaoro AV. 2020 The longer the better: evidence that narwhal tusks are sexually selected. *Biol. Lett.* **16**: 20190950. <http://dx.doi.org/10.1098/rsbl.2019.0950>

Received: 24 December 2019

Accepted: 24 February 2020

Subject Areas:

behaviour, ecology, evolution

Keywords:

animal weapons, animal signals, sexual selection, exaggerated trait, allometry

Author for correspondence:

Zackary A. Graham

e-mail: zgraham1@asu.edu

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.4880298>.

Evolutionary biology

The longer the better: evidence that narwhal tusks are sexually selected

Zackary A. Graham¹, Eva Garde², Mads Peter Heide-Jørgensen² and Alexandre V. Palaoro³

¹School of Life Sciences, Arizona State University, Tempe, AZ 85287, USA

²Greenland Institute of Natural Resources, Box 570, DK-3900 Nuuk, Greenland

³LUTA do Departamento de Ecologia e Biologia Evolutiva, UNIFESP, Brazil

ZAG, 0000-0002-6132-2885; AVP, 0000-0002-8629-0728

Once thought to be the magical horn of a unicorn, narwhal tusks are one of the most charismatic structures in biology. Despite years of speculation, little is known about the tusk's function, because narwhals spend most of their lives hidden underneath the Arctic ice. Some hypotheses propose that the tusk has sexual functions as a weapon or as a signal. By contrast, other hypotheses propose that the tusk functions as an environmental sensor. Since assessing the tusks function in nature is difficult, we can use the morphological relationships of tusk size with body size to understand this mysterious trait. To do so, we collected morphology data on 245 adult male narwhals over the course of 35 years. Based on the disproportional growth and large variation in tusk length we found, we provide the best evidence to date that narwhal tusks are indeed sexually selected. By combining our results on tusk scaling with known material properties of the tusk, we suggest that the narwhal tusk is a sexually selected signal that is used during male–male contests.

1. Introduction

Protruding from the head and reaching nearly 3 m in length, the tusks of narwhals (*Monodon monoceros*) are one of the most charismatic structures in biology. Despite immense speculation, the function of the tusk remains unclear. Based on the tusk's anatomy, a recent study proposed that narwhal tusks sense chemical changes in their environment [1]. By contrast, reports of head scarring, broken tusks and tusks impaled in the sides of male narwhals suggest that males use their tusks as weapons during aggression [2–4]. Observations of 'tusking', where two narwhals cross and rub their tusks together, suggest that the tusk is used for communication during intra- or intersexual interactions [4] (figure 1). Unfortunately, narwhals spend most of their lives in inaccessible areas of the Arctic which makes these behaviours nearly impossible to study [3]. Additionally, almost all male narwhals are tusked, while females rarely develop a tusk [2,5]. Importantly, although narwhal tusks are generally sexually dimorphic, this sexual dimorphism alone does not provide sufficient evidence for sexual selection, because other selective pressures, such as differences in foraging behaviour, can lead to sexual dimorphism as well (i.e. ecological selection; [6–8]). Since we currently have no way of directly assessing the function of the tusk in nature, we can use the morphological relationships of tusk size with body size to better understand the function of this exaggerated trait [9,10].

The scaling relationship of a trait with body size has historically been used to provide evidence regarding the type of selection acting on that trait [11]. When comparing individuals of the same age, sexually selected traits often exhibit disproportional growth, i.e. hyperallometry [12]. That is, for a given body size, sexually selected traits are often larger than expected in the largest

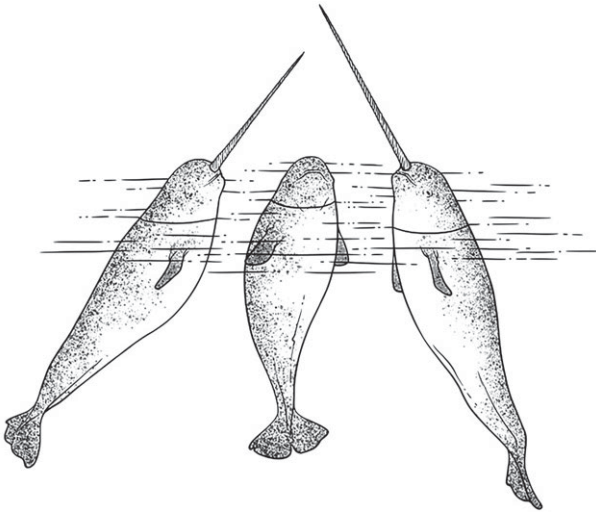


Figure 1. This narwhal (*Monodon monoceros*) behaviour, called tusking, has been recorded between two males with a female present, and with two or more males with no female present. Visual observations and photographs of this behaviour were used to recreate this image.

individuals [11,13–19]. Using a dataset of 35 narwhals of different ages, Best [20] proposed that narwhal tusks are sexually selected solely based on tusk hyperallometry. However, we now know that non-sexual traits, such as lizard cranial horns, can also scale hyperallometrically without being sexually selected [9,17,21]. Furthermore, Best [20] combined juveniles and adults in one analysis, which limits the conclusions because reaching sexual maturity influences trait growth (i.e. ontogenetic allometry [22]). Therefore, a first step towards understanding the function of the narwhal tusk should be to examine how the tusk scales with the body size of adults only (i.e. static allometry).

A second step that is not addressed in previous studies is to compare the variation between the tusk and a trait that is selected for non-sexual functions [9,10]. Sexual selection typically amplifies individual differences, because individuals with more resources are expected to produce larger than average traits, while individuals with less resources produce smaller than average traits [23,24]. Conversely, if a trait that is vital for survival is smaller or larger than average, individuals are expected to perform worse and suffer fitness costs [25]. Thus, when we compare a putatively sexually selected trait to a non-sexually selected trait, we expect the trait that is under sexual selection to be more variable than the trait selected for non-sexual functions [10]. Since some of these methods have already been used to understand the function of morphological traits in extinct species [10,26–29] and were validated in extant species [10], we can apply these methods to understand enigmatic traits such as the narwhal tusk.

Here, we studied the morphological scaling and variance of 245 adult male narwhals, collected from 1983 to 2018. First, we examined the scaling relationship between body size and tusk length and compared it to the scaling relationship between body size and our reference trait, fluke width. If the tusk is sexually selected, we expect a higher variance and a steeper scaling in comparison to our reference trait. If the tusk, however, is selected for non-sexual functions, we expect equal variance and a similar scaling to the reference trait.

2. Material and methods

(a) Data collection

Morphology data (body length, fluke width and tusk length) and sex were collected from narwhals in Greenland from 1983 to 2018. Samples and data were collected through the Greenland Institute of Natural Resources (GINR) using a narwhal specific sampling scheme prepared by the GINR. The sex of the animal was determined either by the reproductive organs or by the presence (male) or absence (female) of a tusk. Male narwhals were considered adults when they reached 400 cm [30]. For our analyses, we only included adult males because we wanted to investigate the scaling relationships of individuals of the same age (i.e. static allometry [22])—adding sexually immature individuals would change the properties of the scaling relationship (i.e. ontogenetic allometry [22]).

(b) Statistical analysis

We predicted that if the male tusk is sexually selected, the tusk would have a steeper scaling value (greater values of slope, β) when compared to the fluke width scaling value. To test this hypothesis, we first ran three separate models for each trait (tusk length and fluke width): (i) a linear model, (ii) a quadratic model and (iii) a nonlinear exponential model to determine which model best described our data. For each trait, we then compared the fit of the three models using AIC [31]. The model with the lowest AIC value was used as the best fit model (using the threshold of $\Delta\text{AIC} > 2$ to discard the other models), and we used the parameters estimated by that model on further analyses. If the models tied ($\Delta\text{AIC} < 2$), we used the simplest model. In all models, we used the size of the trait (i.e. tusk or fluke) as our dependent variable and body length as our independent variable. After model selection, we compared the slopes of models with their 95% confidence intervals. We conducted all analyses using base R for linear and quadratic models, the *nlme* package for the exponential model [32] and *bbmle* package for the AIC tests [33].

We also predicted that if the narwhal tusk is sexually selected, we expect greater variation in tusk length compared to the variation in fluke width. To test this hypothesis, we used two analyses. First, we calculated the coefficients of variation (CV) for each trait and bootstrapped the CV to have a measure of reliability. We bootstrapped the CV using a standard non-parametric formula by sampling our data with replacement and calculating the CV. We performed 10 000 iterations and calculated the confidence interval of the CV using the *boot* package [34]. Second, we built two linear mixed regression models with different error structures and compared how they fit the data. Standard regression models use a unitary error structure (e.g. variance of the entire dataset) to calculate the best fit models. However, some traits might have higher variance than other traits, and in these cases, models tend to be ‘heteroskedastic’. Thus, we also built a second model that use two error structures: one error structure taken from tusk length data and another error structure taken from fluke width data [35]. Both models use trait size as the dependent variable, and body length, the type of trait (i.e. tusk or fluke) and their interactions as the independent variables. In our second model, we used individual as a random effect because tusk length and fluke width came from the same animal. Error structure models were compared using the same AIC thresholds from the allometry analysis.

3. Results

Tusk length was best fit by a quadratic model, whereas fluke width was best fit by a linear model (table 1 and figure 2a).

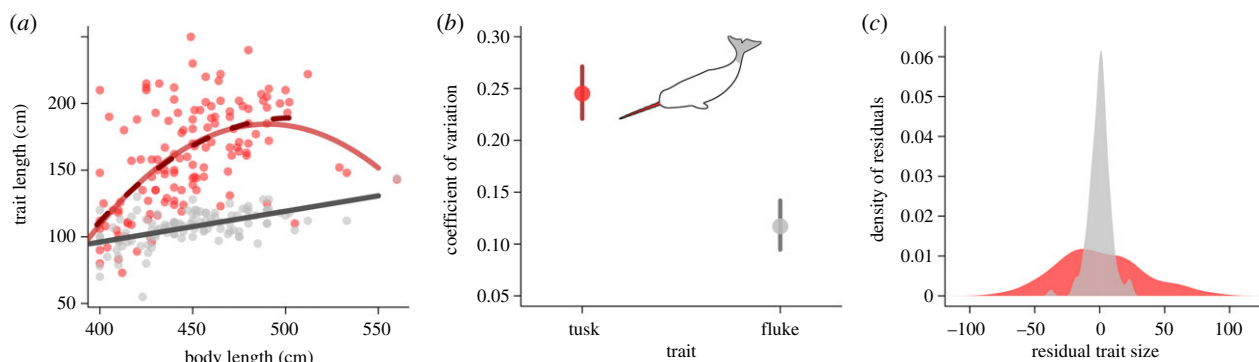


Figure 2. (a) The scaling relationship between narwhal (*Monodon monoceros*) body size and tusk length (solid red) demonstrates the steep scaling of the tusk ($y = -2036.5 + 9.06 \times x - 0.009 \times x^2$). When we removed three outliers that likely drive the downward slope of our data, an asymptote of tusk allocation appears (dashed red; $y = -1640 + 7.26 \times x - 0.007 \times x^2$). Fluke width (grey), on the other hand, demonstrates the shallow scaling of a non-sexually selected trait ($y = 3.689 + 0.23 \times x$). (b,c) Coefficients of variation and residual variation for tusk length (red) and fluke width (grey) demonstrates considerable variation in tusk length, but not fluke width, consistent with the hypothesis that the tusk is sexually selected.

Table 1. Model comparisons for tusk length allometry, fluke width allometry and variance error structures. For each model, the number of parameters (k), the log-likelihood (ll), the Akaike information criterion (AIC) and the Akaike weight (w) are reported. Linear model: $y \sim a + b \times x$; quadratic model: $y \sim a + b \times x + c \times x^2$; exponential model: $y \sim a + \exp(b \times x)$.

	k	log-likelihood	AIC	Δ AIC	w
(a) tusk length allometry					
quadratic model	4	−649.0	1306.1	0.0	1
linear model	3	−658.8	1323.6	17.6	<0.0001
exponential model	3	−664.4	1334.8	28.8	<0.0001
(b) fluke width allometry					
linear model	3	−432.1	870.1	0.0	0.550
quadratic model	4	−431.5	870.9	0.8	0.363
exponential model	3	−433.9	873.8	3.7	0.088
(c) variance error structure					
two error structures	8	−1095.4	2206.8	0.0	1
common error structure	7	−1156.2	2326.5	119.7	<0.0001

Based on the best fit models, tusk length increased with body size with a strong, hyperallometric slope ($\beta_1 = 9.06$ [5.36; 12.75, 95% CI], β_2 (or x^2) = -0.009 [−0.013; −0.005]; figure 2a). Interestingly, only three narwhals were larger than 5.2 m, and all these individuals had very small tusks (figure 2a). To assess the influence of these three individuals in our analysis, we reran the models without these three individuals, but results were similar ($\beta_1 = 7.26$ [1.25; 13.26, 95% CI], $\beta_2 = -0.007$ [−0.013; −0.0005]; figure 2a, dashed line). By contrast, fluke width increased with body size with a much shallower slope ($\beta_1 = 0.23$ [0.16; 0.29]; figure 2a). That is, larger males allocate relatively more into tusk length than smaller males. Our reference trait (fluke width), on the other hand, also increased as body size increased, although with a much shallower slope (table 1 and figure 2a). Furthermore, tusk length had a higher CV than fluke width (figure 2b), and the residuals of tusk length were also larger than the residuals of fluke width (table 1 and figure 2c).

4. Discussion

The hyperallometric scaling and large variation in the tusks supports the hypothesis that narwhal tusks are sexually

selected (figure 2; electronic supplementary material, figure S1 and table S1). Sexually selected signals used in male–male competition are more likely to exhibit hyperallometry when compared to other sexually selected traits, because the information being signalled is simple: ‘I am bigger than you’ [9]. To convey this message, males exaggerate the size of their signals which facilitate the detection of size discrepancies between individuals, reducing the likelihood of engaging in potentially dangerous fights [9]. Using the tusk as a signal might explain the tusking behaviour observed in male narwhals (figure 1; [4]). Tusking may be a ritualized behaviour used to assess the fighting ability of opponents and avoid potentially costly fights [36]. In this scenario, fully fledged aggression should be rare, because competitors should attempt to settle contests through signalling [37,38].

However, using the tusk purely as a signal does not explain why head scarring and broken tusks occur. Adult male narwhals possess significantly more scars on their heads compared to juvenile males and females [3,4], similar to the scarring found in other cetaceans that are known to fight [39,40]. Similar injury patterns are also common in other animals that possess signals that also function as weapons [36,41,42]. Additionally, 40–60% of adult males have damaged or broken tusks [2,4], which should be common if

narwhals used their tusks in fights [43]. Interestingly, tusks cannot withstand 'ramming' forces, which suggest that the tusk is not used for direct stabs [44,45]. However, tusks can withstand lateral strikes without breaking, which might explain the head scarring [44,45]. Considering that the tusk length scaling reaches an asymptote, then tusk length may be constrained by breaking when becoming too long [46] or there are large metabolic costs incurred when individuals produce and maintain massive tusks (but see [47]). Indeed, biomechanical limits to the size and elaboration of sexually selected traits are common [48–50]. Thus, when combining our results of tusk hyperallometry with the known material properties of narwhal tusks, it suggests that the tusk is likely used as an aggressive signal during contests.

An alternative hypothesis is that the tusk functions as a signal during mate choice [9]. Signals used in mate choice should also scale hyperallometrically based on a similar logic to aggressive signals. For example, male fiddler crab claws scale hyperallometrically and are used both in mate attraction and as aggressive signals during territorial disputes [51]. Moreover, if the tusk plays a role in mate choice, we may expect that the size of the tusk gives information about the quality of the wielder. If only the highest quality males produce and adorn larger-than-average tusks, then it can also serve as an honest signal to females or males (i.e. handicap signal, [23]). However, little is currently known about mating behaviour and the role of mate choice in narwhals.

Importantly, despite being sexually selected, the tusk might also possess other functions outside of sexual signalling or aggression. For example, the sexually selected claws of many crustaceans function as weapons during territorial contests, but they also can function as signals in male–male combat and female mate choice [41,52–54]. Additionally, the same claws play a role in chemical communication and prey capture [55,56]. In narwhals, the tusk might also possess other functions related to sensing the environment and in rare cases, catching prey [1]. Thus, although we have supported

the hypothesis that the tusk is sexually selected, large tusks may benefit narwhals in non-sexual acts that we are currently unaware of. Proclaiming that a trait has a single function can hinder our understanding of trait evolution, because the multiple hypothesis for a trait's function are not always mutually exclusive.

Overall, our evidence supports the hypothesis that the tusk functions both as a sexually selected weapon and sexually selected signal during male–male contests. However, further evaluations of the narwhal's ecology are warranted. Because female narwhals sometimes develop a tusk, investigations into anatomical, morphological and behavioural differences between tusked males and tusked females may shed light on the tusk's importance during non-sexual functions. Furthermore, population and seasonal differences into tusk investment may reveal the tusks relative importance during pre- and post-copulatory mating. Lastly, continuing efforts to collect behavioural data on narwhals (e.g. using drones) will provide new insights into the social structure and behaviour of this unique species. Although we do not discard other possibilities, based on the large amount of morphological data we gathered here, we suggest that the narwhal tusk likely functions as a signal and a weapon during aggressive disputes.

Data accessibility. R scripts will be made available upon request. Raw data have been archived in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.s1rn8pk43> [57].

Authors' contributions. This study was conceived by Z.A.G. and A.V.P.; E.G. and M.P.H.J. collected the data; Z.A.G. and A.V.P. analysed the data and drafted the manuscript. All authors edited the manuscript. All authors approved the final version of the manuscript and agree to be held accountable for the content therein.

Competing interests. We declare we have no competing interests.

Funding. We received no funding for this study.

Acknowledgements. We thank Michael Angilletta for helpful comments and discussions that have significantly improved the manuscript.

References

1. Nweeia MT *et al.* 2014 Sensory ability in the narwhal tooth organ system. *Anat. Rec.* **297**, 599–617. (doi:10.1002/ar.22886)
2. Porsild MP. 1922 Scattered observations on narwhals. *J. Mammal.* **3**, 8–13. (doi:10.2307/1373444)
3. Gerson HB, Hickie JP. 1985 Head scarring on male narwhals (*Monodon monoceros*): evidence for aggressive tusk use. *Can. J. Zool.* **63**, 2083–2087. (doi:10.1139/z85-306)
4. Silverman HB, Dunbar MJ. 1980 Aggressive tusk use by the narwhal (*Monodon monoceros* L.). *Nature* **284**, 57–58. (doi:10.1038/284057a0)
5. Hay KA. 1984 *The life history of the narwhal (Monodon monoceros L.) in the eastern Canadian Arctic*. Montreal, Canada: McGill University.
6. Temeles EJ, Pan IL, Brennan JL, Horwitt JN. 2000 Evidence for ecological causation of sexual dimorphism in a hummingbird. *Science*. **289**, 441–443. (doi:10.1126/science.289.5478.441)
7. Slatkin M. 1984 Ecological causes of sexual dimorphism. *Evolution*. **38**, 622–630. (doi:10.1111/j.1558-5646.1984.tb00327.x)
8. Shine R. 1989 Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Q. Rev. Biol.* **64**, 419–461. (doi:10.1086/416458)
9. Eberhard WG, Rodríguez RL, Huber BA, Speck B, Miller H, Buzatto BA, Machado G. 2018 Sexual selection and static allometry: the importance of function. *Q. Rev. Biol.* **93**, 207–250. (doi:10.1086/699410)
10. O'Brien DM, Allen CE, Van Kleeck MJ, Hone D, Knell R, Knapp A, Christiansen S, Emlen DJ. 2018 On the evolution of extreme structures: static scaling and the function of sexually selected signals. *Anim. Behav.* **144**, 95–108. (doi:10.1016/j.anbehav.2018.08.005)
11. Kodric-Brown A, Sibly RM, Brown JH. 2006 The allometry of ornaments and weapons. *Proc. Natl Acad. Sci. USA* **103**, 8733–8738. (doi:10.1073/pnas.0602994103)
12. Huxley JS. 1924 Constant differential growth-ratios and their significance. *Nature*. **114**, 895–896. (doi:10.1038/114895a0)
13. Kawano K. 1997 Cost of evolving exaggerated mandibles in stag beetles (Coleoptera: Lucanidae). *Ann. Entomol. Soc. Am.* **90**, 453–461. (doi:10.1093/aesa/90.4.453)
14. Emlen DJ, Nijhout HF. 2000 The development and evolution of exaggerated morphologies in insects. *Annu. Rev. Entomol.* **45**, 661–708. (doi:10.1146/annurev.ento.45.1.661)
15. McCullough EL, Ledger KJ, O'Brien DM, Emlen DJ. 2015 Variation in the allometry of exaggerated rhinoceros beetle horns. *Anim. Behav.* **109**, 133–140. (doi:10.1016/j.anbehav.2015.08.013)
16. Miller CW, Emlen DJ. 2010 Across- and within-population differences in the size and scaling relationship of a sexually selected trait in *Leptoscelsis tricolor* (Hemiptera: Coreidae). *Ann. Entomol. Soc. Am.* **103**, 209–215. (doi:10.1603/AN09039)

17. Bonduriansky R. 2007 Sexual selection and allometry: a critical reappraisal of the evidence and ideas. *Evolution*. **61**, 838–849. (doi:10.1111/j.1558-5646.2007.00081.x)
18. Simmons LW, Tomkins JL. 1996 Sexual selection and the allometry of earwig forceps. *Evol. Ecol.* **10**, 97–104. (doi:10.1007/BF01239350)
19. Harrison JF. 2017 Do performance–safety tradeoffs cause hypometric metabolic scaling in animals? *Trends Ecol. Evol.* **32**, 653–664. (doi:10.1016/j.tree.2017.05.008)
20. Best RC. 1981 The tusk of the narwhal (*Monodon monoceros* L.): interpretation of its function (Mammalia: Cetacea). *Can. J. Zool.* **59**, 2386–2393. (doi:10.1139/z81-319)
21. Bergmann PJ, Berk CP. 2012 The evolution of positive allometry of weaponry in horned lizards (*Phrynosoma*). *Evol. Biol.* **39**, 311–323. (doi:10.1007/s11692-011-9147-2)
22. Pélabon C, Bolstad GH, Egset CK, Cheverud JM, Pavlicev M, Rosenqvist G. 2013 On the relationship between ontogenetic and static allometry. *Am. Nat.* **181**, 195–212. (doi:10.1086/668820)
23. Grafen A. 1990 Biological signals as handicaps. *J. Theor. Biol.* **144**, 517–546. (doi:10.1016/S0022-5193(05)80088-8)
24. Andersson MB. 1994 *Sexual selection*. Princeton, NJ: Princeton University Press.
25. Arnold SJ. 1983 Morphology, performance and fitness. *Integr. Comp. Biol.* **23**, 347–361. (doi:10.1093/icb/23.2.347)
26. Knapp A, Knell RJ, Farke AA, Loewen MA, Hone DWE. 2018 Patterns of divergence in the morphology of ceratopsian dinosaurs: sympatry is not a driver of ornament evolution. *Proc. R. Soc. B* **285**, 20180312. (doi:10.1098/rspb.2018.0312)
27. O'Brien DM. 2019 Static scaling and the evolution of extreme canine size in a saber-toothed cat (*Smilodon fatalis*). *Integr. Comp. Biol.* **59**, 1303–1311. (doi:10.1093/icb/icz054)
28. Gould SJ. 1974 The origin and function of 'bizarre' structures: antler size and skull size in the 'Irish elk,' *Megaloceros giganteus*. *Evolution*. **28**, 191–220.
29. Knell RJ, Fortey RA. 2005 Trilobite spines and beetle horns: sexual selection in the Palaeozoic? *Biol. Lett.* **1**, 196–199. (doi:10.1098/rsbl.2005.0304)
30. Garde E, Hansen SH, Ditlevsen S, Tvermosegaard KB, Hansen J, Harding KC, Heide-Jørgensen MP. 2015 Life history parameters of narwhals (*Monodon monoceros*) from Greenland. *J. Mammal.* **96**, 866–879. (doi:10.1093/jmammal/gyv110)
31. Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edn. New York, NY: Springer.
32. Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. 2018 *nlme*: Linear and nonlinear mixed effects models. R package version 3.1-137. See <https://CRAN.R-project.org/>.
33. Bolker B, R Development Core Team. 2017 *bbmle*: Tools for general maximum likelihood estimation. R package version 1.0.20. See <https://CRAN.R-project.org/>.
34. Canty A, Ripley BD. 2019 *boot*: Bootstrap R (S-Plus) functions. R package version 1.3-24. See <https://CRAN.R-project.org/>.
35. Pekár S, Brabec M. 2016 Marginal models via GLS: a convenient yet neglected tool for the analysis of correlated data in the behavioural sciences. *Ethology*. **122**, 621–631. (doi:10.1111/eth.12514)
36. Palaoro AV, Briffa M. 2017 Weaponry and defenses in fighting animals: how allometry can alter predictions from contest theory. *Behav. Ecol.* **28**, 328–336. (doi:10.1093/beheco/arw163)
37. Hardy ICW, Briffa M. 2013 *Animal contests*. Cambridge, UK: Cambridge University Press.
38. Pinto NS, Palaoro AV, Peixoto PEC. 2019 All by myself? Meta-analysis of animal contests shows stronger support for self than for mutual assessment models. *Biol. Rev.* **94**, 1430–1442. (doi:10.1111/brev.12509)
39. Marley SA, Cheney B, Thompson PM. 2013 Using tooth rakes to monitor population and sex differences in aggressive behaviour in bottlenose dolphins (*Tursiops truncatus*). *Aquat. Mamm.* **39**, 107–115. (doi:10.1578/AM.39.2.2013.107)
40. MacLeod CD. 1998 Intraspecific scarring in odontocete cetaceans: an indicator of male 'quality' in aggressive social interactions? *J. Zool.* **244**, 71–77. (doi:10.1017/S0952836998001083)
41. Dennenmoser S, Christy JH. 2013 The design of a beautiful weapon: compensation for opposing sexual selection on a trait with two functions. *Evolution*. **67**, 1181–1188. (doi:10.1111/evo.12018)
42. Lane SM, Briffa M. 2017 The price of attack: rethinking damage costs in animal contests. *Anim. Behav.* **126**, 23–29. (doi:10.1016/j.anbehav.2017.01.015)
43. Jennings DJ, Boys RJ, Gammell MP. 2017 Weapon damage is associated with contest dynamics but not mating success in fallow deer (*Dama dama*). *Biol. Lett.* **13**, 20170565. (doi:10.1098/rsbl.2017.0565)
44. Currey JD, Brear K, Zioupos P. 1994 Dependence of mechanical properties on fibre angle in narwhal tusk, a highly oriented biological composite. *J. Biomech.* **27**, 885–897. (doi:10.1016/0021-9290(94)90261-5)
45. Brear K, Currey JD, Kingsley MCS, Ramsay M. 1993 The mechanical design of the tusk of the narwhal (*Monodon monoceros*: Cetacea). *J. Zool.* **230**, 411–423. (doi:10.1111/j.1469-7998.1993.tb02693.x)
46. McCullough EL. 2014 Mechanical limits to maximum weapon size in a giant rhinoceros beetle. *Proc. R. Soc. B* **281**, 20140696. (doi:10.1098/rspb.2014.0696)
47. Somjee U, Woods H, Duell M, Miller C. 2018 The hidden cost of sexually selected traits: the metabolic expense of maintaining a sexually selected weapon. *Proc. R. Soc. B* **285**, 20181685. (doi:10.1098/rspb.2018.1685)
48. Lemaitre JF, Vanpé C, Plard F, Gaillard JM. 2014 The allometry between secondary sexual traits and body size is nonlinear among cervids. *Biol. Lett.* **10**, 20130869. (doi:10.1098/rsbl.2013.0869)
49. Pomfret JC, Knell RJ. 2006 Sexual selection and horn allometry in the dung beetle *Euoniticellus intermedius*. *Anim. Behav.* **71**, 567–576. (doi:10.1016/j.anbehav.2005.05.023)
50. Knell RJ, Pomfret JC, Tomkins JL. 2004 The limits of elaboration: curved allometries reveal the constraints on mandible size in stag beetles. *Proc. R. Soc. Lond. B* **271**, 523–528. (doi:10.1098/rspb.2003.2641)
51. Crane J. 2015 *Fiddler crabs of the world: Ocypodidae: Genus Uca*. Princeton, NJ: Princeton University Press.
52. Wilson RS, Angilletta MJ. 2015 Dishonest signaling during aggressive interactions: theory and empirical evidence. In *Animal signaling and function: an integrative approach* (eds DJ Irschick, M Briffa, J Podos). Hoboken, NJ: John Wiley & Sons.
53. Bywater CL, Angilletta MJ, Wilson RS. 2008 Weapon size is a reliable indicator of strength and social dominance in female slender crayfish (*Cherax dispar*). *Funct. Ecol.* **22**, 311–316. (doi:10.1111/j.1365-2435.2008.01379.x)
54. Moore P. 2007 Agonistic behavior in freshwater crayfish: the influence of intrinsic and extrinsic factors on aggressive behavior and dominance. In *Evolutionary ecology of social and sexual systems: crustacea as model organisms* (eds J Duffy, M Thiel), pp. 90–114. New York, NY: Oxford University Press.
55. Mariappan P, Balasundaram C, Schmitz B. 2000 Decapod crustacean chelipeds: an overview. *J. Biosci.* **25**, 301–313. (doi:10.1007/BF02703939)
56. Fujiwara S, Kawai H. 2016 Crabs grab strongly depending on mechanical advantages of pinching and disarticulation of chela. *J. Morphol.* **277**, 1259–1272. (doi:10.1002/jmor.20573)
57. Graham ZA, Garde E, Heide-Jørgensen MP, Palaoro AV. 2020 Data from: The longer the better: evidence that narwhal tusks are sexually selected. Dryad Digital Repository. (doi:10.5061/dryad.s1rn8pk43)