Comment

Ornament Complexity Is Correlated with Sexual Selection

(A Comment on Raia et al., "Cope's Rule and the Universal Scaling Law of Ornament Complexity")

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ABSTRACT: Raia et al. propose that the evolution of the shape and complexity of animal ornaments (e.g., deer antlers) can be explained by interspecific variation in body size and is not influenced by sexual selection. They claim to show that ornament complexity is related to body size by an 0.25-power law and argue that this finding precludes a role for sexual selection in the evolution of ornament complexity. However, their study does not test alternative hypotheses and mismeasures antler shape allometry by omitting much of the published data. We show that an index of sexual selection (sexual size dimorphism) is positively correlated with size-corrected antler complexity and that the allometric slope of complexity is substantially greater than 0.25, contra Raia et al. We conclude that sexual selection and physical constraints both affect the evolution of antler shape.

Keywords: allometry, antlers, Cope's rule, deer, morphology, weapons.

Animal weaponry, including deer antlers, fiddler crab claws, and beetle horns, are traditionally regarded as adaptations to intraspecific contests over resources (e.g., Darwin 1871; Kodric-Brown et al. 2006). In particular, weapons are commonly used by males fighting over access to females, leading to the hypothesis that large and elaborate weapons have evolved in response to sexual selection. Numerous interspecific studies have claimed support for this hypothesis (e.g., Andersson 1994; Kodric-Brown et al. 2006; Emlen 2008), and the hypothesis that sexual selection explains much of the diversity in weapon shape and size appears to be widely accepted.

Recently, Raia et al. (2015a, p. 165) made the intriguing claim that "although sexual selection may control size in most ornaments, it does not influence their shape." They argue instead that the evolution of ornament shape and complexity is "a simple by-product of body size increase through time within clades" (i.e., Cope's rule; p. 166). The crux of their hypothesis is that trait complexity should be expected to increase with body size because of ontogenetic processes and physical constraints; by analogy, an oak sapling has a less complex network of branch forks than a fully grown tree. Thus, whenever related species differ in size (e.g., when descendant species are larger than their ancestors, as with Cope's rule), Raia et al.'s theory states that one should expect to see interspecific variation in complexity even in the absence of interspecific variation in selection on those traits (e.g., from sexual selection)—a conclusion with which we agree.

Furthermore, Raia et al. propose that the complexity of traits should scale with an allometric slope of 0.25 in the absence of sexual selection. This hypothesis stems from the empirical observation that the scaling exponent of developmental time on body size appears to be 0.25 (e.g., West et al. 2001; Roff 2002). Raia et al. suggest that complexity will have the same allometric slope as development time, because of the aforementioned increase in complexity during ontogeny.

Raia et al.'s 0.25-scaling "null model" is potentially useful, but it makes the unstated assumption that complexity increases linearly with development time. If complexity instead shows a diminishing or accelerating relationship with development time, then the allometric slopes of complexity and development time will be different. Formally, if the allometric scaling of development time (DT) is $DT \propto mass^{0.25}$ and complexity $\propto DT^a$ (where a is a scaling exponent), then complexity $\propto mass^{0.25a}$; thus, Raia et al.'s hypothesis is correct only in the special case in which complexity increases linearly with DT ($a = 1$). Although this assumption might be valid, it was apparently not discussed; we suggest that this assumption warrants careful scrutiny by researchers considering using Raia et al.'s approach.
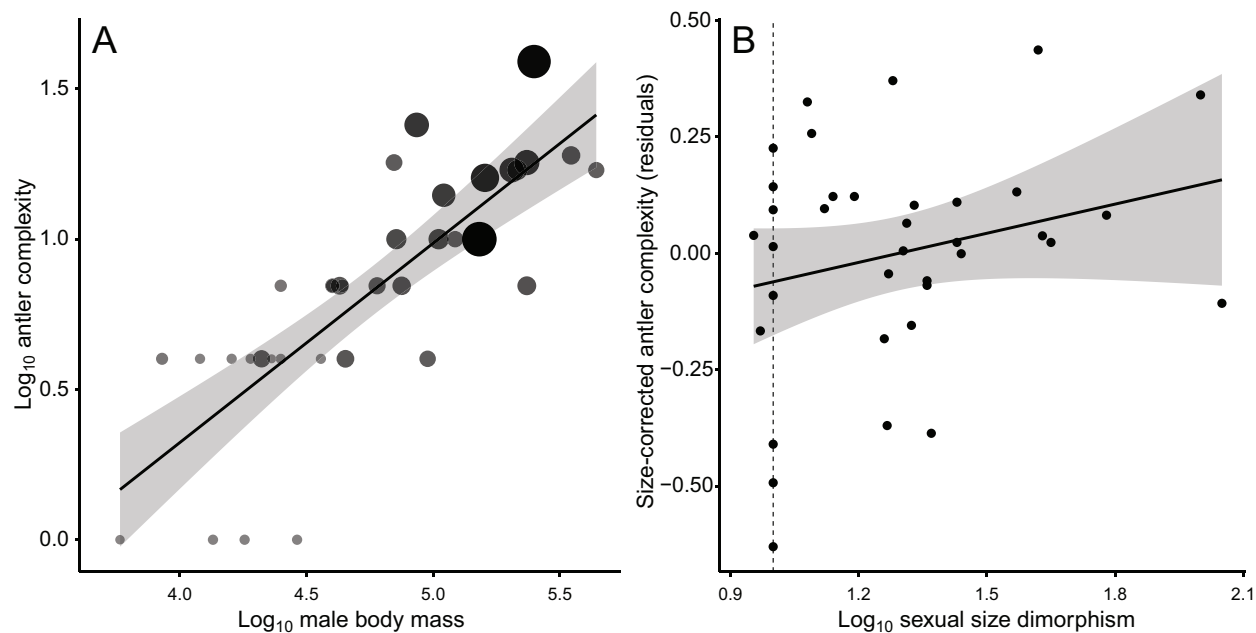
Figure 1: Body size and sexual size dimorphism (SSD) both predict the complexity of antler shape ($n = 36$ species). *A*, Larger, darker points denote species with higher SSD. Note that larger points tend to be above the regression line. *B*, The residuals from an ordinary least squares regression of complexity on body size tend to be higher in species with high SSD. The dashed line indicates the absence of SSD, and data points to the right of it correspond to species in which males are larger than females.

In their allometric analyses of deer antlers, ceratopsian dinosaur frills, and ammonite shell sutures (a nonornamental trait), Raia et al. found that the 95% confidence limits on the allometric slope of complexity included 0.25 for all three taxa, leading them to conclude that sexual selection probably does not act on the shapes of deer antlers and dinosaur frills. We believe that Raia et al.'s study does not support this conclusion. Our principal argument is that it is fallacious to conclude that factor A (sexual selection) is uncorrelated with factor B (ornament complexity) simply because factor B is correlated with factor C (body size). Instead, one should test directly whether factors A and B are correlated. Furthermore, one should not take the failure to reject a null hypothesis to mean that the null hypothesis is correct. However, as we shall see, our expanded analysis of

deer antlers reaches a different conclusion regarding shape allometry.

We first collated data on sexual size dimorphism (SSD, a reliable proxy for the strength of sexual selection in deer; Pérez-Barbería et al. 2002) and antler complexity (measured by Strahler number, following Raia et al.) in 36 deer species. We tested whether SSD explains variation in antler complexity after controlling for body size, using phylogenetic generalized least squares multiple regression (see the appendix). We found that $\log_{10}$ male body size (slope $= 0.36$; 95% CI [confidence interval] $= 0.12-0.59$; $t = 3.00$, $P = .005$) and $\log_{10}$ SSD (slope $= 1.26$; 95% CI $= 0.33-2.18$; $t = 2.67$, $P = .012$) were both positively correlated with $\log_{10}$ ornament complexity (fig. 1). Thus, sexual selection appears to explain a considerable amount of variance in antler com-

Table 1: Model comparison of three models of the scaling of $\log_{10}$ antler complexity (y) with $\log_{10}$ body size (x)

Model	R^2	df	ΔAIC	Intercept (a)	Slope (β)	Quadratic term (γ)
$y \sim a + \beta x + \gamma x^2$	.77	62	...	3.04	-1.43 (-2.97 to .10)	**.20** (.04–.37)
$y \sim a + \beta x$	.75	63	4.25	**-1.41**	**.48** (.36–.61)	...
$y \sim a + .25x$	.69	64	15.0	$-.286$	.25 (n/a)	...

Note: The top model contained both the linear and quadratic effects of body size. The second-best model, which included the linear effect only, provided a greatly improved fit over a model in which the slope was constrained to be 0.25 (ΔAIC $= 10.75$). R^2 was calculated as $1 - $ (residual sum of squares)/(total sum of squares), ΔAIC is in reference to the top model, numbers in parentheses are 95% confidence intervals, and parameter estimates in boldface differ significantly from 0 ($\alpha = 0.05$). AIC = Akaike information criterion; n/a = not applicable.
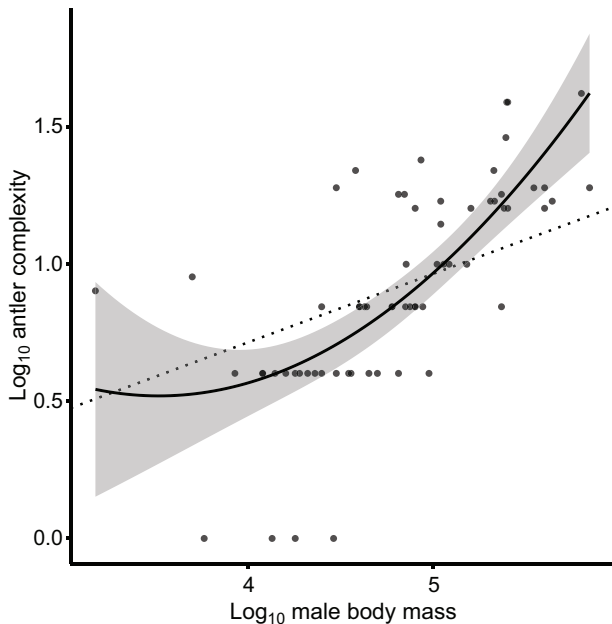
Figure 2: There is a steep, nonlinear relationship between log body size and log antler complexity. The null hypothesis of Raia et al. (2015*a*), that complexity scales linearly with log body size with a slope of 0.25, was not supported. For comparison, the dotted line has a slope of 0.25 and an intercept that minimizes the sum of the squared residuals (table 1).

plexity, even after increases in complexity with body size are accounted for with a multiple regression.

We next tested Raia et al.'s claim that log antler complexity scales linearly with log body size with a slope of 0.25, using their deer data set (i.e., the 39 species listed in the Dryad Data Repository: http://dx.doi.org/10.5061 /dryad.50dr8 [Raia et al. 2015*b*]; in places, Raia et al. report that there were 41 species) supplemented with 28 additional species for which male body size data are available in the literature (Plard et al. 2011; Sibly et al. 2012). Using ordinary least squares regression, we found that the allometric slope of antler complexity was 0.48 ($t_{63} = 7.65, P < .0001$) and that its 95% confidence limits did not overlap 0.25 (see table 1). Our estimate is thus somewhat steeper than the slope estimated in Raia et al. (i.e., 0.346), which narrowly included 0.25 in its 95% confidence limits (Raia et al. give the 95% CI as 0.247–0.446 in their figure 3 and as 0.201–0.449 in their "Results" section). In addition, we found that a quadratic curve provided a significantly improved fit to the relationship between log size and complexity (table 1). This quadratic relationship reflects the fact that the largest deer have especially complex antlers (fig. 2; table 1; linear effect of body size: $t = -1.86, P = .067$; quadratic effect: $t = 2.50, P = .015$). This result is not unique to our expanded data set: a quadratic fit is bet-

ter than a linear one for the 39 species in Raia et al. (ΔAIC [Akaike information criterion] $= 4.05$). We note that the largest deer species are also the ones with the strongest sexual size dimorphism and sexual selection (Loison et al. 1999), suggesting that differences in the strength of sexual selection between large and small species might explain this quadratic relationship.

In summary, both of our analyses suggest that sexual selection has played a role in the evolution of antler complexity. We showed, first, that a commonly used index of the intensity of sexual selection (SSD) is correlated with size-corrected antler complexity and, second, that antler complexity scales with greater than 0.25 power, which implies that it has been the object of sexual selection.

Despite disagreeing with its conclusions, we believe that Raia et al.'s article is valuable, in that it highlights that ornament evolution has most commonly been studied in terms of size only, rather than shape or complexity. Future work could further investigate the evolution of the shape of ornaments and weapons, perhaps using morphometric methods (e.g., Klingenburg 2010) more sophisticated than the Strahler number used in their study, which largely reflects the number of forks in the antlers. The manifold uses of antlers in defense, signaling, and fighting have likely shaped their size and shape in many hitherto unappreciated ways. Raia et al. (2015*a*) also reaffirm the importance of ontogenetic and evolutionary constraints in explaining phenotypic diversity, alongside adaptation.

Data Sharing.   Our expanded data set and the R code to reproduce our analyses and figures are available in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad .ft70n (Holman and Bro-Jørgensen 2016).

APPENDIX

Data Collection and Analysis

We collected male and female body size data on 36 antlered deer species from references cited in Sibly et al. (2012) and Plard et al. (2011). We then computed the Strahler number for each species not represented in Raia et al. (2015*a*), following their methods, using photographs found online through exhaustive Google searches. If photographs of multiple individuals were found for a given species, we picked the one with the most complex antlers.

We used the phylogeny of Bininda-Emonds et al. (2007). We performed phylogenetically controlled multiple regression, using the *gls* function in the *nlme* package for R and using the expected covariance structure assuming a Brownian model of evolution (computed with the *corBrownian* function in the R package *ape*). We calculated sexual size dimorphism as male mass divided by female mass.

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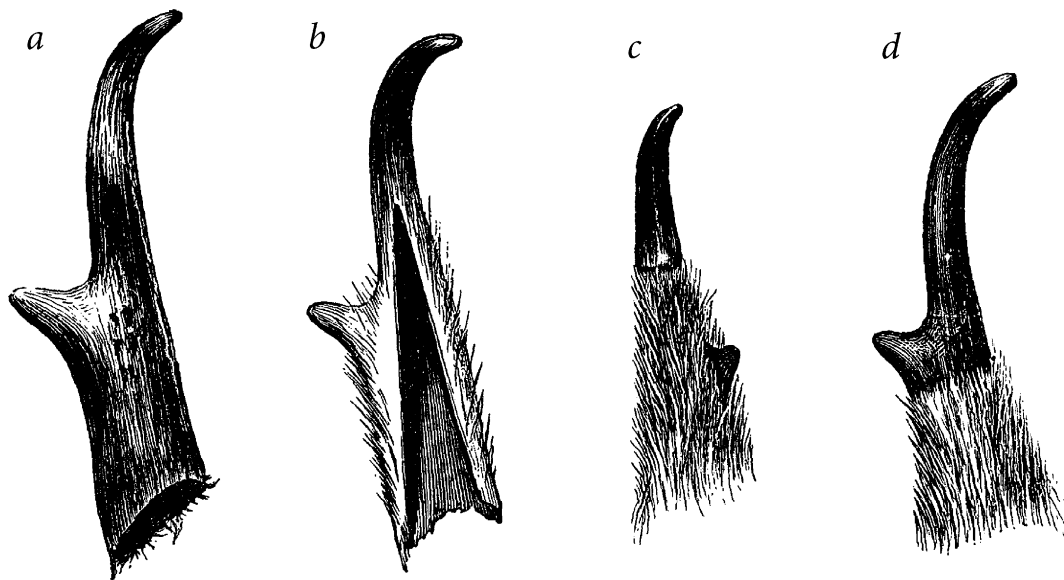
"For the last four years I have had an antelope under my own observation, and have watched carefully the process of development of the horns. . . . [a] The horn just shed. [b] A longitudinal section showing the manner in which the hairs pass through the horns. [c] The appearance of the horn in the month of January. [d] Its appearance in April." From "The Prong-Horn Antelope" by W. J. Hays (*The American Naturalist* 1868, 2:131–133).