Reply

From Evolutionary Allometry to Sexual Display

(A Reply to Holman and Bro-Jørgensen)

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ABSTRACT: Conventional wisdom holds that the complex shapes of deer antlers are produced under the sole influence of sexual selection. We questioned this view by demonstrating that trends for increased body size evolution passively yield more-complex ornaments, even in organisms where no effect of sexual selection is possible, with similar allometric slopes. Recent investigations suggest that sexual selection on antlers of larger deer species is stronger than that in smaller species; hence, the use of conspicuous antlers for display in large male deer is a secondary function driven by especially intense sexual selection on these large-bodied species. Since ancestral deer were small and had very simple antlers, such an intense selection on antlers shape was probably absent in early deer. Therefore, the evolution of complex ornaments is coupled with body size evolution, even in deer.

Keywords: antler, sexual selection, display.

Recently, we (Raia et al. 2015) tested the idea that the evolution of ornament complexity is a by-product of body size increase through time, namely, Cope's rule. Ornaments develop through ontogeny and usually become more complex and elaborate with age (García-Ruiz et al. 1990; Geist 1998). Consequently, the more an individual grows, the more complex its ornamental structures will be, because time to maturation increases with body size (Calder 1984). Moving from ontogenetic to evolutionary allometry, this increase in complexity through ontogeny implies that larger daughter species will inherit more-complex ornaments than their smaller parent species—which is expected if Cope's rule holds. This prediction generates a testable hypothesis: because time to maturation scales among species (i.e., evolutionary allometry) to the 0.25 power of body size (Lindstedt and Calder 1981; Calder 1984), we predicted that, all else being equal, or-

nament complexity should also scale to the 0.25 power. To test for this, we assembled a large data set on phylogeny, complexity, and body sizes in three very different groups of animals and ornaments. Specifically, since the effect of sexual selection is generally held responsible for the evolution of ornament size and shape (West-Eberhard 1983; Emlen 2008), we examined one clade for which the importance of sexual selection in the evolution of the ornament is obvious: deer and their antlers. Another group bore ornaments of uncertain function (the frill in ceratopsian dinosaurs). In our third group, sexual selection is highly unlikely to be related to ornamentation: the suture line in ammonoid cephalopods (which was covered in tissue in the living organisms and therefore could not have been used for sexual display). We found that the phylogenetic relationship between body size and complexity holds and that the allometric scaling exponent is not different from 0.25 in all three groups.

Holman and Bro-Jørgensen (2016) recently extended our data set for deer only, using the same measure of antler complexity we used (the "Strahler number"; Strahler 1957). The exponent of their allometric scaling regression was 0.48 (95% confidence interval: 0.36–0.61), significantly higher than 0.25. They also used phylogenetic generalized least squares to regress sexual size dimorphism (SSD), a reliable index of the strength of sexual selection in deer, against (the log of) antler complexity. They found that a quadratic regression fits better than a linear model, indicating that males of larger species have disproportionately complex antlers. They concluded that "the largest deer species are also the ones with the strongest sexual size dimorphism and sexual selection" and that "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." The former statement agrees with reports indicating that the intensity of sexual selection is stronger in larger deer species (Clutton-Brock

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et al. 1980; Bro-Jørgensen 2007) The latter is in full compliance with our hypothesis.

We are glad that our article attracted interest, and we applaud Holman and Bro-Jørgensen's enlarged data set and reanalysis. In Raia et al. (2015), we claimed that the increase of ornament complexity is due to Cope's rule. We thus argued against the very common, conventional view that ornament shape is solely controlled by sexual selection in the same way as ornament size is (Gould 1974; West-Eberhard 1983; Anderson 1994; Møller and Birkhead 1994; Emlen 2008). We posit that the mechanism that drove increased complexity (i.e., evolutionary allometry) is not derived from its function (i.e., sexual selection). Hence, the switch from antlers used in male-male combat to antlers used in sexual display is not necessarily a product of sexual selection. This is, we contend, not the same as saying that sexual selection does not matter to the evolution of deer antlers. Indeed, in selecting deer for our analysis, we (Raia et al. 2015, p. 167) emphasized that they were chosen exactly because "sexual selection is obviously at play in deer antler evolution (Geist 1998)." Thus, the interpretation remains the same: larger deer would have more complex antlers irrespective of sexual selection, and, very importantly, large antlers either were *recruited* for sexual display passively (if the allometry is 0.25 or similar) or were further shaped by sexual selection (if the scaling is steeper than 0.25, as found by Holman and Bro-Jørgensen). But large antlers were not necessarily *produced* for display. In this regard, the findings of Holman and Bro-Jørgensen are especially important, as they suggest, to us, that sexual selection might have emphasized selection on complexity in deer over that found in dinosaurs and ammonites.

A couple of observations merit consideration here. First, since geologically older deer were small and had small and simple antlers (Geist 1998), the intensity of sexual selection in deer became more important over time, if Holman and Bro-Jørgensen's conclusions are correct. Although we are unaware of any study predicting an increase in the importance of sexual selection (and presumably SSD) over time, this would be very interesting to investigate. Second, even today small species in all the deer tribes (e.g., brocket deer *Mazama*, *Pudu*, and especially tufted deer *Elaphodus*, whose antlers are hidden by a tuft) have exceptionally simple antlers (Geist 1966). These antlers are not used for sexual display but are usually used in male-male combat (Geist 1998). This implies that, even under Holman and Bro-Jørgensen's perspective, sexual dis-

play did not primarily target antler shape during the early stages of deer evolution. That is, antler complexity evolved for reasons unrelated to sexual selection and was secondarily recruited to the goal of sexual display. This is not at odds with Holman and Bro-Jørgensen's conclusions. The new results further suggest that sexual selection (to which sexual display fully pertains) is more important in large than in small deer.

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