Journal of Zoology

Journal of Zoology. Print ISSN 0952-8369

LETTER

Bizarre structures in dinosaurs: species recognition or sexual selection? A response to Padian and Horner

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Editor: Steven Le Comber

doi:10.1111/j.1469-7998.2010.00758.x

Since the mid-1970s, most investigators have agreed that the 'bizarre' structures (here referred to as 'exaggerated' structures) of dinosaurs – for example, the horns and frills of ceratopsids, the crests of lambeosaurine hadrosaurids, the domes of pachycephalosaurs – functioned first and foremost as signalling and combat structures used in mate competition (Farlow & Dodson, 1975; Hopson, 1975; Molnar, 1977; Spassov, 1979; Ostrom & Wellnhoffer, 1986; Sampson, 1997, 2001; Dodson, Forster & Sampson, 2004). Padian & Horner (2010) argue that the mate competition hypothesis is not supported by available evidence, citing in particular the lack of data documenting sexual dimorphism within dinosaur species. In place of the mate competition model, they present a challenging and novel alternative, suggesting these traits functioned as species recognition features for identifying conspecifics, thereby facilitating social interactions such as herding, mating and parental care.

Padian & Horner offer a pair of tests for distinguishing paleontological examples of exaggerated traits evolving under the influence of species recognition from those resulting primarily from sexual selection. The first test relates to the patterns of diversification of exaggerated structures, predicted to be random under the influence of species recognition and directional if driven by sexual selection. The second test invokes evidence of geographic overlap of closely related, contemporaneous species, thought to be a necessary condition for the evolution of exaggerated structures under the influence of species recognition (in part so as to avoid unwanted matings). These authors argue that known examples of exaggerated structures among dinosaurs pass both of these tests, indicating that species recognition is the preferred (though not necessarily sole) explanation.

Padian & Horner highlight a major problem common to most previous studies addressing the function of dinosaurian exaggerated structures – lack of phylogenetic context. Comprehensive testing of adaptation hypotheses requires mapping of relevant characters onto independently derived phylogenies in order to search for evidence of evolutionary assembly of the purported adaptation. They also underline the importance of assessing the full range of alternative hypotheses as rigorously as possible, rather than accepting one explanation as the default. We fully support both of these contentions. Nevertheless, we disagree with several of the paper's central conclusions, including: (1) the necessary correlation of overt sexual dimorphism and sexual selection; (2) the required linkage between sexual selection with a directional pattern of diversification; (3) evidence for the geographical overlap of multiple closely related dinosaur taxa bearing exaggerated structures. In addition to countering these claims, we propose two alternative predictions that allow putative species recognition traits to be distinguished from sexually selected ones. With regard to the exaggerated structures of dinosaurs, the species recognition hypothesis fails both of these tests, and the sexual selection hypothesis remains by far the best-supported explanation.

Citing Darwin (1871), Padian & Horner claim that sexual dimorphism is effectively the *sine qua non* of sexual selection. They argue further that the apparent absence of sexual dimorphism in dinosaurian exaggerated characters is compelling evidence against the mate competition hypothesis. Yet with few exceptions, sample sizes for individual dinosaur species are too small to conduct statistical tests for the presence of sexual dimorphism (Sampson, 1997), so any inference drawn from such an observation is weak at best. More importantly, and as argued previously for dinosaurs (Sampson, 2001), evidence derived from vertebrates demonstrates that sexual selection is not necessarily correlated with overt sexual dimorphism. Among mammalian megaherbivores, sexual dimorphism tends to be least in small-bodied forms, greatest in medium-sized forms, and reduced in large-bodied forms (Walther, 1966; Estes, 1974; Geist, 1974, 1977, 1978; Jarman, 1983; Stankowich & Caro, 2009). In bovids, for example, the sexes of small species (<20 kg) and large species (>300 kg) tend to exhibit minimal dimorphism, whereas species between these extremes (80–300 kg) often show marked sexual differences. The relative lack of dimorphism in megaherbivore mammals (>300 kg) is particularly prevalent among gregarious, herd-forming species inhabiting open environments (Jarman, 1983; Stankowich & Caro, 2009).

Although bovids use their horns for a variety of purposes – from food acquisition to warding off predators – it is clear that in males at least they function predominantly in competition for mates (Andersson, 1994). In contrast, female hornedness in large-bodied, gregarious, open-living bovids appears to be related primarily to predator defense, and secondarily to intrasexual selection (Stankowich & Caro, 2009). Ceratopsid and hadrosaurid dinosaurs certainly qualify as megaherbivores, with most taxa as large or larger than the largest bovids, and the documentation of monodominant bonebeds for many ceratopsid and hadrosaurid species (Sampson, 2001; Dodson *et al.*, 2004) suggests that at least some forms lived in large, mixed-sex groups, or 'herds', often in open, savannah-like settings. In short, an apparent lack of sexual dimorphism cannot be put forth as evidence against the mate competition hypothesis; rather this observation is fully consistent with the pattern present in extant horned mammals.

With regard to the alternative hypothesis postulated by Padian & Horner, to our knowledge species recognition has not been documented as a key factor in the evolution of exaggerated traits among any extant animals. Nor, as far as we are aware, are there any documented examples of exaggerated morphological traits being used primarily for species recognition in living animals, although some cases exist of such characters possessing a secondary function in species recognition (e.g. colour patches on the dewlaps of *Anolis* lizards; Losos, 1985; Nicholson, Harmon & Losos, 2007; Vanhooydonck *et al.*, 2009). Nevertheless, although the exaggerated traits of modern animals do not seem to have evolved for this purpose, it is conceivable that dinosaurs followed a different evolutionary trajectory.

As the first of their two tests, Padian & Horner (2010) propose that traits under sexual or natural selection should show directional change through time that ought to be visible within clades, whereas species recognition traits are unlikely to experience directional selection. They conclude that the apparent lack of directional evolution of exaggerated structures within dinosaur clades is more consistent with a species recognition interpretation than with one based on sexual selection. In our view, a central problem of this test is the assumption that traits under directional selection evolve slowly enough for directional change to be evident on phylogenies of extinct clades. Among extant clades bearing exaggerated characters that clearly function first and foremost in mate competition (e.g. Caro *et al.*, 2003; Emlen *et al.*, 2005; Nicholson *et al.*, 2007), some published phylogenies demonstrate apparently random patterns of diversification. Perhaps the best example comes from the Coleoptera; research over the last 20 years has demonstrated unambiguously that beetle horns are used as weapons in contests between males for access to mates (Knell, in press). There is no reason to think beetle horns play any role in species recognition; the insects generally encounter each other in dark tunnels and horns are not used in any described way in interactions between males and females (Kotiaho, 2002). Furthermore, in many species only some males carry horns, whereas others do not (e.g. Emlen, 1997; Moczek & Emlen, 2000). Species recognition in these beetles, as in many other species of insect, is most likely mediated by odour based on their cuticular hydrocarbons (Singer, 1998). In contrast to the first prediction of Padian & Horner, these beetles exhibit no directional change in horn morphologies within clades, a fact commented on by Darwin (1871):

> In the several sub-divisions of the family, the differences in structure of the horns do not run parallel, as I am informed by Mr. Bates, with their more important and characteristic differences; thus within the same natural section of the genus Onthophagus, there are species which have either a single cephalic horn, or two distinct horns.

Emlen et al. (2005) have recently verified Bates' observations using a phylogeny of 48 species of *Onthophagus*; Emlen counted at least 25 gains and losses of horns within this clade, with no indication of any directional trend in horn morphology. There is little question that, when present, these horns have an adaptive function, allowing males to increase their fitness by increasing their number of matings, so the lack of directional change likely results from the gains and losses occurring too rapidly for any directional change to be evident. Horn losses appear to be causally linked to changes to ecological variables such as population density or sex ratios favouring hornless males (Moczek, 2003; Pomfret & Knell, 2008). Studies of introduced populations of horned beetles have shown measurable changes in horn size and frequency after <40 years, apparently linked to densities of the introduced populations (Moczek, 2003). Although exaggerated structures in dinosaurs (e.g. horns, frills, crests and domes) would have evolved more slowly than beetle horns due to longer generation times, it is nonetheless possible that they showed a similar amount of evolutionary lability, particularly over macroevolutionary timescales. If so, especially given the relatively low temporal resolution characteristic of the Mesozoic vertebrate record, we should not be surprised to find a lack of evidence for directional morphological change in exaggerated characters evolving under sexual selection.

The second test of the species recognition hypothesis proposed by Padian & Horner is that species with exaggerated traits should occur in sympatry with others bearing similar features at some point during the evolution of these traits. This contention is founded on the idea that traits used in species recognition should be more divergent when species occur in sympatry. Thus, the songs of closely related sympatric pairs of antbird (Thamnophilidae) differ from each other more than the songs of closely related allopatric pairs (Seddon, 2005). Similarly, island-dwelling species of wildfowl (Anseriformes) that live in sympatry with few congeners are than less brightly coloured than anseriforms sharing the same habitat with more congeners (Figuerola & Green, 2000).

This prediction has several problems as applied to Mesozoic dinosaurs. The first is that the proposed correlation does not seem to be universal among extant animals, weakening any inferences based upon the fossil record. For example, in *Anolis* lizards, although an interspecific study has shown that dewlap colour patch diversity is predicted by the number of sympatric congenerics on an island (Vanhooydonck *et al.*, 2009), a detailed interspecific study found no evidence for a similar effect between species (Nicholson *et al.*, 2007). Another problem with particular relevance to the present discussion is that multiple contemporaneous, closely related species with overlapping geographic ranges is consistent with traits evolving under sexual selection as well as species recognition (i.e. multiple, co-existing taxa within a clade spawning new forms distinguished primarily on the basis of sexually selected mating signals).

More problematic still is the fact that the dinosaur fossil record does not support the second prediction of Padian & Horner. They cite several examples of multiple, contemporaneous, closely related dinosaur species bearing bizarre structures (2010: table 2). Yet most of these examples span millions of years and a range of environments, bringing into question whether or not the animals within a given clade actually co-existed in the same habitats. Of the examples given, by far the best documented – stratigraphically and paleontologically – is the Late Cretaceous (Campanian) Dinosaur Provincial Park in Alberta, Canada, for which the authors cite the occurrence of 10 hadrosaur species, four pachycephalosaur species and at least 10 ceratopsid species. Yet a recent review of Dinosaur Park Formation ornithischians (Ryan & Evans, 2005) concluded that many dinosaur taxa had relatively short species durations (<1 million years), and that the dinosaurs may be divided into successive faunal communities characterized by one or two species each of hadrosaurines, lambeosaurines, centrosaurines and chasmosaurines (the single exception is a time slice that may record three co-occuring lambeosaurines). This conclusion appears to apply to all reasonably well-sampled formations from the Campanian Western Interior Basin of North America (Gates *et al.*, 2010; Sampson & Loewen, 2010), arguably the best sampled continent-scale 'slice' of time and geography known for the entire Mesozoic. To highlight a single example from the Dinosaur Park Formation (Ryan & Evans, 2005), it seems difficult to maintain that the centrosaurine ceratopsid *Centrosaurus apertus* evolved its highly derived horn and frill morphologies in order to distinguish conspecifics from individuals of its contemporary, the chasmosaurine *Chasmosaurus russelli*, with which it last shared a common ancestor more than 5 million years prior. Depending on the primary mode of macroevolutionary change (cladogenetic vs. anagenetic), it is certainly conceivable, perhaps even likely, that sister taxa within these clades (e.g. *C. apertus* and *Styracosaurus albertensis* within centrosaurine ceratopsids) lived briefly side-by-side in ecological time. Yet if the elaborate and highly divergent signalling structures of these taxa had evolved predominantly under the influence of mate recognition, it seems improbable that such energetically expensive structures would be maintained virtually unchanged for the duration of the species. In short, although not conclusive, the dinosaur fossil record presently does not support the general claim of multiple, co-occurring, closely related taxa, as predicted by the species recognition hypothesis of Padian & Horner.

Having commented on the two tests put forth by Padian & Horner, we here propose an additional pair of tests based on signalling theory that might permit differentiation of traits selected primarily for species recognition from those resulting from conventional sexual selection. The first is based upon the relative predicted costs of species recognition versus sexually selected signals. According to the species recognition hypothesis, the signal is used primarily to allow conspecifics to recognize the bearer of the signal so that some mutually beneficial social behaviour (e.g. herding, reproduction) can occur. We argue that in such a system the interests of the signaller and receiver coincide and there is no benefit to either party from signalling dishonestly. Modelling studies have shown that under these circumstances a system based on low- or zero-cost signals can be evolutionarily stable (Maynard Smith & Harper, 2003): thus, we argue that signalling structures that function predominantly for species recognition should not impose significant costs upon the bearer. This contention may account for the lack of structural traits used primarily for species recognition in extant species; in the *Anolis* lizards referred to earlier, for example, Vanhooydonck *et al.* (2009) found that dewlap size was best explained by sexual and natural selection, whereas the (less costly) colours were associated with species recognition. In contrast, sexually selected traits are thought to act as signals of individual quality, either to compete with opponents or to attract females. This means that a benefit to the signaller can be conferred if the receiver can be deceived, and these traits are believed to be costly to the bearer in order to maintain honesty (Andersson, 1994; Maynard Smith & Harper, 2003). The horns and frills of ceratopsians, the crests of hadrosaurs and the plates of stegosaurs were large and elaborate structures that would have imposed a significant cost on the bearer, requiring significant resources to grow, maintain and carry. On this basis alone, species recognition is an improbable explanation for the exaggerated structures of dinosaurs.

With regard to our second test, species recognition signals are predicted to differ from signals of quality, as used in sexual or social selection, in the extent of intraspecific variation. Species recognition signals are likely to exhibit minimal variation within a species, because high levels of variation would increase the probability of error. Conversely, sexually selected traits frequently, though not invariably, show condition-dependent expression leading to a great deal of intraspecific variation and strong positive allometry (Cotton, Fowler & Pomiankowski, 2004; Tomkins *et al.*, 2004, 2010; Bonduriansky, 2007), resulting in larger animals carrying much larger traits relative to body size than do smaller animals. Positive intraspecific allometry of exaggerated traits has recently been proposed as evidence for sexual selection operating on the anterior spines of trilobites (Knell & Fortey, 2005) and the crests of *Pteranodon* (Tomkins *et al.*, 2010). Thus, although other factors (e.g. phylogenetic history, biomechanics, morphological integration) could conceivably yield similar patterns, evidence of strong positive allometry is consistent with the mate competition hypothesis and appears to run counter to the species recognition hypothesis (see Tomkins *et al.*, 2010, for additional discussion).

Among the best documented examples of exaggerated structures within Dinosauria are the crests of hadrosaurs (Dodson, 1975; Evans, 2010). A summary of allometric slopes calculated by Evans (2010) indicates strong positive allometry in the bony crests of a variety of hadrosaurid taxa. Analysis of crest height (variable 9; relative to basal skull length) for a sample ($N = 7$) of skulls pertaining to a single species, *Hypacrosaurus altispinus*, resulted in a strongly and significantly positive intraspecific allometric coefficient (reduced major axis slope of 4.97; 95% CIs 3.40–6.54). Although it is conceivable that this conclusion results from faulty taxonomy (two or more taxa mistakenly placed within a single species, artificially inflating variation), we see no evidence to support such a claim, and numerous other taxa, among ceratopsids (Sampson, Ryan & Tanke, 1997; Dodson *et al.*, 2004) as well as hadrosaurids, appear to exhibit similarly high levels of variation in their exaggerated structures. Assuming that the allometric slope for *H. altispinus* documented by Evans (2010) is reasonably accurate, it is steeper even than the majority of those calculated for modern sexually selected structures (Tomkins *et al.*, 2010). For the reasons cited above, the presence of strong positive allometry in the exaggerated structures of dinosaurs constitutes strong evidence against a species recognition function and is fully consistent with a mate competition function.

If exaggerated structures functioned to facilitate species recognition relating to behaviours other than mating (e.g. herding, parental care), one might further predict that these features would show species-specific development as early in ontogeny as possible. Instead, studies of ontogenetic variation of exaggerated structures in at least hadrosaurs (Dodson, 1975; Evans, 2010) and ceratopsids (Sampson *et al.*, 1997; Dodson *et al.*, 2004) demonstrate that these features underwent delayed development, exhibiting the adult condition at or near the onset of adult body size. A parallel developmental pattern has been documented for extant taxa bearing hornlike structures that appear to function first and foremost in mate competition (e.g. Geist, 1966; Jarman, 1983). Clearly, more quantitative analyses of this variation in exaggerated structures are needed before general conclusions can be made with confidence. Nevertheless, data currently available strongly support a sexual selection function for these traits.

In sum, we agree with Padian & Horner that pluralistic explanations are likely necessary for a full functional understanding of exaggerated, or 'bizarre', structures in dinosaurs. Species recognition is by no means unlikely as a secondary function for some of these structures, but their large and costly nature coupled with their high variability within species indicates strongly that their primary function involved mate competition, either as weaponry used in intrasexual agonistic behaviours, or as ornaments used in intra- and intersexual interactions.

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