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The species recognition hypothesis explains exaggerated structures in non-avialan dinosaurs better than sexual selection does



L'hypothèse de la reconnaissance de l'espèce explique mieux que la sélection naturelle des structures exagérées chez les dinosaures non aviens

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ABSTRACT

Several hypotheses have been proposed to explain "bizarre structures" in dinosaurs and other extinct animals (e.g., mechanical function and several kinds of intra- and interspecific display). Recent evidence and tests for species recognition as a possible driver of these structures have been proposed, in particular as an alternative to traditional hypotheses of function and sexual selection, which have fallen short. Advocates of sexual selection and mechanical function have advanced untested hypotheses claiming that species recognition cannot be an important process in evolution. We address these claims and show that they are based on misreading of the evidence and of previous literature. We also acknowledge that there have been historically differing definitions of sexual selection, which have greatly impeded understanding of the whole phenomenon of mate attraction and choice. Particularly in fossil animals, it is impossible to accept any hypothesis as the "default" that does not require evidence or testing to establish it.

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RÉSUMÉ

Certaines hypothèses ont été proposées pour expliquer des «structures bizarres» chez les dinosaures ou chez d'autres animaux disparus (par exemple fonction mécanique, différentes sortes d'affichage intra- et interspécifique). Des preuves et tests récents pour une reconnaissance de l'espèce en tant que facteur déterminant de ces structures ont été proposés, en particulier comme alternative aux hypothèses traditionnelles de sélection sexuelle et de fonction, mais ont été un échec. Les avocats de la sélection sexuelle et de la fonction mécanique ont avancé des hypothèses non testées, affirmant que la reconnaissance de l'espèce ne peut constituer un processus important au cours de l'évolution. Nous présentons ces affirmations et montrons qu'elles sont fondées sur une lecture erronée des preuves et de la littérature antérieure. Nous admettons aussi qu'il y a eu historiquement différentes définitions de la sélection sexuelle, qui ont gêné la compréhension du phénomène

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d'attraction et de choix du partenaire dans son ensemble. En particulier, chez les animaux fossiles, il est impossible d'accepter quelque hypothèse que ce soit de défaut (ou de manque) qui ne requière de preuve ou de test pour l'établir.

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1. Introduction

Several mechanisms have been historically advanced to explain variations in the bizarre skeletal structures of dinosaurs such as horns, frills, plates, spikes, crests, and domes (Main et al., 2005; Padian and Horner, 2011a, 2011b), including mechanical functions and several kinds of display (intraspecific and interspecific, including species recognition, mate recognition, social selection, and sexual selection). The considerable difference of opinion on the relative importance of such mechanisms and how to recognize them proceeds from two main sources. First, different workers use different definitions, some strongly altered from their original meanings. Second, no mechanisms can be assumed to have been prevalent in extinct animals based on weak analogy to living animals; there must be specific and diagnostic comparisons. However difficult it is to understand the behavior of living animals, it is much harder to understand what behaviors were associated with structural changes in extinct ones. "Default" hypotheses for these structures cannot be accepted merely on vague comparisons to selected living examples.

Our position is that Darwin defined sexual selection for a specific reason and that it requires specific criteria, but these criteria have been lost as the recent generation of biologists has neglected to read his work and has instead reduced his concept to a vague formulation of mating advantage, however it is acquired. In so doing the concepts of mate recognition, mate choice, and mate competition have been frequently confused with and even equated with sexual selection. We show that there is considerable value in differentiating among these concepts and respecting Darwin's original formulation. In turn, we think that the concept of species recognition is far more important than usually recognized, has been traditionally neglected by biologists, and is testable, either by itself or in concert with other processes, as a promoter of species differentiation. This does not mean that it explains everything or most things, but it should not be dismissed. There is now a considerable sample of fossil material available for testing in its morphological, stratigraphic, ecological, and geographic contexts.

In a recent paper, Hone and Naish (2013) make several statements about the interpretation of exaggerated or "bizarre" structures (Padian and Horner, 2011a, 2011b) in non-avialan dinosaurs that are incorrect. They claim that species recognition could not have been important in extinct animals because (according to them) it is not observed, or not important, in living animals. They recur to discredited arguments about sexual selection in non-avialan dinosaurs, even though every case purported to demonstrate sexual selection in these dinosaurs (and other Mesozoic archosaurs) has been rejected or shown to have

no evidentiary basis. In contrast, species recognition, as we define it (and there are several definitions in the literature), is probably more important than heretofore recognized in both living and extinct animals, and it likely worked in concert with other processes to promote species diversity and morphological evolution.

Here we evaluate the claims of various authors about sexual selection and species recognition as they relate to extinct animals, and we reset the concepts of species recognition, sexual selection, and related terms in a logical hierarchical scheme.

2. Claim 1. Only processes that have been observed in available living animals (i.e., those animals that have been adequately studied to date) were present in extinct animals

For example, Hone and Naish (2013) claim that "multifunctionality for many such [bizarre] structures is probable, given extant analogues"; however, "invoking species recognition as the primary selective mechanism driving the evolution of such structures is problematic given the lack of evidence for this in extant species"; that "fossil animals must have been subject to the same selection pressures as extant ones" (how can one know "selection pressures" in extinct animals?); and that "nonavialan dinosaurs were likely similar to extant animals and probably used multiple signals as identifiers" (our emphases).

These arguments violate the concept of *uniformitarianism*, the philosophical foundation of science. True uniformitarianism holds only that the *laws of nature* are immanent, and by no means can one assume that the processes and patterns that governed extinct creatures and their environments are restricted by what is available to observe in the present day. So it is incorrect to claim that because we have not yet observed (or looked for, or intensively studied) a process in today's world, the process could not have existed in the past or was not important.

Moreover, arguments cannot be justified solely on the basis of analogies, because they do not provide evidence for anything, and are merely rhetorical devices. To substantiate analogies, *specific* structures between analogized groups must be identical in order to postulate similar functions. For example, dinosaur cranial ornamentations are vastly different than they are in dimorphic birds and mammals. On the other hand, Darwin's (1859) classic analogy between artificial and natural selection works because he was able to show that both processes depend upon natural, inherited variations that succeed differentially under given circumstances; in fact, his comparison was ultimately based on the homology of genetics.

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