Letters Response

Response to Revilla, and Buckley and Ruxton: the resource dispersion hypothesis

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We agree with Revilla [1] that the resource dispersion hypothesis (RDH) indeed lacks comprehensive evidence in any one specific case; however, this deficiency results from a lack of good tests, rather than from the failure of any tests [2]. Revilla's claim that 'we only need evidence against one of its assumptions and/or predictions to invalidate it', is too sweeping. RDH cannot be rejected just because it does not work everywhere or is difficult to test. Ecological models can only be refined into theories by discovering where they do not work, as well as where they do [3]. The costs of group living that Revilla cites do not detract from the proposition that heterogeneous resources will lower those costs compared with homogenous resources. Revilla sees a 'conceptual gap' between the RDH mechanism and a causal means of group formation because he incorrectly assumes that wherever resources are heterogeneous, RDH automatically predicts animals to live in groups. RDH was always a facilitating, rather than a causal, factor leading to group formation [4,5]. We agree that 'resource patchiness alone' is not enough to explain group living (indeed, we have previously outlined why simultaneous dispersal costs are crucial [6,7]) – RDH is not exclusive of other theories.

The 'future value' of food

Many of the heterogeneous resources that RDH would predict to affect animal distributions are not food, and therefore need not deplete (water holes, nesting sites, etc.). Depletion might also be of little significance in 'rich patch cases' of RDH [4]. Additionally, some food resources (e.g. worms, fruit, nectar, and terrestrial insects) might replenish rapidly enough to eliminate serious future competition costs [8,9]. Buckley and Ruxton [10] question whether RDH still holds in the remaining subset of scenarios when depletion might be significant. However, temporal independence of resources serves as a modelling simplification, and there are three reasons why depletion need not challenge the RDH:

First, resource depletion affects both primary and secondary animals. Thus, primaries will experience lower resource availability in the environment, so territories would be scaled up to compensate.

Second, if competition associated with depletion incurs a cost to primaries, RDH nevertheless predicts that, where resources are heterogeneous, such costs will be lower (and hence group living more favoured) regardless of the level of depletion.

Third, even if secondaries impose some magnified costs owing to resource depletion (i.e. depletion becomes disproportionately larger, or longer lasting, with increasing group size), costs of depletion can still be minimized short of secondaries being evicted from the territory: (a) Secondaries might often put up with lower food security than that of primaries if the costs are still better than dispersing, but, moreover, they might need fewer resources anyway if they do not breed (or are low ranking, smaller etc.); (b) in practice, animals are rarely egalitarian, rather they tend to be despotic and structured in their interactions. Simple simulations, prompted by Buckley and Ruxton's letter, indicate that secondaries are easily supported in such a scenario despite depletion.

Buckley and Ruxton remind us of the complications in predator-prey relationships, and between any organism and their resources, and thereby warn us to keep a keen naturalistic eye on theoretical simplifications. They are right to cite resource depletion as influencing food availability, but it does not conflict with the predictions of RDH.

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0169-5347/03/$ - see front matter
doi:10.1016/S0169-5347(03)00155-1

Book Reviews

Counting the pages of books about dinosaurs and birds

Mesozoic Birds: Above the Heads of Dinosaurs edited by Luis M. Chiappe and Lawrence M. Witmer. University of California Press, 2002 £66 hbk (532 pages) ISBN 0 520 20094 2
Dinosaurs of the Air by Gregory S. Paul. The Johns Hopkins University Press, 2002. US$49.95 hbk (460 pages) ISBN 0 8018 6763 0

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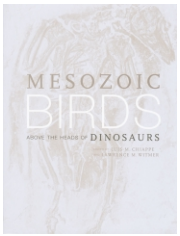

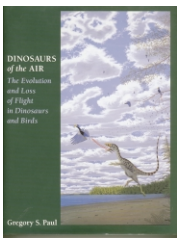

The past few years have been an amazing time for students of bird origins – exceptional new feathered and nonfeathered theropod dinosaurs, birds such as *Rahonavis* that don't look like birds [1], theropods, such as alvarezsaurs and the four-winged *Microraptor*, that do look like birds [2,3], even fake birds ('*Archaeoraptor*') that aren't even birds at all [4], have been discovered and described at an alarming pace. Because the number of new species of Mesozoic birds discovered and described over the past ten years more than triples those known for much of the past two centuries, keeping up with the recent literature in this area can be more than a little confusing. It is helpful then to sometimes consult books, and you could do worse than to read these two recent offerings.

Although essentially dealing with the same subject matter – the early fossil record of birds and their dinosaurian relatives – *Mesozoic Birds: Above the Heads of Dinosaurs* and *Dinosaurs of the Air* couldn't be more different. In the first of these two volumes, Chiappe and Witmer have assembled a sequence of authored papers (many addressing topics of interest for the first time) that deal with specific subjects tied together within the general arena of Mesozoic avian evolution. This book is primarily a collection of research contributions whereas Paul's thesis in *Dinosaurs of the Air* is to present a summary of the dinosaur and bird fossil record and to interpret it in light of his own ideas regarding the origin and evolution of flight. The first book then is less suitable for a general readership and the latter is eminently so; both fill a niche and have been long anticipated by the scientific community.

One great advantage of *Mesozoic Birds* is that it presents a status report of an active field of enquiry. Several chapters present detailed descriptions of taxa hitherto known only from short initial reports in the primary literature (*Shuvuuia* and *Vorona*), or summarize anatomical information pertaining to tantalizingly incomplete but informative fossils (*Avimimus* and *Alvarezsaurus*). Fossil material discussed in this book is very well presented, both adequately described and evaluated in context with the use of convincing character analyses. Descriptive chapters are augmented with contributions presenting 'state-of-the-game' systematic analyses for non-avian theropods (Clark *et al.*) and basal birds (Chiappe) that bring readers up-to-speed with the current consensus. The editors of *Mesozoic Birds*, Chiappe and Witmer, have certainly achieved their goal – to synthesize this diverse field of study (comprising topics such as the origin of birds and the evolution of their flight with the taxonomy of *Archaeopteryx* and reviews of feathers, histology and tracks) without appearing clumsy (and more importantly, out-of-date). As is the case with many edited amalgamations of co-authored papers, *Mesozoic Birds* was long in the pipeline, a fact that is happily not reflected by the bulk of its chapters.

By contrast, and departing somewhat from current consensus, Paul's lavishly illustrated *Dinosaurs of the Air* is a work of art, albeit hanging by a thread of science. Readers will be left in no doubt about the artistic ability of the author and, indeed, about his ability to summarize effectively literature pertaining to the origin of birds in a concise and engaging manner. I would certainly recommend *Dinosaurs of the Air* to anyone entering the field for the first time – it is exceptionally well illustrated and provides a great introduction to the major fossil groups of dinosaurs and birds. Enough said? No, because there is a thread inherent to *Dinosaurs of the Air* that comes to the fore in later chapters – Paul has an agenda with this book. Following the opening (and very informative) descriptive and anatomical chapters, Paul draws us into his ideas about the evolution of flightlessness; in short, the hypothesis that many familiar groups of dinosaurs (troodontids and oviraptorosaurs among them) do not

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