distinguishing between these processes of coevolution. Similarly, both sets of authors suggest that direct fitness costs of manipulative males might be more than offset by benefits accrued through production of manipulative sons. This view echoes the earlier 'sexy son' hypothesis [4], which has neither theoretical nor empirical support (e.g. [5,6]). In the context of sexual conflict, the idea had been already been modeled in the 1970s [5]. More recently, sexy son effects were investigated in a genetic model of sexually antagonistic coevolution [8]. Although costly female resistance easily led to the exaggeration of manipulative male traits, the inclusion of sexy sons had no effect on the equilibrium values of either trait. This result has a long and consistent history [9].

Another form of indirect selection on female preference, the so-called 'good genes' effects, can shift equilibrium values of male and female traits, and has received little attention in analyses of sexually antagonistic coevolution [7,10]. We noted that these indirect effects are likely to occur, but that theory suggests they will be relatively weak [2]. We do agree with Eberhard and Cordero and with Córdoba-Aguilar and Contreras-Garduño that, in the end, their relative strength in nature will only be resolved by experiments, and that more experiments are required. We do not agree that attempts have not been made to assess indirect benefits in those species where direct costs have been assayed. One of us made an initial attempt at such an experiment (in the field) over ten years ago [11], and more recent experiments, by Holland, Rice, and Promislow [12–14], collectively do not make a strong case for substantial good gene effects. Future experiments might do so.

Córdoba-Aguilar and Contreras-Garduño make several claims that puzzle us. For example, in no place did we argue that males usually emerge at the 'forefront' in conflicts, or that males 'take over' the reproductive 'decisions' of females, or that such takeovers give rise to unending coevolution. The closest we came to this was a healthy distance, when we stated that 'neither sex can be said to win a conflict' [2]. Two of Córdoba-Aguilar and Contreras-Garduño's prescriptions – studying female traits influencing fertilization, and mapping traits on phylogenies –are interesting but ill defined at best, and in spite of their claims, both types have been conducted and were cited [2].

Eberhard and Cordero would like to see fitness assays of direct and indirect selection in wild populations. So would we; although we think that this is a tall order given the obstacles that Eberhard and Cordero note in assaying these same effects in the lab. Both sets of authors would also like to see more taxa included in sexual conflict research. We agree and therefore ended our review with 'The taxonomic breadth and range of phenotypic traits that are involved in sexual conflict…remains unclear' [2]. We hope that our optimism will encourage further theoretical analysis and careful empirical work in a diverse array of taxa.

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Letters

'Big bang' for Tertiary birds?

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I enjoyed Feduccia's [1] recent article in *TREE* where he reiterates his hypothesis that the radiation of modern birds (Neornithes) occurred in an 'explosive manner' in the aftermath of the 'Cretaceous–Tertiary (K–T) cataclysm' [2]. I note, however, that this argument [1,2] is based primarily on counts of the number of fossil neornithine genera, before and after the K–T boundary. Feduccia's 'big bang' hypothesis does not consider the fact that molecular clock studies are becoming increasingly less discordant with the fossil record as both calibration and rate

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estimation methods are refined [3,4]. Furthermore, phylogenetic interpretations of the fossil record do not support an 'explosive' model for the modern avian radiation [5]; the debate is not cut and dried [1,2].

Although some earlier molecular clock studies placed all neornithine divergences deep in the Cretaceous [6,7], recent studies have noted that the accuracy of genetic time estimations are dependent on the establishment of a phylogenetic framework for Neornithes as well as simply knowledge of their numbers and ages [4,5]. Molecular watchmakers accept that, given knowledge of the neornithine record, most internal calibrations are problematic [4]. I do, however, wish to echo Feduccia's assertion [1] that the other 'major problem' inherent to this discussion is assignment of fossil fragments from the Cretaceous to modern orders on the basis of little or no evidence [8,9]. Irrespective of which side of the K–T boundary is being considered, convincing placement of a fossil within a clade of Neornithes requires characters that are demonstrably diagnostic (via cladistic methods) to the lineage in question [5]. The waters have been muddied considerably in this respect as referrals of Cretaceous fossil bones to modern clades on the basis of informally evaluated characters and intuitive systematic assessments have been commonplace [8,9]. Feduccia glosses over the fact that there are large numbers of well dated and phylogenetically constrained fossil modern birds known from rocks of Eocene age and younger – the placement of these taxa within the tree of Neornithes (as it is developed by neontologists) corroborates some clade divergences before the K–T boundary [5], which is less discordant with recent molecular clock estimates. It is time, therefore, to move beyond the current debate.

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'Big bang' for Tertiary birds? A reply

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In a recent Opinion article in *TREE* [1], Feduccia maintains his support for an explosive radiation of modern (neornithine) birds from a late Cretaceous shorebird-like ancestor. However, we think the relevant data do not show this and that Feduccia does not clarify the exact composition of his 'transitional shorebirds'.

Feduccia's 'big bang' theory [2] has moved tinamous, ratites, waterfowl and flamingos to the base of the neornithine radiation [3]. However, he does not take into account attempts to address the transitional charadriiform hypothesis with a molecular phylogenetic approach [4,5]: he claims that genetic studies focus on taxa (modern charadriiforms, paleognaths and galloanserines) that are not relevant to the source of the modern radiation [1]. If so, then it would be appropriate for Feduccia to specify the relevant taxa rather than referring 'transitional' shorebirds, 'paleognaths' and 'some other' lineages [1] to the base of the neornithine radiation.

Because no Cretaceous fossil flamingos, ratites or tinamous have yet been found, Feduccia favors an ecological concept [6] over a direct interpretation of the fossil record. Several fossils from the Cretaceous [7,8] do point to Mesozoic neornithines, but Feduccia does not take into account those with limited character diagnosis [3].

Feduccia also claims that the temporal discrepancy between molecules and fossils indicates that either the molecular or fossil-bird tempo is wrong [1,3]. It might be that neither data set is wrong; they might simply reflect different signals. A Cretaceous origin for many neornithine clades [4,5] should not be interpreted as direct support for the presence of modern albatrosses or pelicans alongside more archaic birds [1]. It is plausible that the diversification of major bird clades did take place near the Cretaceous–Tertiary (K–T) boundary, as indicated for various mammals [9]. Molecular studies at this scale are still limited, and we can only guess whether the patterns observed in disparate lineages (Cretaceous ratites, passerines and anseriforms) document the exception or the rule [4,5]. Hence, neither clocks nor fossils undisputedly confirm whether crown neornithines passed 'unblemished'

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