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Ecological modelling, size distributions and taphonomic size bias in dinosaur faunas: reply to Brown *et al.*

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Understanding dinosaur palaeobiology requires appropriate reconstruction and interpretation of the fossil record. Brown *et al.* [1] question our interpretation and the modelling approach used [2]. Here we address their concerns.

Fossil record. Brown *et al.* [1] suggest that the observed scarcity of small dinosaurs in global datasets results from taphonomic and researcher bias towards larger taxa. They highlight the fact that recent descriptions of small taxa reduce left-skewness in body size distributions. Nonetheless, reduced skewness does not contradict our original prediction, so long as the proportion of smaller-sized taxa remains low relative to modern mammalian ecosystems. Moreover, fig. 1a of Brown *et al.* [1] could also be interpreted as evidence that, despite new finds, a ‘gap’ in the range from approximately 32 to 2000 kg is a stable finding since the early twentieth century up to 2012. Whether or not this gap is based on the mechanism we propose, it seems that it has not been filled by new findings for over a century.

Brown *et al.* cite evidence that species accumulation curves over time for smaller taxa from the Dinosaur Park Formation (DPF) show no sign of asymptoting [3]. Closer inspection reveals this is true only for theropods, not ornithischians. One conclusion could be that we already have a good understanding of sauropod and ornithischian diversity (although new finds could easily refute this idea), whereas many small theropods await discovery. Another interpretation, more relevant to our hypothesis, could be that the DPF lacks sauropods, yet it is the extreme sizes that this particular group reached which had the major influence on vertebrate faunas in our model. Conceivably, our prediction of reduced niche opportunities for small species could be under-expressed in dinosaur assemblages lacking extreme giants.

Model. Brown *et al.* stated that, because interspecific competition was the only limiting factor in our model, all populations would inevitably decline towards extinction, leaving only one surviving taxon, probably the smallest. The latter conclusion is strange, since they (mistakenly) claimed that our model assumed constant fecundity across species. The former claim is based on the fact that our model lacks (density-dependent) intraspecific competition. Yet, this is certainly not the only factor that might regulate natural populations—interspecific competition, predation, extrinsic factors such as climate, and other factors can all be limiting to a greater or lesser degree. While we agree that intraspecific competition is probably limiting in many cases, we deliberately excluded it to avoid additional assumptions about variation in carrying capacities. Inclusion of this parameter, however, would not alter the fact that, in our model, smaller dinosaur species faced greater competition pressure than larger ones.

We are aware that our model is ‘simplistic’, ‘deterministic’ and lacks ‘temporal dynamics over ecological and evolutionary time scales’ ([2]; p. 11 of supplementary material), and agree that testing our results in models which

include temporal dynamics is an important next step. But it is not possible to simply translate our deterministic model into one of temporal dynamics, especially for extinct size-structured populations for which information on ages at sexual maturity, reproductive output and other demographic changes during ontogeny are lacking for a wide variety of species and size classes. Including an expanded array of ecological interactions would also be interesting, but would probably make effects of size-specific competition difficult to discern from those of the overall array.

Our major purpose was to highlight the fact that different roles of juvenile stages probably made dinosaur ecosystems function differently from mammal ones. Modelling these differences does not require a high degree of complexity; our simplistic model proved a useful step towards unravelling how these two ecosystems did differ. To our knowledge, potential consequences of the longer series of ontogenetic size stages have not been explored in detail in dinosaur palaeobiology. Our prediction of a size-gap in dinosaurs due to higher interspecific competition was a theoretical concept that appeared in a deterministic model and was robust to numerous variations in the original settings. The model itself

simply represents the logical conclusion that smaller-bodied dinosaurs had reduced niche opportunity, assuming niches are size-specific. Several model outcomes matched observations from the fossil record, indicating that dinosaur size distributions could be expected to differ from those of mammals, and offering one potential, additional explanation for the failure of non-avian dinosaurs to recover after the K-T event. How this effect would be modified—attenuated or reinforced—when considering specific trophic or taxonomic groups (we note an earlier omission that theropods lack the left-skewed distribution observed in sauropods and ornithischians), varying scenarios of parental care or density-dependent intraspecific effects and temporal dynamics, remains to be investigated. Given their ontogenetic complexity, however, it is difficult to see how size-specific competition would not be important for dinosaur communities. Hence, if no size gap were found, we probably need an explanation for why not; until such an explanation is presented, our fundamental assumption remains interesting. We eagerly await new findings, such as those presented by Brown *et al.* that will lead to development of more realistic models, and a broader understanding of dinosaur ecosystems.

References

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