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Response to Comment on “The influence of juvenile dinosaurs on community structure and diversity”

Katlin M. Schroeder^{1*}, S. Kathleen Lyons², Felisa A. Smith¹

¹Department of Biology, University of New Mexico, Albuquerque, NM, USA. ²School of Biological Sciences, University of Nebraska, Lincoln, NE, USA.

*Corresponding author. Email: maguire@unm.edu

The analysis of dinosaur ecology hinges on the appropriate reconstruction and analysis of dinosaur biodiversity. Benson *et al.* question the data used in our analysis and our subsequent interpretation of the results. We address these concerns and show that their reanalysis is flawed. Indeed, when occurrences are filtered to include only valid taxa, their revised dataset strengthens our earlier conclusions.

Benson *et al.* (1) questioned our finding (2) of a persistent carnivore body size gap in dinosaur communities. Specifically, they argued that (i) we omitted communities at odds with our hypothesis, (ii) our data were pseudoreplicated and biased toward Late Cretaceous North America, and (iii) we overlooked important taphonomic biases. We believe these critiques to be unfounded and explain in detail below.

Benson *et al.* suggest that nonconforming communities were omitted from our dataset and suggest additional formations to use. These suggestions stem from a flawed assessment of community availability. Our community dataset consisted of formations containing at least four valid taxa. Conversely, Benson *et al.* used raw occurrence data from the Paleobiology Database (paleobiodb.org) and selected formations “that include more than four dinosaur-yielding localities.” This method is invalid, as occurrences are not equivalent to taxonomic diversity. For example, downloaded data for the Hell Creek Formation yielded 323 genus or species occurrences, but 284 of these were duplicates. Of the 39 unique taxa, three were avian, five were synonymous with other taxa, and seven were taxa that have never been found in the Hell Creek. The difference between the raw PBDB download and the vetted taxonomic data corresponded to a 92.6% error rate.

Moreover, Benson *et al.* suggest the inclusion of several questionable sites, including the Kem Kem Group, which consists of two separate formations containing only three carnivorous taxa identifiable below the family level. Ironically, the Kem Kem Group is perhaps most well-known for its potential taphonomic and collection biases toward large-bodied theropods (3) represented by hundreds of occurrences of vaguely identifiable shed teeth.

Similarly, they argue for inclusion of the Broome Sandstone, which consists entirely of ichnotaxa, for which mass estimation, trophic identification, and comparison to known body fossils is extremely difficult (4). Instead, our analyses relied on an extensively vetted dataset recording the presence of valid taxa, sufficiently identifiable for mass estimation and trophic assignment, regardless of their frequency in the fossil record. We focused on communities containing both herbivores and carnivores so that analyses of trophic guilds could be performed within the same formation, although five monotrophic communities were also included from underrepresented continents/time periods. When examining formations that fit our criteria, the communities remaining to analyze (and indeed those we used) are simply the most taxonomically diverse communities available (Fig. 1E); it is telling that many of these same communities were selected independently in a similar analysis by a separate research group (5).

Despite our concerns about the validity of data, we reran our earlier analysis to evaluate the influence of these additional, though problematic, communities. Including every community possible after proper taxonomic vetting, as well as the communities of concern noted by Benson *et al.* (Fig. 2), increased our carnivore dataset from 39 to 56 communities. Of these, 75% exhibited a carnivore body size gap (Fig. 1A). Of the 14 communities without a body size gap, most did not contain megatheropods. Of the five remaining communities, all but one were included in our original analysis. Overall, adding communities increased support for our original hypothesis from 89% to 91% of communities (Fig. 1D). We did not predict that a body size gap would be found in all communities, as Benson *et al.* claim, but rather that a gap should be found only in com-

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munities with megatheropods. Similarly, our results did not suggest that gap-containing communities were entirely devoid of carnivores between 100 and 1000 kg, only that a gap of at least an order of magnitude existed most frequently within this body size range—for example, the body size gap between *Dakotaraptor* (285 kg) and *Tyrannosaurus* (6428 kg) in the Hell Creek.

Benson *et al.* argue that the divergence between our global and community-level datasets arose from differences in taxonomic, spatial, and temporal sampling. To demonstrate this, Benson *et al.* pooled our community data ($n = 43$) and compared this “globally treated” set to the median community distribution. However, this is not a global dataset, because it excluded many taxa from poorly preserved/depauperate localities not characterized as communities and potentially introduced taphonomic bias. Further, Benson *et al.* did not constrain their comparison of global and community datasets by trophic guild. Thus, it is unsurprising that they found similarities between their “globally treated” and the community median; we demonstrated that community herbivore body size distributions were not significantly different from their global distribution (2).

Benson *et al.* also noted that our dataset oversampled Late Cretaceous North America. Although their calculation of this oversampling is exacerbated by the inappropriate use of raw occurrence data [Fig. 1, B and C, “Occurrences (PBDB)”] over taxonomic diversity (Fig. 1, B and C, “Global”), this was a valid point. It is unclear, however, why an overabundance of North American formations would bias results if they were indeed a product of taphonomic processes, as Benson *et al.* proposed. Regardless, the consistency in results from the original to the new carnivore community datasets suggested that our observed patterns were not driven by oversampling (Fig. 1D), as the new temporal and spatial extents were nearly identical to the global data. The critique that the Western Interior Basin formations were autocorrelated was particularly weak, and moreover antithetical to the concern about data exclusion. The formations criticized do not all overlap temporally, span up to 14° of latitude, and share as little as 7% of their taxa. Nonetheless, results were robust to this critique; when we collapsed these “autocorrelated” communities into single formations, 90% of all remaining formations supported our hypothesis.

Oddly, Benson *et al.* asserted that our communities were undersampled because many contained fewer than 10 carnivores. The source of this threshold is unclear: Certainly, communities with fewer than 10 carnivores are studied frequently in the literature (6, 7). Benson *et al.* also took issue with our use of body size bins. Not only is the use of body size bins standard practice (8), the carnivore

body size gap surpasses 2000 kg of separation on average, exceeding the size of 83% of the body size bins filled by carnivores (Fig. 1A).

The final class of critique offered by Benson *et al.* dealt with taphonomic processes. The possibility of size-dependent preservation and collection was given special attention in our paper’s first paragraph (2). We agree that taphonomic bias could result in the recovery of fewer small-bodied dinosaurs—specifically, those below 100 kg (9, 10). However, many (57%) of the carnivores in our global dataset were below 100 kg, indicating that these size classes were well represented. The body size gap we identified is above 100 kg; moreover, it is not random, but rather is correlated with the presence of megatheropods. Thus, it was unlikely that bias against small-bodied dinosaurs drove our results. It is also difficult to envision a taphonomic mechanism that selectively targeted single trophic guilds, as communities with carnivore body size gaps did not contain similar body size gaps in their herbivore distributions. This, while taphonomically inexplicable, was ecologically realistic, as resource acquisition and partitioning may have varied drastically between carnivorous and herbivorous dinosaurs as a result of herbivores’ high digestive efficiency (11), vertical food partitioning, and consumption of food at the organ level (12, 13).

Finally, Benson *et al.* asserted that modern mammals do not exhibit bimodality at the continental scale, whereas fossil mammals do. This is inaccurate; modern assemblages are multimodal, and there was no gap in fossil mammals prior to 40 million years ago (14). The emergence of a body size gap in the Oligocene has been linked to a loss of arboreal mammals (15), not a change in taphonomy. Indeed, no taphonomic process has been identified that would differentially preserve small- and large-bodied taxa while excluding preservation of medium-sized animals.

We are indebted to Benson *et al.* for their interest in our paper, and in particular their suggestion to include more communities in our analysis; doing so strengthened our arguments and conclusions about the carnivore body size gap hypothesis. The possibility raised by Benson *et al.* of temporal variation in the presence of the carnivore gap is an intriguing one, and one that we discussed in depth in our paper (2). Indeed, our original results demonstrated that body size gaps were smaller in Jurassic communities; we hypothesized that this resulted from larger average prey body mass available in the Jurassic, increased competition from endothermic dromaeosaurs in the Cretaceous, and increased potential for ontogenetic niche shift in Cretaceous theropods (2). We agree with Benson *et al.* that dinosaur ontogenetic niche shift, and the evolutionary drivers behind it, are exciting avenues of research and look forward to continuing advances in this field.

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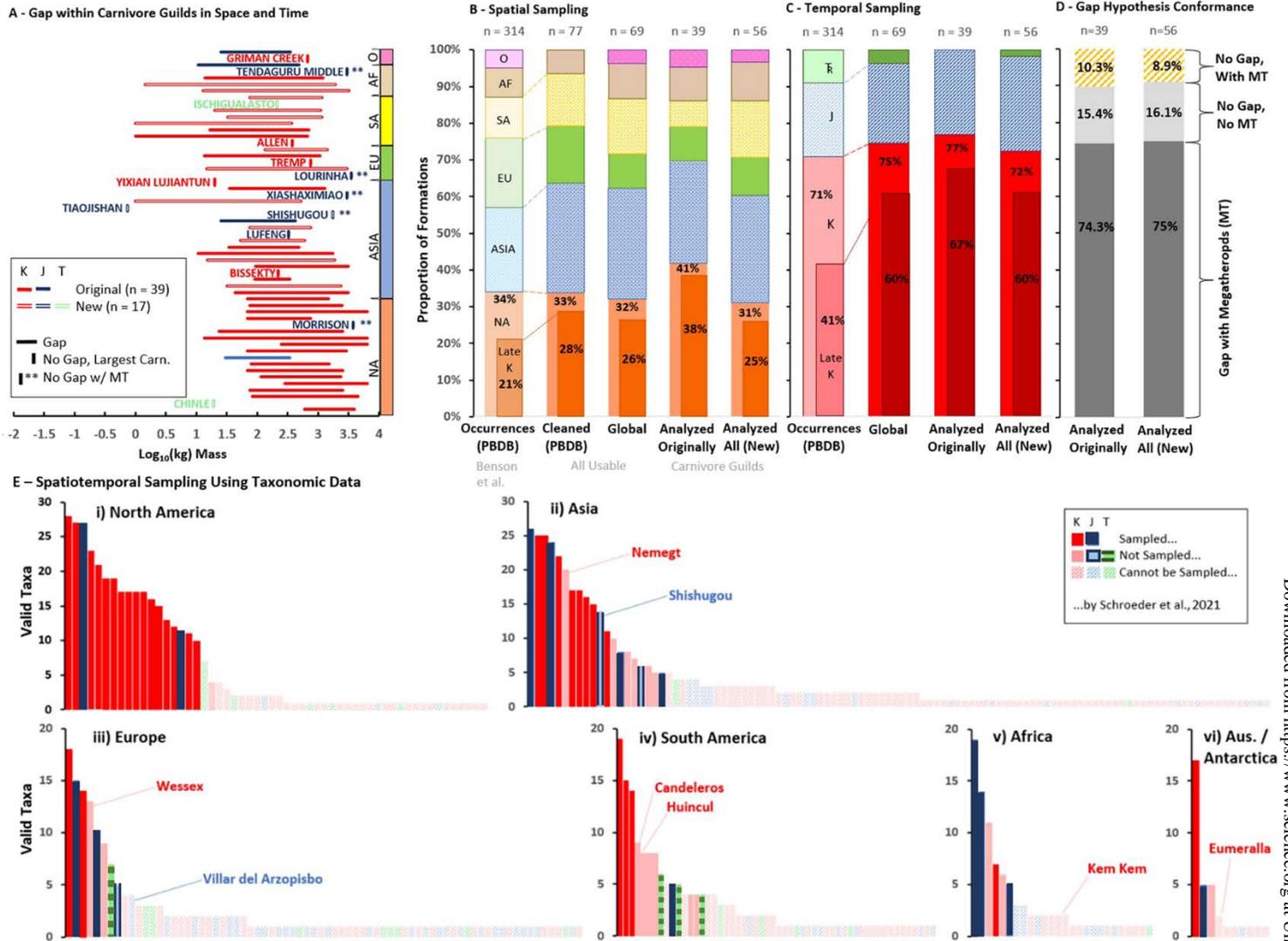


Fig. 1. Comparison of occurrence data (PBDB) and available formations based on actual taxonomic data from the PBDB and those analyzed by Schroeder *et al.* across time and geography. (A) The carnivore gap for all available communities, shown in horizontal lines irrespective of body size bin. Communities lacking a gap are named. For non-gap communities, the mass of the largest carnivore is shown by a vertical bar. Communities not in support of the original hypothesis are followed by a double asterisk. MT, megatheropods. **(B and C)** Spatial distribution (B) and temporal distribution (C) of PBDB formations based on occurrences ($n = 314$) and the available formations using taxa, the global dataset, the original set of analyzed communities, and the inclusive set of communities. **(D)** The proportion of communities that support or do not support the original gap hypothesis from the original set of communities and the inclusive set of communities. **(E)** Spatial and temporal distribution of all formations represented in the global dataset, highlighting those that were analyzed (solid, dark color), those not included in the original community set (solid, light color), and those not available for analysis because of low taxonomic diversity (hatched, light color).

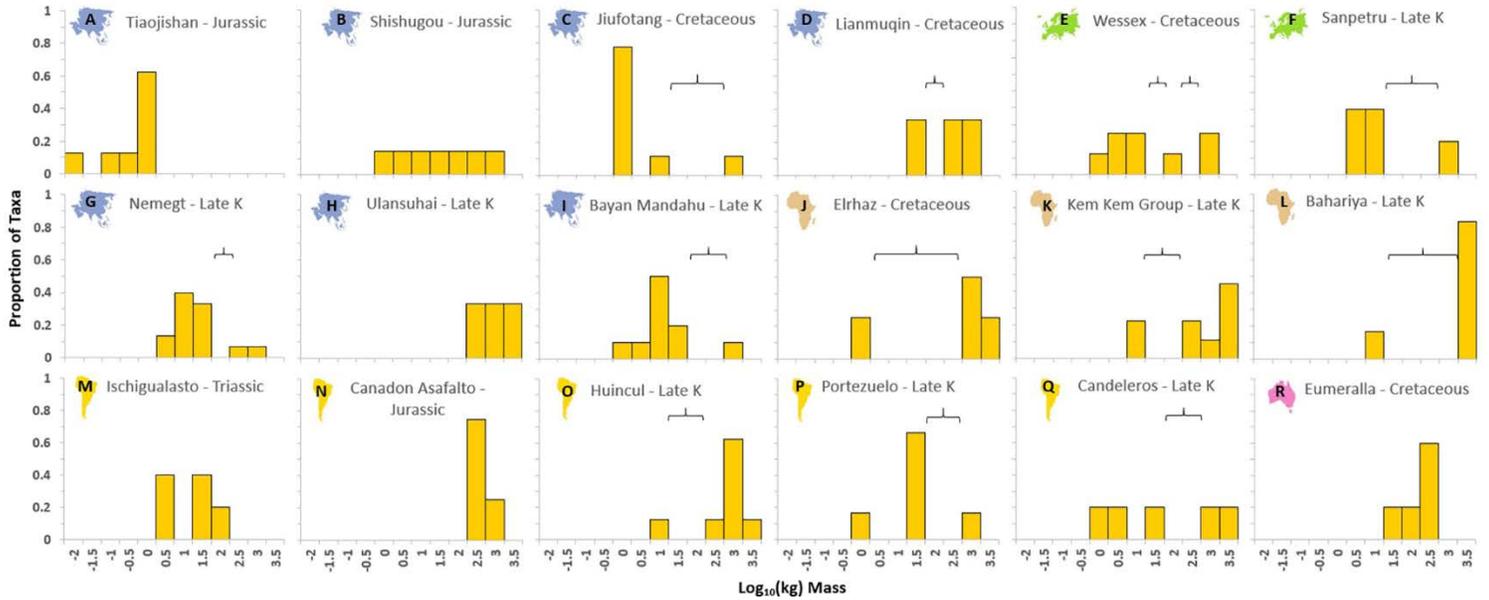


Fig. 2. Body size distributions for all “omitted” formations. Histograms of $\log[\text{body size (kg)}]$ are shown for (A) Tiaojishan Formation, Mid-Late Jurassic of China; (B) Shishugou Formation, Late Jurassic of China; (C) Jiufotang Formation, Early Cretaceous of China, (D) Lianmuqin Formation, Early Cretaceous of China, (E) Wessex Formation, Early Cretaceous of the United Kingdom; (F) Sanpetru Formation, Late Cretaceous of Romania; (G) Nemegt Formation, Late Cretaceous of Mongolia; (H) Ulansuhai Formation, Late Cretaceous of Mongolia; (I) Bayan Mandahu Formation, Late Cretaceous of Mongolia; (J) Elrhaz Formation, Early Cretaceous of Niger; (K) Kem Kem Group, Late Cretaceous of Morocco; (L) Bahariya Formation, Late Cretaceous of Egypt; (M) Ischigualasto Formation, Late Triassic of Argentina; (N) Canadon Asafalto Formation, Early-Mid Jurassic of Argentina; (O) Huincul Formation, Late Cretaceous of Argentina; (P) Portezuelo Formation, Late Cretaceous of Argentina; (Q) Candeleros Formation, Late Cretaceous of Argentina; (R) Eumeralla Formation, Early Cretaceous of Australia. The predator gap present in each formation is indicated by a black bracket, as the gap is not a singular entity, but rather a space of at least one order of magnitude correlated with the size of the largest carnivores in the community. The gap tends to fall between 100 and 1000 kg but is not all-encompassing of this area, nor necessarily bound entirely within it. Gaps were not shown in communities containing only large carnivores (Ulansuhai and Canadon Asafalto), although these would be interpreted as supporting the carnivore gap hypothesis. In the interest of capturing all possible “gap fillers” and addressing even depauperate communities mentioned by Benson *et al.*, rough mass estimates were made for taxa identifiable to family level and above for Kem Kem and Eumeralla.

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