Comment on the influence of juvenile dinosaurs on community structure and diversity

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Abstract: Schroeder *et al*., (Reports, 26 February 2021, p. 941) reported a size gap among predatory dinosaur species. We argue that the supporting dataset is skewed towards Late Cretaceous North America, and the gap was likely absent during other intervals in most geographic regions. We urge broader consideration of this hypothesis, with quantitative evaluation of preservational and dataset biases.

Main Text: Schroeder *et al. (1)* reported a gap in the body size distribution of predatory dinosaurs. They argued that this was caused by the presence of >1,000 kg megapredators, which as giant oviparous animals, produced hatchlings that grew through several orders of magnitude (*2*), traversing distinct ecological niches as they grew (ontogenetic niche shifts). Under this hypothesis (*1*), juvenile megapredators competitively excluded smaller-bodied species, causing a 'predator size gap' at 100–1,000 kg. Schroeder *et al.* (*1*) state that this size gap was absent from the global body size distribution but present within communities. If so, this could reflect the effects of competitive exclusion on community assembly from a broader species pool. However, we argue instead that it occurs because different datasets were used to characterize 'global' and 'community' signals.

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Using the community dataset, we captured community signal as the median relative frequencies of body size classes, and global signal by pooling all species (omitting potential duplicates), this approach recovers almost identical global and community body size distributions (Fig. 1A-B). The different global pattern shown by Schroeder *et al.* (*1*) (Fig. 1A) is based on a more inclusive dataset. This dataset includes species from a larger set of communities, and the absence of a predator gap here suggests that those communities often lacked the gap. 'Gap fillers' are common in the Jurassic–Early Cretaceous, especially among megalosauroids, abelisauroids, and tyrannosauroids, which often coexisted with allosauroid or megalosauroid megapredators. We argue, therefore, that the reported predator size gap does not result from processes of community assembly, but the omission of non-conforming data.

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There could be good reasons to exclude some communities, such as low sampling intensity or size-biased preservation. We searched for patterns using the 314 formations from the Paleobiology Database (paleobiodb.org) that include more than four dinosaur-yielding localities. We find that the dataset preferentially over-samples the Late Cretaceous of North America (Fig. 2) and exacerbates this bias by pseudoreplication of formations: 12% represent geographic extensions of strict lateral equivalents (e.g., Oldman≈Judith River≈Two Medicine; Lance≈Hell Creek≈Laramie≈Scollard (*3*)). Late Cretaceous formations of North America comprise just 21% of the input formations but are 35% of the published dataset (*1*) and 67% of figured exemplars (Fig. 2A). The late Campanian Western Interior Basin of North America is represented six times in the data, but equivalent-aged communities in Asia, Africa and Europe only once.

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The hypothesis of Schroeder *et al.* (*1*) predicts that the size gap should be widespread in time and space, emerging as a definitional feature of dinosaurian biology. However, it is absent in many formations, especially from the Jurassic (Fig. 2C). Furthermore, many well-sampled formations from distinct regions and time intervals were omitted from the published data without explanation (Fig. 2D). These include the Nemegt Formation (Mongolia), Shishugou Formation (China), Huincul Formation (Argentina), and Wessex Formation (United Kingdom) (Fig. 1), all of which contain species within the predator size gap (Fig. 1).

Our different opinion also arises also because we view the dinosaur assemblages of most formations as incomplete samples of the underlying community, as indicated by objective measures of sampling rate (*4*). Of the 43 formations analyzed, only four record more than 10 predator species, and 70% of them have <5 species, suggesting a major sampling deficiency for most of their selected formations (Fig. 2D), even among their figured exemplars (e.g. Cloverly Formation; N = 3 predators). Because of their methodological decisions, poorly sampled assemblages will always contain 'gaps' due to the high count of histogram bins ($N_{bins} = 10$).

Size-dependent preservation and detection distort face-value body size distributions (*5*–*7*). This possibility was dismissed by Schroeder *et al.* (*1*), but such biases are systematic and become compounded, not ameliorated, at larger study scales. For example, extant mammals do not have bimodal body size distributions, but bimodality is widespread in fossil mammals (*7*-*8*), suggesting a preservational interpretation of many ‘size gaps’ in the fossil record. Preservational bias also influences other claims, such as the assertion that the body size distribution of dinosaurs was negatively skewed, with most dinosaur species having large body sizes (*1*,*9*). Instead, quantitative assessments demonstrate strong, ten-fold biases against the preservation of small–medium-sized dinosaurs indicating a large, but hidden, species richness of smaller predators even in well-sampled formations (*6*,*7*,*10*).

In short, we argue that Schroeder *et al*. (*1*) present a biased and pseudoreplicated sample, contain important omissions of evidence, and include interpretations based on the unfounded assumption that taphonomic biases are not important. These issues are compounded by their biological interpretations, which make coarse assumptions regarding the distribution of ontogenetic niche shifts among dinosaurs. For example, small-bodied theropods also underwent these shifts, as evidenced by dietary proxies (*11*), and literature cited by Schroeder *et al*. (*1*) to support their claim of that ontogenetic niche shifts varied among megatheropod groups actually conclude the opposite or are equivocal (*12*,*13*). Furthermore, large-bodied herbivorous dinosaurs grew through several orders of magnitude and must have shown size-dependent ontogenetic niche shifts (*14*), but a ‘herbivore size gap’ is absent (*1*).

We therefore conclude that the ‘predator size gap’ was not widespread in Mesozoic communities. Further, that where it did occur, it may not have resulted from competitive exclusion by juvenile megapredators. The predator size gap may be exclusive to the Late Cretaceous of North America (Fig. 2), with tyrannosaurids outsizing other predators as a product of their evolutionary history (*15*). Various other macroevolutionary and macroecological hypotheses might explain this pattern and largely remain untested, including historical factors such as selective extinctions of non-coelurosaurian theropods, along with ecosystem upheavals during the ‘Cretaceous Terrestrial Revolution’. While we disagree with the findings of Schroeder et al. (*1*), we appreciate the motivation to explore important hypotheses of dinosaur biology. However, such hypotheses can only be tested through critical evaluations of fossil record body-size frequency distributions, which are incomplete and biased by size-dependent preservation and may have varied substantially through space and time.

References and Notes

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Figure captions

Fig. 1. Body size distributions from reanalysis of the published dataset (*1*) (A-B) and for communities excluded from the published dataset (C-F). Histograms of log-body size (kg) for **A,** Global treatment of the published dataset (*1*) (grey fill) compared to the unpublished global dataset (white fill); **B,** Community-level treatment of the published dataset; **C,** Shishugou Formation, Late Jurassic of China; **D,** Wessex Formation, Early Cretaceous of the United Kingdom; **E,** Huincul Formation, Late Cretaceous of Argentina; **F,** Nemegt Formation, Late Cretaceous of Mongolia. Histogram bins introduce arbitrary gaps, so short vertical line segments are used to indicate individual species-body masses in C-F. The hypothesised predator size gap is indicated by a horizontal bar.

Fig. 2. Comparison of dinosaur yielding formations sampled by Schroeder *et al. (1)* compared to the Paleobiology Database (PBDB). Spatial (**A**), and temporal (**B**) distribution of PBDB formations with more than four dinosaur-yielding localities (n=314), compared to those analyzed (n=43) and figured (n=9) by Schroeder *et al. (1)*. **C**, Temporal distribution of the predator gap within formations analyzed by of Schroeder *et al. (1)* (n=43). **D**, Spatial (landmass) and temporal (geological period, color) distribution of the PBDB formations (n=314) with more than four dinosaur-yielding localities, highlighting which were analyzed (solid color) and figured (*) by Schroeder *et al. (1)*. Percentages in D indicate proportions of highest-sampled formations (max n=30) included in the published data of Schroeder *et al. (1)*. In B-D red = Cretaceous, blue = Jurassic, green = Triassic.