

PALEONTOLOGY

The influence of juvenile dinosaurs on community structure and diversity

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Despite dominating biodiversity in the Mesozoic, dinosaurs were not speciose. Oviparity constrained even gigantic dinosaurs to less than 15 kg at birth; growth through multiple morphologies led to the consumption of different resources at each stage. Such disparity between neonates and adults could have influenced the structure and diversity of dinosaur communities. Here, we quantified this effect for 43 communities across 136 million years and seven continents. We found that megatheropods (more than 1000 kg) such as tyrannosaurs had specific effects on dinosaur community structure. Although herbivores spanned the body size range, communities with megatheropods lacked carnivores weighing 100 to 1000 kg. We demonstrate that juvenile megatheropods likely filled the mesocarnivore niche, resulting in reduced overall taxonomic diversity. The consistency of this pattern suggests that ontogenetic niche shift was an important factor in generating dinosaur community structure and diversity.

Dinosaurs were the dominant terrestrial vertebrates for >150 million years, yet their species diversity, particularly at sizes <60 kg, remained well below that of other fossil groups (1). Moreover, their overall body size distribution differed from other vertebrates. Because small-bodied vertebrates can finely partition resources and have high turnover between environments (2, 3), they typically have the highest diversity across regions. Yet curiously, large-bodied dinosaurs were the most diverse. This was particularly true for herbivorous sauropods and ornithischians, whereas the predominantly carnivorous theropods exhibited a more uniform range of sizes globally (4). Although the preponderance of large-bodied forms may be partially due to taphonomy (5), some 90% of dinosaur species <60 kg would have to be missing from the fossil record for the body mass distribution of dinosaurs to resemble that of extinct mammals, which display a pattern less skewed by size (4). Rather, dinosaurs' global body mass distribution patterns may have been linked to their physiology; as oviparous organisms, the largest dinosaurs grew from disproportionately small infants (6). Many dinosaurs exhibited marked morphological differences between juveniles and adults (7, 8), resulting in the utilization of different resources through growth and development (9–12), a relatively rare terrestrial life history strategy observed mostly in large egg-laying reptiles (13). Moreover, rapid growth combined with low adult survivorship (14–16) resulted in large populations of juvenile dinosaurs (17) that may have competed with dinosaurs that were small and medium-sized as adults.

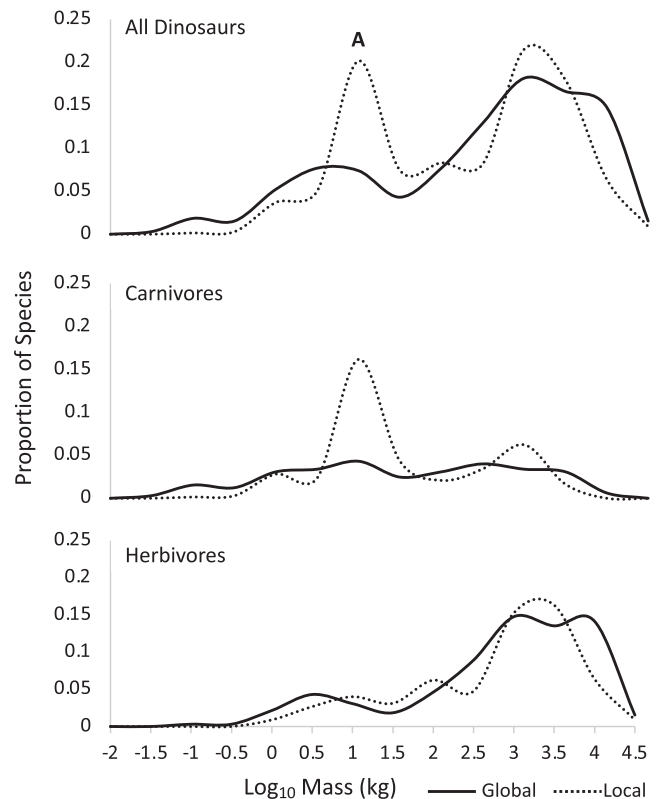
Here, we tested whether low dinosaur species diversity and their unusual body size distribution was, at least partially, due to the large disparity between neonate and adult body size, with juveniles of larger-bodied species filling ecological niches that might have otherwise been available to other taxa. This concept of “ontogenetic niche shift” (ONS) in dinosaurs is widely assumed based on modern correlates (10, 13, 14, 18, 19). For example, based on modeling of hypothetical dinosaur communities, Codron *et al.* (9, 11) predicted that ONS led to reduced diversity of dinosaurs

weighing between 1 and 1000 kg. Despite these predictions, little work has empirically explored juveniles' influence on community structure and overall dinosaur diversity (11, 19). Thus, we examined small-scale body size patterns for evidence of competitive interactions using fossil evidence from dozens of communities representing a wide variety of environments spanning most of dinosaur evolution and evaluated the potential effects of spatial scale and trophic affiliation using well-constrained groups of biologically interacting species.

Our analyses are based on 43 dinosaur communities constructed from data extracted from the Paleobiology Database (20, 21) (table S1). From this baseline, each species' occurrence and taxonomic validity were checked individually against the literature, with taxa deemed synonymous by most experts removed and new taxa absent from the Paleobiology Database added. Masses were derived using averages from the primary literature (table S1). Wherever possible, formations were limited to smaller subsets of cooccurring species. Our dataset represents seven continents spanning 136 million years and includes >550 species. We predicted that dinosaur communities with strong local drivers would diverge from the global distribution (2, 22, 23). Because ecological interactions such as competition might not have influenced carnivorous and herbivorous dinosaurs equally (24), the shape of each carnivore and herbivore dinosaur guild within each

Fig. 1. Community divergence from global distributions.

Distributions comparing 1303 global taxa with local community taxa (median). Overall, global taxa are more left skewed and communities are more bimodal. “A” indicates the largest deviation from the global distribution; the same deviation is clearly shown in the carnivore distribution.



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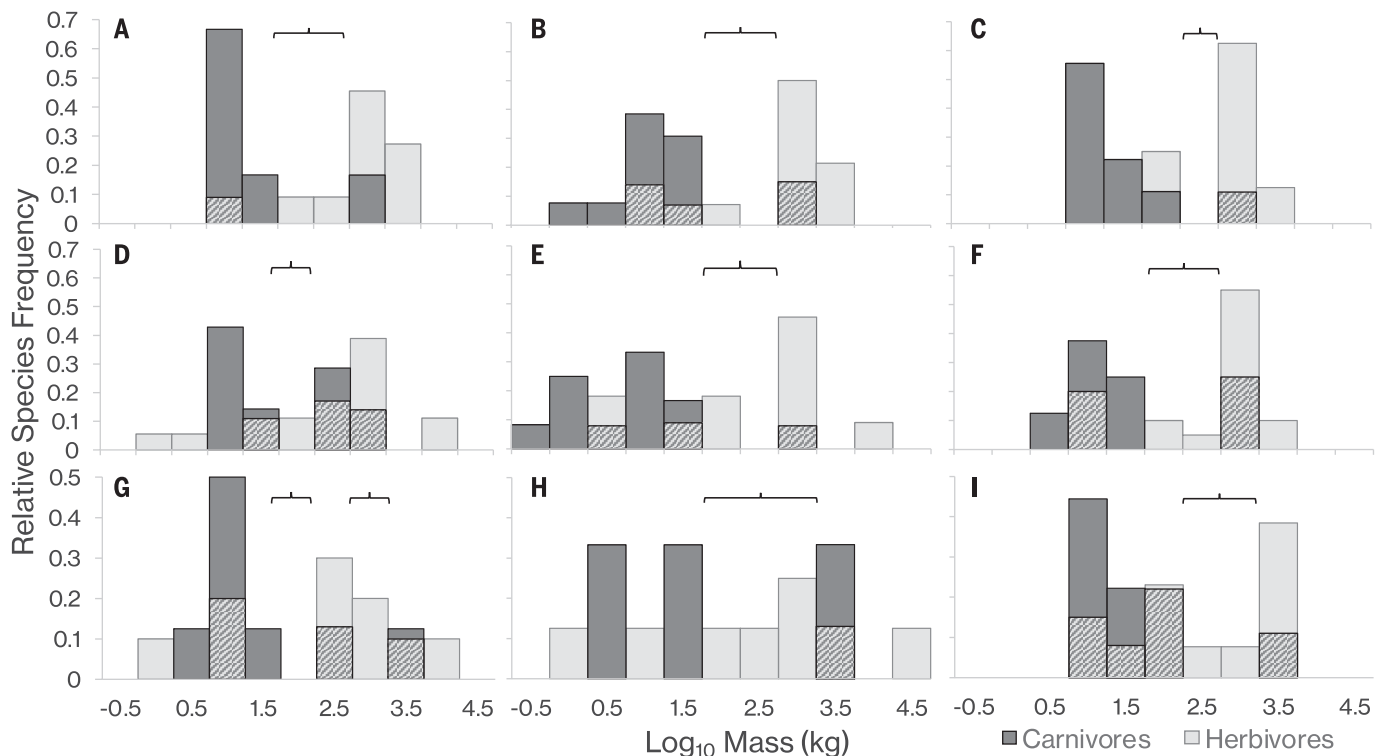


Fig. 2. Community mass-species distributions of nine formations. The formations shown are as follows: (A) Judith River, (B) Dinosaur Park, (C) Two Medicine, (D) Bayan Shireh, (E) Barun Goyot, (F) Horseshoe Canyon, (G) Cedar Mountain, (H) Cloverly, (I) Hell Creek. Brackets illustrate the gaps in carnivore distributions.

community was compared against the global distribution (4).

We found that the overall body size distributions within communities were consistently bimodal regardless of continent, taxa, and time, resulting in less-extreme skew toward large size than evidenced in the global distribution (global skew = -0.577 , community average skew = -0.365 ; table S2). The disparity between the local and global distributions was driven primarily by small (10 to 100 kg) carnivorous dinosaurs (table S4 and Fig. 1); when examined separately, local herbivore body mass distributions closely reflect their global distribution, suggesting that ecological interactions have little effect on their distribution [$P < 0.05$ in 40% of communities, Kolmogorov–Smirnov (K-S) test; table S3].

By contrast, most carnivorous guilds within communities differed from the global carnivore pattern ($P < 0.05$ for 64% of communities, K-S test; table S4), as predicted for strong local interactions. Pairwise comparisons between carnivore guild distributions were nonsignificant in 92% of tests ($\alpha = 0.05$, two-tailed t test with Bonferroni correction for multiple comparisons: $\alpha = 0.000058$ nonsignificant in 99.7%, table S7) despite differing variances, means, and sample sizes, suggesting similar underlying drivers across communities. The only exceptions are formations lacking megatheropods

(carnivores >1000 kg) (e.g., Tremp and Bissekty), those dominated by very small taxa (e.g., Yixian), or those containing multiple sauropods (e.g., Morrison and Lameta), where the availability of multiple enormous prey species may have reduced interspecific competition and allowed the coexistence of an unusually diverse assortment of carnivores.

Community distributions exhibited a persistent lack of carnivorous dinosaurs weighing between 100 and 1000 kg (Fig. 2). The least likely body size of carnivorous taxa was consistently in the 100- to 300-kg range (fig. S1). For perspective, if the modern mammal carnivore assemblage of Kruger National Park were similarly structured, there would be no carnivores between the size of an African lion (190 kg) and a bat-eared fox (4 kg) (Fig. 3). The carnivore “gap” was above the expected limit of taphonomic size bias against small dinosaurs (5), and the drivers of such bias were unlikely to have selectively affected carnivores but not herbivores, suggesting that the gap represents a true biological signal. Moreover, it is unlikely that other clades such as mammals or crocodylomorphs occupied this body size niche because no known Mesozoic mammals exceeded 15 kg (22), and crocodylomorphs were predominantly semiaquatic after the Triassic (25). Furthermore, the width of the carnivore body size gap is correlated with the size of the

largest carnivore (Kendall rank $\tau = 0.437$, $P = 0.000652$). The presence of megatheropods in the community decreased the likelihood of cooccurring species between 100 and 1000 kg even further (table S5). Formations without megatheropods, such as Yixian Lujiantun, did not exhibit body size discontinuities in their carnivorous dinosaur assemblages.

Although the overall distribution of carnivore body size was consistent, the gap itself was dynamic. From the Jurassic to the Cretaceous, the size gap in carnivore species shifted toward larger sizes, mirroring the evolutionary increase in overall dinosaur size (26), and widened from an average of 436 kg to >2060 kg. We suspect that the shift and expansion of the body size gap was caused by a number of changes from the Jurassic to the Cretaceous resulting in increased competition, including (i) decrease by half of average prey body mass, limiting the potential for size partitioning (26); (ii) the diversification of small, potentially endothermic carnivorous dinosaurs (27); and (iii) heightened ONS in Cretaceous megatheropods.

A smaller size gap was found in Jurassic communities, which were characterized by multiple large allosauroids and medium-sized ceratosaurs. Allosauroida was a morphologically diverse clade (28), which likely facilitated the cooccurrence of multiple carnivores within

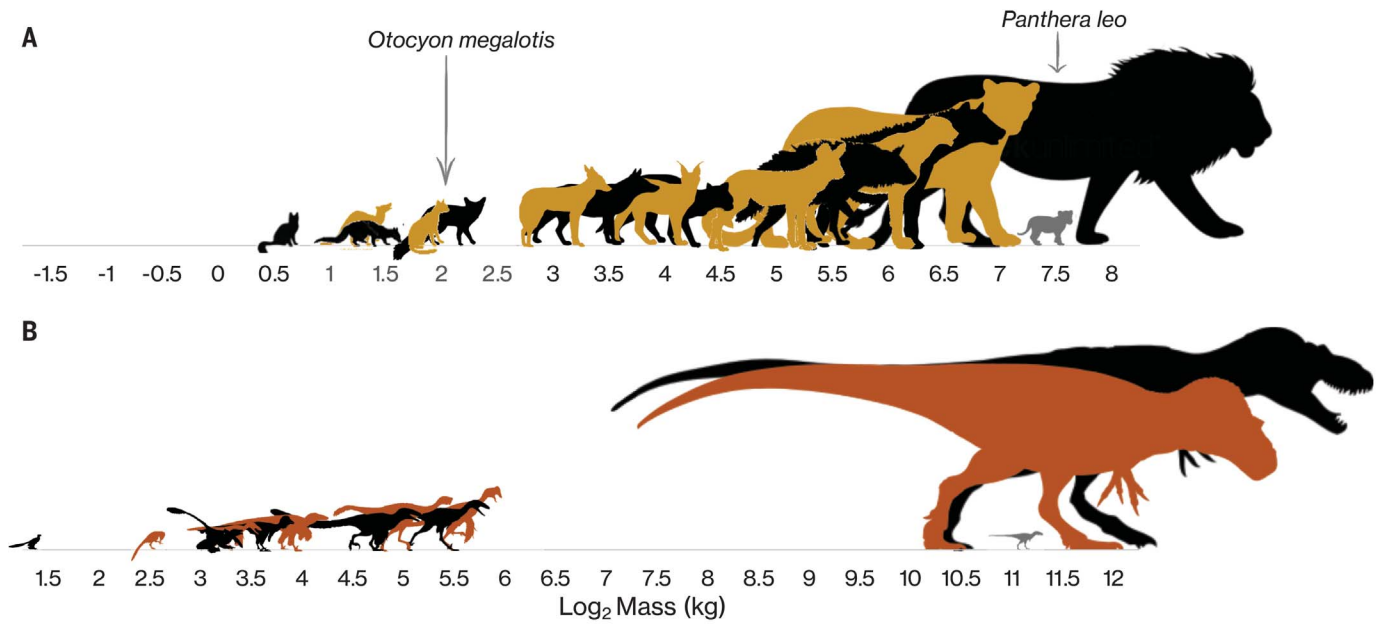


Fig. 3. The dinosaur gap versus modern carnivorous mammals. (A) Carnivorous mammals of Kruger National Park organized to scale by mass. (B) Carnivorous dinosaurs of Dinosaur Park Formation if the largest carnivore were scaled equally to the largest mammalian carnivore in Kruger. Infants (gray) of the largest species shown below adult to show relative growth requirement.

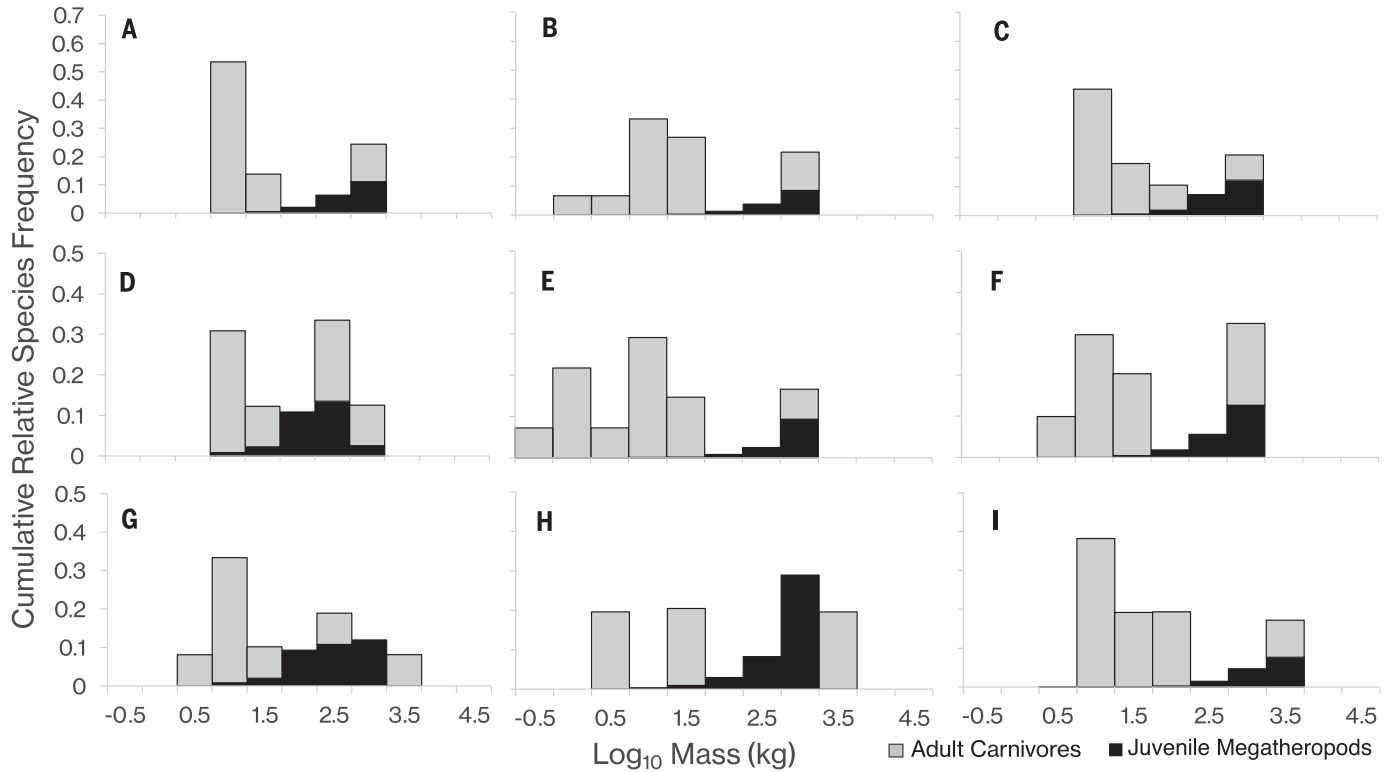


Fig. 4. Community mass-species distributions with juvenile megatheropods as morphospecies stacked with adult conspecifics. The formations shown are as follows: (A) Judith River, (B) Dinosaur Park, (C) Two Medicine, (D) Bayan Shireh, (E) Barun Goyot, (F) Horseshoe Canyon, (G) Cedar Mountain, (H) Cloverly, (I) Hell Creek. The influence of juveniles was highest within the carnivore gap and was proportional to at least 60% of adults in all measured communities. Megatheropods <3000 kg exerted the most influence, matching or outweighing their adult conspecifics in more than half of the measured formations.

communities. Juvenile allosaurs were more similar to adults than Cretaceous megatheropods (29), resulting in fewer feeding niche shifts through ontogeny. Predation on sauropods (30) may have reduced allosaurs' competition with ceratosaurs, which have been associated with piscivory or omnivory, respectively (31). This relatively high morphological differentiation and associated dietary niche partitioning combined with limited ONS in megatheropods may have allowed for the coexistence of large- and medium-sized Jurassic carnivores.

The end of the Jurassic saw a drastic reduction in the diversity of both sauropods and stegosaurs and may have led to the disappearance of many allosauroid taxa (32). Replacing the diverse megatheropod guilds of the Jurassic were Cretaceous communities dominated by a single clade: tyrannosaurs in the north and abelisaurs in the south. Both tyrannosaurs and abelisaurs have been associated with extensive morphological changes through ontogeny (7, 33). Concurrent diversification of dromaeosaurs added competitive pressure on the truncated prey base (34). The ornithischian prey that replaced sauropods likely traveled in multigenerational herds (35), limiting the possibility of predation of isolated juveniles. We suggest that competition for a limited prey source by both large and small carnivores, and the broadening of megatheropod niches, resulted in a widening of the carnivore gap.

For juvenile megatheropods to exclude smaller species from the community, they must represent a non-negligible proportion (>50%) of the biomass. Moreover, juvenile peak biomass must fall predominantly within the carnivore gap. To evaluate the effect of juveniles [<16 years of age (12, 33)] on community composition, we calculated the proportion of juvenile biomass using published growth rates derived from lines of arrested growth and survivorship curves based on relative age abundance from mass-death assemblages recorded in the fossil record (17, 36–38).

We calculated biomass through ontogeny for 1000 individual cohorts of six tyrannosaurs and four allosaurs by multiplying the mass (M_a) and survivorship (S_a) at age in years (a) such that the proportion of any species' biomass represented by juveniles (BM_J) is as follows:

$$BM_J = \sum \left(\frac{M_1 * S_1}{\sum(M_1 * S_1, M_2 * S_2 \dots M_{max} * S_{max})} \right),$$

$$\left(\frac{M_2 * S_2}{\sum(M_1 * S_1 \dots M_{max} * S_{max})} \right) \dots$$

$$\left(\frac{M_{16} * S_{16}}{\sum(M_1 * S_1 \dots M_{max} * S_{max})} \right) \quad (1)$$

We then related BM_J to the proportion of mass contained in adults, set to 1, so that relative

juvenile species proportion (RSP_J) is equal to the following:

$$RSP_J = BM_J * \left[\frac{1}{1 - BM_J} \right] \quad (2)$$

For example, if juveniles represented 60% of the biomass of *Tyrannosaurus rex*, then the juvenile “morphospecies” would be equivalent to 1.5× the taxonomic species. Tyrannosaurs and other megatheropods did not live long past somatic maturity (16), and their juvenile growth rate approached that of mammals and birds (12). This supports our finding that megatheropod biomass peaked at sexual maturity (16 to 19 years of age) and followed a log-normal distribution (fig. S2). For all 10 species examined, juvenile biomass was proportional to least 60% of adult conspecifics (table S6) and exceeded adult biomass in five tyrannosaur species. Substantial proportions of juvenile biomass, including peak biomass, fell within the range of the size gap in all communities (Fig. 4). Thus, juvenile megatheropods represented taxonomically identical but ecologically disparate morphospecies within their communities, with the greatest potential influence in the mass range of 300 to 1000 kg. Our results support the hypothesis that juvenile megatheropods effectively filled the niche of medium-sized carnivores, or mesocarnivores and therefore likely limited diversification of theropods with adult body sizes that fell within this range.

That large carnivorous dinosaurs may have filled multiple niches through ontogeny is not a new assertion (7, 9, 11, 12, 32), yet despite their morphological disparity, adults and juveniles continue to be grouped together in diversity indices, which is accurate taxonomically but not ecologically. Our analysis demonstrates the influence that juvenile megatheropods would have had as morphospecies on their community. We found a gap in the community body size distribution of carnivorous dinosaurs regardless of continent, biome, formation size, or species examined. Our analysis demonstrates that this gap was likely filled by juvenile megatheropods and suggests that low taxonomic diversity in carnivorous dinosaurs was not caused solely by taphonomy or collection bias but rather by competition for resources within and among body size niches filled by juveniles. Dinosaurs existed in a specialized terrestrial community structure, largely organized as a result of their extreme size, ovipary, and resulting ontogenetic niche shift. The “grow fast, die young” approach of megatheropods resulted in a predominance of juveniles in communities, filling the morphological and functional role of mesocarnivores, which as a result are absent from the fossil record as

individual species, artificially deflating diversity indices of dinosaurs as a whole.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 and S2
Tables S1 to S7
References (39–378)
MDAR Reproducibility Checklist

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Not enough room

Modern carnivore communities include species that span a range of body sizes. For example, on the African savannah, there are small species (mongooses), medium species (wild dogs), and large species (lions). This variation reflects available prey sources that best suit each group. Carnivorous dinosaur communities, however, were missing species that fall into the middle, or mesocarnivore, group as adults. Schroeder *et al.* looked across communities, space, and time and found that this absence appears to have been driven by the distinctive biology of dinosaurs, in which giant adults start out as tiny hatchlings. Growing juvenile dinosaurs thus filled the other niches and limited trophic species diversity.

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