Size-driven preservational and macroecological biases in the latest Maastrichtian terrestrial vertebrate assemblages of North America

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Abstract.—The end-Cretaceous (K/Pg) mass extinction event is the most recent and well-understood of the “big five” and triggered establishment of modern terrestrial ecosystem structure. Despite the depth of research into this event, our knowledge of upper Maastrichtian terrestrial deposits globally relies primarily on assemblage-level data limited to a few well-sampled formations in North America, the Hell Creek and Lance Formations. These assemblages disproportionally affect our interpretations of this important interval. Multiple investigations have quantified diversity patterns within these assemblages, but the potential effect of formation-level size-dependent taphonomic biases and their implications on extinction dynamics remains unexplored. Here, the relationship between taphonomy and body size of the Hell Creek Formation and Lance Formation dinosaurs and mammals are quantitatively analyzed. Small-bodied dinosaur taxa (<70 kg) are consistently less complete, unlikely to be articulated, and delayed in their description relative to their large-bodied counterparts. Family-level abundance (particularly skeletons) is strongly tied to body mass, and the relative abundance of juveniles of large-bodied taxa similarly is underrepresented. Mammals show similar but nonsignificant trends. The results are remarkably similar to those from the Campanian-aged Dinosaur Park Formation, suggesting a widespread strong taphonomic bias against the preservation of small taxa, which will result in their seemingly depauperate diversity within the assemblage. This taphonomically skewed view of diversity and abundance of small-bodied taxa amid our best late Maastrichtian samples has significant implications for understanding speciation and extinction dynamics (e.g., size-dependent extinction selectivity) across the K/Pg boundary.

Introduction

The transition from the Mesozoic to the Cenozoic (66 Ma) marks one of the largest terrestrial mass extinction events in Earth’s history, shifting vertebrate ecosystems from dinosaur dominated to mammal dominated (Brusatte et al. 2015). As the most recent of the “big five” mass extinctions, the Cretaceous–Paleogene (K/Pg) extinction has been studied intensely, resulting in one of the best-sampled fossil records of these major mass extinctions (Sloan 1976; Russell 1977; Alvarez et al. 1980; Clemens et al. 1981; Krassilov 1981; Benton 1985; Galbreath 1988; Archibald 1992; Clemens 1992; Novacek 1999; Buffetaut 2004; Archibald and MacLeod 2007; Krug et al. 2009; Archibald et al. 2010; Schulte et al. 2010; Larson et al. 2016; Bazzi et al. 2018; Schoene et al. 2019). Accordingly, it is arguably our best window into the causes and consequences of mass extinctions and provides invaluable insights into our current biodiversity crisis (Novacek and Cleland 2001; Barnosky et al. 2011; Payne et al. 2016). However, substage-level understandings of diversity...
dynamics, ecological interactions, and abundance patterns of terrestrial vertebrates leading up to the K/Pg transition are limited to a few basins worldwide (Brusatte et al. 2015). Of these, the Hell Creek Formation and equivalent terrestrial beds in the Western Interior Basin of the northwestern United States represent, by far, the best studied and sampled example of a latest Maastrichtian dinosaur-dominated ecosystem (Fig. 1, Supplementary Table 1).

As the Hell Creek Formation and equivalent beds provide a fossiliferous, accessible, and meter-scale framework for detailed diversity studies, these deposits have served as the model for understanding the tempo and mode of terrestrial vertebrate extinctions at the K/Pg for well over three decades (Pearson et al. 2002; Russell and Manabe 2002; Horner et al. 2011; Lyson et al. 2011; Tobin et al. 2014; Wilson et al. 2014a; Sprain et al. 2015; Fastovsky and Bercovici 2016; DePalma et al. 2019; García-Girón et al. 2021). Meter-scale analyses of the diversity/richness, taxonomic composition, and relative abundances of individual taxa...
leading up to and through the K/Pg boundary include mammals (Wilson 2005, 2014; Wilson 2013; DeBey and Wilson 2014, 2017), amphibians (Wilson et al. 2014b), turtles and lizards (Longrich et al. 2012; Holroyd et al. 2014), and dinosaurs (Sloan et al. 1986; Sheehan et al. 1991, 2000; Fastovsky and Sheehan 2005; Fastovsky and Weishampel 2005; Horner et al. 2011; Longrich et al. 2011; Lyson et al. 2011; Stein 2019), as well as the entire fauna (Pearson et al. 2002; DePalma et al. 2019). In terms of temporal resolution and fossil abundance, nowhere else in the world comes close to the Hell Creek and Lance Formations, which have generated approximately one-third of dinosaur occurrences for the entire Maastrichtian stage globally (Fig. 1, Supplementary Table 1). Because of the sheer amount of data from the Hell Creek Formation, its inclusion into global-scale analyses, particularly for the Maastrichtian, will inevitably swamp the signal. Accordingly, to understand the role the Hell Creek fauna plays in larger-scale datasets aimed at assessing diversity dynamics (e.g., Wilson 2014), it is paramount that we first explore the underlying taphonomic and sampling biases present within these important deposits. For instance, historical collections for museum display specimens were biased toward complete Triceratops skulls from the Hell Creek Formation. These biases resulted in the preferential sampling of sandstone and siltstone lithologies for museum display specimens to the exclusion of mudstone facies, which preserve incomplete but taxonomically and ontogenetically important specimens (Goodwin and Horner 2010). The recognition of such collection biases led to their subsequent rectification and, eventually, to a much better understanding of dinosaur growth, evolution, and diversity during this time (Horner and Goodwin 2006, 2008; Goodwin and Horner 2010; Horner et al. 2011; Lyson and Longrich 2011; Scannella et al. 2014).

By contrast, detailed studies that explore the potential of preservational (taphonomic) biases to skew our view of faunal composition in the Hell Creek Formation, and equivalent, are rare (but see Wilson 2008; Stein 2019). Dinosaur-dominated assemblages often show distinct differences from modern, generally mammal-dominated, assemblages, with one of the largest distinctions being the pattern of body-size distributions (O’Gorman and Hone 2013). Modern terrestrial assemblages show a consistent positive skew in the body-size distribution, with a higher diversity (i.e., richness) of small taxa and lower diversity of large taxa (Blackburn and Gaston 1994, 1996; Clauset and Erwin 2008). By contrast, dinosaur-dominated assemblages often show a negative skew, with higher diversity of larger taxa and lower diversity of small taxa (Barrett et al. 2009; Butler et al. 2011; O’Gorman and Hone 2013; Benson 2018). As a result, research regarding dinosaur assemblages took two contrasting viewpoints when inferring the mechanisms behind these differential size distributions.

On the one hand, the pattern of dinosaur size distributions can be interpreted as a real biological phenomenon; the result of intrinsic ecological or physiological differences between mammals and dinosaurs, such as through the competitive exclusion of small-bodied dinosaurs by juveniles of larger species (Richmond 1965; Varricchio 2011; Codron et al. 2012, 2013; O’Gorman and Hone 2013; Schroeder et al. 2021). On the other hand, a negatively skewed body-size distribution pattern may result from large taphonomic and/or collection biases toward large-bodied taxa (Behrensmeyer et al. 1979; Farlow 1993; Peczkis 1994; Farlow et al. 1995; Brown et al. 2013a,b; Benson 2018; Darroch et al. 2021). Such a bias was detected and quantified in the Dinosaur Park Formation (Brown et al. 2013a,b), is supported by contrasting body-size distributions between Recent and fossil (last 10 Ma) mammals (Benson 2018), and contrasts with typically positively skewed size distributions in Lagerstätte-type deposits of the Jehol (Benson 2018). In addition to the physiological and ecological ramifications of body-size distributions, the debate regarding the relative importance of taphonomic versus biological factors in shaping these patterns has major implications for interpretations of extinction mechanisms. Body size is implicated as a major factor for extinction vulnerability (Raup 1986; Gaston and Blackburn 1995; Jablonski et al. 1996; Cardillo and Bromham 2001; Cardillo et al. 2005; Olden et al. 2007; Payne and Heim 2020), including as a
hypothesized extinction filter at the end-Cretaceous extinction event (Bakker 1977; Russell 1977; Buffetaut 1990; Archibald 2011; Wilson 2013; Benson et al. 2014; Berv and Field 2018).

Given that the Hell Creek and Lance Formations disproportionately shape our understanding of diversity and extinction at the Mesozoic twilight, our study examines the taphonomic body-size patterns within these formations. We specifically concentrate on dinosaurs, which span a very large body-mass range that allows us to test the effects of body mass on preservation across several orders of magnitude. We compare the assemblage-level effect of body size on various taphonomic indicators, similar to work previously done for the Dinosaur Park Formation (Brown et al. 2013a, b); test for the presence and magnitude of the relationships; and identify biases that impact our understanding of extinction dynamics at the K/Pg boundary.

Methods

Hell Creek Formation and Lance Formation Dinosaur Faunal Dataset

Recent debate regarding the taxonomic validity and synonymy of dinosaur species from the Hell Creek Formation, particularly relating to the effects of ontogeny (Boyd et al. 2009; Horner and Goodwin 2009; Ott and Larson 2010; Scannella and Horner 2010, 2011; Campione and Evans 2011; Parke 2011; Longrich and Field 2012; Larson 2013; Brusatte et al. 2016; Schmerge and Rothschild 2016; Woodward et al. 2020), has resulted in a lack of consensus regarding the alpha-level taxonomic diversity of dinosaurs in this formation. To account for this uncertainty, we assembled two faunal lists for the Hell Creek Formation, one that considers the majority of recently synonymized taxa as valid taxa on their own (“maximum taxonomic split” list, \( N_{\text{Hell Creek split}} = 35 \) species; Supplementary Table 2) and another that considers all recently synonymized taxa as indeed junior synonyms (“maximum taxonomic lump” list, \( N_{\text{Hell Creek lump}} = 25 \) species; Supplementary Table 2). A complete list of taxa considered valid in the split dataset and subjective junior synonymy under the lumped dataset is included in Supplementary Table 2. These contrasting faunal lists allow assessment of the effects of taxonomic opinion on taphonomic correlations.

We also tested the effect of paleobiogeographic and/or formational boundary faunas, considering that the dinosaur fauna was likely geographically cosmopolitan, at least within Laramidia (Lehman 1987, 2001; but see Vavrek and Larsson 2010; Lucas et al. 2016). In a secondary analysis, we assembled a faunal list for the Lance Formation and combined it with that of the Hell Creek Formation. As with the exclusively Hell Creek faunal lists, we created a maximum taxonomic split and maximum taxonomic lump version of the combined Hell Creek + Lance fauna (Supplementary Table 2). This combined faunal list consists of 43 taxa for the maximum taxonomic split version (\( N_{\text{Hell Creek + Lance split}} \)) and 33 taxa for the maximum taxonomic lump version (\( N_{\text{Hell Creek + Lance lump}} \)). The main differences between the Hell Creek and Hell Creek + Lance faunal lists is the inclusion of multiple avian taxa known only from the Lance.

Dinosaur Body-Mass Estimation

Adult body mass was estimated for all dinosaur taxa (Supplementary Table 2). The majority of these estimates were made using predictive equations generated from linear regressions of limb measurements and body mass in extant taxa. A majority of the body-mass estimates (52%) were taken from Benson et al. (2018), which utilizes the quadrupedal and bipedal scaling formulae of Campione and Evans (2012) and Campione et al. (2014) that is based on the minimum circumference of the femur and humerus. In several cases, for which comparatively little skeletal material is known for a species, body mass was estimated based on a close relative of similar size (e.g., *Triarchuncus* was based on *Albertonykus*, *Acheroraptor* was based on *Sauritholestes*, and *Densversaurus* was based on *Edmontonia*), or scaled relative to comparable elements (e.g., *Sphaerotherolus buchholtziae* was based on dome length from *Stegoceras validum*, which has a comparable frontoparietal dome length). In other cases, a single body-mass estimate was used for closely related taxa of similar body
size; for instance, *Thescelosaurus garbani* and *Bugenosaurus infernalis* were both based on *Thes-
celosaurus neglectus*. Body-mass estimates for taxa known only from teeth (e.g., *Richardoestesia isosceles*, *Paronychodon* sp.) were based on estimates of closely related taxa known from more complete material, such as *Richardoestesia gilmori*, *Dracoceous albertensis*, and *Troodon inequalis* (Carbone et al. 2011). Mass estimates for the avian sample (approximately one-third of the fauna) were derived from Longrich et al. (2011), which uses scaling of the coracoid, though see Field et al. (2013) and Serrano et al. (2015) for additional scaling estimates.

Dinosaur Taxonomic Completeness Index and Taphonomic Mode

Each dinosaur species in the dataset was quantified in terms of its known completeness using the Skeletal Completeness Metric 2 of Mannion and Upchurch (2010), as modified by Brown et al. (2013b) (Supplementary Table 2). This metric examines all skeletal material for each species and determines the average percentage completeness for that species by dividing the skeleton into nine equally weighted regions; for more details, see Brown et al. (2013b). The completeness index also attempts to account for differential completeness between the formations and the effect of synonymy. Each species was also assigned a taphonomic mode following the classification of Eberth and Currie (2005), as implemented in Brown et al. (2013b). The most complete specimen reported in the literature from each taxon was assigned to a taphonomic mode that represents an ordered but categorical disarticulation continuum, from A, articulated (multiple bones from the same skeleton present, with more than 50% of these in natural life position), to B, associated (multiple bones from the same skeleton present, with 50% or fewer of these in natural life position), to C, isolated (individual bones/teeth fully removed from the context of the rest of the skeleton).

Dinosaur Species Discovery Curve Analysis

To assess the effect of body size on the identification of diversity in these units over time, species discovery curves (see Steyskal 1965; Soberón and Llorente 1993; Solow and Smith 2005; Bebber et al. 2007) were generated by compiling the dates of the first description for all dinosaur taxa in all lists from the literature (Supplementary Table 2). These dates considered the differential description dates of the same taxon between the Hell Creek and the Hell Creek + Lance faunal lists. The effect that synonymy may have on certain taxa was also taken into account. For each species, we determined “year of description” \(Y_{D0}\), which is the year of publication of the first description of that species based on Hell Creek material, following the methods of Brown et al. (2013b). For each species, we also calculated “time to description” \(t_{D0}\), which is the difference between the year of description for that species and the year 1883, when the Hell Creek taxa were first described (Cope 1883).

To test differences in discovery rates between taxa in the small and large size classes, the cumulative number of known taxa was plotted across a discovery timeline divided into 10-year bins. Although the current decade (2020–2029) is graphed, it is excluded from the analysis due to obvious incompleteness. Four models were fit to the data: linear \(y = mx + b\), logarithmic \(y = m\log_{10}x + b\), power \(y = bx^m\), and exponential \(y = be^{xm}\). Model fit was evaluated using the Akaike information criterion (AIC). Delta AIC values of 0 were considered the optimal model, with a threshold of 2.0 used to contrast the support of suboptimal models.

Dinosaur Census and Family-Level Comparisons

In the last four decades, there have been six major surveys or censuses of dinosaur richness and relative abundances within the Hell Creek Formation or Hell Creek Formation and coeval deposits (Lehman 1987; White et al. 1998; Russell and Manabe 2002; Horner et al. 2011; Lyson and Longrich 2011; Stein 2019) (Supplementary Table 3). Some of these surveys use abundance data based on articulated/associated skeletons, while others are based on more exhaustive datasets including microvertebrate sites. Data on relative abundance at the family level from these surveys were collected and plotted against average body mass for each family-level clade (derived from the taxonomically lumped datasets). Family body mass was estimated as the average mass of all taxa assigned to that family.
using the maximum taxonomic lumped dataset. The dataset of Stein (2019) is not directly comparable with the other surveys because Ankylosauridae & Nodosauridae, Troodontidae & Dromaeosauridae, and Leptoceratopsidae & Ceratopsidae were grouped in the analysis. Family-level abundance was analyzed as this is the taxonomic rank used most consistently in the published surveys. However, under a taxonomic lumped framework, many of these families become monospecific (i.e., Tyrannosauridae, Hadrosauridae, Thescelosauridae, Leptoceratopsidae, Ankylosauridae, Nodosauridae, Ornithomimidae, Alvarezsauridae, Troodontidae, Caenagnathidae) with the pattern therefore also at least partly consistent with a species-level analysis.

Specimen-Level Intraspecific Dinosaur Abundances as a Factor of Body Mass

We also investigated the effect of body size on taphonomic metrics at the intraspecific level in the most common large dinosaur taxa. Individuals of those taxa passed through most of the adult body-size bins used in this analysis throughout their ontogeny. We predict that, if body size is a taphonomic filter, correlations recovered at the interspecific level should be evident across the growth series of the largest-bodied species in the dataset. To test this, we compiled growth series of the four largest and most abundant dinosaurs in the Hell Creek Formation (Tyrannosaurus rex \[n=25\], Edmontosaurus annectens \[n=16\], Triceratops horridus, and Triceratops prorsus \[n=18\]) by collecting measurement data from articulated or associated specimens. Due to the limited number of overlapping bones among these taxa, several size proxies were used to maximize sampling. Proxies consisted of femur circumference and tooth-row length for T. rex, quadrant height for E. annectens, and basal-skull length for Triceratops. Data were collected from the literature (Forster 1996; Horner and Goodwin 2006; Larson 2008; Campione and Evans 2011) with additional specimen data from personal observations collected by all the authors (Supplementary Table 4). Here, we focused on articulated and associated skeletons or skulls, which comprise the most diagnostic fossils for these taxa; isolated and/or scattered bone-bed elements were not included. Data for Tyrannosaurus femora represent articulated or associated skeletons, whereas data for Tyrannosaurus dentaries and Edmontosaurus and Triceratops skulls represent articulated or associated skulls.

The faunal survey of Horner et al. (2011) also contains relative abundance data of associated skeletons at four different size/age classes (small/juvenile, medium/subadult, large/adult, extra-large/large adult) of multiple taxa. To quantify the effect of body size on relative abundance within a taxon within the formation, the relative abundances of these different size classes were compared for the four most common genera (Triceratops, Tyrannosaurus, Edmontosaurus, and Thescelosaurus).

Hell Creek Formation Mammals

Although much of the project concentrates on the fossil record of dinosaurs, given their large range of body masses, a subset of parallel analyses was performed on the Hell Creek Formation mammal assemblage. A mammal faunal list was compiled from Archibald and colleagues (2011) and Wilson (2013, 2014), with a total of 31 taxa, including 11 multituberculates, 12 metatherians, and 8 eutherians (Supplementary Table 5). Estimated body mass for each species was obtained from Wilson (2013). For each species, skeletal completeness was calculated using the same method as for dinosaurs (Supplementary Table 5). As the record of Hell Creek mammals is predominantly teeth and jaws, the taphonomic modes were expanded to reflect this, being divided into four ordinal categories: isolated teeth, teeth in isolated jaws, associated skulls, and articulated skulls/skeleton (Supplementary Table 5), representing a coarse disarticulation gradient. Both completeness and taphonomic mode indices relied on published specimen data. These data were used to visually and statistically test the pattern of completeness and taphonomic mode across body size in the mammal assemblage.

Statistical Analyses

All analyses were conducted in R statistical language (v. 4.0.2; R Core Team 2009) following the methods of Brown et al. (2013b). Body-mass estimates were log transformed (base 10) or
ranked depending on the analysis. Completeness metrics were also log transformed (base 10) depending on the analysis. Body mass (log10 kg), completeness (%), and \( t_{DE} \) (years) all represent ratio data, whereas taphonomic mode (i.e., articulated, associated, isolated) and size class (i.e., small, large) are ordinal data. Correlations were tested using the function `cor.test` (package: stats), with Pearson, Spearman, or Kendall methods depending on the assumptions of analysis and data type. Correlations between ratio data variables were tested using the Pearson correlation, while those including ordinal data used Spearman or Kendall. While the parametric assumptions of the Pearson correlation are met for the various dinosaur ratio datasets, given the magnitude of the body-mass range and the distribution of the completeness/timing data (raw not residuals), nonparametric correlations (converting ratio data variables to rank) were also performed (Spearman or Kendall) to test the sensitivity of these results and the allow a more direct comparison with the mammal results. While the dinosaur ratio datasets meet the assumptions of Pearson, the mammal datasets (mass and completeness) are not bivariate normal, and only nonparametric tests are used (Spearman).

Statistical comparisons between size classes were performed using the functions `chisq.test` (stats) and `t.test` (stats). Linear models were analyzed using the function `lm` (stats), whereas the nonlinear models were fit with `nls` (stats). Model fit was assessed using the function `AIC` (stats).

The global occurrence of Maastrichtian rock formations was projected onto the present-day global map (Fig. 1) using the function `symbols` (package: graphics) and the “coastlineWorld” dataset in the package `oce` (v. 1.2-0) (Kelley et al. 2016). Occurrence data were downloaded from the Paleobiology Database (https://paleobiodb.org) on 27 August 2020, using the following parameters: time interval = Maastrichtian-age (72.1–66 Ma), Taxon = Dinosauria.

**Results**

**Hell Creek Formation and Lance Formation Dinosaurs**

**Correlation between Body Mass and Completeness.**—Taxonomic skeletal completeness has a consistent, strong, and significant positive correlation with log body mass (Pearson’s product-moment correlation \( r = 0.74–0.76, \ p << 0.001 \)) (Fig. 2, Table 1). These results are consistent across the Hell Creek and Hell Creek + Lance faunal lists and between the two taxonomic permutations (lumping and splitting). While the parametric assumptions are met, given the magnitude of the body-mass range, the correlation was also tested using ranked body mass (rather than absolute estimated body mass) and ranked completeness, and remains both strong and significant (Kendall’s rank correlation \( \tau = 0.69–0.72, \ p << 0.001 \) (Table 1).

When the dinosaur faunal lists are segregated into Ornithischia and Theropoda, body mass is significantly correlated with completeness for all eight theropod treatments and half (4/8) of the ornithischian treatments (the taxonomic split treatments; Table 1). The taxonomically lumped ornithischian treatments, while still showing relatively strong correlations (\( r = 0.59, \ \tau = 0.49 \)), were not significant, although this may be a by-product of having the smallest sample sizes and few taxa below the size threshold (Table 1).

When the taxa are ranked in increasing mass and plotted against their completeness index, a clear trend exists: small-bodied taxa (≥70 kg) are relatively incomplete, and larger taxa (≥100 kg) are relatively complete (Fig. 3). At a threshold (i.e., 60–100 kg), this pattern is similar to that identified using the sliding mean difference method in the Dinosaur Park Formation (Brown et al. 2013b). Likewise, this division allows the Hell Creek Formation dinosaur assemblage to be divided into two, more isotaphonomic (i.e., more preservational equivalent) size classes: small taxa (<70 kg) and large taxa (>70 kg), for subsequent analyses.

In all cases, taxa smaller than 70 kg are <17% complete and no more than 2% complete if Dracorex is not considered valid. If Dracorex is considered invalid (e.g., Horner and Goodwin 2009; Goodwin and Evans 2016), there is no overlap in completeness between the small- and large-size classes. For the taxonomically lumped datasets, the mean and median completeness are 1.5% and 1%, respectively, for
taxa <70 kg and 64% and 81%, respectively, for the taxa >70 kg (Fig. 2B,D, Table 2). For the taxonomically split datasets, the mean and median completeness are 2.4% and 1.1% for taxa <70 kg and 58% and 64% for the taxa >70 kg, respectively (Fig. 2 A,C, Table 2). The small-size class is consistently and significantly less complete than the large-size class in all treatments (Table 2).

Correlation between Body Mass and Taphonomic Mode.—We recovered strong and significant positive correlations between rank body mass and taphonomic mode for all treatments of the Hell Creek + Lance taxa ($\rho = 0.83$–0.86, $p << 0.001$; Table 3). When divided into large- and small-size classes (threshold $\approx 70$ kg, based on completeness—see “Correlation between Body Mass and Completeness”), there are also strong associations between size class and taphonomic mode ($\chi^2 = 25.0$–36.1, $p << 0.001$). In all cases, the small-size classes are predominated by taxa represented only from isolated material, whereas the large-size classes are predominated by taxa known from articulated specimens (Fig. 4).

Correlation of Body Mass and Time to Description ($t_{De}$).—There are strong and significant negative correlations between the length of time until a taxon is described ($t_{De}$) and log body mass ($r = -0.63$ to $-0.79$, $p << 0.001$, $\rho = -0.63$–0.79, $n = 35$–53, $p << 0.001$; Table 3).
Pearson) (Fig. 5, Table 4). In all cases, this correlation is also significant under a nonparametric rank body mass ($\rho$ = −0.47 to −0.75, $p << 0.001$, Spearman) (Table 4). The larger the species’ body size, the earlier it was identified and described, and conversely, the smaller the species, the more time, on average, before it was described. If the $t_{De}$ between the two size classes (<70 kg and ≥70 kg) is compared, then there is a significant ($p < 0.005$) bimodality in all cases, with mean $t_{De}$ of large taxa (57–70 years) approximately half that of small taxa (111–123 years); median values are even more divergent (Fig. 5, Table 4).

**Discovery Rates and Taxon Body Mass.**—Differential $t_{De}$ between the large- and small-size classes (Fig. 5, Table 4) suggests that there may be differential rates of discovery (i.e., discovery curves) between these two size classes. In these analyses, both taxonomic splitting/lumping and formation splitting/lumping significantly affect the model fitting of the cumulative description rates, at least for large taxa (Fig. 6, Table 5). In all datasets, the discovery rates of large-bodied taxa are initially high and relatively constant, but the preferred model for the curve varies from a constant linear rate model (Hell Creek, Lump), an exponentially increasing rate model (Hell Creek, Split), and, finally, a power decreasing rate model (Hell Creek/Lance, Lump and Split) (Table 5, Fig. 6). In half the cases, we cannot reject at least one of the suboptimal models, based on a ∆AIC < 2 and equivalently elevated Akaike weights relative to the optimal model (identified with an asterisk in Table 5). These model ambiguities are almost exclusive to the large-size class taxa, for which we generally cannot reject a broadly constant rate of discovery (i.e., linear model). By contrast, the discovery rates of small-size class taxa show a sharp increase through time (Fig. 6); in all cases, rates are best described by exponential models regardless of taxonomic lumping/splitting or formation (Table 5).

**Change in Dinosaur Body-Size Distribution through Collection History.**—We recover a strong shift in our knowledge of dinosaur body-size distributions as a function of collection history over the last 100 years (Fig. 7). In the Hell Creek and Lance Formations (Fig. 7A), dinosaur discoveries before the 1970s were almost exclusively of larger-bodied taxa, with a few notable exceptions (e.g., *Cimolopteryx rara*: 0.5 kg, described in 1892 [Marsh 1892]). In the Dinosaur Park Formation, dinosaurs between 10 and 1000 kg were rare before 1920 and became increasingly better sampled toward the present day, but taxa <10 kg were unknown until the last three decades (Fig. 7B). Changes in these distributions are supported by significant trends in the size distribution skewness (Fig. 7C). Necessarily, initial years have much lower diversity, which is problematic for

### Table 1. Correlations of estimated taxon body mass (log10 and ranked) and taxon completeness for all Hell Creek Formation dinosaur taxa, as well as Ornithischia and Theropoda subsets. Significance at: **$\alpha = 0.01$, ***$\alpha = 0.001$, ns = not significant.

| Formation          | Taxonomy | Size class | Sample | Log10 mass (Pearson) | Ranked mass (Kendall) |
|--------------------|----------|------------|--------|----------------------|-----------------------|
|                    |          | Size | (n)   | Min. (kg) | Max. (kg) | $r$ | $p$-value | Sig. | $\tau$ | $p$-value | Sig. |
| Hell Creek         | Dinosauria | Lump  | 25    | 0.26 | 13,274 | 0.74 | 2.20E-05*** | 0.74 | 2.20E-05*** |
|                    |          |       |       |      |       |     |           |      |         |           |     |
|                    | Ornithischia | 9    | 16.14 | 13,274 | 0.59 | 0.096 | ns  | 0.49 | 7.97E-02 ns |
|                    | Theropoda | 16   | 0.26 | 6403 | 0.76 | 7.22E-04*** | 0.67 | 9.05E-04 *** |
|                    | Dinosauria | 35   | 0.26 | 13,274 | 0.74 | 3.40E-07*** | 0.67 | 7.46E-08 *** |
|                    |          |       |       |      |       |     |           |      |         |           |     |
|                    | Ornithischia | 15   | 16.14 | 13,274 | 0.67 | 6.15E-03 ** | 0.53 | 7.68E-03 ** |
|                    | Theropoda | 20   | 0.26 | 6403 | 0.74 | 7.14E-04*** | 0.60 | 7.50E-04 *** |
| Hell Creek and Lance | Dinosauria | Lump | 33   | 0.19 | 13,274 | 0.76 | 2.46E-07*** | 0.71 | 1.12E-07 *** |
|                    |          |       |       |      |       |     |           |      |         |           |     |
|                    | Ornithischia | 9    | 16.14 | 13,274 | 0.59 | 9.50E-02 ns | 0.49 | 7.97E-02 ns |
|                    | Theropoda | 24   | 0.19 | 6403 | 0.75 | 2.40E-05*** | 0.64 | 9.68E-05 *** |
|                    | Dinosauria | 43   | 0.19 | 13,274 | 0.75 | 5.34E-09*** | 0.72 | 2.48E-10 *** |
|                    |          |       |       |      |       |     |           |      |         |           |     |
|                    | Ornithischia | 15   | 16.14 | 13,274 | 0.67 | 6.15E-03 ** | 0.53 | 7.68E-03 ** |
|                    | Theropoda | 28   | 0.19 | 6403 | 0.73 | 9.54E-06*** | 0.65 | 1.56E-05 *** |
FIGURE 3. Charts showing completeness and taphonomic mode as a function of estimated ranked body mass for all Hell Creek Dinosaur taxa. A, Hell Creek: taxonomic split; B, Hell Creek: taxonomic lump; C, Hell Creek and Lance: taxonomic split; D, Hell Creek and Lance: taxonomic lump. The colors of the bars follow major taxonomic groupings. Boxes under the completeness graphs indicate taphonomic mode (A, articulated; B, associated; C, isolated). Numbers in B and D correlate to numbered taxa in A and C, respectively. Taxa in gray are excluded from lumped analyses. *Note Acheroraptor (11 and 19) changes rank position based on synonymy.
qualifying the skewness, but as sampling improved from the 1920s onward, both rock units reveal a relatively steady increase in skewness, from strong negative skews to more symmetric distributions. This increase in skewness indicates that both formational units became less dominated by large taxa, as improved sampling progressively (or exponentially; Fig. 6) filled in the diversity of small-bodied taxa. Regardless of whether the initial decades are dropped, body-mass skewness is strongly and significantly positively correlated with research year in both the Hell Creek/Lance (\( r = 0.92, p = 0.00002 \)) and Dinosaur Park (\( r = 0.78, p = 0.0041 \)) Formations.

Correlation of Family-Level Body Mass and Relative Abundance.—There are strong positive correlations (\( r = 0.40–0.90 \)) between average family-level body mass and relative abundance (percentage of the dinosaur fauna accounted for by that family) in five of the seven datasets from the previous Hell Creek dinosaur faunal surveys (Lehman 1987; White et al. 1998; Russell and Manabe 2002; Horner et al. 2011; Lyson and Longrich 2011; Stein 2019) (Fig. 8, Supplementary Table 6). Data on the abundance of articulated/associated skeletons from the Stein (2019) data show the strongest correlation (\( \rho = 0.90, p = 0.002 \)), while data encompassing large counts of isolated elements (including teeth) have the lowest (\( \rho = 0.40, p = 0.22 \)), revealing the difference in perceived relative abundance due to taphonomic mode. The lack of significance when using the Russell and Manabe (2002) data is likely due to both Ankylosauridae and Nodosauridae having very low relative abundances despite their large body size. These correlations (especially when looking at associated/articulated specimens) are consistent regardless of sample size or survey year, suggesting that the pattern is not strongly related to sampling intensity.

Ontogimorph (Semaphoran) Abundances as a Factor of Body Mass.—Histograms showing the frequency of specimens in each size class illustrate a consistent pattern across all three taxa (\textit{Triceratops}, \textit{Tyrannosaurus}, and \textit{Edmontosaurus}) and all measurements (Fig. 9A–D). In all cases,
Figure 4. Histograms illustrating the size distribution of Hell Creek dinosaur taxa. In all cases, the top histogram illustrates the size distribution of all Hell Creek dinosaur taxa, whereas the bottom three are segregated based on taphonomic modes: black, articulated (mode A); gray, associated (mode B); white, isolated (mode C). A, Hell Creek: taxonomic split; B, Hell Creek: taxonomic lump; C, Hell Creek and Lance: taxonomic split; D, Hell Creek and Lance: taxonomic lump.
FIGURE 5. Correlations between years until description and estimated body mass (log10 kg) for all Hell Creek Dinosaur taxa. A, Hell Creek: taxonomic split; B, Hell Creek: taxonomic lump; C, Hell Creek and Lance: taxonomic split; D, Hell Creek and Lance: taxonomic lump. Point shape/color indicates the large (blue diamond) or small (red circle) size classes. Point fill shade indicates taphonomic mode: solid, articulated; partial, associated; hollow, isolated. Dashed lines indicate the best-fit lines, while solid gray and hollow dotted areas indicate 95% confidence and 95% prediction intervals, respectively. Box plots above indicate the distributions of completeness by size class.
the majority of specimens form a relatively normal distribution around the average adult size, with very few subadults and even fewer juvenile specimens preserved. The *Tyrannosaurus* femur circumference measurements also allow estimation of body mass through the ontogenetic sample, with 90% of articulated/associated specimens in the 1000–10,000 kg size bin, 10% in the 100–1000 kg size bin, and no specimens in the <100 kg size bin.

The survey data of Horner et al. (2011) show consistent patterns of relative abundance of the four different size/age classes within each of the four most abundant Hell Creek taxa (*Triceratops*, *Tyrannosaurus*, *Edmontosaurus*, and *Thescelosaurus*). In all cases, the most common size class is the large/adult, with fewer medium/subadult specimens and even fewer small/juvenile specimens (Fig. 9E). Extra-large/large adult specimens are also relatively rare in all taxa (Fig. 9E).

**Hell Creek Formation and Lance Formation Mammals.**—Contrasting the pattern for dinosaurs, the correlation between mass (rank mass) and skeletal completeness within the mammal dataset is much weaker (Spearman \( \rho = 0.08 \)) and nonsignificant (\( p = 0.66 \)), though still positive (Fig. 10A,B). Despite this nonsignificant result, two of the three largest taxa (*Meniscoessus robustus* and *Didelphodon vorax*; Fig. 10C).

### Table 4. Correlation between time to description (the number of years till the description of a taxon) and its body mass (both log10 and ranked). Significance at: *** \( \alpha = 0.001 \).

| Formation                  | Taxonomy | \( r \)   | \( p \)-value | Sig. | \( p \)   | \( p \)-value | Sig. |
|----------------------------|----------|-----------|--------------|------|-----------|--------------|------|
| Hell Creek                 | Lump     | -0.79     | 3.34E-06 *** |      | -0.69     | 1.53E-04 *** |      |
|                            | Split    | -0.75     | 1.92E-07 *** |      | -0.75     | 4.56E-07 *** |      |
| Hell Creek and Lance       | Lump     | -0.63     | 9.14E-05 *** |      | -0.47     | 6.28E-03 *** |      |
|                            | Split    | -0.63     | 9.14E-05 *** |      | -0.47     | 6.28E-03 *** |      |

**Discussion**

**Presence of Taphonomic Size Bias in the Dinosaur Assemblage**

The strong and highly significant correlations of dinosaur taxon body mass with skeletal completeness, taphonomic mode of preservation, and time to description (\( t_{De} \)) indicate that small body size is a proxy for low completeness and disarticulation and a predictor of discovery rate at the taxon level. Importantly, the three parameters (completeness, taphonomic mode, and \( t_{De} \)) are independent metrics, with no fundamental basis to expect a relationship. For instance, one can have a very complete yet associated specimen or, likewise, a very incomplete yet articulated specimen. Also independent from these relationships is the positive correlation between body mass and relative abundance at the family level as well as the low abundance of small (juvenile) specimens of larger taxa. We are unaware of any single ecological mechanism that can explain our recovered patterns. Accordingly, multiple separate ecological mechanisms, such as juvenile allopatry, ontogenetic competition, ontogenetic niche shifts, and true rarity of small taxa, would need to be invoked to explain these individual correlations. By contrast, a single strong taphonomic, preservational bias (likely combined with collection biases) toward large taxa can explain all of our empirical observations.

Support for this interpretation can be found in actualistic taphonomic studies. In terrestrial ecosystems, large bones and skeletons are more resistant to processes such as biological destruction (e.g., carnivory and scavenging) as well as physical and chemical weathering,
whereas small skeletons and bones are more susceptible to these processes and therefore more likely to be destroyed before fossilization (Behrensmeyer et al. 1979; Behrensmeyer and Dechant Boaz 1980; Lyman 1984; Kidwell and Flessa 1996; Arribas and Palmqvist 1998; Brand et al. 2003a). A bias toward preserving large bones alone can decrease the completeness and abundance of small skeletons, independent of whether the individual pertains to a small-bodied species or a juvenile of a larger taxon. This decrease in abundance and completeness will reduce representation in the taphocoenosis, resulting in the eventual loss
of faunal compositional fidelity (presence/absence) through the apparent absence of small taxa. Indeed, such size-dependent losses in compositional fidelity were demonstrated through live–dead experiments on extant ecosystems (Behrensmeyer et al. 1979). The presence of a strong taphonomic bias against the skeletal completeness, articulation, time to initial description, and abundance of small dinosaurs in the Hell Creek Formation assemblage suggests that there may also be a bias against the discovery of other small taxa, unequally reducing the compositional fidelity of the small-bodied portion of the entire fauna.

The suggestion of a strong taphonomic bias to explain our various observations does not exclude the possibility that Mesozoic dinosaurs had unique intrinsic physiologies and/or ecologies that may have influenced these patterns, as taphonomic and biological explanations are not mutually exclusive. However, we suggest that biological explanations (Codron et al. 2012; O’Gorman and Hone 2013; Schroeder et al. 2021), especially those that invoke “non-analogue” systems (sensu Williams and Jackson 2007), at least in the context of extant terrestrial vertebrates, should not be invoked to explain patterns that can all be effectively explained by a single taphonomic size bias. Additionally, the low abundance and completeness of ontogimorphs of the taxa with the largest body masses (i.e., megaherbivores and “megatheropods”) demonstrate that a preservation size bias reduces the ability to accurately assess the role of ontogenetic niche shifts in the diversity of small-bodied taxa (Codron et al. 2012; Schroeder et al. 2021). It should also be noted that nonrandom research and collection practices can further compound those associated with differential
FIGURE 7. Histograms illustrating the size distribution of dinosaur taxa in Hell Creek and Lance Formations (A), and Dinosaur Park Formation (B) through historical collection history. C, Plot of skewness (k) of dinosaur size distribution in each decade, showing general reduction in negative skew through time.
preservation due to size, as demonstrated by the evident shift in size distributions over research history (Fig. 7).

The results presented here for the Hell Creek Formation (and Hell Creek/Lance subset), particularly with regard to associations with completeness and taphonomic mode (i.e., level of articulation), echo those previously recovered for the Campanian-aged Dinosaur Park Formation (Brown et al. 2013b). For instance, the size threshold below which completeness and articulation are compromised are nearly identical: ∼60 kg (60–370 kg) for the Dinosaur Park Formation and 62–100 kg for the Hell Creek Formation. Importantly, these size-dependent taphonomic patterns are equivalent despite notable differences in the depositional environments, differences in geographic and geological contexts, different taxa, variable body-mass ranges, and differential collection histories between the two formations. Our results are consistent with some of those obtained by Stein (2019) as part of a broadscale faunal survey of the Hell Creek Formation. Stein (2019) effectively shows a drop in the abundance of articulated and associated skeletons below 200 kg, compared with a discordantly higher abundance of isolated specimens under this threshold. Furthermore, the aforementioned ∼60–100 kg taphonomic threshold is similar to
the 100 kg point of divergence between faunal representations in the bio- and taphocoenoses of modern ecosystems (Behrensmeyer et al. 1979) and the 10–100 kg taphonomic peak observed in fossil mammals from the last 10 Myr (Benson 2018). Although these thresholds are not fixed, and there is a substantial range in absolute terms, their overall relative similarity suggests protracted taphonomic influences on taxa above and below 10–100 kg that transcend taxonomy and diagenesis. There are, however, notable examples where small-bodied taxa were not taphonomically biased, such as the Lagerstätte assemblage of the Early Cretaceous Jehol Biota (Zhou 2014). There, dinosaur body masses show a more typical positively skewed distribution (Benson et al. 2018). It is worth underscoring that local preservational factors and overall fossil abundance likely also dictate the rate at which decent skeletons of small taxa are likely to be found. Even in systems like Dinosaur Park and Hell Creek, exceptional skeletons of small-bodied species can be found, such as the recently described complete skeleton of *Saurornitholestes* from the former unit (Currie and Evans 2020) and, most importantly in the context of this work, the almost complete and articulated hatchling skeleton of *Edmontosaurus annectens* from the Hell Creek (Wosik et al. 2017). These preservational rarities will on average take much effort and time to find but are invaluable to our understanding of latest Cretaceous dinosaur life history, diversity, and paleoecology.

**Magnitude of the Taphonomic Size Bias**

A taphonomic size bias against the preservation of small skeletons parsimoniously explains all correlations of size with the various independent taphonomic indices. The question of how strong this bias is can be addressed to a certain degree by looking at the correlation coefficients. Average correlation coefficients of mass with completeness (mean $r = 0.75$), taphonomic mode (mean $r = 0.84$), time to description ($r = −0.70$), and relative abundance ($r = 0.74$) are all large and suggest that, on average, 56%, 71%, 49%, and 54% of their respective variance can be explained ($r^2$) by estimated body mass of the relevant taxon alone. As

![Graphs showing within-taxon specimen abundances based on measurements of femur circumference, dentary tooth row length, quadrate height, and basal skull length.](image)

**Figure 9.** Within-taxon specimen abundances based on A, *Tyrannosaurus* femur circumferences; B, *Tyrannosaurus* dentary tooth row length; C, *Edmontosaurus* quadrate height; and D, *Triceratops* basal skull length. E, Relative abundances of specimens within four size classes in the four most common genera in the Hell Creek Formation, based on the census of Horner et al. (2011).
such, the taphonomic implication of differential preservation due to body mass is likely the largest single factor shaping most aspects, including the diversity of the Hell Creek dinosaur assemblage.

The correlation coefficients for the Hell Creek Formation are very similar to those obtained from the Campanian-aged Dinosaur Park Formation for the same parameters (Brown et al. 2013b): completeness ($r_{\text{HC}} = 0.75$ vs. $r_{\text{DPF}} = 0.81$), taphonomic mode ($r_{\text{HC}} = 0.84$ vs. $r_{\text{DPF}} = 0.82$), time to description ($r_{\text{HC}} = -0.70$ vs. $r_{\text{DPF}} = -0.62$). This similarity is despite these two formations having different constituent taxa (i.e., the faunas are similar at the family level, but only teeth taxa overlap at the genus level, and notable size differences occur within many families) and disparate collection histories (i.e., the bulk of the diversity resulted from fieldwork conducted by different institutions.

FIGURE 10. Hell Creek mammal assemblage showing absolute body mass (A), taxon-based skeletal completeness (B), and taphonomic mode (C) all ordered by ranked body mass. In A and B: white, Multituberculata; gray, Metatheria; black, Eutheria. In C, black to lightest gray indicates a disarticulation gradient from articulated skull (black), to associated skull (dark gray), to teeth within jaws (medium gray), to isolated teeth (light gray).
and at different times). Together, these results suggest comparable preservational biases against small taxa in these two dinosaur-dominated assemblages.

Accommodating large changes in taxonomic splitting and lumping and the boundaries between the formations of interest effectively acts as a sensitivity analysis for our main results. Here, again, we find significant size-dependent taphonomic patterns, suggesting our results are unlikely to change under different sampling or taxonomic philosophies and further supporting the strength of the taphonomic size bias in the Hell Creek Formation. The low impact of taxonomic lumping and splitting is not solely due to the small portion of debated taxa in the total fauna, as both low completeness and longer $t_{pe}$ are seen within the ontogimorphs as well. When multiple ontogenetic stages of a taxon (either junior synonym or ontogimorphs) are preserved, the larger-sized stages are consistently more complete. For example, *Pachycephalosaurus* (Dracorex = 17%, Stygimoloch = 28%, and Pachycephalosaurus = 40%), *Tyrannosaurus* (Nanotyrannus = 74% and Tyrannosaurus = 100%), and *Acheroraptor* (Acheroraptor = 2% and Dakotaraptor ≈ 12%). Similarly, except for *Acheroraptor*/Dakotaraptor, the large, adult form is generally described first, with the smaller, less mature forms described later (e.g., *Pachycephalosaurus*: 1943; Stygimoloch: 1982; Dracorex: 2006; and Tyrannosaurus: 1905; Nanotyrannus: 1946).

Rates of Description

Historic cumulative description rates of large-bodied dinosaur taxa are characterized by high initial rates, with a decelerating rate, but still increasing count, toward the present time (Fig. 6). By contrast, small-bodied taxa were initially described at a slow rate, but the rates have increased dramatically toward the present (Fig. 6). If these general patterns continue to hold into the future, we would expect to find a reduction in the rate of discovery of new large-bodied taxa from the Hell Creek Formation but a rapid increase in the rate for small-bodied taxa. These rarefaction-like species discovery curves suggest that the known large-bodied portion of the Hell Creek dinosaur fauna is likely approaching a level at which it is representative of the true biological fauna, approximating the biocoenosis. Conversely, the small-bodied portion of the assemblage is likely missing significant diversity that will continue to be discovered in the future, but until such time it should not be assumed that the Hell Creek Formation fossil assemblage represents a relatively complete and/or unbiased picture of the biological fauna of the time. This pattern of constant or slightly slowing discovery rates for large-bodied taxa in the Hell Creek Formation is in stark contrast to the asymptotic pattern recovered in a similar treatment of the Dinosaur Park Formation assemblage (Brown et al. 2013b). Therefore, the Dinosaur Park assemblage may be “further along” (i.e., more mature) in terms of its taxon sampling, suggesting a better understanding of its ancient ecosystem than that of the Hell Creek Formation. These results are congruent with those of Chiarenza and colleagues (2019) based on the interplay between habitat suitability and taphonomic suitability between the Campanian (largely driven by the Dinosaur Park Formation) and Maastrichtian (largely driven by the Hell Creek Formation).

The differential description rates in the Dinosaur Park and Hell Creek formations are commensurate with the changing skewness of the body-size distributions through time in both formations, which progress from negatively skewed assemblages to positive skews that are more characteristic of most modern ecosystems (Fig. 7). However, it is worth noting that, in recent years, the Dinosaur Park Formation produced several new large-bodied taxa, specifically ceratopsians, all of which are represented by single, and in most cases very fragmentary, specimens (Longrich 2014; Ryan et al. 2014); this accounts for the recent more negative skew observed in the formation (Fig. 7C).

Implications for Dinosaur Paleoecology

It is well recognized that the fossil record of dinosaurs, and all extinct forms, is woefully incomplete (Wang and Dodson 2006; Barrett et al. 2009; Cashmore and Butler 2019), and our current knowledge of dinosaurs will likely change because of future discoveries (Tennant et al. 2018). Previous studies have explored the role of differential sampling in shaping
dinosaur diversity and predicted that upward of 2000 dinosaur species may have been present during the Mesozoic (Wang and Dodson 2006; Starrfelt and Liow 2016). In addition to known sampling factors, the results presented here and elsewhere (Brown et al. 2013a,b; Evans et al. 2013; Benson et al. 2018) implicate body size as a major yet poorly considered factor driving the preservational potential of dinosaurs. Furthermore, our results suggest that in well-sampled Late Cretaceous North American assemblages, most of the missing diversity of dinosaurs will pertain to small-bodied forms.

The biased dearth of small-bodied dinosaur diversity in the Hell Creek Formation, as indicated by both the correlation of mass and taphonomic indicators and the differential rates of description of large and small taxa, will have significant ramifications for our understanding of the dinosaur paleoecology in the ecosystems represented by the Hell Creek assemblages. Notably, both the abundance and the diversity of small taxa would have been far greater than suggested by the fossil assemblage alone. This underrepresentation is highlighted by (1) the occurrence of a highly diverse avian fauna during the Maastrichtian, only recognized in the last decade (Longrich et al. 2011); (2) the fact that the preservation of small-bodied taxa depends on the taphonomic resilience of their bones (such as the frontoparietal domes of pachycephalosaurs; Brown et al. 2013c; Evans et al. 2013); and (3) the exponential accrual of small taxa in the last three decades (Fig. 6). Due to both the low completeness of known small taxa and the number of currently unrecognized taxa that likely existed (e.g., Starrfelt and Liow 2016; Close et al. 2018), the number of ecological niches both available to and occupied by small dinosaurs is, by extension, greatly underappreciated by current assemblage data. Such underrepresentation of diversity within the Hell Creek Formation will have a disproportionately high effect on the inferred complexity and possible interactions within this past ecosystem, as the number of possible ecological interactions scales geometrically to alpha diversity (Valiente-Banuet et al. 2015), with similar implications for reconstructing food web models and ecosystem resilience to secondary extinction cascades (Mitchell et al. 2012). As a result, before interpreting the paleoecology for the latest Maastrichtian, we emphasize the need for a more concerted effort to identify the size-dependent taphonomic factors presented in this study, the outcome of which may allow for the interpretation of the cryptic diversity of small dinosaurs, which is likely underestimated. How generally applicable these results are to the global Mesozoic dinosaur record remains to be tested.

Size-related Taphonomy in Mammals and Other Vertebrate Groups

The patterns observed for dinosaurs may also present, though likely reduced in magnitude, in other taxonomic groups, and our framework provides a new understanding of preservation patterns in the Hell Creek and its equivalents and allows us to make predictions about their fossil record and preserved diversity.

The estimated body masses of Hell Creek Formation mammals range from 4.72 g (Bato don tenuis) to 5.2 kg (Didelphodon vorax) (Wilson et al. 2016). While this range is much less than that of contemporary dinosaurs (≈0.192–13,000 kg; more than five orders of magnitude), it still exceeds three orders of magnitude. Despite this broad size range, even the most massive Hell Creek mammals were well below the ~70 kg taphonomic size threshold seen in the dinosaur assemblage; indeed, the only overlap of mass ranges between the two groups is due to birds. It is unclear from the mass ranges alone if the strong and prevalent size-related taphonomic bias in the dinosaur assemblage should also describe the contemporaneous mammal assemblage.

The results presented here suggest that, while greatly reduced in strength, a similar but non-significant positive association between body mass and completeness and taphonomic mode in Maastrichtian fossil mammals (Fig. 10) is recorded. Two of the three most massive mammal taxa, the multituberculate Meniscoesous robustus and the stagodontid metatherian Didelphodon vorax, are the only specimens known from associated or articulated skulls and are also the most complete (Fig. 10; Supplementary Table 5). The latter of these is by far the largest
taxon, and it is represented by at least one complete skull, several partial crania, isolated postcranial elements, and an unpublished associated skeleton (Bryant 1989; Wilson et al. 2016). The lower magnitude and lack of significance of the effect in the mammal assemblage relative to the dinosaur assemblage is likely due, in part, to the more restricted body-mass range of mammals (and their lower absolute sizes), as well as the limited range of completeness scores, which both act to reduce the ranges over which correlations can be calculated, and the use of rank as opposed to values (particularly for mass). It is also important to point out that the Cretaceous mammal fossil record is dominated by taphonomically resistant but highly diagnostic teeth, a departure from the fossil record of most dinosaurs. As a result, while a size-related taphonomic bias may be present in these mammals, its impact on the alpha taxonomy, richness patterns, and our ultimate understanding of mammalian evolution and extinction is more limited than for dinosaurs. While any taphonomic bias may not strongly limit our understanding of taxonomic diversity, our understanding of morphological and ecological diversity and phylogenetic relationships is likely to be heavily impacted. This also highlights that even if size-related taphonomic biases act at similar magnitude for disparate clades (which they are unlikely to), they are likely to have disparate effects on these clades based on novel anatomical, ecological, or behavioral factors.

Based on our results for dinosaurs, and to a lesser extent mammals, we hypothesize that these size biases are also present in the fossil record of other terrestrial groups, such as lizards. A survey of the literature reveals that there are no lizards known from articulated or associated material in the Hell Creek or equivalent formations (Estes et al. 1969; Estes and Berberian 1970; Longrich et al. 2012), supporting the presence of a strong size bias across all terrestrial vertebrate taxa in these depositional systems. Furthermore, we predict that when associated specimens of these taxa are found, they will most likely be from the largest taxa. Such a prediction appears to hold for lizards, as *Palaeosaniwa canadensis*, the largest lizard in the Hell Creek (~6 kg) and the largest terrestrial lizard from the Cretaceous (Longrich et al. 2012), is also the only taxon known from an associated skeleton (i.e., skull, vertebrae, limbs), although this specimen remains undescribed (Bryant 1989). The strong size bias against small skeletons in other groups of terrestrial vertebrates, such as lizards, fundamentally limits our abilities to understand their diversity and ecology, along with their roles in contemporary ecosystems.

Interestingly, crocodilians, champsosaurs, and especially turtles may be less affected by body-size biases, as most taxa are known from largely complete associated specimens (Gilmore 1910, 1911; Hutchison and Archibald 1986; Holroyd and Hutchison 2002; Holroyd et al. 2014). We suggest that their preservation as associated or articulated specimens is related to their aquatic, freshwater ecology, directly associated with the sediment-carrying medium (Noto 2011). Increased preservation potential in turtles is likely also due to the carapace and plastron in turtles (Brand et al. 2003b). Disarticulation experiments also suggest an environmental role in this body-size taphonomy, with larger specimens taking significantly longer to disarticulate in terrestrial environments, but this size effect being negligible in aqueous settings (Brand et al. 2003a). Taken together, these studies highlight that while body size is a major factor in taphonomy, it is not the only factor, and other factors such as the ecology and anatomy of specific groups can exacerbate (e.g., birds) (Turvey and Blackburn 2011; Mitchell 2015) or counteract (e.g., turtles) (Brand et al. 2003b) the body-size patterns. This interplay between size-specific and size-independent preservational factors is an important area of future research.

Implications for End-Cretaceous Mass Extinction

As the Hell Creek Formation is one of the few well-sampled examples of a late Maastrichtian assemblage globally, our understanding of its diversity and paleoecology is paramount to our interpretations of mass extinction dynamics at the end of the Cretaceous (e.g., Sheehan and Fastovsky 1992; Fastovsky and Sheehan 2005; Wilson et al. 2014a; Fastovsky and Bercovici 2016; DePalma et al. 2019). Many authors
have discussed the possibility that the end-Cretaceous dinosaur mass extinction was size dependent (Bakker 1977; Russell 1977; Buffetaut 1990; Benson et al. 2014), with a disproportionate effect on larger taxa. If, however, our understanding of the dinosaur size distribution within this formation is taphonomically biased against small taxa, as we revealed here, then a size-independent extinction of all non-avian dinosaurs will appear to be size selective against large-bodied taxa. Concomitantly, if small-bodied taxa were more diverse than currently understood, as would be the case under our taphonomy-biased framework, then their extinction may have been just as severe as for the large taxa but would have gone undetected. The discovery that many contemporaneous small-bodied taxa, such as avians, lizards, and mammals, underwent similarly dramatic losses in diversity across the K/Pg boundary suggests that the mass extinction may not have been as size selective as previously thought (Wilson 2005, 2013, 2014; Longrich et al. 2011, 2012, 2016; Wilson et al. 2014b; Hallday et al. 2016) and supports the hypothesis that taphonomic filters have clouded our ability to grasp the true magnitude and specificity of this event.

The strongest extinction selectivity has been proposed for body sizes >25 kg for the terrestrial and freshwater realms (Bakker 1977; Russell 1977; Sheehan and Fastovsky 1992; Buffetaut 2006). Virtually no species above this body-mass threshold survived the K/Pg extinction event. Survivorship below this threshold was variable but could be high in certain groups, such as turtles, crocodylomorphs, and choristoderes (Holroyd et al. 2014; Chiarenza et al. 2020). Even for clades entirely below this size threshold (e.g., mammals, squamates), body size remains a major filter for survivorship through this interval, disproportionately impacting larger taxa (Longrich et al. 2012; Wilson 2013, 2014). Further, the Hell Creek mammals also show a pattern consistent with an adaptive decrease in mean body size related to increasing temperatures in the latest Maastrichtian (Wilson 2005, 2014). The differential extinction selectivity, both between and within major clades, related to factors such as body size and various ecological niches and behaviors remains an intriguing question.

Our Hell Creek dataset suggests that our knowledge of dinosaur diversity below this body-size threshold is particularly poor, especially when compared with Lagerstätte, such as the Jehol Biota, that preserve a notably large diversity of feathered dinosaur and birds that were likely below 25 kg in body mass (Benson et al. 2018). The preservational biases against small-bodied taxa quantified here add to a growing list of paleobiological biases effecting species richness/abundance patterns, including this important latest Cretaceous interval. These include investigations into the role of outcrop area, sea level, and sampling (Butler et al. 2011; Lloyd 2011; Smith and McGowan 2011; Upchurch et al. 2011; Cleary et al. 2018); the interplay between ecological habitat suitability and taphonomic/depositional suitability (Chiarenza et al. 2019); and historical collection biases (Goodwin and Horner 2010). Until the true faunal assemblage and size distribution of the Hell Creek can be adequately determined or modeled, discussions regarding the end-Cretaceous mass extinction, particularly those involving body size or size selectivity, must consider the potential effects of unequal size-dependent taphonomic, preservation, and collection biases as alternate explanations of putative extinction dynamics.

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