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# Ecological Specialization in Fossil Mammals Explains Cope's Rule

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ABSTRACT: Cope's rule is the trend toward increasing body size in a lineage over geological time. The rule has been explained either as passive diffusion away from a small initial body size or as an active trend upheld by the ecological and evolutionary advantages that large body size confers. An explicit and phylogenetically informed analysis of body size evolution in Cenozoic mammals shows that body size increases significantly in most inclusive clades. This increase occurs through temporal substitution of incumbent species by larger-sized close relatives within the clades. These late-appearing species have smaller spatial and temporal ranges and are rarer than the incumbents they replace, traits that are typical of ecological specialists. Cope's rule, accordingly, appears to derive mainly from increasing ecological specialization and clade-level niche expansion rather than from active selection for larger size. However, overlain on a net trend toward average size increase, significant pulses in origination of large-sized species are concentrated in periods of global cooling. These pulses plausibly record direct selection for larger body size according to Bergmann's rule, which thus appears to be independent of but concomitant with Cope's.

*Keywords:* Cope's rule, Bergmann's rule, mammals, ecological specialization, range size, body size.

## Introduction

Of the many empirical "laws" of evolution tentatively attributed to E. D. Cope (Simpson 1953; Rensch 1954; but see Polly 1998), the one known today as Cope's rule posits a trend toward increasing body size in a lineage over geological time (Cope 1887). This rule has received mixed support in the scientific literature. Among terrestrial vertebrates, it has been shown to apply to fossil mammals (Stanley 1973; Alroy 1998; Finarelli 2007) and to Mesozoic reptiles (Hone and Benton 2007). Besides these supportive cases, mixed or inconclusive evidence comes from studies pertaining to the earliest ruminants (Gingerich 1974), early amniotes (Laurin 2004), Mesozoic birds (Butler and Goswami 2008; Hone et al. 2008), and extant mammals (Clauset and Erwin 2008; Monroe and Bokma 2010).

As Cope's rule represents a large-scale evolutionary trend, two sorts of opposing explanations could be advanced for it: it is either generated by a passive mechanism or driven by selection (McShea 1994; Wagner 1996). In the particular context of Cope's rule, a "passive drive" hypothesis depicts body size evolution as diffusion away from a lower boundary of minimum size (Stanley 1973; Gould 1988; Clauset and Erwin 2008). As such, an increase in variance and mean body size through time is expected to occur within lineages (Gould 1988). For instance, passive drive assumes from empirical observation the existence of a 2-g lower limit to body size in mammals (Clauset and Erwin 2008). Because of that limit, evolution would have been constrained to produce more large-sized than small-sized species (Stanley 1973; Clauset and Erwin 2008).

In contrast, the "active drive" hypothesis seeks the competitive advantages of being large as the causation behind Cope's rule (Kingsolver and Pfennig 2004; Hone and Benton 2005). Active drive presumes that larger sizes are preferentially favored because large size confers ecological advantages over smaller competitors (e.g., better resource provisioning, larger niche breadth, larger range size, and increased longevity), provided that these advantages are not offset by the corresponding disadvantages of being large (such as longer generation time and higher absolute energy requirement) and assuming that they translate into higher evolutionary fitness for clades of large-sized organisms (Brown and Sibly 2006).

Unfortunately, explicit tests of active drive at the macroevolutionary level have to date been exceedingly rare and mostly confined to invertebrates (Arnold et al. 1995;

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Novack-Gottshall and Lanier 2008). Those studies have used traits such as size-related survival of major perturbations (Arnold et al. 1995), size-biased origination and extinction dynamics, and species duration (Novack-Gottshall and Lanier 2008) to test the active drive hypothesis. Here we provide the first, to our knowledge, explicit and phylogenetically informed test for active drive in body size evolution in mammals. We compiled a species-level tree ($n = 554$) of extinct large mammals living during the Cenozoic by expanding on published phylogenies introduced in Meloro et al. (2008), Raia (2010), and Raia et al. (2010; see the appendix, available online, for details). The smallest species in the tree is the Miocene mustelid *Plesiomeles pusilla*, estimated to be 200 g in size. The largest species is the late Miocene *Deinotherium giganteum*, a giant (≈11,000 kg) proboscidean. The average body size in our data set is 71.8 kg, and the median is 69.0 kg. Using this phylogenetic tree, we tested whether Cope's rule applied. We then contrasted the body sizes, range sizes, commonness, and stratigraphic duration of species to their phylogenetically closest relatives after collating species in the chronological order of appearance in the fossil record. For active drive to apply, we presume that species should be substituted in time by larger, more common, geographically more widespread, and longer-lived relatives. Whereas range size and commonness are obvious signs of the ecological "success" of a species, phyletic longevity is herein assumed to represent the natural outcome of this success in evolutionary time (Wilson 1987; Jablonski and Hunt 2006).

## Material and Methods

### *Species Data and Geostatistics*

A description of and the methods used to construct the phylogenetic tree are available from Dryad (http://dx.doi.org/10.5061/dryad.8bn8431n). We compiled a database of occurrences of mammals as provided by the Paleobiology Database (http://www.paleodb.org) and the Neogene of the Old World Database (http://www.helsinki.fi/science/now/). Our data set includes 554 extinct species that are distributed worldwide and that cover the time interval from circa 60 Ma to the recent. The stratigraphic duration of each species was computed as the difference in million years between the species' first and last occurrence in the fossil record. Extinct species' body sizes either were taken from the source databases or published papers or are estimates based on regressions of individual bone measurements versus known body size (equations in Damuth and MacFadden 1990).

We first detected the actual position of all fossil localities by using their paleocoordinates. The Paleobiology Database provides the correct position of a specific fossil locality related to its measured age. For the remaining localities, we computed the paleolatitudes and paleolongitudes by using PointTracker software (http://www.scotese.com).

The fossil record was divided into temporal intervals (time bins) of 1 million years (myr) long and then 2 myr long. Both temporal resolutions were used for the analyses. Only the results for the 1-myr temporal resolution are reported here. The results for the 2-myr temporal resolution are available in the appendix.

Each species covers temporally a set of $n \geq 1$ consecutive time bins. In reference to the time bins where they occur, species are heretofore indicated either as "first occurring" in the oldest time bin they cover or as "incumbent" for each younger time bin.

Using ESRI ArcGis 9.3, we computed the range sizes ($km^2$) of species by considering the minimum convex polygon (MCP) identified by localities' geographic distributions in each time bin. The data were then projected in the Mollweide equal area projection. The areas of MCPs computed in this way could not be used as the species' range sizes because they include seas and portions of lakes that could overestimate the real range size of the taxa. To overcome this problem, in ESRI ArcGis 9.3 we drew two different sea shapefiles (one for the Miocene and another for the Pleistocene/Recent time periods) by removing age-specific world maps of the Reconstructed Shapefile Library (http://www.scotese.com) from a rectangular polygon spreading from $+180$ and $-180$ decimal degrees in longitude and from $+90$ and $-90$ degrees in latitude. In this way, the areas of polygons were computed after removing the portions occupied by water bodies from the MCPs. Although this procedure for computing range size in extinct species is now becoming routine in the paleobiological literature (Lyons 2003, 2005; Carotenuto et al. 2010; Heim and Peters 2011; Raia et al. 2011), it inevitably somewhat misestimates actual range sizes because the fossil record is discontinuous and time bins are unevenly represented. In this case this is not a problem, however, since we compared range sizes of different species in the same time bin, using one and the same sample of the fossil record for each pairwise comparison (see below). Species commonness was computed as the ratio of the number of occurrences of each species to the number of total fossil localities in a specific time bin (Jernvall and Fortelius 2004; Raia et al. 2006; Carotenuto et al. 2010).

### *Testing whether Cope's Rule Applies*

To investigate whether the data support Cope's rule, we first calculated the median body size per time bin. Second, for each time bin *i* we recorded which species have their first occurrence in the fossil record in *i*. We then tested whether these first-occurring species tended to be larger than the median body size of the species present in the previous time bin ($i - 1$). We did this by contrasting the observed proportion of "large" (greater than the median body size in $i - 1$) first-occurring species to a null model of unbiased first occurrences of either large or small species by means of a likelihood ratio test, as described in Finarelli (2007). This test assumes that the unbiased proportion of first-occurring species being either smaller or larger than the median body size of the species in the previous time bin is 0.5 and then assesses significant deviations from this proportion by means of binomial likelihood calculation (Finarelli 2007).

This same procedure was applied to extinction (last occurrences in the fossil record). We also calculated the correlation between body size and first-appearance age for each species within clades, which by Cope's rule should be negative.

It has been noted that for Cope's rule to apply, body size within lineages should not increase on average only; the smallest size should increase as well (Jablonski 1997; Brown and Sibly 2006). Therefore, we computed the net trend of both the minimum and the maximum body size for 43 clades included in the tree, corresponding to taxonomic orders or families, to see whether both the minimum and the maximum body size per clade increased through time.

### *Relationship between Diversification Rate and Body Size*

If diversification rate scales positively with body size, Cope's rule would be explained by the faster pace of origination of large-sized versus small-sized species, regardless of whether large body size confers higher evolutionary fitness. Estimating the change in diversification rate in a phylogeny of living species could be problematic (Quental and Marshall 2010; Losos 2011), especially because living-species phylogenies do not consider past extinction (Rabosky 2010; Tarver and Donoghue 2011). Fossil phylogenies consider past extinction. Phylogenetically explicit methods for computing rates from fossil phylogenies are becoming available (Ezard and Purvis 2009; Liow et al. 2010). We computed speciation and extinction rates within time bins by using the package paleoPhylo (Ezard and Purvis 2009) in R, as follows: within a given time bin, the number of speciation events is the number of branches that bifurcate into daughter branches that cross the younger but not the older time boundary of the bin. Similarly, extinctions are the number of branches crossing the older but not the younger time boundary, thus representing branches that terminate within the time bin without giving birth to daughter branches. Dividing these speciation and extinction numbers for the sum branch lengths that fall within the bin gives the speciation $\lambda$ and extinction $\mu$ rates (i.e., the number of events per unit of time; Ezard and Purvis 2009). The difference $\lambda - \mu$ is the diversification rate within the time bin. Diversification rates were correlated with the mean body size of the species that lived in that time bin. If size-related change in diversification rate drives Cope's rule, then as body size increases in time the diversification rate should increase as well.

### *The Mechanisms behind Cope's Rule*

After determining whether Cope's rule applies to our data, we tested the active drive hypothesis by comparing the body size, range size, commonness, and stratigraphic duration of each first-occurring species in a given time bin with its phylogenetically closest relative living in that time bin that was already present in the previous one (i.e., the species taken for comparison is not also first occurring but incumbent). The closest phylogenetic relative is here defined as the species having the smallest patristic distance (the shortest distance of summed branch lengths separating two species in the tree, down to the most recent common ancestor for the pair) to the first-occurring species. This choice is justified by guild competition theory, which indicates that a species' fiercest competitors are very likely its closest relatives, to the extent that guilds are often defined on taxonomic grounds (e.g., the mustelid guild and the canid guild) and intraguild competition often drives character displacement (Dayan and Simberloff 2005).

For active drive to apply, body size, range size, commonness, and stratigraphic duration of the first-occurring species should be higher, on average, than those of their incumbent competitors. Range size and occupancy trajectories tend to have an unimodal course over a species' existence (Jernvall and Fortelius 2004; Foote et al. 2007; Carotenuto et al. 2010). As such, per-time-bin measures of these variables could be misleading (e.g., comparing a species on the ascending phase of its trajectory to a species at its peak). For this reason, pairwise comparisons of range sizes and occupancies were performed by using both the lifetime range and the occupancy for each species and then computing these variables per time bin.

Our record is composed of 554 species, four of them occurring in the first time bin, 61–62 Ma. For each of the 550 remaining species first occurring in the record in a given time bin, there is a single pairwise comparison to an incumbent species. Among them, we selected species pairs whose geographic ranges overlap or at least touch each other, taking geographic overlap as minimum evidence of potential competition between the two species. By applying this criterion, we selected 325 pairwise comparisons out of 550. By applying the 2-myr temporal resolution, 400 pairwise comparisons were valid. By computing range size and commonness per time bin, we obtained 84 valid pairwise comparisons for 1-myr-long intervals and 116 valid pairwise comparisons for 2-myr-long intervals.

## Results

Cope's rule applies to our data. There is a 10-fold increase in mean body size during the Cenozoic, with a minimum apparently coincident with the early Paleocene-Eocene thermal maximum (fig. 1). Significant pulses in origination of large species occur in five distinct time bins, twice in the Pliocene, twice in the Miocene, and once in the Eocene, at 37–38 Ma. Qualitatively the same results apply when using a 2-myr-long time bin resolution (table A1, available online; fig. A1, available online), with the interesting exception that an additional origination pulse at 30–32 Ma is apparent by using the 2-myr resolution, mostly in clear coincidence with the first onset of the Antarctic glaciation (fig. A1; table A2, available online). Irrespective of the sampling interval used, origination pulses tended to occur during cooling periods throughout the Cenozoic and have intensified from the middle Miocene global cooling (Abels et al. 2005) onward (table 1). This is particularly evident when plotting the paleotemperature curve along with the body size trend, as we did in figure 1.

In contrast to the multiple origination events, significant pulses of extinction of large-sized species occurred only twice (table 1). The first was in the 53–54 Ma (early Eocene) time bin, when we document the extinction of a number of North American limnocyonine creodonts. This pulse could well be an artifact of our record, since only five creodonts and two phenacodontid "condylarths" are present in our record in that particular time interval. The second pulse occurred in the latest temporal interval (0–1 Ma) and clearly corresponded to the end-Pleistocene megafauna extinction. By using a 2-myr temporal resolution, this latter extinction pulse is still apparent, and an additional pulse appeared at the 32–34-Ma interval (fig. A1; table A2), just before the abrupt cooling at the Eocene-Oligocene boundary.

The correlation between first-occurrence age and body size is negative and significant for most clades, at the levels of order, family, and even subfamily (table 2; fig. 2). Most notably, negative correlations accrue to crown group Artiodactyla, Perissodactyla, and Carnivora, which account for some 95% of the species in our tree (fig. 2).

In the 43 taxonomically relevant clades analyzed, the smallest size increased through time 29 times, the largest size 38 times (table 2; fig. 2). Both figures deviate significantly from a 1 : 1 ratio, in support of Cope's rule. This means that, at least in our data (which are necessarily incomplete given that we did not consider the entire fossil record), Cope's rule is supported.

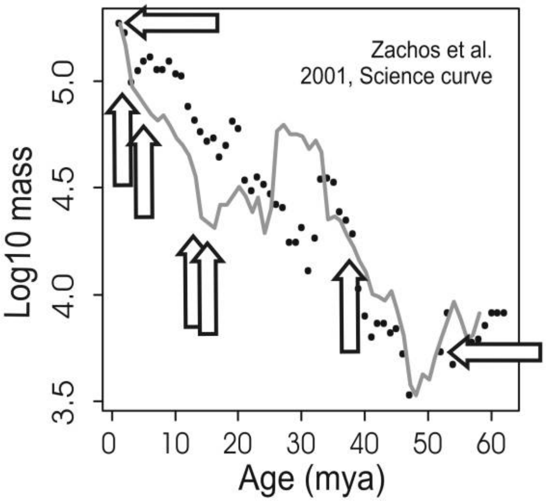

**Figure 1:** Plot of mean size (dots) per time bin versus age. Horizontal arrows designate pulses of significant high extinction of large-sized species, as in table 1. Vertical arrows designate pulses of significant high origination of large-sized species, as in table 1. The gray line represents the mean $^{18}$O values per time bin taken from Zachos et al. (2001) by calculating the average value per million years.

The relationship between body size and diversification rate is significantly negative with both temporal resolutions (table A3, available online). Using the 1-myr-long bins, Pearson's product-moment correlation is $-0.481$ ($t = -4.035$, df $= 54$, $P < .001$). Using the 2-myr-long bins, the correlation is $-0.510$ ($t = -3.141$, df $= 28$, $P = .004$). We repeated the tests excluding the last 5 myr (6 myr with the 2-myr temporal resolution) to avoid biases from oversampling the most recent intervals (the Pull of the Recent; Jablonski et al. 2003). Without the most recent time bins, the relationship between diversification rate and body size remains significant and negative (1-myr bins: $r = -0.450$, $P < .001$; 2-myr bins: $r = -0.405$, $P = .036$; table A3). This means that Cope's rule is not explained by faster diversification in lineages of large-sized species.

We found that the body size of the first-occurring species is larger than that of their incumbent closest relative more often than expected by chance, as predicted by Cope's rule (table 3). In contrast to the active drive hypothesis, we found strong evidence that commonness, range size, and even stratigraphic duration are significantly smaller for first-occurring species than for resident species.

Of the 325 selected pairwise comparisons, the first-occurring species' body size is larger 198 times, which strongly deviates from a 1 : 1 ratio, supporting Cope's rule ($P \ll .001$). The first-occurring species' range size is larger

**Table 1:** Likelihood ratios (LRs) for median body size

| Interval | $LR_{\text{origination}}$ | $LR_{\text{extinction}}$ |
|---|---|---|
| 0–1 Ma | 1.4 | **$4 \times 10^{31}$** |
| 1–2 Ma | **$3.7 \times 10^{5}$** | 2.3 |
| 2–3 Ma | 1 | 1.2 |
| 3–4 Ma | 1 | 1.5 |
| 4–5 Ma | **47.5** | 1.3 |
| 5–6 Ma | 2.6 | 1.7 |
| 6–7 Ma | 1.4 | 3.2 |
| 7–8 Ma | 1.1 | 1 |
| 8–9 Ma | 1.3 | 1.1 |
| 9–10 Ma | 1.6 | 3.9 |
| 10–11 Ma | 2.4 | 1 |
| 11–12 Ma | **27.7** | 2.6 |
| 12–13 Ma | 2.3 | 1 |
| 13–14 Ma | **17.8** | 1 |
| 14–15 Ma | 1.7 | 1 |
| 15–16 Ma | 2 | 1.2 |
| 16–17 Ma | 3.1 | 1.2 |
| 17–18 Ma | 7.4 | 1.3 |
| 18–19 Ma | 1 | 1.7 |
| 19–20 Ma | 4.8 | 1.4 |
| 20–21 Ma | 1 | 1.1 |
| 21–22 Ma | 1 | 1 |
| 22–23 Ma | 1.2 | 1 |
| 23–24 Ma | 4 | 1.2 |
| 24–25 Ma | 2.6 | 2.6 |
| 25–26 Ma | 1.1 | 1.7 |
| 26–27 Ma | 2 | 1 |
| 27–28 Ma | 1 | 2 |
| 28–29 Ma | 1.2 | 1 |
| 29–30 Ma | 4 | 1 |
| 30–31 Ma | 4 | 1 |
| 31–32 Ma | 4 | 1 |
| 32–33 Ma | 2 | 4 |
| 33–34 Ma | 1.7 | 1.1 |
| 34–35 Ma | 2 | 1 |
| 35–36 Ma | 2 | 1.2 |
| 36–37 Ma | 8 | 1 |
| 37–38 Ma | **16** | 2 |
| 38–39 Ma | 1.2 | 2 |
| 39–40 Ma | 1 | 8 |
| 40–41 Ma | 1 | 2 |
| 41–42 Ma | 2 | 1.2 |
| 42–43 Ma | 2 | 1 |
| 43–44 Ma | 1.2 | 2 |
| 44–45 Ma | 1 | 1 |
| 45–46 Ma | 2 | 1 |
| 46–47 Ma | 1 | 1 |
| 51–52 Ma | 1 | 2 |
| 52–53 Ma | 1 | 4 |
| 53–54 Ma | 1 | **16** |
| 54–55 Ma | 2 | 1.2 |
| 55–56 Ma | 1.4 | 1 |
| 56–57 Ma | 2 | 1 |
| 57–58 Ma | 4 | 1 |
| 58–59 Ma | 2 | 2 |
| 59–60 Ma | 1 | 1 |
| 60–61 Ma | 1 | 1 |
| 61–62 Ma | 1 | 1 |

Note: LRs show that the median body size of species originating and becoming extinct in each time interval is larger than the median body size of all species in the previous time interval. Significant values (in boldface) are interpreted as pulses of origination or extinction of large-sized species.

than that of its closest resident relative only 90 times ($P \ll .001$). It is more common only 144 times ($P = .023$) and lives for longer (in the record) only 147 times ($P = .048$; table 3). Since the same resident species may appear more than once in our computation, we removed at random multiple occurrences of incumbents 100 times to avoid pseudoreplication and calculated 95% confidence intervals for pairwise comparisons of each variable in the replicated sets (table 3). The confidence intervals thus calculated confirm the insights obtained from analyzing the 325 pairwise comparisons of the entire data set (table 3). Using 2-myr time bins gave even stronger results (table A4, available online).

The procedure we applied for comparing range size and commonness of first-occurring versus resident species takes the entire range size over a species' existence. This is appropriate because species tend to both start and end small in terms of range size and commonness (Jernvall and Fortelius 2004; Foote et al. 2007; Carotenuto et al. 2010). Yet the difference in range size and commonness between first-occurring and resident species might be inflated by the significant relationship between range size and duration ($r = 0.183$, $t = 4.367$, $P \ll .001$), which holds even after application of a phylogenetic correction under the Brownian motion ($P \ll .001$, $\text{df} = 552$, Akaike Information Criterion = 2,877.9, log likelihood = −1,435.9). For this reason, we calculated the species range sizes and total number of occurrences on a per-million-year-long interval base. Then we recomputed pairwise comparisons per time bin, still maintaining the range overlap criterion for inclusion. For each species within each pairwise comparison, we took the average of the range sizes over all the time bins where it occurred and used the averages for comparison. Since the relationship between range size and time is unimodal (Jernvall and Fortelius 2004; Foote et al. 2007; Carotenuto et al. 2010), this procedure avoids comparing species in either the declining or the ascending phase of their range size and commonness curve while removing artificial range size inflation in long-lasting species. With the 1-myr-long time bins, the range size of the first-occurring species is larger than that of its closest resident relative only 33 times in 84 valid comparisons ($P_{\text{binomial}} = .031$). The resident species has higher occurrence 34 times ($P_{\text{binomial}} = .051$). With the 2-myr-long time bins, the results are qualitatively the same (table A5, available online). It is important to note that, irrespective of the measure taken for comparison, range size and commonness of first-occurring species are always significantly smaller than those of their closest incumbent relatives.

## Discussion

Our results clearly contradict the active drive hypothesis. We found convincing evidence that when a species first

**Table 2:** Size trends within selected taxonomic groups

| Taxonomic group | *n* | *r* | *P* | Smallest size trend | Largest size trend |
|---|---|---|---|---|---|
| Phenacodontidae | 5 | −.025 | .968 | Increase | Decrease |
| Artiodactyla | 267 | −.442 | <.001* | Increase | Increase |
| Tylopoda | 35 | −.881 | <.001* | Increase | Increase |
| Camelidae | 22 | −.635 | .002* | Decrease | Increase |
| Laminae | 8 | −.176 | .677 | Decrease | Increase |
| Protoceratidae | 12 | −.915 | <.001* | Increase | Increase |
| Oreodontoidea | 22 | −.615 | .002* | Increase | Increase |
| Merycoidodontinae | 18 | −.551 | .018* | Increase | Increase |
| Suoidea | 42 | −.148 | .35 | Increase | Increase |
| Tayassuidae | 11 | −.555 | .076 | Increase | Increase |
| Tragulidae | 12 | −.54 | .07 | Increase | Increase |
| Antilocapridae | 9 | −.625 | .072 | Increase | Increase |
| Giraffidae | 16 | −.083 | .759 | Increase | Increase |
| Paleotragini | 9 | −.191 | .623 | Increase | Increase |
| Cervoids | 48 | −.694 | <.001* | Increase | Increase |
| Muntiacinae | 15 | −.312 | .258 | Increase | Increase |
| Cervinae | 19 | −.6 | .007* | Increase | Increase |
| Bovidae | 79 | −.399 | <.001* | Decrease | Increase |
| Bovinae | 25 | −.832 | <.001* | Increase | Increase |
| Boselaphini | 12 | −.96 | <.001* | Increase | Increase |
| Antilopini | 28 | −.055 | .781 | Decrease | Increase |
| Caprini | 6 | −.521 | .289 | Increase | Increase |
| Ovibovini | 6 | −.782 | .066 | Increase | Increase |
| Perissodactyla | 88 | −.284 | .007* | Increase | Increase |
| Ceratomorpha | 33 | −.278 | .117 | Decrease | Increase |
| Aceratheriinae | 16 | −.449 | .081 | Decrease | Decrease |
| Equidae | 53 | −.609 | <.001* | Increase | Increase |
| Hipparionini | 30 | −.141 | .457 | Increase | Decrease |
| Carnivora | 164 | −.25 | .001* | Decrease | Increase |
| Arctoids | 114 | −.096 | .308 | Decrease | Increase |
| Ursidae | 15 | −.334 | .223 | Decrease | Increase |
| Mephitidae | 8 | −.294 | .48 | Increase | Increase |
| Mustelidae | 35 | −.351 | .039* | Decrease | Increase |
| Canidae | 40 | −.604 | <.001* | Decrease | Increase |
| Borophaginae | 20 | −.886 | <.001* | Increase | Increase |
| Caninae | 14 | −.596 | .024* | Increase | Increase |
| Feloids | 50 | −.463 | .001* | Increase | Increase |
| Hyaenidae | 20 | −.447 | .048* | Increase | Increase |
| Felidae | 22 | .116 | .607 | Decrease | Decrease |
| Machairodontini | 15 | −.194 | .488 | Increase | Decrease |
| Felini | 7 | −.4 | .374 | Decrease | Increase |
| Creodonta | 10 | −.805 | .005* | Increase | Increase |
| Proboscidea | 20 | .054 | .822 | Decrease | Increase |

Note: $n$ = number of species, $r$ = correlation between body size and time using the first-appearance data for the species within the group, $P$ = probability that $r$ is significantly different from 0. The last two columns indicate whether the lower and upper size boundaries of the group increase or decrease over the group's history. Significant correlations are indicated by an asterisk.

occurs in the fossil record, it fares no better than its living competitors in terms of commonness, geographic range size, and stratigraphic duration, although it tends to be larger.

Provided that mortality and resource availability are constant, evolution should favor smaller body size because smaller organisms have a higher production rate (Brown and Sibly 2006). Thus, a likely explanation for Cope's rule should involve changes in either mortality or resource availability.

Our data suggest that size increase is associated with a niche shift toward specialized morphotypes, suggesting ex-

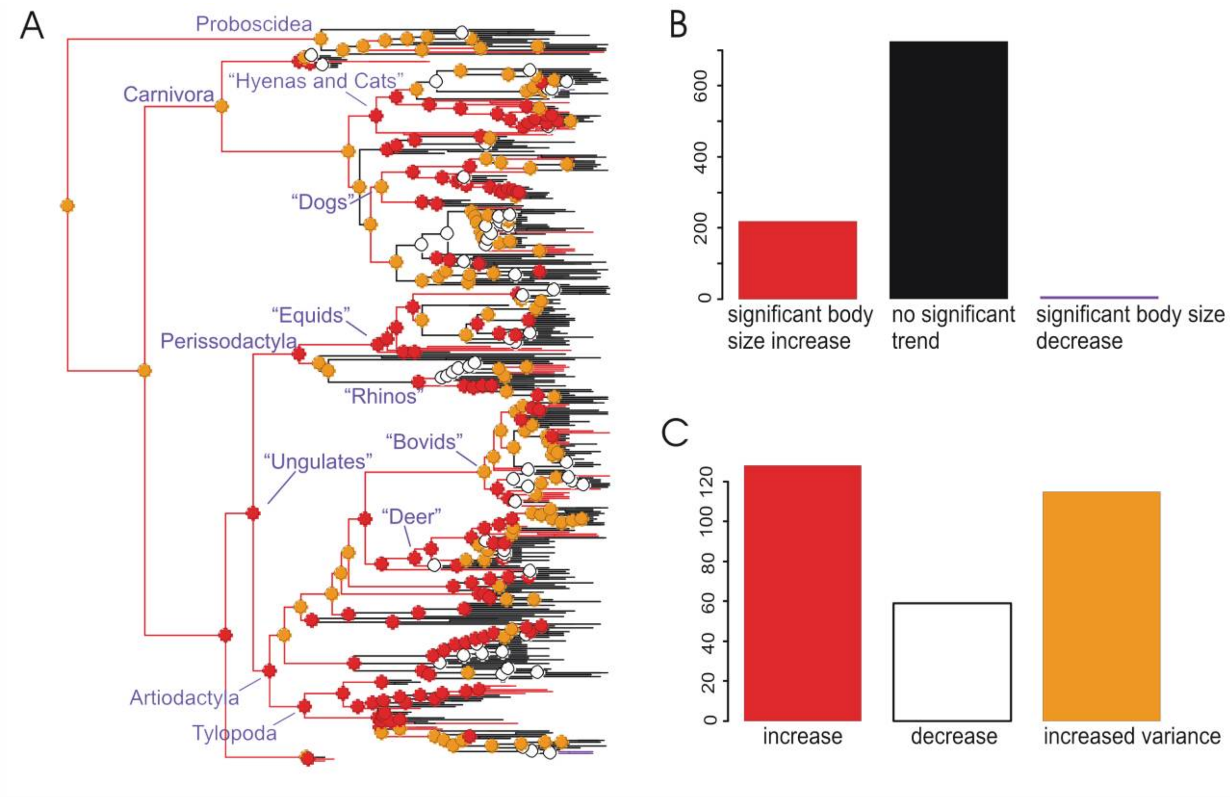

**Figure 2:** Patterns of size changes mapped on the phylogeny and their relative frequencies. In *A*, clades showing a significant correlation between body size and first-appearance datum per clade (at $P < .05$) are shown in red. Clades for which body size significantly decreased through time are shown in purple. Clades for which the relationship is not significant are shown in black. The red circles indicate clades for which both the smallest and the largest species body size increased over time. Orange circles designate clades for which the largest but not the smallest body size increased through time, thereby causing an increase in the size spectrum of the clade. White circles designate clades for which both the smallest and the largest body size decreased through time. In *B*, the frequency of significance of the relationships between body size and first-appearance datum per clade are reported. In *C*, the frequency of instances of size increase, decrease in both maximum and minimum body size through time, and increased variance over all the clades are shown.

ploitation of new resources. Among ungulates, for example, the acquisition of grass feeding was accompanied by a significant increase in body size (Raia et al. 2010). This is usually attributed to the high content of cellulose fibers in grass, requiring a long digestion time and, therefore, the lower mass-specific energy requirement that comes with larger size (Clauss and Hummel 2005). Grazing ruminants similarly appear to be mainly short-lived, large-sized, rapidly diversifying, and geographically restricted specialists (Raia et al. 2011). Most carnivore clades evolved into highly specialized and typically large-sized hypercarnivores or bone crackers only late in their history; examples include at least canids (Van Valkenburgh et al. 2004; Finarelli 2007), hyenas (Ferretti 2007), and machairodont cats (Slater and Van Valkenburgh 2008).

Dietary specialization is inversely correlated to abundance and geographic range size (Brown 1984). In keeping with this, our first-occurring species are larger but less common and widespread than their incumbent relatives. Furthermore, dietary and habitat specialization are directly correlated with extinction rate in large mammals (Van Valkenburgh et al. 2004; Hernández Fernández and Vrba 2005), which would account for the lower stratigraphic duration of first-occurring species in our data.

We found that diversification rate scales negatively with body size. Furthermore, the relationship between duration and body size is not significant ($t = 0.699$, $\mathrm{df} = 552$, $P = .485$, $r = 0.030$). This means that although smaller mammals probably diversify faster than larger mammals and stratigraphic duration is independent of body size, species within clades tended to be replaced by larger and shorter-lived forms. This is also expected because smaller mammals have a suite of behavioral and ecological attrib-

**Table 3:** Ecological pairwise comparisons of first-occurring species versus their phylogenetically closest relatives (incumbents)

| | Mean ratio | No. first-occurring > incumbent | P | 95% CI, replicated sets |
|---|---|---|---|---|
| Body size | 1.236 | 193 | <.001 | 1.277–1.470 |
| Range size | .703 | 90 | <.001 | .735–.881 |
| Commonness | .535 | 143 | .023 | .521–.663 |
| Duration | .638 | 147 | .048 | .612–.921 |

Note: The temporal resolution used is 1 million years. The total number of comparisons is 325. Mean ratio = mean ratio between the two species' values (newcomer/closest incumbent relative), no. first-occurring > incumbent = number of times the first-occurring species' value is larger than that of its phylogenetically closest incumbent relative for each variable, $P$ = $P$ value for deviation from a 1 : 1 ratio, 95% CI = 95% confidence intervals drawn from replicated sets where each incumbent species was taken only once.

utes that make them less prone to extinction risk (Liow et al. 2009).

Kingsolver and Pfennig (2004) have contended that the microevolutionary advantage of being large could turn into a macroevolutionary trend toward an increase in body size. Our results point to a more complicated scenario. Large, inclusive clades tend to include small and morphologically unspecialized species at the beginning (Ciampaglio et al. 2001). Then, clades expand by invasion of new ecospace (Sahney et al. 2010), through the evolution of key innovations (Vermeij 2006; Benton 2009; Raia et al. 2011), or following major extinction events (Sahney et al. 2010). These new ecospaces are filled secondarily by increasingly specialized species (Ciampaglio et al. 2001; Meloro and Raia 2010), which we found are larger than the species they replace. Besides body size increase, specialization should prompt reduction in average range size and long-term increase in biodiversity. These predictions are confirmed by observations reported in many fossil groups. For example, it has been noted that as paleodiversity increased in time, cosmopolitan species were reduced in number (Benton 2010). That the world is nevertheless not full of large specialists is explained by the lack of very specialized morphotypes early in the history of animal clades (Ciampaglio et al. 2001; Meloro and Raia 2010), by the negative relationship between body size and diversification, and by the positive relationship between extinction risk and both body size and range size (Cardillo 2003; Liow et al. 2009).

The climatic evolution of the Cenozoic would certainly have promoted a process such as we suggest by offering new resources in the expanding open habitats (Janis 2008; Eronen et al. 2009). These in turn prompted the evolution of large-sized ungulates and provided to carnivorous mammals a favorable landscape for the evolution of bone cracking and diet specialization in feeding on megaherbivores. Other studies have found a direct connection between body size evolution and climate change (Hunt and Roy 2006). The extent to which cooling alone, through Bergmann's rule (Meiri and Dayan 2003; Smith et al. 2010), could account for our results is difficult to assess. Most peaks in origination of large-sized mammals were concentrated in the Neogene, when the climate cooled and open habitats expanded (fig. 1), but the concentration of significant cases of size increase to the more inclusive clades within the phylogeny (fig. 2) argues against a process of simple climatic forcing. Furthermore, the neat and linear relationship between time and average body size per interval (fig. 1) suggests that size increase was in place before cooling intensified in the Neogene. It is most probable that the effects of Cope's and Bergmann's rules have been conflated since the Miocene, thereby promoting the origination pulses of large-sized mammals superimposed on an existing trend toward size increase. Conceptually, the extent to which direct, physiologically driven selection for larger body size has occurred could be regarded as the degree to which Bergmann's rule is independent from Cope's.

The connection of Bergmann's rule with Cope's is not the only such linkage that our results suggest. Essential to Edward Drinker Cope's neo-Lamarckist creed, especially in his later years, was the belief that adaptation is the main force in evolution, driving lineages from the unspecialized to the specialized and from the simple to the complex by the process of "kinetogenesis" (Bowler 1977). Although based on assumptions no longer considered valid, his model of adaptive evolution by means of inheritance of acquired characteristics produced generalities that make equally good sense in a theoretical framework based on natural selection. Regardless of whether Cope's rule was really Cope's (Polly 1998), it is the process of adaptive evolution, not its underlying mechanism, that forms the theoretical underpinnings of Cope's more mature empirical rules.

The acquisition of new morphotypes (and ensuing invasion of new ecospaces)—which Cope recognized, even without having the morphotype concept at hand—can, in a contemporary framework, be comfortably attributed to the exploration of new resources and habitats by specialized forms. The early dominance in evolving clades of unspecialized small-sized forms and the subsequent niche expansion provided by new specialized morphotypes o larger size appears to us to be the most likely fundamental driver of Cope's rule of size increase in mammals.

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