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Where the Wild Things Are: Investigating Body Size as a Mechanism for Persistence

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WHERE THE WILD THINGS ARE: INVESTIGATING BODY SIZE AS A MECHANISM FOR PERSISTENCE

BY

Meghan Anne Balk
B.S., University of California, Davis, 2010

DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of

Doctor of Philosophy in Biology

The University of New Mexico
Albuquerque, New Mexico

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DEDICATION

To my mother and late father: thank you for teaching me to love learning, for prioritizing education, empowering me, and making it possible for me to pursue a career in science.

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ABSTRACT

Body size is a trait under selection. Genetic drift, climate, diet quality, and biotic interactions all select upon body size at the population, species, and community levels. These factors can be important in the context of rapidly changing climate. One of the ways an animal can persist in its environment is through morphological adaptation *in situ*. Here, I investigate four questions relating to the evolution of body size: (1) what is the limit in body size change in response to climatic change; (2) how does body size influence the thermal tolerances of animals; (3) how does body size evolve over space and time; and (4) what are body size relationships between predators and their prey. I employ both the fossil and modern record, take both a macro- and micro- approach, and investigate both the terrestrial and marine realms. Overall, my dissertation demonstrates that species overwhelming evolve body size as a mechanism to persist in their environments.

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INTRODUCTION

Body size influences ecology and evolution at many levels of biotic organization. For example, a species' mass scales with its generation time, growth rate, life span, ingestion rate, and home range size (Kleiber 1932; Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Ernest et al. 2003). At the community- and ecosystem- levels, body size distributions of species can yield insights into the way that energy flows through a system (Brown & Nicoletto 1991; Chown & Gaston 1997; Loreau et al. 2001; Woodward et al. 2005). Knowing that body size is important means that it is critical to understand the selection pressures acting upon it. These might include abiotic, physiological, evolutionary, and biotic factors – all of which can shift the mean body size of animal populations. To investigate the drivers and consequences of body size, I look to the both paleo- and modern record, explore both the terrestrial and marine realm, and look at both micro- and macro- level at the geographic scale and level of biotic organization.

Temperature exerts selective pressure on populations. Survivorship depends on the ability to retain or dissipate heat (Brown & Lee 1969). Larger individuals within a population, with a higher volume to surface area ratio, may struggle to dissipate heat, and vice versa for smaller individuals. Populations may experience differential mortality such that larger animals die during warming events, and smaller animals die during cooling events (Smith et al. 1998). This may be one mechanism underlying the ecogeographic pattern called Bergmann's Rule, wherein species with in a genus (or populations within a species) are larger in colder environments and smaller in warmer environments (Bergmann 1847; Mayr 1956). Majority of mammals (>70%) conform to the Bergmann's Rule (Millien et al. 2006). This pattern has also been shown to exist over evolutionary scales (Smith et al. 1995). Recent work suggests that it may be easier for species to evolve a smaller size than a larger size (Evans et al. 2012). In chapter one I examine the role of body size in adapting to climate change. Specifically, I take a microevolutionary approach to test the potential asymmetry in rates of body size change during periods of global warming versus cooling on: is it easier to evolve smaller or larger body size? We employ the fossil record of the bushy-tailed woodrat, *Neotoma cinerea*. Our data consists of over 130 geogreferenced and radiocarbon dated paleomidden sites across the western USA to answer this question. *Neotoma cinerea* conforms to Bergmann's rule across its expansive geographic distribution, as well as through time (Brown & Lee 1969; Smith et al. 1995; Smith & Betancourt 2006). We find no bias in the recovery of paleomiddens during warmer or cooler temperatures. However, populations at the periphery may have been challenged by temperature change; northern populations seem to become locally extirpated during cold events, and southern populations went extinct during warming events. Still, adaptation *in situ* via body size change is a necessary mechanism for *N. cinerea* to persist during climatic changes.

A species' thermal physiology is also influenced by body size. As predicted by Bergmann's rule, larger species should be able to tolerate colder temperatures and small species warmer temperatures. The thermal neutral zone (TNZ) is the range of temperatures endotherms can tolerate a without exerting energy to generate or dissipate heat. All else being equal, it is expected that animal thermal neutral zone should match their thermal environment perfectly (e.g., Janzen 1967; Stevens 1989; Hughes et al. 1996;

Gaston & Chown 1999; Addo-Bediako et al. 2000). Remarkably, endotherm TNZs often do *not* align with the range of environmental temperatures experienced (see Khaliq et al. 2014; Khaliq et al. 2015). We suspect the limitation for endotherms' thermal physiology to parallel the temperatures in their environment may be due to a trade-off between the upper and lower critical thermal temperatures – the boundaries of the TNZ. In chapter two I quantify the role of body size and other body-size independent adaptations in setting endotherm thermal tolerance. Using critical thermal temperature data for ~300 mammals and ~200 birds, we test for a potential trade-off in the ability of animals to evolve warm- and cold- tolerance. We find that for every increase of 1˚C in upper critical thermal temperature, 3˚C of lower critical thermal temperatures are lost; this relationship holds even after standardizing for body size. This ultimately results in species' TNZ either shrinking and shifting up, or expanding but shifting downward. This trade-off may explain why animals cannot persist in all thermal environments without behavioral adaptations or other body-size independent adaptations.

Of course, evolutionary changes in body size can occur without selective pressures. It is possible for populations to drift over time. Thus, it is necessary to test whether populations underwent random or directed evolution. Typically, the three modes of evolution that can occur are: an unbiased random walk (stochastic), a general random walk (stasis), or directional evolution in body size. A tremendous system to test the question of body size change is that of *Carcharocles megalodon*. This shark is the ultimate species in a paraphyletic lineage of megatooth sharks spanning from the early Eocene to the late Pliocene. Anecdotal evidence suggested that lineages within the megatooth shark clade increased in body size over time. There is reason to believe that selection for a larger body size would be advantageous: larger sharks can potentially eat a broader range of prey (Estrada et al. 2006; Lucifora et al. 2009). In chapter three I investigate the evolutionary patterns of body size change in one megatooth shark, *Carcharocles megalodon*, through time and across space. We characterized the length, width, and tooth position of over 600 *C. megalodon* teeth from around the globe to compare body size distributions during the Middle Miocene, Late Miocene, and Pliocene and between oceanic basins. We find that *C. megalodon* had a left-skewed body size distribution, which remained constant across space and time. Further, our analyses suggest that the evolution body size of *C. megalodon* exhibited stasis throughout its duration. We suggest hypotheses to explain this pattern: 1) larger body size must have been favored as larger sharks can take a broader range of prey (Estrada et al. 2006; Lucifora et al. 2009); 2) sharks have long generation times (Martin et al. 1992), thus potentially preventing rapid adaptation to changing environmental conditions (Martin et al. 1992; Pimiento et al. 2013). Large body size, but not necessarily body size adaptation, may have allowed *C. megalodon* be a cosmopolitan shark.

Biotic interactions – notoriously hard to test in the natural environment – may cause shifts in population body size distributions via competitive exclusion or may lead to the evolution of larger body size through predation pressure. In the literature, there is an uncited 'truth' that prey species evolve larger body sizes to avoid predation (e.g., O'Gorman & Hone 2012). In chapter four I explore the drivers of predator-prey body size relationships in the marine realm. A recent study by Carbone et al. (2014) posits that minimum prey size should decrease as predator body size increases in the marine realm since smaller prey, such as sardines and krill, are abundant and clumped in the environment. Further, research by Lucifora et al. (2009) and Estrada et al. (2006) have documented that throughout a sharks' lifespan, the range of prey size increases. Here, we gather body size and ecological data for ~500 species of sharks and ~1,000 prey items to quantify the relationship between predators and their prey. Interestingly, we do not recover the pattern that the minimum prey size decreases with increasing body size of the shark. Further, we find that the broadening of prey size by larger sharks is due to an increase in the maximum prey size that a predator can consume. Additionally, the larger prey items in a shark's diet tends to be those most at risk for extinction. The potential removal of these species would reduce the size range of prey available to sharks by half. This may have cascading effects in the environment, and lead to increased competition among shark species. Ultimately, we find that larger body size for the predator may be advantageous.

My dissertation has relied heavily upon large, open-access datasets, which have been collected by many persons, resulting in hundreds to thousands of hours of hard field work. The advent of these data repositories has allowed for large-scale questions to be answered, identify patterns, and start to understand mechanisms underlying those patterns, such as those evaluated here. I have begun and hope to continue to contribute data to these open-source data repositories. It cannot be underestimated the role open-access data plays in paleoecological, biogeographical, macroecological, macroevolutionary, and macrophysiological studies.

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CHAPTER 1

ADAPTATION *IN SITU*: AN UNDERAPPRECIATED REPSONSE TO CLIAMTE CHANGE

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KEY WORDS: mammals, body size, climate change, late Quaternary, adaptation *in situ*

ABSTRACT:

When scientists assess the consequences of future environmental change on vertebrates, they focus on the most likely outcomes: movement and extirpation of organisms. However, adaptation *in situ* is also a potential mechanism and may be increasingly important as movement is constrained by extensive urbanization and habitat fragmentation. Since the last deglaciation comparable environmental shifts resulted in broadscale biotic reorganization. Thus, the past provides a natural experiment to investigate how animals responded to climatic stresses. We quantify the adaptive capability of a small mammal (*Neotoma cinerea*) to cope with warming and cooling events over the late Quaternary. While the geographic range expanded northward and contracted in the south, within the modern limits, populations generally adapted *in situ* with little difference between warming and cooling events. Our results suggest adaptation may be an underestimated response to future climatic change.

INTRODUCTION:

A major focus of conservation biology is characterizing the response of organisms, communities, and ecosystems to anthropogenic climatic change. Ample evidence suggests that many taxa have already been affected by climate shifts over the past half century (Chen *et al.*, 2011, Parmesan, 2006, Parmesan & Yohe, 2003, Walther *et al.*, 2002). The predicted increase of 2–4.5°C over the next 100 years (Stocker *et al.*, 2013) will likely cause further disruptions in biological systems (Barnosky *et al.*, 2012). The responses of animals to future climatic change probably will include multiple strategies. Of the potential responses, changes in abundance or distribution, which are the quickest and most likely, have been emphasized in the literature. However, estimates suggest that 55.5% of terrestrial ecosystems are altered by humans (Ellis *et al.*, 2010), restricting the ability of species to shift their geographic range (Rowe & Terry, 2014, Selwood *et al.*, 2015) to more favorable conditions.

When documenting the response of organisms to climate change, meta-analyses of past studies have mostly excluded adaptation or physiological responses – a potentially important strategy for coping with past and future climate change. Several intriguing studies on small vertebrates suggest that populations can locally adapt to increased temperature within 13–18 generations (Haugen & Vøllestad, 2000), despite the general perception that adaptation operates at time scales too slow for populations to cope with anthropogenic climatic change (e.g., Bradshaw & Holzapfel, 2006, Hetem *et al.*, 2014, Hoffmann & Sgro, 2011, Huntley, 2007). These studies have engendered some reconsideration of the adaptive potential of species (Bell & Gonzalez, 2011, Hoffmann

& Sgro, 2011, Smith & Betancourt, 2006, Smith *et al.*, 1995), but the limits and extent to which adaptation is possible remains elusive. For instance, previous work suggests that evolutionary decreases in body size are easier to achieve than increases (Evans *et al.*, 2012), so adapting to warming may be easier than cooling. While potential asymmetries in the phenotypic response to warming versus cooling have been examined in plants (Wang *et al.*, 2014), the potential asymmetries in the morphological response of mammals are not well understood.

Modern and historical studies investigating species' responses to climate change are limited by the restricted range of temperature change over the past 100-years, and do not capture the predicted 2–4.5˚C temperature increase in the 21st Century (Stocker *et al.*, 2013). Over the late Quaternary, climate changes of comparable magnitude occurred. Importantly, virtually all extant taxa successfully coped with these temperature shifts (Hof *et al.*, 2011). In response to past climatic change, populations both shifted their geographic range (Graham, 1986, Jackson & Overpeck, 2000, Lenoir & Svenning, 2015) and adapted *in situ* (Smith & Betancourt, 2006). In particular, North American animals successfully coped with 6–10˚C of warming in as little as 20 years (Alley *et al.*, 1993, Peteet, 1995) at the terminus of the Younger Dryas (11,690-11,590 ybp).

Here, we use a paleoecological perspective to examine the adaptive capability of the bushy-tailed woodrat, *Neotoma cinerea*, to past climate change. Our late Quaternary time frame encompasses the Last Glacial Maximum (21,000 ybp), as well as several significant abrupt warming and cooling events over the Holocene (last 11,000 years).

Using the well-resolved paleomidden record, we characterize the potential asymmetry in the morphological response of *Neotoma cinerea* to warming versus cooling climates. Specifically, we ask: (i) Were animals able to adapt equally well to warming versus cooling over the late Quaternary? (ii) Did the ability to adapt *in situ* vary with position within their modern geographic range? (iii) Did the direction, magnitude, or rate of climatic shifts ever exceed their thermal adaptive threshold?

Our analysis employs the paleomidden record created by *Neotoma cinerea*, the largest and most-cold tolerant species of North American woodrats. Their current distribution ranges from the Canadian Arctic to the Colorado Plateau, but was shifted considerably southward during the Pleistocene (Smith, 1997) (Fig. 1a). All woodrat species construct middens, or debris piles, which can be preserved for thousands of years in caves and rock shelters in arid and semi-arid areas (Betancourt *et al.*, 1990) (Fig. 1b-d). Analysis of plant macrofossils preserved in middens yielded detailed reconstructions of the late Quaternary vegetation history and dynamics in western North America (Betancourt *et al.*, 1990). Additionally, 100–1000s of fecal pellets are preserved in middens. Studies have shown that the width of fecal pellets is a robust proxy for body size (Smith, 1995, Smith & Betancourt, 2006).

Body size is a trait that influences an animals' thermal ecology. The majority of mammals (70%) conform to Bergmann's Rule (Millien *et al.*, 2006), an eco-geographic pattern wherein populations within a species (or species within a genus) are smaller in warmer habitats and larger in cooler habitats (Bergmann, 1847, Mayr, 1956). Bergmann's Rule also holds temporally for some taxa (Smith *et al.*, 1995), and has been postulated as a mechanism for coping with anthropogenic climate warming (Millien *et al.*, 2006). Woodrats display a robust relationship with temperature (Brown & Lee, 1969, Smith & Betancourt, 2006, Smith *et al.*, 1995) (Fig. S1a). Across their temporal and geographic range, populations conform to Bergmann's Rule (Brown & Lee, 1969, Smith *et al.*, 1995) (Fig. S1b).

Over the late Quaternary, *Neotoma* responded to climate change in a variety of ways: their geographic range shifted northward and contracted in the south substantially (Betancourt *et al.*, 1990), and they adapted *in situ* in the direction predicted by Bergmann's Rule at many localities (Brown & Lee, 1969, Smith & Betancourt, 2006). Modern populations at the edges of the range, possibly already at their physiological limits, may be vulnerable to future anthropogenic temperature shifts. For example, populations in the southern portion occupy higher elevations than populations in the north (Smith, 1997). For these populations, there may be insufficient elevational relief to allow retreat upwards as climate warms. Likewise, for northern populations, moving downslope may not provide enough temperature difference to cope with cooling temperatures experienced during the late Quaternary. Thus, adaptation via body size changes may be the only viable option. Populations at the center of the range, however, have more environmental 'space' to cope escape temperature changes.

MATERIALS & METHODS:

We use presence or absence of *Neotoma cinerea* middens in the paleorecord to examine potential asymmetries in their thermal response to climate over the late Quaternary.

Additionally, we quantify the rate of morphological change of *N. cinerea* populations and compare with the rate of temperature change to test populations' ability to adapt *in situ*. We restrict our analysis to records unambiguously attributed to *Neotoma cinerea*. Our dataset includes 34 georeferenced paleomidden localities, with 189 radiocarbon-dated pellet samples, spanning the limits of their modern geographic range, and what would have been the central-to-northern limits of their geographic range during the late Pleistocene (Smith, 1997) (Fig. 1a; Table S3).

We acknowledge that our paleomidden series is not perfect. For example, sampling effort of paleomiddens may be dependent on the question an investigator is seeking to answer and so may be selective in sampling, or may not sample paleomiddens in areas which are inaccessible (JL Betancourt, personal communication). Likewise, areas that have been sampled repeatedly for many years tend to have more paleomiddens from all time periods. In many cases, however, investigators tend to look for older paleomiddens rather than modern middens (Felisa Smith, personal communication). Therefore, we do not believe the paleomiddens were collected in any known systematic way; no one type of paleomidden was preferred over any other. Finally, many sites are 'missing' from our analyses due to lack of radiocarbon dates or because the associated pellets have not been measured. There are at least 169 paleomiddens whose pellets have not been measured for mass estimates, and 38 paleomiddens that have mass estimates but have not been radiocarbon dated.

Temperature records were obtained from the Greenland Ice Sheet Project 2 (GISP2), which provides the best well-resolved, continuous, global temperature proxy spanning the late Quaternary (Alley, 2000). Importantly, the GISP2 record captures the major features of millennial-scale temperature variations across the Northern Hemisphere over this time interval (Clark *et al.*, 2013*,* Viau *et al.*, 2006). Finer-scale temperature reconstructions from pollen (century to millennial-scale) or tree rings (annual- to decadal-scale) averaged for temperature across North America are available for some locations, but are extremely patchy in their temporal and spatial coverage (Viau *et al.*, 2006); none extend as far into the Pleistocene as the woodrat paleomidden record.

We calculated the temperature anomaly as the difference from the last 1,000-year temperature mean from the GISP2 temperature-record (following Jouzel et al., 2007). The GISP2 temperature data was binned in 100-year intervals, and the temperature over that interval was averaged. Due to the nature of the ice core data, the temperature record is more resolved towards the present. Thus, the number of temperature records per bin increases as the time approaches the present. To make the temperature and paleomidden records comparable, we averaged ± 50 years of temperature anomalies centered on the calibrated age of the paleomidden. We then averaged temperature anomalies into 100-year bins. Although binning dampens some high-amplitude, low-frequency temperature spikes, it generally corresponds to the temporal uncertainty around the paleomidden radiocarbon dates (~100 years). The maximum rate of temperature shifts was the maximum difference of temperature within each 100-year bin (see Table S1).

The overall distribution of temperatures and temperature shifts during midden formation was compared to the overall distribution in the GISP2 record over the last 25,000 years using Kolmogrov-Smirnov test and unpaired Wilcoxon Signed-Rank test to assess if middens were formed equally during warming as cooling events. If the estimated paleomidden temperatures are representative of the entire GISP2 temperature record (i.e., paleomiddens are sampled from all temperature regimes), we expect a non-significant difference for the Kolmogorov-Smirnov and Wilcoxon Signed-Rank tests. We only performed analyses on sites and time periods with >5 samples.

Majority of middens recovered are middle to late Holocene (last 5,000 years; n = 104/164) (Fig. 1d), which coincides with warmer temperatures. This phenomenon, where younger fossils, or middens, are more likely to be recovered since older fossils or middens have a greater chance of degrading, is found in many paleontological studies and is termed the "pull of the recent" effect (Raup, 1979). Both our study and previous studies on *Neotoma sp.* paleomiddens do find more paleomiddens within the last 20,000 years than older (Betancourt *et al.*, 1990). Although we recognize this issue, the decay function of middens remains unknown. Partly, this is because decay rates may be site-specific. Middens in wet environments or that experience flash floods will not be preserved. For example, middens at lower elevations in Titus Canyon in Death Valley, CA would be compromised or erased by periodic flooding events and we would therefore not be able to recover a record of those populations. Similarly, middens in the northern part of the geographic range may be erased or compromised due to repeated freezing events. Further, older middens decrease with effective moisture (cooler summers and, in some cases, more precipitation) from south to north (from low to high elevations) as areas containing older middens are increasingly patchy in northern latitudes and higher elevations. For our study, not correcting for the pull of the recent may result in a signal of midden formation occurring more during warmer climates that may not be real. To ameliorate any bias caused by the high preponderance of paleomiddens recovered over the last 5,000 years – when temperatures are warmer, we used a sliding window of 5,000-year intervals to test the distribution of temperatures and temperature shifts. Additionally, we binned paleomidden samples into three different latitudinal bands containing ~30 samples that encompass microhabitats in which animals may respond differently to climate: South (35-37˚N), Central (40-42˚N), and Northern (44.5-46.5˚N), to assess regional differences in the response to climate change.

We also calculated the rate of body size change using darwins (*d*): ln $(x_2/x_1)/\Delta t$, where x is body size and Δt is the time interval in millions of years (Gingerich, 1983). Similarly, rates of temperature change were calculated in darwins: ln $(T_2/T_1)/\Delta t$, where T is the average temperature anomaly during midden formation. Darwins are a useful unit to compare rates of proportional change over a standardized time interval within a single species. Because darwins can be influenced by varying temporal intervals (Gingerich, 1983), we only used temporal intervals within 100–1,000 years. Likewise, we compared the rate of temperature shifts during midden formation to the rate of body size change using a Kolmogrov-Smirnov test. Further, we perform a simple regression of body size shifts during cooling and warming events.

RESULTS:

Within the modern geographic range, we found no asymmetry in the ability of woodrat populations to persist to different climate regimes over the last 25,000 years. Within each

5,000-year interval, we found no change (Kolmogrov-Smirnov test: p-values > 0.05; Table S1) in midden formation during warmer or cooler climatic conditions. Indeed, temperatures during midden deposition closely mirrored the frequency of temperatures within the GISP2 record (Fig. 2a). Moreover, *N. cinerea* populations persisted during temperatures that were 22°C cooler up to 3°C warmer found in the GISP2 record over the last 25,000 years (Fig. 2a,b).

The magnitude of temperature changes also did not influence persistence patterns. Despite an average warming of 0.7˚C and average cooling was 0.5˚C, there was no asymmetry in the response of woodrats (Kolmogrov-Smirnov test: p-values > 0.05; Table S1) to the thermal shifts in each 5,000-year interval. These results were robust and qualitatively similar regardless of how middens were binned (Table S1). Animals persisted even during the most abrupt events (e.g., up to 8˚C 100-years^{-1}) (Fig. 2c,d) – rates that exceed those expected for future anthropogenic warming.

As expected, we found possible climatic conditions that may have caused local extirpations at the periphery of or outside their modern range. We found a temporal gap in both the midden and fossil record at the extreme northern latitudes (44.5–46.5˚N); neither woodrat middens nor bones in sediment from caves and open sites have been reported from 25,000 to 11,500 years ago (Table S2). This coincides with an apparent dearth of middens from the northern edge during the coldest temperatures (Fig. 3a,b). Middens older and younger than this interval were recovered from the northern edge (Table S3). The absence of middens could mean that populations encountered conditions that exceeded their ability to adapt *in situ*, and/or modify their elevational extent. It is also possible that the apparent absence of middens or bone assemblages during the cold interval could be attributed to inadequate sampling effort in the northern part of *N. cinerea* range, or increasingly poor midden preservation at higher latitudes due to increased effective moisture with lower temperature (Betancourt *et al.*, 1990).

The middle Holocene was several degrees warmer than today, but this warmer climate did not negatively influence the recovery of paleomiddens at the center or the southern boundary of sites included in our study (Fig. 3c-g). Animals at these southern sites (35–37˚N) even persisted during the greatest temperature shifts: 8˚C warming and 2˚C cooling during the late Pleistocene (Fig. 3h). It should be noted, however, that these locations (35–37˚N) were close to the center of the Pleistocene geographic range (Smith, 1997). As expected, populations at the edges of their Pleistocene geographic range appear to become locally extirpated as climate warmed (southern populations not included in this dataset) or cooled (northern populations). Still, populations in the center of the Pleistocene geographic range (35–42˚N) persisted during temperature shifts in the past comparable to projected shifts in climate (Fig. 3c-f).

The overall distribution of evolutionary rates of body size change does not significantly differ from that of the rate temperature change over the late Quaternary (Kolmogrov-Smirnov test: p-value = 0.23) (Fig. 4), suggesting that animals were adapting in step with environmental challenges. Moreover, contrary to our expectations, the rates of body size decreases were not systematically higher than increases; getting smaller was not evolutionarily ‘easier’. Similarly, we find body size shifts do not correlate to cooling (Fig. S2a) or warming (Fig. S2b) events. The fastest rate of decrease was 2661*d*

(203g/153 yr); the fastest rate of increase was comparable, at 2550*d* (103g /117 yr). These extremely rapid rates of body size change correspond with those found in studies performing artificial, or directed, evolution (Gingerich, 1983, Reznick *et al.*, 1997). Moreover, we find that body size was evolutionarily labile; the mean rate of body size change was 2*d*, somewhat higher than the average for the vertebrate fossil record (Gingerich, 1983). Woodrat populations changed body mass quickly and presumably in response to climate (Smith & Betancourt, 2006, Smith *et al.*, 1995). Of course, baseline temperatures were lower in the past, so there may have been more thermal scope for adaptation; future temperature increases may challenge populations, particularly those at the southern edge.

DISCUSSION:

Although rates of temperature change exceeded rates of body size change, populations still persisted. Multiple strategies for coping with changing temperatures may account for this conundrum. First, individuals modify their thermal environment by hiding in rock shelters (Betancourt *et al.*, 1990). For example, a related species, *Neotoma lepida*, are known to stay in their cooler dens until outside temperatures lower below their thermal critical temperature (Murray & Smith, 2012). As long as individuals have enough 'cool' hours to forage, then warmer temperatures may not pose a problem or cause selection against an extreme body size (Fig. S1b), and vice versa for cold temperatures. Second, since individuals with larger body sizes have a wider range of environmental temperatures that they can tolerate, they may be more tolerant against temperature change. Increasing or decreasing temperatures may not affect persistence of populations with a larger mean body as it would for populations starting at a smaller mean body size. Finally, the apparent persistence could be due to the wide temporal windows. Truly extreme temperature events may be short-lived relative to the 100-year interval. Even if these extreme events resulted in extirpation, it would not be captured by the time-averaging of the paleomidden record.

Recent studies confirm that morphological change may be the most feasible option for some species to persist during current and future climatic change (Barnosky *et al.*, 2003, Blois & Hadly, 2009, Thompson, 1998). Our study demonstrates that majority of *N. cinerea* populations adapted equally well to warming and cooling events over the late Quaternary, but that peripheral populations were challenged. The rates of climatic shifts did not exceed their thermal adaptive threshold. Climate change may be an issue at the physiological edges of the geographic range, but within the core, populations may well be able to adapt even to rapid shifts. We provide a framework for testing the direction of morphological change in response to concurrent climatic change. Our study suggests that for some mammals, adaptation may be a viable option for coping with anthropogenic climate change.

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Figure 1. Location and spatial-temporal extent of middens included in the study. (a) Spatial distribution of *Neotoma cinerea* middens examined (orange circles) across the western USA. Size of circle is scaled by number of middens recovered from each location. Tan area represents the current geographic range of *N. cinerea*. (b) *Neotoma cinerea*, the bushy-tailed woodrat. (c) An indurated midden from Death Valley National Park, California. (d) Sampling of middens in 500-year bins throughout the late Quaternary from 40,000 years ago to modern (orange histogram) with the GISP2 ice core temperature anomaly overlaid (blue). Note that younger samples are more prevalent, which also coincides with warmer temperatures in the GISP2 record.

Figure 2. Temperature and midden record. GISP2 temperature anomalies (blue); estimated temperature when midden was formed (orange). (a) Comparison of binned temperature record in 100-year bins from the GISP2 and temperature during midden formation. Middens are recovered throughout the range of temperatures occurring over the late Quaternary. (b) Frequency distribution of temperature shifts in 100-year bins of the temperature record and estimated temperature in 100-year bins centered on midden formation for all temperature shifts experienced. (c) Comparison of temperature shifts in 100-year bins and those occurring during midden formation. (d) Frequency distribution of temperature shifts in 100-year bins of the temperature record and estimated temperature shifts of midden formation. Notice a preponderance of middens from 5,000 years ago to present, when there is little fluctuation in temperature. To avoid the 'pull of the recent', we used a sliding window of 5,000 years (Table S3).

Figure 3. Temperature profile across *Neotoma cinerea* geographic range. (a,c,e,g,) Comparisons of the frequencies of temperatures during formation of middens (a,c,e in orange) to the GISP2 temperature record (g in blue). (b,d,f,h) Comparisons of the frequency of the maximum temperature shifts within 100-year intervals of when the middens were formed (b,d,f in orange) to the GISP2 temperature record (h in blue). Note that our 'southern edge' was close to the center of *N. cinerea*'s distribution during the Pleistocene. Thus, our analysis excludes the southern-most edge of their Pleistocene distribution.

Figure 4. Rates of temperature change and morphological change calculated in *darwins*. The distribution of rates of population mean body mass change (in orange) is not significantly different from the distribution of rates of temperature change (in blue) over the late Quaternary (Kolmogorov-Smirnov test p-value = 0.24). Binning smoothed out eight extreme rates of temperature change: four decreasing temperature rates of -12,381*d*; -7,457*d*; -5,586*d*; -10,643*d*; and four increasing temperature rates of 5,598*d*; 7,482*d*; 6,786*d*; 11,004*d*.

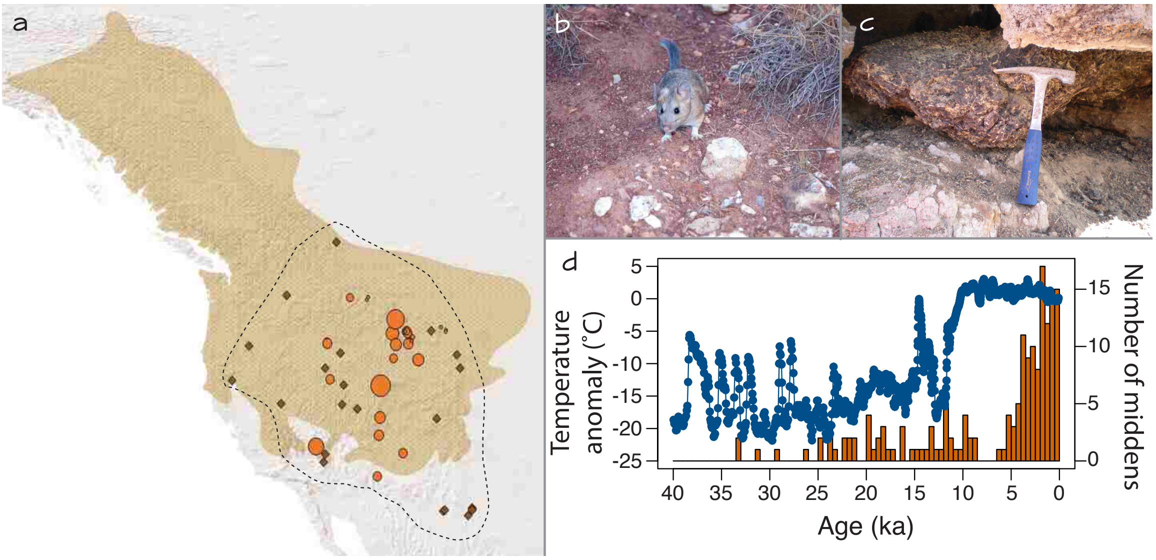
a
b
c
d
Temperature anomaly (˚C)
5
0
-5
-10
-15
-20
-25
40
35
30
25
20
15
10
5
0
Age (ka)
Number of middens
15
10
5
0

Figure 1.

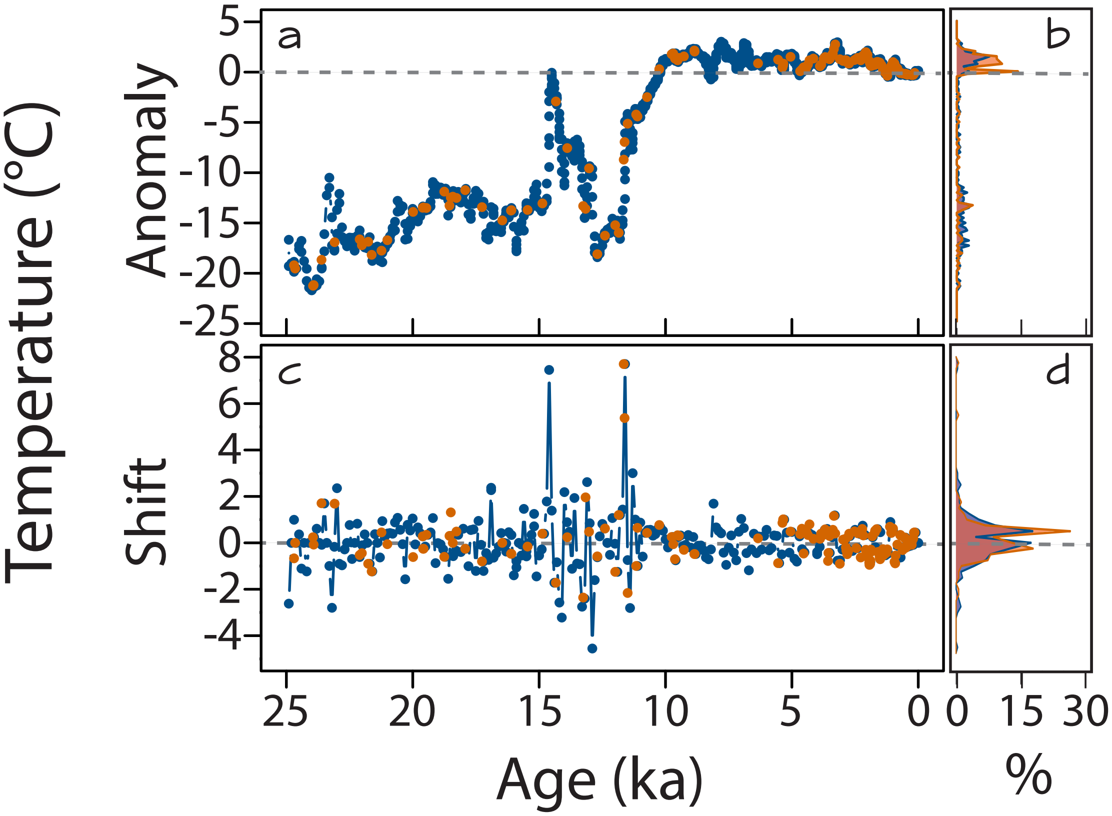
Temperature (°C)
Anomaly
Shift
a
b
c
d
5
0
-5
-10
-15
-20
-25
8
6
4
2
0
-2
-4
25
20
15
10
5
0
0
15
30
Age (ka)
%

Figure 2.

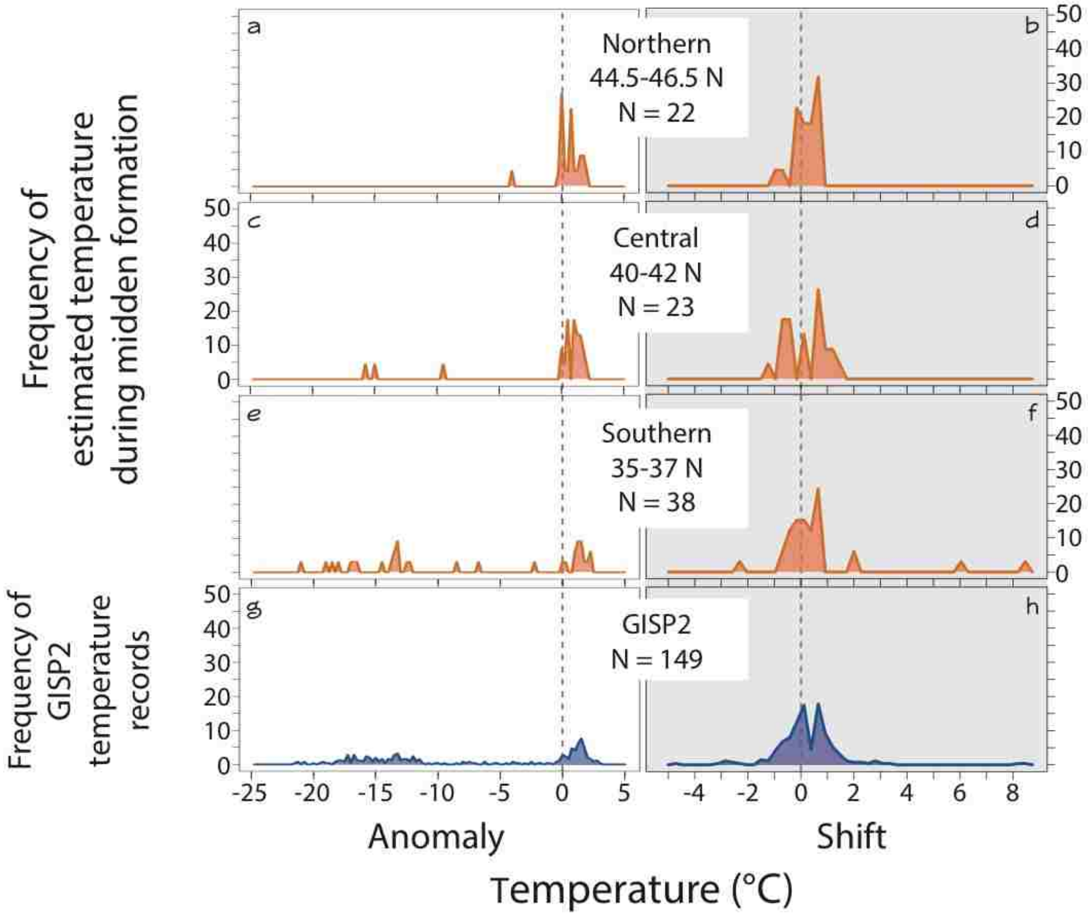
a
b
c
d
e
f
g
h
Northern
44.5-46.5 N
N = 22
Central
40-42 N
N = 23
Southern
35-37 N
N = 38
GISP2
N = 149
Frequency of estimated temperature during midden formation
Frequency of GISP2 temperature records
0
10
20
30
40
50
-25
-20
-15
-10
-5
0
5
-4
-2
0
2
4
6
8
Anomaly
Shift
Temperature (°C)

Figure 3.

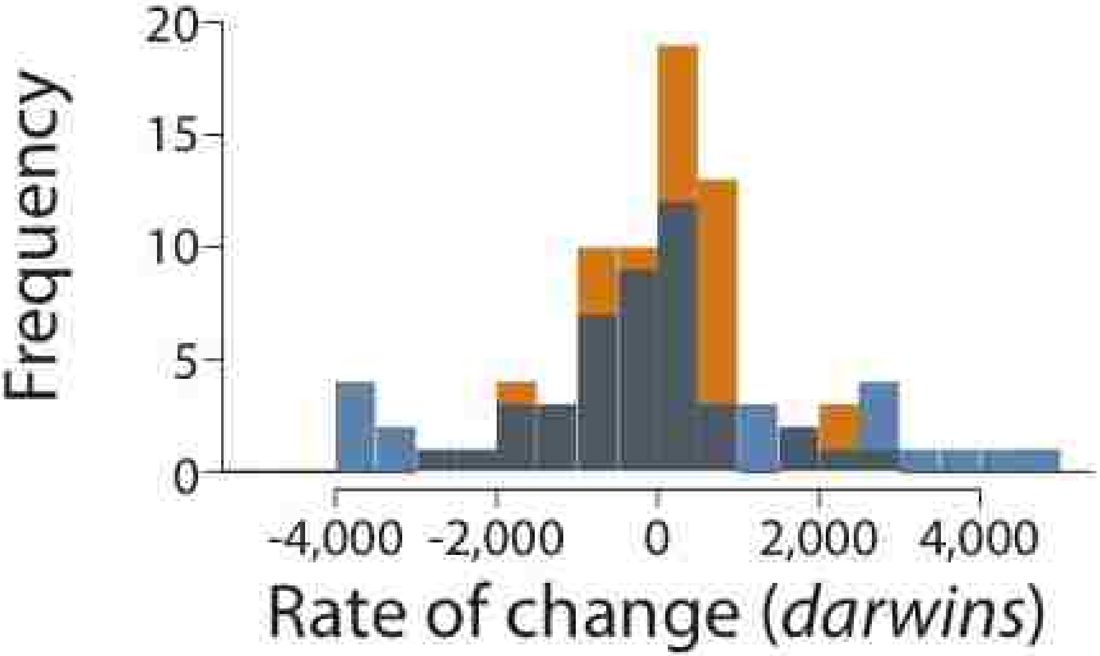
Frequency
20
15
10
5
0
-4,000
-2,000
0
2,000
4,000
Rate of change (*darwins*)

Figure 4.

SUPPLEMENTAL MATERIALS

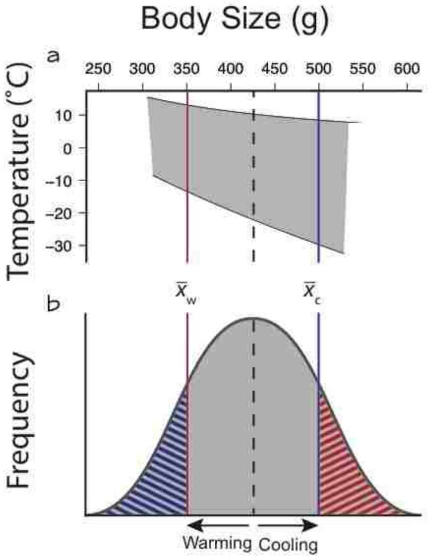

Figure S1. Relationship between temperature and body size for populations of *Neotoma cinerea*. (a) The realized thermal niche (shaded gray) is bounded by the mean July temperature (upper black regression line) and the mean January temperature (lower regression line) animals experience throughout their modern geographic range (equations from Smith & Betancourt, 2006). Larger animals can tolerate colder temperatures and a wider range of temperatures; smaller animals can tolerate warmer upper temperatures, but a narrower overall range of temperature. (b) The morphological response of a hypothetical population with a mean body size around 400g to warming and cooling of 2˚C. As climate warms, the largest animals are selected against, driving the mean population body size down by ~95g. Conversely, smaller animals would be thermally disadvantaged during cooling events, and mean population body size increases by ~155g. This suggests that it may be easier to get smaller, as less change in body size is required. However, if temperature shifts outside of the adaptive zone, then persistence requires elevational shifts in addition to morphological adaptation.

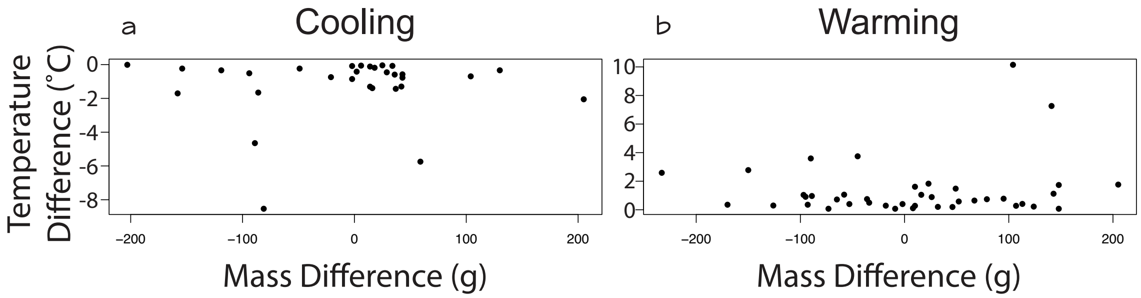

Figure S2. Plots of body size change during cooling and warming temperature shifts. Body size change is not significantly correlated with (a) cooling events (slope = 0.001, R^2 = 0.004, p-value = 0.74) or (b) warming events (slope = 0.003, R^2 = 0.02, p-value = 0.42).

Table S1. Results for temperature anomaly (relative to 1,000-year mean) and shifts in 100-year bins compared to the estimated temperatures during midden formation over the last 25,000 years using a Kolmogorov-Smirnov and un-paired Wilcoxon Signed-Rank tests. Shifts are calculated in three ways: (1) the difference between the latest recorded temperature and the earliest recorded temperature in each 100-year bin (Shift$_1$); (2) the maximum difference for all possible temperatures, regardless of chronology, for each 100-year bin (Shift$_2$); (3) maximum from the first differences of the temperatures in each 100-year bin (Shift$_3$). Of note, interpretation of results does not differ based on method of calculating shifts.

			Anomaly		**Shift$_1$**		**Shift$_2$**		**Shift$_3$**	
Locality	Window (ka)	N	KS Test	Wilcoxon Signed-Rank Test	KS Test	Wilcoxon Signed-Rank Test	KS Test	Wilcoxon Signed-Rank Test	KS Test	Wilcoxon Signed-Rank Test
All	25–0	163	>0.01	>0.01	0.39	0.84	0.48	0.96	0.03	0.92
	5–0	104	0.80	0.37	0.96	0.68	0.94	0.78	0.74	0.63
	6–1	80	0.63	0.36	0.77	0.60	0.83	0.75	0.79	0.45
	7–2	52	1.00	0.99	0.20	0.07	0.20	0.07	0.08	0.04
	8–3	34	0.95	0.43	0.04	0.01	0.01	0.01	0.01	0.01
	9–4	16	0.28	0.08	0.20	0.07	0.13	0.07	0.26	0.13
	10–5	14	0.98	0.92	0.82	0.55	0.90	0.64	0.86	0.60
	11–6	11	0.88	0.53	1.00	0.76	0.99	0.70	0.68	0.72
	12–7	17	0.31	0.37	0.84	0.79	0.97	0.84	1.00	0.94
	13–8	19	0.97	0.88	0.95	0.90	0.91	0.96	0.95	1.00
	14–9	21	1.00	0.79	1.00	0.83	1.00	0.78	1.00	0.76
	15–10	17	0.96	0.60	0.99	0.86	0.99	0.82	0.99	0.81
	16–11	16	0.99	0.79	0.95	0.81	0.99	0.83	1.00	0.97
	17–12	12	0.79	0.97	0.94	0.91	0.92	0.88	0.95	0.75

	18–13	12	0.55	0.80	0.65	0.66	0.85	0.76	0.80	0.55
	19–14	13	0.47	0.53	0.98	0.98	0.98	1.00	0.99	0.92
	20–15	16	0.17	0.45	0.94	0.78	0.96	0.93	0.95	0.81
	21–16	15	0.08	0.16	0.48	0.36	0.52	0.42	0.44	0.31
	22–17	16	0.66	0.60	0.64	0.36	0.69	0.43	0.66	0.34
	23–18	16	0.69	0.66	0.76	0.37	0.76	0.37	0.68	0.38
	24–19	15	0.71	0.35	0.52	0.34	0.52	0.34	0.36	0.36
	25–20	12	0.21	0.10	0.72	0.62	0.72	0.62	0.76	0.81
Northern	25–0	22	0.00	0.00	0.32	0.66	0.23	0.79	0.11	0.90
	5–0	20	0.33	0.13	0.99	0.95	0.75	0.88	0.77	0.93
	6–1	14	0.71	0.49	0.88	0.90	0.91	0.87	0.97	0.88
	7–2	7	0.53	0.28	0.84	0.56	0.94	0.64	0.81	0.36
	8–3	5	0.16	0.20	0.46	0.33	0.47	0.43	0.53	0.20
	9–4	1	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	10–5	1	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	11–6	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	12–7	1	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	13–8	1	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	14–9	1	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	15–10	1	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	16–11	1	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	17–12	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	18–13	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	19–14	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	20–15	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	21–16	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	22–17	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	23–18	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	24–19	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	25–20	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A

Middle	25–0	23	0.00	0.00	0.94	0.59	0.68	0.73	0.39	0.86
	5–0	16	0.89	0.90	0.41	0.22	0.09	0.16	0.32	0.53
	6–1	14	0.85	0.45	0.57	0.46	0.10	0.39	0.41	0.80
	7–2	9	0.99	0.63	0.95	0.88	0.75	0.74	0.74	0.73
	8–3	4	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	9–4	2	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	10–5	3	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	11–6	3	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	12–7	5	0.60	0.41	0.99	0.78	0.95	0.71	0.98	0.98
	13–8	5	0.98	0.95	0.99	0.78	0.97	0.66	0.99	0.98
	14–9	6	0.86	0.77	1.00	0.91	0.98	0.68	1.00	0.96
	15–10	4	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	16–11	3	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	17–12	1	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	18–13	1	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	19–14	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	20–15	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	21–16	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	22–17	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	23–18	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	24–19	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	25–20	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Southern	25–0	33	0.95	0.94	0.93	0.87	0.87	0.98	0.82	0.88
	5–0	7	0.83	0.72	0.74	0.79	0.68	0.78	0.92	0.64
	6–1	7	0.80	0.54	0.94	0.98	0.92	1.00	0.97	0.81
	7–2	6	0.64	0.63	0.14	0.28	0.14	0.28	0.17	0.31
	8–3	4	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	9–4	5	0.92	0.76	0.60	0.63	0.90	0.70	0.87	0.91
	10–5	7	0.90	0.42	0.76	0.36	0.81	0.29	0.72	0.39
	11–6	8	0.91	0.51	0.74	0.34	0.80	0.29	0.82	0.57
	12–7	9	0.95	0.67	0.91	1.00	0.91	0.94	0.91	0.67

	13–8	10	0.53	0.28	0.81	0.90	0.76	0.94	0.81	0.91
	14–9	9	0.66	0.39	0.91	1.00	0.91	0.99	0.91	0.98
	15–10	5	0.98	0.58	0.60	0.49	0.59	0.53	0.60	0.73
	16–11	5	0.98	0.63	0.60	0.48	0.58	0.60	0.61	0.74
	17–12	4	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	18–13	4	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	19–14	6	0.64	0.80	0.59	0.69	0.58	0.61	0.87	0.95
	20–15	8	0.76	0.92	0.98	0.96	0.95	0.83	0.98	0.86
	21–16	7	0.65	0.49	0.80	0.69	0.80	0.79	0.86	0.50
	22–17	7	0.57	0.51	0.80	0.67	0.82	0.74	0.83	0.58
	23–18	7	0.66	0.47	0.87	0.78	0.87	0.78	0.86	0.76
	24–19	7	0.66	0.33	0.85	0.89	0.85	0.89	0.88	0.82
	25–20	6	0.34	0.25	0.69	0.88	0.69	0.88	0.80	0.61

Table S2. *Neotoma cinerea* fossil localities from 40,000 years ago to 10,000 years ago and references shown in Figure 1A.

Site Name	Latitude	Longitude	Age Range	Reference(s)
Medicine Lodge Creek	44.25	-107.50	11,001–11,011	(Walker, 1987)
Deer Creek Cave	41.75	-115.37	11,680–11,127	(Heaton, 1985, Ziegler, 1963)
Upper Sloth Cave	31.87	-104.75	13,360–12,939	(Harris, 1985, Logan & Black, 1979, Van Devender *et al.*, 1975)
Smith Creek Cave	39.33	-114.08	14, 004–10,472	(Bryan, 1979, Mead *et al.*, 1992, Mead *et al.*, 1982)
Marmes Rockshelter	46.62	-118.20	14,170–10,191	(Gustafson, 1972, Lyman & Livingston, 1983, Sheppard *et al.*, 1987)
Danger Cave	40.62	-114.00	15,332–11,779	(Currey *et al.*, 1984, Grayson, 1988, Jennings, 1957, Madsen, 1980, Scott *et al.*, 1983)

Shelter Cave	32.18	-106.60	15,332–11,417	(Harris, 1977, Harris, 1985, Stock, 1932, Thompson *et al.*, 1980)
Bell Cave	41.75	-105.37	16,048–11,417	(Walker, 1987, Zeimans & Walker, 1974)
Wilson Butte Cave	42.77	-114.22	17,474–11,341	(Crane & Griffin, 1966, Gruhn, 1961, Lundelius *et al.*, 1983)
Haystack Cave	38.37	-107.12	18,140–14,008	(Emslie, 1986)
Potosi Mountain Midden 2	36.00	-115.38	19,625–13,854	(Mead & Murray, 1991)
Connley Cave No. 4	43.25	-121.00	21,286 –10,305	(Bedwell, 1973, Grayson, 1979)
Kokoweef Cave	35.42	-115.50	23,956–11,417	(Goodwin & Reynolds, 1989, Reynolds *et al.*, 1991)
Samwel Cave	40.92	-122.23	25,600–19,603	(Feranec *et al.*, 2007, Harris, 1985)
Crystal Ball Cave	39.00	-113.00	27,608–11,417	(Heaton, 1985)

January Cave	50.19	-114.52	27,721-11,417	(Burns, 1990)
Little Box Elder Cave	42.62	-105.62	28,734–10,421	(Anderson, 1968, Indeck, 1987, Walker, 1987)
Hidden Cave	39.37	-106.50	30,041–11,417	(Grayson, 1985, Thomas, 1985, Thompson *et al.*, 1986)
Conkling Cavern	32.25	-104.50	30,041–11,417	(Harris, 1977, Harris, 1985, Smartt, 1977)
Dark Canyon Cave	32.25	-104.50	20,041–24,084	(Harris, 1977, Harris, 1985)
Dry Cave	32.37	-104.48	35,407–12,757	(Harris, 1970, Harris, 1980, Harris, 1984, Harris, 1985, Harris, 1987)

Table S3. Midden data used in our study. Analyses were restricted to only include intact indurated middens, and further limited middens to only those with an estimated mean body mass of at least 325g to ensure all populations represent *Neotoma cinerea* and not possibly other *Neotoma* species (Smith & Betancourt, 2003).

Locality	State	Lat.	Long.	Elev. (m)	^{14}C	^{14}C SD	Age[1]	Mass est. (g)	Est. Temp. (˚C)	Max. Temp. Shift (˚C)	Collected / Measured By
Allen Canyon	UT	37.47	109.35	2195.00	11310.00	200.00	13161	347	-13.59	1.96	(Betancourt, 1984)
Arco Hills	ID	43.39	113.08	1926.00	2400.00	185.00	2451	351	1.34	-0.23	(Smith & Betancourt, 2003)
Arco Hills	ID	43.39	113.08	1926.00	3315.00	150.00	3550	418	1.32	-0.43	(Smith & Betancourt, 2003)
Arco Hills	ID	43.39	113.08	1926.00	3880.00	140.00	4299	329	1.17	0.80	(Smith & Betancourt, 2003)
Atlatl Cave	NM	36.05	107.59	1910.00	0.00	25.00	0	419			(Betancourt & Davis, 1984)
Atlatl Cave	NM	36.05	107.59	1910.00	1960.00	120.00	1907	455	0.83	0.17	(Betancourt & Davis, 1984)
Atlatl Cave	NM	36.05	107.59	1910.00	2780.00	120.00	2889	396	1.20		(Betancourt & Davis, 1984)
Atlatl Cave	NM	36.05	107.59	1910.00	5550.00	130.00	6337	442	0.88	0.20	(Betancourt & Davis, 1984)
Atlatl Cave	NM	36.05	107.59	1910.00	8290.00	150.00	9274	345	1.57	-0.30	(Betancourt & Davis, 1984)

Atlatl Cave	NM	36.05	107.59	1910.00	9460.00	160.00	10732	479	-2.48	0.43	(Betancourt & Davis, 1984)
Atlatl Cave	NM	36.05	107.59	1910.00	10080.00	140.00	11650	516	-8.71	7.70	(Betancourt & Davis, 1984)
Beaver Creek Canyon	MT	46.47	111.52	1169.23	192.00		196	342	-0.27	0.20	(Norris, 2006)
Beaver Creek Canyon	MT	46.47	111.52	1169.23	356.00		419	394	-0.25	0.11	(Norris, 2006)
Beaver Creek Canyon	MT	46.47	111.52	1169.23	1570.00		1455	363	0.68	-0.35	(Norris, 2006)
Bird's Eye Canyon/ Creek	WY	43.23	108.05	1645.00	90.00	45.00	45	491			Betancourt et al. unpublished
Bison Alcove	UT	38.44	109.30	1317.00	405.00	100.00	453	501	-0.22	-0.16	(Mead *et al.*, 1991)
Bison Alcove	UT	38.44	109.30	1317.00	1930.00	80.00	1872	504	0.62	-0.29	(Mead *et al.*, 1991)
Bison Alcove	UT	38.44	109.30	1317.00	3058.00	38.00	3281	533	2.77	0.40	(Mead *et al.*, 1991)
Bison Alcove	UT	38.44	109.30	1317.00	12420.00	210.00	14340	513	-2.91	-1.72	(Mead *et al.*, 1991)
Bison Alcove	UT	38.44	109.30	1317.00	14910.00	100.00	17924	565	-11.73	-0.26	(Mead *et al.*, 1991)
Bison Alcove	UT	38.44	109.30	1317.00	15250.00	100.00	18492	597	-12.48	1.31	(Mead *et al.*, 1991)
Bison Alcove	UT	38.44	109.30	1317.00	16490.00	170.00	19610	607	-13.49	0.28	(Mead *et al.*, 1991)
Bison Alcove	UT	38.44	109.30	1317.00	17910.00	110.00	21237	543	-17.75	0.45	(Mead *et al.*, 1991)
Bison Alcove	UT	38.44	109.30	1317.00	18480.00	100.00	22101	542	-16.63	-0.53	(Mead *et al.*, 1991)

Bison Alcove	UT	38.44	109.30	1317.00	20050.00	160.00	23948	560	-21.25	0.24	(Mead *et al.*, 1991)
Bison Alcove	UT	38.44	109.30	1317.00	20680.00	140.00	24653	582	-19.53	0.00	(Mead *et al.*, 1991)
Brokenback Canyon	WY	44.06	107.25	1569.23	2095.00	75.00	2067	357	1.97	-0.30	(Lyford *et al.*, 2003)
Brokenback Canyon	WY	44.06	107.25	1581.00	2200.00	60.00	2212	381	1.46	0.60	(Lyford *et al.*, 2003)
Brokenback Canyon	WY	44.06	107.25	1763.08	3144.00			347			(Lyford *et al.*, 2003)
Brokenback Canyon	WY	44.06	107.25	1769.00	887.00			355			(Lyford *et al.*, 2003)
Cook's Canyon	WY	43.59	107.14	1784.62	2695.00	75.00	2794	446	0.95	-0.42	Betancourt et al. unpublished
Cook's Canyon	WY	43.59	107.14	1895.38	4620.00	90.00	5336	379	0.85	1.01	Betancourt et al. unpublished
Cook's Canyon	WY	43.59	107.14	1969.23	500.00	65.00	526	360	-0.17	0.22	Betancourt et al. unpublished
Coyote Hills	NM				13830.00	165.00	16114	332	-13.77	-0.47	Betancourt unpublished
CR	UT				0.00		0	372			
Dutch John Mountain	UT	40.57	109.25	2021.00	0.00	25.00	0	527			(Lyford *et al.*, 2003)
Dutch John Mountain	UT	40.57	109.25	2029.00	0.00	25.00	0	498			(Lyford *et al.*, 2003)
Dutch John Mountain	UT	40.57	109.25	2030.00	1495.00	60.00	1377	537	0.11	-0.54	(Lyford *et al.*, 2003)
Dutch John Mountain	UT	40.57	109.25	2030.00	1985.00	50.00	1929	345	1.06	-0.95	(Lyford *et al.*, 2003)
Dutch John Mountain	UT	40.57	109.25	2030.00	2255.00	50.00	2279	409	1.19	-0.63	(Lyford *et al.*, 2003)
Dutch John Mountain	UT	40.57	109.25	2030.00	2945.00	70.00	3105	415	1.28	-0.90	(Lyford *et al.*, 2003)
Dutch John Mountain	UT	40.57	109.25	2030.00	4650.00	85.00	5374	392	0.46	0.86	(Lyford *et al.*, 2003)

Dutch John Mountain	UT	40.57	109.25	2030.00	8455.00	75.00	9471	440	1.41	0.30	(Lyford *et al.*, 2003)
Dutch John Mountain	UT	40.57	109.25	2030.77	4100.00	60.00	4607	344	0.26	0.61	(Lyford *et al.*, 2003)
Dutch John Mountain	UT	40.57	109.25	2030.77	9100.00	70.00	10247	329	0.29	0.77	(Lyford *et al.*, 2003)
Dutch John Mountain	UT	40.57	109.25	2049.23	579.00	40.00	506	414	-0.16	-0.18	(Lyford *et al.*, 2003)
Dutch John Mountain	UT	40.57	109.25	2061.54	2170.00	70.00	2170	375	1.68	0.32	(Lyford *et al.*, 2003)
Dutch John Mountain	UT	40.57	109.25	2080.00	1990.00	70.00	1937	355	1.11	-0.86	(Lyford *et al.*, 2003)
Dutch John Mountain	UT	40.57	109.25		410.00	50.00	474	453	-0.21	-0.18	(Lyford *et al.*, 2003)
Dutch John Mountain	UT	40.57	109.25		1630.00	70.00	1521	544	0.92	-0.64	(Lyford *et al.*, 2003)
Dutch John Mountain	UT	40.57	109.25		2610.00	50.00	2737	575	0.87	0.39	(Lyford *et al.*, 2003)
Dutch John Mountain	UT	40.57	109.25		2630.00	60.00	2747	504	0.85	0.29	(Lyford *et al.*, 2003)
Dutch John Mountain	UT	40.57	109.25		10180.00	140.00	11851	375	-15.97	1.20	(Lyford *et al.*, 2003)
Dutch John Mountain	UT	40.57	109.25		35170.00	710.00	40494				(Lyford *et al.*, 2003)
Dutch John Mountain	UT	40.57	109.25		23120.00	190.00	27743				(Lyford *et al.*, 2003)
Fishmouth Cave	UT	37.25	109.38	1520.00	0.00	25.00	0	378			(Betancourt, 1984)
Fishmouth Cave	UT	37.25	109.38	1520.00	0.00	25.00	0	389			(Betancourt, 1984)
Fishmouth Cave	UT	37.25	109.38	1546.00	0.00	25.00	0	333			(Betancourt, 1984)
Fishmouth Cave	UT	37.25	109.39	1585.00	3550.00	60.00	3839	343	0.74	0.39	(Betancourt, 1984)

Fishmouth Cave	UT	37.25	109.39	1585.00	9700.00	110.00	11106	342	-4.40	0.65	(Betancourt, 1984)
Fishmouth Cave	UT	37.25	109.39	1585.00	10540.00	300.00	12392	380	-16.27	0.62	(Betancourt, 1984)
Fishmouth Cave	UT	37.25	109.39	1585.00	12770.00	140.00	14873	409	-13.05	0.39	(Betancourt, 1984)
Fishmouth Cave	UT	37.25	109.39	1585.00	13800.00	320.00	16098	480	-13.74	-0.47	(Betancourt, 1984)
Hidden Mouth Cave	ID	43.57	113.26	2255.00	3160.00	80.00	3379	446	1.84	0.56	(Smith & Betancourt, 2003)
Hidden Mouth Cave	ID	43.57	113.26	2255.00	3555.00	85.00	3845	456	0.74	0.39	(Smith & Betancourt, 2003)
Hidden Mouth Cave	ID	43.57	113.26	2255.00	3985.00	85.00	4446	468	0.36	0.44	(Smith & Betancourt, 2003)
Homestead Cave	UT	41.00	113.00	1406.00	1020.00	40.00	935	340	0.84	-0.82	(Madsen *et al.*, 2001)
Homestead Cave	UT	41.00	113.00	1406.00	1200.00	50.00	1119	341	0.28	0.69	(Madsen *et al.*, 2001)
Homestead Cave	UT	41.00	113.00	1406.00	2025.00	775.00	2009	408	1.72	-0.61	(Madsen *et al.*, 2001)
Homestead Cave	UT	41.00	113.00	1406.00	3480.00	40.00	3745	336	1.34	0.35	(Madsen *et al.*, 2001)
Homestead Cave	UT	41.00	113.00	1406.00	8675.00	235.00	9698	399	1.84	-0.06	(Madsen *et al.*, 2001)
Homestead Cave	UT	41.00	113.00	1406.00	10255.00	180.00	11989	396	-15.23	-1.25	(Madsen *et al.*, 2001)
Homestead Cave	UT	41.00	113.00	1406.00	11168.00	208.00	13027	438	-9.56	0.48	(Madsen *et al.*, 2001)
Inyan Kara Drainage	SD	44.49	104.79	1280.00	153.00		145	376	-0.08	0.45	(Norris *et al.*, 2016)
Lander-Twin Creek	WY	42.40	108.30	1876.92	380.00	80.00	436	342	-0.23	-0.14	Lyford unpublished

Lander-Twin Creek	WY	42.40	108.30	1886.15	100.00	0.50	150	432	-0.10	0.44	Lyford unpublished
Lander-Twin Creek	WY	42.40	108.30	1907.69	99.30	0.74	169	413	-0.17	0.44	Lyford unpublished
Lander-Twin Creek	WY	42.40	108.30	1907.69	1930.00	50.00	1873	449	0.65	-0.39	Lyford unpublished
Little Belt Mountains	MT	46.51	110.18	1575.38	377.00		438	339	-0.23	-0.14	(Norris *et al.*, 2016)
Little Belt Mountains	MT	46.33	110.27	1600.00	368.00		430	380	-0.24	-0.14	(Norris *et al.*, 2016)
Lower Canyon Creek	WY	44.02	107.20	1581.00	1280.00	50.00	1222	361	-0.35	-0.28	(Lyford *et al.*, 2003)
Lower Canyon Creek	WY	44.02	107.20	1581.00	1740.00	50.00	1650	385	1.00	0.59	(Lyford *et al.*, 2003)
Lower Canyon Creek	WY	44.02	107.20	1581.00	1880.00	45.00	1822	384	0.66	0.29	(Lyford *et al.*, 2003)
Lower Canyon Creek	WY	44.02	107.20	1593.00	1635.00	70.00	1527	377	0.96	-0.56	(Lyford *et al.*, 2003)
Lyman Lake	AZ	34.50	109.50	1880.00	1690.00	50.00	1588	381	0.98	-0.40	Koehler unpublished; (Anderson *et al.*, 2000)
Lyman Lake	AZ	34.50	109.50	1880.00	3110.00	60.00	3334	346	2.31	1.16	Koehler unpublished; (Anderson *et al.*, 2000)
Lyman Lake	AZ	34.50	109.50	1880.00	10020.00	70.00	11502	426	-5.12	-2.16	Koehler unpublished; (Anderson *et al.*, 2000)

Lyman Lake	AZ	34.50	109.50	1880.00	12090.00	100.00	13887	424	-7.56	0.24	Koehler unpublished; (Anderson *et al.*, 2000)
Lyman Lake	AZ	34.50	109.50	1880.00	15540.00	180.00	18750	414	-11.89	-0.60	Koehler unpublished; (Anderson *et al.*, 2000)
Lyman Lake	AZ	34.50	109.50	1880.00	16460.00	100.00	19574	487	-13.80	-0.25	Koehler unpublished; (Anderson *et al.*, 2000)
Lyman Lake	AZ	34.50	109.50	1880.00	16480.00	90.00	19594	466	-13.48	-0.25	Koehler unpublished; (Anderson *et al.*, 2000)
Medicine Lodge Canyon	WY	44.19	107.32	1640.00	4810.00	90.00	5549	349	1.23	-0.87	(Lyford *et al.*, 2003)
Miller Creek	SD	44.30	104.42		795.00		709	382	-0.10	0.34	(Norris, 2006)
Perry Park Golf Course	WY				210.00	50.00	230	451	-0.31	0.11	Betancourt unpublished
Perry Park Golf Course	WY				1420.00	60.00	1320	467	-0.02	-0.47	Betancourt unpublished
Pictograph Cave	ID	43.41	113.20	1900.00	3970.00	85.00	4427	394	0.45	0.47	Betancourt unpublished
Pictograph Cave	ID	43.41	113.20	1900.00	4050.00	140.00	4539	369	0.49	-0.46	Betancourt unpublished
Pryor Mountains	MT	44.08	108.38	1490.00	1785.00	80.00	1706	419	0.77	0.52	(Lyford *et al.*, 2003)
Pryor Mountains	MT	44.08	108.38	1490.00	3190.00	80.00	3409	389	1.70	0.44	(Lyford *et al.*, 2003)
Pryor Mountains	MT	45.07	108.38	1500.00	490.00	70.00	521	335	-0.16	0.20	(Lyford *et al.*, 2003)

Pryor Mountains	MT	44.08	108.38	1518.00	1660.00	50.00	1510	345	0.88	-0.71	(Lyford *et al.*, 2003)
Pryor Mountains	MT	44.08	108.38	1518.00	3285.00	75.00	3507	357	1.29	0.30	(Lyford *et al.*, 2003)
Pryor Mountains	MT	44.08	108.38	1524.00	1160.00	70.00	1071	403	0.60	0.43	(Lyford *et al.*, 2003)
Pryor Mountains	MT	44.08	108.38	1554.00	2370.00	75.00	2393	458	1.42	0.41	(Lyford *et al.*, 2003)
Redbird Canyon	SD	43.79	104.02	1470.77	344.00			439			(Norris, 2006)
Redbird Canyon	SD	43.79	104.02	1492.31	1090.00			419			(Norris, 2006)
Redbird Canyon	SD	43.79	104.02	1520.00	196.00			515			(Norris, 2006)
Redbird Canyon	SD	43.81	104.00	1560.00	0.00			374			(Norris, 2006)
Redbird Canyon	SD	43.81	104.00	1560.00	2580.00			520			(Norris, 2006)
Redbird Canyon	SD	43.81	104.00	1560.00	3554.00			482			(Norris, 2006)
Rocky Canyon	ID	43.40	113.20	1798.00	455.00	70.00	500	366	-0.17	-0.21	(Smith & Betancourt, 2003)
Rocky Canyon	ID	43.40	113.20	1798.00	645.00	65.00	621	434	-0.15	-0.31	(Smith & Betancourt, 2003)
Rocky Canyon	ID	43.40	113.20	1798.00	795.00	65.00	713	362	-0.09	0.34	(Smith & Betancourt, 2003)
Rocky Canyon	ID	43.40	113.20	1798.00	1950.00	75.00	1894	332	0.77	-0.76	(Smith & Betancourt, 2003)
Rocky Canyon	ID	43.40	113.20	1798.00	2100.00	85.00	2075	381	1.98	-0.30	(Smith & Betancourt, 2003)

Rocky Canyon	ID	43.40	113.20	1798.00	2770.00	75.00	2864	374	1.19	-0.20	(Smith & Betancourt, 2003)
Rocky Canyon	ID	43.40	113.20	1798.00	3180.00	80.00	3399	435	1.76	0.45	(Smith & Betancourt, 2003)
Rocky Canyon	ID	43.40	113.20	1798.00	3925.00	85.00	4367	362	0.76	0.34	(Smith & Betancourt, 2003)
Southern Bighorn Mountains	MT	45.02	108.15	1274.00	460.00	65.00	504	376	-0.16	-0.18	(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Southern Bighorn Mountains	MT	45.02	108.15	1274.00	915.00	65.00	830	330	0.37	-0.08	(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Southern Bighorn Mountains	MT	45.02	108.15	1274.00	1880.00	70.00	1819	338	0.67	0.29	(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Southern Bighorn Mountains	MT	45.02	108.15	1274.00	2860.00	75.00	2976	447	1.11	0.14	(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Southern Bighorn Mountains	MT	45.02	108.15	1274.00	3285.00	90.00	3509	348	1.30	-0.30	(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Southern Bighorn Mountains	MT	45.02	108.15	1311.00	1795.00	70.00	1718	375	0.73	0.45	(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Southern Bighorn Mountains	MT	45.02	108.15	1311.00	3340.00	75.00	3571	344	1.45	-0.78	(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Southern Bighorn Mountains	MT	45.02	108.15	1372.00	1515.00	70.00	1398	371	0.25	-0.27	(Lyford *et al.*, 2002, Lyford *et al.*, 2003)

Southern Bighorn Mountains	MT	45.02	108.15	1372.00	9740.00	90.00	11162	331	-4.21	-1.00	(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Southern Bighorn Mountains	MT	45.02	108.15	1402.00	1160.00	65.00	1070	403	0.60	0.43	(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Southern Bighorn Mountains	MT	45.02	108.15	1402.00	1570.00	70.00	1454	384	0.68	-0.35	(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Southern Bighorn Mountains	MT	45.02	108.15	1402.00	4440.00	90.00	5057	334	1.52	0.49	(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Southern Bighorn Mountains	MT	45.02	108.15	1524.00	1415.00	65.00	1317	360	-0.02	-0.47	(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Southern Bighorn Mountains	MT	45.02	108.15	1582.00	3180.00	60.00	3398	368	1.76	0.45	(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Southern Bighorn Mountains	MT	45.02	108.15	1582.00	3210.00	80.00	3428.00	390	1.64	0.37	(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Southern Bighorn Mountains	MT	45.02	108.15	1591.00	2665.00	75.00	2771	343	0.87	-0.34	(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Southern Bighorn Mountains	MT	45.02	108.15		450.00	50.00	501	435	-0.17	-0.21	(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Southern Bighorn Mountains	MT	45.02	108.15		26720.00	250.00	32007				(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Southern Bighorn Mountains	MT	45.02	108.15		27050.00	4290.00	32082				(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
T Hill	WY	43.39	108.12.07	1440.00	18190.00	710.00	21629	430	-18.16	-1.23	Betancourt unpublished

T Hill	WY	43.39	108.12.07	1440.00	18300.00	690.00	21767	388	-16.86	-0.90	Betancourt unpublished
Ten Sleep Canyon	WY	44.03	107.30	1957.00	1145.00		1054	431	0.70	0.53	(Lyford *et al.*, 2003)
Titus Canyon	CA	36.49	117.08	582.00	2427.00	37.00	2523	334	1.20	0.50	(Smith *et al.*, 2009)
Titus Canyon	CA	36.49	117.08	582.00	10720.00	66.00	12697	357	-18.10	-0.58	(Smith *et al.*, 2009)
Titus Canyon	CA	36.50	114.04	1015.00	3781.00	42.00	4150	420	1.34	0.18	(Smith *et al.*, 2009)
Titus Canyon	CA	36.50	117.04	1030.00	14085.00	40.00	16459	421	-14.74	0.00	(Smith *et al.*, 2009)
Titus Canyon	CA	36.50	117.04	1030.00	14013.00	76.00	17261	407	-13.43	-0.80	(Smith *et al.*, 2009)
Titus Canyon	CA	36.50	117.04	1030.00	16768.00	96.00	19991	529	-13.90	-0.61	(Smith *et al.*, 2009)
Titus Canyon	CA	36.51	117.04	1114.00	19760.00	80.00	23612	327	-18.67	4.08	(Smith *et al.*, 2009)
Titus Canyon	CA	36.51	117.04	1154.00	7987.00	47.00	8861	397	2.14	-0.48	(Smith *et al.*, 2009)
Titus Canyon	CA	36.51	117.04	1154.00	13273.00	73.00	15456	342	-13.70	-0.16	(Smith *et al.*, 2009)
Titus Canyon	CA	36.51	117.03	1190.00	11406.00	60.00	13255	483	-13.31	-2.36	(Smith *et al.*, 2009)
Titus Canyon	CA	36.51	117.03	1200.00	1310.00	15.00	1265	325	-0.16	-0.43	(Smith *et al.*, 2009)
Titus Canyon	CA	36.51	117.03	1200.00	16340.00	50.00	19457	404	-13.51	-0.35	(Smith *et al.*, 2009)
Titus Canyon	CA	36.51	117.03	1200.00	17740.00	100.00	21004	446	-16.71	-0.06	(Smith *et al.*, 2009)
Titus Canyon	CA	36.51	117.03	1200.00	17660.00	120.00	22018	590	-17.21	-0.44	(Smith *et al.*, 2009)
Titus Canyon	CA	36.51	117.03	1200.00	20020.00	120.00	23919	503	-21.17	-0.08	(Smith *et al.*, 2009)

Titus Canyon	CA	36.51	117.03	1200.00	20710.00	160.00	24701	355	-19.20	-0.67	(Smith *et al.*, 2009)
Titus Canyon	CA	36.51	117.04	1220.00	3433.00	37.00	3713	390	1.41	0.37	(Smith *et al.*, 2009)
Titus Canyon	CA	36.51	117.04	1220.00	4116.00	39.00	4677	371	0.10	0.37	(Smith *et al.*, 2009)
Titus Canyon	CA	36.51	117.04	1249.00	24340.00	200.00	29116	471		0.00	(Smith *et al.*, 2009)
Titus Canyon	CA	36.51	117.04	1249.00	26080.00	230.00	31318	549		0.00	(Smith *et al.*, 2009)
Titus Canyon	CA	36.51	117.04	1249.00	28070.00	210.00	33439	464		0.00	(Smith *et al.*, 2009)
Titus Canyon	CA	36.51	117.04	1249.00	28120.00	210.00	33491	420		0.00	(Smith *et al.*, 2009)
Titus Canyon	CA	36.51	117.04	1249.00	24340.00	200.00	29116	471			(Smith *et al.*, 2009)
Titus Canyon	CA	36.51	117.03	1250.00	15056.00	84.00	18274	470	-12.51	0.49	(Smith *et al.*, 2009)
Titus Canyon	CA	36.51	117.03	1250.00	15331.00	84.00	18413	456	-12.39	0.00	(Smith *et al.*, 2009)
Titus Canyon	CA	36.51	117.03	1250.00	15295.00	45.00	18544	430	-13.28	0.30	(Smith *et al.*, 2009)
Titus Canyon	CA	36.5	117.03	1345.00	21690.00	100.00	26100	512			(Smith *et al.*, 2009)
Upper Titus Canyon	CA	36.50	117.03	1345.00	19400.00	120.00	23092	532	-16.91	1.69	(Smith *et al.*, 2009)
Upper Titus Canyon	CA	36.50	117.03	1345.00	21690.00	100.00	26100	512		0.00	(Smith *et al.*, 2009)
Upper Titus Canyon	CA	36.50	117.02	1400.00	10065.00	25.00	11618	372	-6.96	5.38	(Smith *et al.*, 2009)
Upper Titus Canyon	CA	36.49	117.00	1559.00	8642.00	65.00	9628	380	1.36	1.69	(Smith *et al.*, 2009)
Upper Titus Canyon	CA	36.49	117.00	1559.00	8749.00	49.00	9751	378	1.77	0.25	(Smith *et al.*, 2009)

Upper Titus Canyon	CA	36.49	117.00	1576.00	7976.00	47.00	8849	392	2.04	-0.48	(Smith *et al.*, 2009)
Upper Titus Canyon	CA	36.49	117.00	1576.00	8543.00	49.00	9522	398	1.17	0.33	(Smith *et al.*, 2009)
Western Bighorn Mountains	WY	44.20	107.43	1787.69	989.00		909	338	0.64	-0.88	(Norris *et al.*, 2016)
Western Bighorn Mountains	WY	44.19	104.44	1840.00	972.00		894	326	0.50	-0.55	(Norris *et al.*, 2016)
Western Bighorn Mountains	WY	44.22	107.33	1855.38	1700.00	50.00	1600	482	1.02	-0.40	(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Western Bighorn Mountains	WY	44.22	107.33	1883.08	4630.00	90.00	5348	333	0.67	1.00	(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Western Bighorn Mountains	WY	44.22	107.33	1892.00	225.00	40.00	253	400	-0.30	-0.09	(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Western Bighorn Mountains	WY	44.22	107.33	1892.00	1100.00	40.00	997	420	1.01	0.62	(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Western Bighorn Mountains	WY	44.15	107.37	2129.23	1997.00			362			(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Western Bighorn Mountains	WY	44.18	107.36	2153.85	1072.00			374			(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Western Bighorn Mountains	WY	44.18	107.36	2154.00	921.00			430			(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Western Bighorn Mountains	WY	44.18	107.36	2154.00	1121.00			367			(Lyford *et al.*, 2002, Lyford *et al.*, 2003)

Western Bighorn Mountains	WY	44.18	107.36	2209.23	2401.00			384			(Lyford *et al.*, 2002, Lyford *et al.*, 2003)
Wind River Canyon	WY	43.34	108.12	1367.00	2750.00	75.00	2843	407	1.16	-0.33	(Jackson *et al.*, 2002, Lyford *et al.*, 2003)
Wind River Canyon	WY	43.34	108.12	1416.00	2710.00	80.00	2807	461	1.03	-0.49	(Jackson *et al.*, 2002, Lyford *et al.*, 2003)
Wind River Canyon	WY	43.34	108.12	1416.00	3430.00	80.00	3682	409	1.50	0.58	(Jackson *et al.*, 2002, Lyford *et al.*, 2003)
Wind River Canyon	WY	43.34	108.12	1416.00	3590.00	60.00	3890	344	0.60	0.18	(Jackson *et al.*, 2002, Lyford *et al.*, 2003)
Wind River Canyon	WY	43.34	108.12	1421.00	1970.00	75.00	1915	427	0.92	-0.89	(Jackson *et al.*, 2002, Lyford *et al.*, 2003)
Wind River Canyon	WY	43.34	108.12	1431.00	3260.00	80.00	3480	415	1.42	0.47	(Jackson *et al.*, 2002, Lyford *et al.*, 2003)
Wind River Canyon	WY	43.34	108.12	1431.00	3590.00	80.00	3890	372	0.60	0.18	(Jackson *et al.*, 2002, Lyford *et al.*, 2003)
Wind River Canyon	WY	43.34	108.12	1455.00	375.00	45.00	442	480	-0.23	-0.14	(Jackson *et al.*, 2002, Lyford *et al.*, 2003)
Wind River Canyon	WY	43.34	108.12	1455.00	767.00	43.00	691	460	-0.06	0.31	(Jackson *et al.*, 2002, Lyford *et al.*, 2003)

[1] Age is in calendar years

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CHAPTER 2

CONSTRAINTS AND TRADE-OFFS IN ENDOTHERMIC THERMAL REGULATION

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ABSTRACT:

The range of environmental temperatures a species can tolerate while minimizing the energetic costs of thermoregulation – the thermal neutral zone – is determined by a balance between heat production and heat dissipation. However, in most mammals and birds, the thermal neutral zone does not correlate well with the range of environmental temperatures experienced. A mismatch between the range of temperatures a species can tolerate and their thermal environment may be explained by a potential trade-off between the upper and lower bounds of the thermal neutral zone. Here, we employ data for 85 mammals and 33 birds to examine: (1) do mammals and birds both show similar patterns in how thermal critical temperatures vary with body size?; (2) what is the relationship between the upper and lower critical thermal temperatures?; and (3) are there any environmental or ecological variables that influence this relationship? We find that birds and mammals do indeed show similar trends. For both groups, a trade-off exists between the upper and lower thermal critical temperatures; 57% of mammals and 66% of birds show a shift in their thermal critical temperatures in concert rather than expanding or contracting their thermal neutral zone. Surprisingly, environmental and ecological variables do not influence the strength or direction of this relationship. Evidence of a trade-off means that strong physiological constraints operate on adaptations to both extremes of the thermal environment, and provides a mechanism for observed mismatch between species' thermal tolerances and their thermal environment.

INTRODUCTION:

Understanding the extent physiological traits interact with the thermal environment to determine species distributions has long been of interest to biogeographers (Dobzhansky, T. 1950, Gaston, K. J. et al. 2009, Humboldt, A. V. 1817, Janzen, D. H. 1967). A number of hypotheses have proposed links between species' thermal tolerances and the range of temperatures experienced throughout their geographic ranges (Bozinovic, F. et al. 2011, Pither, J. 2003). Ongoing climatic change increases the urgency to understand the how species' physiology matches or mismatches to their environment (Huey, R. B. et al. 2000, Huey, R. B. et al. 2009, Khaliq, I. et al. 2014, Sunday, J. M. et al. 2011). Here, a macrophysiological approach is useful to elucidate potential mechanisms for the influences and drivers of species' thermal physiology across space.

The climactic variability hypothesis (CVH) predicts that environments with a wide range of temperatures should select for individuals with broad thermal tolerances (Gaston, K. J. and Chown 1999, S. L., Janzen, D. H. 1967, Stevens, G. C. 1989). For endothermic birds and mammals, maintaining an optimal body temperature requires the expenditure of energy when individuals experience environmental temperatures outside their thermal neutral zone (TNZ) (Figure 1). Consequently, there should be selection to minimize energetic demands by favoring individuals with TNZs that closely match the range of temperatures encountered in their environments. While recent macrophysiological analyses support the CVH in birds, they have rejected the hypothesis in mammals (Khaliq, I. et al. 2014). Furthermore, species in both groups tend to demonstrate a mismatch between their thermal tolerances (defined as the upper and lower critical temperatures or the upper and lower bounds of the TNZ, respectively) and the environmental temperatures where they persist (Araújo, M. B. et al. 2013). This mismatch between species' thermal tolerance and their thermal environment appears to become more extreme at high latitudes, where the annual breadth of temperatures is highest (Khaliq, I. et al. 2014).

Species, of course, can evolve morphologies that help maintain homeostasis in the thermal environment. In mammals, body size influences the TNZ (Riek, A. and Gieiser, F. 2013) through its effect on both metabolic rate (B) and thermal conductance (C) (Figure 1). While both traits increase with body size, B increases more rapidly with size than does thermal conductance, although both are sub-linear (slope = 0.64–0.73 and 0.51–0.57, respectively) (Fristoe, T. S. et al. 2015). This results in a higher ratio of B to C in larger animals (Fristoe, T. S. et al. 2015, Riek, A. and Gieiser, F. 2013), an expansion of the TNZ with increasing body size, but a shifting of both the upper thermal critical temperature (T_{UC}) and lower thermal critical temperature (T_{LC}) downward (Riek, A. and Gieiser, F. 2013). Consequently, evolution of larger body size is associated with increased tolerance to colder temperatures at the expense of heat tolerance; the opposite is true for smaller body sizes. This relationship remains untested in birds (Riek, A. and Gieiser, F. 2013).

The apparent mismatch between thermal physiology and environmental temperatures implies that biophysical constraints could potentially limit the ability of animals to adapt to a wide range of environments. Despite the important influence of body size on thermal physiology, mass-independent changes in B and C also play a role in allowing birds and mammals across the body size spectrum to adapt to a wide range of thermal environments (Fristoe, T. S. et al. 2015). Such adaptations should also be subject to physiological trade-offs, with a positive relationship expected between mass-corrected T_{UC} and T_{LC}. Mass-independent adaptations that increase T_{UC} (increased heat tolerance) should be accompanied by increases to mass-independent T_{LC} (decreased cold tolerance) in species occupying 'hot' environments, and vice versa for species inhabiting colder environments. Despite the potential benefits of expanding the TNZ, especially in temperate environments as predicted by the CVH, adaptations that increase T_{UC} and decrease T_{LC} (expanding the TNZ) should be difficult to achieve and rarely occur. An absence of such a trade-off would be suggested by a lack of or a positive relationship between mass-corrected T_{UC} and T_{LC}.

Many species have behavioral adaptations that potentially reduce exposure to temperatures that exceed their TNZ. Small mammals, for example, often burrow to escape extreme heat (Reichman, O. J. and Smith, S. C. 1990, Kinlaw, A. 1999) or cold (Merritt, J. F. 1986). Or, animals may augment their activity time to be active only during times of the day that are favorable (Murray, I. W. and Smith, F. A. 2012, Ruf, T. and Geiser, F. 2015). Such changes in behavior may be expressed more in animals at higher latitudes, which tend to have increased seasonality, or in species with large geographic ranges encompassing different microclimates.

The lifestyle of animals may also play a vital role in the selection for a broader TNZ. Herbivores and omnivores, which can store food (Sherry, D. F. 1989, Sklepkovych, B. O. and Montevecchi, W. A. 1996), or switch to a different diet depending on the season (Taylor, L. R. 1984), may not experience direct selection for a broad TNZ. Conversely, large herbivores, which cannot shelter from extreme temperatures, often travel to more favorable microhabitats to escape cold (Telfer, E. S. and Kelsall, J. P. 1984) or heat (McKechnie, A. E. et al. 2012), and this may be under selection for a broad TNZ. Carnivores, too, rarely hibernate, and often forage year-round (Geiser, F. 2013), and may similarly experience selection for a broad TNZ.

Further, where an animal lives may impose selection on thermal tolerance. Animals with larger geographic ranges, possibly inhabiting a wider range of thermal environments, may experience selection for wider thermal tolerances (Janzen, D. H. 1967, Sizling, A. L. et al. 2009, Stevens, G. C. 1989, Whittaker, R. H. 1967). Similarly, animals occurring at higher latitudes, with increased seasonality (Sizling, A. L. et al. 2009, Stevens, G. C. 1989), may also have undergone selection for wider thermal tolerances. Therefore, it is expected that geographic range and/or latitude should influence the TNZ.

Here we explore the constraints and trade-offs faced by endotherms when adapting to the thermal environment by analyzing the relationship between the upper- and lower- bounds of the TNZ as a proxy for thermal tolerance for endothermic animals. Specifically, we address the following questions: (1) do mammals and birds show the same pattern between thermal critical temperatures and body size?; (2) what is the relationship between upper and lower thermal critical temperatures?; (3) what environmental and ecological variables influence this relationship? Given potential constraints to the evolution of an expanded upper or lower thermal critical temperature, we expect both mammals and birds to have a trade-off, resulting in a positive relationship. Further, it is likely that activity time, lifestyle, and geographic range should influence this relationship.

MATERIALS & METHODS:

Our dataset includes 85 mammalian and 33 avian species. These species cover 15 orders of mammals, ranging in size from 4 to 25000g, and 8 orders of birds, ranging in size from 6.3 to 1390g. For both mammals and birds, we include species whose geographic range centroid was from 45˚S to 50˚N, with approximately equal numbers from the southern hemisphere (45 mammals; 12 birds) and northern hemisphere (40 mammals; 21 birds).

Data for endotherms were extracted from various sources. Upper and lower thermal critical temperatures (˚C) for mammals and birds were extracted from the literature (Khaliq, I. et al. 2014, Wolf, B.O et al. 2016). Following Wolf et al. (2016), only studies that included more than two individuals with clear upticks in metabolic rate near the upper and lower bounds of the TNZ were included. We also obtained body mass (g), body temperature (˚C), and latitude (˚N) of capture from original literature. To investigate the role of the environment on thermal critical temperatures, the geographic range area for each species was extracted using maps available on the International Union for the Conservation of Nature (IUCN 2015). Using the WorldClim temperature data (Hijmans, R. J. et al. 2005), we calculated the average minimum and maximum temperatures (E_{MIN}

and E_{MAX}, respectively) from the geographic range using the program ArcGIS (ESRI 2011). Given the vastly different lifestyles of endotherms, ecological data for mammals and birds, including diet (herbivore, omnivore, carnivore) and activity cycle (diurnal, nocturnal, crepuscular/cathemeral) were extracted from the PanTHERIA database (Jones, K. E. et al. 2009) and the Eltonian traits dataset (Wilman, H. et al. 2014). Additionally, maximum clade credibility trees for both mammals (Fritz, S. A. et al. 2009, Kuhn, T. S. et al. 2011) and birds (Jetz, W. et al. 2012) were generated using BEAST (Drummond, A. J. and Rambaut, A. 2007) to examine the role of shared evolutionary history on thermal critical temperatures.

We assessed the potential influence of body size for both birds and mammals on thermal critical temperatures by using general least squares (GLS) regression. Residuals from this analysis were used to calculate mass-corrected upper thermal critical temperature (mcT_{UC}) and mass-corrected lower thermal critical temperature (mcT_{LC}). The relationships between both raw T_{UC} and T_{LC} as well as mcT_{UC} and mcT_{LC} were characterized using OLS regression analysis. We calculated the percentage of species that have an expanded versus contracted TNZ, as well as a TNZ that was shifted upwards or downwards.

For all analyses, phylogenetic signal for upper and lower thermal critical temperatures was calculated using Blomberg's K and Pagel's λ. Because values close to one suggest that there is a phylogenetic signal (as seen for mammal lower thermal critical temperature) (Blomberg, S. P. et al. 2003), we employ a phylogenetic general least squares (PGLS) using the *R* packages (R Team 2013) *nmle* (Pinheiro, J. et al. 2016) and *caper* (Orme , D. 2013) only for values above 0.5. Any POLS that resulted in a negative lambda value were omitted from the results. We used Akaike information criterion (AIC) to evaluate support for the GLS compared to the PGLS.

The influence of environmental and ecological variables on the potential trade-off between mcT_{UC} and mcT_{LC} was also examined. Since latitude is often used as a proxy for temperature and seasonality, raw and mass-corrected upper and lower thermal critical temperatures against latitude were examined using an GLS regression. Likewise, how upper critical thermal temperature changed as a function of average maximum environmental temperature (E_{MAX}), and how lower critical thermal temperature changed across average minimum environmental temperature (E_{MIN}) was examined using an GLS. Additionally, species were coded by their activity cycle (diurnal, crepuscular/cathemeral, nocturnal), diet (herbivore, omnivore, and carnivore), geographic area (km^2), and geographical zone (˚). A third of the mammals in our dataset are nocturnal, 10% are diurnal, and 13% are crepuscular or cathemeral, and 44% are not coded. Birds are primarily diurnal (86%), with 10% in our dataset being nocturnal. These variables potentially influence how an animal interacts with its' environment, and therefore may influence the relationship between upper and lower thermal critical temperatures.

RESULTS:

We find thermal critical temperatures in mammals and birds follow the same trend with body size (Figure 2a; Table 1). An earlier study (Riek, A. and Gieiser, F. 2013) found that both upper and lower thermal critical temperatures decrease with increasing body size (slope = -0.027, -0.194, respectively). We find a similar trend, although the slope is substantially different (slope = -1.10, -2.44, respectively). There is greater support for a phylogenetic signal for mammals than the GLS relationship ($\lambda = 0.9$; AIC: (GLS) 477.4, (POLS) 473.4), which perhaps is not surprising given the high broad-sense heritability (>94%) among species within genus (Smith, F. A. et al. 2004). The trend is the same for birds (slope = -1.96, -5.71; Figure 2b; Table 1). However, in birds the ordinary least squares received more support than the POLS; this may be because body size has not been found to be consistently heritable in birds at the higher taxonomic levels (Smith, F. A. and Lyons, S. K. 2013).

For both mammals and birds, lower critical thermal temperature decreases more rapidly with body size than does upper critical thermal temperature (mammals: slope = -1.10 (upper), -2.44 (lower); birds: slope = -1.96 (upper), -5.71 (lower)). In fact, the R^2 value for T_{UC} and body size for both mammals and birds is extremely low ($R^2 = 0.09$, 0.12, for mammals and birds respectively). The result of the combined relationship of upper and lower thermal critical temperatures with body size is that the thermal neutral zone increases with increasing body size.

We found a potential trade-off between upper and lower thermal critical temperature for both birds and mammals (Figure 3a,b; Table 1). There is a positive relationship between upper and lower thermal critical temperatures (mammals: df = 83, slope = 0.45, $R^2 = 0.38$, p-value < 0.001; birds: df = 30, slope = 0.27, $R^2 = 0.23$, p-value = 0.007). Likewise, our analysis suggests a general positive trend between mass-corrected upper and lower thermal critical temperatures for both mammals and birds (mammals: df = 83, slope = 0.71, R^2 = 0.32, p-value < 0.001; birds: df = 31, slope = 0.23, R^2 = 0.08, p-value = 0.065; Figure 3c,d; Table 1). Further, the trend is significant (p-value < 0.001) for mammals, and 57% of species fall within the predicted quadrants (upper right or lower left quadrants). While a positive relationship between mass-corrected upper and lower thermal critical temperatures is seen for both birds and mammals, it is only marginally significant for birds (Table 1). Still, 66% of avian species fall in the two quadrants predicted if a trade-off exists.

Despite a decreasing trend in environmental temperatures with latitude, endotherm thermal critical temperatures generally do not follow a latitudinal trend. As expected, average maximum temperature weakly decreases with latitude, although it is only significant for mammals (mammals: df = 83, slope = -0.10, R^2 = 0.067, p-value = 0.038; birds: df = 25, slope = -0.11, R^2 = 0.047, p-value = 0.142; Figure 4a,b). Similarly, the relationship between upper thermal critical temperatures in endothermic species also decreases weakly with latitude (mammals: df = 82, slope = -0.04, R^2 = 0.01, p-value = 0.140; birds: df = 30, slope = -0.01, R^2 = 0.00, p-value = 0.862; Figure 4a,b; Table 2). But, unlike average minimum temperature, which does decrease with latitude (mammals: df = 83, slope = -0.53, R^2 = 0.41, p-value < 0.001; birds: df = 25, slope = -0.76, R^2 = 0.63, p-value < 0.001; Figure 4a,b; Table 2), mammal lower thermal critical temperatures surprisingly do not change with latitude (df = 83, slope = 0.01, R^2 = 0.00, p-value = 0.864; Figure 4a; Table 2), and still do not change after standardizing for body size (df =

83, slope = -0.01, R^2 = 0.00, p-value = 0.801). Birds, by contrast, do show a significant decrease in T_{LC} with latitude (df = 30, slope = -0.30, R^2 = 0.31, p-value < 0.001; Figure 4b; Table 2), but this trend disappears after standardizing for body size (df = 30, slope = -0.13, R^2 = 0.08, p-value = 0.069).

We find weakly or non-significant relationships between critical thermal temperatures and environmental temperatures. For mammals, there is a lack of a relationship between upper and lower thermal critical temperatures with environmental temperatures (lower: df = 49, slope = 0.01, R^2 = 0.00, p-value = 0.821; upper: df = 49, slope = 0.16, R^2 = 0.03, p-value = 0.119; Figure 5a-d; Table 2). Although this relationship becomes slightly significant after standardizing for body size, it only explains 6% of the variation (lower: df = 49, slope = -0.01, R^2 = 0.00, p-value = 0.838; upper: df = 49, slope = 0.20, R^2 = 0.06, p-value = 0.044; Figure 5e,g; Table 2). Birds, which do show a relationship between lower thermal critical temperature and latitude, also have a significant relationship between both upper and lower thermal critical temperatures and environmental temperature (lower: df = 25, slope = 0.29, R^2 = 0.26, p-value = 0.004; upper: df = 25, slope = 0.35, R^2 = 0.15, p-value = 0.024; Figure 5a-d; Table 2). These relationships become insignificant when standardizing for body size (lower: df = 25, slope = 0.12, R^2 = 0.04, p-value = 0.169; upper: df = 25, slope = 0.25, R^2 = 0.07, p-value = 0.097; Figure 5f,h; Table 2). Although E_{MIN} is strongly correlated with absolute latitude, thermal critical temperatures do not follow a similar trend.

We expected that the degree animals avoid or modify their exposure to the thermal environment could contribute to the observed trade-off. Despite different activity cycles among mammals, we found no effect on the relationship between thermal critical temperatures and activity cycle (p-value = 0.343; Figure 6a). We did, however, find that birds, majority of which are diurnal, had a significant effect of activity cycle was found on the relationship between thermal critical temperatures (p-value = 0.042; Figure 6b). Trophic styles, potentially indicating how a species interacts with its environment, also did not influence the relationship between thermal critical temperatures for both mammals and birds (mammals: p-value = 0.5; birds: p-values > 0.05; Figure 6c,d). Even differences in geographic range size, potentially indicating a wider thermal breadth, or latitude, a proxy for seasonality, do not influence the relationship between upper and lower thermal critical temperatures (geographic range: mammals p-value = 0.978, birds p-value = 0.953; latitude: mammals p-value = 0.627, birds p-value = 0.391; Figure 6e-h).

DISCUSSION:

We find differences in the way that birds and mammal physiology interacts with environmental temperatures. Not surprisingly, we find that body size affects thermal physiology of animals (Figure 2). While larger animals have a broader thermal neutral zone (Figure 4), the overall TNZ tends to be shifted downward suggesting a loss of heat tolerance to gain cold tolerance. Thus, there is a trade-off between animal size and thermal tolerance: larger animals, which cannot escape their thermal environment as readily, have a wider TNZ; smaller animals, which often escape in hospitable thermal environments (McCain, C. M. and King, S. R. B. 2014), have a narrower TNZ.

We find a clear positive relationship between T_{UC} and T_{LC} (Figure 3), consistent with predictions derived from the Scholander-Irving model (Scholander, P. F. et al. 1950). This likely plays a role in explaining the observed mismatch between an animals' thermal physiology and their thermal environment (Khaliq, I. et al. 2015). The CVH predicts a negative relationship between mass-corrected T_{UC} and mass-corrected T_{LC} such that TNZ is expanded for animals living in seasonal environments. A positive relationship suggests a trade-off in thermal adaptation: a slope of one indicates a commensurate trade-off between T_{UC} and T_{LC} while a slope differing from one indicates that an expansion at one end of the TNZ is accompanied by a disproportionate decrease at the other end (Figure 1).

Overall, endotherm thermal critical temperatures are not correlated with absolute latitude nor environmental temperatures. Only birds show a trend with lower thermal critical temperature and latitude (Figure 4b; Table 2), but this disappears after correcting for body size (Figure 4d; Table 2). Data scale may account for the lack of correlation between thermal critical temperatures and the environment, which may not be detectible at such a large geographic range. Some species of ectotherms display population-level differences in thermal tolerances across their geographic range (Angilletta, M. J., Jr. et al. 2002, Huey, R. B. 1991). Further, the coarse scale of the environmental temperature data may not be representative of the microhabitats selected by species. The result is site-specific adaptations that may not be reflected at such a large scale.

Given the various ways that endotherms can hide or modify their environment, it is astounding that none of these variables influence the relationship between thermal critical temperatures. Competing trade-offs in predation risk, foraging time, and selection of microhabitats may contribute to the lack of significance in any individual factor (Figure 6). For instance, avoidance of the thermal environment does not appear to affect the observed trade-off in thermal physiology. Activity cycle, for mammals at least, may not be solely driven by the thermal environment; much research suggests that competition and predation may drive how animals petition the temporal niche (Kronfeld-Schor, N. and Dayan, T. 2013, Smith, F. 1992, Smith, F. A. 1995). It is probable that forage behavior, which changes seasonally, may influence the relationship between thermal critical temperatures. However, coarse dietary guilds are highly related to body size. Therefore, correcting for body size may eliminate any influence of trophic levels on the observed trade-off. While geographic area could indicate that animals inhabit multiple biomes, it also assumes that populations are continuous throughout. However, many species occupy microhabitats, or may change elevation with latitude to maintain a similar thermal environment throughout their range.

There is an explicit trade-off in adapting to either the upper or lower temperatures in the thermal environments: evolutionary changes in metabolic rate (B) or body temperature (T_b) will shift both thermal critical temperatures (T_{UC} and T_{LC}) in the same direction. Decreasing heat production through the evolution of lower B results in a raised T_{UC} and a higher heat-tolerance, but also raises T_{LC} and decreases cold tolerance. Adaptations that influence thermal conductance will likely affect both C_{MIN} and C_{MAX}, and will shift both thermal critical temperatures together. For example, evolving denser pelage would increase tolerance to cold but be detrimental in heat. The slope of the trade-off may reflect the relationship between C_{MIN} and C_{MAX} such that an increase in C_{MAX} is accompanied by three times the increase in C_{MIN} (Figure 1). Despite the greater cost to cold tolerance, species appear to sacrifice a greater amount of cold tolerance for only slightly more heat tolerance.

The observed trade-off places very real constraints on how animals interact with their thermal environment, and impose limitations for coping with future climate change. Over the next century not only is temperature predicted to increase, but extreme heat waves will also increase in frequency (IPCC 2012). For many endotherms, their T_{UC} exceeds current average warm temperatures in their environment (Khaliq, I. et al. 2015) (Figure 4). However, animals may not be able to tolerate future extreme (and prolonged) warming events. In fact, high mortality in response to unusually severe heat waves is documented for passerine birds in Australia (McKechnie, A. E. et al. 2012). Even though some species can regulate their exposure to thermal environment via behavior, it comes at the expense of greater activity time to forage for food and to search for a mate (Murray, I. W. and Smith, F. A. 2012). Despite this, the fitness costs of a mismatched thermal tolerance to the thermal environment are not well understood.

Understanding the evolutionary and ecological constraints on thermal physiology can help answer age-old questions, such as what drives biodiversity gradients across the globe, as well as answer pressing questions, such as how species will respond to current and future climatic change. Given that latitude and other ecological variables fail to explain the observed trade-off suggests that the mechanism is physiological. The trade-off between the upper and lower critical temperatures may be driven by the asymmetric relationship between minimum and maximum thermal conductance (C_{MIN} and C_{MAX}, respectively). This trade-off in upper and lower critical temperatures explains the observed mismatch between endotherms and their thermal environment, as well as hints at mechanisms preventing species from occupying certain thermal environments.

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DATA ACCESSIBILITY: All data on critical thermal temperature and body size were from Khaliq et al. (Khaliq, I. et al.). All environmental temperature data were extracted from Fristoe et al. (Fristoe, T. S. et al.). Generated data (mcT_{UC}; mcT_{LC}) are available in the manuscript as Tables 3 & 4.

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Table 1. Results of general linear models from figures 1 and 2. Residuals for mcT_{UC} and mcT_{LC} are from the GLS relationship between $\log_{10}$ body size and the thermal critical temperatures. We used a RMA for the relationship between mcT_{UC} and mcT_{LC}.

Group	Model	df	Slope	R^2	p-value
Mammals	$T_{UC} \sim T_{LC}$	295	0.56	0.33	<0.001
	$Log(M) \sim T_{UC}$	295	-0.65	0.04	<0.001
	$Log(M) \sim T_{LC}$	295	-3.1	0.31	<0.001
	$mcT_{UC} \sim mcT_{LC}$	295	0.66	0.33	<0.001
Birds	$T_{UC} \sim T_{LC}$	159	0.56	0.33	<0.001
	$Log(M) \sim T_{UC}$	159	-1.12	0.04	0.012
	$Log(M) \sim T_{LC}$	159	-6.01	0.35	<0.001
	$mcT_{UC} \sim mcT_{LC}$	159	0.69	0.34	<0.001

Table 2. Results for thermal critical temperatures with latitude and environmental temperatures. Significant results are in bold.

Group	Model	df	Slope	R^2	p-value
Mammals	$T_{LC} \sim Latitude$	83	0.01	0.00	0.864
	$T_{UC} \sim Latitude$	83	-0.04	0.01	0.140
	$mcT_{LC} \sim Latitude$	83	-0.01	0.00	0.801
	$mcT_{UC} \sim Latitude$	83	-0.05	0.03	0.070
	$T_{LC} \sim E_{MIN}$	49	0.01	0.00	0.821
	$T_{UC} \sim E_{MAX}$	49	0.16	0.03	0.119
	$mcT_{LC} \sim E_{MIN}$	49	-0.01	0.00	0.838
	$mcT_{UC} \sim E_{MAX}$	49	0.20	0.06	**0.044**
Birds	$T_{LC} \sim Latitude$	30	-0.30	0.31	**<0.001**
	$T_{UC} \sim Latitude$	30	-0.01	0.00	0.862
	$mcT_{LC} \sim Latitude$	30	-0.13	0.08	0.069
	$mcT_{UC} \sim Latitude$	30	0.05	0.00	0.341
	$T_{LC} \sim E_{MIN}$	25	0.29	0.26	**0.004**
	$T_{UC} \sim E_{MAX}$	25	0.35	0.15	**0.024**
	$mcT_{LC} \sim E_{MIN}$	25	0.12	0.04	0.169
	$mcT_{UC} \sim E_{MAX}$	25	0.25	0.07	0.097

Table 3. Mass-corrected upper and lower thermal critical temperatures for mammalian species.

Order	Binomial	mass-corrected T_{UC}	mass-corrected T_{LC}
Rodentia	*Abrothrix andinus*	-0.05	-1.60
Rodentia	*Abrothrix longipilis*	-1.95	-0.88
Rodentia	*Ammospermophilus leucurus*	0.44	3.69
Aotidae	*Aotus trivirgatus*	-2.43	3.19
Rodentia	*Apodemus agrarius*	-6.71	-3.77
Rodentia	*Apodemus speciosus*	-4.14	-3.60
Chiroptera	*Artibeus jamaicensis*	1.08	-3.11
Chiroptera	*Artibeus lituratus*	2.29	-2.65
Diprotodontia	*Bettongia gaimardi*	-12.19	-14.27
Rodentia	*Cabassous centralis*	0.70	4.09
Carnivora	*Canis latrans*	-5.34	-0.39
Rodentia	*Cannomys badius*	1.55	0.78
Chiroptera	*Carollia perspicillata*	0.55	-0.29
Diprotodontia	*Cercartetus lepidus*	-1.55	-0.52
Diprotodontia	*Cercartetus nanus*	1.29	3.35
Diprotodontia	*Cercopithecus mitis*	-3.42	-17.56
Eulipotyphla	*Crocidura russula*	0.38	-2.17
Eulipotyphla	*Crocidura suaveolens*	0.16	-2.67
Rodentia	*Cryptomys damarensis*	-2.44	-0.04
Rodentia	*Cynomys ludovicianus*	2.61	5.28
Chiroptera	*Cynopterus brachyotis*	2.99	1.69
Dasyuromorphia	*Dasycercus cristicauda*	3.39	2.57
Didelphimorpha	*Didelphis virginiana*	2.12	-1.58
Chiroptera	*Diphylla ecaudata*	-4.15	-2.63
Rodentia	*Dipodomys microps*	-1.81	-0.86
Macroscelidae	*Elephantulus edwardii*	2.13	4.49
Erinaceomorpha	*Erinaceus concolor*	-1.03	2.46
Rodentia	*Gerbillurus paeba*	1.05	3.88
Rodentia	*Gerbillurus setzeri*	0.89	4.11
Rodentia	*Gerbillurus tytonis*	0.79	3.85
Rodentia	*Gerbillurus vallinus*	1.01	4.83
Rodentia	*Gerbillus pusillus*	3.47	1.93
Chiroptera	*Glossophaga soricina*	0.54	1.65
Rodentia	*Hystrix africaeaustralis*	-4.31	1.68
Rodentia	*Jaculus jaculus*	1.32	5.42
Rodentia	*Jaculus orientalis*	-0.38	1.08

Diprotodontia	*Lagorchestes conspicillatus*	3.03	1.21
Diprotodontia	*Lasiorhinus latifrons*	8.09	3.58
Chiroptera	*Lasiurus cinereus*	-0.15	1.36
Lagomorpha	*Lepus alleni*	3.14	1.45
Chiroptera	*Macroderma gigas*	1.49	2.80
Peramelemorpha	*Macrotis lagotis*	2.56	2.18
Didelphimorpha	*Marmosa lepida*	1.49	3.79
Rodentia	*Megadontomys thomasi*	1.51	0.84
Rodentia	*Micaelamys namaquensis*	0.74	-1.35
Rodentia	*Microtus longicaudus*	-0.67	-2.16
Rodentia	*Mystromys albicaudatus*	-3.57	-7.34
Carnivora	*Nasua nasua*	1.22	1.64
Chiroptera	*Noctilio leporinus*	4.23	0.21
Rodentia	*Notomys alexis*	-0.08	3.53
Rodentia	*Notomys cervinus*	-0.05	4.59
Rodentia	*Onychomys torridus*	0.67	0.97
Rodentia	*Otomys irroratus*	-5.49	-3.15
Artiodactyla	*Pecari tajacu*	3.99	6.34
Rodentia	*Peromyscus crinitus*	0.71	0.07
Diprotodontia	*Petauroides volans*	-7.38	-6.69
Diprotodontia	*Petaurus breviceps*	-2.42	-0.01
Chiroptera	*Phyllostomus discolor*	2.94	-3.43
Chiroptera	*Phyllostomus hastatus*	1.38	-2.45
Rodentia	*Phyllotis darwini*	0.21	-0.33
Diprotodontia	*Potorous tridactylus*	-2.39	-4.71
Carnivora	*Potos flavus*	-2.02	-0.90
Hyracoidae	*Procavia capensis*	2.98	3.10
Diprotodontia	*Pseudocheirus peregrinus*	-0.01	0.02
Chiroptera	*Pteronotus quadridens*	3.02	-0.47
Chiroptera	*Pteropus scapulatus*	2.17	-1.70
Rodentia	*Rattus villosissimus*	1.90	3.70
Diprotodontia	*Setonix brachyurus*	0.53	-3.79
Rodentia	*Spermophilus beecheyi*	-2.68	-0.37
Chiroptera	*Sturnira erythromos*	-1.92	-3.72
Carnivora	*Suricata suricatta*	0.48	5.00
Lagomorpha	*Sylvilagus audubonii*	7.37	2.75
Chiroptera	*Tadarida brasiliensis*	-1.69	-2.86
Rodentia	*Tamias minimus*	0.14	-1.99
Rodentia	*Tamias striatus*	-1.58	1.14
Rodentia	*Thallomys paedulcus*	2.46	0.42

Rodentia	*Thomomys bottae*	-3.37	1.11
Rodentia	*Thomomys talpoides*	-1.51	-1.21
Rodentia	*Thomomys umbrinus*	1.38	-0.44
Didelphimorpha	*Thylamys elegans*	1.03	-0.74
Artiodactyla	*Tragulus javanicus*	-3.21	2.28
Scandentia	*Tupaia belangeri*	1.76	0.89
Chiroptera	*Vespadelus vulturnus*	-1.77	-3.08
Carnivora	*Vulpes macrotis*	0.86	-2.17
Carnivora	*Vulpes zerda*	-0.39	-1.32

Table 4. Mass-corrected upper and lower thermal critical temperatures for avian species.

Order	Binomial	mass-corrected T_{UC}	mass-correct T_{LC}
Passeriformes	*Alaemon alaudipes*	1.44	5.56
Galliformes	*Alectoris chukar*	5.10	3.14
Passeriformes	*Amadina fasciata*	1.27	1.91
Strigiformes	*Bubo virginianus*	-1.07	1.29
Psittaciformes	*Cacatua roseicapilla*	-1.38	-0.25
Galliformes	*Callipepla gambelii*	6.96	9.84
Apodiformes	*Collocalia esculenta*	-3.52	0.11
Apodiformes	*Collocalia vanikorensis*	-3.07	-0.07
Columbiformes	*Columba livia*	2.58	2.10
Falconiformes	*Daptrius ater*	0.86	-2.03
Columbiformes	*Ducula zoeae*	-1.94	-1.96
Passeriformes	*Eremalauda dunni*	4.42	2.86
Passeriformes	*Erythrura gouldiae*	1.18	2.35
Passeriformes	*Estrilda troglodytes*	0.43	4.46
Columbiformes	*Geophaps plumifera*	3.67	7.99
Columbiformes	*Hemiphaga novaeseelandiae*	-3.98	-1.07
Galliformes	*Lagopus leucura*	3.78	-15.79
Galliformes	*Leipoa ocellata*	4.01	3.81
Passeriformes	*Lonchura fuscans*	1.76	-0.56
Passeriformes	*Malurus cyaneus*	-2.36	-4.93
Strigiformes	*Megascops asio*	-0.94	2.14
Psittaciformes	*Melopsittacus undulatus*	4.84	1.58
Passeriformes	*Mirafra erythrocephala*	-1.24	-0.05
Psittaciformes	*Myiopsitta monachus*	3.08	-0.77
Passeriformes	*Passer domesticus*	-1.48	-8.37
Passeriformes	*Pica nuttalli*	-1.38	-10.19
Passeriformes	*Pica pica*	-2.34	-2.57
Passeriformes	*Sporophila aurita*	2.09	-1.30
Strigiformes	*Strix occidentalis*	-8.55	-3.40
Galliformes	*Syrmaticus ellioti*	-2.48	3.14
Galliformes	*Syrmaticus humiae*	-4.85	1.71
Coraciiformes	*Todus mexicanus*	-5.59	-2.58
Strigiformes	*Tyto alba*	-1.31	1.93

Figure 1. Relationship between metabolic rate (B), thermal conductance (C), and body temperature (T_b), and the thermal critical temperatures. For a given thermal neutral zone (TNZ), B and T_b change both the upper (T_{UC}) and lower (T_{LC}) critical temperatures proportionately. Minimum thermal conductance (C_{MIN}), by contrast, only determines a species' T_{LC}. We suggest a new term, maximum thermal conductance (C_{MAX}), which relates to a species' T_{UC}. C_{MIN} and C_{MAX} must change disproportionate to one another, thus causing a trade-off between T_{UC} and T_{LC}.

Figure 2. Thermal ciritical temperatures change with body mass. For both (a) mammals and (b) birds, upper (red closed circles; black line) and lower (blue closed circles; gray line) thermal critical temperatures decrease with increasing body size. The R^2 value for T_{UC} for both mammals and birds, however, is low and not biologically meaningful. The result of this trend is that TNZ increases with increasing body size. Results are reported in Table 1.

Figure 3. Relationship between thermal critical temperatures. Mammals show a significant relationship; 57% of species fall along this trend line. 66% of bird species fall either within the two quadrants predicted by a trade-off. For both (a) mammals and (b) birds, the relationship between T_{UC} and T_{LC} are significant (p-values <0.01). (c) Mammals show a significant relationship for mcT_{UC} versus mcT_{LC}; (d) birds do now show a significant relationship. Results are reported in Table 1.

Figure 4. Relationship between temperature and latitude for mammals and birds. Species' thermal critical temperatures are closed circles; T_{UC} and mcT_{UC} values are in dark red and T_{LC} and mcT_{LC} values are in dark blue. For each species, the average warmest (light red open circles) and average coldest (light blue open circles) temperatures across a species' geographic range were extracted. (a) Mammals show no relationship between their thermal critical temperatures and latitude; likewise, E_{MAX} does not vary with latitude (df = 83, slope = -0.10, R^2 = 0.067, p-value = 0.038), and E_{MIN} shows a strong negative trend with increasing latitude (df = 83, slope = -0.53, R^2 = 0.41, p-value < 0.001). (b) Birds show similar results to mammals, except T_{LC} in birds does decrease with increasing absolute latitude. The environmental temperatures across bird geographic ranges changes in the same trend as mammals (E_{MAX}: df = 25, slope = -0.11, R^2 = 0.047, p-value = 0.142; E_{MIN}: df = 25, slope = -0.76, R^2 = 0.63, p-value < 0.001). Both (c) mammals and (d) birds show no relationship between mcT_{UC} and mcT_{LC} with latitude. Results are reported in Table 2.

Figure 5. Thermal critical temperatures versus environmental temperatures. Lower thermal critical temperatures have no relationship with coldest environmental temperature for (a) mammals and (b) birds. Similarly, upper thermal critical temperatures do not vary with warmest environmental temperature for (c) mammals and (d) birds. For both (e) mammals and (f) birds, mass-corrected lower thermal critical temperature is not related to E_{MIN}. Finally, mass-corrected upper thermal critical temperatures for (g) mammals and (h) birds is not related to E_{MAX}. Notice the lack of a consistent relationship

for thermal critical temperatures with environmental temperatures. Results are reported in Table 2.

Figure 6. The influence of ecological variables on the relationship between thermal critical temperatures. For both (a,c,e,g) mammals and (b,d,f,h) birds, ecological variables do not explain the observed tradeoff. (a,b) Activity cycle (nocturnal, purple; diurnal, gold; crepuscular/cahtemeral, blue) is not a significant predictor of the relationship. (c,d) Trophic level (carnivore, red; omnivore, gold; herbivore, green) is also not a predictor of the observed trade-off. Neither is (e,f) geographic range (small, red to large, purple) nor (g,h) latitude (tropical, green; subtropical, orange; temperate, blue). Species lacking data are shown in light gray.

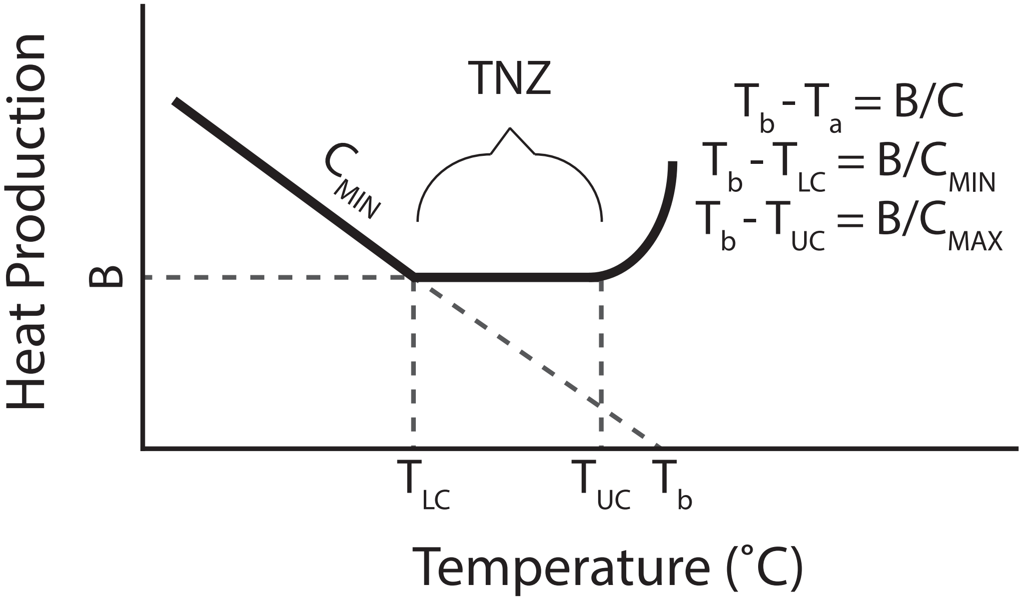
Heat Production
B
TNZ
C_{MIN}
$T_b - T_a = B/C$
$T_b - T_{LC} = B/C_{MIN}$
$T_b - T_{UC} = B/C_{MAX}$
T_{LC}
T_{UC}
T_b
Temperature (˚C)

Figure 1.

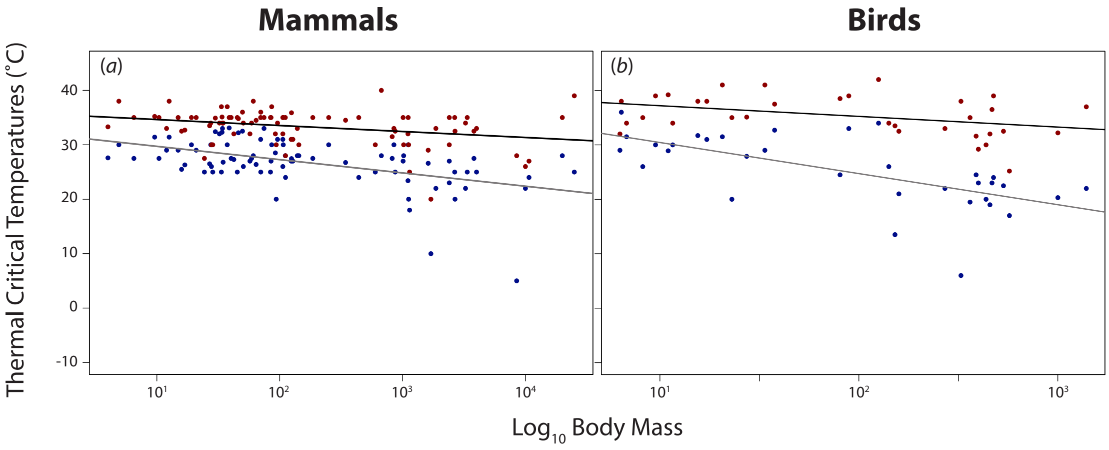
Mammals
Birds
(a)
(b)
Thermal Critical Temperatures (°C)
40
30
20
10
0
-10
10^1
10^2
10^3
10^4
10^1
10^2
10^3
Log_{10} Body Mass

Figure 2.

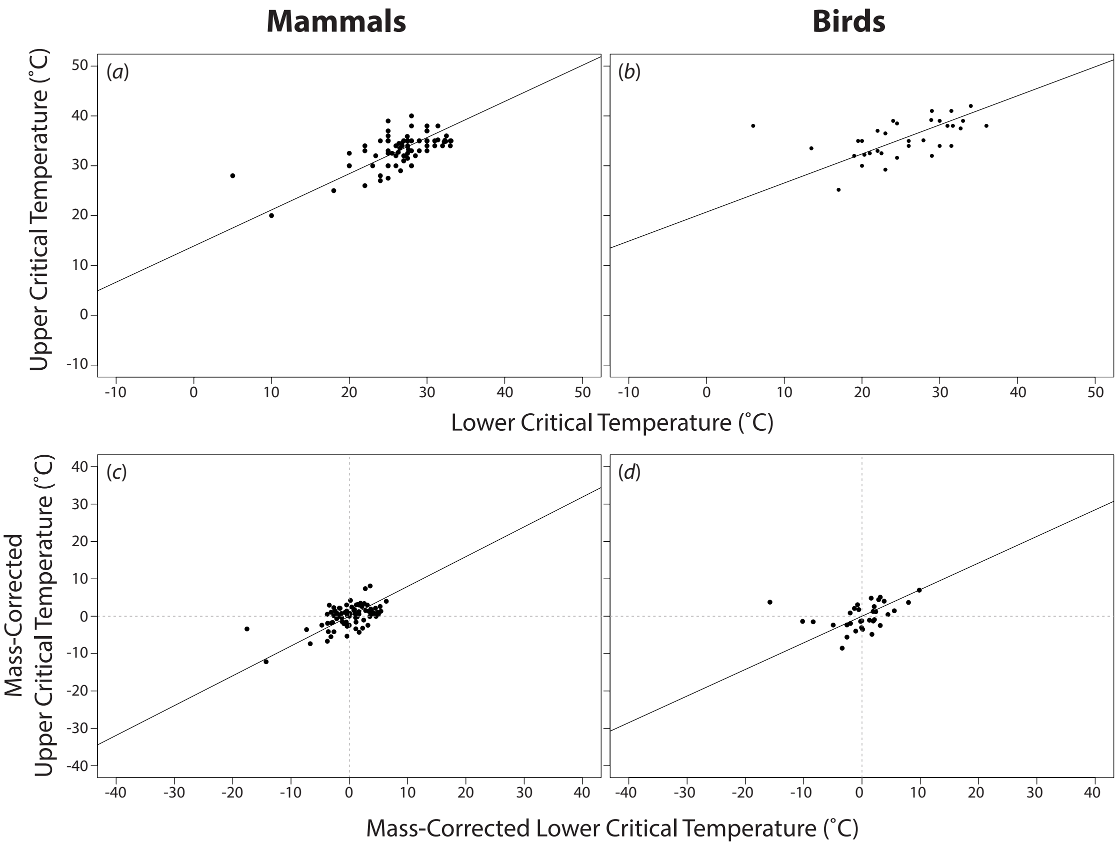
Mammals
Birds
(a)
(b)
(c)
(d)
Upper Critical Temperature (˚C)
Lower Critical Temperature (˚C)
Mass-Corrected Upper Critical Temperature (˚C)
Mass-Corrected Lower Critical Temperature (˚C)
50
40
30
20
10
0
-10
-40
-30
-20
-10
0
10
20
30
40

Figure 3.

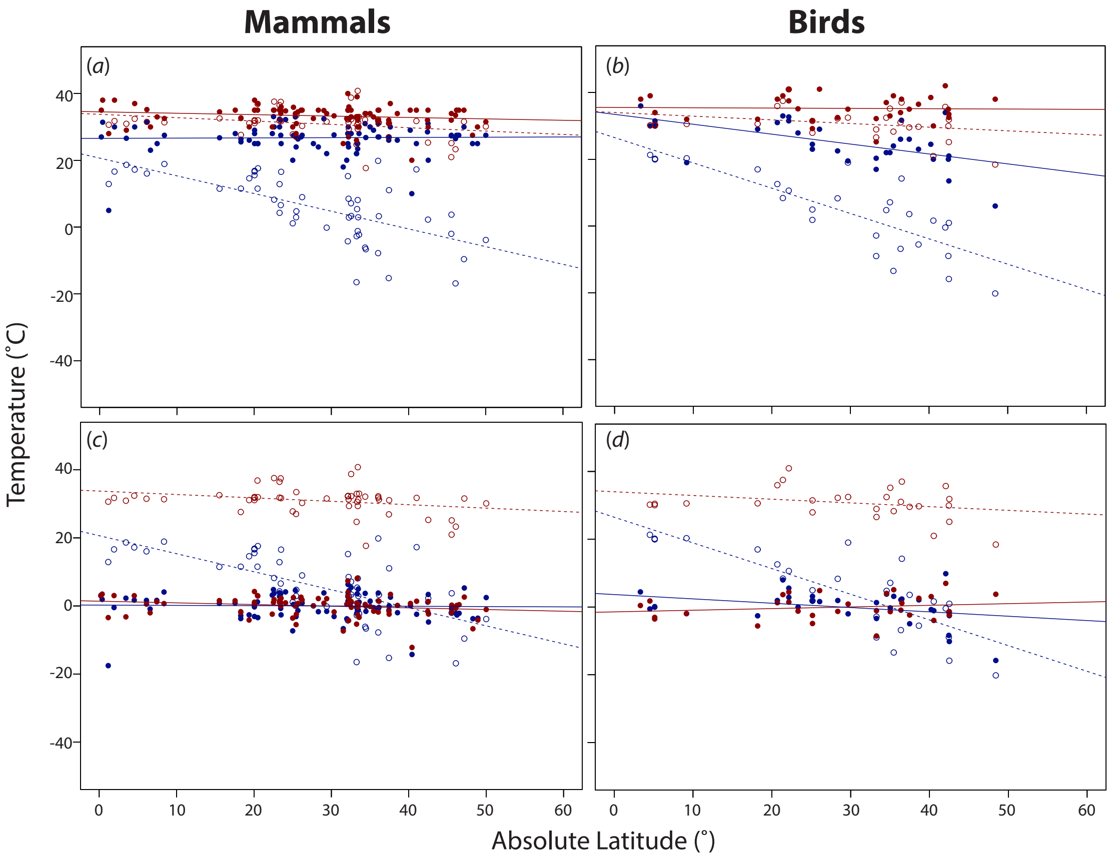
Mammals
Birds
(a)
(b)
(c)
(d)
Temperature (˚C)
40
20
0
-20
-40
0
10
20
30
40
50
60
Absolute Latitude (˚)

Figure 4.

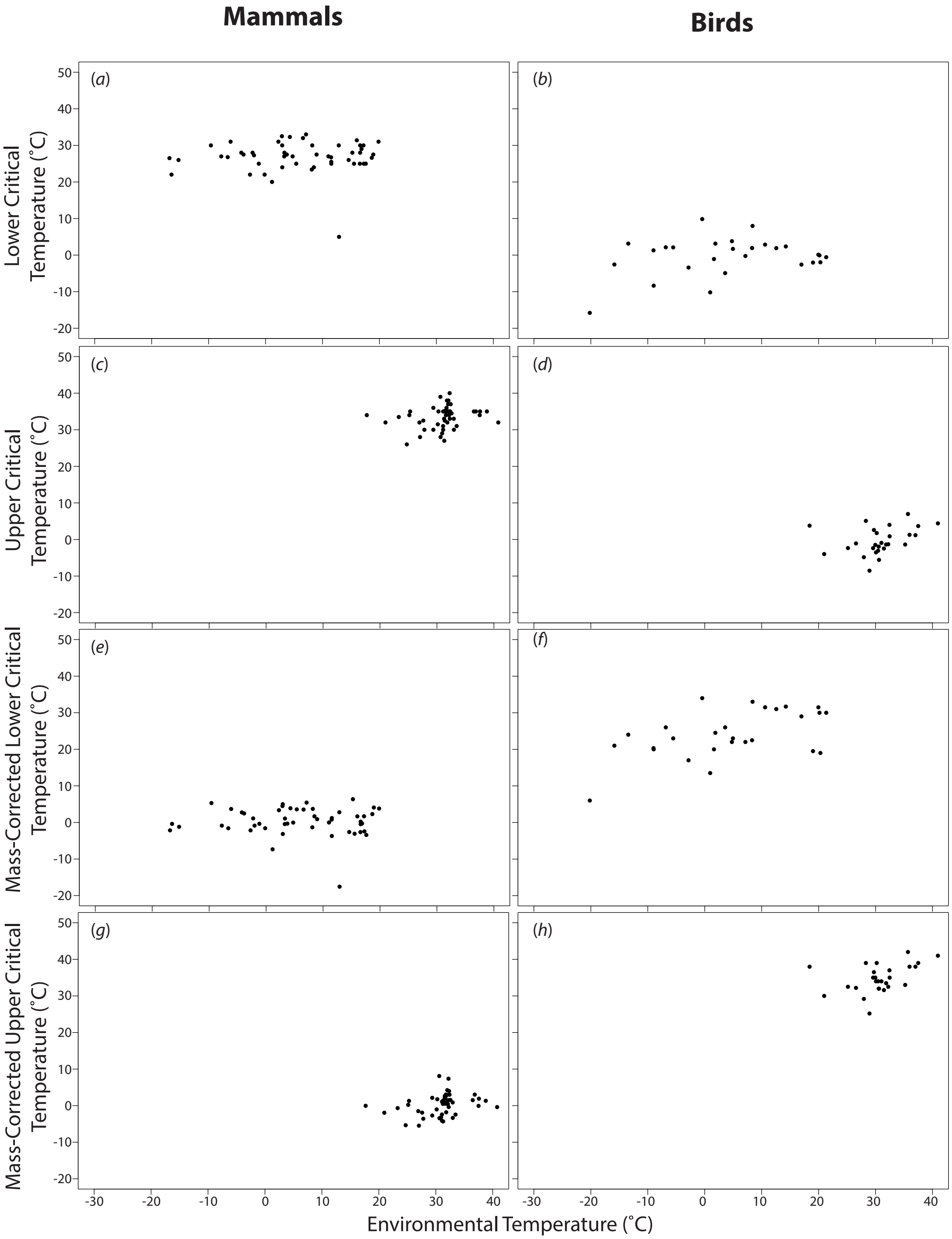
Mammals
Birds
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
Lower Critical Temperature (˚C)
Upper Critical Temperature (˚C)
Mass-Corrected Lower Critical Temperature (˚C)
Mass-Corrected Upper Critical Temperature (˚C)
50
40
30
20
10
0
-10
-20
-30
-20
-10
0
10
20
30
40
Environmental Temperature (˚C)

Figure 5.

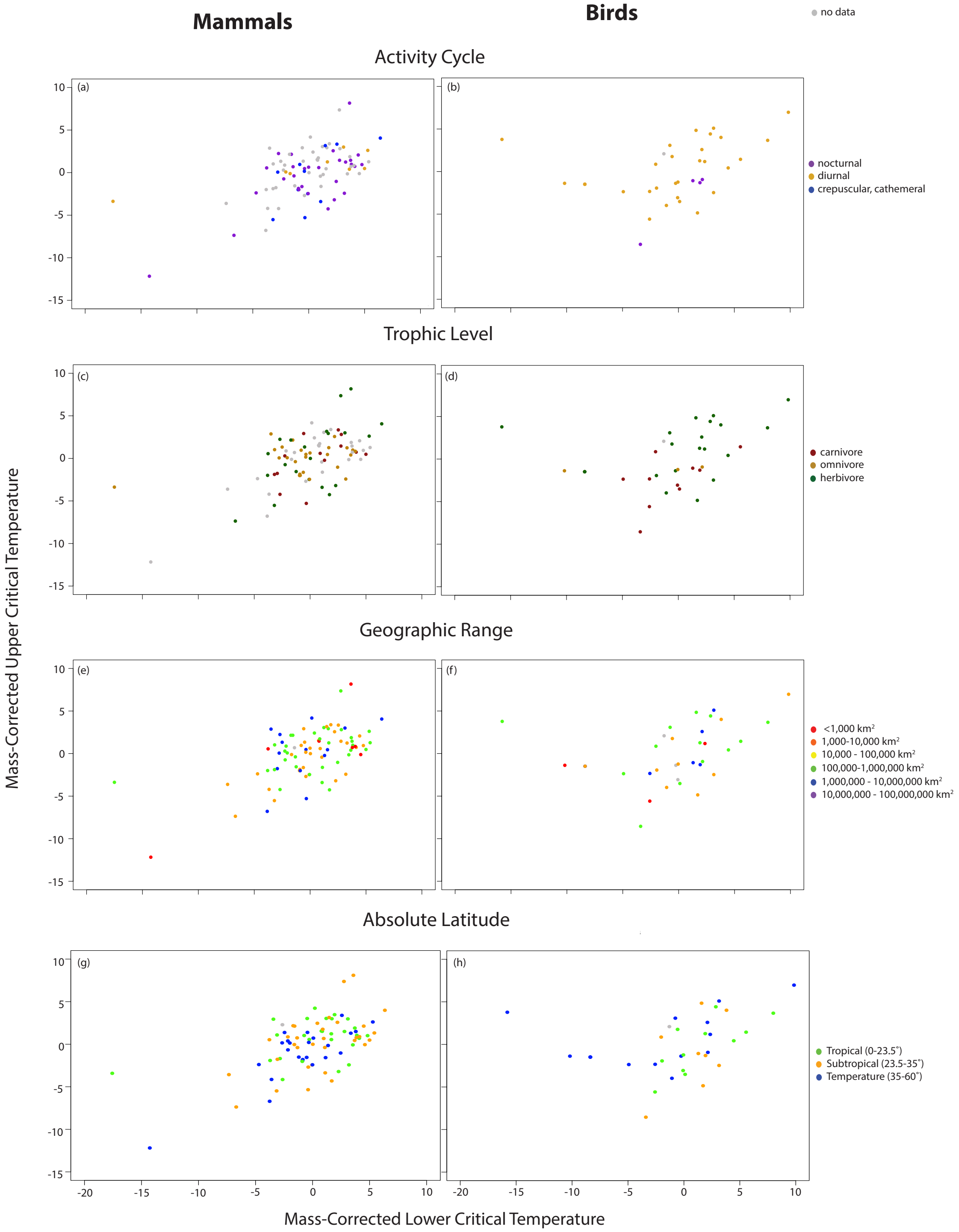
Mammals
Birds
● no data
Activity Cycle
(a)
(b)
● nocturnal
● diurnal
● crepuscular, cathemeral
Trophic Level
(c)
(d)
● carnivore
● omnivore
● herbivore
Geographic Range
(e)
(f)
● <1,000 km^2
● 1,000-10,000 km^2
● 10,000 - 100,000 km^2
● 100,000-1,000,000 km^2
● 1,000,000 - 10,000,000 km^2
● 10,000,000 - 100,000,000 km^2
Absolute Latitude
(g)
(h)
● Tropical (0-23.5°)
● Subtropical (23.5-35°)
● Temperature (35-60°)
Mass-Corrected Upper Critical Temperature
10
5
0
-5
-10
-15
Mass-Corrected Lower Critical Temperature
-20
-15
-10
-5
0
5
10

Figure 6.

CHAPTER 3

THE EXTINCT GIANT SHARK *CARCAROCLES MEGALODON*: A MODEL FOR UNDERSTANDING LONG-TERM MICROEVOLUTIONARY BODY SIZE TRENDS

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ABSTRACT:

The extinct shark *Carcharocles megalodon* is one of the largest marine apex predators ever to exist. Nonetheless, little is known about its body-size variations through time and space. Here, we studied the body size trends of *C. megalodon* through its temporal and geographic range to better understand its ecology and evolution. Given that this species was the last of the megatooth lineage, a group of species that shows a purported size increase through time, we hypothesized that *C. megalodon* also displayed this trend, increasing in size over time and reaching its largest size prior to extinction. We found that *C. megalodon* body-size distribution was left-skewed (suggesting a long-term selective pressure favoring larger individuals), and presented significant geographic variation (possibly as a result of the heterogeneous ecological constraints of this cosmopolitan species) over geologic time. Finally, we found that stasis was the general mode of size evolution of *C. megalodon* (i.e., no net changes over time), contrasting with the trends of the megatooth lineage and our hypothesis. Given that *C. megalodon* is a relatively long-lived species with a widely-distributed fossil record, we further used this study system to provide a deep-time perspective to the understanding of the body size trends of marine apex predators. For instance, our results suggest that (1) a selective pressure in predatory sharks for consuming a broader range of prey may favor larger individuals and produce left-skewed distributions on a geologic time scale; (2) body-size variations in cosmopolitan apex marine predators may depend on their interactions with geographically discrete communities; and (3) the inherent characteristics of shark species can produce stable sizes over geologic time, regardless of the size trends of their lineages.

INTRODUCTION:

The extinct megatooth shark *Carcharocles megalodon* is the largest shark ever to exist (Gottfried et al. 1996). From its tooth size and morphology, it was inferred to have been an apex predator that reached up to ~ 18mof total length (TL) (Gottfried et al. 1996; Pimiento et al. 2010; Pimiento et al. 2013a). Furthermore, given the nearly global distribution of its fossil record, *C. megalodon* is considered to have been a cosmopolitan species that lived from ca. 15.9 Ma (middle Miocene) to ca. 2.6Ma (Pliocene/Pleistocene boundary) (Applegate and Espinosa-Arrubarrena 1996; Gottfried et al. 1996; Purdy 1996; Purdy et al. 2001; Cappetta 2012; Pimiento and Clements 2014).

Apex predators are animals with no predatory pressures. Usually they are large-bodied vertebrates that can move over large areas, thus interacting with different communities. Most importantly, apex predators are pivotal in maintaining ecosystem stability, and their elimination can produce cascading effects throughout entire food webs (Myers et al. 2007; Terborgh et al. 2010; Estes et al. 2011). Accordingly, the extinction of *C. megalodon* potentially affected the structure and function of ancient ecosystems (Pimiento and Clements 2014). The causes of its extinction are still unknown.

The phylogenetic relationships of *C. megalodon* have mainly been studied on the basis of its relatedness to the great white shark, *Carcharodon carcharias* (e.g., Long and Waggoner 1996; Martin 1996). To our knowledge, no phylogenies for this species have ever taken into consideration all its ancestors. Thus, the taxonomy of *C. megalodon* has long been debated, with a number of possible interpretations. For instance, some authors place it in the genus Carcharodon (family Lamnidae) (e.g., Applegate and Espinosa-Arrubarrena 1996; Gottfried et al. 1996; Purdy 1996), whereas others place it in the genus Carcharocles (Family Otodontidae) (e.g., Ward and Bonavia 2001; Nyberg et al. 2006; Ehret et al. 2009; Ehret 2010; Pimiento et al. 2010; Cappetta 2012). Using the most recent morphological evidence (e.g., Nyberg et al. 2006; Ehret et al. 2009), we follow the second interpretation.

Regardless of its taxonomic assignment, it is widely accepted that *C. megalodon* is the largest member of the megatooth lineage, an extinct group of large predatory sharks. It has been proposed that the megatooth sharks comprise a series of chronospecies (i.e., a group of species that evolve via anagenesis and that gradually replace each other in an evolutionary scale [Benton and Pearson 2001]) that are distinguished from each other in the fossil record by the morphological changes of their teeth (Ward and Bonavia 2001). These changes include the loss of lateral cusplets (Ward and Bonavia 2001; Ehret 2010; Pimiento et al. 2010; Pimiento et al. 2013b); broadening of tooth crowns; and, of most relevance to this study, size increase through geologic time (Ehret 2010). Because tooth size has been demonstrated to be a good proxy of body size in lamnoid sharks (Gottfried et al. 1996; Shimada 2003; Pimiento et al. 2010), we can infer that the observed chronoclinal tooth size trend of the megatooth linage (Fig. 1) translates into a macroevolutionary body-size increase over geologic time.

Body size has long been of interest to scientists, not only because it is a relatively easy trait to quantify in both living and fossil organisms (Peters 1983; Maurer et al. 1992;

Kingsolver and Pfennig 2004; Smith et al. 2008), but also because it correlates with many ecological and evolutionary patterns (Peters 1983; Calder 1996; Smith et al. 2008). For example, body-size distributions are an important component of community structure and thus are often studied to infer selection pressures (Peters 1983; Werner and Gilliam 1984; Bell et al. 2006). Furthermore, body size is highly correlated with geographic distribution, making it the most common and repeatable relationship studied in macroecology (Lyons and Smith 2010).

Body size has important implications for a species' ecology. Many clades have a log-skewed (right-skewed on logarithmic axes) body-size distribution pattern, where the majority of species are small and a few are large (Kozlowski and Gawelczyk 2002; O'Gorman and Hone 2013). This pattern has been demonstrated in mammals, birds, reptiles, amphibians, and fish, but not in dinosaurs (left-skewed) or snakes (not skewed) (Boback and Guyer 2003; Lyons and Smith 2010; O'Gorman and Hone 2013). Moreover, body size patterns are driven by clade- or region- specific mechanisms, which produce both positive and negative correlations between body size and latitude (Cushman et al. 1993; Atkinson 1994). It has also been argued that body-size distributions are invariant along latitudinal gradients (Roy et al. 2000). To our knowledge, there have been no studies investigating body-size trends (either body size distributions or body-size geographic patterns) at the species level of any marine apex predator over a geologic time scale.

Little is known about the body-size trends of the extinct apex predatory shark *C.*

megalodon over geologic time. Because body size predictably scales with many aspects of species' biology, here we study body-size trends of *C. megalodon* across time and space as a means to better understand the ecology and evolution of this species. Given that *C. megalodon* was the largest of a lineage with a purported body-size increase over time, we hypothesize that this species increased in size through time, reaching its largest size prior to extinction. In order to reach our research objectives and test our hypothesis, we estimated the body size of individuals from a large sample across regions and time periods, compared trends through the species' temporal and geographic range, and tested its general mode of size evolution. Our results provide novel information on the macroecological patterns of this extinct giant shark. Moreover, because *C. megalodon* is a long-lived species (~14 Myr) with a widely-distributed fossil record, it represents an ideal study system to provide a deep-time perspective to the understanding of body-size trends of marine apex predators.

METHODS:

Museum Collections Survey

We did an online search of natural history museums throughout the world that house specimens encompassing the species' known temporal and latitudinal range. In order to identify which of these museums contain sufficient material, we explored their databases and/or requested a list of specimens. As a result of this process, we visited the following museum collections: the British Museum of History Museum (NHM); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN); Museo de La Plata (UNLP); Museo de Historia Natural de la Universidad de San Marcos, Lima (UNMSM); Museo

Nacional de Historia Natural de Chile (MNHN); Florida Museum of Natural History (FLMNH); Natural History Museum of Los Angeles County (LACM); San Diego Natural History Museum (SDNHM); University of California Museum of Paleontology (UCMP); and Smithsonian Institution National Museum of Natural History (USNM). After examining their specimens for signs of abrasion (as an indicator of redeposition; e.g., Boessenecker et al. 2014), we selected only well-preserved, relatively complete specimens with adequate stratigraphic information for inclusion in our study.

Tooth Measurements

We measured tooth crown height (CH) and width (CW) of a total of 544 *C. megalodon* specimens from 32 localities, 26 formations, and nine countries (Fig. 2). Another 51 specimens were measured; however, they either showed signs of redeposition or lacked sufficient stratigraphic information to be included in our analyses. These include 30 teeth from the Red Crag Formation (U.K.) that were clearly eroded, and 21 specimens from the Middle Globigerina Limestone (Malta) that did not have accurate stratigraphic information. These teeth are all deposited in the NHM collection.

Body-Size Estimations

We estimated the total length (TL) of *C. megalodon* teeth measured following the methods described in Pimiento et al. (2010), where the tooth CH is used to calculate TL based on the regressions from Shimada (2003) on the great white shark (*Carcharodon carcharias*), which is considered a modern analogue of *C. megalodon*. Accordingly, every tooth position in the jaw corresponds to a regression equation that calculates body size. As in Pimiento et al. (2010), we assigned a range of plausible positions to each tooth and estimated TL of every specimen by calculating it from the average among the different positions where every tooth could have belonged.

We then created a matrix of data (available in online supplemental materials) consisting of specimen number, CH, CW, tooth position, TL, geologic age (maximum, minimum and median), epoch, stage, formation, locality, stratigraphic level, country, ocean, latitude and collection. Our data collection covers a large portion of *C. megalodon*'s geographic distribution range (Pacific, Atlantic, and Indian oceans; Northern and Southern Hemispheres). Despite these efforts, we were not able to obtain samples from northern Europe, Asia, or southern Africa, where there are known *C. megalodon* records. Nonetheless, our matrix represents the most comprehensive data set of body-size estimations for this species and, of most relevance for this work, includes all body size ranges and hence, life stages. We did not exclude any tooth size, as we are not interested in maximum length, but in quantifying overall patterns of body size including all life stages and habitats.

Geological Age Assessment

For each specimen studied, we examined the accompanying label and used collection databases to verify the age assignment. Additionally, we studied a number of supplementary references that further documented or refined the age of the localities from which the specimens were recovered. This process was aided by using the Paleobiology Database (http://paleobiodb.org).

General Statistical Comparisons

In order to assess *C. megalodon* body-size trends through time, we calculated the moments (minimum [Min] and maximum [Max] values, mean, mode, skewness, and kurtosis) of the distribution of the TL data. We also divided the data into three time slices based on the age range of the specimens studied (middle Miocene, late Miocene, and Pliocene), following the geologic time scale of Gradstein et al. (2012). We did not subdivide Pliocene into early and late so as to maintain a relatively equitable time span for each slice. Finally, we calculated the moments of the distribution of TL for each time period and made pairwise comparisons of all distributions, using Kolmogorov-Smirnov (KS) tests.

Geographic Statistical Comparisons

In order to assess how trends in body size of *C. megalodon* vary across space, we plotted TL by absolute latitude, hemisphere, and ocean. Furthermore, we calculated the linear regression between body size and latitude, as well as compared body size by hemisphere and by ocean, using a Welch two-sample t-test and a Tukey test, respectively. Finally, we repeated the comparisons for each time slice. All analyses in this study were made using the statistical software R (R Development Core Team 2012).

Evolutionary Models

To test our hypothesis (H1 = *Carcharocles megalodon* increased in size through time, reaching its largest size prior to extinction) we used the methods of Hunt (2006, 2008) and Hunt and Carrano (2010). We tested three common models of trait evolution: random walk (UWR), where evolutionary increments are independent and equally likely to increase or decrease; directional evolution (GWR), which features a trend of increasing (or decreasing) trait values over time; and stasis, with trajectories that show fluctuations around a steady mean. We used the R package paleoTS (Hunt 2008) to fit these models to our time series of body sizes. This package uses maximum-likelihood estimation to fit these models and the small-sample-size Akaike Information Criterion (AICc) as a measure of model support (Hunt and Carrano 2010). Furthermore, it aids the interpretation of AICc scores by converting them to Akaike weights, which are the proportional support that each model receives.

Our general statistics and geographic analyses over time used three time slices: middle Miocene, late Miocene, and Pliocene. However, for our evolutionary models we used the total number of bins that resulted from estimating the mean age of each sample. For each resulting bin, we calculated the mean, variance, and sample size of the TL data, which formed the basis for the time-series analysis in paleoTS (available in online supplemental materials).

Supplementary Analyses

Megatooth sharks have diagnathic heterodonty (i.e., differences in the tooth morphology of the upper and lower dentition) (Purdy et al. 2001). Moreover, antero-posteriorly through the jaw, there is a slight initial tooth-size increase followed by a progressive decrease that continues to the last tooth. Because of this tooth-size variability within individuals, we calculated TL of each specimen based on a position-specific regression equation and drew our analyses on the basis of such estimations. Nonetheless, it could be argued that this approach warrants some caution, as TL estimations were based in a modern analogue (*C. carcharias*). To counteract this issue, we repeated all of our analyses using the raw tooth size data (available in online supplemental materials) and contrasted them with our main results using TL. Our conclusions are still based on the results obtained from the analyses data, as they represent a more robust estimation of the body size of *C. megalodon*.

RESULTS & DISCUSSION:

Ecology

General Body-Size Patterns

Total Length (TL) estimates for *Carcharocles megalodon* range from 2.20 to 17.90m (mean=10.02m, mode = 10.54m) (Table 1). The distribution of *C. megalodon* body sizes was left-skewed on a log scale (Table 1, Fig. 3A), with larger individuals found more frequently than smaller individuals. Above the species level, body-size distributions are usually right-skewed (Kozlowski and Gawelczyk 2002; O'Gorman and Hone 2013). At narrower taxonomic levels, species' body sizes are influenced by their unique physiological constraints, ecological relationships, and selective pressures (e.g., McClain et al. 2015). These sets of characteristics result in species having sizes relatively close to their optimum, which in turn shapes their distribution of body-size frequencies (Kozlowski and Gawelczyk 2002).

Optimum size is the size at which there is no ecological advantage to evolving larger or smaller size, and has often been defined as the most frequent size found across a broad scale (Maurer et al. 1992; Brown et al. 1993). The most frequent TL value of *C. megalodon* in a geologic time scale is 10.54m (mode in Table 1, peak in Fig. 3A). However, it is noteworthy that the optimum size of a species can vary across populations and ontogeny, and can also be taphonomically biased in the fossil record. Regardless, our broad scale results show a higher frequency of larger individuals (left-skewed distribution) and a modal value at 10.54m that may have shaped this trend.

When comparing *C. megalodon* body-size patterns throughout time (Fig. 3B), we obtained similar moments for each time slice studied (Table 1), with the middle Miocene slice showing a significantly different distribution, lower mode, and less negative skewness relative to the general trend (Table 1). Despite these differences, a left-skewed body-size distribution and a mode around 10.54m (between 9.32 and 11.59 m) were maintained through time. All these trends are supported by the raw data (Supplementary Table S1, Supplementary Fig. S1).

Geographic Trends of Body Size

No correlation (R^2= 0.01) was found between TL estimates and absolute latitude (Table 2, Fig. 4A), suggesting that body size did not vary systematically along a latitudinal gradient. Of note, midlatitudes lack fossil occurrences, lower-latitude fossil occurrences are all from the Pliocene (white dots), and higher latitudes are dominated by middle Miocene fossil occurrences (black dots) (Fig. 4A). Whether these patterns are biological or due to sampling bias requires further investigation. Consequently, our geographic distribution results must be interpreted with caution, as they might be influenced by our sampling and/or the availability of outcrops in certain areas and subsequent deposition in major collections (e.g., Uhen and Pyenson 2007).

Significant differences were found between *C. megalodon* body sizes from the Northern Hemisphere relative to the Southern Hemisphere (Table 2). Notably, the Southern Hemisphere has a larger mean body size (Fig. 4B) (Northern n=426, mean=9.58m, 78.30% of total sample; Southern n=118, mean=11.62m, 21.69% of the total sample). Similarly, significant differences were found between samples from the Atlantic and Pacific oceans, with the Pacific having a larger mean value (Pacific n=188, mean=10.90 m, 34.55% of the total sample; Atlantic n=350, mean=9.53m, 64.33%). No significant differences were found between *C. megalodon* body sizes from the Indian Ocean relative to the Atlantic or the Pacific (Table 2, Fig. 4C); however, the low sample size of the Indian Ocean (Indian n=6, mean=11.03m, 1.10% of the total sample) severely limits the statistical power.

The differences in mean sizes across hemispheres and oceans could be due to both environmental (e.g., water depth, ocean currents, resource availability, productivity) and biological (e.g., sexual segregation, habitat use, home range) reasons. On the other hand, it could also be due to sampling and taphonomic biases. For instance, the larger mean size found in the Southern Hemisphere could be the result of a lack of systematic collecting efforts, as most of the southern samples are from the Bahia Formation (Mina

Fosforita, Chile, #1 in Fig. 2); these come from illegal confiscations and are biased toward larger teeth (R. Otero personal communication 2013). Similarly, Atlantic specimens come mostly from high latitudes. Even though *C. megalodon* is well known from tropical Atlantic and Caribbean localities (see Pimiento et al. 2013a for a review), large natural history collections from the tropics are lacking, and our samples from the Caribbean included only one collection (Gatun Formation, Panama, #6 in Fig. 2).

In spite of our sampling limitations, we were able to collect a relatively large number of specimens (544) from a broad time range (~14 Myr). Collectively, these specimens suggest that *C. megalodon* body size differs significantly between hemispheres and among ocean basins, but not across a latitudinal gradient. This body-size pattern across space reflects the widespread distribution of *C. megalodon*, which may be a result of its geographically structured populations facing diverse ecological constraints (hence the differences between hemispheres and oceans), even though the species had a cosmopolitan range (hence the lack of a latitudinal gradient).

Similar to the overall pattern, there was no correlation between body size and absolute latitude within any time period. The middle Miocene was particularly similar to the overall relationship (Table 2, Fig. 4D). Also, *C. megalodon* was significantly larger in the Southern Hemisphere and in the Pacific Ocean during the middle and late Miocene (Table 2, Fig. 4E,F). Even when in the Pliocene *C. megalodon* appeared to have slightly larger sizes in the Northern Hemisphere and in the Atlantic Ocean, these differences were not significant (Table 2).

The raw data support each of these trends (Supplementary Table S2, Supplementary Fig. S2), with the Southern Hemisphere having significantly larger tooth sizes throughout all time periods. Although the Indian Ocean data reveal significantly larger tooth sizes both in the total sample and in the Pliocene, this disparity lacks statistical power given the small sample size of the Indian Ocean (n=6, 1.10% of the total sample). Nevertheless, taken together, our results suggest that the differences in *C. megalodon* body size across space are maintained throughout time.

Evolution

Evolutionary Body-Size Mode

[H1*: Carcharocles megalodon* increased in size through time, reaching its largest size prior to extinction]. When testing for the three models of trait evolution, we found that stasis is the one that best fits our data, accounting for 97% of the Akaike weight and greatly outperforming the UWR and GWR models (Table 3). This trend is supported even when using raw data (Supplementary Table S3, Supplementary Fig. S3). We therefore reject our hypothesis of body-size increase through time. This result contrasts with the size increase trend seen in the megatooth lineage (Fig. 5).

Stasis in body size was previously proposed for *C. megalodon* on the basis of dental measurements (Pimiento et al. 2010). However, because the aim of that work was to compare tooth measurements (not body size) from a particular area (nursery), the comparisons were made using only three localities, based on a limited sample size, and not statistically tested. Conversely, here we used rigorous quantitative methods (i.e., Hunt 2006, 2008; Hunt and Carrano 2010) to test for different hypotheses of mode of trait body-size evolution.

Although stasis has been widely studied, no consensus has been reached on the causal mechanisms (Estes and Arnold 2007; Hunt 2007; Hunt and Rabosky 2014). It has been proposed that stasis could be caused by stabilizing natural selection, genetic and environmental constraints, resource competition, habitat selection, and/or geographic structure, among others (Eldredge et al. 2005; Estes and Arnold 2007; Hunt 2007; Hunt and Rabosky 2014). From these, stabilizing selection and geographic structure are particularly supported (Hunt 2007). Stabilizing selection causes a species' size to be relatively close to its optimum (Kozlowski and Gawelczyk 2002) and when this optimum does not change much over time, stasis is observed. Similarly, the geographic range of a widespread species can cause stasis due to spatially heterogeneous natural selection acting across semi-isolated populations (Eldredge et al. 2005; Hunt 2007; Hunt and Rabosky 2014). Accordingly, stasis is common when a taxon has widespread distributions, lives in variable environments, and is insensitive to environmental fluctuations (Sheldon 1996; Benton and Pearson 2001). Because *C. megalodon* body size is both invariant in terms of size frequency distributions (keeping a relatively constant modal [optimum?] value) and variant across hemispheres and oceans over geologic time, stabilizing selection and/or geographic structure may be (either mutually or exclusively) the mechanisms causing stasis in this species.

Broader Implications

To our knowledge, body-size trends of large predatory sharks have never been studied before over geologic time. Our results have three broader implications that provide a deep-time perspective to the understanding of the body-size trends of marine apex predators:

1. The left-skewed distribution of *C. megalodon* body size, both in the total temporal range and throughout the different periods studied, suggests a selective pressure favoring larger individuals. At ecological scales, and despite body-form similarities between large and small predatory sharks (Irschick and Hammerschlag 2014), larger individuals tend to prey upon larger animals (Lucifora et al. 2009). This trend is related to an ontogenetic dietary shift whereby smaller individuals avoid large (possibly dangerous) prey, whereas larger individuals consume a broader range of prey sizes (Lucifora et al. 2009; Estrada et al. 2006). This pattern has also been observed across different species of terrestrial predators (Peters 1983; Carbone et al. 1999). The left-skewed distribution of *C. megalodon* body size may therefore be the result of a long-term selective pressure on marine predatory sharks that favors consumption of a broader range of prey, increasing their impact in the structure of food webs (e.g., Steneck 2013).

2. Given the widespread distribution of a large cosmopolitan apex predator such as *C. megalodon*, the body-size variations found across oceans and hemispheres may be a result of the heterogeneous ecological conditions that they faced. Currently, sympatric populations of cosmopolitan predatory marine mammals such as the killer whale

(*Orcinus orca*) are genetically distinguishable. This might be a result of assortative mating, which eventually produces morphological (e.g., body size) and behavioral differences between populations through generations (Hoelzel and Dover 1961). Similarly, the great white shark (*Carcharodon carcharias*) has demographically isolated populations due to their high degree of site fidelity (Jorgensen et al. 2009). Our study of *C. megalodon* body size trends through space and geologic time suggests that the ecological distinctiveness of geographically discrete populations of large cosmopolitan marine apex predators may shape their body-size trends in deep time.

3. Finally, the lack of size change in *C. megalodon* throughout geologic time contrasts with the size increase trend observed not only in the megatooth lineage but also in other lineages of marine predators such as toothed whales (Odontoceti) (Pyenson and Sponberg 2011). Given that sharks have slower evolutionary rates than mammals (Martin et al. 1992), the lack of body-size change in *C. megalodon* may be the result of the inherent characteristics of shark species, which potentially make them particularly resilient to environmental changes (Martin et al. 1992; Pimiento et al. 2013a). A disconnection between micro- and macro- evolutionary body-size patterns (i.e., stasis in the species vs. size increase in the lineage) could be an evolutionary consequence of such characteristics. The macroevolutionary mechanisms that produce the body-size increase in lineages of large marine predators are the subject of a future investigation.

CONCLUSIONS:

We found that *Carcharocles megalodon* body size had a left-skewed distribution and was significantly different between hemispheres and ocean basins through geologic time. In addition, we found stasis as the mode of size evolution of *C. megalodon*, and thus reject our hypothesis of body-size increase over geologic time. Given that *C. megalodon* is a long-lived giant predator with a fossil record of ~14 Myr, it represents an excellent study system to provide a deep-time perspective to the understanding of body-size trends of marine apex predators. For instance, this study suggests that (1) a selective pressure in predatory sharks for consuming a broader range of prey may favor larger individuals and produce left-skewed distributions over geologic time, (2) body-size variations in cosmopolitan large apex predators may depend on the predators' interactions within geographically discrete communities, and (3) the inherent characteristics of shark species can produce a lack of net size changes over geologic time, even though the species' lineage shows size increase. Future research on body-size patterns of additional large apex predators (e.g., other megatooth sharks, toothed whales, plesiosaurs, mosasaurs, archaeocetes) would allow a more complete understanding of the macroevolutionary mechanisms that produce body-size increases, the evolution of gigantism, and the role of body size in extinction risk.

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TABLE 1. Descriptive statistics of *Carcharocles megalodon* body size (m) through time. Significant values in bold. Codes: P=Pliocene (5.33–2.58 Ma), LM= late Miocene (11.61–5.33 Ma), MM=middle Miocene (15.97–11.61 Ma).

	n	Min	Max	Mean	Mean (log 10)	Mode	Mode (log 10)	Skew (log 10)	Kurtosis (log 10)	*p*-value (K.S.)
All	544	2.20	17.90	10.02	0.97	10.54	1.02	-0.84	0.43	
P	260	2.92	17.68	10.29	0.99	10.18	1.01	-0.79	0.69	
LM	170	2.20	17.00	10.22	0.98	11.59	1.06	-1.13	1.37	0.58
MM	114	2.81	17.90	9.12	0.92	9.32	0.97	-0.37	-0.93	**0.02**

TABLE 2. Statistical comparisons of *Carcharocles megalodon* body size (m) trends through time across space. Significant values in bold. P=Pliocene (5.33–2.58 Ma), LM= late Miocene (11.61–5.33 Ma), MM=middle Miocene (15.97–11.61 Ma).

	Latitude	Hemisphere		Ocean					
		North-South		Atlantic-Indian		Indian-Pacific		Atlantic-Pacific	
	R^2	*p*-value	*t*	*p*-value	*t*	*p*-value	*t*	*p*-value	*t*
All	0.01	**<0.01**	-7.17	0.50	1.07	1.00	-0.09	**<0.01**	4.47
P	0.11	0.53	0.65	0.88	0.47	0.38	-1.30	0.22	1.65
LM	0.19	**<0.01**	-8.11	0.64	0.87	1.00	-0.02	**<0.01**	5.04
MM	0.07	**<0.01**	-3.95	0.48	1.12	0.99	0.14	**<0.01**	6.73

TABLE 3. Model-fitting results for *Carcharocles megalodon* body size trends. Largest Akaike weight (best fit) in bold.

	LogL	AICc	Akaike weight
GRW	-36.22	77.37	0.004
URW	-36.36	75.00	0.016
Stasis	-30.80	66.53	**0.981**

FIGURE 1. Schematic representation of the changes in tooth morphology within the megatooth lineage: cusplet loss, broadening of tooth crowns, and size increase. Scheme based on the work of Ehret (2010).

FIGURE 2. Geographic locations of *Carcharocles megalodon* collections included in this study. 1. Bahia Inglesa Fm., Mina Fosforita, late Miocene (MNHN). 2. Basal Black Rock Fm., Beaumaris, Pliocene; Batesford Fm., Batesford, Middle Miocene; Muddy Creek Fm., Hamilton, late Miocene (NHM). 3. Bone Valley Fm., Payne Creek Mine, Fort Green Mine SW, North Palmetto Mine, Achan Mine, Palmetto Mine (Agrico) and Chicora Mine (FLMNH); Tamiami Fm., East Coast Aggregates, Pliocene (FLMNH). 4. Calvert Fm., Parkers Creek and Scientists Cliff, middle Miocene localities (USNM and LACM). 5. Capistrano Fm., Laguna Hill and Antigua; Purisima Fm., Steamer's Lane, late Miocene (LACM, UCMP and SDNHM). 6. Chucunaque Fm., late Miocene; Gatun Fm., YPA017, YPA021 and YPA032, late Miocene and YPA033, middle Miocene (FLMNH). 7. Loxton Sand Fm. Sunlands Pumping Station, Pliocene (NHM). 8. Monterey Fm., Altamira, El Toro and Leisure World, middle Miocene; San Mateo Fm., Lawrence Canyon, late Miocene and Lawrence Canyon upper gravel unit, Pliocene; Topanga Fm., Cook's Corner, middle Miocene (LACM and SDNHM). 9. Onzole Fm., Punta la Gorda and Punta la Colorada, Pliocene (NHM). 10. Paraná Fm., late Miocene (MACN and UNLP). 11. Pisco Fm., Cerro Colorado, middle Miocene; Montemar, Cerro Los Quesos, Cerro La Bruja, Yesera Amara, Ocucaje, Agua de las Lomas, late Miocene (UNMSM). 12. Pungo River Fm., Middle Miocene (USNM). 13. Punta del Diablo Fm., late Miocene (UNLP). 14. Rosarito Beach Fm., Mesa los Indios, middle Miocene (SDNHM). 15. Temblor Fm.,

Shark Tooth Hill, middle Miocene (LACM and UCMP). 16. Tirabuzon Fm., Baja, Pliocene; Ysidro Fm., Santa Rita, middle Miocene (LACM and SDNHM). 17. Wanganui, Wellington, Pliocene (NHM). 18. Yorktown Fm., Pliocene (LACM and USNM).

FIGURE 3. *Carcharocles megalodon* body-size distributions (note log10 scale). The density curve is in gray. A, General body-size distribution. B, Body-size distributions through time.

FIGURE 4. Geographic trends in *Carcharocles megalodon* body size. A, Body size by latitude. The dashed line represents best-fit linear regression model. Black dots represent the middle Miocene (MM) samples, gray dots the late Miocene (LM) samples, and white dots the Pliocene (P) samples. B, Boxplot showing body size by hemisphere. C, Boxplot showing body size by ocean. D, Body size by absolute latitude through time. E, Boxplots showing body size by hemisphere through time. F, Boxplots showing body size by oceanic region through time.

FIGURE 5. Evolutionary trajectory of *Carcharocles megalodon* body size. Bars represent standard errors of the mean.

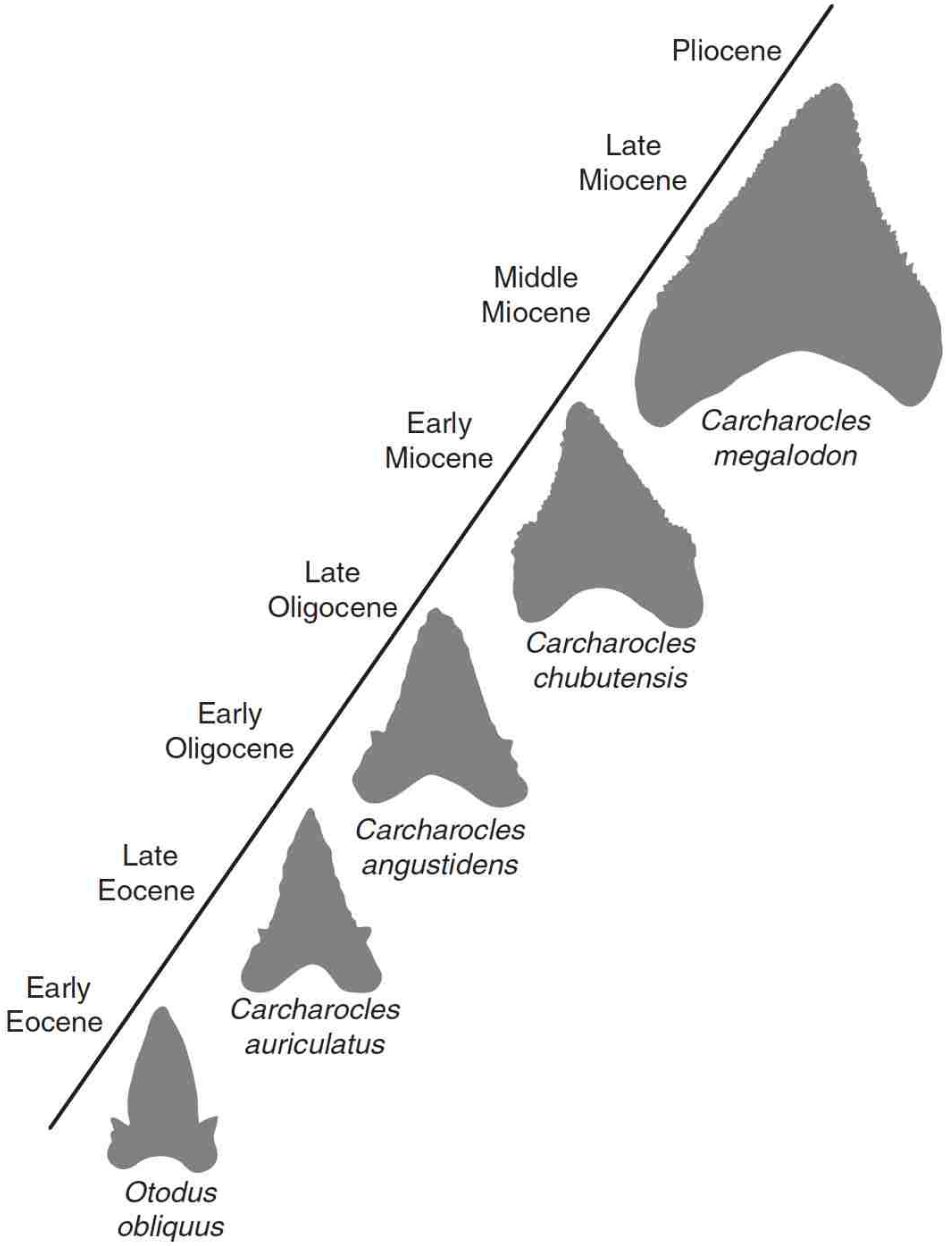

Pliocene
Late Miocene
Middle Miocene
Early Miocene
Late Oligocene
Early Oligocene
Late Eocene
Early Eocene
Carcharocles megalodon
Carcharocles chubutensis
Carcharocles angustidens
Carcharocles auriculatus
Otodus obliquus

Figure 1.

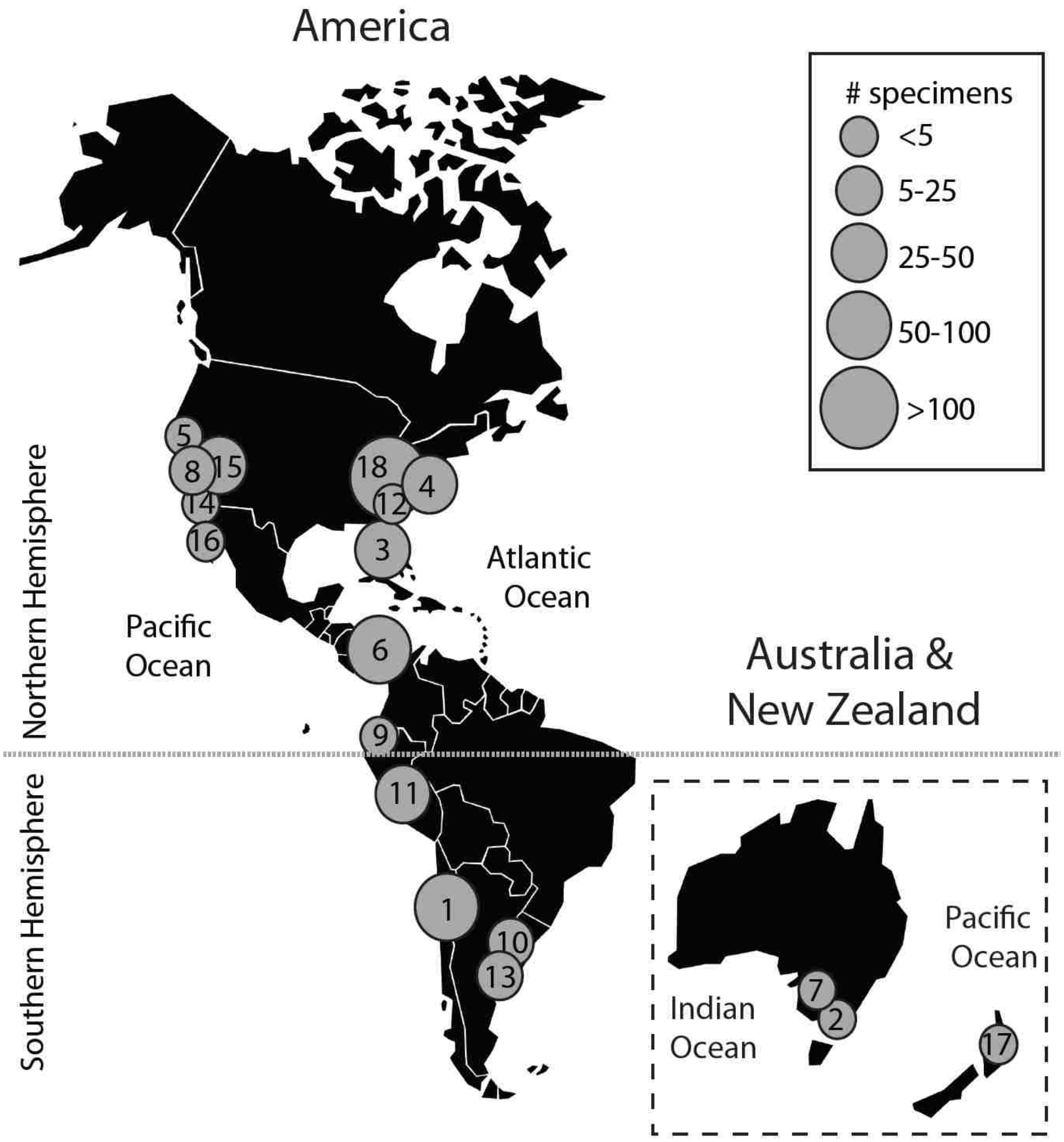

America
specimens
<5
5-25
25-50
50-100
>100
Northern Hemisphere
Southern Hemisphere
Pacific Ocean
Atlantic Ocean
Australia & New Zealand
Indian Ocean
Pacific Ocean
5
8
15
14
16
18
12
4
3
6
9
11
1
10
13
7
2
17

Figure 2.

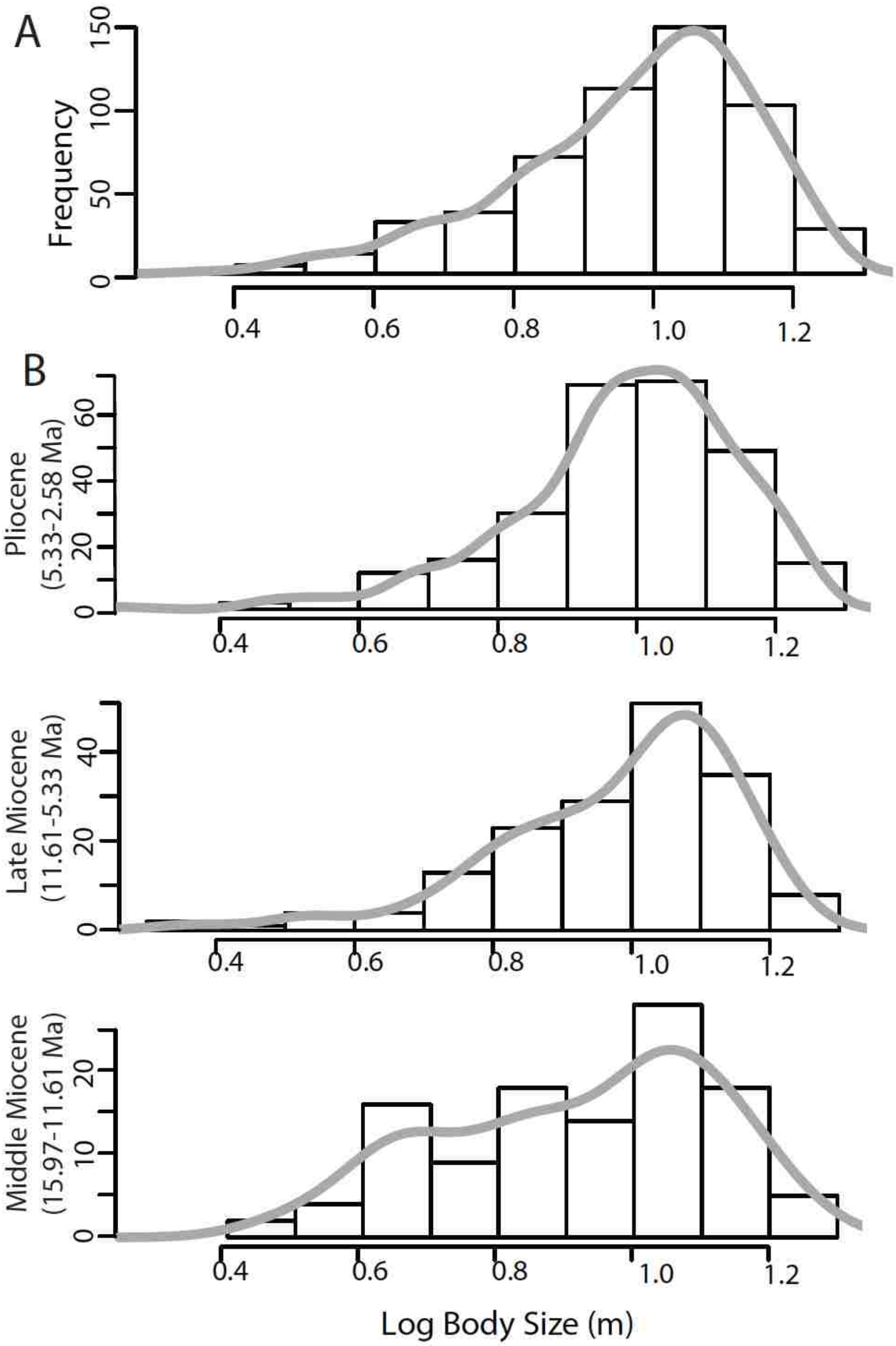
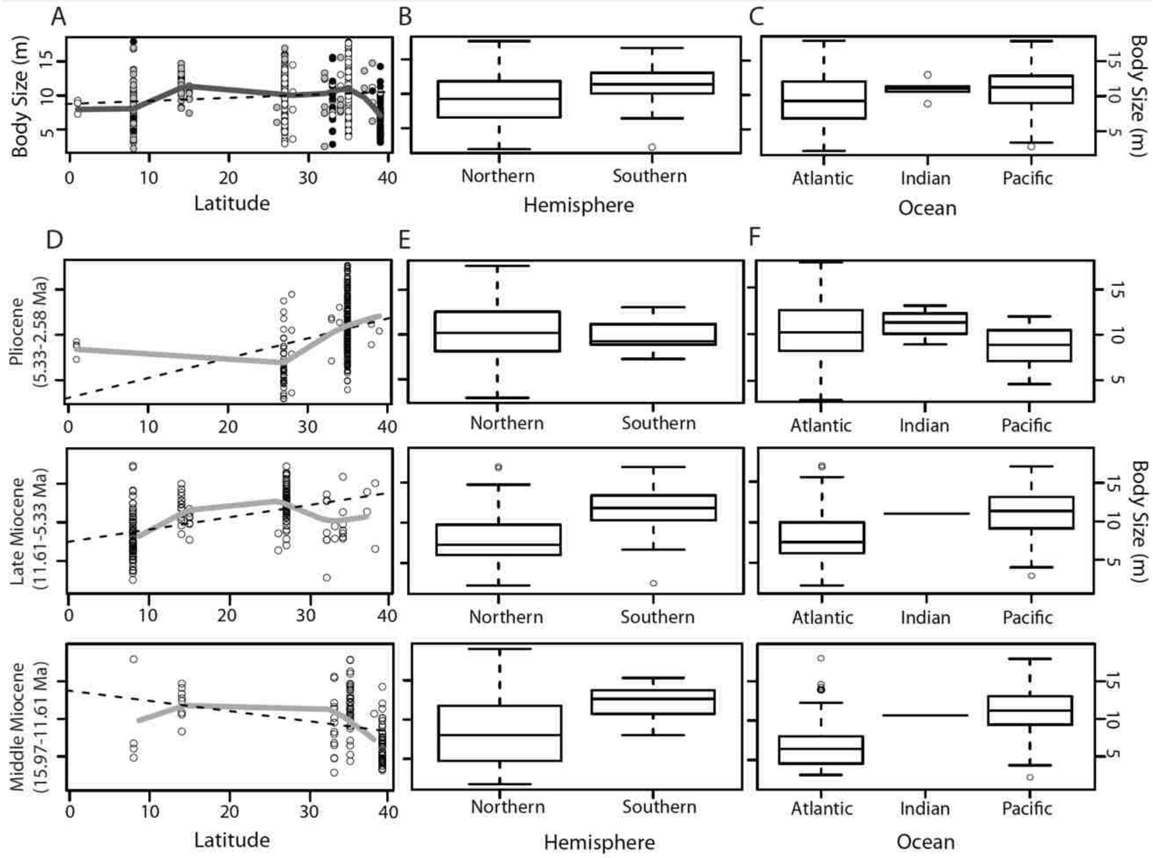

A
Frequency
0
50
100
150
0.4
0.6
0.8
1.0
1.2
B
Pliocene (5.33-2.58 Ma)
0
20
40
60
0.4
0.6
0.8
1.0
1.2
Late Miocene (11.61-5.33 Ma)
0
20
40
0.4
0.6
0.8
1.0
1.2
Middle Miocene (15.97-11.61 Ma)
0
10
20
0.4
0.6
0.8
1.0
1.2
Log Body Size (m)

Figure 3.



A
B
C
Body Size (m)
15
10
5
0
10
20
30
40
Latitude
Northern
Southern
Hemisphere
Atlantic
Indian
Pacific
Ocean
Body Size (m)
D
E
F
Pliocene (5.33-2.58 Ma)
Late Miocene (11.61-5.33 Ma)
Middle Miocene (15.97-11.61 Ma)

Figure 4.

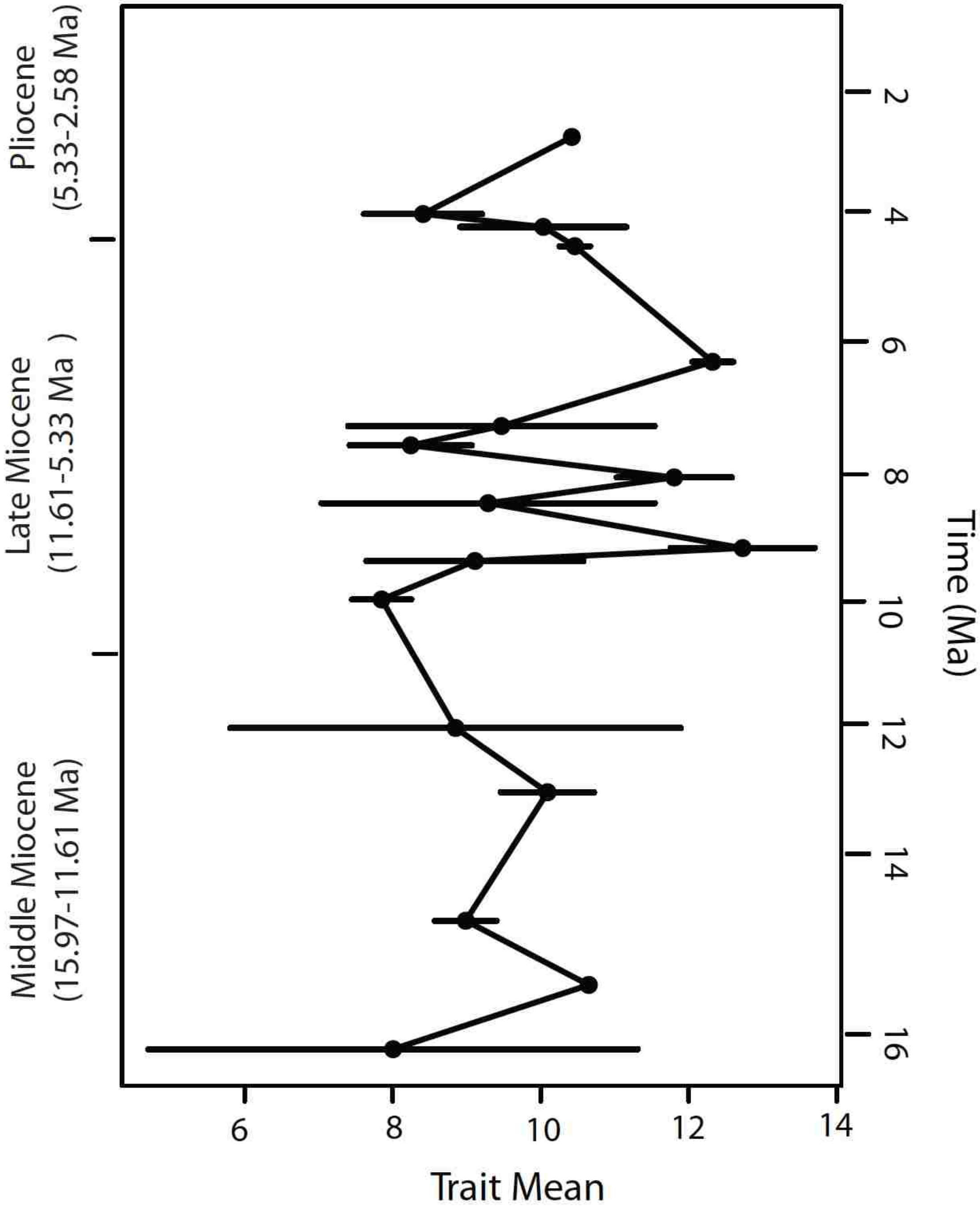

Pliocene
(5.33-2.58 Ma)
Late Miocene
(11.61-5.33 Ma)
Middle Miocene
(15.97-11.61 Ma)
Time (Ma)
2
4
6
8
10
12
14
16
Trait Mean
6
8
10
12
14

Figure 5.

APPENDICES

Appendix 1. Shark tooth measurements.

Collection	Catalogue	CH	CW	Tooth Position	Total Length	Ma Max	Ma Min	Epoch	Stage	Formation	Locality	Stratigraphy	Country	Ocean	Hemisphere
MNHN	CP 1	107.22	115.64	A1-A2	12.68	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 10	112.91	104.52	a1-a2	16.01	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 11	83.88	85.43	a1-a2	11.87	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 12	99.87	98.43	A1-A2	11.81	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 13	107.18	123.38	L1-L2	14.86	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 14	62.18	84.95	L3-L5, l3-l5	16.05	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 15	112.7	107.3	a1-a2	15.98	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 16	85.73	87.63	a1-a2	12.13	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 17	93.84	76.47	a1-a2	13.29	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 18	91.13	100.55	A1-A2	10.78	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 2	96.09	103.47	A1-A2	11.37	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 20	90.49	82.49	a1-a2	12.81	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 21	69.02	70.75	a1-a2	9.75	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 22	72.92	70.38	a1-a2	10.31	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 23	98.89	87.05	A1-A2	11.7	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 24	114.44	118.58	A1-A2	13.53	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 26	65.45	84.9	L1-L4	9.83	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 27	47.42	53.38	a1-a2	6.68	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 28	69.64	72.64	l1-l3	14.27	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 29	66.16	74.61	L1-L5	11.43	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 3	102.75	102.91	a1-a1	14.56	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern

MNHN	CP 30	59.24	84.69	L1-L5	10.24	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 31	49.1	55.25	L1-L5	8.49	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 32	52.93	58.79	L1-L3	7.48	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 34	42.97	67.97	L1-L7	12.47	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 35	42.89	59.95	L1-L7	12.45	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 36	55.19	73.89	L1-L7	16.06	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 38	73.48	85.41	A1-A2	8.7	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 39	93.13	86.8	a1-a2	13.19	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 4	82.46	92.57	l1-l3	16.91	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 40	108.31	109.18	A1-A2	12.81	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 41	88.55	103.15	A1-A2	10.48	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 42	73.04	80.78	A1-L1	9.24	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 43	98.01	105.59	A1-A2	11.59	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 45	39.92	58.52	L3-L7	13.98	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 46	80.03	96.49	L1-L3	11.29	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 47	41.77	64.45	L3-L7	14.64	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 48	84.86	93.8	a1-l1	12.97	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 49	42.43	59.53	L3-L5, l3-l5	10.91	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 5	91.28	94.07	A1-A2	10.8	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 51	74.42	82.38	l1-l2	13.69	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 52	34.36	53.91	L3-L7	12	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 53	31.93	52.45	L3-L6, l3-l6	11.76	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 54	37.88	58.87	L3-L6, l3-l6	14.02	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 55	42.88	65.71	L3-L6, l3-l6	15.92	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 56	43.19	63.76	L3-L5, l3-l5	11.1	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern

MNHN	CP 57	42.09	66.62	L3-L5, l3-l5	10.82	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 58	92.65	85.13	a1-a2	13.12	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 59	76.83	89.28	l1-l3	15.75	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 6	106.7	105.89	a1-a1	15.12	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 60	80.8	93.95	L1-L3	11.4	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 61	88.96	96.26	a1-a2	12.59	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 62	100.86	128.51	A1-A2	11.93	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 63	95.22	113.32	a1-a2	13.49	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 64	115.77	116.05	A1-A2	13.69	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 65	99.16	106.11	A1-L1	12.53	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 66	110.49	127.96	L1-L2	15.32	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 67	102.78	118.9	A1-A2	12.16	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 68	97.87	119.34	L1-L2	13.57	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 69	98.03	114.77	L1-L2	13.6	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 7	93.77	103.4	a1-a2	13.28	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 8	96.35	105.76	A1-A2	11.4	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
MNHN	CP 9	92.61	104.19	A1-A2	11	7.3	5.3	LM	Messinian	Bahia Inglesa	Mina Fosforita	Unit 5	Chile	Pacific	Southern
NHM	P13932	78.9	70.02	a1-a2	11.16	5.0	3.4	P	Zanclean	Basal Black Rock Sandstone	Beaumaris	Cheltenhamian to Kalimnan	Australia	Indian	Southern
NHM	P5209	67.5	67.5	A1-A2, L1-L3	8.91	5.0	3.4	P	Zanclean	Basal Black Rock Sandstone	Beaumaris	Cheltenhamian to Kalimnan	Australia	Indian	Southern
NHM	P27667	90.02	71.45	A1-A2	10.65	16.5	15.5	MM	Langhian	Batesford	Batesford	Batesfordian	Australia	Indian	Southern
FLMNH	UF 132588	29.39	31.74	A1-A2	3.49	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 132593	33.39	30.31	a1-a2	4.68	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 132595	35.15	33.33	A1-A2	4.17	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 17839a_2_LR	32.54	37.17	a1-a2	4.56	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA

FLMNH	UF 17839b_1_LR	30.79	33.65	l1-l3	6.27	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 17840a_1_LR	42.07	46.9	L1-L5	7.28	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 17840a_2_LR	27.04	33.15	l1-l5	7.94	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 17840a_3_LR	35.01	40.32	L1-L5	6.06	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 17840a_4_LR	21.32	21.79	a1-a2	2.96	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 17850c1_LR	49.38	53.44	A1-A2	5.85	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 17850c2_LR	46.12	48.92	l1-l5	13.75	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 17872b_1_LR	45.82	53.95	L1-L5	7.92	10.3	4.9	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 17872b_10_LR	31.69	31.45	a1-l1	4.99	10.3	4.9	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 17872b_11_LR	20.8	31.9	l1-l5	6.04	10.3	4.9	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 17872b_2_LR	35.44	34.14	a1-a2	4.97	10.3	4.9	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 17872b_3_LR	38.27	44.85	L4-L6	11.78	10.3	4.9	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 17872b_6_LR	23.42	26.6	a1-a2	3.26	10.3	4.9	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 17872b_7_LR	24.61	25.81	A1-A2	2.92	10.3	4.9	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 17872b_8_LR	33.61	36.15	a1-a2	4.71	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 17980	46.97	44.03	a1-a2	6.61	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 209164	40.73	46.42	L1-L5	7.04	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 209170	55.81	59.78	L1-L5	9.65	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 217140	75.22	78.71	L1-L3	10.61	10.3	4.9	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 217225	67.29	69.81	A1-A2	7.96	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 228479	42.78	46.06	a1-a2	6.02	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 228480	50.59	56.49	L1-L5	8.75	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 229804	20.82	29.92	L5-L8	12.53	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 229807	33.74	33.35	l1-l3	6.88	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 234583	81.14	79.81	A1-A2	9.6	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA

FLMNH	UF 24715b_1_LR	44.6	41.4	a1-a2	6.27	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 24715b_2_LR	38.16	38.44	L1-L3	5.4	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 24715b_3_LR	45.86	46.35	A1-A2	5.43	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 24715b_4_LR	35.59	33.22	a1-a2	4.99	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 24715b_6_LR	41.33	43.13	A1-A2	4.9	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 24715b_7_LR	31.94	43.68	L3-L6	8.51	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 300	73.66	70.7	A1-A2	8.72	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 55973b_1_LR	29.58	35.05	l1-l3	6.02	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
FLMNH	UF 55973b_2_LR	35.24	38.67	a1-l1	5.56	5.3	3.6	P	Zanclean	Bone Valley		US East	Atlantic	Northern	WNA
MNH	ACC NO. 413905	35.6	43.6	L1-L6	7.99	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	DJB 1029	26.64	27.1	a1-a2	3.72	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	DJB 1061	29.76	36	L1-L3	4.22	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	DJB 1566	26.23	29.4	A1-A2	3.11	13.8	11.6	MM	Serravallian	Calvert	Scientists Cliff	US East	Atlantic	Northern	WNA
MNH	DJB 1596	33.92	35.6	A1-A2	4	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	DJB 1766	34.9	36.8	l1-l3	7.06	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	DJB 1860	52.15	64.41	L1-L3	7.44	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	DJB 1933	80.05	62.85	a1-a2	11.31	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	DJB 1975	39.5	60.07	A1-A2	6.58	13.8	11.6	MM	Serravallian	Calvert	Scientists Cliff	US East	Atlantic	Northern	WNA
MNH	DJB 2009	17.53	25	l1-l6	6.84	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	DJB 2090	68.75	67.8	a1-a2	9.71	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	DJB 2372	57.56	62.85	A1-A2	6.81	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	DJB 2464	25.59	33.92	L5-L7	12.02	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	DJB 850	55.46	57.3	A1-A2	6.57	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
LACM	LACM 58931	43.7	45.92	L1-L5	7.56	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	No number	24.81	23.7	l1-l2	4.6	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA

MNH	No number	33.49	47.1	L1-L3	4.75	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	PAL 535357	27.59	32.1	L1-L6	6.17	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	R.O. 411148	21.25	32.3	l3-l7	14.24	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 171156	50.83	73.8	L1-L3	7.18	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 171157	21.72	31.2	l1-l5	6.32	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 171170	14.84	22.3	L3-L7	5.04	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 171182	31.27	35.9	A1-A2	3.71	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 182307	75.1	94.87	A1-A2	8.89	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 24956.1	22.08	23.8	l1-l2	4.1	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 24956.2	52.69	61.2	L1-L3	7.44	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 25929	37	43.27	A1-A2	4.39	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 26189	39.8	36.3	a1-a2	5.59	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 282935.1	34.08	39.57	l1-l5	10.09	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 282935.2	36.41	46.59	A1-A2	4.32	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 282935.3	22.23	25.47	a1-a3	3.33	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 282935.4	30.77	26.41	a1-a2	4.3	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 282935.5	27.77	33.2	A1-A2	3.3	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 293100	21.52	36.25	L5-L7	10.04	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 337208	26.41	32.68	L3-L7	9.17	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 475290	27.36	30.6	l1-l3	5.57	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 475297	19.26	34	L1-L6	4.28	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 475299	33	30.4	a1-a2	4.62	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 475303	38.14	34.4	a1-a2	5.35	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 475304	36.79	30.7	a1-a2	5.16	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 475306	30.51	39.8	L1-L3	4.33	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA

MNH	USNM 475347	48.7	52.13	a1-a2	7.52	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 489136	68.08	87.11	A1-A2	8.06	13.8	11.6	MM	Serravallian	Calvert	Scientists Cliff	US East	Atlantic	Northern	WNA
MNH	USNM 489137	46.08	43.86	A1-A2	5.4	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 494369	45.36	44.17	a1-a3	6.83	13.8	11.6	MM	Serravallian	Calvert	Scientists Cliff	US East	Atlantic	Northern	WNA
MNH	USNM 494370	69.89	102.6	A1-A2	8.27	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
MNH	USNM 495294	38.08	39.5	A1-A2	4.51	16.0	13.8	MM	Langhian	Calvert	Parkers Creek	US East	Atlantic	Northern	WNA
LACM	LACM 58936	92.9		A1-A2	10.99	7.3	5.3	LM	Messinian	Capistrano	Laguna Hill	US West	Pacific	Northern	ENP
SDNHM	SDNHM 125566	52.51		A1-A2	6.22	11.6	3.6	LM	Messinian	Capistrano	Antigua at Monarch Beach?	US West	Pacific	Northern	ENP
SDNHM	SDNHM 53167	105.2	98.19	L1-L5	14.73	11.6	3.6	LM	Messinian	Capistrano	Antigua at Monarch Beach?	US West	Pacific	Northern	ENP
FLMNH	UF 275053	16.31	22.98	L5-L7, l3-l6	6.64	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275085	71.72	69.121928	A1-A2	8.49	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275086	41.1	40.87804	L1-L5	7.11	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275096	32.66	33.08	L1-L5	5.65	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275097	79.49	76.288976	a1-a3	12.13	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275099.1	39.92	39.789608	a1-a3	6.05	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275099.2	20.33	21.719792	L5-L7, l3-l6	8.39	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275107	51.2552	50.25	L1-L5, l1-l5	12.09	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275108	59.23	57.601152	a1-a3	9.01	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275109	27.23	24.83	L1-L5	4.72	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275110	43.95	38.66	A1-A2	5.21	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275114	82.44	79.010056	A1-A2	9.75	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275116	86.93	85.4	A1-A2	10.28	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275117.1	28.59	30.24	A1-A2	3.39	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275118	87.8	83.95412	A1-A2	10.39	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275127	34.11	34.430464	a1-l5	8.24	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275128	27.6	28.42564	L1-L5	4.78	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP

FLMNH	UF 275129	40.38	40.213912	a1-a3	6.12	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275131	66.61	64.408464	A1-A2	7.88	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275132	78.02	74.933048	A1-A2	9.23	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275133	50.34	49.401016	A1-A2	5.96	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275134	37.36	37.428264	A1-A2	4.43	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275136	43.51	43.101024	a1-a3	6.6	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275137	65.17	63.080208	L1-L5	11.26	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275139	55.50856	54.2	A1-A2	6.57	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	UF 275151	47.25	46.5508	l1-l3	9.66	11.5	9.7	LM	Tortonian	Chucunaque		Panama	Pacific	Northern	ECP
FLMNH	AT04-17-1	43.8	43.2	a1-a2	6.2	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	AT04-41-2	56.4	60.3	A1-A2	6.7	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	AT06-9-1	60.1	57.7	A1-A2	7.1	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	CTPA 6671	72.3	74.7	A1-A2	8.6	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 237898	50	53	A1-A2	5.9	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 237914	46.4	31.4	L1-L5	8	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 237949	32.9	35.7	A1-A2	3.9	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 237950	54.2	47.7	a2	7.3	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 237951	17.6	26.8	L1-L5	3.1	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 237952	31.3	43.2	L1-L5	5.4	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 237953	24.5	30.9	l1-l5	7.2	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 237954	41.2	41.7	A1-A2	4.9	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 237955	28.5	28.4	A1-A2	3.4	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 237956	28.1	44.9	l4-l6	16.8	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 237957	19.4	26.7	L6-L9	13.8	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 237959	16	16.1	a1-a2	2.2	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 242801	27.5	31.2	L1-L5	6.4	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 242802	41	45.1	L1-L5	7.1	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 242803	34.7	40.8	L1-L5	6	12.0	9.0	LM	Tortonian	Gatun	YPA021	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 242804	34.7	34.7	L1-L5	6.9	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern

FLMNH	UF 245844	11.2	20.6	l5-l7	10	12.0	9.0	LM	Tortonian	Gatun	YPA021	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 245852	70.9	73.2	L2-L3	10.8	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 245885	36.6	39.6	L1-L3	5.2	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 245886	40.5	45.6	L1-L5	7	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 245925	19.2	23.2	L6-L8	13.7	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 245995	63.2	62.2	a3	11	12.0	9.0	LM	Tortonian	Gatun	YPA021	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 245996	25.9	31.8	l2-l6	13.1	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 246002	24.5	35	L5-L7	11.5	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 246003	45.4	52.4	L1-L3	6.4	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 246846	28.2	28.2	L1-L3	3.5	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 247248	61.8	61.8	A1-A2	8.6	12.0	9.0	LM	Tortonian	Gatun	YPA017	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 247250	40.7	40.7	a1-a2	4.8	12.0	11.0	MM	Serravallian	Gatun	YPA033	Lowermost Gatun	Panama	Atlantic	Northern
FLMNH	UF 247251	45.1	45.1	a1-a2	6	12.0	11.0	MM	Serravallian	Gatun	YPA033	Lowermost Gatun	Panama	Atlantic	Northern
FLMNH	UF 247252	48.2	48.2	L1-L5	7.8	12.0	9.0	LM	Tortonian	Gatun	YPA032	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 247254	63.4	63.4	L1-L5	8.7	12.0	9.0	LM	Tortonian	Gatun	YPA032	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 257576	43.9	43.9	a1-a2	6.7	12.0	11.0	MM	Serravallian	Gatun	YPA033	Lowermost Gatun	Panama	Atlantic	Northern
FLMNH	UF 257577	39.7	39.7	L5-L7	17	12.0	9.0	LM	Tortonian	Gatun	YPA030	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 257578	51.1	51.1	A1-A2	5.9	12.0	9.0	LM	Tortonian	Gatun	YPA032	Lower Gatun	Panama	Atlantic	Northern
FLMNH	UF 257579	41.2	41.2	L5-L7	17.9	12.0	11.0	MM	Serravallian	Gatun	YPA033	Lowermost Gatun	Panama	Atlantic	Northern
FLMNH	UF 266953	22.5	22.5	L6-L8	9.6	12.0	9.0	LM	Tortonian	Gatun	YPA032	Lower Gatun	Panama	Atlantic	Northern
NHM	P15216.1	96	96.5	A1-A2	11.36	5.3	3.6	P	Zanclean	Loxton Sand		Australia	Indian	Southern	Ind
NHM	P15216.2	94	93	L1-L2	13.04	5.3	3.6	P	Zanclean	Loxton Sand		Australia	Indian	Southern	Ind
LACM	LACM 10153.1	38.09		l1-l5	11.31	20.4	13.8	MM	Burdigalian	Monterey		Altamira Shale	US West	Pacific	Northern
LACM	LACM 10153.2	33.54		a1-a2	4.7	20.4	13.8	MM	Burdigalian	Monterey		Altamira Shale	US West	Pacific	Northern
LACM	LACM 144941	40.2	42	A1-A2	4.76	10.3	4.9	MM	Tortonian	Monterey	El Toro		US West	Pacific	Northern
LACM	LACM 58935	85.21	102.45	A1-A2	10.08	13.8	11.6	MM	Serravallian	Monterey	Leisure World	US West	Pacific	Northern	ENP
LACM	LACM 59052	82.5	93.99	L1-L5	11.56	13.8	11.6	MM	Serravallian	Monterey	Leisure World	US West	Pacific	Northern	ENP

SDNHM	SDNHM 98715.1	35.42		L5-L7	15.4	13.8	11.6	MM	Serravallian	Monterey	Leisure World?	US West	Pacific	Northern	ENP
SDNHM	SDNHM 98715.2	45.94		a1-a2	6.47	13.8	11.6	MM	Serravallian	Monterey	Leisure World?	US West	Pacific	Northern	ENP
SDNHM	SDNHM 98715.3	27.04		l1-l5	7.94	13.8	11.6	MM	Serravallian	Monterey	Leisure World?	US West	Pacific	Northern	ENP
NHM	P37925	93.45	100.05	A1-A2	11.05	15.5	15.0	LM	Tortonian	Muddy Creek	Muddy Creek near Hamilton	Balcombian	Australia	Indian	Southern
NHM	P59278	62.5	56.5	L1-L3	8.82	5.3	2.6	P	Zanclean	Onzole			Ecuador	Pacific	Southern
NHM	P59279	65.5	46.8	a1-a2	9.25	5.3	2.6	P	Zanclean	Onzole			Ecuador	Pacific	Southern
NHM	p59280	75	61.9	A1-A2	8.87	5.3	2.6	P	Zanclean	Onzole			Ecuador	Pacific	Southern
NHM	P59281	61.5	69.9	A1-A2	7.28	5.3	2.6	P	Zanclean	Onzole			Ecuador	Pacific	Southern
UNLP	21.245	87.63	86.41	a1-a2	12.4	11.6	7.3	LM	Tortonian	Parana			Argentina	Atlantic	Southern
MACN	9326.1	17.05	24.12	L1-L5	2.49	11.6	7.3	LM	Tortonian	Parana			Argentina	Atlantic	Southern
MACN	14328.1	70.19		A1-A2	8.31	11.6	7.3	LM	Tortonian	Parana			Argentina	Atlantic	Southern
MACN	14328.1	42.66	52.62	L1-L5	7.38	11.6	7.3	LM	Tortonian	Parana			Argentina	Atlantic	Southern
MACN	14328.1	76.85	88.82	L1-L5	13.27	11.6	7.3	LM	Tortonian	Parana			Argentina	Atlantic	Southern
UNLP	40-v-31-1	48.71	53.36	a1-a3	7.4	11.6	7.3	LM	Tortonian	Parana			Argentina	Atlantic	Southern
UNLP	86-v-1-159	94.38	106.41	A2-L2	12.53	11.6	7.3	LM	Tortonian	Parana			Argentina	Atlantic	Southern
UNMSM	MUSM 2088	62.5	50.89	A1-A2	7.4	8.7	6.45	LM	Messinian	Pisco	Montemar		Peru	Pacific	Southern
UNMSM	MUSM 2089	53.49		L1-L5	9.25	13.8	11.6	MM	Serravallian	Pisco	Cerro Los Quesos	Peru	Pacific	Southern	ESP
UNMSM	MUSM 2090	75.69		a1-a2	10.7	13.8	11.6	MM	Serravallian	Pisco	Cerro Los Quesos	Peru	Pacific	Southern	ESP
UNMSM	MUSM 2091	84.35		A1-A2	9.98	13.8	11.6	MM	Serravallian	Pisco	Cerro Los Quesos	Peru	Pacific	Southern	ESP
UNMSM	MUSM 2092	105.75	111.31	A1-A2	12.51	13.8	11.6	MM	Serravallian	Pisco	Cerro Los Quesos	Peru	Pacific	Southern	ESP
UNMSM	MUSM 2093	105.48	124.86	A1-A2	12.48	13.8	11.6	MM	Serravallian	Pisco	Cerro Los Quesos	Peru	Pacific	Southern	ESP
UNMSM	MUSM 2094	81.59	69.72	a1-a2	11.54			LM	Messinian	Pisco	Cerro La Bruja	Peru	Pacific	Southern	ESP
UNMSM	MUSM 2095	81.8	70.07	a1-a2	11.57			LM	Tortonian	Pisco	Yesera Amara	Peru	Pacific	Southern	ESP
UNMSM	MUSM 2096	104.34	89.6	A1-A2	12.34	14.0	12.0	MM	Serravallian	Pisco	Cerro Colorado	Peru	Pacific	Southern	ESP
UNMSM	MUSM 2097	90.18	81.02	L1-L3	12.72	14.0	12.0	MM	Serravallian	Pisco	Cerro Colorado	Peru	Pacific	Southern	ESP
UNMSM	MUSM 2098	89.08	70.25	A1-A2	10.54	14.0	12.0	MM	Serravallian	Pisco	Cerro Colorado	Peru	Pacific	Southern	ESP

UNMSM	MUSM 2099	91.22	78.85	A1-A2	10.79	14.0	12.0	MM	Serravallian	Pisco	Cerro Colorado	Peru	Pacific	Southern	ESP
UNMSM	MUSM 2100	70.02	64.52	A1-A2	8.29	14.0	12.0	MM	Serravallian	Pisco	Cerro Colorado	Peru	Pacific	Southern	ESP
UNMSM	MUSM 2101	40.21		L3-L7	14.081	14.0	12.0	MM	Serravallian	Pisco	Cerro Colorado	Peru	Pacific	Southern	ESP
UNMSM	MUSM 2102	49.14	36.84	l1-l5	14.673	14.0	12.0	MM	Serravallian	Pisco	Cerro Colorado	Peru	Pacific	Southern	ESP
UNMSM	MUSM 2103	44.67	43.14	l1-l5	13.312	14.0	12.0	MM	Serravallian	Pisco	Cerro Colorado	Peru	Pacific	Southern	ESP
UNMSM	MUSM 2105	25.47	39.36	L5-L7	11.96			LM	Tortonian	Pisco	Yesera Amara	Peru	Pacific	Southern	ESP
UNMSM	MUSM 2106	16.01	18.67	l5-l7	14.66			LM	Tortonian	Pisco	Yesera Amara	Peru	Pacific	Southern	ESP
UNMSM	MUSM 2107	114.45	116.7	A1-A2	13.53	9.23	6.87	LM	Tortonian-Messinian	Pisco	Ocucaje		Peru	Pacific	Southern
UNMSM	MUSM 2108	85.48	104.34	L1-L3	12.05	9.23	6.87	LM	Tortonian-Messinian	Pisco	Ocucaje		Peru	Pacific	Southern
UNMSM	MUSM 2109	75.94	72.57	L1-L5	13.12	9.23	6.87	LM	Tortonian-Messinian	Pisco	Ocucaje		Peru	Pacific	Southern
UNMSM	MUSM 2110	34.89	37.43	l1-l5	10.33	9.23	6.87	LM	Tortonian-Messinian	Pisco	Ocucaje		Peru	Pacific	Southern
UNMSM	MUSM 2111	75.29	71.03	L2-L4	11.49	9.23	6.87	LM	Tortonian-Messinian	Pisco	Ocucaje		Peru	Pacific	Southern
UNMSM	MUSM 2112	91.68	115.99	L2-L4	13.98	9.23	6.87	LM	Tortonian-Messinian	Pisco	Ocucaje		Peru	Pacific	Southern
UNMSM	MUSM 2113	10.02	23.77	L6-L7, l6-l7	8.13	9.23	6.87	LM	Tortonian-Messinian	Pisco	Ocucaje		Peru	Pacific	Southern
UNMSM	MUSM 634-1	80.55	93.13	A1-A2	9.53	8.7	6.45	MM	Tortonian	Pisco	Agua de las Lomas	Peru	Pacific	Southern	ESP
UNMSM	MUSM 634-2	76.81	69.77	a1-a2	10.86	8.7	6.45	MM	Tortonian	Pisco	Agua de las Lomas	Peru	Pacific	Southern	ESP
UNMSM	MUSM 634-3	88.17	68.57	A1-A2	10.43	8.7	6.45	MM	Tortonian	Pisco	Agua de las Lomas	Peru	Pacific	Southern	ESP
UNMSM	MUSM 634-4	79.82	94.07	A1-A2	9.44	8.7	6.45	MM	Tortonian	Pisco	Agua de las Lomas	Peru	Pacific	Southern	ESP
UNMSM	MUSM 634-5	59.58	54.36	L1-L5	10.3	8.7	6.45	MM	Tortonian	Pisco	Agua de las Lomas	Peru	Pacific	Southern	ESP
UNMSM	MUSM 635	96.3	114.68	A1-A2	11.39	8.7	6.45	MM	Tortonian	Pisco	Agua de las Lomas	Peru	Pacific	Southern	ESP
MNH	USNM 280567	45.52	43.93	a1-a2	6.41	13.8	11.6	MM	Serravallian	Pungo River		US East	Atlantic	Northern	WNA
MNH	USNM 295331	103.54	95.36	A1-A2	12.25	13.8	11.6	MM	Serravallian	Pungo River		US East	Atlantic	Northern	WNA
MNH	USNM 355806	67.6	79.61	l1-l3	13.9	13.8	11.6	MM	Serravallian	Pungo River		US East	Atlantic	Northern	WNA
MNH	USNM 355820	84.68	88.75	L1-L5	14.623	13.8	11.6	MM	Serravallian	Pungo River		US East	Atlantic	Northern	WNA
UNLP	76-V-14142.1	58.35		a1-a2	8.23	5.3	3.6	LM	Messinian-Zanclean	Punta del Diablo		Argentina	Atlantic	Southern	WSA

UNLP	76-V-14142.2	53.63		a1-a2	7.56	5.3	3.6	LM	Messinian-Zanclean	Punta del Diablo		Argentina	Atlantic	Southern	WSA
UNLP	86-II-10-13	84.66	89.29	l1-l2	15.57	5.3	3.6	LM	Messinian-Zanclean	Punta del Diablo		Argentina	Atlantic	Southern	WSA
UNLP	86-II-10-7410.1	66.59		a1-a2	9.41	5.3	3.6	LM	Messinian-Zanclean	Punta del Diablo		Argentina	Atlantic	Southern	WSA
UNLP	86-II-10-7410.2	65.58		A1-A2	7.76	5.3	3.6	LM	Messinian-Zanclean	Punta del Diablo		Argentina	Atlantic	Southern	WSA
UNLP	86-II-10-7410.3	72.69		A1-A2	8.6	5.3	3.6	LM	Messinian-Zanclean	Punta del Diablo		Argentina	Atlantic	Southern	WSA
UCMP	UCMP 219502	115.06	118.74	A1-A2	13.61	11.6	5.3	LM	Tortonian-Messinian	Purisima			US West	Pacific	Northern
SDNHM	SDNHM 67595	47.75	60.99	L1-L3	6.75	13.8	11.6	MM	Serravallian	Rosarito Beach	Mesa Los Indios	Mexico	Pacific	Northern	ENP
SDNHM	SDNHM 77901	17.8	25.79	L5-L7	8.23	13.8	11.6	MM	Serravallian	Rosarito Beach	Mesa Los Indios	Mexico	Pacific	Northern	ENP
UCMP	UCMP 111745	10.58	22.22	L1-L7, l1-l5	2.81	13.8	11.6	MM	Serravallian	Rosarito Beach	La Mision 1	Mexico	Pacific	Northern	ENP
LACM	LACM 131149	63.8		A1-A2	7.55	7.3	5.3	LM	Messinian	San Mateo	Lawrence Canyon	US West	Pacific	Northern	ENP
SDNHM	SDNHM 23617	65.2		L1-L5	9.15	7.3	5.3	LM	Messinian	San Mateo	Lawrence Canyon	US West	Pacific	Northern	ENP
SDNHM	SDNHM 23959	84.8	90.52	L1-L5	11.88	5.3	2.6	P	Zanclean	San Mateo	Lawrence Canyon upper gravel unit	US West	Pacific	Northern	ENP
SDNHM	SDNHM 24448	82.76		L1-L3	11.67	5.3	2.6	P	Zanclean	San Mateo	Lawrence Canyon upper gravel unit	US West	Pacific	Northern	ENP
SDNHM	SDNHM 77430	24.3	27.22	l1-l5	7.11	5.3	2.6	P	Zanclean	San Mateo	Lawrence Canyon upper gravel unit	US West	Pacific	Northern	ENP
FLMNH	UF 259902	56.03		a1-a2	7.9	5.3	3.6	P	Zanclean	Tamiami	East Coast Aggregates	US West	Atlantic	Northern	ENP
FLMNH	UF 259903	27.72	27.68	L4-L8	14.47	5.3	3.6	P	Zanclean	Tamiami	East Coast Aggregates	US West	Atlantic	Northern	ENP
FLMNH	UF 259907	30.19	35.58	A1-A2	3.58	5.3	3.6	P	Zanclean	Tamiami	East Coast Aggregates	US West	Atlantic	Northern	ENP
FLMNH	UF 259908	74.4		L1-L3	10.5	5.3	3.6	P	Zanclean	Tamiami	East Coast Aggregates	US West	Atlantic	Northern	ENP
UCMP	Acc.4311 1968	66.02	60.82	a1-a2	10.21	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
UCMP	Acc.4311.1	36.55	45.35	A1-A2	4.33	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
UCMP	Acc.4311.2	43.89		A1-A2	5.2	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM - Pathology	74.4	97.68	L1-L3	10.5	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern

LACM	LACM 10140	86.7	89.98	L1-L5	12.15	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM 10147	90.2	94.33	L1-L3	12.72	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM 10148.1	97.1	86.07	l1-l2	17.84	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM 10148.2	44.2	51.21	L4-L7	15.98	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM 10149	85.8	89.7	L1-L3	12.1	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM 115396	103.8	94.51	L1-L3	14.63	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM 123651	80.6	84.58	L1-L5	11.3	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM 129862	81.86	102.76	L1-L5	16.28	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM 129863	102.4	106.54	A1-A2	12.11	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM 133455	73.5	84.83	A1-A2	8.7	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM 149395	74	66.03	a1-a2	10.46	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM 149396	89.3	88.05	L1-L6	17.78	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM 149397	99.8	92.75	a1-a2	14.14	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM 149398	96.9		a1-a2	13.73	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM 149518	63.8	58.42	a1-a2	9.01	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM 149519	49.7	68.44	L1-L6	9.86	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM 149520	72.1	82.91	L1-L6	14.34	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM 149522	90.5		L1-L4	12.62	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM 156332	83.4	92.11	A1-A2	9.87	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM 156333	50.3	61.23	L1-L5	7.07	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM 58926	62.3	64.96	l1-l3	12.76	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM 58928	79.8	81.28	a1-a2	11.29	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
LACM	LACM 59060	63.88	65.19	L1-L3	9.02	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
SDNHM	SDNHM 99741	95.3	101.96	A1-A2	11.27	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern
SDNHM	SDNHM 99773	18.4	33.78	L6-L8	13.08	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern

SDNHM	SDNHM 99774	79.3		L1-L3	11.19	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern	
SDNHM	SDNHM 99776	110.6	108.14	A1-A2	14.56	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern	
UCMP	UCMP 190987	89.21	107.8	A1-A2	10.55	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern	
UCMP	UCMP 23876	88.94		A1-A2	10.52	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern	
UCMP	UCMP 65586	92.64	111.02	A1-A2	10.96	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern	
UCMP	UCMP 81659	98.21	101.49	A1-A2	11.62	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern	
UCMP	UCMP 81660	69.55	64.41	a1-a2	10.76	16.0	13.8	MM	Langhian	Temblor	Shark tooth Hill	Round Mountain Silt	US West	Pacific	Northern	
LACM	LACM 29065	43.5	42.86	L1-L3	6.15	5.3	2.6	P	Tortonian	Tirabuzon	Baja?		Mexico	Pacific	Northern	
LACM	LACM 29076	32.9		L1-L3	4.66	5.3	2.6	P	Tortonian	Tirabuzon	Baja?		Mexico	Pacific	Northern	
LACM	LACM 129670	67.08		L1-L3	9.47	16.0	13.8	MM	Langhian	Topanga	Cook's Corner?	US West	Pacific	Northern	ENP	
SDNHM	SDNHM 14013	102.2		A1-A2	12.09	16.0	13.8	MM	Langhian	Topanga	Cook's Corner?	US West	Pacific	Northern	ENP	
SDNHM	SDNHM 14015	43.1		L4-L7	15.58	16.0	13.8	MM	Langhian	Topanga	Cook's Corner?	US West	Pacific	Northern	ENP	
NHM	P27667	90.02	71.45	A1-A2	10.42	5.3	0.3	P	Zanclean	Wanganui			New Zealand	Pacific	Southern	
LACM	LACM 10041	43.5	46.4	l1-l5	12.96	5.3	3.6	P	Zanclean	Yorktown			US East	Atlantic	Northern	
LACM	LACM 10042	61.9	62.42	L1-L5	10.7	5.3	3.6	P	Zanclean	Yorktown			US East	Atlantic	Northern	
LACM	LACM 10043	55.1	58.24	A1-A2	6.52	5.3	3.6	P	Zanclean	Yorktown			US East	Atlantic	Northern	
LACM	LACM 10044	36.6	50.31	L3-L6	9.78	5.3	3.6	P	Zanclean	Yorktown			US East	Atlantic	Northern	
LACM	LACM 10046	31.8	42.99	L3-L6	8.47	5.3	3.6	P	Zanclean	Yorktown			US East	Atlantic	Northern	
LACM	LACM 10047	52.3	51.72	a1-a2	7.37	5.3	3.6	P	Zanclean	Yorktown			US East	Atlantic	Northern	
LACM	LACM 10049	46.6	50.19	L3-L7	16.36	5.3	3.6	P	Zanclean	Yorktown			US East	Atlantic	Northern	
LACM	LACM 10050	52.4	57.13	L1-L3	7.4	5.3	3.6	P	Zanclean	Yorktown			US East	Atlantic	Northern	
LACM	LACM 10051	59.9	57.43	a1-a2	8.45	5.3	3.6	P	Zanclean	Yorktown			US East	Atlantic	Northern	
LACM	LACM 10052	20.9	26.77	l1-l5	6.07	5.3	3.6	P	Zanclean	Yorktown			US East	Atlantic	Northern	
LACM	LACM 10053	51.9	51.66	a1-a2	7.31	5.3	3.6	P	Zanclean	Yorktown			US East	Atlantic	Northern	
LACM	LACM 10054	63.3	67.98	a1-a2	8.94	5.3	3.6	P	Zanclean	Yorktown			US East	Atlantic	Northern	
LACM	LACM 10055	59.1	72.57	L1-L3	8.35	5.3	3.6	P	Zanclean	Yorktown			US East	Atlantic	Northern	
LACM	LACM 10056	83.7	81.41	L1-L3	11.8	5.3	3.6	P	Zanclean	Yorktown			US East	Atlantic	Northern	

LACM	LACM 10057	59.9	53.5	L1-L5	10.35	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
LACM	LACM 10059	33.3	54.78	L5-L7	15.77	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
LACM	LACM 10061	33.3	50.11	L1-L7	9.63	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
LACM	LACM 10062	42.2	46.22	L1-L7	12.24	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
LACM	LACM 10063	83.7	80.03	L1-L3, l1-l3	14.49	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
LACM	LACM 10064	28.2	32.82	a1-a2	3.94	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
LACM	LACM 10066	41.3	50.57	L3-L7,l3-l7	16.16	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
LACM	LACM 10067	19.1	27.92	L5-L7	8.87	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
LACM	LACM 10068	61.5	43.82	a1-a2	8.68	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
LACM	LACM 10070	48.5	51.25	L1-L5	8.38	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
LACM	LACM 10071	41.8	41.71	A1-A2	4.95	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
LACM	LACM 11180	23.6	31.01	l3-l7	15.89	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 175642	71.14	69.93	l1-l4	17.07	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 256331	71.22	73.22	L1-L4	10.7	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 256334	61.59	65.13	L1-L3	8.7	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 279258	82.64	86.87	A1-A2	9.78	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 279259	68.46	68.55	l1-l3	14.03	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 279260	58.61	60.29	L1-L3	8.28	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 279261	58.49	72.88	l2-l4	15.24	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 279262	45.71	56.59	L1-L3	6.46	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 279267	62.65	55.56	a1-a3	9.54	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 279279	51.8	51.92	a1-l3	9.2	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 279280	51.66	50.64	l1-l2	9.52	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 279281	52.41	55.79	l1-l5	15.67	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 279282	59.06	53.56	l1-l3	12.09	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 279283	50.54	53.54	A1-A2	5.99	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 279288	50.67	51.87	A1-A2	6	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 279407	46.35	37.87	a1-a3	7.03	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern

MNH	USNM 279415	73.87	71.51	A1-A2	8.74	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 279424	56.08	60.02	A1-A2	6.64	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 279425	51.2	69.14	L1-L4	7.7	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 279432	79.26	62.96	A1-A2	9.38	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 281392	101.12	90.25	a1-a3	15.45	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 287699	54.43	49.93	l1-l3	11.14	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 287708	41.24	46.38	A1-A2	4.89	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 287709	63.35	72.84	a1-a3	9.65	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 292978	61.26	71.37	L1-L3	8.65	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 292990	51.27	50.99	a1-a2	7.22	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 293746	44.37	45.54	l1-l5	13.22	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 293748	46.7	59.3	L1-L5	8.07	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 293752	49.64	60.49	L1-L5	8.58	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 293754	49.25	50.86	a1-a2	6.94	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 293758	69.46	84.35	L1-L5	12	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 295339	73.19	67.97	l1-l3	15	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 299740	102.04	107.88	A1-A2	12.07	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 339918	84.55	96.59	a1-l1	13.39	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348165	25.6	47.44	L6-L8, l3-l6	13.91	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348166	19.69	34.55	L6-L8, l3-l6	10.56	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348168	39.51	55.37	L1-L5	6.83	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348178	42.29	56.88	l1-l5	12.59	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348265	70.22	76.04	L1-L5	12.13	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348277	81.48	91.35	L1-L5	14.07	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348278	83.24	96.42	L1-L3	11.74	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348279	76.59	79.13	l1-l2	14.09	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348280	79.02	76.78	A1-A2	9.35	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348283	75.63	65.52	l1-l3	15.51	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern

MNH	USNM 348286	72.69	78.89	L1-L5	12.56	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348305	75.11	75.52	l1-l2	13.82	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348307	74.66	67.59	l1-l3	15.31	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348308	68.75	57.91	a2-l1	11.12	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348337	80.88	86.77	L1-L3	11.41	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348375	42.76	65.06	L4-L5, l4-l5	14.07	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348381	57.2	65.97	L1-L5	9.88	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348406	64.88	71.21	L1-L3	9.16	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348410	65.41	70.44	L1-L3	9.23	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348418	57.8	63.39	L1-L5	9.99	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348420	67.6	75.71	L1-L5	11.68	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348429	55.48	53.65	a1-a3	8.44	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348431	54.23	53.98	a1-a3	8.25	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348436	63.66	56.01	a1-a3	9.7	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348445	69.94	70.64	a1-a3	10.66	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348446	67.98	69.95	L1-L5	11.74	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348448	55.71	65.52	L1-L5	9.63	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348449	63.2	71.63	L1-L5	10.92	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348450	61.3	72.22	L1-L5	10.59	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348451	58.62	67	L2-L5	10.57	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348452	63.95	76.83	L1-L3	9.03	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348453	61.68	69.91	L1-L4	9.27	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348454	65.42	71.47	L1-L5	11.3	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348455	62.68	75.97	l1-l3	12.84	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348456	66.39	67.91	A1-A2	7.86	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348457	74.14	73.72	L1-L5	12.81	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348460	61.5	67.77	A1-A2	7.28	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348461	76.6	76.31	a1-a2	10.83	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348462	73.92	81.25	l1-l3	15.15	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern

MNH	USNM 348466	53.16	62.72	l2-l5	17.53	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348471	47.65	57.34	a1-a2	6.71	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348472	70.27	81.37	l1-l4	16.86	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348512	82.61	89.83	L1-L5	14.27	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348514	68	75.91	L1-L4	10.21	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348515	74.23	72.63	L1-L5	12.82	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348516	52.4	52.7	a1-a3	7.96	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348517	72.78	74.19	l1-l3	14.92	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNm 348521	48.83	57.1	A1-A2	5.78	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348524	57.85	59.98	A1-A2	6.85	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348525	62.73	57.39	a1-a3	9.55	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348530	55.57	50.19	l1-l3	11.38	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348532	61.28	55.4	a1-a3	9.33	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348535	60.42	58.7	L1-L3	8.53	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 348540	69.64	72.44	A1-L1	6.61	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 350928	66.76	63.36	a1-a3	10.17	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 350929	62.92	69.23	L1-L3	8.88	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 350932	66.91	71.4	L1-L2	9.3	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 350935	46	65.43	L4-L5, l4-l5	15.16	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 350936	63.5	73.24	L1-L3	8.96	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 350939	67.82	73.48	a1-a3	10.33	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 350940	80.43	85.39	A2-L2	10.68	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 350941	73.22	89.42	A1-A2	8.66	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 350942	81.34	86.35	L1-L5	14.05	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 350991	79.9	81.67	a1-a3	12.19	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 350992	67.87	77.84	L1-L3	9.58	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 350993	79.69	79.13	L1-L3	11.24	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 350994	83.53	72.3	a1-a3	12.75	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 350995	84.28	83.7	A2-L1	11.1	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern

MNH	USNM 350996	71.54	97.84	L1-L5	12.36	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 350997	84.86	82.53	a1-a2	12.01	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 351100	85.93	81.07	l1-l2	15.8	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 353735	82.09	87.49	A1-A2	9.71	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 353738	82.43	83.52	A1-A2	9.75	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355714	64.71	76.76	L1-L5	11.18	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355715	77.48	79.07	A2-L1	6.8	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355716	69.37	73.64	A1-A2	8.21	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355718	78.17	81.38	L1-L5	13.5	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355726	90.02	82.6	a1-a2	12.74	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355728	65.23	87.93	L3-L5	12.74	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355736	70.04	72.66	L1-L3	9.88	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355740	71.5	72.81	L1-L5	12.35	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355742	69.56	74.32	A1-A2	8.23	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355743	68.93	83.6	L1-L4	10.35	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355746	73.15	81.26	l1-l4	17.56	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355749	76.65	90.75	l1-l3	15.72	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355752	72.04	70.83	a1-a3	10.98	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355756	66.84	75.23	A1-A2	7.91	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355760	74.88	92.57	A1-A2	8.86	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355761	72.35	84.9	L1-L4	10.86	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355763	69.28	76.37	l1-l3	14.2	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355767	72.81	82.73	L1-L3	10.27	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355772	78.56	79.41	l1-l2	14.45	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355776	75.11	88.21	L1-L3	10.6	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355777	79.52	74.8	a1-a2	11.25	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355780	76.35	83.75	a1-a3	11.65	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355781	59.02	67.71	l1-l5	17.68	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355782	65.48	76.35	A1-A2	7.75	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern

MNH	USNM 355822	102.13	116.39	A1-A2	12.08	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355854	76.16	71.91	a1-a2	10.77	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355855	75.2	77.47	a2-a3	11.47	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355858	78.71	89.19	l1-l2	14.48	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355860	73.73	79.82	A1-A2	8.72	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355864	70.49	72.84	a1-a2	9.96	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355866	83.59	89.61	L1-L4	12.55	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355870	100.65	111.25	L1-L5	17.38	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355871	90.14	92.97	A1-A2	10.66	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355872	98.78	122	A1-A2	11.68	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355874	94.67	91.52	a2-L1	15.32	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355880	89.37	88.32	l1-l2	16.43	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355885	98.89	108.59	L1-L5	17.07	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355886	87.24	106.53	A2-L1	11.49	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355887	92.12	101.25	A1-A2	10.9	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355890	82.59	79.11	a1-a3	12.6	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355894	96.62	86.05	a1-a2	13.69	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355895	69.31	86.11	A1-A2	8.2	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355904	65.41	76.64	L1-L2	9.09	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355917	60.93	70.89	a1-a3	9.28	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355928	31.56	48.49	L6-L8, l3-l6	17.29	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 355938	70.25	66.64	a1-a2	9.93	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 356968	87.25	102.49	L1-L2	12.11	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 356969	72.51	76.48	l1-l3	14.86	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 356972	68.88	87.24	L3-L5	13.45	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 356973	82.48	84.66	A1-A2	9.76	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 356975	60	58.48	l1-l3	12.29	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 356976	32.2	51.18	L6-L8, l3-l6	17.65	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern

MNH	USNM 356980	85.16	84.95	a1-a2	12.05	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 392159	66.39	71.06	a2-l2	11.24	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 392160	74.8	72.89	L1-L5	12.92	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 392161	73.56	75.79	A1-A2	8.7	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 392162	71.05	71.3	a1-a2	10.04	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 392171	57.26	57.28	l1-l4	13.7	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 482310	87.7	99.59	A1-A2	10.37	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 482311	83.95	105.59	L1-L4	12.6	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 482313	94.39	92.57	A1-A2	11.17	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 530191	77.17	87.57	L1-L4	11.59	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 530192	43.32	49.87	l3-l5	16.17	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 530606	89.46	79.39	a1-a2	12.67	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 530607	75.85	87.1	A1-A2	8.98	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 530608	64.92	72.06	A1-A2	7.68	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 531643	92.81	107.19	A1-A2	10.98	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 537789.1	54.16	69.57	L1-L5	9.36	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM 537789.2	45.53	50.28	l1-l4	10.86	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM182108	83.64	78.08	A1-A2	9.9	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
MNH	USNM293744	43.66	54.87	L5-L7	13.48	5.3	3.6	P	Zanclean	Yorktown		US East	Atlantic	Northern
SDNHM	SDNHM 86291.1	50.9	51.6	A1-A2	6.03	11.6	5.3	LM	Tortonian	Ysidro	Santa Rita	Mexico	Pacific	Northern
SDNHM	SDNHM 86291.2	37.64		L1-L5, l1-l5	8.23	11.6	5.3	LM	Tortonian	Ysidro	Santa Rita	Mexico	Pacific	Northern

Appendix 2. Values used for evolutionary models.

Sample Mean TL	Sample Variance	Sample Size	Sample Mean Age (Ma)
8.01	21.85	2	2.8
10.65	0.00	1	4.0
8.99	14.38	83	4.2
10.09	11.45	29	4.5
8.85	37.02	4	6.3
7.85	9.91	62	7.3
9.11	15.03	7	7.6
12.73	2.83	3	8.1
9.29	15.21	3	8.5
11.80	4.21	7	9.2
8.24	11.54	17	9.4
9.47	8.57	2	10.0
12.32	5.05	66	12.0
10.46	10.37	246	13.0
10.04	2.53	2	15.0
8.41	5.74	9	16.0
10.42	0.00	1	17.0

CHAPTER 4

BIG FISH EAT LITTLE FISH: THE RELATIONSHIP BETWEEN PREDATORS AND THEIR PREY IN A MARINE SYSTEM

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ABSTRACT:

Human activities, such as over-fishing, pollution, and climatic change, are increasingly stressing Earth's oceans. These anthropogenic impacts effect many levels of biotic organization, from the individual to entire ecosystems. Understanding the relationships between species in threatened systems may provide insight into how to mitigate anthropogenic impacts. Trophic relationships, as an example, describe energy-flow through ecosystems. Thus, predator-prey body size relationships reveal how energy flows through a system and potentially predict how the removal of apex predators or the removal of prey species alter energy fluxes. Previous studies have used a community-level approach to understand the scaling relationships between predators and their prey, including foraging parameters such as search time and handling time. However, examining these relationships at a broader scale could elucidate patterns in these relationships and predict mechanisms influencing the relationship between predator-prey relationships. Here, we determine the body size relationship between a group of marine apex predators and their prey using a dataset constructed from the literature. We examine ecological and evolutionary variables that influence the size of prey taken by predators. Finally, we assess if the removal of prey species that are considered moderately to highly vulnerable alter the size of prey available for predators. We find that larger sharks on average larger prey than smaller congeners. But, smaller prey items are not absent from their diet. Rather, we find that larger predators take an increased size range of prey as larger predators tend to incorporate larger prey species without removing small prey items from their diet. Bottom-dwelling species tend to take a smaller size range of prey items than species in other habitats, possibly due to reduced productivity in these

habitats. Many of the shark species consume prey at risk of extinction. If prey items that are considered most at risk of extinction are removed from predator diets, the size range of prey available is reduced by half, and this disproportionately affects larger sharks.

INTRODUCTION:

We live in the Anthropocene (Crutzen 2006): a time when human impacts are fundamentally changing the biotic world (Dirzo et al. 2014; McCauley et al. 2015). Defaunation, which includes both extinction and declines in species abundance (Dirzo et al. 2014), can result in the loss of ecosystem function through changes in nutrient cycling and transfer of energy (Boyer & Jetz 2014). Further, the defaunation occurring in the Anthropocene has been markedly size-selective, disproportionately targeting larger-bodied taxa (Lyons et al. 2004; Dirzo et al. 2014; Payne et al. 2016). These changing body-size distributions within communities may have cascading effects, altering biochemical cycles, landscape structure, and diversity (Dirzo et al. 2014; Doughty et al. 2016; Malhi et al. 2016; Smith et al. 2016). Indeed, the loss of large apex predators fundamentally alters ecosystem dynamics, a phenomenon termed trophic downgrading (Estes et al. 1998; Estes et al. 2011).

Apex consumers play a unique role in ecosystem structure. These species are generally large and mobile (Harestad & Bunnel 1979), and can be critical in the transportation of nutrients (McCauley et al. 2012; Doughty et al. 2013). The loss of the top trophic level can lead to devastating consequences for ecosystems (Estes et al. 2011). For example, the loss of large fish in the Baltic Sea led to a 20% reduction of silica production (Katz et al. 2009). Likewise, the loss of terrestrial megafauna in the Pleistocene resulted in phosphate limitation in the Amazon due to the reduction in connectivity that megafauna provided (Doughty et al. 2013).

In marine systems, the top consumer is often a shark. Currently, 62.6% of shark species are threatened globally (Dulvy et al. 2014), primarily from the unsustainable fin-trade, habitat loss, and mortality as fishing by-catch. As humans decrease the abundance of the largest individuals and species from an ecosystem, lower trophic levels are targeted by the fishing industry, a phenomenon termed "fishing down the food web" (Pauly et al. 1998). However, human activities do not solely target apex predators. Hunting and fishing at lower trophic levels affects abundance and increases competition among predators for smaller prey items (Woodward & Hildrew 2002). This may result in indirect, negative bottom-up effects on apex consumers (Cury et al. 2011; Smith et al. 2011). Therefore, understanding predator-prey relationships is the first step in unraveling the indirect impact of humans on these ecosystems.

Four different hypotheses have been proposed to describe the relationship between predators and the size of their prey. First, both maximum and minimum prey body size might increase with predator body size (Fig. 1a). This could be expected under an optimal foraging scenario, where larger predators, which have a higher absolute metabolic rate, consume larger prey and avoid smaller, less profitable prey items (MacArthur & Pianka 1966; Charnov 1976; Costa 2009). This results in an invariant range of prey sizes as predator size increases. Second, maximum prey size increases while minimum prey size decreases as predators get larger (Fig. 1b). For minimum prey size to decrease with increasing predator size, small prey items must be sufficiently abundant in the environment and/or special morphology may be needed to capture large quantities of small prey items. This results in larger animals consuming a greater size range of prey.

Third, maximum prey size increases with predator size, but no relationship is found between minimum prey size and predator size (Fig. 1c). This relationship should only be possible if small prey items are sufficiently abundant in the environment. Finally, the null hypothesis is that of no relationship between maximum and minimum prey size with predator size (Fig. 1d). This scenario appears unlikely as larger predators, with a larger gape and higher absolute metabolic rate, should forage for more valuable, larger prey items. For hypotheses (1), (2), and (3), larger prey items can be incorporated in the diet as predator gape size increases (Peters 1983; Vézina 1985; Diaz 1994). Further, hypotheses (2) and (3) suggest that sharks are more opportunistic than selective (Motta & Wilga 2001).

Previous work has yielded conflicting results about the relationship between predator and prey body size. In general, a positive relationship between maximum and mean prey size by predator size has been reported across aquatic, terrestrial, and marine taxa (Cohen et al. 1993; Carbone et al. 1999; Costa 2009), larval fish predators (Pepin & Penney 1997), and as fish body size increases through ontogeny (Scharf et al. 2000; Estrada et al. 2006; Lucifora et al. 2009). The relationship between minimum prey body size and predators, however, is not as clear. In terrestrial systems, minimum prey size increases with predator body size for both ectotherms and endotherms (Carbone et al. 2014). In contrast, marine systems show an increase in minimum prey size with increasing predator size for some marine communities (Costa 2009), but a decrease for others (Costa 2009; Carbone et al. 2014; Tucker & Rogers 2014). The range of prey size consumed has a slightly clearer relationship. In general, as predator size increases the range of prey sizes consumed also increases (Cohen et al. 1993; Scharf et al. 2000). It is thought that this relationship is generated by incorporating larger prey items faster than smaller prey items drop out (Cohen et al. 1993; Scharf et al. 2000). While this holds for some marine fish communities, the evidence is mixed for sharks (Lucifora et al. 2009; Heupel et al. 2014).

Additionally, environmental or evolutionary factors may influence the relationship between predator-prey body size. For example, more productive habitats, such as coral reefs, tend to have greater species richness and consequently more complex food webs (Abrams 1993; Pauly & Christensen 1995; Brose et al. 2006). Because these more complex food webs typically include more trophic links and a broader size spectrum of both predators and prey items (Elton 1927; Hutchinson & MacArthur 1959; Oksanen et al. 1981; Takimoto et al. 2012), predators in these habitats may be more generalist foragers (Kassen 2002). So, minimum prey size should not increase with predator size, and we would expect that the variance in prey size would increase with predator size in productive habitats but not in non-productive habitats. Furthermore, there should be a positive influence of habitat-type and depth on predator-prey body size relationships. Alternatively, it might be expected that productive habitats – with greater species richness – may promote specialization of predators (Evans et al. 2005). Predators in food-limited environments however, may be driven towards highly specialized diets to ensure successful capture of prey items when encountered; this has primarily been described in extreme environments, such as the deep-sea (Snelgrove & Smith 2002). This would lead to a positive effect on trophic level and a negative effect of habitat type on these relationships. Or, predators in food-limited environments may be generalists, taking advantage of any food source encountered (Evans et al. 2005). This would result in no relationship between prey size variance and predator size. These hypotheses for the influence of ecological variables are not mutually exclusive and are habitat-specific.

A macroecological approach for understanding body size relationships between predators and their prey may reveal pathways to extinction for large predators (Carbone et al. 2007). Much of previous studies investigating predator-prey relationships have been restricted geographically or to only discrete communities (Dickie et al. 1987; Cohen et al. 1993; Persson et al. 1996; Scharf et al. 2000; Jennings & Warr 2003; Layman et al. 2005). For the few studies that have looked across a wide range of taxa or large geographic scales, their findings are rarely applied to conservation (Etnier & Fowler 2005; Carbone et al. 2007).

Here, we characterize patterns and explore drivers of predator-prey body size relationships in marine systems. We construct a larger and more precise dataset of sharks and their prey items than previously published (Cortés 1999; Carbone et al. 2014). Specifically, we ask: (1) which, if any, metrics of prey size change with predator size? (2) Do larger predators eat larger prey than their congeners? (3) What ecological variables influence the size of prey taken by a predator? To date, only the minimum size of prey captured has been studied in sharks, and potential drivers of these relationships have yet to be tested. Our results can potentially aid in understanding the potential impact of defaunation across trophic levels in the marine system.

METHODS:

Data

We obtained data for shark species from FishBase (Froese & Pauly 2016). Shark body size ranged over two orders of magnitude from 22 cm (smalleye pygmy shark) to 2000 cm (whale shark), and spanned 33 families, 85 genera, and 237 species. We include samples across ocean basins, with 125 species from the Atlantic, 159 species from the Pacific, and 136 species from the Indian. Our coverage is global, with 60 species from the northern hemisphere, 68 in the southern hemisphere, and 135 species spanning both hemispheres. Our dataset also includes species that forage across three orders of magnitude of depth, from a maximum average depth of 2100 m to a minimum average depth of 2 m.

For each shark species, we extracted the body size data reported in FishBase (Froese & Pauly 2016). We preferentially used maximum length of males, but then used the following hierarchy if that was not available: (1) maximum length female, (2) common length male, (3) common length female. We also pulled a variety of ecological data for each shark species. Factors considered in our analysis were those hypothesized to influence prey choice. The variables examined included trophic level, habitat, and average depth of occurrence, all of which were obtained from FishBase (see ECOLOGY table for specific definitions). Lastly, to understand the potential role of relatedness between groups on these patterns, we use a shark phylogeny created by Vélez-Zuazo & Argnarsson (Vélez-Zuazo & Agnarsson 2011).

We collected data on the prey items found in shark stomachs from the literature. Often, prey item abundance per shark stomach sample as well as the total number of shark specimens collected were not reported, so diet information is aggregated by species. In total, 706 prey items (280 families, 508 genera, and 662 species) were reported for the 237 shark species. The size of prey items ranged from 0.05 cm (a small copepod) to 180 cm (a sheep). Prey taxa include a wide range of clades: cephalopods, cnidarians, ctenophores, mammals, crustaceans, various marine worms, echinoderms, mollusks, and fish. A few reported prey items were unusual. For example, a sheep was reported in the stomach of a tiger shark (*Galeocerdo cuvier*), and both coal and plastic were found in the stomach of the blackmouth catshark (*Galeus melastomus*). This suggests scavenging, although in the literature this is reportedly rare (Motta & Wilga 2001). Overall, however, terrestrial and human-made materials were seldom found.

For all prey, we obtained information on length and vulnerability status from FishBase (Froese & Pauly 2016), SeaLifeBase (Palomares & Pauly 2016), and the primary literature. When possible, maximum length was preferred over average length. For prey items that could not be identified to species, we used generic, familial, or ordinal means. We also collected vulnerability status for fish prey items from FishBase. Traits related to vulnerability account for 30% of the variation seen in threatened fish populations (Cheung et al. 2005; Strona 2014). To be considered a vulnerable prey item in our analyses, a prey must have a vulnerability status of 50/100 or greater, which translates to “moderately vulnerable”.

Analyses

For each shark species, we calculated the mean, maximum, minimum, and variance of prey size. We ran Ordinary Least Squares (OLS) regressions of these metrics against the size of the shark. Some shark species were closely related and therefore presumably share morphological structures that may limit the size of prey captured. Consequently, we also employed a phylogenetic general least squares regression (PGLS) (Felsenstein 1985). The tree used only overlaps with 217 species; we pruned the dataset to match and run these analyses. All analyses were repeated using OLS (OLS_phylo) and PGLS (PGLS_phylo) using the APE package in the computer program *R* (Paradis et al. 2004; R Team 2013) for the relationships between mean, maximum, and minimum prey size. Negative lambda values, which are not evolutionary meaningful (Swenson 2014), were excluded. Results from the OLS_phylo and PGLS_phylo regressions were compared using Akaike Information Criterion (AIC).

The influence of trophic level, habitat, and depth, on predator-prey relationships were quantified using OLS. We created a full model that included all variables and all two-way interactions. Then, we selectively excluded any variance inflation factor greater than 10, which suggests multicollinearity in the data (O'Brien 2007). We kept only the most significant variables for our final model. The final OLS_phylo model was then compared to PGLS_phylo model using AIC.

To assess biases in our data, we conducted a series of sensitivity analyses. Prey items with missing size values were replaced with the averages of either their genus or family.

Additionally, we tested if the level of prey identification influenced our results by creating nested subsets of the data at the specific, generic, familial, and ordinal level. While all slopes changed for each permutation, they changed in the same direction as the results without replacing missing values, and further none of the slopes were significantly different (Table S1).

RESULTS:

We found significant relationships between predators and the maximum and mean prey size consumed. A positive relationship between maximum prey size and shark length was recovered (slope = 0.86, df = 112, R^2 = 0.15, p-value <0.001, Fig. 3; Table 1). This relationship held even after reducing the data to include only the highest quality prey identification at the specific level (Table S1). Similarly, a positive relationship between mean prey size and shark was found (slope = 0.65, df = 112, R^2 = 0.14, p-value <0.001; Fig. 3; Table 1). This relationship was robust to biases in the data (Table S1). After including phylogenic information, we found a stronger relationship between predator and prey body size (lambda = 0.85, slope = 0.86, df = 93, R^2 = 0.75, p-value <0.001; Table 2).

Minimum prey size and shark length was not correlated (slope = -0.02, df = 112, p-value 0.94; Fig. 3; Table 1). When reducing the dataset to the lowest level of identification, no pattern with minimum prey size was recovered (Table S1). While the PGLS has a negative slope, the findings were non-significant (lambda = 0.25, slope = -0.16, df = 93, p-value = 0.62; Table 2).

As shark size increased, the size range of prey also increased (slope = 0.86, df = 78, p-value < 0.001; Fig. 3; Table 1). Correcting for phylogeny only strengthened the relationship (lambda = 0.31, slope = 1.98, df = 69, p-value < 0.001; Table 2). Moreover, the relationship was not sensitive to the level of prey item identification (Table S1).

Trophic level of the predator positively influenced the size and range of prey selected by predators. For both maximum and mean prey size of a predator, sharks with higher trophic levels consumed larger prey than other sharks at the same body size (p-value <0.001; Table 3). Prey size variance for sharks was also influenced by trophic level, where sharks with a higher trophic level consumed a wider size range of prey items (p-value = 0.001; Table 3).

We also found an influence of habitat type on predator-prey relationships. For both maximum and mean prey size of a predator we found that pelagic (open-water) predators consumed smaller prey on average (p-values <0.0001; Table 3). Interestingly, demersal sharks, which reside or feed closer to the sea-floor, consumed larger than average prey (p-value = 0.048; Table 3) and consumed a larger range of prey sizes (p-value = 0.025; Table 3).

Depth broadly affected predator-prey relationships. Shallow water (<200 m) sharks consumed a larger range of prey sizes (p-value = 0.048; Table 3) than deep water species. However, sharks that inhabit shallow waters, but were associated a benthic substrate, generally consumed a narrower size range of prey items (p-values = 0.014, 0.008, respectively; Table 3).

Interestingly, over half of the sharks in our study (129 out of 237; 54%) had at least one prey item in their diet considered vulnerable based on FishBase criteria. Many of the vulnerable fish tended to be the larger prey items in a shark's diet (Fig. 4). We computed the change in the slope of prey size variance if all moderate to highly vulnerable species went extinct. We found that the slope for prey size variance decreased from 2.1 to 1.0 – a reduction of nearly 50% (Fig. 4; Table 2). Importantly, this disproportionately affected larger sharks. Additionally, seven sharks in the dataset *only* consumed vulnerable species.

DISCUSSION:

Our findings support the third hypothesis: no relationship is found between minimum prey size and predator size (Fig. 1c). This pattern appears to arise because these marine apex predators may be opportunistic foragers, except in near-bottom habitats (Fig. 2e; Table 3). Further, larger predators eat a wider size range of prey items, which is driven by taking larger prey items than smaller predators. However, larger prey items tend to be those that are at most risk for extinction (locally or globally). In addition to humans directly contributing to shark population declines by fishing, there is another, insidious bottom-up effect of prey items potentially being removed from the food web. This affects larger sharks more than smaller sharks, and may lead to increased competition between the two size classes.

We find that larger sharks consume prey items smaller than themselves, and on average consume prey larger than smaller congeners (Fig. 2b). So, big fish eat little fish, but proportionate to their body size. These results are consistent with previous work, which has found slopes between 0.5 to 1.2 (Emerson et al. 1994; Petchey & Dunne 2012). Previously, a positive relationship has been confirmed for various marine communities (Costa 2009) and terrestrial mammals (Carbone et al. 1999; Carbone et al. 2007). Three explanations for an increase in maximum prey size are: (1) increased gape of the predator; (2) increase in metabolic rate that requires eating larger prey; (3) increased incidences of scavenging by larger predators. There is ample evidence for (1) that predators are limited by gape size (Scharf et al. 2000). However, this is not consistently true for sharks (García et al. 2008). Previous studies, too, have found that (2) metabolic rate is a major determinate of prey size in large carnivores (Carbone et al. 1999; Carbone et al. 2014). Of course, our data does not distinguish prey items that have been actively hunted from those scavenged. However, feeding studies on shark species suggest that sharks are active hunters (Motta & Wilga 2001).

The lack of relationship between minimum prey size and the size of sharks is intriguing (Fig. 1c,d; Fig. 2c; Table 1). This leads to two possible scenarios: Small prey items (e.g., zooplankton, krill) are abundant in the oceans and often clumped, making it advantageous for all sized predators to eat small prey items. Or, this relationship could be driven by a few species if the smallest (smalleye pygmy shark) and some of the largest sharks (e.g., whale shark, megamouth shark, and basking shark) specialize on small prey items. When removing the two large-bodied filter-feeding sharks, the relationship becomes positive

(Fig. S2; slope = 3.77, $R^2 = 0.18$, p-value <0.001). This suggests that a combination of body size and unique morphologies, such as filter feeding, drives the above relationship.

Given the incorporation of larger prey items, variance increases with predator size (Fig. 2e). Importantly, this is not a sampling bias of sharks (Fig. S1). That is, larger sharks are selectively taking a larger size range of prey. The increase in variance could be due to larger sharks eating within the same group (e.g., cephalopods), but incorporating larger species. The increase in variance could also be due to larger sharks being more generalist feeders. Species count data from predator diets across their range is needed to directly answer this question. Nonetheless, increased variance with body size suggests that sharks are more opportunistic than not, and are generally more catholic in their diets. Further, shark diet may be more guided by limitations in gape size rather than energetics, as found for some marine communities and terrestrial mammals (Carbone et al. 1999; Costa 2009).

Habitat, and by extension productivity, of where a predator inhabits does affect the size of prey consumed. Near bottom or bottom-dwelling animals in shallow water show a decrease in the range of prey items taken. This may be dependent on unique morphology of the shark, such as smooth-hound sharks (Genus *Mustelus*), which have plate-like teeth for crushing prey. Or, a decrease in prey size could be driven by energetics, where these areas tend to be less productive and therefore have reduced diversity (Paine 1966) and possibly a reduced range of prey sizes (Takimoto et al. 2012). So, even if a predator species is a generalist, supporting hypothesis (3), there is a smaller range of prey from which to choose.

The reliance of sharks on vulnerable prey may have conservation implications for these large marine predators. While sharks are threatened by humans due to fin-fishing, being caught as by-catch, and habitat destruction (Dulvy et al. 2014), there may be another indirect avenue by which humans are threatening sharks. Fishing down the food web (Pauly et al. 1988; Smith et al. 2011) results in many important prey species becoming less abundant. Thus, apex predators are threatened by both bottom-up and top-down effects. Interestingly, this is size-selective; the reduction of moderate to highly vulnerable prey affects larger predators more than smaller ones (Fig. 3). Human-mediated activities, such as climatic and habitat change, may push vulnerable prey species – larger-bodied species, species with small geographic ranges, etc. (Cheung et al. 2005; García et al. 2008) – to extinction. Removing these important links in the food web could cause a collapse of ecosystems.

Several factors may complicate the interpretation of our results. For example, the abundance of prey items in the diet is often not recorded. Some of the variation in our results may arise because abundance was not considered. We also lack information on the sample sizes of individual shark stomachs sampled. Thus, each documented prey item is given equal weight. Additionally, when a prey item is reported, the identification is often not verified, or is often identified to a higher taxonomic level. Researchers are often making these identifications in the field, rarely with voucher specimens or *DNA* identification. However, it should be noted that estimating body size at the generic, familial, and ordinal level, as well as reducing the dataset based on level of identification did not make a significant difference in our results (Table S1).

Our study uses a high-quality dataset of shark diet to test hypotheses about predator-prey body size relationships, test ecological and evolutionary variables that may drive them, and to identify potential human impacts. We show that shark predator-prey body size relationships are remarkably similar to patterns found in other, disparate environments. Like marine and terrestrial mammals as well as terrestrial ectotherms, we find that these large, ectothermic, marine species also show a positive relationship between maximum and mean prey size and predator size (Carbone et al. 1999; Costa et al. 2008; Tucker and Rogers 2014). Further, our results suggest that sharks may be opportunistic feeders, and that the relationship between prey and predator size are driven by morphology, trophic position, and habitat. Importantly, the vulnerability of fish is possibly another avenue to extinction for these apex predators in addition to direct human impacts.

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DATA ACCESSABILITY:

All generated data (shark length, mean prey size, maximum prey size, minimum prey size, prey size variance) as well as prey body size data are available in the supplementary materials.

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Table 1. Results for relationships shown in figures 3 and 4. We report the slope, standard error (SE), intercept, degrees of freedom (Tedford & Gustafson 1977), r-squared values, and p-values for all relationships. Significant values in bold.

Model	Prey Length (cm)	Slope	SE	Intercept	*df*	R^2	p-value
$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	All	0.80	0.06	-0.46	1049	0.13	**<0.001**
$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	Mean	0.65	0.15	0.00	112	0.14	**<0.001**
$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	Minimum	-0.02	0.24	0.79	112	0.00	0.936
$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	Maximum	0.86	0.19	-0.18	112	0.15	**<0.001**
$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	Variance	2.12	0.33	-1.88	78	0.33	**<0.001**
$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	Variance (minus vulnerable species)	1.03	0.33	0.15	33	0.20	**0.003**

Table 2. Ordinary least squares and phylogenetic generalized least squares results. These relationships use a reduced dataset that reflects the species found in the phylogenetic tree. We report the lambda values for all PGLS analyses. Additionally, we report the slope, standard error (SE), intercept, degrees of freedom (Tedford & Gustafson 1977), p-value, and Akaike Information Criterion (AIC) for all relationships. Only the OLS relationship between maximum prey size and predator size is shown as the phylogenetic analyses resulted in negative lambda values. The most supported model is in bold.

Model	**Prey Length (cm)**	**Lambda**	**Slope**	**SE**	**Intercept**	***df***	**p-value**	**AIC**
$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$, OLS	Maximum		0.71	0.21	0.21	93	0.001	
$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$, PGLS	Mean	0.85	0.85	0.21	-0.47	93	<0.001	**137.05**
$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$, OLS	Mean		0.53	0.17	0.32	93	0.002	148.44
$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$, PGLS	Minimum	0.25	-0.16	0.31	1.18	93	0.62	**241.38**
$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$, OLS	Minimum		-0.13	0.28	1.09	93	0.64	244.73
$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$, PGLS	Variance	0.31	1.98	0.37	-1.56	69	<0.001	**180.40**
$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$, OLS	Variance		1.71	0.34	-0.92	69	<0.001	182.05

Table 3. Important variables for predator-prey body size models. Reported are the significant variables only from the model of prey length versus predator length with the following variables and all two-way interactions: habitat (pelagic, reef-associated, benthopelagic), trophic level, and depth (shallow, <200 m, or deep, >200 m). Under direction, "+" means larger or wider range of prey size than average, and "-" indicates smaller or narrower range of prey size than average.

Prey Size (cm)	Model	Variable(s)	p-value	Direction
Maximum	*~ Predator Size (cm) + Trophic level + Habitat + Depth + Habitat : Depth*	*Predator Size (cm)*	<0.001	+
		Trophic level	<0.001	+
		Pelagic	<0.001	-
Mean	*~ Predator Size (cm) + Trophic level + Habitat + Depth + Habitat : Depth*	*Predator Size (cm)*	<0.001	+
		Trophic level	<0.001	+
		Demersal	0.048	+
		Pelagic	<0.001	-
Variance	*~ Predator Size (cm) + Trophic level + Depth + Habitat + Habitat : Depth*	*Predator Size (cm)*	0.002	+
		Trophic level	0.001	+
		Shallow	0.048	+
		Demersal	0.025	+
		Benthopelagic : Shallow	0.014	-
		Demersal : Shallow	0.008	-

Fig. 1. Four hypotheses for predator-prey relationships. (a) Minimum prey size increases because larger species, with higher absolute metabolic rates, selectively forage for larger prey. For all sizes of predators, the variance of prey size remains constant. This has been shown in some marine communities (Costa 2009) as well as for terrestrial ecto- and endo- therms (Carbone et al. 2014). (b) Minimum prey size decreases with increasing predator size (Carbone et al. 2014). This might arise because smaller prey, such as krill, tend to be more clumped in oceanic environments, making it energetically efficient for large predators to eat small prey. At the same time, increased gape size and energetic demands may require some larger predators to eat larger prey. (c) No relationship between minimum prey size and predator size in the marine environment; small and large predators may both be able to eat small prey since they tend to be clumped. Still, some larger predators may need to eat larger prey items. (d) No relationship between both maximum and minimum prey size with predator size.

Fig. 2. Relationships between prey size and predator size. A positive relationship exists between (a) all prey items for each shark species (slope = 0.8; df = 1049; $R^2 = 0.13$; p-value < 0.001). Dashed lines are the 99th and 1st quantile). With increasing shark body size, (b) maximum prey item size also increases, driving the predator-prey body size relationship (slope = 0.86; df = 112; $R^2 = 0.15$; p-value < 0.001). Likewise, a positive relationship exists between (c) mean prey item size for each shark species (slope = 0.65; df = 112; $R^2 = 0.14$; p-value < 0.001). No relationship is recovered between (d) minimum prey item size for each shark species (slope = -0.02; df = 112; $R^2 = 0$; p-value = 0.94). As larger predators consume larger prey sizes, the prey size variance (e)

also increases (slope = 2.12; df = 78; SE = 0.33; $R^2 = 0.33$; p-value < 0.001). Results are also reported in Table 1.

Fig. 3. Prey species that are vulnerable in shark's diet (in red). (a) Prey items (primarily fish) that are vulnerable tend to be the larger prey items. Lines represent the quantiles (99^{th} and 1^{st} are dashed lines). (b) Effects of removing prey items on the variance of prey sharks consume. Shark diets containing threatened prey species are shown in red. (c) If these prey items ultimately became extinct or severely removed from the oceans, the variance in prey size from (b) decreases by half (black vs. red line) (see Table 1).

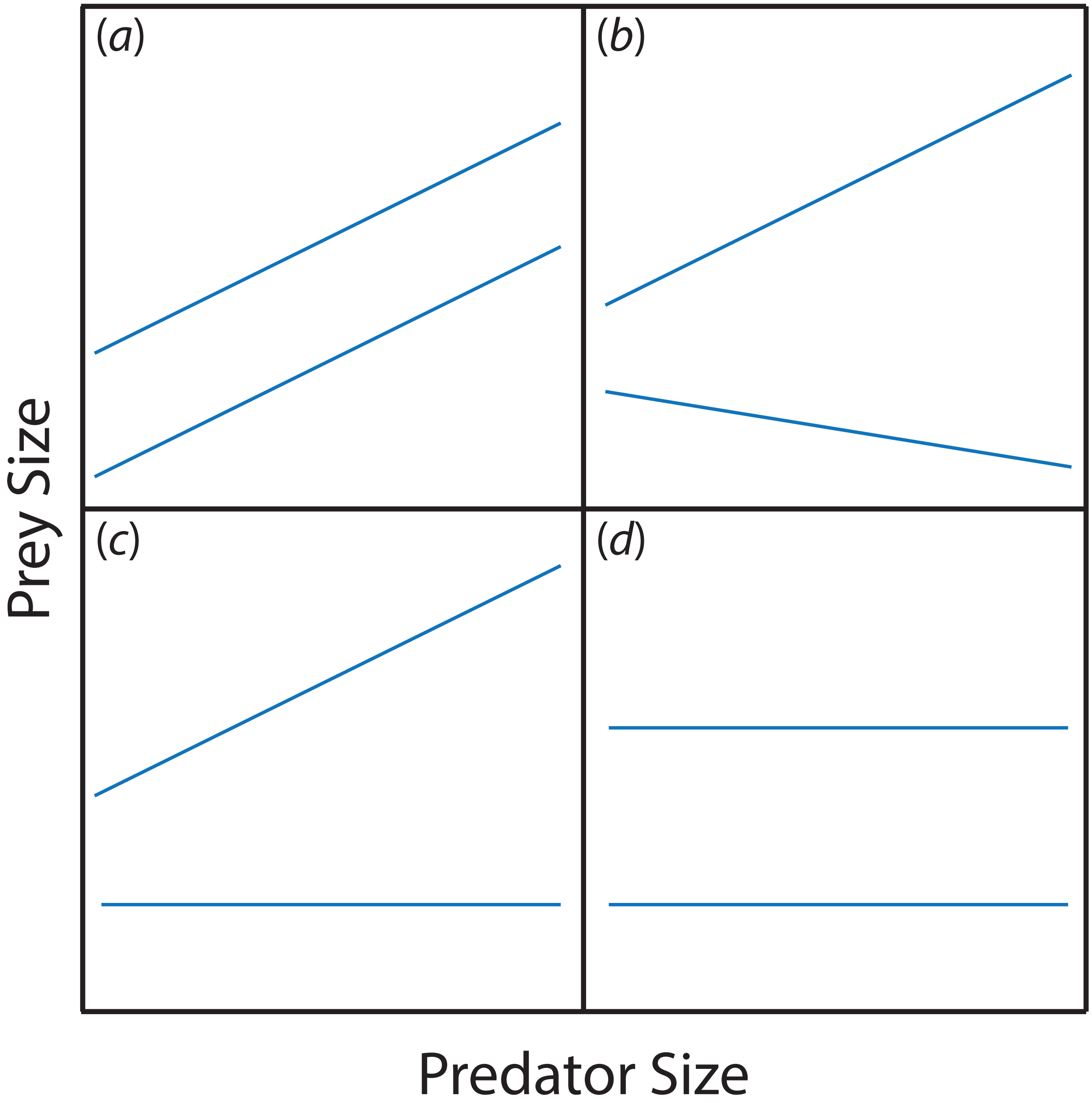


Figure 1.

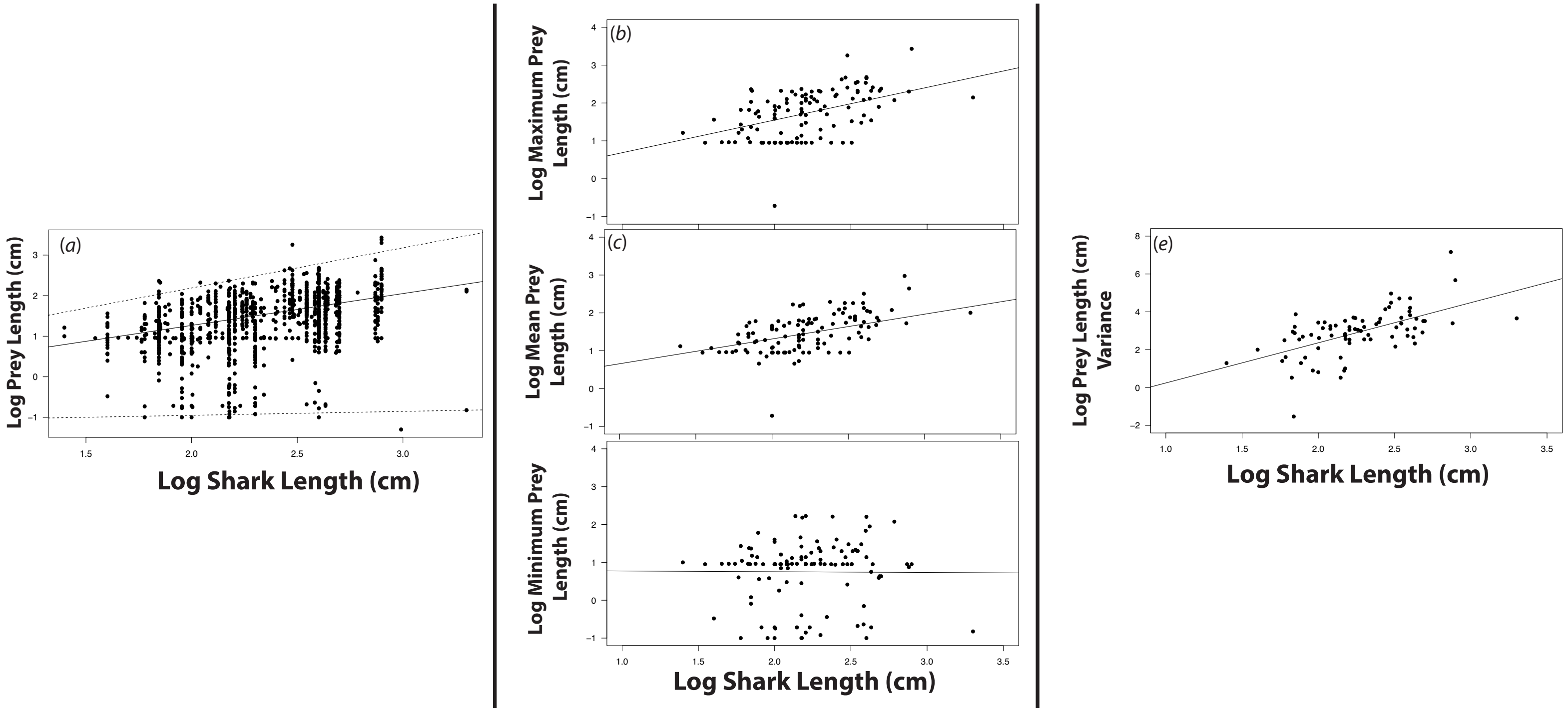

(a)
Log Prey Length (cm)
3
2
1
0
−1
1.5
2.0
2.5
3.0
Log Shark Length (cm)
(b)
Log Maximum Prey Length (cm)
4
3
2
1
0
−1
(c)
Log Mean Prey Length (cm)
4
3
2
1
0
−1
Log Minimum Prey Length (cm)
4
3
2
1
0
−1
1.0
1.5
2.0
2.5
3.0
3.5
Log Shark Length (cm)
(e)
Log Prey Length (cm) Variance
8
6
4
2
0
−2
1.0
1.5
2.0
2.5
3.0
3.5
Log Shark Length (cm)

Figure 2.

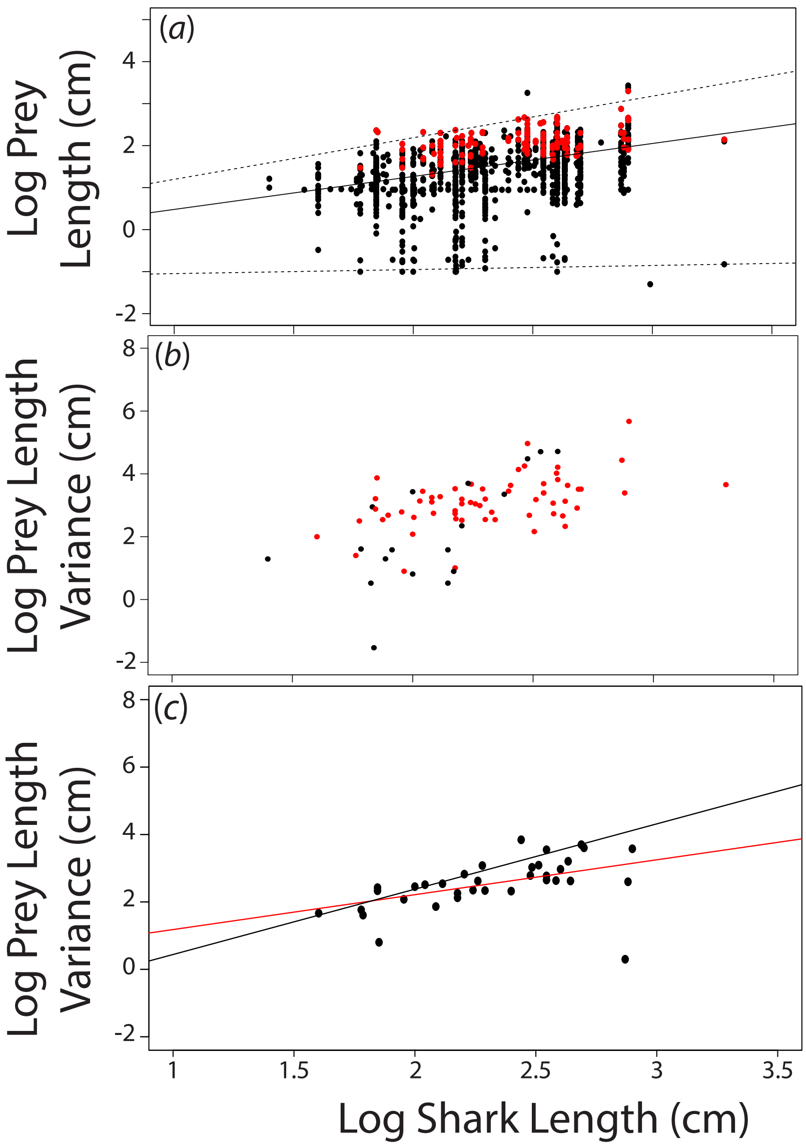
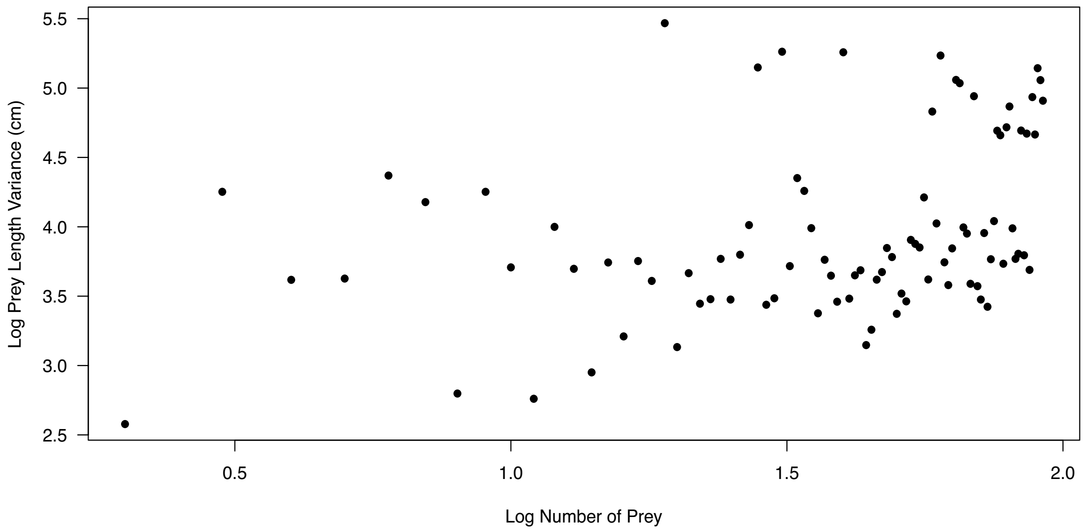

(a)
(b)
(c)
Log Prey Length (cm)
Log Prey Length Variance (cm)
Log Prey Length Variance (cm)
Log Shark Length (cm)
4
2
0
-2
8
6
4
2
0
-2
8
6
4
2
0
-2
1
1.5
2
2.5
3
3.5

Figure 3.

SUPPLEMENTAL MATERIALS

(*a*) **Randomized**



(*b*) **Observed**

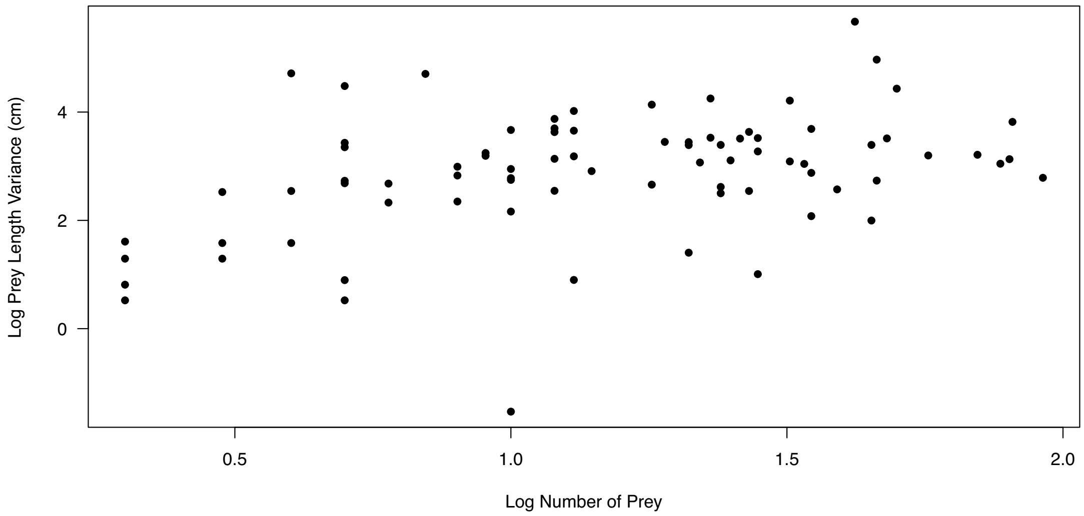


Figure S1. Relationship between sampling and increased variance. (a) Randomized variance as a function of sampling (slope = 0.59, SE = ±0.17, $R^2 = 0.11$, p-value <0.001). (b) Observed variance as a function of sampling (slope = 1.05, SE = ±0.28, $R^2 = 0.14$, p-value <0.001). Note that slopes are non-overlapping. Thus, the increase in variance is due to sharks selectively increasing variance of prey size.

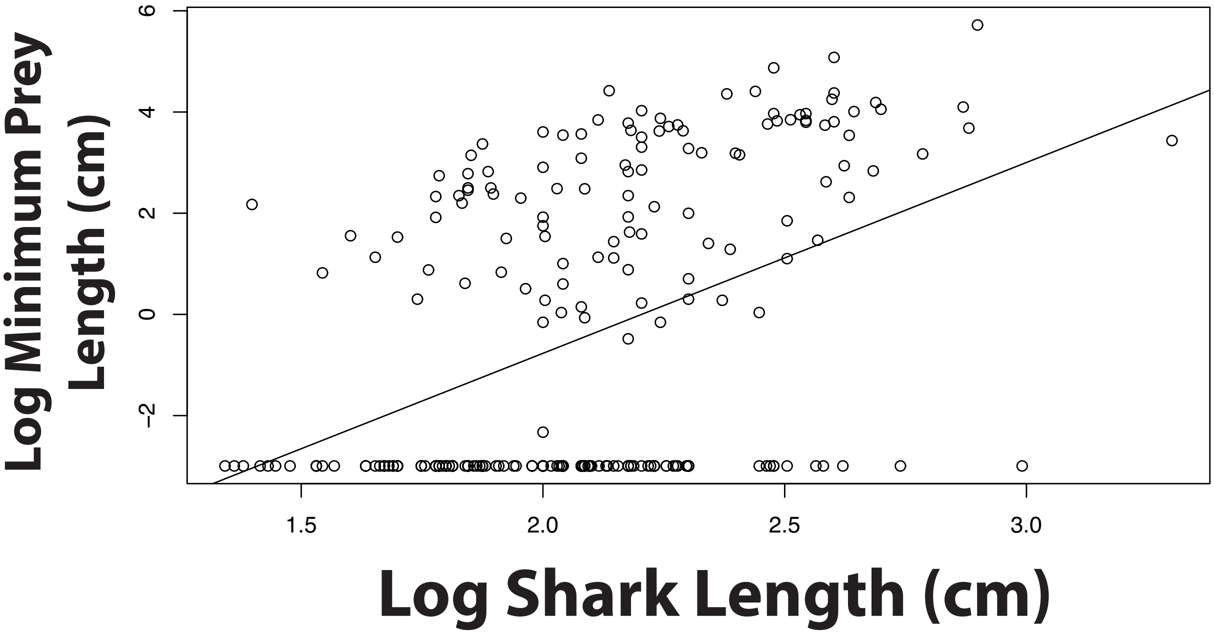


Figure S2. Predator-prey body size relationships after specialized filter feeders are removed. Minimum prey size as predator size increases is significantly different from when filter feeders are included. Minimum prey size versus predator size (slope = 3.77; $R^2 = 0.18$; p-value <0.001).

Table S1. Results for sensitivity analyses for relationships shown in Fig. 2. Different values (generic minimum, mean, and maximum size; familial minimum, mean, and maximum size) were substituted for missing data. Further, the data was subsetted based on degree of accuracy of prey identity: at the specific level; specific and generic levels; specific, generic, and familial levels; specific, generic, familial, and ordinal levels.

Plot	Subset	Equation	Slope	SE	Intercept	*df*	R^2	p-value	Bonferroni
All Prey Items	Full dataset	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	0.80	0.06	-0.46	1049	0.13	<0.001	<0.001
	Specific level	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	0.91	0.08	-0.75	735	0.14	<0.001	<0.001
	Specific & Generic levels	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	0.85	0.07	-0.58	887	0.13	<0.001	<0.001
	Specific, Generic, & Familial levels	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	0.81	0.06	-0.47	997	0.14	<0.001	<0.001
	Specific, Generic,	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	0.80	0.06	-0.45	1041	0.13	<0.001	<0.001

	Familial, & Ordinal levels								
	Full dataset	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$ *NAs = Family minimum*	0.92	0.07	-0.85	1197	0.14	<0.001	<0.001
	Full dataset	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$ *NAs = Family maximum*	0.77	0.06	-0.42	1197	0.13	<0.001	<0.001
	Full dataset	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$ *NAs = Family mean*	0.81	0.06	-0.53	1197	0.14	<0.001	<0.001
	Full dataset	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$ *NAs = Genus minimum*	0.83	0.06	-0.60	1124	0.13	<0.001	<0.001
	Full dataset	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$ *NAs = Genus maximum*	0.80	0.06	-0.49	1124	0.13	<0.001	<0.001
	Full dataset	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$ *NAs = Genus mean*	0.81	0.06	-0.52	1124	0.13	<0.001	<0.001
Mean Prey Length (cm)	Full dataset	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	0.65	0.15	0.00	112	0.14	<0.001	<0.001
	Specific level	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	0.74	0.24	-0.16	72	0.11	0.002	0.012

	Specific & Generic levels	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	0.68	0.21	-0.00	82	0.10	0.002	0.009
	Specific, Generic, & Familial levels	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	0.70	0.18	-0.05	97	0.12	<0.001	<0.001
	Specific, Generic, Familial, & Ordinal levels	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	0.65	0.15	0.01	112	0.14	<0.001	<0.001
Minimum Prey Length (cm)	Full dataset	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	-0.02	0.24	0.79	112	0.00	0.936	1
	Specific level	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	0.43	0.35	-0.33	72	0.00	0.231	1
	Specific & Generic levels	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	0.33	0.33	-0.02	82	0.00	0.322	1
	Specific, Generic, &	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	0.09	0.28	0.56	97	0.00	0.745	1

Maximum Prey Length (cm)	Familial levels								
	Full dataset	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	-0.02	0.24	0.79	112	0.00	0.936	1
	Full dataset	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	0.86	0.19	-0.18	112	0.15	<0.001	<0.001
	Specific level	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	0.82	0.28	0.01	72	0.10	0.004	0.020
	Specific & Generic levels	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	0.78	0.25	0.12	82	0.10	0.003	0.013
	Specific, Generic, & Familial levels	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	0.90	0.23	-0.20	97	0.14	<0.001	<0.001
	Full dataset	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	0.86	0.19	-0.18	112	0.15	<0.001	<0.001
Prey Length	Full dataset	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	2.12	0.33	-1.88	78	0.33	<0.001	<0.001

(cm) **Variance**	Specific level	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	1.87	0.36	-1.09	56	0.32	<0.001	<0.001
	Specific & Generic levels	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	1.75	0.32	-0.90	65	0.30	<0.001	<0.001
	Specific, Generic, & Familial levels	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	1.79	0.32	-1.04	70	0.31	<0.001	<0.001
	Full dataset	$Log_{10}Length_{PREY} \sim Log_{10}Length_{PREDATOR}$	2.14	0.33	-1.92	78	0.34	<0.001	<0.001

Table S2. Generated data (mean, minimum, maximum, and variance of prey size) for each shark species.

Binomial	Shark Length (cm)	Mean Prey Length (cm)	Minimum Prey Length (cm)	Maximum Prey Length (cm)	Prey Length Variance (cm)
Alopias pelagicus	383.0	44.0	0.2	120.0	1170.0
Alopias superciliosus	488.0	74.5	4.3	210.0	3234.7
Alopias vulpinus	760.0	53.0	7.5	200.0	2478.9
Apristurus brunneus	68.0	44.8	23.7	65.9	888.7
Asymbolus vincenti	61.0	15.5	11.0	20.0	40.5
Carcharhinus albimarginatus	300.0	132.0	8.9	255.0	30276.4
Carcharhinus amblyrhynchos	255.0	93.4	40.2	166.5	4287.0
Carcharhinus amboinensis	280.0	8.9	8.9	8.9	NA
Carcharhinus brachyurus	325.0	76.3	19.8	130.0	1520.8
Carcharhinus cautus	150.0	26.1	26.1	26.1	NA
Carcharhinus falciformis	350.0	64.4	0.2	210.0	2465.6
Carcharhinus galapagensis	370.0	30.0	30.0	30.0	NA
Carcharhinus isodon	190.0	67.7	36.0	110.0	977.2
Carcharhinus leucas	350.0	71.0	20.0	360.0	4883.5
Carcharhinus limbatus	275.0	122.8	19.8	420.0	13751.4
Carcharhinus longimanus	396.0	182.3	68.3	341.5	10488.9
Carcharhinus melanopterus	200.0	11.7	11.7	11.7	NA
Carcharhinus obscurus	420.0	113.0	89.0	130.0	457.0
Carcharhinus plumbeus	250.0	51.0	8.7	152.0	2818.9
Carcharhinus porosus	150.0	63.1	12.0	234.0	3358.5
Carcharhinus sorrah	160.0	8.9	8.9	8.9	NA
Carcharhinus tilstoni	200.0	19.8	19.8	19.8	NA
Carcharodon carcharias	792.0	442.1	8.9	2700.0	468114.0
Centrophorus granulosus	160.0	168.0	168.0	168.0	NA
Centrophorus moluccensis	100.0	45.7	8.9	82.5	2708.6
Centrophorus squamosus	160.0	59.8	9.2	115.0	1558.5
Centroscyllium fabricii	107.0	36.0	1.8	78.0	1367.9
Centroscymnus coelolepis	120.0	45.6	3.0	100.0	1277.6
Centroscymnus crepidater	130.0	9.2	9.2	9.2	NA
Cephaloscyllium isabellum	100.0	8.9	8.9	8.9	NA
Cephaloscyllium umbratile	120.0	45.5	10.7	126.6	1759.0
Cetorhinus maximus	980.0	0.1	0.1	0.1	NA

Chiloscyllium arabicum	78.0	60.6	60.6	60.6	NA
Chlamydoselachus anguineus	200.0	31.9	9.2	65.0	352.5
Dalatias licha	182.0	53.7	9.2	125.1	1106.1
Deania calcea	122.0	23.8	7.0	64.0	558.4
Deania profundorum	79.0	18.0	3.6	43.3	484.2
Echinorhinus cookei	400.0	321.0	160.0	482.0	51842.0
Etmopterus bigelowi	67.0	10.5	9.2	11.7	3.3
Etmopterus gracilispinis	35.0	8.9	8.9	8.9	NA
Etmopterus granulosus	60.0	27.0	27.0	27.0	NA
Etmopterus pusillus	50.0	9.2	9.2	9.2	NA
Etmopterus spinax	60.0	16.4	0.1	65.9	316.5
Furgaleus macki	160.0	19.5	8.9	30.0	222.1
Galeocerdo cuvier	740.0	946.9	8.9	18000.0	14534426.7
Galeorhinus galeus	195.0	70.3	23.7	210.0	3315.5
Galeus eastmani	40.0	11.7	0.3	36.3	99.7
Galeus melastomus	90.0	19.2	0.1	110.0	610.7
Galeus nipponensis	70.0	27.5	0.8	230.0	1622.5
Galeus polli	45.0	9.2	9.2	9.2	NA
Ginglymostoma cirratum	430.0	20.1	5.6	34.8	212.7
Gollum attenuatus	109.2	8.9	8.9	8.9	NA
Hemigaleus microstoma	110.0	8.9	8.9	8.9	NA
Hemipristis elongata	240.0	194.9	161.4	228.3	2240.8
Heptranchias perlo	140.0	10.5	9.2	11.7	3.3
Heterodontus mexicanus	70.0	23.2	23.2	23.2	NA
Hexanchus griseus	482.0	47.6	3.9	79.2	809.9
Holohalaelurus regani	69.0	9.0	8.9	9.2	0.0
Iago omanensis	58.0	10.0	4.0	16.3	25.3
Isogomphodon oxyrhynchus	160.0	27.2	13.7	48.1	334.9
Isurus oxyrinchus	400.0	134.1	13.7	455.0	16342.8
Lamna ditropis	305.0	54.9	30.0	76.0	477.8
Lamna nasus	350.0	81.0	20.0	193.0	2456.7
Leptocharias smithii	82.0	4.6	0.2	8.9	38.1
Mitsukurina owstoni	385.0	22.9	0.7	47.0	538.6
Mustelus antarcticus	175.0	68.8	8.9	200.0	4687.5
Mustelus canis	150.0	5.3	2.8	8.9	10.2
Mustelus fasciatus	150.0	22.4	0.4	69.0	672.3
Mustelus griseus	101.0	12.3	0.2	65.0	413.7
Mustelus lenticulatus	151.0	12.3	0.1	58.0	372.3
Mustelus manazo	220.0	15.5	0.4	50.0	349.9
Mustelus mustelus	200.0	15.5	0.1	200.0	1576.1

Mustelus palumbes	120.0	8.9	8.9	8.9	NA
Mustelus schmitti	92.0	7.0	3.8	8.9	8.0
Nasolamia velox	150.0	13.7	13.7	13.7	NA
Nebrius ferrugineus	320.0	21.1	8.9	33.0	145.4
Negaprion brevirostris	340.0	180.8	21.5	340.0	50721.1
Notorynchus cepedianus	300.0	182.3	2.6	1800.0	92750.0
Orectolobus maculatus	320.0	8.9	8.9	8.9	NA
Paragaleus pectoralis	140.0	4.6	0.2	8.9	38.1
Parmaturus xaniurus	55.0	9.2	9.2	9.2	NA
Poroderma africanum	101.0	8.9	8.9	8.9	NA
Poroderma pantherinum	84.0	8.9	8.9	8.9	NA
Prionace glauca	400.0	57.7	0.1	458.0	6574.5
Pristiophorus cirratus	137.0	166.5	166.5	166.5	NA
Rhincodon typus	2000.0	100.7	0.2	140.0	4524.7
Rhizoprionodon acutus	175.0	8.9	8.9	8.9	NA
Rhizoprionodon lalandii	77.0	16.8	13.7	20.0	19.6
Rhizoprionodon porosus	110.0	16.1	16.1	16.1	NA
Schroederichthys bivius	70.0	28.4	1.2	107.5	756.4
Scoliodon laticaudus	100.0	40.0	40.0	40.0	NA
Scyliorhinus canicula	100.0	11.9	0.1	50.0	119.6
Scyliorhinus capensis	122.0	8.9	8.9	8.9	NA
Scyliorhinus stellaris	170.0	50.1	0.2	100.0	4980.8
Somniosus microcephalus	291.5	99.2	13.7	470.0	17774.7
Somniosus pacificus	440.0	106.3	8.9	258.0	4296.9
Sphyrna lewini	430.0	42.3	0.2	210.0	1348.5
Sphyrna mokarran	610.0	119.0	119.0	119.0	NA
Sphyrna tudes	148.0	47.7	45.7	49.7	7.9
Sphyrna zygaena	500.0	62.7	4.3	239.0	3257.8
Squaliolus laticaudus	25.0	13.1	10.0	16.3	19.6
Squalus acanthias	160.0	35.1	0.1	130.0	1113.1
Squalus blainville	100.0	0.2	0.2	0.2	NA
Squalus megalops	71.0	55.5	15.0	210.0	7459.3
Squalus melanurus	75.0	29.1	9.2	52.9	348.4
Squalus mitsukurii	110.0	60.5	7.0	210.0	2786.0
Squatina dumeril	152.0	152.0	152.0	152.0	NA
Squatina guggenheim	130.0	54.5	13.0	200.0	1878.7
Squatina squatina	244.0	25.0	25.0	25.0	NA
Squatina tergocellata	100.0	36.8	35.0	38.6	6.5
Stegostoma fasciatum	235.0	8.9	8.9	8.9	NA
Triaenodon obesus	213.0	40.6	8.9	81.4	601.9

Triakis megalopterus	174.0	54.4	18.0	145.0	1227.4
Triakis scyllium	150.0	18.4	0.1	100.0	544.5