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Encephalization in Commensal Raccoons: A Unique Test of the Cognitive Buffer Hypothesis

Peter M. Anderson
East Tennessee State University

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Encephalization in Commensal Raccoons: A Unique Test of the Cognitive Buffer Hypothesis

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by
Peter Anderson
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Steven C. Wallace, Chair
Christopher Widga
Timothy Andrew Joyner

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ABSTRACT

Encephalization in Commensal Raccoons: A Unique Test of the Cognitive Buffer Hypothesis

by

Peter Anderson

This study investigated selective pressures associated with encephalization in mammals and discussed broader implications. Relative brain size as measured by EQ (Encephalization Quotient) was compared between ecological categories. Omnivores had higher average EQ than ecological specialists. Since specialists are disproportionately affected by extinction events, selection for ecological generalism is proposed as encephalization mechanism. This mechanism may reinforce the more widely known Cognitive Buffer Hypothesis (CBH)—the idea that possessing relatively large brains has buffered lineages against environmental change. CBH is tested here by comparing EQs in *Procyon lotor* (raccoon) in urban and rural environments. CBH predicts that raccoons in the most radically altered environment, the city, experience the strongest selection for encephalization. Urban raccoons studied here exhibit a higher EQ. Although results are preliminary, data suggest that encephalization is accelerated during abrupt periods of environmental change. Finally, implications for the evolution of biological complexity more generally are discussed.

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CHAPTER 1

INTRODUCTION

Fitness and Complexity

Biological evolution is a conspicuous phenomenon in an otherwise chaotic, lifeless universe. The bewildering diversity of organisms on Earth were born right out of its lifeless rocks and oceans (Pleyer et al. 2018). This story of evolution contextualizes the human condition—we as researchers are trying to understand it, but we are also active participants. Inherent in natural selection (by definition) is increasing reproductive efficiency (Darwin 1859), but another product of natural selection—complexity—is not so self-evidently consequential. In other words, the process by which natural selection produces fitness is well understood; yet the process by which it produces complexity is currently far more obscure (Hazen et al. 2007).

Life on Earth has undoubtedly increased in complexity over the course of evolution (Bogonovich 2011). Simple nucleic acids gave rise to chemically sophisticated replicating single cells (Erhan 1977), which gave rise to multicellular organisms (Donoghue and Antcliffe 2010), which gave rise to such impressive problem solvers as octopuses and humans; the latter of which gave rise to technological advancement, a new player in the story that is unbeholden to the usual constraints of biological evolution. Of course, not all lineages have undergone complexification to the same degree and are doing just fine—bacteria outnumber eukaryotes by a wide margin, after all. Still, even such “simple” life forms are descended from organisms that are simpler still. Prokaryotic complexity evolved relatively early in life’s history—but still resulted in cells that rely on an intricate chemical symphony to survive and replicate. Only after an endosymbiotic breakthrough (Knoll 2000), at the inception of the eukaryotic lineage, could those lineages begin to reach a new threshold of complexity, gradually layering new kinds of emerging composite structures (such as tissues and organs) into this increasingly impressive suite of interdependencies that allow multicellular organisms to survive and thrive. This evolutionary trajectory toward ever-more complex varieties is a conspicuous pattern, and one that I think deserves more serious scientific scrutiny than it currently receives.

Before proceeding any further, let me dispel any potential misunderstandings that may arise if this language elicits the idea of an evolutionary “goal.” Evolution does not have goals; it is merely a consequence of competing replicators. When Charles Darwin (1859) defined the fours tenets of natural selection, he did not describe fitness as a “goal”, but as a *consequence* of those tenets. There was no *mind* that guided organisms toward fitness—there was variation, competition, overproduction, and differential reproductive success. In the same vein, this thesis is intended to posit the possibility that complexity, like fitness, is a *consequence* of some as yet uncharacterized features of competing lineages on a broad scale. Please keep that distinction in mind going forward.

So why would life become more complex? Was Earth’s production of such organisms contingent upon a huge number of accidents and coincidences or was it a predictable consequence of competing replicators? In other words, how delicately does Earth-life complexity in its current form—with neurons and muscles, segmentation and regional differentiation, organ systems and eusocial colonies—hinge on a specific set of sequential evolutionary events? Would even the slightest deviation from that sequence result in a landscape devoid of complex multicellular organisms, instead occupied only by bacteria, or protists, or perhaps some manifestation of complexity that would escape even the vaguest biological categorization? Or, would such deviations only change the “players” at any given time, but still result in similar levels of complexity? Answers to such questions potentially have significance to our place in the immense, bizarre universe we inhabit. The question of what has led to the development of such remarkable complexity on Earth may influence discussions of complex life's rarity or commonality throughout the universe. That is not to say that contingency vs. direct selection for features associated with complexity is perfectly straightforward or that it can provide definitive answers to those grand philosophical inquiries, but it is a question worth asking, and an interesting puzzle.

Complexity itself cannot be the subject of natural selection; it is an abstraction, a meaningful abstraction, but an abstraction nonetheless. One could imagine a scenario in which humans selectively breed, say, a fern based on the complexity of its leaf-branching patters, but nature does not discriminate based on such abstractions. In determining fitness, nature is only concerned with how well an organism propagates itself. What I will be arguing in this thesis is that there are characteristics *associated with* complexity that can be subject to direct selection, and that long-term selection for those characteristics has been an important factor in the development of complex life. I will provide some preliminary data that is supportive of this selective process. However, an important question needs to be addressed first: how can one possibly measure and meaningfully compare complexity?

To approach this topic, I will focus on one of the many realms of biological complexity—neural complexity. Nervous systems allow organisms to interact intimately and immediately with a complex, chaotic environment. Evolution of complex brains is the subject of much evolutionary debate and speculation, likely because the evolution of complex brains so completely captures (and contains) our imaginations, and allows these discussions in the first place. I chose to focus on the evolution of the brain as a proxy for increasing complexity because of the brain's appeal to popular interest, and also because the brain is tangible, leaves fossil evidence, and can be measured.

Relative brain size—that is, brain mass relative to body mass—can indicate the degree to which an animal devotes its metabolic resources for behavioral, cognitive, or perceptive capacity (Sol et al. 2007). Animals with larger brains are generally able to exhibit more complex behavior, and hence more successfully map out and predict the environment and respond accordingly. Relative brain size is imperfect, but is often used to approximate and compare cognitive sophistication within and between species. Furthermore, it is easy to measure, and in many cases, it leaves fossil evidence (Finarelli 2011).

Thesis Statement

This thesis will present preliminary statistical support for a simple mechanism for encephalization. My argument that this mechanism exists is contingent upon two fundamental premises:

1. Ecologically specialized animals are generally more susceptible to extinction than ecologically generalistic animals when the environment changes.
2. Ecologically specialized animals are generally less encephalized (and more behaviorally simplistic) than ecologically generalistic animals.

My argument is also contingent on at least two assumptions:

1. Raccoons represent mammals in general.
2. Mammals are good representatives for vertebrates in general.

I will argue that from these premises, encephalization is a predictable result—since environmental changes favor more encephalized, generalist animals, whose descendants radiate into the newly empty niches and raise the bar, so to speak, in the evolutionary brains race.

Experimental Approach

First premise is already well substantiated in the current literature (Abramson et al. 2011). The second, surprisingly, has barely been explored. Several papers have indicated that generalistic birds are more encephalized than specialized birds (Shultz et al. 2005; Sol et al. 2005; Overington et al. 2011), but the same cannot be said for mammals. The first major portion of this thesis will seek to characterize relative brain size based on ecological specialization in mammals to evaluate the second premise of this mechanism for encephalization.

Second major portion of this thesis will seek to observe this mechanism in action, utilizing the abrupt shift of today's biogeographic landscape—altered in large part by anthropogenic sources. In the novel environment of human cities, we may observe commensals adapting rapidly. Raccoons are an ideal species to test such predictions, because urban raccoons tend to remain in cities as genetically distinct populations (Prange et al. 2003), so control and experimental groups are straightforward and easy to define. Control group is comprised of the forest dwellers whose environment closely resembles that of their more distant ancestors, and the experimental group includes the city dwellers, whose environment is radically different.

This thesis is only an introduction to the idea that abrupt environmental change disproportionately selects for more highly encephalized generalists. With limitations in data and experimental design inherent in a two-year process, definitive support or refutation of this evolutionary mechanism is only preliminary. I do, however, hope to lay a solid framework for future research in this area. I also hope to make a compelling argument that this mechanism has been an important factor in encephalization, and further, that it may reflect a deeper evolutionary principal that applies to other aspects in the evolution of complexity. For instance, perhaps metabolically flexible (and therefore chemically more complex) prokaryotes were similarly buffered against environmental change, eventually culminating in some possessing enough biochemical complexity to transcend the confines of the prokaryotic paradigm.

CHAPTER 2

LITERATURE REVIEW

Ultimately, this thesis boils down to two empirical studies looking at encephalization patterns. First, I sought to characterize encephalization in multiple mammalian species based on ecological characteristics. Second, I sought to characterize encephalization in a single species (*Procyon lotor*) based on proximity to cities. Both of these studies were aimed at testing predictions of broad evolutionary patterns of encephalization and increasing biological complexity. I intended for my thesis to be an important part of a much larger scientific puzzle. As such, this literature review will reflect that process—it will begin discussing literature relevant to that larger scientific puzzle and will then begin to "zoom in" toward literature dealing more with the concrete details relevant to my limited empirical studies. Thus, this chapter will be a bit more theoretical than Chapters 3 and 4 (which will describe experiments and will be intended for different publications).

Astrobiology

We are not the first to wonder about the existence of life beyond Earth. The question of whether we are alone in the universe is not new, but with emerging technologies we are in a unique position now to ask and answer questions relating to the existence of extraterrestrial life or lack thereof. Combining physics, chemistry, biology, geology, and astronomy, the emerging interdisciplinary field of astrobiology seeks to answer questions about the emergence of life on Earth and the likelihood of its emergence elsewhere (Marais 1999). Although perspectives vary wildly in terms of hypothesized answers to this question, most astrobiologists who have written about the discipline would agree that the discovery of habitable exoplanets in the 1990s has made the search more optimistic (Dominik and Zarnecki 2011; Drake 2011; Cady 2014). Since that first discovery, more than 4,000 exoplanets have been confirmed and 30 have been confirmed to be rocky planets similar in size to Earth with orbital distances that permit the existence of liquid water (Brennan 2019).

Western civilization has a history of anthropocentricism, wherein mankind is the final product of an omnipotent God's creation or that the sun and the stars revolve around the Earth. In many cases, subsequent science has overturned those assumptions, reducing our position in the universe from undisputed center of everything to impossibly small and fragile stowaways. What the discovery of Extra-Terrestrial Intelligence (ETI) would mean for anthropocentrism is unclear. One perspective from Steven J. Dick (1996, p. 137) is that the belief in ETI is a non-anthropocentric worldview, where life on Earth is a small subset of what he calls the "biophysical cosmology". In his words, if ETI is discovered, "the debate so far [of Mankind's significance] will have been a minor prelude."

On the other hand, some advocate just the opposite, that the "cosmic imperative," the tendency for the universe to bring about intelligent life, hints that life itself is the inevitable incarnation of some grand design (Christian De Duve 2011). Because of this philosophical argument, some theologians have begun to reinterpret their scriptures (O'Meara 2014) in terms of mankind as just one of God's "children" so to speak, and some have even gone so far as to suggest that, for instance, each life-bearing planet should host a unique incarnation of Jesus Christ (Peters 2011). Still others suggest that even if the laws of physics are fine-tuned to bring about intelligent life, the existence of infinite universes with varying laws of physics guarantees that at least some of them will happen to have the right laws to bring about living things, and so the conditions of our universe aren't actually so inconceivably unlikely (Greene 2011).

Existence of multiple universes may forever be outside the scope of empirical science, but the essence of its argument mirrors the often-cited argument for the existence of ETI within this universe—that the vastness of space and sheer number of possible habitable worlds guarantees the repeated development of ETI, even if that development is fleetingly unlikely (Mash 1993). This appeal to big numbers is a common argument for the existence of ETI, and is referred to as the “Brute Force Argument” (Mash 1993, p. 205). One version of this argument proposed by Lucretius (1951) depends on one possible cosmic arrangement of our universe—one that is truly infinite (as yet, cosmologists have not reached a consensus on the margins of the universe). This “Lucretian Style Brute Force Argument” is characterized by Mash (1993) as any possibility, no matter how fleetingly unlikely, is guaranteed in an infinite set—flipping a coin and it coming up heads 2^{100} times in a row will happen eventually if you keep flipping forever.

Lucretian Style Brute Force argument is seductive. Mere existence of intelligent life on Earth indicates that such is a possible configuration of matter and energy, and therefore has a finite possibility and is bound to occur and recur in an infinite universe. The universe may not actually be infinite, however, and although trillions upon trillions of stars that we observe seem infinite, the difference between 100 trillion and infinity is unimaginable, and therefore the *probability* of life’s emergence genuinely matters. Whether the probability of a planet developing is low, very low, or infinitesimally low could mean the difference between a universe teeming with civilizations and one in which the development of microbes is one-of-a-kind.

Probability of intelligent life’s emergence is commonly discussed in terms of the Drake Equation, which calculates the number of technological civilizations in the Milky Way as a function of individual probabilities, each necessary for intelligent life’s emergence (Marais 1999; Dick 2006; Bogonovich 2011; Davies 2011). Versatility of the Drake Equation is highlighted by

Roy Mash (1993), who ascribes to the equation a bipartisan utility—arguers on both sides of the debate reference the equation. He points out that the higher the number one starts out with, the more likely some will be left over when the other fractions have reduced the number—buttressing the Lucretian Style Brute Force Argument. Additionally, according to Mash (1993), the Drake Equation divides the issue into manageable chunks. Usefulness of isolating factors for different disciplines is critical for the ability of such a multi-faceted subject to be scientifically evaluated in a meaningful way, for many of the astronomical variables, in the words of C. de Duve, “are not for the biologist to judge” (2011, p. 623).

Then which variables *are* for the biologist to judge? Most clearly, f_l, the fraction of suitable planets on which life actually appears, and f_i, the fraction of life bearing planets on which intelligent life evolves, exist within the realm of biological inquiry, albeit with implicit assumptions about the ability to extrapolate themes of biology on Earth to the universe at large. To make such extrapolations, argues Mash, depends on “the assumption of [Earth’s] mediocrity” (1993, p. 213)

Assessment of Earth’s Mediocrity

A few authors have argued that making this assumption is not completely unfounded. As summarized in “Astrobiology: A New Frontier for 21st Century Paleontologists,” Sherry L. Cady (1988) notes a common argument in favor of some degree of mediocrity in the initial formation of life on Earth—namely that it appears to have formed very quickly, geologically speaking, within 200-300 million years after the Earth had stabilized from its tumultuous formation (De Duve 1995). There exists evidence of life on Earth as early as 3.45 billion years ago (Schopf 1992), and this was presumably preceded by a least common ancestor (LCA) that existed long before (De Duve 2011). Experimental synthesis of amino acids from inorganic reactants in the

Stanley Miller experiment proved that the building blocks of life, at least, can form under "mediocre" environmental conditions, and further, those building blocks have been found in exogenous space debris that has fallen to Earth (Glavin et al. 2010). Furthermore, the relative chemical makeup of living things on Earth is reflective of the relative chemical makeup of matter detected in space, and so the ingredients of life appear to be relatively common and ubiquitous throughout the cosmos (De Duve 2011).

Other authors have argued that some of Earth's characteristics are quite unique and therefore the assumption of Earth's mediocrity is unfounded. For one, these scientists argue, Earth is in orbit around an atypical star system called a K-dwarf star, which is a much rarer star type than the far more common G-dwarf stars that make up the majority of stars in the universe; according to Hagg-Misra et al. (2018), the evolution of "conscious observers" hinges on the presence of heavier elements more common in K-dwarf systems (Haqq-Misra et al. 2018). Other characteristics that potentially undermine the assumption of Earth's mediocrity include the unusually large and stabilizing moon orbiting the Earth, which may not only be unique in the solar system but quite rare throughout the universe (Redd 2011). Additionally, the existence and position of Jupiter, a rather large and epiphyseal gas giant that attracts otherwise-threatening asteroids, is unique (Morbidelli et al. 2005). Earth also has an unusually circular orbit—less than five percent of discovered exoplanets have eccentricities equal to or less than Earth's (Smith 2017).

At its core, life is the consequence of a process in which complex organic molecules replicate themselves and natural selection begins to refine them, and its initiation is hypothesized by some chemists to have been triggered by an autocatalytic feedback mechanism in marine hydrothermal vents (Wachtershauser 2006). Those two steps: 1. the chemistry *leading to* replicating molecules and 2. Selection *on them* are formally distinguished Christian de Duve in "Life as a Cosmic Imperative" (2011). The verdict may still be out on the precise probability of this autocatalytic feedback mechanism initiating elsewhere, but in the current literature, it would seem that a significant proportion of biologists expect that—because of its relatively immediacy of development on Earth, the commonality of its ingredients, and the conceivability of its chemical ancestry—this first biological variable of the Drake Equation, f_l, has a value not especially close to zero, and there must therefore be millions of planets on which simple life takes its roots. Although there are critics (Mash 1993; Smith 2017), who argue for instance that the evolution of DNA must have itself depended on "many fortuitous accidents" (Smith 2017, p. 326) even they concede that simple life is likely enough to occur in appreciable numbers throughout the cosmos. The main skepticism revolves around the evolution of those simple precursors into complex, intelligent life.

A few authors have argued that simple life is common, but that complex life is rare. One such interpretation is laid out in Ward and Brownlee's book *Rare Earth: Why Complex Life is Uncommon in the Universe* (Ward et al. 2000). Their argument revolves around the principal of contingency—the precise sequence of events that led to the current complexity of Earth's ecosystems is so unique that they are unlikely to occur more than once (Knoll 2000; Bogonovich 2011; Jablonski 2017). This argument is reflected in Gould's tape analogy—if we were to rewind the tape of Earth's history and replay it, a completely different sequence of evolutionary events would transpire (Gould 1989). Implicit in this sort of argument is the assumption that the precise sequence of evolutionary events that took place on Earth is *required* to bring about complex life forms. Surely, the evolution of *humanity* is contingent on an infinite number of coincidences, but that is to imply that the evolution of humanity is the only possible incarnation of complexity that qualifies as intelligent. If we were to replay Gould's tape again, we would no doubt see a different evolutionary story, but would the reiterated evolution of complexity result in anything remotely familiar?

Whether the pattern of evolving complexity on Earth's ecosystems can be generalized as an inherent property of "biophysical cosmology" or is merely an accident of contingency is hotly disputed. A review by Andrew Knoll entitled "Directionality in the History of Life: Diffusion from the Left Wall or Repeated Scaling of the Right" (2000) critically evaluated perspectives on this debate and serves as a useful analysis in addressing this question. I find his analysis to be especially informative, so the remainder of this section will focus on his article.

As in the "steps" that were thought to have led from chemical precursors to the first metabolically active cells, biologists have similarly delineated the complexification of life on Earth in a series of steps, or as Andrew Knoll referred to them, "megatrajectories" (2000, p. 2). Each megatrajectory refers to a major evolutionary step that was required for life to achieve its current state of complexity, and in order for life to transcend one megatrajectory into the next, a major biological restructuring, whether metabolic or physiological, was required in order to increase the ecospace available for exploitation.

Knoll (2000) named three authors before him to highlight a continuum of interpretation for the increasing complexity of life: Christian de Duve (2011) asserted that this pattern is deterministic, and that active selection will invariably bring about complexity. On the opposite side of the spectrum is Steven Jay Gould, who argued for the concept of "evolutionary diffusion" away from a static "left wall" of minimal complexity and size. This left wall of minimum size and complexity occurs at the starting point of a "megatrajectory," and only because of undirectional diffusion of variance does life move away from the left wall, simply because there is nowhere else for it to go, much like the diffusion of a gas moving away from its starting point. The last author Knoll chose to illustrate the continuum was Geerat Vermeij (1999). Vermeij agreed (1999) with some of Gould's interpretations about bounding left walls and "diffusive evolution," but also saw room for directionality. In the views of Vermeij, Gould was correct to identify bounding left walls, but should also include bounding right walls, which can only be surmounted by new Superkingdoms of organisms such as Eukaryotes and multicellular organisms.

Knoll, in the rest of that paper, went on to elaborate and expand upon each of the six megatrajectories. A theme he observed is that in each, diffusive evolution creates variants that can take advantage of a new realm of ecospace, but once those variants exist, directional selection quickly improves their efficiency in exploiting it, until they reach a bounding right wall defined by metabolic and physiological constraints. The maximum complexity may exist at the right wall for a long period of time, until a restructuring allows a lineage to overcome those constraints. For instance, single celled eukaryotes are limited in size and complexity by the need for a limited surface area to volume ratio, but the advent of multicellularity allowed them to increase in size by adding more cells and increase in complexity by specializing cells for different purposes. Since multiple cells being identical is likely to be the left wall condition for the "aquatic multicellularity" megatrajectory, any variation to this pattern would bring about differentiation of cells, a diffusive process. After this differentiation exists, directional selection takes over as the dominant force, until cell specialization becomes pronounced and efficient.

Whether the evolution of complexity occurs diffusively or is driven by selection has implications for the predictability with which it will occur elsewhere. If evolutionary diffusion is the predominant factor in complexification, then the complexity of Earth's ecosystems may more precariously hinge on the principal of contingency. On the other hand, if active selection is the predominant factor, then complexity should be a more predictable outcome. The difference in these interpretations means a differing value for the f_i variable: its relative position between 0 and 1.

Much research has been devoted to the study of human and primate intelligence (e.g., Leonard 1975; Iriki and Sakura 2008; Soligo 2013; Kamilar and Baden 2014). Marc Bogonovich described this field as the study of the “human intelligence phenomenon” (2011, p. 113). The other subdiscipline of intelligence research is focused on the evolution of intelligence in the whole of the animal kingdom, which he deemed the “broad-sense intelligence phenomenon” (2011, p. 114). He asserted that although people tend to be more interested in the human intelligence phenomenon, the f_i component of the Drake equation revolves around broad-sense intelligence. Much like the observed steady and consistent increase in complexity outlined in Vermeij’s megatrajectories, Russell (1983) demonstrated a steady, positive correlation between the log of the maximum encephalization quotient and time over the last 542 million years.

Once again, this pattern is clear, but as was the case for complexity in general, “the interpretation of this pattern has proven contentious” (Knoll 2000, p. 1). Was this increase observed by Russell due to diffusive or directional evolutionary forces? Bogonovich (2011) suggested that the statistical probability of a diffusive or directional model is testable, and he simulated a stochastic scenario in which diffusion was the sole force. Encephalization should still occur, since random iterations move this measure of complexity away from the left wall, but the rate of encephalization should be different in either case. To his surprise, EQ did not take a major dive during mass extinctions, and suggested that perhaps if extinction likelihood had been higher, EQ would not have risen as rapidly. His comment echoed the sentiment of Ward and

Brownlee (2000), that the emergence of intelligence is remarkable in spite of such major extinction events. Could there be a simpler explanation? Could it be that complex, intelligent life did not evolve *in spite of* high rates of extinction, but instead *because of* high extinction rates?

Relative Brain Size - What Can it Tell Us?

Many authors use relative brain size as a proxy for behavioral complexity (Chanziti 2003; Marino et al. 2004; Finarelli and Flynn 2007). Some are critical of the use of cranial capacity as a metric. For instance, Roth et al (2010) suggest that the number of neurons or neural connections should be more appropriate, and that in some measures of intelligence, absolute brain size is a better predictor of performance than relative brain size (Roth et al. 2010). To explain this, he discusses the concept of neuron density: individual neurons in larger brains are less able to communicate directly with as much of the brain as a percentage. This creates the need for more compartmentalization and lamination (layering) of the brain, which improves its functionality, regardless of body size. Another critic of relative brain size as a proxy for behavioral complexity is Deacon (1990). In “Rethinking Mammalian Brain Evolution,” he criticized the use of relative brain size and argued for the use of relative brain proportions as a more accurate predictor of intelligence. He further argued that developmental homologies of brain expansion are the real reason for what other authors claimed to be analogous. He argued that the complexities of neural development prevent the question from “being grappled with in a meaningful way” (Deacon 1990, p. 629). Additionally, Soligo (2013, p. 1) argued that “brain reorganization, not relative brain size, characterizes anthropoid brain evolution.” He claimed that the predictive power of Encephalization Quotient (EQ) is greatly overestimated, and that mosaic changes are responsible for increases in behavioral complexity. However, he still observed a general increase in relative brain size in some lineages of his phylogenetic analysis.

Deacon, Roth, and Soligo are just a few examples of a camp who decry the use of relative brain size to explain behavioral complexity. However, they appear to be outnumbered by authors who either disagree or have simply capitulated to the fact that encephalization is the best proxy we have to use, especially in extinct fauna. For instance, Finlay and Darlington (1995, p. 1578) examined the relative brain components of 131 species of primates, bats, and insectivores and found that the sizes of individual brain components were "highly predictable from absolute brain size." Most importantly, perhaps, in discussing the proponents of the validity of EQ, is a study that sought to directly measure the relationship between EQ and problem-solving ability (Benson-Amram et al. 2016). Benson-Amram presented various species of carnivorans to a food puzzle box, and the success with which they solved those puzzles was significantly more correlated with relative brain size than with any other measured variable.

A review authored by Striedter attempted to analyze the varying opinions on the subject in "Precis of Principals of Brain Evolution." In it, he noted that although absolute brain size and relative brain structure proportions are important predictors of intelligence, EQ is a reasonable metric (Striedter 2006). Furthermore, there exists empirical support for the relationship between relative brain size and behavioral complexity (Daniel et al. 2012; Benson-Amram et al. 2016), but most authors admit that the metric is imperfect and is only a proxy. Nevertheless, many researchers measure EQ to study the evolution of the brain, especially in extinct fauna. Finarelli (2007) has used EQ to document the evolution of the brain in caniform carnivorans and Marino (2004) has done similar work in toothed whales. The fossil record leaves behind plenty of evidence to document *how* the brain has evolved, but without contextual evidence for each case, it can be difficult to study *why* the brain evolved the way it did in any selected group.

EQ and Fitness

A great deal of research, as emphasized in the last section, has been devoted to the predictive power of encephalization in behavioral complexity, and there is a precarious consensus that encephalization is a reasonable proxy. Whether this encephalization translates into a selective advantage is perhaps a more relevant to the question of whether the evolution of behavioral complexity is a diffusive process or a directional one. A few studies have sought to address this question—more often in birds than in mammals. Sol et al. (2007) garnered empirical support for encephalization’s selective advantage. They found a strong negative correlation between relative brain size and annual adult mortality, supporting the cognitive buffer hypothesis (2007), the idea that big brains are especially advantageous in novel environments. A subsequent study published by Sol (2012) found that invasive bird species that scored higher as ecological opportunists outcompeted native species in urban environments.

Ecological opportunism, one could argue, requires a higher degree of behavioral flexibility than does ecological specialization, with opportunists being better able to modify their foraging strategies in varying environments. Interestingly, a correlation between resource generalism, brain size, and resilience to population decline was observed by Schultz et al (2005). Whereas many bird species in Britain are in sharp decline as a result of human disruption of their habitat, researchers found that birds with relatively larger brains and less resource specialization sustained less population decline over the period of study. This result brings me to another piece of support for the idea that higher extinction rates tend to select for encephalization—generalists fare better during periods of high background extinction, and generalists tend to be more behaviorally flexible.

In addition to these avian case studies in the effect of relative brain size on survival, a similar pattern was seen in mammals (Sol et al. 2008). In it, Sol formally defined the brain size-environmental change hypothesis: “Such enhanced behavioral flexibility [conferred by encephalization] is predicted to carry fitness benefits to individuals facing novel or altered environmental conditions, a theory known as the brain size–environmental change hypothesis” (2008, p. 63), which he says is part of the more general cognitive buffer hypothesis. As part of that study, researchers compiled data on 100 species that were recently introduced to non-indigenous environments and measured their relative success at becoming and remaining established.

As Bogonovich stated with regards to designing empirical experimentation to infer patterns in the evolution of intelligence, “…the goal is to look for evolutionary experiments in the various biogeographically isolated regions of the past” (2011, p. 116). I agree with this suggestion; however, I think he may have done well to include not just those experiments of the past, but those of the present. If you want to find evolutionary experiments, look no further than industrialized landscapes. Humans are altering the environment in significant ways, and the shuffling of species occurring because of human activity will surely alter the course of evolution for many lineages, as did the shuffling of species during the great American interchange (Sato et al. 2012). An examination of populations in varying degrees of urbanization provides a perfect means to test the effect that those environments have on the physiology and encephalization of the isolated populations. This response to urbanization has been tested to some degree by the previously cited studies on birds and mammals (Sol et al. 2007; Daniel et al. 2008; Shultz et al. 2010) , but Snell-Rood (2013) spoke directly to the effect of urbanization.

Snell-Rood (2013) predicted that urban populations of selected mammal species would show greater encephalization than rural populations, and that this difference would exaggerate over the period of study from 1920-2010. Measurements were taken from museum collections. She and her colleagues found that urban environments did select for increased encephalization, particularly in highly fecund species. They also found that this increase in encephalization occurred most rapidly in the beginning of the colonization process. Interestingly, in several species, they observed an increase in the encephalization of the rural populations as well, suggesting that some aspect of living in rural environments may have also selecting for higher cognition, perhaps (as suggested by the authors) because of logging, agriculture, or some other human activity—or alternatively that the variation in cognitive capacity may be due to variation in nutrition, as nitrogen has become more prevalent in the last 100 years. All of the specimens they chose to analyze were from counties in Minnesota. It is also possible that gene flow reduced separation in urban and rural populations. A similar analysis with rural populations that are farther-removed from urban settings may further clarify this trend. I would like to expand upon this research with the present thesis, except that I would like to focus on fewer species. Snell-Rood et al. (2013) analyzed 10 species, listed below:

Blarina brevicauda (Northern short-tailed shrew)
Clethrionomys gapperi (Red-backed vole)
Eptesicus fuscus (Big brown bat)
Geomys bursarius (Plains pocket gopher)
Myotis lucifugus (Little brown bat)
Microtus pennsylvanicus (Meadow vole)
Peromyscus leucopus (White-footed mouse)
Sciurus carolinensis (Eastern gray squirrel)
Sorex cinereus (Cinereus shrew)

Tamiasciurus hudsonicus (American red squirrel)

Although Snell-Rood included raccoons in her study, they were excluded from the analysis. Raccoons are the quintessential generalists, they thrive in urban areas like Chicago and Manhattan, and they belong to clade Musteloidea, which is ecologically diverse compared to other carnivorans (Sato et al. 2012). Stanton et al. (2017) has demonstrated raccoons are clever by subjecting them to a cognitive test requiring the subjects to use stones to displace water in order to obtain food. Two of the ten raccoons solved this puzzle, which only the cleverest bird species (*Corvus moneduloides*) had previously been able to do (Jelbert et al. 2014), and a third raccoon found an alternative solution by flipping the entire experimental apparatus over, much to the bemusement of the researchers.

Summary

Within the interdisciplinary field of astrobiology, several testable hypotheses about the evolution of complexity are being explored. Whether this evolution of complexity is due to diffusive evolution or active selection has implications for the f_i variable of the Drake Equation, such that active selection for complexity or characteristic associated with complexity predicts a higher value of f_i than in the case of diffusive evolution. One measurement of complexity, encephalization, is of interest to researchers and has been extensively studied and discussed. Heated debate surrounds the validity of relative brain size as an indication of behavioral complexity, the generally preferred term to “intelligence.” Nonetheless, encephalization quotient, or EQ, has been demonstrated to be a reasonable approximation for behavioral complexity and is assessed by many researchers. Whether encephalization confers a selective advantage in novel environments (the brain size-environmental change hypothesis – part of the more general Cognitive Buffer Hypothesis) has not been extensively studied, but in those few studies that have examined the relative encephalization of birds and mammals introduced to novel environments, preliminary support has been found in support of the cognitive buffer hypothesis. To the best of my knowledge, only one study has looked specifically at the difference in encephalization between urban and rural populations of mammals, and despite sampling issues, they found some support for the hypothesis that urban environments select for increased encephalization. A similar study on raccoons, with a larger sample size over a wider range, might yield more explanatory results. Increased encephalization in commensal raccoons would suggest that novel environments select for increased behavioral flexibility, supporting the cognitive buffer hypothesis, and providing some evidence that encephalization is the result of direct selection in times of abrupt environmental flux. This result would be of interest to astrobiologists, because it suggests that the evolution of complexity is a predictable consequence of natural selection, rather than a fluke of contingency as is the argument of proponents of the Rare Earth Hypothesis.

CHAPTER 3

OMNIVORY AND BRAIN SIZE

Introduction

What led to the evolution of large, complex brains? This evolutionary enlargement of the brain, referred to as “encephalization”, has profound implications for a diverse range of disciplines—from paleontology and evolutionary psychology to philosophy and the development of artificial intelligence. Clearly, disproportionately large brains (relative to body size) are one of the major features that allowed humans to adapt so well, and it is widely recognized that the brain is in some way involved in manifesting that elusive concept, “intelligence.” The precise nature of the relationship between the brain and intelligent behavior has been hotly disputed, with some arguing that absolute brain mass, or total number of neurons, is the best predictor of intelligent behavior (Roth et al. 2010), whereas others argue that brain size relative to body size is a better predictor (Sol et al. 2008). In spite of these disputes, most experts will agree that relative brain size is at least a reasonable approximation for intelligence, and it is used by most preeminent paleoneurologists (Finarelli 2007). Additional experimental evidence has recently been mounting to support this assumption, such as the finding that relative brain size is positively associated with problem-solving abilities in mammalian carnivores (Benson-Abram et al. 2016), and that relative brain size predicted the success of mammals introduced to new environments (Sol et al. 2008). Similar conclusions have been reached in studies on birds as well, with Shultz et al. (2010) finding that larger brained, more omnivorous birds were more successful through England’s industrialization, and Sol et al (2007) finding a negative correlation between brain size and mortality. In general, all vertebrate groups, excluding agnathans, which lack a cerebellum, possess the same number of brain divisions and have lineages that have undergone encephalization—generally accompanied by increases in behavioral complexity (Northcutt

2002). For the above reasons, this thesis will proceed with the assumption that relative brain size is a reasonable proxy for intelligent behavior in mammals, as well as other vertebrate groups.

In any case, this encephalization process is well documented. A study by Russel (1983) demonstrated that the natural log of the maximally encephalized animal against time has a very clear linear increase. This observation introduced an intriguing directionality in evolution, brain size relative to body size tends to increase. Interpretation of this pattern, however, has proven controversial (Knoll 2000). Does relative brain size tend to increase as a result of evolutionary diffusion—with encephalization being an unremarkable inevitability when minimal size and complexity must have been the initial state—or is encephalization a predictable consequence of animals evolving throughout time?

One modern and strong proponent of the latter perspective is Cambridge paleontologist Simon Conway Morris (who received his initial notoriety by introducing the idea of the Cambrian Explosion), who has written books that are critical of Gould's interpretation (who thought that evolution was wholly unpredictable and random). For example, in *Runes of Evolution: How the Universe Became Self-Aware*, Morris (2015) highlighted the innumerable instances of evolutionary convergence across the biosphere—from the fusiform bodies of fast swimmers like dolphins, sharks, and ichthyosaurs, to the camera eyes of vertebrates and octopuses, just to name a few. Since so many separate lineages have reached similar evolutionary solutions to similar problems, Morris argued, then perhaps evolution behaves more predictably than previously estimated. Whether these convergences are "true" or not, Morris (2015) concedes, is impossible to say with absolute certainty. For instance, the common ancestor of octopuses and vertebrates may share genetic homologies for photoreceptive cells that makes their analogous camera eyes less remarkable. Analogies between more distant relatives (like the injecting cnidocytes in Cnidarians and the injecting stingers of scorpions or fangs of snakes) may provide more powerful evidence for the predictability of evolution, but even they share features—DNA or lipid bilayers—that some would argue make those analogies actually "deep homologies" (Shubin 2009).

How can the study of brain sizes in mammals even begin to inform interpretations of these broad conceptual dilemmas? Well, a link between omnivory and brain size might suggest an evolutionary mechanism for the steady encephalization observed. Before explaining this mechanism, I would like to briefly address a widely-held assumption that I think should be reevaluated—that assumption being that greater extinction rates should have a net negative effect on not just ecosystem complexity, but also on behavioral complexity. One good example of this is in the discussion of Marc Bogonovich's "Intelligence's likelihood and evolutionary timeframe" (2011). In regard to Russel's aforementioned demonstration of maximal EQ increase over time, Bogonovich (2011) runs a series of models that attempt to map the maximal EQ over time by simulating diffusive evolutionary parameters. Maximal EQ still rises, albeit less regularly, and human-level EQ is never reached in the model. While interpreting the model, Bogonovich (2011) states that "if the extinction likelihood [a model parameter] was lower, EQ drops would presumably be less likely in any particular model iteration." Furthermore, Bogonovich (2011) states that the actual maximal EQ increase seen by Russel is surprising, since EQ drops were not observed during major mass extinction events. Maybe this pattern should not be so surprising. Maybe his presumption (held currently by many) that extinction negatively impacts organismal complexity is unfounded.

Such an effect might be the case since extinction is thought to generally affect specialists more negatively than generalists (Regan 2001; Vasquez 2002; Price 2012). Being highly specialized is advantageous for efficiently exploiting a particular niche, but the ebb and flow of environmental change that marks geologic history can often make those specializations a liability (Barriga 2015). For instance, the giant panda might not be able to survive if bamboo were to suddenly disappear, whereas a black bear could likely survive if one of its many food sources were to disappear. Generalists might not as efficiently exploit one particular niche, but the wider breadth of their niche may afford them faster adaptability in periods of environmental flux (Vázquez and Simberloff 2002). To be so adaptable may be more cognitively demanding, requiring a greater behavioral repertoire, which may be reflected in a larger relative brain size (Holekamp et al. 2013). Such is the reason for the present study. The question that seems unsatisfactorily addressed in the literature is whether or not generalists (omnivores) have larger relative brains than specialists (carnivores and herbivores).

However, the present study is by no means the first to correlate relative brain size against ecological characteristics. For instance, a positive correlation is well documented between relative brain size and arboreality (Eisenberg 1981), the idea being that navigation in trees requires precise interaction with a more complex 3-dimensional space. Another positive correlation is observed between nocturnality and relative brain size, perhaps resulting from a need for more nervous tissue to successfully navigate in the absence of visual stimuli (Harvey and Krebs 1990). Relationship between sociality and relative brain size is less universal across animal lineages. Some of the most highly encephalized animals, such as humans and cetaceans, are highly social, and this sociality is often argued to have initiated the intraspecific competition that led to such marked encephalization (Fox et al. 2017). However, in other lineages, such as non-hominid primates, sociality does not seem to be correlated at all with brain size (DeCasien 2017).

Although the relationship between resource specialization and brain size has not yet been adequately explored in mammals, there does exist compelling evidence for the relationship in birds. Schultz et al. (2010) demonstrated that in declining bird populations in the UK, two major factors were associated with resistance to those declines—resource generalization and relative brain size. Thus, those two factors were independently associated with resistance to population decline, but the authors did not examine the statistical association between those two factors themselves.

Here I address this relationship in a diverse sample of mammal taxa. Central to the question of this study is whether or not omnivory is associated with relative brain size. Other ecological categories were analyzed to ensure that the methods used here were at least able to reproduce what is already widely accepted with regards to arboreality and nocturnality. Sociality was also explored to add to the developing conversation with regard to the complex evolutionary relationship between sociality and encephalization. If a positive correlation between omnivory and relative brain size was found, then some support would be garnered for the hypothesis that the resilience of generalists in changing environmental conditions acts as a potential direct selective mechanism for the observed encephalization throughout geologic history.

Limitations

Though the present study was meant to examine correlations of EQ across a wide-range of mammalian taxa, the dataset nonetheless was still weighted more heavily in some taxa than for others. For instance, 20 specimens of *Procyon lotor* were measured, while only one specimen of *Potus flavus* was measured. Furthermore, the dataset was generally weighted towards members of Musteloidea and the majority of measurements were taken from members of Carnivora. Given this restricted phylogenetic range, broadly-scoped conclusions made from these data rely on assumptions—patterns in this group of animals may not be consistent in other groups. However, the inclusion of members of other outside Musteloidea could potentially skew results, because even though EQ is meant to correct for phylogenetic disparities (Harvey and Krebs 1990), some have argued that EQ comparisons are less viable with greater phylogenetic distance (Kruska 2005). For this reason, non-musteloid taxa were removed from analysis when possible, but not in the analysis of feeding categories, since non-musteloids were nearly the only herbivore representatives in the available sample. Future studies with a greater variety of taxa and with greater sample sizes would provide a more robust analysis of variance.

Additionally, data for brain mass depended upon estimations from two equations and body mass depended upon estimation from yet another equation, and each of these introduce a margin of error. That error may affect estimations in some taxa more than others. It is unclear in what direction this error may skew the data, if in any particular direction at all. Nonetheless, a more accurate estimation for brain mass and body mass would greatly buttress the explanatory power of a study such as this.

Chapter 1 referenced two assumptions about extrapolation. Here I will address one: that mammals are good representatives for vertebrates in general with regards to brain evolution in response to ecology. First, I would point to some of the evolutionary convergences in birds and mammals—two clades that are quite phylogenetically disparate (Page 2000). In spite of reproductive and gross morphological differences, mammals and birds have undergone surprisingly similar encephalization (Jerison 1971). In fact, some researchers have found that the position and size of the cerebral cortex in mammals is similar to the position and size of the bird’s telencephalon (Güntürkün 2016), and both structures have been shown to be involved in mental capacities that are thought to be associated with intelligent thought and behavior

(Güntürkün 2016), although both structures are derived from different embryological tissues Streidter (1997). These convergences seem to imply mammal brain evolution can in some cases reflect brain evolution in distant evolutionary relatives. For this reason, I argue that using mammal brain evolution as a model for broader evolutionary themes is at least partly justified.

Materials and Methods

Ecological Classification

Animals were categorized according to four ecological characteristics: feeding category (herbivore, omnivore, mesocarnivore, or hypercarnivore), nocturnality and diurnality, locomotory style (cursorial, scansorial, natatorial, or arboreal), and sociality (solitary or social). To maintain a consistent standard by which to categorize, Animal Diversity Webpage, funded by the NSF, was followed. For instance, in the "behavior" section of the entry for *Procyon lotor*, "key behaviors" are listed (Fox 2001). Those key behaviors classified *Procyon lotor* as nocturnal, scansorial, and solitary. Feeding categories were obtained from the "food habits" section, and if a taxon was labelled with both "omnivore" and "carnivore," it was placed into the "mesocarnivore" category for the present study. If a taxon was not identified to species (*Nasua* sp., *Aonyx* sp., and *Odocoileus* sp.), it was categorized based on characteristics of a species within that genus (the assumption that these characteristics can apply to other members of the genus is not always valid) *Canis dirus* was the only fossil specimen, categorized according to the characteristics listed for *Canis lupis*. This categorization, too, relies on the assumption that the dire wolf lives similarly to the gray wolf, an assumption that has been called in to question recently (Figueirido et al 2015). In some instances, locomotory style was not explicitly listed as any of the categories present. If the animal was not considered to be scansorial, arboreal, or natatorial, it was placed into the cursorial category, which came to encompass not just animals adapted for fast running but also those that spend most of their time moving over solid ground (this generalization was made with the assumption that locomotion on flat ground is similarly cognitively demanding when compared to swimming or climbing in 3 dimensions). All taxa are listed alongside their sample size, ecological classifications, and mean and standard deviation for EQ in Table 1.

Table 1 Species Ecological Categorization

Taxon	N	Feeding category	Nocturnality / Diurnality	Locomotion	Sociality	$\overline{\text{EQ}}$(SD)
Procyon lotor	24	Omnivore	Nocturnal	Scansorial	Solitary	1.64(0.21)
Ailurus fulgens	4	Herbivore	Nocturnal	Arboreal	Solitary	2.17(0.26)
Nasua nasua	2	Omnivore	Nocturnal	Scansorial	Social	1.64(0.09)
Procyon cancrivorus	1	Mesocarnivore	Nocturnal	Scansorial	Solitary	1.66
Nasua narica	1	Omnivore	Diurnal	Scansorial	Solitary	2.11
Bassariscus astutus	2	Omnivore	Nocturnal	Scansorial	Solitary	1.75(0.17)
Nasua sp.	1	Omnivore	Diurnal	Scansorial	Solitary	1.95
Potus flavus	1	Herbivore	Nocturnal	Arboreal	Social	1.82
Enhydra lutris	1	Hypercarnivore	Diurnal	Natatorial	Social	1.20
Aonyx cinera	3	Hypercarnivore	Diurnal	Natatorial	Social	1.46(0.12)
Aonyx sp.	1	Hypercarnivore	Diurnal	Natatorial	Social	0.99
Aonyx capensis	1	Hypercarnivore	Diurnal	Natatorial	Social	0.87
Lontra canadensis	10	Hypercarnivore	Diurnal	Natatorial	Social	0.88(0.14)

Mustela nigripes	11	Hypercarnivore	Nocturnal	Cursorial	Solitary	1.45(0.34)
Martes pennanti	9	Mesocarnivore	Nocturnal	Scansorial	Solitary	1.60(0.18)
Gulo gulo	5	Mesocarnivore	Nocturnal	Cursorial	Solitary	1.13(0.10)
Lynx rufus	4	Hypercarnivore	Nocturnal	Scansorial	Solitary	2.02(0.57)
Crocuta crocuta	2	Hypercarnivore	Diurnal	Cursorial	Social	1.36(0.43)
Canis dirus	1	Hypercarnivore	Nocturnal	Cursorial	Social	.69
Canis lupus	3	Hypercarnivore	Nocturnal	Cursorial	Social	.84(0.25)
Canis latrans	1	Hypercarnivore	Nocturnal	Cursoiral	Social	1.03
Ursus arctos middendorffi	1	Omnivore	Diurnal	Cursorial	Social	1.11
Odocoileus sp.	11	Herbivore	Diurnal	Cursorial	Solitary	0.81(0.12)

Taxon, sample size (N), feeding category, nocturnality, locomotory style, sociality, and mean encephalization quotient. EQ is represented as the mean for that taxon, and the standard deviations for samples larger than one are listed in parentheses beside the mean.

Estimation of Brain Volume and Brain mass

All specimens were obtained from the vertebrate modern collections at East Tennessee State University. Cranial dimensions and the width of the occipital condyle were measured to the nearest millimeter using dial calipers. For braincase, length (L), width (W), and height (H) were measured along three orthogonal axes (Figure 1). Length was defined as the distance between the nasal-frontal suture and the most posterior point of the occipital bone, excluding the occipital condyle and sagittal crest. Braincase width was measured as the widest point of the braincase along the parietal bones, behind the zygomatic arch. Height was measured as the distance between the most ventral point of the basioccipital to the top of the braincase, excluding the sagittal crest if present.

Using these three measurements, cranial capacity was estimated following Finarelli (2006), which was shown to estimate endocranial volume with 98.3% accuracy:

$$\ln(\text{brain volume}) = -6.23 + 1.06\ln(\mathrm{H}) + 0.28\ln(\mathrm{L}) + 1.27(\mathrm{W})$$

Encephalization quotient (EQ), which was the target metric of this study (explained more fully in its own section below), was defined as the relationship between brain mass and body mass, so brain volume had to be converted to brain mass following Benson-Amram et al. (2016):

$$\text{brain mass} = 1.147 \times \text{brain volume}^{0.976}$$

Estimation of Body Mass

Widths of the occipital condyles were measured in millimeters using calipers. Sarko et al. (2010) analyzed the predictive accuracy of a number of potential osteological characters in a wide variety of mammals, and found occipital condyle breadth to be the best predictor of body size, with a correlation coefficient of 0.928 ($p<0.001$), using the following equation:

$$\log(\text{Body weight}) = -2.098 + 4.623 \times \log(\text{Occipital condyle width})$$

Encephalization quotient

Brain weight and body weight scale allometrically, as larger animals do not require as much nervous tissue per gram of body weight to perform the same behaviors (Soligo, 2013).

Therefore, EQ, which is a measure of an animal’s deviation from the expected result, is often used to approximate behavioral complexity. EQ values greater than 1 are larger than expected for a given body mass, and EQ values less than 1 are smaller than expected for a given body mass. Following Finarelli and Flynn (2007):

$$\mathrm{EQ} = \frac{\text{brain weight}}{11.22 \times \text{body weight}^{0.76}}$$

Results

Feeding behavior

One-way ANOVA indicated that mean EQs between feeding categories were statistically different (F=6.068, p=0.001). Descriptive statistics indicated omnivores had the highest mean EQ (1.64 ± 0.22), followed by mesocarnivores (1.47 ± 0.32), hypercarnivores (1.24 ± 0.46) and finally herbivores (1.22 ± 0.64) (Figure 1 and Table 2). The data set failed the test of homogeneity of variances with a Levene statistic of 9.978 and a significance value of 0.000. For this reason, a Tamhane test was used to evaluate post-hoc comparisons, as it is robust to violation of the assumption of equal variances.

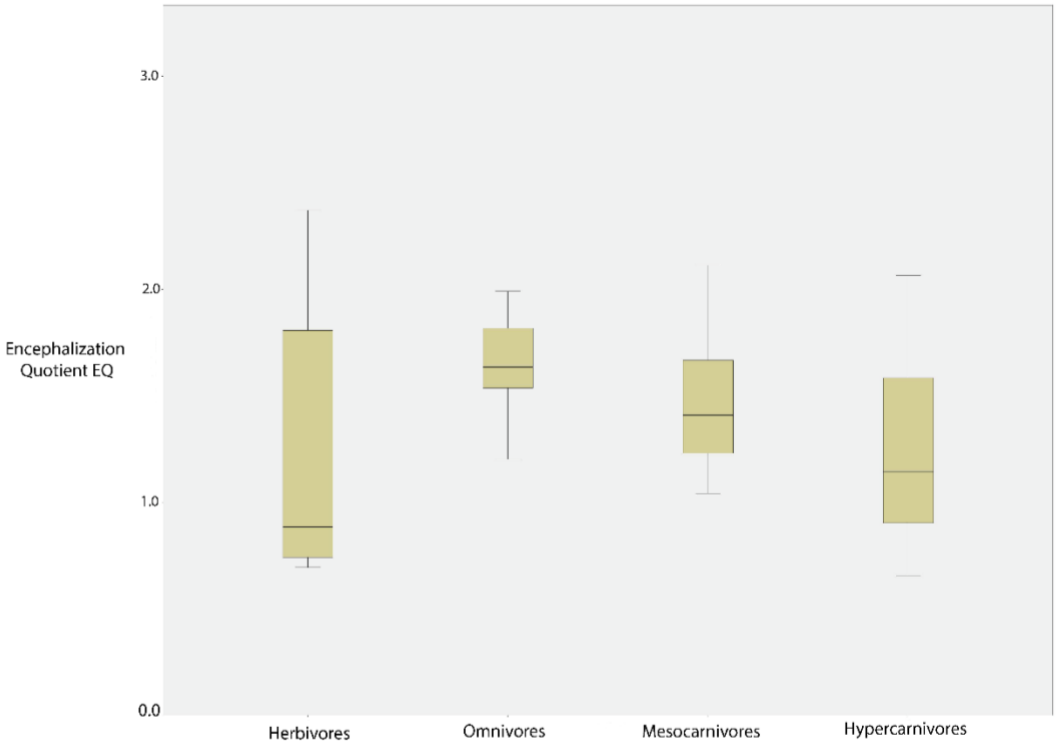


Figure 1. Encephalization Quotient Versus Feeding Strategy. Herbivores = animals with a diet consisting of plants, rarely if ever eating meat. Omnivores = animals with flexible diets. Mesocarnivores = animals adapted for eating meat but can and often do eat plants. Hypercarnivores = animals with diets that consist of meat, rarely if ever eating plants. Center line for each corresponds with median EQ of sample, which delineates quartile 2 (below line) and quartile 3 (above line). Lines above and below box represent quartiles 4 and 1, respectively.

Table 2. Descriptive Statistics for EQ by Feeding Category

Variable	**Herbivore**$_{(16)}$	**Omnivore**$_{(29)}$	**Mesocarnivore**$_{(15)}$	**Hypercarnivore**$_{(39)}$
EQ	$1.22(0.64)_{\mathrm{O}}$	$1.64(0.22)_{\mathrm{Herb,\ Hyp}}$	1.47(0.32)	$1.24(0.46)_{\mathrm{O}}$

Abbreviations: Herb, herbivore; Hyp, hypercarnivore; M, mesocarnivore; O, Omnivore. Data is represented as mean encephalization quotient (EQ) and standard deviation (SD). Subscripts beside feeding category represent sample size. Superscripts represent groups with statistically significant differences between the means.

Nocturnality / Diurnality

One-way ANOVA indicated a statistically significant difference between the means of nocturnal and diurnal animals (F=21.6, p=0.000). This difference was statistically significant, with a Levene statistic of 0.88 and a significance value of 0.242. Mean EQ of diurnal and nocturnal animals was 1.13 ± 0.32 and 1.57 ± 0.40, respectively (Table 3 and Figure 2).

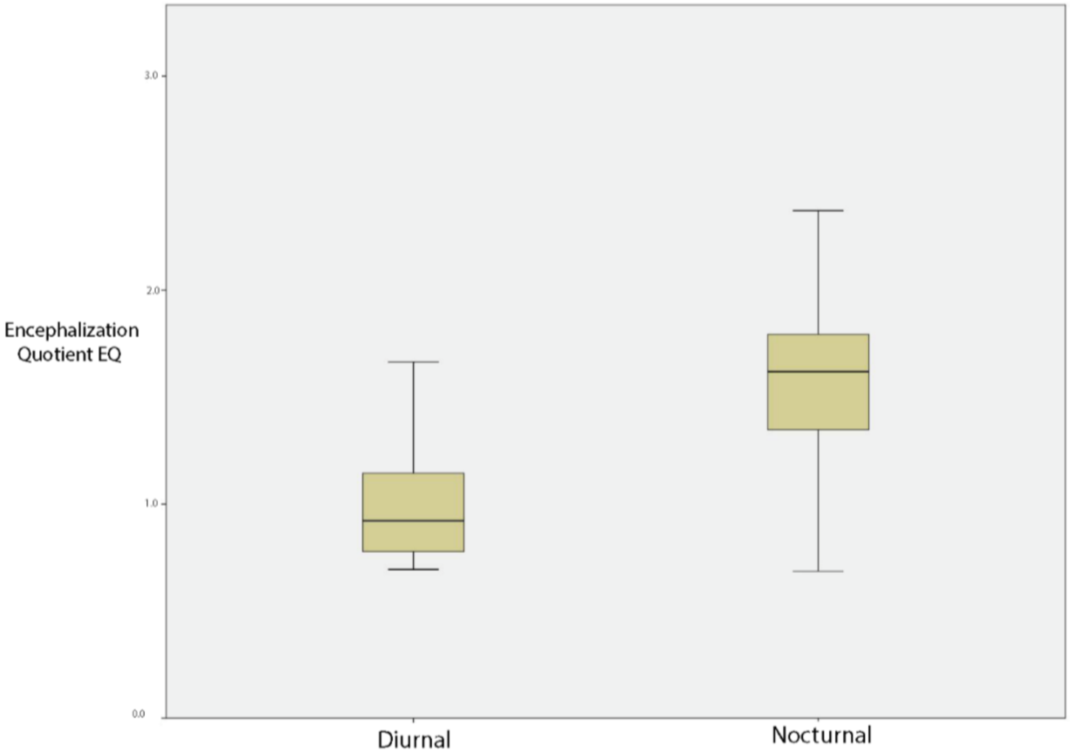


Figure 2. Encephalization Quotient Versus Nocturnality and Diurnality. Diurnal = animals that are more active during the day. Nocturnal = animals that are more active during the night. Designations based on Animal Diversity Webpage. Center line for each corresponds with median EQ of sample, which delineates quartile 2 (below line) and quartile 3 (above line). Lines above and below box represent quartile 4 and 1, respectively.

Table 3. Descriptive Statistics for EQ by Nocturnality and Diurnality

Variable	**Diurnal**$_{(22)}$	**Nocturnal**$_{(66)}$
EQ	1.13(0.34)	1.64(0.22)

Data is represented as mean encephalization quotient (EQ) and standard deviation (SD). Subscripts beside feeding category represent sample size.

Locomotion

One-way ANOVA indicated statistically significant differences in mean EQ by locomotory category (F = 22.13, p=0.000). Descriptive statistics indicated arboreal animals had the highest mean EQ (2.10 ± 0.28), followed by scansorial animals (1.66 ± 0.21), cursorial animals (1.35 ± 0.47) and finally natatorial animals (1.02 ± 0.25) (Figure 3 and Table 4). A Levene statistic of 1.557 (p=0.205) allowed the use of a Scheffe post-hoc test to evaluate statistically significant differences. That differences in means were statistically significant was further supported by one-way ANOVA between groups comparison significance of less than 0.001, permitting the use of a post-hoc Scheffe test.

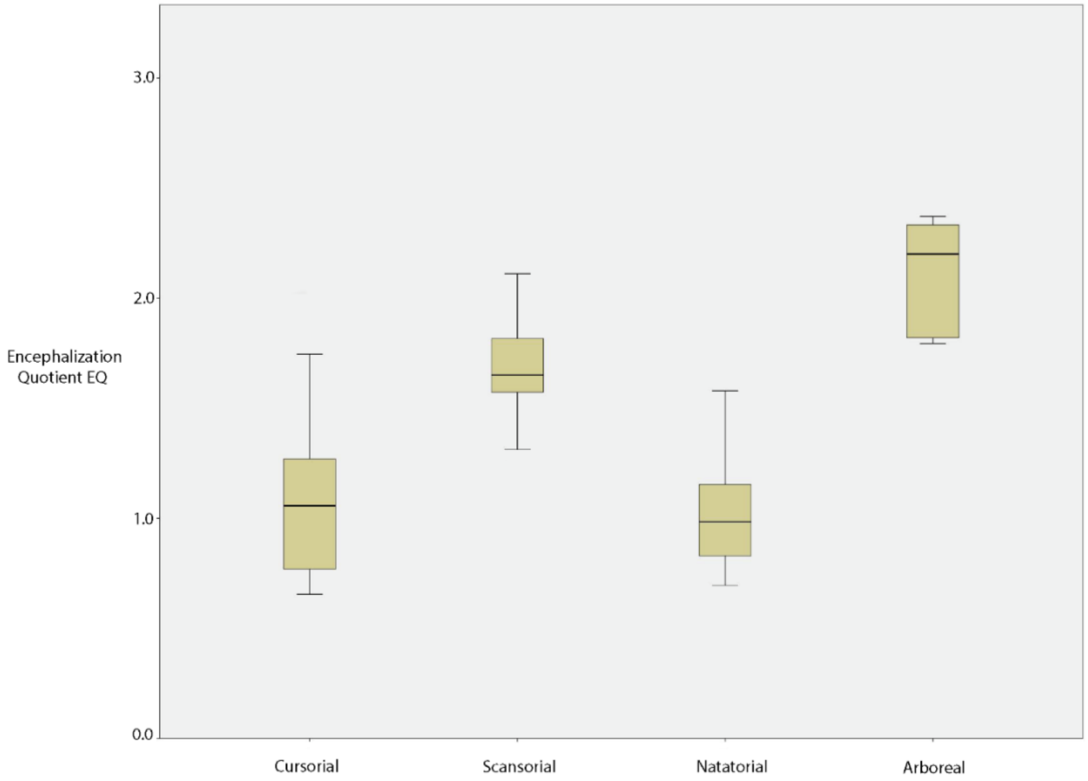


Figure 3. Encephalization Quotient Versus Locomotory Style. Cursorial = animals adapted primarily for moving on dry land. Scansorial = animals with limited adaptations for navigating trees. Natatorial = animals adapted for moving in water. Arboreal = animals well adapted for navigating trees. Center line for each corresponds with median EQ of sample, which delineates quartile 2 (below line) and quartile 3 (above line). Lines above and below box represent quartile 4 and 1, respectively.

Table 4. Descriptive Statistics for EQ by Locomotory Style

Variable	**Cursorial**$_{(28)}$	**Scansorial**$_{(38)}$	**Natatorial**$_{(17)}$	**Arboreal**$_{(5)}$
EQ	1.35(0.47)$_{\text{Sc, Arb}}$	1.65(0.21)$_{\text{Cur, Na}}$	1.02(0.25)$_{\text{Sc, Arb}}$	2.10(0.28)$_{\text{Cur, Na}}$

Abbreviations: Arb, arboreal; Cur, cursorial; Na, natatorial; Sc, scansorial. Data is represented as mean encephalization quotient (EQ) and standard deviation (SD). Subscripts beside locomotory style represent sample size. Superscripts represent groups with statistically significant differences between the means.

Sociality

One-way ANOVA indicated a statistically significant difference between the mean EQs of solitary and social animals (F=42.95, p=0.000). Mean EQ was higher in solitary animals (1.62 ± 0.36) than in social animals (1.09 ± 0.34) (Table 5 and Figure 4).

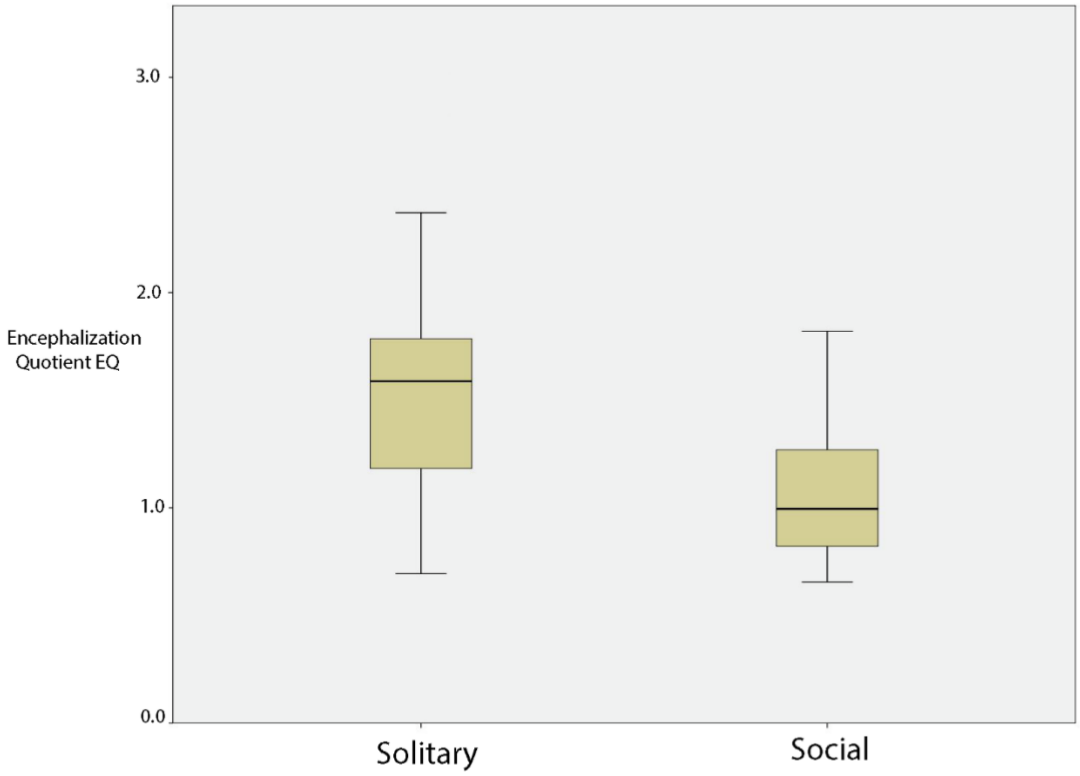


Figure 4. Encephalization Quotient Versus Sociality. Solitary = animals that rarely congregate except for mating and childrearing. Social = animals that congregate regularly. Center line for each corresponds with median EQ of sample, which delineates quartile 2 (below line) and quartile 3 (above line). Lines above and below box represent quartile 4 and 1, respectively.

Table 5. Descriptive Statistics for EQ by Sociality

Variable	**Solitary$_{(61)}$**	**Social$_{(27)}$**
EQ	1.62(0.36)	1.09(0.34)

Data is represented as mean encephalization quotient (EQ) and standard deviation (SD) in parentheses. Subscripts next to feeding category represent sample size.

Discussion

Omnivory was positively associated with higher EQs, supporting the initial hypothesis. The smallest brain sizes seen in specialists may indicate that more specialized lifestyles require less brain power to operate (of course, more cognitive power is needed to chase down and kill prey than to feed on unmoving plant material, as is evident in the data). In contrast, the ability to succeed with a wider range of available resources may require more abstract cognitive reasoning. In omnivores, all mean differences were statistically significant except between themselves and mesocarnivores. This is unsurprising, since mesocarnivores are to some degree omnivorous. While the greater EQ of omnivores compared to mesocarnivores was not statistically significant, it still provides some preliminary support that the more specialized a diet becomes, the less brainpower it will require. Conversely, the more omnivorous the more brain tissue the animal will require. Statistically significant differences between nocturnal animals and diurnal animals was not surprising. Nocturnal mammals navigate an environment with less visual stimuli, and thus require more cognitive processing to accurately interact with the environment. Likewise, locomotory style supports findings of other studies that have found arboreality to be positively associated with brain size, as navigation within a complex 3D environments requires significant spatial reasoning, which is not a neurologically simple accomplishment (Roth et al., 2010). Whereas tree-climbing ability was expected to be positively correlated with EQ, it was not expected that natatorial animals would score the lowest, because they also navigate a 3D environment. Perhaps because they don't interact with this 3D environment in as complex of a way as in scansorial or arboreal animals, they don't need as much processing power. Climbing requires tactile grasping ability, an understanding of a 3D environment riddled with far more complex and nuanced obstacles, the possibility of death or injury from falling, and competence with lever mechanics of limb segments and tree limbs, being able to modify the relative position and direction of each joint, including pronation and supination. Natatorial animals, on the other hand, have adapted to swimming by modifying limbs in various ways, such as forelimbs into flippers, which are far less cognitively demanding to operate. Large brains in cetaceans must be attributable to factors other than locomotion. Many have argued that large brains in cetaceans result from selection forces in an increasingly complex social structure (Marino, 2002; Marino et al. 2004; Al et al. 2017), but some argue that the development of echolocation may have been a more significant contributor (Marino 2000). Certainly, the varying hypotheses of brain evolution may depend on the taxa. However, evolutionary theorists, like most scientists, seek out the most parsimonious answers. It may the case that sociality is the primary driver of encephalization when some threshold of communicative ability is reached and a positive feedback loop of selection is initiated. As previously mentioned, significant support exists to suggest that a social feedback mechanism was a strong pressure in the encephalization of hominins and cetaceans (Kamilar and Baden 2014).

A growing body of encephalization research, however, now including this study, suggests that sociality alone cannot fully explain the extraordinary brain expansion seen in mammals and birds. In fact, results presented here suggest that sociality is in general negatively correlated with encephalization. While social interactions can apply a selective pressure for encephalization, it is possible that cognitive functions diffuse in social groups—making individuals less responsible for as wide a range of behaviors at any one time. For instance, in a herd of buffalo, the entire herd will be alerted if a single individual detects a threat (Quenette 1990). Such a social alert mechanism may reduce the sensory needs of the individual.

If this pattern—of larger brains in omnivorous animals—is observed across a broader range of the animal kingdom (and preliminary evidence exists to support at least as much is the case in birds (Shultz 2005)), then a potential mechanism may be proposed for the consistent encephalization pattern seen through geologic history. Being generalistic is cognitively demanding, but buffers animals against environmental change and extinction. Mass extinctions may therefore play a pivotal role in encephalization events, by selectively eliminating ecologically specialized organisms. If this is true, then perhaps the evolution of complex and intelligent life is not as unlikely as proponents of the contingency hypothesis (the idea that evolution of any complex life was contingent on a huge number of effectively irreplicable accidents (Smith 2017)) would argue.

CHAPTER 4

CRANIAL EVOLUTION OF *PROCYON LOTOR* IN RESPONSE TO URBAN ENVIRONMENTS

Introduction

Raccoons range across most of North America and where it is invasive and/or introduced. Unlike many native species, *P. lotor* has not been displaced in areas where its range overlaps with city limits. In fact, many populations of raccoons thrive alongside humans, living an existence that is far removed from their rural relatives. Living in shadows, eating food either thrown out or inadequately guarded by humans, these urban raccoons have been subjected to a unique set of selective pressures for many generations (Clark 1994). Of course, these populations aren't completely isolated; some gene flow doubtlessly exists, but as long as within-population gene flow is significantly higher than between-population, difference in selective pressures might result in measurable adaptations in urban vs rural raccoon populations. If so, what would those adaptations be, and why?

A primarily human-food based diet could relax selection for a strong bite and a pronounced dentition, since human food is often processed and easy to ingest (Eng 2013). One might also expect urban raccoons to have developed a smaller jaw and simpler teeth, investing those metabolic resources in other functions. Additionally, and perhaps more interestingly, the urban environment might be selecting for quite different behavioral dispositions. Living in cities and feeding largely off of human garbage may require a vastly different set of skills than that of the forest raccoon. Might this selection bring about differences in brain morphology?

This question, as it relates to mammals in general, was formally addressed by Snell-rood et al. (2013), who predicted that urban populations of selected mammal species (raccoons excluded) would show greater encephalization than rural populations. Eight out of the ten species examined were more encephalized in urban environments. Although not mentioned in Snell-rood's article, the observed difference in cranial capacity between urban and rural populations functions as a test for the Cognitive Buffer Hypothesis (CBH)—the idea that bigger brains buffer animals against environmental change. If true, the CBH has important implications for the evolution of large brains in general. If environmental change selects for encephalization, then relatively large brains and the commensurate level of cognitive sophistication are unsurprising evolutionary results.

To qualify the preceding statement, I must first address an assumption that some readers may be averse to—namely, that relatively large brains are "commensurate" with behavioral sophistication. Not all researchers agree that relative brain size corresponds with complex behavior, some arguing that neuron density (Roth et al. 2010), relative proportion of brain components (Finlay and Darlington 1995), absolute brain size (Beals et al. 1984), or some combination therein (Holekamp et al. 2013) is a better predictor. However, there is a precarious consensus that since brain tissue is metabolically expensive (and therefore the selective advantages to maintaining such expensive tissue must outweigh the cost) and that neuron density is relatively consistent within vertebrates (Striedter 2006), relative brain size is a reasonable proxy for complexity of cognition or behavior. In this study, interpretations will follow the assumption that relative brain size corresponds to behavioral complexity.

To compare relative brain size between and within species, encephalization quotient (EQ) is often used. This quotient measures the residual of the regression of the logarithm of an animal's brain mass to body mass ratio—in other words, how far an animal's brain mass deviates from what is expected for an animal of that size. EQ is measured as a ratio to 1—an animal whose brain is twice what is expected for a given body mass is 2. An animal whose brain is half of what is expected is 0.5. Humans, for instance, have an EQ of about 8.

In addition to EQ, the following study will examine several other aspects of raccoon craniomandibular morphology—tooth row length, brain case dimensions, etc. (See Table 6 for all variables measured). Unlike the Snell-rood example, this study will more closely examine a single species, across a much wider range.

Methods

Physical Measurements

All specimens in this study are housed in one of four museum collections: East Tennessee State University (ETSU), The Field Museum of Natural History (FMNH), the Oklahoma Museum of Natural History (OMNH), and the Florida Museum of Natural History (FLMNH). Brain case dimensions and occipital condyle were measured using dial calipers. Dorsal, lateral, and ventral photographs were taken of both the mandible and cranium for each individual along with a scale bar to take additional measurements after leaving the collections. Following Finarelli (2006), the height, width, and length of the brain case are were measured to estimate brain size (Figure 5).

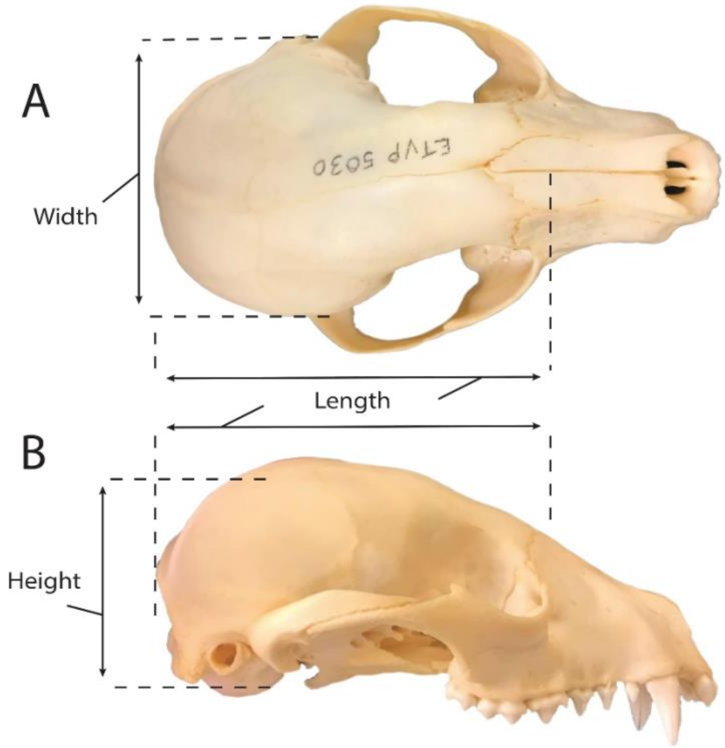


Figure 5. Cranial Caliper Measurements. A) Dorsal and B) Lateral views indicating brain case dimensions. Brain case height was measured as the distance between the top and bottom of the brain case, excluding sagittal crests when present (some of the older forest-dwelling males had prominent ones). Brain case width was measured as the distance between the widest points of the brain case. Brain case length was measured as the distance between the nasal-frontal suture and the back of the brain case. Figure by Salem Smith.

Additional craniomandibular measurements followed Fiscio (2007), measuring the length of the upper tooth row (LUPT), width of the upper tooth row (WUTR), breadth between the base of the upper canines (or canine width – CW), and length of the lower tooth row (LLTR) (Figure 6). In addition to the measurements used by Fiscio (2007), the photographs were used to also measure the skull length (SL) and the length of the lower M1 (M1), as these measurements were shown by Van Valkenberg (1990) to be useful in estimating body size. Estimates from these characteristics were used in addition to occipital condyle breadth (OCB) to approximate body mass in kg following Sarko (2010).

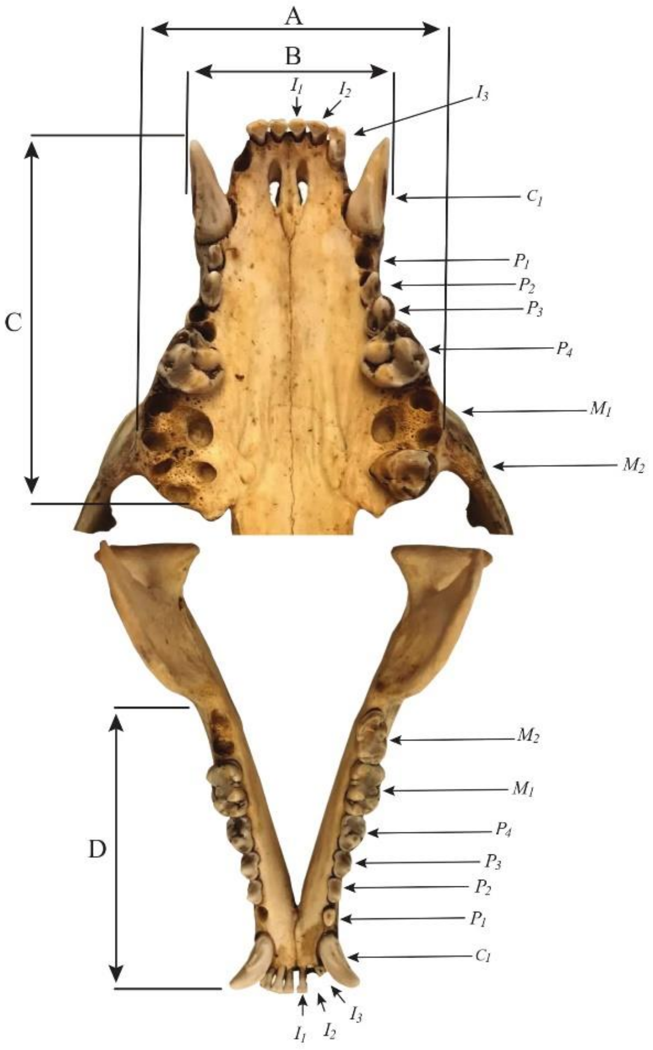


Figure 6. Dental Measurements. A) upper tooth row width (UTRW). B) Distance between base of upper canines, or canine width (CW). C) upper tooth row length (UTRL). D) lower tooth row length. M = molar. P = premolar. C = canine. I = incisor. Figure by Salem Smith.

Encephalization Quotient

Cranial measurements were transformed to Encephalizaton quotient using equations in Table 6.

Table 6. Cranial Transformation Equations

Variable	**Equation**	**Source**
Brain volume	$\ln(\text{brain volume}) = -6.23 + 1.06\ln(\text{H}) + 0.28\ln(\text{L}) + 1.27(\text{W})$	Finarelli 2006
Brain mass	$\text{brain mass} = 1.147 \times \text{brain volume}^{0.976}$	Benson-Abram et al. 2016
Body mass_1	$\log(\text{Body mass}) = -2.098 + 4.623 \times \log(\text{Occipital condyle width})$	Sarko et al. 2010
Body mass_2	$\text{Body mass} = 10^{(-2.27 + 2.97 * \log(\text{M1}))}$	B. Van Valkenburgh 2004
Body mass_3	$\text{Body mass} = 10^{(-5.59 + 3.13 * \log(\text{SL}))}$	B. Van Valkenburgh 2004
Encephalization Quotient	$\text{EQ} = \dfrac{\text{brain weight}}{11.22 \times \text{body mass}^{0.76}}$	Finarelli and Flynn 2007

M1 = length of first molar. SL = skull length. H = height of brain case. L = length of brain case. W = width of braincase.

Craniomandibular Proportions

Ratios were calculated for brain case dimensions: length over height, width over height, and width over length. Other variables obtained from imageJ (Figure 6) in addition to skull length, lower M1 length, occipital condyle breadth, and zygomatic arch breadth were converted to proportions in a different way. Following Coleman (2008), the relative size of each other measurement was compared to the geometric mean (Table 7), wherein each estimate is multiplied by one another, and the product is taken to the n-root, where n is the number of terms.

Table 7. Craniomandibular Proportions

Variable	**Acquisition**
Width between upper canines (UCW)	$UCW/_{GM}$
Upper tooth row width (UTRW)	$UTRW/_{GM}$
Upper tooth row length (UTRL)	$UTRL/_{GM}$
Lower tooth row length (LTRL)	$LTRL/_{GM}$
Skull length (SL)	$SL/_{GM}$
Lower M1 Length (M1)	$M1/_{GM}$
Zygomatic arch breadth (ZAB)	$ZAB/_{GM}$
Brain case length (BL)	$BL/_{BW}$
Brain case width (BW)	$BW/_{BH}$
Brain case height (BH)	$BH/_{BL}$
Occipital condyle breadth (OCB)	$OCW/_{GM}$

(GM = geometric mean). Ratios of linear measurements of skull dimensions to geometric mean, used to analyze relative proportions between commensal and rural raccoon population.

Urban and Rural Categorization

Excel files containing specimen ID numbers and latitude and longitude (provided by museums) were inserted into ArcGIS and laid over a world base map (Figure 7). Latitude and longitude were used to “Display XY Positions.” The 2010 urban boundary shapefile, downloaded from the US Census Bureau’s website, was incorporated into the map (Figure 8). Using the ArcMAP function “select object from location,” object IDs (raccoon occurrences) were selected to be “completely within the boundary layer.” Selected specimens were categorized as Urban and the remaining specimens were categorized as Rural. These two groups were compared.

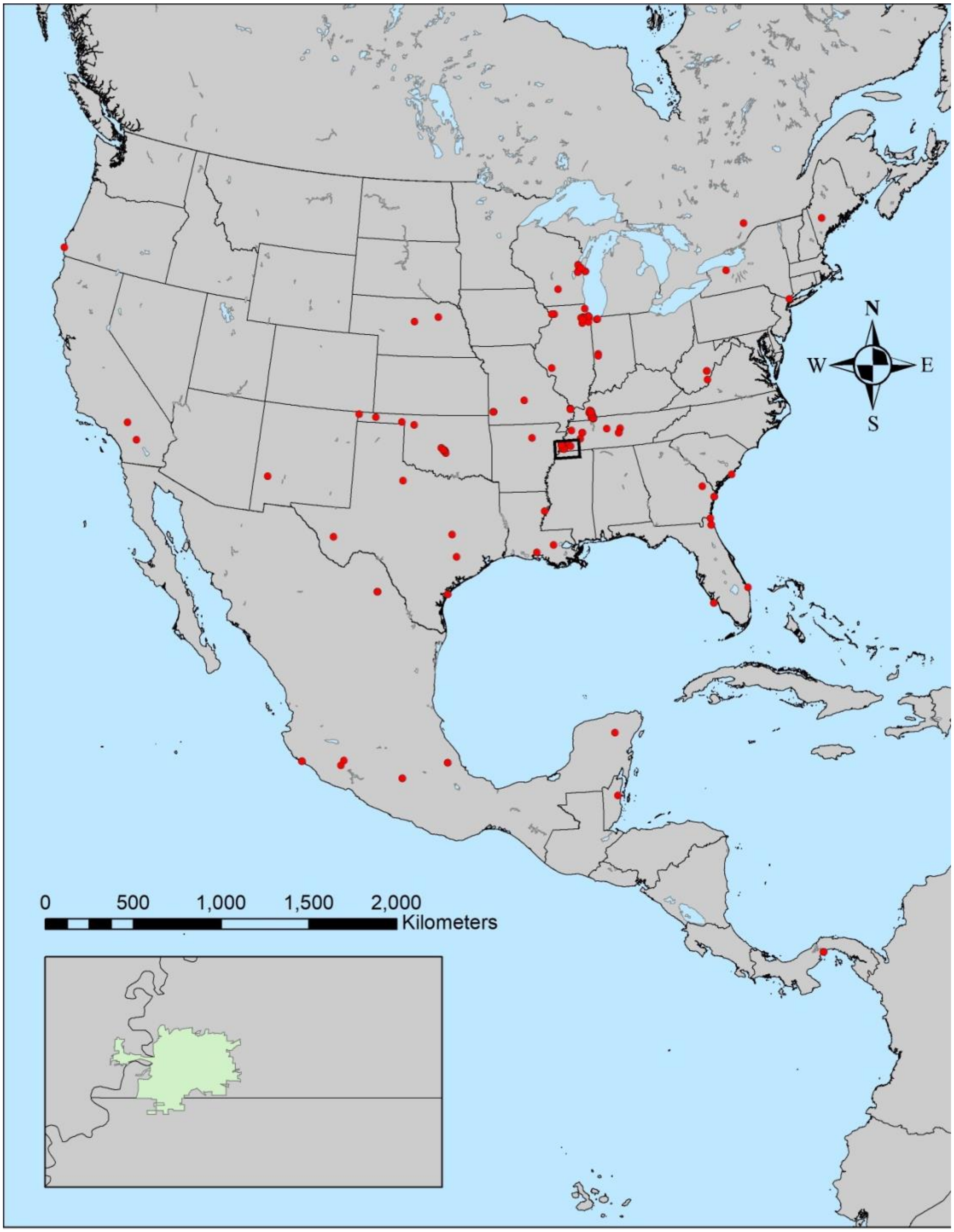
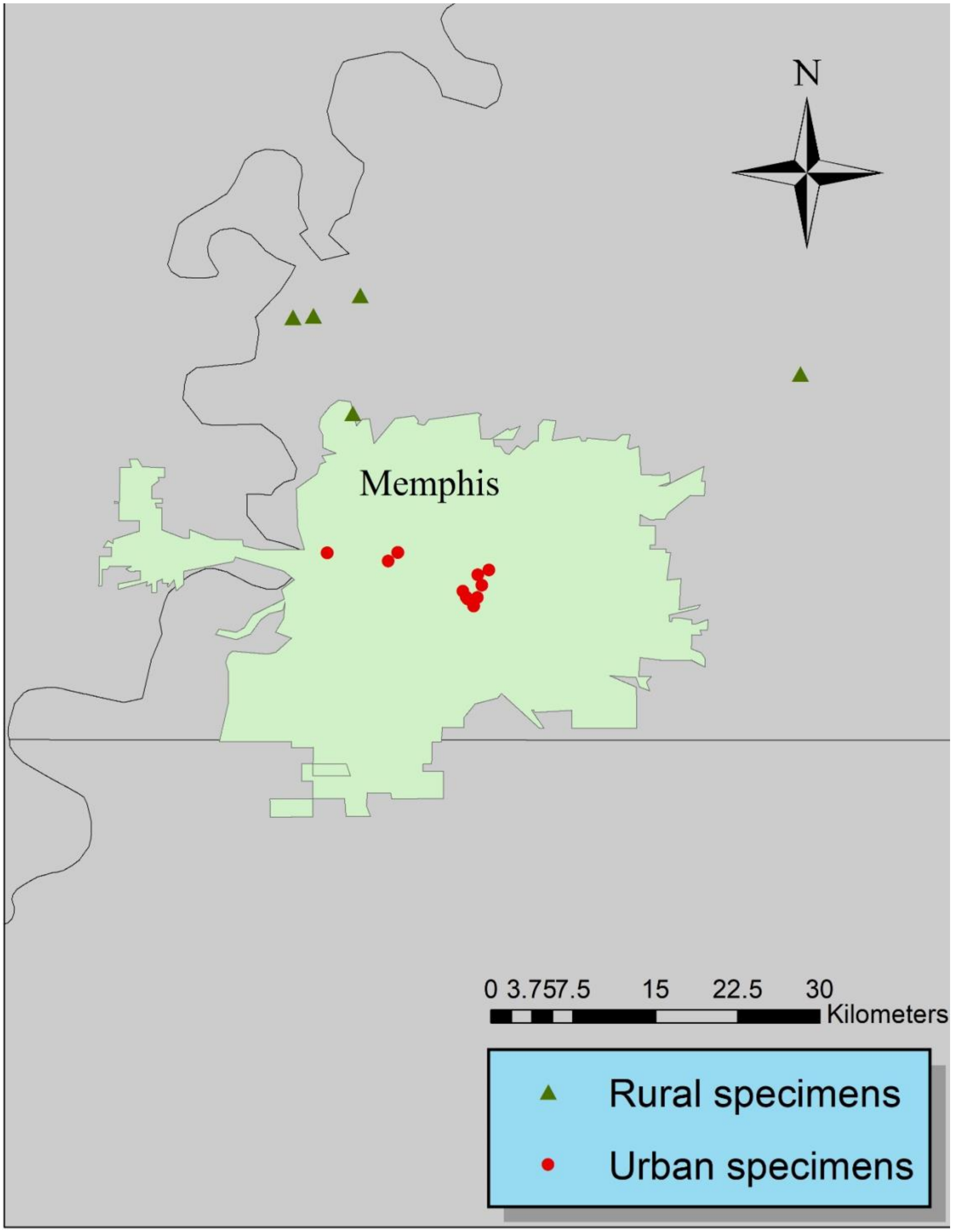


Figure 7. **Specimen Coordinates on ArcMap.** Raccoon specimen locations across North America. Small box around Memphis area is used to illustrate urban / rural categorization in Figure 4.4.

Figure 8. Urban Shapefile. Memphis area highlighted with urban shapefile overlaid. Specimens inside these shapefiles were designated as urban. Those outside were designated rural.



Statistical Analysis

All analyses were performed in SPSS. Analyses of variance (ANOVAs) was used to compare EQs of urban and rural groups. Another set of ANOVAs were used to compare the EQs of rural, urban and suburban. In each set of ANOVAs, EQs were calculated from the average of the weight estimates of the three cranial correlates to body mass. Each ANOVA was subjected to a test of homogeneity of variances. If groups were found not to have homogenous variances, Scheffe and Tamhane post-hoc tests were performed. In addition to EQs, the other craniomandibular metrics as ratios to the geometric mean were analyzed.

Results

Mean and standard deviation of each variable are listed below (Table 8), along with results for a Levene test for homogeneity of variances, a robust test of equality of means, and the ANOVA significance test. Two results are shown for EQ—one before the addition of Florida specimens and one after, as the inclusion of Florida specimens had a pronounced impact on the results of the analysis. Of the other variables examined, the between-group difference in absolute body mass was statistically significant, but none of the others as related to the geometric mean were statistically significant, although upper canine width to geometric mean (UCW/GM) and upper tooth row width to geometric mean (UTRW/GM) were close, with between group significances of 0.088 and 0.078 respectively.

Table 8. Descriptive Statistics for Selected Craniomandibular Proportions

Variable	**Mean ± SD**		**Homogeneity of variances**		**Robust Tests of Equality of Means**		**ANOVA significance**
	Urban	Rural	Levene	Significance	Statistic	Significance	
Upper canine breadth	0.50 ± 0.25	0.55 ± 0.19	10.0	0.002	2.2	0.15	0.109
Upper tooth row length	0.72 ± 0.35	0.80 ± 0.28	9.2	0.003	2.6	0.11	0.084
Skull length	2.4 ± 1.0	2.6 ± 0.91	5.3	0.023	1.6	0.21	0.180
Zygomatic arch breadth	1.47 ± 0.67	1.56 ± 0.55	5.3	0.022	1.1	0.30	0.268
Encephalization Quotient Including Florida*	1.49 ± 0.27	1.41 ± 0.30	0.016	0.90	4.1	0.045	0.047
Encephalization Quotient Excluding Florida*	1.46 ± 0.17	1.31 ± 0.25	0.401	0.430	1.7	0.037	0.001
Body mass (kg)*	4.53 ± 0.97	4.94 ± 1.1	0.55	0.46	6.7	0.011	0.017

Analysis of variance between urban and rural specimens. Only variables that scored below 0.30 for ANOVA significance were listed here. (*) = comparisons that fell below 0.05 ANOVA significance, indicating a statistically significant difference between the two groups.

Discussion

As was the case in Snell-rood’s (2013) example, this study has suggested that the urban environment has exerted selection in favor of higher encephalization. While ontogenetic influences of human food resources cannot be ruled out with this experimental design, the evidence at least provides some preliminary support that the urban environment is imposing some selective pressures on cognition and behavior as reflected in relative brain size. A nuanced evaluation of the environmental constraints that correspond with this encephalization event may point to such features of the city as its spatial complexity—climbing buildings and fences may be more challenging than climbing trees; its enforcement of nocturnality—requiring more somatosensory neurons; or even the presence of humans themselves—who often implement clever tricks to exterminate them. More broadly, however, and taken together with other studies, I suggest that this may reflect the general tendency in evolution for environmental change to favor the most behaviorally adaptable animals, and that this general tendency may be an important influence in the phylogenetically widespread encephalization observed across the animal kingdom.

Differences between the two groups also suggest a less pronounced jaw in urban populations, with UCW/GM and UTRW/GM values being lower, albeit with less statistical significance than the EQ comparison. There may be a multitude of different explanations for a less pronounced jaw in urban raccoons, so any speculation as to evolutionary forces responsible would be out of place. Reduction in jaw size may be adaptive for many features of the urban environment.

This study is only preliminary. Raccoon phenotypes may vary depending on other aspects of the environment and even individual cities are likely to have different selective pressures from one another. Most of the specimens in this study were from the Midwest (Oklahoma, Tennessee, Kentucky, Missouri, and Arkansas). The more pronounced effects may be seen in raccoons that live in the hearts of bigger, denser cities such as New York or Los Angeles. Urbanization is a relatively new environmental phenomenon, and evolutionary responses to it are meaningful case studies in the larger story of evolution.

As for the validity of using raccoons as a model—one of the two assumptions about extrapolation from Chapter 1—I can only point to work that has been done previously. Relative brain sizes differing between urban and rural populations was seen in another collection of mammal taxa (Sol et al. 2008), and the same has been shown in birds (Kark et al. 2007; Shultz et al. 2010). This pattern—of encephalization differing in urban and rural populations—being observed now in this study as well, further points to a potential evolutionary consequence of urbanization on at least some commensals.

CHAPTER 5

DISCUSSION

Scope and limitations

In the end, the results presented here appear to support several interesting trends in relation to encephalization. First, omnivory is positively associated with encephalization in mammals and supports the argument that city living is positively associated with encephalization in raccoons. Such results are scientifically valuable in and of themselves, but they may be interpreted in a number of ways. My argument on behalf of the proposed mechanism for evolution of complexity depends on abstract reasoning that is not entirely quantifiable—not least with the data collected as part of a two-year Master's thesis—and relies on several assumptions that are disputable. Nonetheless, I think it is a reasonable argument and it is at least preliminarily supported by the data. Furthermore, I think the experimental approach is an important one for future research, in both the pursuit of a better understanding of broad scale evolutionary patterns, and in understanding how nature is adapting to humans in this ever-changing landscape. Perhaps the latter is a more practical consideration, but I find the former more interesting.

So while I want to stress the importance of these findings and their potential relevance to this complex biosphere, I also hope to reiterate and remind both myself and the reader not to overinterpret the data; which can and often does lead to all manner of unfortunate misunderstandings (Rizak and Hrudey 2006). I do not plan to assert that these findings are proof-positive that simple life will invariably evolve into featherless bipeds or anything. That being said, however, I do think I will have laid the foundation for a compelling argument as to why complexity is a predictable consequence of competing replicators in variable environmental conditions. This thesis is an introduction to that argument, one that I hope to pursue further in my academic career.

Argument summary

Without rehashing too much of what has been covered in previous chapters, my general thesis is as follows: If generalists are more highly encephalized than specialists, and if generalists are better able to survive in periods of environmental flux, then periods of environmental flux will disproportionately select for more encephalized individuals. The second and third chapters were meant to address the two premises, and the fourth chapter was meant to observe the effect. I will discuss how well the experimental approaches achieved those ends, but first, I think the abstract argument itself deserves some elaboration, in light of some good questions and feedback received in the development of this thesis.

First of all, what is meant by a “generalist” or a “specialist” here? For most of this thesis, animal behavior has been the focus, but generalism can apply to other features of various clades of organisms (Machovsky-Capuska 2016). Broadly speaking, a generalist is any organism that can respond adaptively to a greater variety of environmental conditions, while a specialist is very efficient at exploiting a narrower niche (Cariani 2001). This of course can be just as true of plants as of animals. Plants don’t have nervous systems, but they do interact in complex ways with their environment (Felton 2008), responding to light levels and chemical concentrations (Biella et al. 2019), and some plants are more generalistic than others, able to survive in different biomes, while other plants are confined to much more narrow niches (Fine et al. 2006). The same goes for fungi (Badet et al. 2017), for protists (Orsi et al. 2012) and bacteria (Kwon et al. 2017). There is always a give and take between efficiency in exploiting a particular niche and flexibility in being able to exploit many. As discussed earlier, such interactions disproportionately favor those with more niche flexibility when the environment undergoes significant changes (Vasquez and Simberloff 2002; Balisi et al. 2018). If the Earth's environment had been completely unchanging for its entire existence, one might suspect that every niche would be occupied by an organism that exploits it with near-perfect efficiency, a planet of absolute specialists (Tajika 2017). Clearly such perfection does not exist, and the Earth has undergone radical, sometimes rapid and extreme changes, leading to repeated episodes of chaotic mass extinctions (Jablonski 1984). Maybe it was these episodes and similar environmental changes that created strong selective conditions in favor of niche flexibility.

Environmental change may therefore select for generalism (Vasquez and Simberloff 2002; Balisi et al. 2018), but how does that relate to complexity? Is there an association between generalism and complexity, and if there is, what kind of association is it? This thesis has primarily only discussed generalism as it pertains to feeding behavior, and complexity as it pertains to encephalization quotient, both of which are far from perfect proxies. Sure, omnivores do have a bit more niche flexibility in general (Schultz et al. 2005), but not all plant foraging (or prey hunting) behaviors are cognitively equivalent (Deacon 1990); and in any case, feeding ecology is only one dimension of an animal's behavioral repertoire (Begon et al. 2009). Omnivory was an earnest but rough approach to get at generalism, and encephalization quotient was an earnest but rough approach to get at complexity. I'll discuss more about the utility of those approximations in the next section, but first I want to discuss this association between generalism and complexity more broadly.

Evolution of complexity has repeated one conspicuous pattern—one that has taken different physical forms but has served the same in purpose—compartmentalization (Paegel 2010). Time and time again, organisms have solved existential problems by dividing labor asymmetrically among their component parts, or as an alternative way to describe the same thing—join forces and *become* component parts of a new whole. Eukaryotes were able to compartmentalize various cellular functions into organelles (Gabaldón and Pittis 2015), which were each able to become very specialized in their own right. The differentiated cell as a whole was thusly able to perform a greater variety of functions, making it more generalistic, and since the eukaryotic cell was compartmentalized, it had an additional layer of interdependent systems, making it more complex than the prokaryotic cell. In this way, the eukaryotic cell was able to expand its niche breadth by adding a new layer of complexity, one of compartmentalization and subsequent specialization of subcomponents (Knoll 2000).

This same pattern of compartmentalization and specialization of parts was repeated—multicellular organisms enlisted individual cells to become specialized component parts, which further compartmentalized into composite structures like tissues, organs, and organ systems (Wake 1990). Specialization of those component parts into distinct entities, such as digestive or nervous systems, each allowed the organism as a whole to be able to withstand a greater variety of conditions during its lifetime; and the additional compartmentalization added a layer of complexity to the organism as a whole. The same pattern has also occurred in eusocial animals, in which individual organisms became the specialized component parts to the more general colony, or superorganism, as a whole (Nowak et al. 2010). One might also argue that something similar is going on in human societies, in which people specialize into different professions (Cochran and Harpending 2009), although it’s more difficult to argue that “society” is some kind of biological unit (Queller and Strassman 2009).

So does this compartmentalization have anything to do with brain and behavior? Absolutely it does. Compartmentalization is a feature that underpins both behavior (Changizi

2005) and brain structure (Herrup and Kuemerle 1997). Intelligent, generalistic behavior emerges when an animal's compartmentalized brain succeeds at engaging particular brain subcomponents in response to certain combinations of stimuli (Rabaglia 2011). A successful generalistic organism, whether it be a single cell or a mammal, is one that has *the capacity* to perform many specialized functions, but only performs them when necessary (Goldsby 2009). A cell should only produce lactase in the presence of lactose (Dzialanski et al. 2016), and a hominid should only initialize a particular sequence of specialized brain components when throwing a spear (Urbin 2012)—and another sequence when interpreting a facial expression (Sprengelmeyer 1998).

This sort of division and subdivision of labor is fundamental to the architecture of biological complexity. Some authors have discussed this evolutionary tendency in terms of competition versus cooperation between component parts (Queller and Strassman 2009; Díaz-Muñoz et al. 2016) and others in terms of ecospace exploitation (Knoll 2000). Organismal compartmentalization is a clear evolutionary pattern but one whose selective mechanisms are currently poorly understood (Díaz-Muñoz et al. 2016). However, one key feature, which I hope to emphasize, is clear—more complex organisms are more highly subdivided with more specialized subcomponents (Fragan 2018), and are as such able to withstand a greater variety of environmental conditions (Gabaldón and Pittis 2015). I believe that this relationship between compartmentalization and organismal flexibility is an important one—one that may be at the heart of the evolution of complexity.

Effectiveness of Experimental Design

A great deal of thought went in to trying to find an empirical means to compare complexity of generalistic organisms to specialist organisms. Encephalization was a quantifiable metric that was readily available and could be argued to reflect some aspect of complexity. Feeding ecology was discrete and straightforward enough, so the experimental design for Chapter 3 seemed self-evident: compare EQ between ecological specialists and generalists and see if the hypothesis holds true. The hypothesis was supported (omnivores were more highly encephalized than herbivores or carnivores), but the meaning of that finding only transmits to the broader argument about complexity and generalism if the reader accepts three major assumptions: 1. Omnivory reflects organismal generalism. 2. EQ reflects complexity. 3. The species used in analysis are a good reflection of mammals in general. The third assumption would have been better supported with a more phylogenetically even sample. The herbivore category was comprised mostly of ungulates, which are phylogenetically distant from the others, which were mostly caniform carnivorans. Even though encephalization quotient is supposed to be applicable across wide phylogenies (Harvey and Krebs 1990), a better sampling of species would have made the case better. In any case, all the data can really say is that of the limited species measured, omnivores were more highly encephalized. It does not say that generalistic organisms are more complex than specialized ones, although it is consistent with that prediction.

Far more data were collected for Chapter 4, and I think the data clearly indicate that city-dwelling raccoons are on average more highly encephalized than forest dwelling raccoons. This prediction arose from the idea that the environmental flux of urbanization would strongly select for more generalistic individuals, whose generalism would be reflected in higher EQs. Once again, for the correlation to transmit to my broader argument, one would need to accept at least two assumptions: 1. Raccoons are a good representative of animals adapting to urban environments in general. 2. It is the environmental flux associated with urbanization that selected for encephalization generally, and not some other selective pressure present in cities. Results are very interesting nonetheless. Once again, I do not argue that those results prove that changing environments select for complexity. However, the data are at least consistent with predictions arising from my thesis framework.

Future Directions

Museum collections and accompanying data provide a great tool for analyzing how animals are adapting to human influence. Comparing quantifiable features within those collections is straightforward and unambiguous. Today’s world and its ecosystems are changing rapidly, and evolutionary change is therefore not unlikely to be observable in many commensal species. This experimental design could be implemented for a wide range of different projects. One message that might be important to relay to museum and university collections is perhaps to consider temporal sampling. Some museums will collect, for instance, twenty raccoons between 1970 and 1980 and then decide that they are done collecting raccoons from that point on. They might, however, consider keeping a more temporally variable collection. It is possible that observable evolutionary changes are occurring in contemporary decades and that change might be important to document. Also, the cooperation of commercial trappers could be helpful to collect data.

Characterizing EQ and other ecological variables is a worthwhile endeavor, and one that could have been done much more effectively and thoroughly with a broader sampling of vertebrate taxa. Even without accepting the assumptions that omnivory reflects generalisticness and that encephalization reflects complexity, the relationship between ecology and brain morphology can inform many different evolutionary discussions. Additionally, if one could more thoroughly characterize the relationship between EQ and ecological generalism in various taxa, then perhaps one could better understand some of the reasons that such impressive brains have evolved in so many different lineages.

I do believe that there are as-yet undefined mechanisms of evolution that will shed light on the evolution of complexity. Could biological complexity be a predictable consequence of evolution in a changing world, or was Earth just very, *very* lucky? In this thesis, I have argued that selection for generalism in changing conditions may have contributed to increased behavioral complexity in mammals, since behavioral complexity is associated with generalism. In this discussion chapter, I have suggested that the aforementioned association may reflect a more fundamental principal of biology than just brains and tooth rows. I hope to approach this topic from various angles in future research. Experiments in this thesis provided insight into the evolution of brain size in mammals, and I hope the surrounding discussion provoked a bit of thought about broader themes of evolution. The evolution of complexity is what has ultimately allowed us to have this discussion. That evolutionary process is worth understanding.

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APPENDICES

Appendix A: Raw Data for Chapter 3

Collection	**Taxon**	**Length**	**Width**	**Height**	**Occipital Condyle Breadth**
ETSU	*Ailurus fulgens*	64	46.5	49	23
ETSU	*Ailurus fulgens*	67	43.5	42.7	23.5
ETSU	*Ailurus fulgens*	72	48	45	23
ETSU	*Ailurus fulgens*	84	43	51	23.7
ETSU	*Aonyx capensis*	89.5	61	51.2	37
ETSU	*Aonyx cinerea*	52.8	43.7	37.5	23
ETSU	*Aonyx cinerea*	63	49.5	31.8	24.5
ETSU	*Aonyx cinerea*	71	49	38	25.5
ETSU	*Aonyx sp.*	55	47.8	31.2	24.9
ETSU	*Bassariscus astutus*	49.2	33.2	26.1	17.2
ETSU	*Bassariscus astutus*	46.8	31.8	24.9	17.3
ETSU	*Canis dirus*	130	80	70	51
ETSU	*Canis latrans*	91	55.5	52	34
ETSU	*Canis lupus*	104	66	73	46
ETSU	*Canis lupus*	113.5	70	71	41
ETSU	*Canis lupus*	125	74	70	50
ETSU	*Conepatus humboltii*	41	29.2	24.7	17.5
ETSU	*Conepatus humboltii*	41	28.8	22.5	15.8
ETSU	*Conepatus meansi meansi*	50.2	34	28	20.5
ETSU	*Conepatus mesoleucus*	43	34.8	28.3	20.8
ETSU	*Conepatus mesoleucus*	49	34.5	28	20.65
ETSU	*Conepatus semistriatus*	52	36	25.3	21
ETSU	*Conepatus semistriatus*	48.5	32.8	25.5	20
ETSU	*Crocuta crocuta*	140	74	99	42

ETSU	*Crocuta crocuta*	155	87	103		53
ETSU	*Enhydra lutris*	99.5	89	56.7		40.5
ETSU	*Gulo gulo*	102	59	49		32
ETSU	*Gulo gulo*	105	66	49		36
ETSU	*Gulo gulo*	103.5	68.5	49		35.2
ETSU	*Gulo gulo*	107	66	50		36
ETSU	*Gulo gulo*	95	62	45.6		33.5
ETSU	*Lontra canadensis*	69.5	53	36		29.9
ETSU	*Lontra canadensis*	81	56	37		32.5
ETSU	*Lontra canadensis*	62	57.5	37		33
ETSU	*Lontra canadensis*	69	53	37.2		31.2
ETSU	*Lontra canadensis*	69	51	39.5		32
ETSU	*Lontra canadensis*	72	55.1	31.2		29
ETSU	*Lontra canadensis*	66	54.5	38.9		30.2
ETSU	*Lontra canadensis*	57	56.5	36.5		29.5
ETSU	*Lontra canadensis*	57.2	55.5	40.5		29
ETSU	*Lontra canadensis*	58	51.5	35		31.5
ETSU	*Lynx rufus*	89	55	45		27.5
ETSU	*Lynx rufus*	87	52	43		26
ETSU	*Lynx rufus*	78	51	44		22
ETSU	*Lynx rufus*	88	54	41		26
ETSU	*Martes pennanti*	85	47	44		25
ETSU	*Martes pennanti*	72	43	31		23
ETSU	*Martes pennanti*	74	41.5	30.5		21.5
ETSU	*Martes pennanti*	68	41	34		22
ETSU	*Martes pennanti*	83	46	36		25
ETSU	*Martes pennanti*	74	42	35		21.5
ETSU	*Martes pennanti*	69	41	31		21
ETSU	*Martes pennanti*	69	43	29.8		21.5

ETSU	*Martes pennanti*	67.5	40.5	31.5		22.5
ETSU	*Mephitis mephitis*	50	29	21.8		17.9
ETSU	*Mephitis mephitis*	48	27.8	21.9		18
ETSU	*Mephitis mephitis*	48	28.2	21.5		18.05
ETSU	*Mephitis mephitis*	45	27.5	22.5		15.85
ETSU	*Mephitis mephitis*	43.5	26	21.2		16.9
ETSU	*Mephitis mephitis*	51.6	28.1	21		18.75
ETSU	*Mephitis mephitis elongata*	49	27.35	24		18.15
ETSU	*Mephitis mephitis elongata*	44.5	27	21.6		16.1
ETSU	*Mephitis mephitis elongata*	49.5	28.5	22.1		18.5
ETSU	*Mephitis mephitis elongata*	42	26.7	21.2		15.95
ETSU	*Mephitis mephitis elongata*	45	26.9	21.5		15.85
ETSU	*Mephitis mephitis elongata*	45	27	22		15.9
ETSU	*Mephitis mephitis elongata*	47.5	27.9	21.2		16.3
ETSU	*Mephitis mephits elongata*	50	31	22		19
ETSU	*Mustela nigripes*	48	29	23.9		16.5
ETSU	*Mustela nigripes*	47	21	21		16
ETSU	*Mustela nigripes*	40	26	20.5		14.9
ETSU	*Mustela nigripes*	47	28	19		16
ETSU	*Mustela nigripes*	43	26.5	18.5		15.8
ETSU	*Mustela nigripes*	45	28	19		15.5
ETSU	*Mustela nigripes*	46	28	23.3		14.9
ETSU	*Mustela nigripes*	51	30	22		16

ETSU	*Mustela nigripes*	48	31	21	16
ETSU	*Mustela nigripes*	49	26	17	15.5
ETSU	*Mustela nigripes*	50	23	19	17
ETSU	*Nasua narica*	68	44	40.5	23.8
ETSU	*Nasua nasua*	71	44	37	23
ETSU	*Nasua nasua*	78	46	38.3	24.5
ETSU	*Nasua sp.*	63	44.8	38.2	22.2
ETSU	*Neovison vison energumenos (male)*	43	29	22	15.5
ETSU	*Neovison vison evergladensis*	44	26	19.7	16.5
ETSU	*Neovison vison evergladensis*	41	25.5	19.5	16.2
ETSU	*Neovison vison evergladensis*	42.5	26	19.9	16.2
ETSU	*Neovison vison halilmmetes (male)*	44	28	21	16
ETSU	*Neovison vison lutensis (male)*	42.5	25	18	14.85
ETSU	*Neovison vison lutensis (male)*	47.5	26.9	19.9	15.95
ETSU	*Odocoileus sp.*	140	72	85	52
ETSU	*Odocoileus sp.*	134	75	81	51
ETSU	*Odocoileus sp.*	142	69	71	48.5
ETSU	*Odocoileus sp.*	135	69	73.5	47.5
ETSU	*Odocoileus sp.*	136	76	74	49
ETSU	*Odocoileus sp.*	128	69	63	40
ETSU	*Odocoileus sp.*	127	72	70	48
ETSU	*Odocoileus sp.*	113.5	64	58.5	40
ETSU	*Odocoileus sp.*	124	72	72	48
ETSU	*Odocoileus sp.*	133	74	69	45.5

ETSU	*Odocoileus sp.*	124	69	64		42
ETSU	*Potos flavus*	54	33.2	34		19.1
ETSU	*Procyon cancrivorous*	82	52	45		24.8
ETSU	*Procyon lotor*	74.19	48.895	38		23.11
ETSU	*Procyon lotor*	82.2	51.15	43.8		25
ETSU	*Procyon lotor*	73.83	47.68	38.17		24.4
ETSU	*Procyon lotor*	80.63	52.69	39.65		25.04
ETSU	*Procyon lotor*	75	48	38.2		25
ETSU	*Procyon lotor*	77.9	46.7	43		24.1
ETSU	*Procyon lotor*	74.7	47.5	37		24.1
ETSU	*Procyon lotor*	77.2	50.5	39.9		27.3
ETSU	*Procyon lotor*	78.5	48.1	39.15		25.8
ETSU	*Procyon lotor*	76	49	41.1		25.6
ETSU	*Procyon lotor*	77.8	48.9	43		27.2
ETSU	*Procyon lotor*	72	51	42		27
ETSU	*Procyon lotor*	78.7	46.5	39.8		27.2
ETSU	*Procyon lotor*	70.1	43	38		24
ETSU	*Procyon lotor*	82	52.5	43		26.5
ETSU	*Procyon lotor*	78	45	39.5		23.1
ETSU	*Procyon lotor*	78	51.2	41		26
ETSU	*Procyon lotor*	78.7	48.2	39.1		25.1
ETSU	*Procyon lotor*	73	49.1	43.5		24.9
ETSU	*Procyon lotor*	73	48.1	41.1		25.3
ETSU	*Procyon lotor*	79.8	59.6	40.7		26.7
ETSU	*Procyon lotor*	78	49	42.8		24.9
ETSU	*Pteronura brasiliensis*	113	78.5	55		41
ETSU	*Taxidea taxus*	75.5	56.5	39.5		31.9
ETSU	*Taxidea taxus*	71	59	40		32.7
ETSU	*Taxidea taxus*	82	60.5	43.5		32.7

Appendix B: Raw Data for Chapter 4

Abbreviations: OMNH = Oklahoma Museum of Natural History. FMNH = Field Museum of Natural History. FLMNH = Florida Museum of Natural History. Lon = longitude. Lat = Latitude. BW = Brain case width. BL = Brain case length. BH = Brain case height. OCW = Occipital condyle breadth. UTRW = Upper tooth row width. UCW = Upper canine width. UTRL = Upper tooth row length. SL = Skull length. ZB = zygomatic arches breadth. LTRW = lower tooth row width. M1 = length of lower first molar. X's represent data that was unobtainable as in the case of a partly damaged skull, or a photo that was taken at an angle, and therefore wasn't meaningfully comparable.

Museum	**Lon**	**Lat**	**BW**	**BL**	**BH**	**OCW**	**UTRW**	**UCW**	**UTRL**	**SL**	**ZB**	**LTRW**	**M1**
OMNH	-88.027	36.9092	40	47	29.2	12.9	x	x	x	x	x	x	x
OMNH	-104.51	19.1324	48.6	75.3	43.7	19.5	27.4	17	24.5	78.9	47.3	39.3	9.3
OMNH	-81.12	31.7935	45	61.5	32.9	20.9	37	18.9	30.9	94.8	55.8	31.6	7.6
OMNH	-89.922	35.123	45	61	33.1	21	37.6	22.1	28.4	96	65	33.3	8.5
OMNH	-87.569	44.1539	43	57.8	29.2	21.2	x	x	x	x	x	x	x
OMNH	-88.139	36.8721	45	66.5	32.3	21.6	37.3	22.3	31.9	107.2	58.8	36.7	9.2
OMNH	-90.077	35.3423	44	62	31	21.7	36.6	20.2	33.7	96.2	55.2	39	9.9
OMNH	-90.06	35.3436	46.8	60	36.3	21.7	x	x	x	x	x	x	x
OMNH	-88.11	44.1496	41	61	29.85	21.9	36.4	19.9	30.2	98.5	54.3	34.5	9.9
OMNH	-89.991	35.1498	45	62.5	33	22	31.3	17.5	27.9	88.6	50.7	34.4	8.6
OMNH	-89.934	35.1119	46	65	34	22	36.2	22.5	30.3	99.9	60	36.5	9.5
OMNH	-94.313	37.1884	45.7	68.2	35.1	22.1	36.8	20.3	31.5	100.3	56.5	40.3	9.8
OMNH	-97.439	35.2225	44	64.2	32.5	22.2	30	16.3	25.4	83.4	51.5	35.2	9.2
OMNH	-87.569	44.1539	46	67	34	22.25	38.6	25.3	29.3	101.3	66.7	35	9.1
OMNH	-90.049	35.1494	41	65	32.9	22.3	34.8	19.6	30.6	91.5	50.5	33	8.3
OMNH	-88.11	44.1496	45	67.5	32.2	22.3	39.2	21.1	29.6	108.5	60.5	37	10.1
OMNH	-89.661	35.2961	46.8	64.1	34.1	22.4	39.7	22.2	34.3	104	66	37.3	10.1
OMNH	-94.313	37.1884	43	61	31.5	22.5	34	18.8	30.9	101	55.9	36.7	9.2
OMNH	-88.045	36.7734	44.2	63	33.2	22.5	35.9	20.9	31.2	98.2	59.8	37	9.4
OMNH	-97.397	35.1384	45	63	33	22.5	36.9	20.6	32.4	101.8	60.8	39.6	10.4

OMNH	-90.077	35.3423	44	66.65	32.3	22.5	37.7	22.2	33	103.1	57.4	40	9.9
OMNH	-90.06	35.3436	45.5	63.5	32	22.5	40.3	22	35.8	102.2	57	40.7	9.8
OMNH	-89.991	35.1498	46	72	34	22.5	42.6	26.1	34.9	120	74.2	39.4	9.2
OMNH	-90.049	35.1494	45.2	67	32.3	22.5	x	x	x	x	x	x	x
OMNH	-87.975	36.5769	46.3	66	34.1	22.75	37.7	23.2	33.8	106.4	59.8	37.9	9
OMNH	-87.988	36.7933	46.8	64	33	22.8	37.6	20.6	31.9	96	56	37.6	10.1
OMNH	-90.077	35.3423	45.1	68.5	34.5	22.8	37.6	21.6	32.4	108	60.5	40.4	10.3
OMNH	-97.45	35.1821	46.5	63.5	32.8	22.8	38.1	24.2	34.4	108.6	62.9	38	10.7
OMNH	-94.313	37.1884	47	63.5	33.9	22.8	40	22	29.6	108.4	69.1	36.9	9.5
OMNH	-89.916	35.1357	47	64	34.7	22.85	43	24.5	30.8	104.9	70.3	36.4	9.4
OMNH	-88.045	36.9309	44.5	64	34	22.85	x	x	x	x	x	x	x
OMNH	-89.991	35.1498	43	64	32	23	35.3	19.4	29.7	95.4	56.6	35.8	9.7
OMNH	-87.569	44.1539	50	72	35.5	23	37.7	24.1	32.5	104.4	64.7	36.2	9.3
OMNH	-87.569	44.1539	46	63.2	32.2	23	39	19	31	96	55.2	x	9
OMNH	-87.569	44.1539	45.1	63.9	33.9	23	40.3	22	33.4	106.2	66.1	39.5	9.9
OMNH	-88.015	36.6151	47	62	33	23	41.9	26	36.4	115.8	66.9	37.6	10
OMNH	-86.399	35.71	46	71	34.9	23	43.7	25	34.5	115.7	77.3	42.3	10.6
OMNH	-88.043	36.6334	47	65	34	23	x	x	x	x	x	x	x
OMNH	-88.706	35.8808	48.1	70	35	23.1	36.9	22.7	31.8	101.1	60.9	39	8.6
OMNH	-94.313	37.1884	48	66.2	33.2	23.1	43.3	24.1	35.9	117.4	70.5	37.8	9.3
OMNH	-89.386	36.0344	44.5	67	31.5	23.2	35.9	20.2	28.5	96.9	58.4	36.4	9.3
OMNH	-87.569	44.1539	47	67.8	32.8	23.2	37.5	19.5	32.3	98.8	57	39.3	9.8
OMNH	-90.077	35.3423	47	68.7	33	23.2	38.8	24	32.1	103.4	60	35	10
OMNH	-87.569	44.1539	46.1	68.6	33.5	23.2	40	24.7	30.7	105	67.7	39.4	10.2
OMNH	-90.06	35.3436	46	68	35.5	23.2	41.2	23.2	31.5	111.3	67.5	34.4	8.4
OMNH	-97.442	35.159	47	69	23.2	23.2	x	x	x	x	x	x	x
OMNH	-90.022	35.3602	47.1	69	32.75	23.3	38.6	22.1	26.6	109	69.4	39.8	10.3
OMNH	-88.045	36.7734	45	63	33	23.5	35.9	20.1	28.8	100.5	61.3	33.4	8.4
OMNH	-90.077	35.3423	44	64	32	23.5	37.6	20.7	31.3	102.8	58.5	34.3	8

OMNH	-89.925	35.1314	44.5	65.35	31.5	23.5	38.5	20.7	29.2	98	65.4	34.5	9.6
OMNH	-89.935	35.1132	44.25	65	34.9	23.5	38.5	20.4	30.8	103	61	36.1	9.7
OMNH	-88.142	36.8889	44	63.7	32.8	23.5	39.7	22.2	33.8	110.1	70.5	37.5	9.9
OMNH	-90.077	35.3423	49	65	35.8	23.5	40.8	23.4	30	110.5	64	38.8	9.5
OMNH	-94.313	37.1884	46.3	71	34	23.5	41.3	24.4	34.6	107.8	67.2	35	9.8
OMNH	-90.06	35.3436	44.5	66.5	32	23.5	41.7	24.2	31.9	109.5	67.7	37.5	9.5
OMNH	-88.015	36.6151	48.85	71.1	35.8	23.5	42.7	26	37	114.1	64.5	35.6	8.9
OMNH	-88.113	37.0006	47.2	71.1	34	23.65	40.5	23.1	34	114.3	68.1	39	9.5
OMNH	-81.12	31.7935	46.9	67.9	34	23.7	32.5	18.5	25	93.4	50.4	36.7	8.5
OMNH	-86.291	35.9303	48.1	72	33.1	23.7	41.3	22.8	32.8	116	67.7	43	11.4
OMNH	-89.929	35.1059	47.9	67.1	33.7	23.75	35.4	21.7	36	101.3	54	39.3	9.5
OMNH	-97.988	42.0697	48.7	63.5	34.5	23.75	38.6	25.1	32.1	104.1	69.4	38.3	9.3
OMNH	-90.06	35.3436	47.1	66	33.1	23.75	40.2	23	35.4	101.2	60.3	37.9	9.8
OMNH	-90.077	35.3423	47	69	35	23.8	37.4	22	30.9	106.4	63.1	33.4	7.9
OMNH	-88.043	36.6334	45.5	64.1	34.1	23.8	40.9	23.2	35	110.5	71.6	38.9	9.7
OMNH	-87.998	36.7314	45	73	33	23.8	41.1	24.6	36.9	118.4	68.3	40.1	9.9
OMNH	-88.064	36.9211	49.9	73	36	23.8	45	25.6	37.7	110	69.3	40	10.1
OMNH	-90.06	35.3436	47	72.3	33.8	23.9	36.6	22.7	32	103.6	61.3	38.5	10
OMNH	-87.926	36.6563	47	67	34	23.9	42	22.3	32.7	111.9	64.6	39.5	9.8
OMNH	-75.758	45.3177	47	67	34	23.9	42.2	26.5	36.3	112.7	71.8	36.4	9.3
OMNH	-97.484	35.2039	44.7	62.4	34	24	34.7	20.7	31	95.6	60.6	37.5	9.3
OMNH	-88.706	35.8808	41	64.5	33.1	24	35.7	20.6	30.7	99.2	63.4	31.8	7.9
OMNH	-90.06	35.3436	48.5	68	34	24	36.2	21.1	29.4	98.7	62.7	36.9	9.5
OMNH	-97.418	35.1841	46	61.2	33.3	24	36.8	22.9	28	104.8	65.5	36.3	9.2
OMNH	-87.569	44.1539	47.2	67.3	35	24	36.8	21.4	33.2	97.3	56.4	43.3	10.8
OMNH	-86.399	35.71	48	69.5	34.7	24	37.2	23.5	31.3	101.3	66.8	40.3	10.2
OMNH	-88.706	35.8808	45.9	69.5	33.5	24	38.3	21.7	33.3	108.7	59	35	8.1
OMNH	-90.06	35.3436	49	69.5	34.2	24	38.4	23.3	29.9	109	69	36.5	8.6
OMNH	-87.929	36.6603	46.1	66.8	32.2	24	38.4	22.2	32	100	61.9	36.3	9.7

OMNH	-87.569	44.1539	45.5	69	34	24	40.3	23.6	34	111	68.1	35	9.4
OMNH	-94.313	37.1884	47.2	65.8	36	24	41.5	20	31.3	103.2	66.5	37.2	9.5
OMNH	-90.06	35.3436	47.5	73	34	24	42.9	23.9	34	117.8	71.3	40.7	10.4
OMNH	-90.049	35.1494	50	69.7	40	24	43.3	23.4	31.1	114.3	67.7	39.5	9.9
OMNH	-97.616	35.3329	46.1	72	32	24	x	x	x	x	x	39.9	10
OMNH	-87.569	44.1539	47	71	33	24	x	x	x	x	x	x	x
OMNH	-79.837	32.765	46	62	32	24	x	x	x	x	x	x	x
OMNH	-94.313	37.1884	50	71.5	36.1	24.1	42	26.4	35.4	110.1	71.8	46.2	10.8
OMNH	-88.045	36.7734	45	68	33	24.15	41.3	25.8	36.3	117.3	70.2	38.2	10.9
OMNH	-99.39	36.4772	49	69.5	35.3	24.2	36	21	31.3	98.2	59.1	37.8	9
OMNH	-90.06	35.3436	42	64.9	33.8	24.2	37.3	20.2	28.7	98.5	60.2	32.4	8.2
OMNH	-102.93	36.8776	44.1	63.5	33.5	24.2	x	x	x	x	x	x	x
OMNH	-89.929	35.1059	46	63.7	34.9	24.2	x	x	x	x	x	x	x
OMNH	-88.857	35.5952	45.2	69	33	24.3	42	23.3	32.9	111.1	69.8	33.7	9.1
OMNH	-89.991	35.1498	45	67	31	24.5	34.5	21.1	30.4	96.6	50.5	39	9
OMNH	-87.569	44.1539	47	63.7	33.8	24.5	38.1	20.3	32	100.9	59.7	41.4	9.9
OMNH	-88.077	36.9804	48.95	69	33.7	24.5	41.9	25.7	35.5	115	66.9	44.7	11.1
OMNH	-89.495	35.2434	47.1	69	33.8	24.5	41.9	24.3	34.5	116.3	64.5	37	8.6
OMNH	-90.06	35.3436	46	71	33.1	24.5	43.1	25	35.4	118.9	67.7	40.2	10.8
OMNH	-94.313	37.1884	47.1	67	34.5	24.5	43.2	24.5	38.2	114.1	64.6	38.9	9.7
OMNH	-88.706	35.8808	48.9	70	35	24.5	47.1	29.3	34.9	121.9	83.5	36	8.9
OMNH	-89.991	35.1498	50	73.5	35.2	24.6	40.8	22.1	31.6	117.2	69	37.9	10
OMNH	-90.06	35.3436	45	70.5	33.7	24.6	41.4	23.1	35.2	119.2	66	36.4	8.8
OMNH	-88.045	36.7734	50	71.5	34	24.75	39.1	24.2	31.4	110.4	66.8	40.9	10.3
OMNH	-90.022	35.3602	46.8	69	35.3	24.75	42.9	25.1	32.6	119.9	76.9	38.2	9.8
OMNH	-94.313	37.1884	46	67.5	32	24.8	40.4	21.1	35.1	115.4	68.8	37.2	9.6
OMNH	-90.028	35.2636	48.5	66	35.5	24.8	40.7	24.1	33.6	109.7	72.8	37.4	9.3
OMNH	-89.938	35.118	47.5	61	31.9	24.8	41.5	22.3	34.4	109.6	64	37.2	8.6
OMNH	-88.045	36.7734	48.5	73	34.9	24.8	x	x	x	x	x	x	x

OMNH	-89.999	35.1426	42.5	62	32.9	24.9	32.6	17.8	27.6	94.7	49.4	35.6	9.1
OMNH	-94.313	37.1884	47.2	68	32	24.9	36.4	22.7	31.2	99.2	55.9	38.5	10.2
OMNH	-97.439	35.2225	46.2	68.2	33.2	24.9	38	23.9	33.8	107.1	66.5	38.7	9.7
OMNH	-87.121	35.9819	47.3	65	33.5	24.9	42	25.1	34.8	120.1	69.6	35.4	9.5
OMNH	-88.064	36.9211	46.75	63.15	33.8	24.9	43.3	24.6	34.5	107	66.8	38.8	9.6
OMNH	-89.991	35.1498	45	69	35	24.9	43.3	24.1	38.7	125.9	68.7	41.3	10.1
OMNH	-90.049	35.1494	45.9	66.2	32	24.9	x	x	x	x	x	x	x
OMNH	-88.056	36.8944	50	72	37.2	24.95	x	x	x	x	x	x	x
OMNH	-89.926	35.113	45.5	71	34.85	25	38.9	23.2	36.9	115.7	63.5	45.3	10.3
OMNH	-87.911	36.5842	45	65	34.8	25	40	23.9	31.2	101.4	68	36.9	9.2
OMNH	-100.16	36.61	49	67.8	33.9	25	40.1	24	34.9	109.9	66.9	40.2	9.9
OMNH	-88.142	36.8889	47	68	34	25	40.4	21.6	34.7	111	62.7	42.5	10.3
OMNH	-88.045	36.7734	44.8	68.5	33	25	41.3	24.6	37.2	117	65.4	40.2	9.7
OMNH	-90.049	35.1494	48.5	71	33.3	25	42.6	26.6	35.3	113.2	69.2	37.9	9.1
OMNH	-101.86	36.7692	46.5	72	35.8	25	45.1	26.2	37.2	124.2	78.3	42	10.9
OMNH	-90.06	35.3436	45.5	69	32.7	25	x	x	x	x	x	x	x
OMNH	-94.313	37.1884	48.3	75	35	25.1	37.4	24.9	34	110.8	68.9	42.4	10
OMNH	-88.05	36.9583	49	74.5	35.3	25.1	38.5	23.2	35.6	109.6	59.9	42.6	10.3
OMNH	-88.142	36.8889	47	73.2	33	25.15	39.2	21.8	34.4	115.8	68.1	38.2	9.3
OMNH	-90.06	35.3436	46	68	36	25.2	39.6	22.2	31.3	109.4	65.9	40.5	10.6
OMNH	-104.51	19.1324	45.1	68.3	32.9	25.4	38.5	22.9	30.3	109.3	61.3	41.6	9.9
OMNH	-89.929	35.1059	48.5	71	33.8	25.5	37.1	21	33.6	105	66.7	38.7	9.4
OMNH	-88.141	36.8992	48	65	35.9	25.5	37.3	21.7	29.6	100.7	59.5	37.2	9.9
OMNH	-81.12	31.7935	47.6	67.8	34.5	25.5	39.7	23.4	34.1	110.6	65.3	39.8	9
OMNH	-90.022	35.3602	47	70.5	35	25.5	40.5	23.1	34.7	110.5	65.9	41.2	10.1
OMNH	-88.142	36.8889	47	69	34	25.5	40.7	24.1	33.7	110.7	66.8	42.9	10.7
OMNH	-90.06	35.3436	47	69.3	33.7	25.5	40.9	23.5	35.6	115.6	73.7	39.3	9.6
OMNH	-86.399	35.71	49.5	72	35	25.5	42.9	25.2	35.4	114.2	76.2	39.6	9.6
OMNH	-90.077	35.3423	46	73.5	34	25.7	35.9	21.2	34.2	106	61.4	41.9	10.1

OMNH	-90.077	35.3423	43.4	63.75	32.7	25.75	39.9	19.5	31.4	103.9	59.3	31.5	8.1
OMNH	-88.045	36.7734	49.8	69.5	34.9	25.8	38.1	22.4	30.9	103.6	64.3	x	x
OMNH	-88.037	36.6292	48.3	67	34	25.8	42.2	26.3	35.4	114.6	76	39.1	10.3
OMNH	-94.313	37.1884	50	77	37.5	25.8	44.3	26.4	35.6	114	76.1	40.9	11
OMNH	-90.022	35.3602	47	69.5	34.9	25.9	36.9	19.8	33.3	108.3	56.2	44.6	11.1
OMNH	-90.06	35.3436	52	76	37.8	26	39.1	22.9	29.6	111	67.8	39.5	10.4
OMNH	-90.049	35.1494	49.5	70	35.5	26	43.2	25.7	32.5	108.2	74.1	31.7	9.1
OMNH	-94.313	37.1884	49.8	73	34.8	26	47.1	28.6	40.1	124.6	75.2	41.3	10.1
OMNH	-94.313	37.1884	51	73	31.75	26	x	x	x	x	x	x	x
OMNH	-104.51	19.1324	47.5	71.5	33.85	26.1	36.4	22.6	32.6	107.4	60.9	41.7	9.6
OMNH	-88.064	36.9211	52	71.8	36.2	26.1	38.8	27	33.3	105	72.1	x	x
OMNH	-81.12	31.7935	46.8	72.5	31.8	26.1	41.6	26.4	37	119.6	68.3	40.1	10.4
OMNH	-94.313	37.1884	48.6	62.2	34.1	26.1	41.6	25.6	33.7	119.8	80	39.6	9.5
OMNH	-94.313	37.1884	45	70.5	34	26.1	42.2	22.5	34	115.8	67.9	39.5	10
OMNH	-94.313	37.1884	50	70	35.8	26.2	x	x	x	x	x	x	x
OMNH	-88.042	36.8514	49	70.5	35.8	26.8	43	23.7	33.3	114.5	66.1	37.6	9.5
OMNH	-88.045	36.7734	48.5	77	41.5	26.9	x	x	x	x	x	43.1	9.9
OMNH	-94.313	37.1884	47.2	72	37.827.1	27	38.4	22.6	33.6	102.8	61.8	37	9.5
OMNH	-97.394	35.1392	47.8	70.5	37.8	27	44.8	27.8	36.4	117.3	71.6	39.9	10.1
OMNH	-88.027	36.9092	49.5	75.2	35.2	27.1	40	24.8	35.9	117.1	70.1	43.8	10.2
OMNH	-90.06	35.3436	49.5	74	37	27.2	43.2	25	38	120.5	72.2	44	10.1
OMNH	-88.142	36.8889	48.7	76	37	27.3	47.7	25.7	39.4	132.5	77.7	40.5	11
OMNH	-97.512	35.2329	48.5	77.8	35.1	27.5	42.5	26.9	37.9	130.5	69.9	41.9	9.8
OMNH	-94.313	37.1884	51	73.5	36.2	28.3	42.4	23.4	34.7	118.8	67.7	41.8	9.6
OMNH	-96.607	29.7502	51	72.5	37.9	29.5	41.5	24.3	31.7	115.1	75.2	40.1	10.35
OMNH	-94.313	37.1884	51.8	84	43.8	31.5	45.3	25.7	38.4	131.4	71.3	42.1	11.5
OMNH	-87.569	44.1539	48	66	34.9	x	44.9	25.3	34	116.9	77.1	39.6	9.9
OMNH	-94.313	37.1884	43	66	32	x	x	x	x	x	x	x	x
OMNH	-88.064	44.1772	33	59	35.7	x	x	x	x	x	x	x	x

OMNH	-87.569	44.1539	45	76	34.7	x	39.3	25.9	33.5	x	68.9	36.9	9.3
OMNH	-97.616	35.3329	x	x	x	x	40.2	25.7	35.6	110.4	69.8	41.5	9.9
OMNH	-87.569	44.1539	x	x	x	x	40.3	22.1	33.6	112.4	70.1	37.2	9.4
OMNH	-90.06	35.3436	x	x	x	x	40.5	23.4	34	117.5	67.4	38	9.4
OMNH	-97.335	35.0582	48.1	68	36.3	x	x	x	x	x	x	x	x
FMNH	-87.827	44.3478	35	43.5	28	16.7	x	x	x	x	x	x	x
FMNH	-88.03	44.4837	39.5	54.3	34	19.7	x	x	x	x	x	x	x
FMNH	-87.827	44.3478	42.7	51.7	35	19.9	x	x	x	x	x	x	x
FMNH	-79.567	8.95	41.85	57	31	20.85	x	x	x	x	x	x	x
FMNH	-88.068	41.6986	42.8	55.5	31.5	21.3	x	x	x	x	x	x	x
FMNH	-87.576	41.7836	49.7	74.5	42	21.5	49.7	30.3	41.6	131.1	81.9	43.3	9.8
FMNH	-87.23	39.7654	45.8	66.9	33.5	21.9	47	24.5	38.2	116.3	73.7	x	x
FMNH	-80.238	38.2351	43.4	64	32.1	22.35	42.3	23.3	34.2	117.5	67.7	39.6	9.1
FMNH	-81.73	32.4099	47.5	67.8	31.3	23	40.2	21	32.9	113.9	72.8	34	9.1
FMNH	-99.32	18.6167	49.5	71	40.7	23.1	x	x	x	x	x	x	x
FMNH	-81.553	30.3995	47.1	70	31.5	23.2	40.1	21.7	35.3	115	68.2	39	10.3
FMNH	-124.42	42.4073	47.2	61.8	33.8	23.2	x	x	x	x	x	x	x
FMNH	-89.352	37.1687	47.5	70	33.5	23.4	42.9	25.7	38.5	115.3	70.3	40.9	10.3
FMNH	-81.553	30.3995	47	69	35.5	23.5	40.9	22.7	34	108	74.5	37.5	10.4
FMNH	-87.037	41.6631	46.7	65.1	34.9	23.5	42.1	24.4	34.8	112.5	76	37.4	9.2
FMNH	-87.65	41.85	41.5	68.5	35.8	23.5	42.9	28	42	115.9	68.9	41.3	9.3
FMNH	-96.879	30.894	45.5	67.5	32.8	23.5	45.6	23.6	42.6	128.3	73	39.2	10.4
FMNH	-89.352	37.1687	46.7	68.2	34.6	23.7	40	24.3	34.6	118.5	69	34.4	8.4
FMNH	-81.553	30.3995	47.2	74	35	23.7	40.9	22.7	38	111.1	61.5	40.4	9.2
FMNH	-89.577	43.3594	49	67	36.5	23.7	41.4	?	35.8	?	65	39.5	10.4
FMNH	-81.547	30.7305	48.1	71.7	30.8	23.7	44.7	24.9	32.3	127.2	77.9	36.5	9.5
FMNH	-89.34	37.1328	46.75	72.2	33.9	23.75	39.1	23.5	35.6	112.3	73.2	36.5	8.6
FMNH	-97.109	27.83	47	66.2	34.7	23.8	32.6	18.7	25.8	95.6	53.2	42.2	9.4
FMNH	-73.879	40.9945	45	71.5	32.7	23.8	37.9	21.2	33.8	110.2	65.7	38.4	9.9

FMNH	-87.093	41.6394	42	65.5	33	23.8	46	22.7	33.5	123.6	69.7	40.2	9.5
FMNH	-88.011	41.8089	45.4	63.4	32	23.9	x	x	x	x	x	x	x
FMNH	-80.238	38.2351	46.1	65.75	34.4	24	29.2	16.5	20.1	76.6	50.1	29.7	7
FMNH	-87.841	42.2586	44	62	33	24	43.5	25.4	38.7	120.8	74.2	40.8	9.6
FMNH	-99.61	41.7965	49.5	73	45	24	52.2	28	39	129	84.2	43.3	10.1
FMNH	-80.298	37.7965	46.3	68	33.95	24.1	41.5	23	34.2	113	71.7	37.3	9.2
FMNH	-91.884	35.7882	44.5	62.5	33	24.1	42.5	25.6	37.5	117.4	73.2	39.9	9.5
FMNH	-84.361	25.8132	45	66.1	32.8	24.5	36.9	20.2	36.9	102.1	55.7	37.1	9
FMNH	-92.293	37.7293	48.5	68.5	39.5	24.5	37.3	21.9	35.8	102.3	60	39.6	9.4
FMNH	-87.208	39.8553	46.2	67	33	24.5	41.1	22.8	36.3	123.9	77	?	?
FMNH	-79.567	8.95	44.8	61	33.1	24.5	x	x	x	x	x	x	x
FMNH	-90.157	42.0945	50	78.5	35.7	24.6	36.5	18.9	35.3	108.5	71	38.1	10.5
FMNH	-90.92	30.2382	44.2	66	32	24.6	36.6	20.6	32.2	103.7	61.9	35.5	8.9
FMNH	-88.008	41.8195	46.5	68	40	24.7	x	x	x	x	x	x	x
FMNH	-101.12	27.8486	45.7	67.8	32.95	24.75	44	22.4	36	114.3	65.2	42.9	10.2
FMNH	-102.49	19.0946	46.3	72	36.5	24.8	48.7	28.4	44.4	129.2	76.3	41.1	10.3
FMNH	-97.109	27.83	50	75.6	37.8	24.9	41.3	25.8	35.1	114.7	70.2	46	11.5
FMNH	-99.32	18.6167	51.1	72	38.5	24.9	x	x	x	x	x	x	x
FMNH	-87.65	41.85	47.8	71	32.8	24.9	x	x	x	x	x	x	x
FMNH	-79.567	8.95	47.85	69.5	33.4	24.95	43.6	25.1	37.6	116.5	76.5	40.9	10.4
FMNH	-82.113	26.4451	47.2	74	38.5	25	33	22	36.2	94.6	68	47.7	11.8
FMNH	-102.36	19.3369	47	73.5	36.5	25	40.2	24.3	35.7	117.2	73.2	44.8	11.5
FMNH	-88.147	41.7859	46	70	36	25	40.5	22.1	34.4	108.9	64.4	36.6	9.5
FMNH	-88.011	41.8311	45.7	73.5	36.7	25	41.6	25.2	39	127	70.3	45	9.9
FMNH	-87.65	41.85	49.8	78.5	34	25	43.7	26.8	37.5	121.2	82.8	42.8	10.2
FMNH	-97.008	19.4214	48	63	32.8	25	44.9	27.3	39.1	122.4	78.5	41.1	11
FMNH	-88.049	41.7707	47	71.2	39.5	25	x	x	x	x	x	x	x
FMNH	-88.108	41.5185	42	68.2	39.5	25	x	x	x	x	x	x	x
FMNH	-117.33	34.5989	48.85	73	32.9	25.1	39.7	25.3	35.3	115	75.8	40.1	9

FMNH	-82.113	26.4451	46.8	66.1	38.8	25.1	39.7	22.5	35	109.6	70.4	44.3	11.5
FMNH	-88.011	41.8089	49.3	67.2	37.1	25.1	x	x	x	x	x	x	x
FMNH	-77.683	43.1501	47.25	67.8	33.8	25.2	43	23	36.9	124.4	71.1	41.1	10.1
FMNH	-90.367	39.333	53	73.5	39.6	25.2	43.6	25.7	37.2	114.6	77.7	40.2	9.5
FMNH	-88.147	41.7859	49	72	31.9	25.2	45.1	24.8	32.5	114.1	78.9	39.1	10.2
FMNH	-79.567	8.95	46.5	71.5	34.9	25.2	x	x	x	x	x	x	x
FMNH	-116.53	33.8284	50.5	75	36.7	25.5	34.9	22.3	28.8	101.8	65.8	41.2	9.6
FMNH	-108.21	33.19	48.7	71.5	39.5	25.5	40.1	25	35.7	110	70.4	34.2	8.5
FMNH	-79.567	8.95	46.85	72	35	25.7	40.6	23.5	39	111.7	69.2	38.7	9.4
FMNH	-103.89	30.4865	46.5	70	34.9	25.75	38	23.8	35.3	108.7	58.3	41.6	9.3
FMNH	-81.553	30.3995	50.7	73.8	38.2	25.8	41.9	24.6	35.9	123.5	81.2	39.3	9.7
FMNH	-101.12	27.8486	48	69.9	35.5	25.8	54.6	33.3	49	154.7	89.8	44.5	10.5
FMNH	-88.38	17.54	50	75	36	25.8	x	x	x	x	x	x	x
FMNH	-101.12	27.8486	48.2	70.8	34	26	40	21.6	38.6	114.5	64.8	43.6	10.8
FMNH	-101.12	27.8486	49.2	74.5	35.5	26	41.6	26.2	39.8	126.4	75.6	46.7	10.8
FMNH	-88.265	20.6012	48.9	79.1	38	26	41.7	23	33.2	123.2	78.2	40.5	9.6
FMNH	-97.109	27.83	49.5	71.8	35.6	26.2	44.4	26.3	38.1	126.4	74.9	44.9	10.8
FMNH	-88.02	44.5192	49.5	77.8	35.2	26.2	49.6	32.4	49.7	140.9	81	41.1	9.5
FMNH	-91.333	31.9832	50.3	74.9	35.5	26.4	38	24.5	33.1	113.5	71.8	41.5	10.3
FMNH	-101.12	27.8486	48.3	72.8	35.5	26.5	41.8	26.2	43	125.5	67.8	54.8	14.1
FMNH	-79.567	8.95	48.2	72	34.9	26.8	37.9	23.2	33	111	71.5	37	9.9
FMNH	-97.109	27.83	49.95	71.3	34.1	26.8	43.1	23.8	36.7	119.1	71.5	41.3	10.7
FMNH	-88.147	41.7858	49.7	74.8	39.5	26.8	45.2	29.9	41.5	129.4	75.3	45.7	10.9
FMNH	-101.12	27.8486	49.9	71.8	35.9	26.9	39.6	23.6	34.8	115.7	68.1	42.9	9.6
FMNH	-101.12	27.8486	47.95	68.9	34.9	27	44.6	24.1	35.5	117.4	70	38.6	9.7
FMNH	-70.21	44.5868	48.5	78.2	35.3	27.1	37.2	22.9	32.3	108.5	65.3	38.4	9.5
FMNH	-97.008	19.4214	43	70.5	41.5	28	42.9	25.7	35.5	112.1	67.2	40.5	10.6
FMNH	-80.238	38.2351	47.2	75	35.15	35.5	41.4	30.4	42.7	123.9	79	38	9.7
FMNH	-89.978	42.0805	51	69.5	44	x	45.1	29.1	34.1	114.7	81	37.5	9.2

FMNH	-80.072	26.9455	47.6	73	31	x	48.2	29.8	35.9	135.4	?	37.6	9
FMNH	-91.906	29.8983	49.5	70	40.7	x	38	22.8	32.8	103.3	72	42.7	11.3
FLMNH	-80.448	25.0861	49.7	68	35.5	23.7	x	x	x	x	x	x	x
FLMNH	-81.719	25.9408	47.3	72.5	34	23.7	x	x	x	x	x	x	x
FLMNH	-84.667	30.2083	48	71.5	35.5	23.7	x	x	x	x	x	x	x
FLMNH	-80.448	25.0861	46	70	33.8	23.8	x	x	x	x	x	x	x
FLMNH	-82.542	29.6512	41.2	73.5	34	23.8	x	x	x	x	x	x	x
FLMNH	-81.304	25.9011	49	72	36	24	x	x	x	x	x	x	x
FLMNH	-81.719	25.9408	48	70	36.6	24	x	x	x	x	x	x	x
FLMNH	-81.42	26.0131	46	73	36	24	x	x	x	x	x	x	x
FLMNH	-81.719	25.9408	46.3	71.5	34	24.2	x	x	x	x	x	x	x
FLMNH	-81.398	26.1144	47.7	71.5	34	24.2	x	x	x	x	x	x	x
FLMNH	-81.719	25.9408	46	72	35	24.7	x	x	x	x	x	x	x
FLMNH	-84.667	30.2083	48	73	35	24.7	x	x	x	x	x	x	x
FLMNH	-81.719	25.9408	47.2	73.5	35.8	24.9	x	x	x	x	x	x	x
FLMNH	-81.369	26.4183	47	72	34.9	24.9	x	x	x	x	x	x	x
FLMNH	-81.719	25.9408	49.5	75	35.8	25.7	x	x	x	x	x	x	x
FLMNH	-80.595	25.1678	50	73	36.3	26.1	x	x	x	x	x	x	x
FLMNH	-82.476	29.2331	47.8	72	34.7	26.3	x	x	x	x	x	x	x

VITA

PETER ANDERSON

Education:	Westfield High School, Westfield, IN, 2008 B.S. Biology, Indiana University, Bloomington, IN, 2014 M.S. Geosceinces: Paleontology, East Tennessee State University, Johnson City, TN, 2020
Professional Experience:	Microbiologist, Mid America Clinical Laboratories, Indianapolis, Indiana, 2014-2015 Biology Teacher, Tindley Accelerated Schools, Indianapolis, Indiana, 2015-2017 Teaching Assistant, East Tennessee State University, Johnson City, Tennessee 2017-2018 Paleontologist, East Tennessee State University, Johnson City, Tennessee 2018-2019