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An Analysis of the Macroevolutionary Dynamics of Diet in Amniotes

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AN ANALYSIS OF THE MACROEVOLUTIONARY DYNAMICS OF DIET IN AMNIOTES

A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the Degree of

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By Frederick Bruce Tolchard

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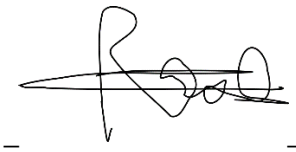
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DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.



_ _____

(Signature of candidate)

Sixteenth_____day of August_____2024_____at Braamfontein Johanneburg, South Africa

ABSTRACT

This doctoral thesis explores the macroevolution of diet in extant amniote lineages and two extinct lineages: early-branching synapsids and non-avian theropod dinosaurs. I collate relative dietary percentages for species- and genus-level taxa in four major amniote lineages (turtles, lizards, birds, and mammals). By applying a rigorous, transparent, and repeatable analytical framework and considering both extant and fossil species, this research enhances our understanding of the intricate interplay between diet, body size, and evolutionary history.

In Chapter One, I employ principal components analysis and k-means cluster analyses on percentile data of different food sources in the dietary compositions of extant amniote taxa to delineate dietary guilds without relying on arbitrary diet classification thresholds. The key findings of this chapter are: (a) invertebrate material is the most widespread food source among different dietary guilds, and (b) the majority of species in all major amniote lineages include some animal-based food in their dietary composition, except mammals.

In Chapter Two I use marginal maximum likelihood modelling to investigate the tempo and directionality of evolutionary transitions between dietary guilds in each major lineage of amniotes. The key findings of this chapter are: (a) invertivory, the ancestral condition of most amniote lineages, is the most evolutionary plastic feeding strategy, (b) evolutionary shifts between specialist herbivorous and faunivorous guilds follow multiple evolutionary pathways through a spectrum of generalist dietary strategies. Evolutionary reversions are frequent at all stages along these evolutionary pathways.

In Chapter Three, I utilize linear modelling and analyses of variance to assess the correlation between diet and body size in each major amniote lineage in a phylogenetic comparative framework. The key findings of this chapter are: (a) neither individual food item percentages nor dietary guild memberships explain body size variance in aggregate among amniotes,

however (b) invertivory and nectarivory are correlated with the lowest body sizes among amniotes.

The synthesis of these results is a macroevolutionary pattern wherein evolutionary shifts occur out of ancestrally invertivorous lineages, through omnivorous and generalist feeding guilds, into specialised carnivorous and herbivorous descendants. Evolutionary shifts out of invertivory often conflate with increased body size.

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GENERAL THESIS INTRO

1. Background

Diet is fundamental to many aspects of amniote biology. These aspects encompass life history, physiology, anatomy, and ecology, among others. Dietary preferences help drive adaptations in anatomy, physiology, and behavior. Dietary classification is a challenging undertaking, given the high variation in feeding habits, and traditional schemes (e.g., faunivory, omnivory, herbivory) belie important differences in patterns of nutrient acquisition. Traits hypothesized to be causally linked to, or strongly affected by, dietary strategy in amniotes include the digestive system, metabolism, tooth structure, locomotion, sensory organs, reproductive strategy, growth rate, behavioral adaptations, habitat and ecological niche (Alcock, 2009; Feldhamer et al., 2020; Gill, 1995; Reece & Rowe, 2017; Vitt & Caldwell, 2013; Wu, 2017). As such, numerous hypotheses have been developed over time to explain the role of diet in shaping macroevolutionary trends in amniotes, and in animals generally.

The earliest Palaeozoic amniotes are often hypothesized to have been invertivorous, or to have fed on small aquatic vertebrates like their amphibian relatives (Modesto et al., 2009; Sahney et al., 2010; Sues, 2000; Sues & Reisz, 1998). The evolution of carnivory (dietary composition consisting nearly entirely of vertebrate meat) from invertivory requires, among others, the evolution of teeth suited for slicing meat rather than piercing and crushing insects (e.g., Van Valen 1969). Carnivores that feed on prey larger than themselves also evolve stronger bite forces relative to their body masses than their invertivorous and piscivorous evolutionary relatives (Christiansen & Wroe, 2007). Beyond oral processing considerations, vertebrate

carrion is easier to digest and more abundant in readily-available energy than invertebrate material, resulting in the evolution of simple digestive systems (Hume, 2003), and reduced activity in carbohydrate-processing enzymes (Schondube et al., 2001) in carnivorous amniotes (Stevens & Hume, 2004). The earliest evolutionary shifts in diet were, thus, from invertivory to carnivory as adapting to a diet of vertebrate prey requires less anatomical and physiological adaptation than does incorporating plant matter into the diet (Sahney et al., 2010).

The earliest unambiguous herbivorous tetrapods evolved in the late Carboniferous (Sues & Reisz 1998). By the Early Triassic, herbivory had evolved multiple times independently in synapsids (e.g., caseids, edaphosaurids, anomodonts, therocephalians, and cynodonts), parareptiles (e.g., pareiasaurs and procolophonids), archosauromorphs (e.g., rhynchosaurs and trilophosaurids), and captorhinid reptiles (Sues, 2000; Sues & Reisz, 1998). Each clade evolved a unique suite of anatomical adaptations for herbivory. For example, anomodont therapsids evolved edentulous beaks (Cruickshank, 1978; King et al., 1989; Sues & Reisz, 1998), while pareiasaur parareptiles developed leaf-shaped teeth for shearing plant material (Sues & Reisz, 1998). In modern taxa too, different taxa have evolved different dental apparatus adapted to a herbivorous diet. Herbivorous iguanid lizards, for example, have evolved labiolingually-compressed, multicusped dentition for shearing through plant material (Cooper Jr & Vitt, 2002; Hotton III, 1955; Hotton et al., 1997; Sokol, 1967). Herbivorous mammals, by contrast, tend to evolve dentition better suited to crushing and grinding plant material (Damuth & Janis, 2011; Gailer & Kaiser, 2014; Janis & Fortelius, 1988; Morales-García et al., 2021).

Vertebrates lack the digestive enzymes necessary to break down plant cell walls and absorb their contents (Sues & Reisz 1998). Early herbivorous amniotes therefore must have evolved endosymbiotic relationships with micro-organisms to facilitate cellulysis, permitting the digestion and metabolism of plant material (Sues & Reisz 1998). Extant herbivorous amniotes, particularly folivores which feed on vegetative plant material, also tend to evolve longer and/or more complex digestive tracts, and increased enzymatic activity, to ferment less-energy dense plant material (M. Clauss et al., 2013; Phoebe D Edwards et al., 2020; Kohl et al., 2016; O'Grady, 2006; O'Grady et al., 2005; Olsen, 2015; Stevens & Hume, 2004). In modern mammals, the primary division between two types of complex herbivorous digestive systems is between foregut-fermenters and hind-gut (or caecum-colon) fermenters (Alexander, 1993; Chivers, 1989; Clauss et al., 2003). Adaptations analogous to the structures involved in hindgut-fermenting have evolved in reptiles and birds as well (Hunt et al., 2019; O'Grady, 2006). The hoatzin is an example of a bird that has converged on the foregut-fermenting (specifically ruminant) anatomy of digestion of fibrous plant material (Grajal, 1995). Herbivorous tetrapods tend to have longer or broader trunks with wider ribcages, relative to overall body size, to accommodate this expanded gut processing apparatus than their faunivorous relatives (Dearing, 1993; Sues, 2000; Sues & Reisz, 1998).

The evolution of herbivory is also accompanied by changes in tooth morphology and jaw musculature. In terms of gross dental morphology, crowns with adaptations for crushing and grinding, such as labiolingual expansion of the crown or complex cusp anatomy, are indicative of increased levels of plant material in the diet in living and extinct amniotes (Paul M. Barrett, 2014; Evans & Pineda-Munoz, 2018; Melstrom, 2017; Norman & Weishampel, 1985; Sues, 2000; Sues & Reisz, 1998). Most extant

herbivorous reptiles, and many extinct ones, have leaf-shaped crowns designed for shearing through plant material as opposed to the complex crowns found in herbivorous mammals (Sokol, 1967; Weishampel & Norman, 1989). Some herbivorous lineages, such as anomodont therapsids, and some lineages of theropod dinosaurs evolve edentulism (Lautenschlager & Porro, 2017; Lautenschlager et al., 2013; Pearson et al., 2013; Rybczynski & Reisz, 2001; Sues, 2000; Sues & Reisz, 1998; L. E. Zanno & P. J. Makovicky, 2011). In addition to dentition, the processing of plant material in the mouth requires enlarged and mechanically advantaged adductor musculature of the jaw (Norman & Weishampel, 1985; Pearson et al., 2013; Sues, 2000; Sues & Reisz, 1998).

Many of the anatomical and physiological phenomena listed above are in reference to dietary extremes; carnivory of large vertebrates, and folivory of vegetative plant material. Reproductive plant structures (e.g., fruits, seeds, and nectar) are a common component of the diets of many modern omnivores (Christiansen & Wroe, 2007; Cork, 1996; Reuter et al., 2023) and herbivores (i.e., frugivores, granivores, and nectarivores). This kind of plant material is easier to digest and more energy-dense than fibrous vegetative plant material (Ayala-Berdon & Schondube, 2011; Brown et al., 1978; Clarke & O'Connor, 2014; Gartrell, 2000; Hulme & Benkman, 2002; Jordano, 2000).

Modern birds and bats, which have evolved lower food retention times in the gut as part of a series of adaptations to reduce energy expenditure to facilitate powered flight, have evolved dietary strategies specialising in reproductive plant structures multiple times (Ayala-Berdon & Schondube, 2011; Daniel Kissling et al., 2009; Karasov & Levey, 1990; Kunz & Ingalls, 1994; Song et al., 2020; Wang et al., 2020).

In particular, nectarivory does not require the evolution of a complex digestive system as nectar and tree sap provide an immediately bioavailable source of energy from easily-digestible carbohydrates (Gartrell, 2000; Mqokeli & Downs, 2013; Teixeira et al., 2013). The consumption of fruit and seeds (frugivory, and granivory respectively) necessitates adaptations to oral and gut processing such as changes in enzymatic activity, but not to the same extent as high-fibre folivory (Bodmer et al., 2006; Bodmer, 1989; Brown et al., 1979; Hulme & Benkman, 2002; Jordano, 2000; Lundgren, 2009). While seeds are a concentrated source of high-quality carbohydrates and energy, the processing of seed husks requires adaptations for grinding in mastication and digestion that is hypothesized to lay grounds for the evolution of folivory in certain lineages like primates (Lambert, 1998; Rosenberger et al., 2011).

Further to the finer detail revealed by separating animal-based food material into invertebrates and vertebrates, and plant-based food into reproductive and vegetative plant structures, the accurate categorization of diet in amniotes remains a difficult task. Many herbivores, such as arboreal mammalian herbivores like koalas and colobine monkeys, incorporate both fibrous and non-fibrous plant material into their diets (Bodmer et al., 2006; Cork, 1996). It is common for nectarivorous and frugivorous birds to supplement their diets with invertebrates as a source of protein and seasonally when their preferred plant-based foods are scarce (Gartrell, 2000; Herrera, 1984). Many lizards incorporate different kinds of plant material opportunistically into an otherwise-invertivorous diet (Cooper Jr & Vitt, 2002; Espinoza et al., 2004; Oonincx et al., 2015; Teixeira et al., 2013). It is also very common for lizards to undergo an ontogenetic shift from invertivory to herbivory (Durtsche, 2000; Mautz & Nagy, 1987; Pough, 1973; Van Leeuwen et al., 2011).

Many faunivores incorporate a combination of vertebrate and invertebrate material (Carbone et al., 1999; Reuter et al., 2023; Van Valen, 1969), and some carnivorous reptiles are invertivorous, or partially invertivorous, as juveniles (Purwandana et al., 2016; Tucker et al., 1996). There are also many amniotes that obligately consume a combination of disparate food types in their regular diets across ontogenetic stages.

Invertebrates and non-fibrous plant material form the most common components of the dietary compositions of omnivorous reptiles, birds, and mammals (Christiansen & Wroe, 2007; Figueras et al., 2021; Jiangzuo & Flynn, 2020; Mulwa et al., 2013; Pineda-Munoz & Alroy, 2014; Reuter et al., 2023). Beyond that, omnivorous taxa include various combinations of different food types in their diets. This broad, grey area in dietary classification in extant amniotes suggests that early instances of evolution of herbivory were from invertivorous ancestors by way of an omnivorous transitional stage (Barrett, 1998; Paul M Barrett, 2014; Barrett et al., 2011; Sahney et al., 2010; Sues & Reisz, 1998). Extant omnivores, especially reptiles, often lack conspicuous adaptations to omnivory that differentiate them from invertivores (Cooper Jr, 2002; Morales-García et al., 2021; Sues, 2000; Sues & Reisz, 1998). Especially from the perspective of oral-processing apparatus, dietary habits of fossil records are only most accurately inferred at the extremes of the dietary spectrum (carnivory, folivory). Therefore, the diets of extinct organisms are often misspecified, resulting in assumptions about the evolution of different dietary strategies in deep time relying on inferences drawn from low-resolution data (Casey & Post, 2011; Davis & Pineda Munoz, 2016).

2. The current study

There are several fundamental questions that remain unanswered about the evolution of diet in amniotes and how it relates to biology and life history traits. For one, research on macroevolutionary trends in extant non-bird reptiles using high-resolution dietary data is currently limited. Such data, and efforts towards developing complex approaches to dietary classification based off it, are present in birds and mammals (Pineda-Munoz & Alroy, 2014; Verde Arregoitia & D'Elía, 2020; Wilman et al., 2014). A better understanding of the diversity of dietary guilds and the patterns of food consumption in extant amniotes would be informative to inferring the kinds of dietary strategies we would expect to see among extinct organisms. Secondly, to my knowledge at the time of writing this thesis, there is no comprehensive review of the directionality, tempo, and pace of evolutionary transitions between precise dietary guilds in all extant amniotes. Numerous studies have attempted to address this issue in individual clades at varying taxonomic levels (Amador & Giannini, 2021; Burin et al., 2016; Meiri, 2008; Olsen, 2015; Price et al., 2012; Reuter et al., 2023), though there is a lack of synthesis. Commonalities in patterns of evolutionary transitions between dietary guilds in extant amniote clades would be informative of the patterns in dietary evolution through deep time. The interplay between refining dietary classification and identifying patterns in evolutionary transitions provides a basis for further investigation of the macroevolutionary relationship between the evolution of diet and other life history traits in amniotes.

A large body of scientific research is dedicated to the evolutionary, biological, and ecological relationship between diet and body size in extinct and extant amniotes alike (Benavidez et al., 2018; Brocklehurst, 2016; Brocklehurst et al., 2017; Carbone

et al., 1999; Case, 1979; Clauss et al., 2003; Clauss et al., 2007; M. Clauss et al., 2013; R. Cooke et al., 2022; Espinoza et al., 2004; Gittleman, 1985; Meiri, 2008; Pineda-Munoz et al., 2016; Price & Hopkins, 2015; Van Damme, 1999; Vitt, 2004; Zanno & Makovicky, 2013). However, there are inconsistencies between the wealth of literature available on the topic in regards to the quality of data used, and the taxonomic range covered. A widely reported phenomenon is the U-shaped curve in body size in amniotes wherein folivores and carnivores tend to larger body sizes, while invertivores, omnivores, and other guilds tend to smaller body sizes. Conventional wisdom holds that herbivorous amniotes tend to larger body size classes than their faunivorous evolutionary relatives to accommodate for their more extensive digestive apparatus (Espinoza et al., 2004). This is commonly referenced as the “Jarman-Bell Principle” following a series of studies in body size distribution in mammalian herbivores (Bell, 1971; Belovsky, 1997; Jarman, 1968). Numerous studies have shown that faunivores cannot sustain themselves at larger body weights, energetically, on a strictly invertivorous diet (Carbone et al., 1999; De Cuyper et al., 2019; Vézina, 1985). There is some debate as to whether this pattern in the distribution of body size along dietary lines is reflective of adaptations in digestive physiology to the kinds of food items consumed, or the product of ecological opportunism or other factors (Brocklehurst et al., 2017; Carbone et al., 1999; Case, 1979; Clauss et al., 2003; Clauss et al., 2007; M. Clauss et al., 2013; Cruz et al., 2011; De Cuyper et al., 2019; Demment & Van Soest, 1985; Espinoza et al., 2004; Franz et al., 2011; Sander et al., 2011; Vitt, 2004).

The gaps in knowledge listed above represent a few opportunities to better refine our existing understanding of the role of diet in shaping the macroevolutionary trends in amniotes. In this thesis, I will address them in a manner that (a) uses the highest

quality data available, and (b) covers a broad range of extant reptiles, birds, and mammals. I will also compare my findings on extant clades with high data resolution to extinct groups with more limited data drawn from inferences from fossil remains. I will then speculate on the nuances in understanding the evolution of diet that are lost in studies on extinct clades and make recommendations regarding the use of diet as an appropriate metric for investigating certain macroevolutionary questions in amniotes.

In Chapter One, I present a transparent, unbiased, repeatable approach to classifying diet in amniotes. I do not believe, given the complex and widely variable dietary strategies that evolved in amniotes through time, that sorting diet into discrete, mutually exclusive categories based on arbitrary parameters is the most appropriate approach to treating diet as a variable in analysis. Rather, I believe that an approach that treats diet as a spectrum of different food types, and seeks to identify patterns in how those food types naturally co-occur in the diets of amniotes, will prove more informative. I will, subsequently, make use of cluster analyses on large datasets of the diets of extant turtles, lizards, birds, and mammals. These datasets are compiled to show the diet of each species as percentage values of different food types (incl. arthropods, gastropods, terrestrial vertebrates, fish, fruit, seed, nectar, and vegetative plant material). I use high-quality existing datasets for birds, and mammals from the EltonTraits database (Wilman et al., 2014). For turtles and lizards, I present novel datasets of detailed proportional dietary data for each species' diet I compiled using literature sources. I use the cluster analyses to generate dietary guilds in each clade, reflecting the natural spread of the dietary data I collected, which I will utilise in the subsequent two chapters.

In Chapter Two I investigate the tempo and directionality of evolutionary transitions between dietary guilds. I will use a combination of marginal maximum likelihood models, and stochastic character mapping to examine differences and similarities in the dynamics of transitions between dietary guilds in turtles, lizards, birds, and mammals. The value of this exercise is that it will illuminate the most common evolutionary pathways between different dietary guilds across the major amniote lineages. To complement these findings, I will repeat the analyses using the simpler "classical" dietary categories of "faunivory" (diet dominated by animal-based food), "herbivory" (diet dominated by plant-based food), and "omnivory" (neither animal- nor plant-based food is dominant in dietary composition). I will run the supplementary analyses in turtles, lizards, birds, and mammals, as well as two fossil clades for comparison; non-mammalian synapsids, and non-avian theropods. I select these lineages as both include multiple independent origins of herbivory (Barrett, 1998; Paul M. Barrett, 2014; Barrett et al., 2011; Hotton et al., 1997; Reisz & Frobisch, 2014; Sues & Reisz, 1998; L. E. Zanno & P. J. Makovicky, 2011). These results will be informative in revealing the finer details in the evolution of diet that are not discernible in analyses using crude dietary categories as is often the case in studies on extinct taxa.

In Chapter Three, I investigate the statistical relationship between diet and body size. I will take a two-fold approach; (a) I will test the correlation between body mass and the percentage of each food type in the diet, and (b) the distribution of body mass ranges between the discrete dietary guilds. I incorporate phylogenetic comparative methods (Felsenstein, 1985) to correct for the non-independence introduced by the underlying phylogenetic structure of the data. As with the analyses in Chapter Two, I will perform a supplementary set of analyses using classical dietary guilds in both the extant and extinct clades. These analyses will reveal (a) if diet is a reliable predictor of, and macroevolutionary correlate to, body mass in amniotes, and (b) if differences in the way diet is classified impact this result. The significance of this for palaeontology, going forward, is to determine whether diet should be used as a factor in assessing macroevolutionary patterns in body mass in amniotes and, if so, which approach at characterising diet is most appropriate when doing so.

CHAPTER ONE

1. Introduction

Diet in amniotes is a complex physiological, behavioral, and ecological phenomenon. The evolution of dietary variation between species over time has played a key role in driving the evolution of variation anatomy, ecophysiology, and behavior as a series of adaptive responses to new dietary ecological niches (Amador & Giannini, 2021; Chivers & Hladik, 1980; Greene, 1982; Grundler & Rabosky, 2021; Jenkins, 1981; Lafuma et al., 2021; Lintulaakso et al., 2023; Losos & Greene, 1988; Melstrom et al., 2021; Miller & Pittman, 2021; Ocampo et al., 2022; Pollard & Puckett, 2021; Pough, 1973; Román-Palacios et al., 2019; Santana et al., 2010) A single species, or even a single individual, can consume different dietary items throughout its life, during different seasons, or even over the course of a single day. Therefore, effectively capturing and classifying diet for a whole species, comprising many individuals, is not straightforward. Because of this, pragmatic classifications of diet are often contingent on informed, but essentially arbitrary decisions. The criteria upon which dietary classification rely may have a measurable impact on the results of scientific studies using diet as a variable (Lintulaakso et al., 2023; Pineda-Munoz & Alroy, 2014; Reuter et al., 2023; Verde Arregoitia & D'Elía, 2021). The collection of dietary data and the classification of diet are, therefore, important considerations before investigating the role of diet in macroevolutionary trends in amniotes.

An understanding of how existing scientific literature categorizes dietary strategy in the animal kingdom begins with the traditional, or "classical", system of classifying animal diet. Under this system, a taxon is placed into either "faunivory", "omnivory", or "herbivory" based on their diets (e.g., Pineda-Munoz and Alroy 2014). From an

ecological perspective, faunivores occupy the higher trophic levels in a given ecosystem, herbivores the lower levels, and omnivores occupy multiple trophic levels (Price & Hopkins, 2015; Price et al., 2012; Tanabe & Namba, 2005). The approximate proportion of animal-based foods relative to plant-based food sources in the dietary composition is the only consideration in classifying an animal into dietary guilds under this system.

Animal-based diets represent the ancestral condition in amniotes (Sues, 2000; Sues & Reisz, 1998). However, there are important differences between different animal food types. The most important distinction is between invertebrate food sources and vertebrate meat. Carnivory on terrestrial vertebrates (Van Valen, 1969) and piscivory (Britt et al., 2009) each require specific adaptations in oral processing anatomy relative to invertivory (Evans & Sanson, 2006; Meloro & O'Higgins, 2011; Sacco & Van Valkenburgh, 2004). The key difference between invertivorous and carnivorous dentition is that the former is adapted to piercing through exoskeletons while the latter is suited to shearing through meat (Van Valen, 1969). In terms of gut-processing apparatus, there is little morphological difference between invertivores and carnivores (De Cuyper et al., 2019; Hume, 2003). Additionally, carnivory has been repeatedly found to necessitate or, at least, facilitate higher average body size in terrestrial amniotes than most forms of invertivory since increased predator size is needed to effectively hunt larger prey which, in turn, provides a higher source of protein and energy (Carbone et al., 1999; Marcus Clauss, Patrick Steuer, et al., 2013; Rob Cooke et al., 2022; Reuter et al., 2023).

Beyond the invertivory-carnivory division, the term "invertebrates" covers a very wide taxonomic range including organisms with wildly different vagility, material

properties, and nutritional value. For example, there are specific anatomical requirements for durophagy (consumption of gastropods, mollusks, crustaceans, and other hard-shelled organisms) including bulbous dentition, stronger jaw musculature, and increased jaw mobility (Dalrymple, 1979; de Souza Leite et al., 2021; Evans & Sanson, 1998, 2006; Figueirido et al., 2013; Hartstone-Rose & Steynder, 2013; Pfaller et al., 2011; Wisniewski et al., 2023) that differentiates it from “soft” invertivory (the consumption mainly of terrestrial arthropods with weaker exoskeletons). Another example is myrmecophagy: the consumption of social insects like ants and termites. The chitinous exoskeletons of their prey require digestive adaptations in the microbiome and enzyme activity (Cavalcanti et al., 2023; Delsuc et al., 2014; Redford, 1987; Zhang et al., 2021). Furthermore, because myrmecophages consume prey that is available in larger concentrations than other insects, facilitating a higher upper body size bound than is expected in other terrestrial insectivores (Cavalcanti et al., 2023; McNab, 1984). There is very little existing research on the different subcategories of invertivory, like durophagy and myrmecophagy, in relation to macroevolutionary trends in amniotes.

In the current study, I use “faunivory” as an inclusive term encompassing dietary strategies composed predominantly of animal-based food material. I use the term “carnivory” to describe a diet composed primarily of the meat of terrestrial vertebrates, and “piscivory” to refer to a diet composed primarily of fish. I use the term “invertivory” to refer to a diet composed primarily of invertebrate material. I use “insectivory” to refer to an invertivorous diet composed primarily of terrestrial arthropods, and “durophagy” to refer to a diet composed of gastropods, mollusks, or crustaceans.

Diets consisting primarily of plant material, or herbivorous diets, have evolved independently multiple times in multiple amniote lineages through time (Sues, 2000; Sues & Reisz, 1998) . Treating “herbivory” as a single, overarching guild in macroevolutionary studies obscures the impact of the important differences of different sub-categories of herbivory introduced by their different ecological and physiological requirements. The most important division within herbivory is between dietary strategies specializing in reproductive (frugivory, granivory, and nectarivory) and vegetative (folivory) plant structures. Nectar and sap are rich in readily-available sugar and energy (Brown et al., 1978; Gartrell, 2000; Teixeira et al., 2013) thus requiring very short retention times in the gut (e.g., in hummingbirds; Karasov and Levey 1990) and less-massive digestive anatomy (Battley & Piersma, 2005). Fruits have the most rapid passage time through the gut of any solid plant structure (Jordano, 2000). Both birds (e.g., Karasov and Levey 1990) and mammals (Bodmer et al., 2006; Bodmer, 1989) and birds (Battley & Piersma, 2005) are able to consume and extract the nutrients from fruit with relatively “simple” digestive anatomy. Seeds are similarly composed of easily digestible material though their husks may necessitate additional oral or gastric processing apparatus (e.g., Arregoitia et al. 2020).

Diets consisting primarily of fibrous vegetative material are the least energetically efficient, from the perspective of digestive physiology, of any other feeding strategy (e.g., Jordano 2000). A wide variety of adaptations have been identified as specialized features of folivorous diets. The evolution of folivory requires a series of complex anatomical and physiological adaptations. These include specialized dentition for grinding fibrous plant material (Damuth & Janis, 2011; Hiiemae, 2000; Janis, 1979; Kay, 1975) and complex gut processing mechanisms (Alexander, 1993;

Bodmer et al., 2006; Franz et al., 2011; Sakaguchi, 2003). Folivores include the largest terrestrial animals alive today (such elephants, giraffes, and large-bodied terrestrial artiodactyls). The evolution of folivory is thought to require a larger gut capacity to extract nutrients from low-quality fibrous food material (Battley & Piersma, 2005; Cork & Foley, 1991; Franz et al., 2011; Grajal, 1995; Stevens & Hume, 2004). This requirement has been hypothesized to drive large body size in folivores (Bell, 1971; Belovsky, 1997; Jarman, 1968). However, many smaller animals (e.g., sloths, koalas, small-to-medium sized birds, and some rodents and other micromammals) have also evolved anatomical and physiological adaptations to consuming fibrous plant material (Cork, 1996; Foley & Cork, 1992; Giné et al., 2022; Kunz & Ingalls, 1994; McNab, 1978; Pauli et al., 2016). This suggests instead that extrinsic factors may explain the apparent correlation between folivory and large body size, such as energy availability in the environment (M. Clauss et al., 2013), or limitations imposed by habitat (Bodmer et al., 2006; Bodmer, 1990; Pineda-Munoz et al., 2016).

I use the term “herbivory” to describe a diet dominated by plant-based food sources. This terminology is frequently used in contemporary research (Atwood et al., 2020; Rob Cooke et al., 2022; Pietczak & Vieira, 2017; Price & Hopkins, 2015; Price et al., 2012). There are several variations within herbivory that necessitate some measure of specialized anatomical and/or physiological adaptation. The terminology I use for these variations in the current study are: “folivory” (a diet composed primarily of high-cellulose plant material; e.g., Edwards and Ullrey 1999), “frugivory” (a diet composed primarily of fruit; e.g., Karasov and Levey 1990), “granivory” (a diet composed primarily of seeds; e.g., Lundgren 2009), “nectarivory” (a diet composed primarily of

nectar or tree sap; e.g., Mqokeli and Downs 2013), and “mixed herbivory” (with diets consisting of inputs from multiple of the above categories).

“Omnivory” is the most poorly defined dietary category of the three classical divisions. The classification of omnivory is problematic because of conflicting definitions which often rest on vague classification criteria. Intuitively, an omnivorous diet consists of animal- and plant-based food sources, with both contributing a meaningful proportion of total energy intake. Some studies have also considered a generally herbivorous or faunivorous diet consisting of two or more different kinds of plant or animal food sources respectively as being “omnivorous” (Burin et al., 2016; Reuter et al., 2023). This is where a challenge in dietary classification is drawn in the distinction between “omnivore” and “generalist”. These terms may be synonyms or may mean different things depending on context (Lopes et al., 2016; Pineda-Munoz & Alroy, 2014; Shipley et al., 2009).

A hypothetical diet consisting of nearly equal proportions of animal- and plant-based material is not reflected the actual proportions of these food sources observed in most amniote diets. In reality, the most frequent components of omnivorous diets in amniotes, when measured by number of species, are invertebrate material and reproductive plant structures (Edwards et al., 2021; Lintulaakso et al., 2023; Reuter et al., 2023). Where dietary composition is quantified in ‘omnivores’, there seems to be a bias in animal diets towards one or the other food source (Cooper Jr & Vitt, 2002). This is unsurprising since (a) invertivory is the most widely accepted ancestral condition for Amniota and several major lineages within it (Figueirido et al., 2010; Lafuma et al., 2021; Modesto et al., 2009; Mueller et al., 2018), and (b) incorporating non-fibrous plant material into an invertivorous diet necessitates less-extensive

anatomical and physiological adaptation than does the addition of fibrous plant material (Battley & Piersma, 2005; Clarke & O'Connor, 2014; Herrera, 1984; Lintulaakso et al., 2023). Some research looking into the morphological correlates to diet in oral and gut processing anatomy has also demonstrated that invertivores and omnivores overlap and occupy the widest morphospace relative to other dietary guilds, pre-adapting them to evolutionary shifts to other feeding strategies (Melstrom et al., 2021; Redford et al., 1984). Furthermore, generalist dietary strategies consisting of either a combination of animal-based (i.e., invertebrates and vertebrates) or plant-based (e.g., fruit and leaves) food sources are also very common among amniotes though the way these are classified is not consistent (Bodmer, 1989; Carbone et al., 1999; Cork, 1996; De Cuyper et al., 2019; Foley & Cork, 1992; Reuter et al., 2023).

There are also challenges in measuring omnivory, and diet in general, from an observational standpoint. Firstly, the diets of many species of amniote vary seasonally (Christian et al., 1996; Cocilio et al., 2016; Degen et al., 1997; Hall et al., 1998; Harcourt, 1986; Joshua et al., 2010; Mulwa et al., 2013; Murphy et al., 2023; Selman & Lindeman, 2018; Storms et al., 2008; van Wyk, 2015). The paucity in reporting on this phenomenon may result in omnivorous taxa being incorrectly identified as faunivorous or herbivorous based on a seasonally-restricted dietary composition (Murphy et al., 2023; Shahar et al., 2001). Secondly, many species in all major amniote lineages opportunistically incorporate food items into their diet outside their typical or preferred range of food sources (Cooper Jr & Vitt, 2002; Furness, 1988; Gormezano & Rockwell, 2013; Meiri, 2018; Reuter et al., 2023; Rosalino et al., 2005). This is often in response to temporal restrictions on food sources available, yet some lizards (Herrel, Vanhooydonck, & Van Damme, 2004; O'Grady, 2006) and

birds (Battley & Piersma, 2005) show changes in the relative sizes of different parts of their digestive tracts in very short timeframes in response to a sudden opportunistic shift in diet. Given the practical limitations on collecting detailed dietary data from wild animals, it is highly probable that seasonal and, especially, opportunistic variations in diet are under-reported (Murphy et al., 2023; Shahar et al., 2001). As such, it is likely that many functionally omnivorous and generalist taxa are widely understood as being specialists. Finally, many species of lepidosaurs, turtles, and archosaurs (including extant birds) are insectivorous in infancy and undergo ontogenetic shifts towards herbivory (Bouchard & Bjorndal, 2006; Drewe et al., 2004; Durtsche, 2000; Foster, 1978; Lopes et al., 2016; Mautz & Nagy, 1987; Mitchell & Eichholz, 2020; Poulin et al., 1994; Van Leeuwen et al., 2011), and carnivory or durophagy (Rieppel & Labhardt, 1979; Tucker et al., 1996; Winkler et al., 2019). This poses less of a challenge to data collection than the previous two situations since the ages of specimens studied is usually reported but is, nonetheless, an important consideration in classifying diet in amniotes. In particular, it is important to consider ontogeny when a shift in diet corresponds with a major shift in ecological and/or trophic niche such as in Komodo dragons (Purwandana et al., 2016), or some sea turtles (Arthur et al., 2008).

In practice, the class “omnivore” is assigned as a wastebasket category for diets that do not fit neatly into herbivory or faunivory (Fagan, 1997; Pineda-Munoz & Alroy, 2014; Price et al., 2012; Reuter et al., 2023; Wisniewski et al., 2023). Treating omnivory as a single, unified category obscures the important nuance in the precise combinations of specific food types that constitute the dietary composition of the animal in question (Lintulaakso et al., 2023). For example, a small omnivorous gekkonid lizard consuming a diet of small arthropods, supplemented with nectar or

tree sap (e.g., *Lygodactylus klugei*; Teixeira et al. 2013) would be biologically quite different from *Ursus americanus*: a large bear that subsists on vegetative and reproductive plant structures alongside a smaller, but substantial, amount of vertebrate meat (Wilman et al., 2014). These considerations would likely influence analysis of the macroevolutionary dynamics of diet but is not accounted for by many classification schemes used in the past.

The classical model of dietary classification is useful in, for example, studies not primarily directed at diet but are rather treating diet as one of many variables. However, as indicated by the lines of evidence explored in the above paragraphs, it does not adequately account for the differences in animal- and plant-based food types and the subsequent effects on the evolution and life history traits of the taxa consuming them.

1.1. Literature review

Many studies have implemented dietary categorization protocols beyond the classical system. A common division made (e.g., Cooke et al. 2022) is the splitting of “faunivory” into “carnivory” and “invertivory”. As mentioned previously, the division between invertivory and carnivory has been demonstrated to correlated with body mass variation among faunivorous taxa (Carbone et al., 1999). A conspicuous gap in the literature is that although diet classification in mammals has received considerable attention, followed by birds, diet classification in other major amniote lineages has been neglected.

Some studies on lepidosaurs and turtles have assigned definition to diet for the purpose of statistical analysis. A common trend here is to treat any taxa with a diet not composed overwhelmingly (>90%) of either plant or animal material as being omnivorous or generalist (Cooper Jr & Vitt, 2002; Herrel, Vanhooydonck, Joachim, et al., 2004; Shipps et al., 2023; Stephens & Wiens, 2003). Cooper Jr and Vitt (2002) determined that herbivory is extremely rare in lizards, accounting for around 3% of all lizard species. Espinoza et al. (2004) defined a carnivorous (insectivorous) liolaemid lizard as having a dietary composition of >90% animal matter, an omnivore as consuming 10-50% plant matter, and a herbivore as consuming >70% plant matter. The gap between the upper bound of omnivory and the lower bound of herbivory is explained by the apparent absence of taxa with a ratio of 50-70% plant material in the diet (Espinoza et al., 2004). Beyond that, there is little synthesis, to my knowledge, of the broad-scale patterns in diet and food usage in turtles or lizards.

Lopes et al. (2016) proposed a comprehensive dietary classification system for birds. These authors proposed that a taxon should be considered a specialist if one food item comprises the majority of its dietary composition and no other dietary category accounts for over 10% (and collectively less than 35%). A food source that accounts for 10-35% of the dietary composition is regarded as having secondary importance. Two food categories would be seen as having equal importance if both form >35% of the total dietary composition. Kissling et al. (2014) developed a system of classification wherein birds were assigned as specialist (further parsed as “herbivore”, “granivore”, “frugivore”, “nectarivore”, “aerial insectivore”, “terrestrial/arboreal insectivore”, “carnivore”, and “scavenger”) of a single food source had an importance rank of 5 or higher out of ten. Burin et al. (2016), similarly, classified birds as omnivores if no food category accounted for more than 50% of a

species' dietary composition. "Specialist" diets, wherein a single food category made up more than 50% of the diet of a given taxon were; "carnivory" (terrestrial vertebrate carrion), "frugivory" (fruit), "granivory" (seeds and nuts), "herbivory" (fibrous plant material), "insectivory" (invertebrates), "nectarivory" (nectar), and "piscivory" (fish).

Mammals have received by far the most attention of any major amniote lineage in studies on dietary classification. Numerous complex dietary classification systems have been proposed for mammals in recent years. This is facilitated by a very rich literature detailing the percentages of different food types in the dietary compositions of mammal species. Kissling et al. (2014) suggested that mammals be assigned to the following non-mutually exclusive dietary guilds based on what food type constitutes an important food source in the animal's diet: "mammal eaters", "insectivores" (invertebrates), "granivores" (seed), "frugivores" (fruit), and "folivores" (fibrous plant material). In a review of the latter paper, Gainsbury et al. (2018) recommended using broader categories (i.e., traditional guilds) owing to inconsistent results in the extrapolation of data where explicit information about an animal's dietary composition is unavailable.

Pineda-Munoz and Alroy (2014) presented a comprehensive review of dietary classification schemes in mammals. This study proposes a multi-layered classification scheme based on primary and secondary food sources in each taxon's diet. The authors recommended that if a single food group accounted for more than 50% of a taxon's diet, it should be considered a specialist feeder of that food type. Any food type that constitutes more than 20% of a taxon's diet should be classified as a secondary diet. The example provided by the authors is "herbivore-frugivore" for

an animal that consumes a diet consisting of >50% fibrous plant material, and >20% fruit (Pineda-Munoz & Alroy, 2014). This study produces an impressive 22 categories and a generalist category for those taxa that do not fit into any specialist category (see Table 1). Reuter et al. (2023) categorized mammalian taxa on the presence or absence of four overarching food categories; invertebrates, vertebrates, fibrous plant material, and non-fibrous plant material.

Lintulaakso et al. (2023) offer the most recent quantitative system of classifying mammalian diets. The study yielded 100 distinct dietary guilds based on the presence and ranked importance of the following food types: the flesh, blood, bones, eggs, larvae, and exudates of animals (separated to invertebrates, terrestrial vertebrates, and fish); the shoots and roots of fungi; the bark, leaves, stems, shoots, roots, nectar, pollen, exudates, buds, flowers, seeds, and fruits of plants; and distinct consideration of ingested minerals and faeces. The authors assessed the nutritional properties of these food types (based on carbohydrate, protein, lipid, and fibre content) and related dietary guild to some metrics of dental complexity. This study drew specific attention to the variation of different sub-types of omnivory with different specific dietary compositions. Most omnivores incorporated some degree of invertebrate material in their diets.

There are also several papers that develop dietary classification schemes in smaller mammalian clades. Verde Arregoitia and D'Elía (2020), categorized rodents into "granivores" (seed-feeders), "frugivores" (fruit-feeders), "folivores" (grass- and leave-feeders), "specialist herbivores" (plant-feeders specializing in other plant material not previously listed), "vermivores" (worm-feeders), "carnivores" (in this instance, feeders of both arthropods and vertebrates), and "omnivores" (simply defined as having more

than one “primary food source”). A taxon being assigned any of these categories, other than omnivory, was contingent on more than 50% of its diet being composed of the relevant food source. In a recent study on evolutionary transitions in dietary strategy in marsupials, Amador and Giannini (2021) categorized taxa first into “animalivory”, “herbivory”, “mycophagy” (fungus-feeding), and “omnivory”. The authors then repeated their study with the same taxa assigned to “insectivory”, “carnivory”, “grass herbivory”, “browse herbivory”, “frugivory”, “nectarivory”, “mycophagy”, “exudivory” (feeding on plant exudates), “granivory”, and “omnivory”. The result was a more nuanced understanding of evolutionary transitions between different strategies than was possible with the lower resolution categories.

The numerous studies that have corrected for biologically important differences between the different animal- and plant-based food sources, that the classical dietary classification system fails to accommodate, have their own limitations. Firstly, most of them rely on arbitrary a priori cut-off values to define the more nuanced guilds (see Table 1). For example, many studies on birds (Burin et al., 2016), and mammals (Amador & Giannini, 2021; Pineda-Munoz & Alroy, 2014; Verde Arregoitia & D’Elía, 2021) define a dietary specialist as a single food category accounting for >50% of the dietary composition of an animal. Many studies on turtles (Stephens & Wiens, 2003) and lizards (Espinoza et al., 2004; Meiri, 2018; Ocampo et al., 2022) use more stringent criteria for defining a dietary specialist (>70% dietary composition). The significance of such guilds to macroevolutionary questions may then be lost or obscured. For example, taxa in a “herbivorous” guild subsisting on a diet of 60% plant material may evolve a different optima for other life history traits

than those in a “herbivorous” consuming a diet of 90% plant material. While dietary guilds defined using arbitrary cut-offs are still biologically informative, they may fail to recognize natural groupings of different food sources in specific proportions. A meaningful proportion of species in a certain lineage may also belong to a dietary guild with a specific dietary composition (e.g., 70% invertebrates, 15% nectar, 15% fruit). A dietary classification system using a priori cut-offs may fail to recognize such a guild. The unique biological and evolutionary characteristics of such a guild, therefore, would be not be accounted for in analysis. Finally, studies investigating the classification of diets in major amniote clades other than mammals are depauperate in the existing scientific literature.

1.2. Aims and objectives

The goal of this chapter it to explore a quantitatively informed, statistically rigorous, and observationally transparent means of investigating diet with the aim of assessing an appropriate system of classification. I will accomplish this goal by examining natural divisions in percentile quantification of different food sources in the dietary compositions of amniotes, compiled at the species level across the tree using and fitting clustering algorithms onto in the data to determine the most optimal divisions. The purpose is to shift the narrative away from an essentialist classification system to one that uses underlying data distributions to make informed categorical assignments and that is more amenable to statistical analysis. The guild structuring is a means of assessing similarity among the distributions of amniote diets, both within and among lineages. They will therefore represent important divisions of the dietary spectrum rather than a rigid system of classification. These guilds will then

serve to (a) evaluate how diet presents itself in terms of which food types naturally tend to co-occur in dietary strategies, and (b) to identify and apply definitions to dietary guilds in a quantifiable, transparent, and repeatable manner, minimizing the use of arbitrary cut-offs for proportional data. I will subsequently deploy these guilds in downstream analysis to investigate evolutionary transitions between dietary strategies and the macroevolutionary relationship between diet and body mass in amniotes.

2. Methods and Materials

2.1. Data collection: overview

I collected diet and body size data for the following lineages: extant turtles (268 taxa), lizards (6726 taxa), birds (9993 taxa), and mammals (5242 taxa). I used pre-existing datasets of diet and body size data for birds and mammals (Wilman et al., 2014). I collected dietary data for the datasets from primary literature sources (e.g., publications detailing dietary assessments from gut contents and field observations, and field guides) for turtles (building on the dataset of Angielczyk et al. 2015), and lizards (building on the dataset of Meiri 2018).

The final dataset for turtles (see below for detailed information), includes each taxon's diet expressed as percentage composed of: invertebrate material ("Inv" – further broken down into arthropod or "Arth", and durophagous or "Duro" material), vertebrate meat ("Vert"), reproductive plant structures ("PlantR") and vegetative plant structures ("PlantO" – also includes fungi and algae). There are also sum totals for all animal-based food material ("AnimalT") and all plant-based food material ("PlantT"). I use carapace length (CL) as the proxy for body size, with those data coming primarily from the dataset of Angielczyk et al. (2015), with occasional references to other literature sources where appropriate.

The final dataset for lizards (see below for detailed information), includes each taxon's diet expressed as percentage composed of: invertebrate material ("**Inv**" – further broken down into arthropod or "**Arth**", and durophagous or "**Duro**" material), vertebrate meat ("**Vert**"), reproductive plant structures ("**PlantR**") and vegetative plant structures ("**PlantO**" – also includes fungi and algae). I use snout-vent-length (SVL) as the proxy for body size because it is the most common size variable employed in the herpetological literature. SVL data was taken from the dataset of Meiri (2018).

I used the "EltonTraits 1.0" (Wilman et al., 2014) datasets for birds and mammals. The EltonTraits database provides a complete dataset of extant birds and mammals (as separate datasets) with the diet of each taxon parsed into percentages for given food categories. Animal-based food categories include invertebrate material ("Inv," not further subdivided), and the following divisions of vertebrate sources; endotherm ("Vend"), ectotherm ("Vect"), scavenged carrion ("Scav"), vertebrate meat of unknown origin ("Vunk"), and fish ("Vfish"). In terms of plant-based food categories, there are fruit ("Fruit"), nectar ("Nect"), seed ("Seed"), and all other plant, fungi, and algae-based food ("PlantO"). For consistency with the turtle and lizard datasets, I summed "Vect", "Vend", "Vunk", "Vfish", and "Scav" into a combined category for total vertebrate material consumed ("**Vtotal**") and for all animal material ("AnimalT" – the sum of "Vtotal" and "Inv"). I also kept a separate category for "**Vfish**" with the remaining vertebrate food sources summed up as "**Vland**". I also summed "**Fruit**", "**Nect**", and "**Seed**" into a combined total for reproductive plant structures ("PlantR"). These datasets each include a column for body mass, expressed in grams as a proxy for body size. Additional columns include data relating to foraging strategy and nocturnality which differ between the bird and mammal datasets (see Wilman et al. 2014, metadata for further details). Percentile values in the EltonTraits database are estimated from qualitative statements from "global handbooks and monographs" (Wilman et al., 2014). These values are, thus, inferred rather than derived from direct observations. As would be expected, there is some discrepancy between the values in this database and those borne from quantitative, observational data (Sebastián-González et al., 2023; Steiner et al., 2022). I critically evaluate the potential shortcomings of this dataset in the discussion section of this chapter.

2.2. Data collection: turtles

I constructed the dietary dataset for turtles based on the dataset of Angielczyk et al. (2015). Most data for body size are sourced directly from Angielczyk et al. (2015). However, I have renamed genera and species where necessary, to reflect the updated taxonomy of Testudines as per Reptile Database. This is consistent with the taxonomy of Thomson et al. (2021), which is also the source of the phylogeny I use for my analyses. My final dataset includes 366 taxa. There are full dietary data for 356 taxa. When cut down to those with matching tree tip-labels, there are 268 taxa in the final dataset for analysis.

The primary data are species diets, recorded as the percentages of different food categories consumed (outlined below). These percentages were determined from information given in primary literature (see Appendices A.3-A.7). Sources of dietary information include quantitative gut and faecal composition analysis, and quantitative observations about the diets of species that researchers have made. In addition to several columns indicating the proportion of each taxon's diet composed of a given food type, I also include columns for the kind of data used to generate those percentages, my level of confidence in those data, and the primary literature from which that information is sourced.

The columns related to taxonomy are as follows:

Family – As per taxonomy of the Reptile Database, reflecting the recent phylogenetic analysis of Thomson et al. (2021).

Species – Binomial as per taxonomy of the Reptile Database, reflecting the phylogenetic analysis of Thomson et al. (2021).

Tree.name – Binomial formatted to match the tip labels on the phylogenetic trees (see Methods). These do not always match the names in the "Species" column.

The columns related to dietary categories are as follows (Note: the following combinations of values add up to 100 – Diet.Arth, Diet.Duro, Diet.Jelly, Diet.Vert, Diet.PlantT, and Diet.PlantO; Diet.Inv, Diet.Vert, Diet.PalntT, and Diet.AnimalT):

Diet.Arth – Percent use of: insects, arachnids, other (largely terrestrial) invertebrates such as worms. Excludes molluscs and crustaceans. “Arth” is shorthand for “arthropod”. Notes: in some limited circumstances, crustaceans (essentially terrestrial isopods) are grouped with Diet.Arth if they are more similar to insects and arachnids in regards to terrestrial habitat.

Diet.Duro – Percent use of: molluscs, crustaceans and other (if any) invertebrates typically seen as part of a durophagous diet (“Duro” is shorthand for “durophagy”). Excludes all insects and arachnids. Notes: in some limited circumstances, crustaceans (overwhelmingly terrestrial isopods) are grouped with Diet.Arth if I judged them to be more similar to insects and arachnids in regards to predation and digestion.

Diet.Jelly – Percent use of: jellyfish, other cnidarians, tunicates, and cephalopods. Notes: the purpose of this category was to reflect the unique physiological adaptations needed for a gelatinivorous diet (e.g., Heaslip et al. 2012). However, given that this food type is restricted to a small number of marine species, it proves to be of little utility in broad statistical analysis. As such, it is combined with Diet.Duro to form “Diet.InvO” for use in analysis.

Diet.Inv – The sum total of Diet.Arth and Diet.InvO; the total contribution of invertebrates in the diet. “Inv” is shorthand for “invertebrate”.

Diet.Vert – Percent use of: any vertebrate meat. “Vert” is shorthand for “vertebrate”.

Diet.PlantR –The total contribution of reproductive parts of plants including fruits, seeds, and nectar. “PlantR” is shorthand for “plant-reproductive”.

Diet.PlantO – All vegetative parts of plants (e.g., leaves, grasses, twigs) and nonanimal food material not mentioned elsewhere. “PlantO” is shorthand for “plant-other”. Notes: algae and fungi are included here largely because for the purposes of consistency with the other datasets (Wilman et al., 2014). Note that the PlantO

category in many turtles is composed of algae, fungi, and aquatic grasses. These may not be directly comparable, from a digestive efficiency point-of view, to fibrous, vegetative terrestrial plant structures.

Diet.PlantT – Sum total of Diet.PlantR and Diet.PlantO. Total contribution of nonanimal food material to the diet. “PlantT” is shorthand for “plant-total”.

Diet.AnimalT – Sum total of Diet.Inv and Diet.Vert. Total contribution of animal food material to the diet. “AnimalT” is shorthand for “animal-total”.

The columns relating to data confidence and data resolution are as follows:

Data.type – a letter indicator (a character) indicating which of the following kinds of data were used to infer the percentage values:

- Volume – The percentage of volume of (usually) stomach or faeces contents of a sample of lizards in a study. Here, the values presented in the dietary categories are, almost always, identical to those presented in the primary source.

- Mass – The percentage of (either dry or wet) mass of (usually) stomach or faeces contents of a sample of lizards in a study. Here, the values presented in the dietary categories are, almost always, identical to those presented in the primary source.

- Item – The percentage of individual items of a given category found in (usually) stomach or faeces contents of a sample of lizards in a study. Here, the values presented in the dietary categories are, usually but not always, identical to those presented in the primary source. In the event that I have subjected the presented values to further interpretation, a detailed motivation for this decision is supplied in the “Notes” column.

- Qualitative – Percentage values are estimated from non-quantitative statements, including direct observation. Additionally, values presented as “percentage/number of lizard stomachs containing a given item” are included here as

the value given is based on the quantity of lizards in a sample rather than the quantity of the consumed food item. In each case, I infer values (usually rounded off to multiples of 5) from descriptions of the diet in text. These values are derived from evidence in the form of statements that convey quantitative information (e.g, “eats mostly fruit” would result in a value for Diet.Fruit over 60%). In addition to wording the text, I also occasionally use the diets of closely related species to infer a specific value (e.g., a species reported as consuming “fruit and insects” in a genus that is, otherwise, habitually insectivorous may get a Diet.PlantR value of 25%, while a genus where all members are omnivorous may receive a Diet.PlantR value of 40%). This is, by far, the most abundant DataType category used. All values chosen under this DataType category will be accompanied by detailed explanation in the “notes” column and/or a protocol category assigned (see below).

Data.confidence – A letter indicator (a character) indicating the strength of my confidence in the data based on the source from where it was extracted. This is expressed as “High”, “Medium”, “Low”, and “Inferred”. “Inferred” refers to data that is either (a) not based on an explicit, direct statement (such as when another taxon is used as a reference point); or (b) if the statement made is vague or very hard to interpret. In any case, data parsed with this category will include a justification in the notes column and, most of the time, a protocol. Notes: while volume and mass data are usually given a higher confidence rank and qualitative data a lower rank, this is not always the case. For example, a qualitative statement like “this turtle taxon feeds exclusively on gastropods” provides higher confidence (“Diet.Arth = 100%) than mass or volume data using a low sample size, a short study time or with other literature sources providing conflicting information. Given that this draws on numerous factors influencing the data, I recommend that the “Data.confidence” variable be used as a filter for sensitivity analyses.

CL – Average carapace length (CL) for each species, expressed in millimetres.

The columns explaining literature sources of data are as follows:

Source.diet – Primary literature source of dietary data.

Source.CL – Source of CL data. This is almost always Angielczyk et al. (2015) unless stated otherwise.

Protocol – As a compliment to the DataType and DataConf columns, the protocol column indicates procedures used for assigning values throughout the dataset. These are also usually accompanied with a more detailed explanation of the decision taken in the notes column of the dataset. The protocols are as follows:

- Standardisation (53 taxa) – This applies to all or some species within a genus being given a “generic” set of values, consistent with other species in the same genus. This is often used for filling in missing data points based on averages of existing ones if it is deemed appropriate to do so. An explanation for the use of this protocol will be provided in the notes column.

- Reference (69 taxa) – This means that values for one species are used for another closely-related species (usually, but not always, cogeneric). This differs from “standardisation” in that it will use the exact values for one particular species rather than averaged or inferred values from multiple species within a genus. This is most commonly used when the qualitative description of a species’ diet is similar to that of another species with higher confidence, or quantitative, data available. An explanation for the use of this protocol is always provided in the “notes” column.

2.3. Data collection: lizards

This dataset is an extension of the dataset in Meiri (2018). It contains all taxa of non-snake squamate included in Meiri’s (2018) dataset (6657 taxa) and does not account for subsequent taxonomic revisions. Meiri’s (2018) dataset includes a “diet” column including qualitative notes on the diets of each taxon where available with varying degrees of detail. The primary modification here is that each species’ diet is recorded as the percentages of different food categories (outlined below) of which it is composed. These percentages were determined from the primary literature (see

Appendices A.4). Sources of dietary information include quantitative gut and faecal composition analysis and quantitative observations about the diets of species that researchers have made. In addition to several columns indicating the proportion of each taxon's diet composed of a given food type, I also include columns for the kind of data used to generate those percentages, my level of confidence in those data, and the primary literature from which that information is sourced (except in the case of those coded using the "Mass import" protocol; see below).

The columns relating to taxonomy are as follows:

Superfamily – As per taxonomy of the Reptile Database, though it reflects taxonomic status of Meiri (2018) and is, therefore, not always currently taxonomically accurate.

Family – As per taxonomy of the Reptile Database, though it reflects taxonomic status of Meiri (2018) and is, therefore, not always currently taxonomically accurate.

Species – Binomial using spelling from Meiri (2018) and thus may not always be consistent with the updated Reptile Database.

Tree.name – Binomial formatted to match the tip labels on the phylogenetic trees (see Methods). These do not always match the names in the "Species" column.

The columns related to dietary categories are as follows (Note: the following combinations of values add up to 100 – Diet.Arth, Diet.Duro, Diet.Vert, Diet.PlantR and Diet.PlantO; Diet.Inv, Diet.Vert, Diet.PlantT, and Diet.AnimalT):

Diet.Arth – Percent use of: insects, arachnids, other (largely terrestrial) invertebrates such as worms. Excludes molluscs and crustaceans. "Arth" is shorthand for "arthropod". Notes: in some limited circumstances, crustaceans (essentially terrestrial isopods) are grouped with Diet.Arth if I judge them to be more similar to insects and arachnids in regards to predation and digestion.

Diet.Duro – Percent use of: molluscs, crustaceans and other (if any) invertebrates typically seen as part of a durophagous diet (“Duro” is shorthand for “durophagy”). Excludes all insects and arachnids. Notes: in some circumstances, crustaceans (essentially terrestrial isopods) are grouped with Diet.Arth if I judge them to be more similar to insects and arachnids in regards to predation and digestion. Many insectivorous species (or species with a Diet.Arth value of 100%), particularly species parsed using the “Mass.import” protocol, may include small (<10%) contributions of gastropods in their diet. Those with Diet.Duro reported are, therefore, mostly taxa with higher consumption.

Diet.Inv – The sum total of Diet.Arth and Diet.Duro; the total contribution of invertebrates in the diet. “Inv” is shorthand for “invertebrate”.

Diet.Vert – Percent use of: any vertebrate meat. “Vert” is shorthand for “vertebrate”. Notes: many insectivorous species (or species with a Diet.Arth value of 100%) opportunistically feed on other lizards (often juvenile conspecifics) though the data here may not reflect that. This is particularly true for species parsed under the MI protocol. In all such instances, however, the vertebrate material constitutes a very small percentage of the diet.

Diet.PlantR –The total contribution of reproductive parts of plants including fruit, flowers, nectar, tree sap, and seeds. “PlantR” is shorthand for “plant-reproductive”.

Diet.PlantO – All vegetative parts of plants (e.g., leaves, grasses, twigs) and nonanimal food material not mentioned elsewhere. “PlantO” is shorthand for “plant other”. Notes: algae and fungi are included here largely because of the extreme rarity of their consumption in lizards. I have not, for example, encountered a lizard with a diet containing high (>20%) fungi consumption. In practical terms, this category refers to leaves, shrubs and grasses. Many lizards with a diet consisting of arthropods and a low (<10%) PlantO likely ingest plant material accidently (Cooper & Vitt 2002).

Diet.PlantT – Sum total of Diet.PlantR and Diet.PlantO. Total contribution of nonanimal food material to the diet. “PlantT” is shorthand for “plant-total”.

Diet.AnimalT – Sum total of Diet.Inv and Diet.Vert. Total contribution of animal food material to the diet. “PlantT” is shorthand for “animal-total”.

The columns relating to data confidence and data resolution are as follows:

Data.type – A letter indicator (a character) indicating which of the following kinds of data is used to infer the percentage values:

- Volume – The percentage of volume of (usually) stomach or faeces contents of a sample of lizards in a study. Here, the values presented in the dietary categories are, almost always, identical to those presented in the primary source.

- Mass – The percentage of (either dry or wet) mass of (usually) stomach or faeces contents of a sample of lizards in a study. Here, the values presented in the dietary categories are, almost always, identical to those presented in the primary source.

- Item – The percentage of individual items of a given category found in (usually) stomach or faeces contents of a sample of lizards in a study. Here, the values presented in the dietary categories are, usually but not always, identical to those presented in the primary source. In the event that I have subjected the presented values to further interpretation, a detailed motivation for this decision will be supplied in the notes column.

- Qualitative – Percentage values are estimated from non-quantitative statements, including direct observation. Additionally, values presented as “percentage/number of lizard stomachs containing a given item” are included here as the value given is based on the quantity of lizards in a sample rather than the quantity of the consumed food item. In each case, I infer values (usually rounded off to multiples of 5) from descriptions of the diet in text. These values convey ordinated levels of consumption of different food sources, and are usually backed up by statements that convey quantitative information (e.g, “eats mostly fruit” would result in a value for Diet.PlantR over 60%). In addition to wording the text, I also occasionally use the diets of closely related species to infer a specific value (e.g., a

species reported as consuming “fruit and insects” in a Genus that is, otherwise, habitually insectivorous may get a Diet.PlantR value of 25%, while a Genus where all members are omnivorous may receive a Diet.PlantR value of 40%). This is, by far, the most abundant DataType category used. All values chosen under this DataType category will be accompanied by an explanation in the notes column and/or a protocol category assigned (see below).

Data.confidence – A letter indicator (a character) indicating the strength of my confidence in the data based on the source from where it was extracted. This is expressed as “High”, “Medium”, “Low”, and “Inferred”. “Inferred” refers to data that is either (a) not based on an explicit, direct statement (such as when another taxon is used as a reference point); or (b) if the statement made is vague or very hard to interpret. In any case, data parsed with this category will include a justification in the notes column and, most of the time, a protocol. Notes: while volume and mass data are usually given a higher confidence rank and qualitative data a lower rank, this is not always the case. For example, a qualitative statement like “this lizard taxon feeds exclusively on ants” provides higher confidence (“Diet.Arth = 100%) than mass or volume data using a low sample size, a short study time or with other literature sources providing conflicting information. Given that this draws on numerous factors influencing the data, I recommend that the DataConf variable be used as a filter for sensitivity analyses.

Other columns relating to life history and ecological traits are as follows:

SVL.maximum – Where available, the maximum recorded snout-vent length (SVL) is shown in millimetres. All of these data are taken directly from Meiri (2018) unless stated otherwise (further explained in the MI protocol section).

SVL.average – Where available, the recorded adult female average SVL is shown in millimetres. All of these data are taken directly from Meiri (2018) unless stated otherwise (further explained in the Mass.import protocol section).

The columns explaining literature sources of data are as follows:

Source.diet – Source of dietary data. This is usually Meiri (2018) – particularly if inputted using the MI protocol – though other sources are used for precision, especially for species that include significant amounts of plant and/or vertebrate material in their diets. Therefore, the dietary data is, at in part, “original information” as opposed to data used unaltered from Meiri (2018).

Source.SVL – Source of SVL data. This is almost always Meiri (2018) unless explicitly stated otherwise.

Protocol – As a compliment to the DataType and DataConf columns, the protocol column indicates the procedures used for assigning values throughout the dataset. These will usually be accompanied with a more detailed explanation of the decision taken in the notes column. The protocols are as follows:

- Mass.import (4731 taxa) – By far, this is the most frequently used protocol. This, in terms of dietary data, refers to lizards given an insectivorous diet (Diet.Arth = 100) on the basis of that classification of the taxon in the Meiri (2018) dataset. In some cases a small value (<10) will be applied to Diet.Vert or Diet.Duro using this protocol with an explanation in the notes column. Usually this is only applied to species with an explicit dietary classification provided in Meiri (2018). In some cases, entire genera will be mass imported (particularly gekkotans and amphisbaenians which are known for being “insectivorous” en masse). All such discrepancies are elaborated on in the notes column. Additionally, any taxa with a diet inputted in my dataset that is NA in the dataset of Meiri (2018) because of this protocol have a data confidence of “inferred” instead of “medium”. All SVL and foraging mode data is obtained by “mass import” by default unless an alternative source is explicitly stated.

- Standardisation (169 taxa) – This applies to all or some members of a genus being given a “generic” set of values. This is often used for filling in missing data points based on averages of existing ones if it is deemed appropriate to do so. An explanation for the use of this protocol will be provided in the notes column.

- Reference (69 taxa) – This means that values for one species are used for another closely-related species (usually, but not always, congeneric). This differs from “standardisation” in that it will use the exact values for one particular species rather than averaged or inferred values from multiple species within a genus. This is most commonly used when the qualitative description of a species’ diet is similar to that of another species with higher confidence, or quantitative, data available. An explanation for the use of this protocol will be provided in the notes column.

- Gehyra.protocol (65 taxa) –This refers to the following distribution of values – DietArth=70, Diet.PlantR=30 – based on an observation of nectar or sap feeding in an otherwise insectivorous lizard. The values chosen are intended to reflect a diet that is primarily arthropod-based but supplemented with nectar/sap feeding, demonstrated with the value of 30% nectar (PlantR). I named the protocol in honour of the first genus I applied it to: *Gehyra* (Edwards et al., 2021). An explanation for any use of this protocol is provided in the notes column.

- Phymaturus.omnivory (3 taxa) – This refers to the split of 25/50/25 for Diets-Arth, PlantR, and PlantO given to *Phymaturus* species described as “omnivorous” without further detail. The values are intended to reflect the range of plant types consumed by liolaemids in general (O'Grady et al., 2005; Vanhooydonck et al., 2010).

- Liolaemus.omnivory (10 taxa) – This refers to the split of 30/50/20 for Diets-Arth, PlantR, and PlantO given to Liolaemus species described as “omnivorous” without further detail. The values are intended to reflect the range of plant types consumed by liolaemids in general. Compared to the analogous *Phymaturus* protocol, I have opted for a higher Diet.Arth value here to reflect the higher overall prevalence of arthropod consumption in *Liolaemus* as opposed to *Phymaturus*.

- O.Grady (12 taxa) – O’Grady (2005) is the primary literature reference for the dietary data of number of *Liolaemus* species. It presents volumetric data but with low sample sizes. I describe this in the notes column and assign a DataConf of “L”. The primary purpose behind this protocol is to simplify potential sensitivity analysis.

2.4. Data ordination and visualisation

Data preparation

In all analyses, in this and the following chapters, I use the arcsine-transformed proportional dietary data and the log-transformed body mass data. Arcsine-transformation is commonly implemented to overcome some of the analytical challenges presented by proportional data in biological and ecological research (Sokal & Rohlf, 1995; Zar, 1999). I arcsine transformed the proportional dietary data to reduce heteroscedasticity and approximate a normal distribution. Arcsine-transformation serves the purpose of equalizing the spread of percentage data, and reducing fluctuation or dispersion in variance, particularly of datasets in which the spread of datapoints are zero- and one hundred percent inflated. This transformation makes proportional data such as percentages more amenable to the assumptions of parametric statistical analyses (e.g., linear regression). Secondly, I log-transformed on all body mass data or body mass proxy data. This decision was guided to mitigate the inherent skewness introduced by the multiplicative nature of body size variation in animals (which spans several orders of magnitude, and to reduce the influence of outliers (Gingerich, 2000; Hunt & Carrano, 2010; Sokal & Rohlf, 1995).

For the sake of convenience and consistency, I refer to different levels of dietary divisions as “first order”, “second order”, and “third order”. The first order categories are the summed totals of animal- and plant-based food material. The second order categories are total invertebrate and vertebrate material (subdivisions of animal material), and total reproductive and vegetative plant structures (subdivisions of plant material). The third-order categories are, subsequently, the least inclusive divisions of the proportional dietary data. The differences in these categories between the datasets include the division of invertebrates into “insectivorous” (terrestrial arthropods) and “durophagous” (mollusks, gastropods, crustaceans) material; the division of reproductive plant structures into fruit, seed, and nectar in the bird and mammal datasets; and the division of vertebrate material into terrestrial vertebrates and fish in the bird and mammal dataset. The first- and second-order divisions are

consistent in definition between the datasets, while the third order divisions vary by clade.

I performed a series of analyses on the arcsine-transformed percentage data to (a) develop a visual representation of dietary variance in each of the major amniote lineages, and (b) determine statistically which combinations of food types are most common in the dietary compositions of different amniote taxa. Unless stated otherwise, all analyses were conducted in the R work environment (R Core Team & Team, 2022).

Principal Components Analysis

I performed principal component analyses (PCA) on the arcsine-transformed percentage dietary data to determine which divisions in the data best explain differences in dietary composition. I used the 'prcomp' function in the base R 'stats' package to compute the PCAs. I ran the analyses using the third-order subdivisions ("Arth", "Duro", "Vert", "PlantR", "PlantO" for turtles and lizards; "Inv", "Vland", "Vfish", "Fruit", "Seed", "Nect", "PlantO" for birds and mammals) as a means of exploring the most important divisions in the dietary data for each major amniote lineage. I also ran the analyses for all major amniote lineages using second-order subdivisions ("Inv", "Vert", "PlantR", and "PlantO") to facilitate direct comparisons between the clades.

Correlation matrix

I calculated correlation matrices between the different dietary items in each clade to demonstrate which dietary items more and less likely co-occur in a taxon's dietary composition. A positive correlation indicates that consumption rates of two dietary

items simultaneously increase at the expense of other dietary items, indicating that two diet items frequently co-occur within the diets of species in the group. A negative correlation indicates a trade-off between two dietary variables in the dietary compositions of taxa such that the one dietary item is anticorrelated with the other. A correlation coefficient at, or close to-, zero (<|0.2|) would indicate that there is no predictable statistical relationship between two dietary items in the dietary compositions of taxa in a given clade. This would be an indicator of either (a) two food types being “mutually exclusive” or seldom co-occurring in the composition of the diets of most taxa, or (b) that the two food sources tend to co-occur in a consistent or predictable ratio such that the increase in one does not cause a linear change in the other (Dziuban & Shirkey, 1974; Steiger, 1980). I compute the correlation matrices using the ‘cor’ function in the base R ‘stats’ package. I ran a set of analyses using the second order dietary categories (“Inv”, “Vert”, “PlantR”, “PlantO”) to facilitate direct comparisons between each major amniote lineage, and a set of analyses using the third-order subdivisions (“Arth”, “Duro”, “Vert”, “PlantR”, “PlantO” for turtles and lizards; “Inv”, “Vland”, “Vfish”, “Fruit”, “Seed”, “Nect”, “PlantO” for birds and mammals) to assess the patterns present within each major lineage.

Cluster analysis

I performed a series of k-means cluster analyses on the arcsine-transformed third-order proportional dietary data to test if there is an optimal number of divisions in the dietary data that may bear utility for dietary classification. I limit this analysis to third-order dietary categories to capture dietary complexity within clades rather than compare them. I use the results to generate dietary guilds for downstream analysis representing biologically informative divisions in the spectrum of diet in each major amniote lineage. I used this method to avoid arbitrary a priori cut-offs and instead use a dietary classification scheme informed a posteriori from the results of cluster analysis. Clustering methods may reveal important insights into natural divisions in dietary data that may not be appreciable using traditional methods. My foremost aim to sufficiently capture dietary complexity as a set of discrete units for use in downstream analysis.

Using k-means clustering, the maximum possible number of distinct clusters for an amniote lineage (k-max) is equal to the unique combinations of different percentages of food types across the dietary dataset. I calculated cluster sizes with k-values set at k-max, k=100, k=50, k=20, k=10, and k=5 for each amniote lineage using the function ‘kmeans’ in the base R ‘stats’ package. I then calculated the distribution of silhouette scores for clusters of different k-values using the “fviz_nbclust” function in the package ‘factoextra’ (Kassambara & Mundt, 2017). The silhouette method is a means of assessing the degree of separation between datapoints in different clusters as a metric of quality of data clustering under a given k-value (Rousseeuw, 1987). I visually inspected the distribution of silhouette scores relative to k-values at each maximum. The purpose of exploring a wide variety of k-values was to assess if silhouette scores could improve such that increasingly large numbers of clusters would better explain divisions in the dataset and to what extent higher values of k optimize separation of the data. It is also informative to see how close to a silhouette score of 1 is statistically attainable as this would provide evidence that dietary compositions can be accurately sub-divided and, by extension, classified. I also deploy the elbow method to visually inspect the range of k-values for a point at which the within sums of squares (WSS) no longer improve by a great margin by adding higher k-values. The WSS is an appropriate metric for determining an optimal number of clusters for use in downstream analysis since it is expected that there would be at least some overlap between different dietary guilds in any classification system, as assessed by the silhouette method. The similarity of dietary compositions of taxa within a guild is, therefore, a useful indicator of biologically informative a guild is than degree of separation between the different guilds.

I assess the and WSS against number of clusters using the “fviz_nbclust” function in the package ‘factoextra’ (Kassambara & Mundt, 2017). I perform the cluster analysis using the function ‘kmeans’ in the base R ‘stats’ package.

Comparative guilds

I also assigned the taxa in each dataset to traditional “faunivore-omnivore-herbivore” classifications. I defined “faunivore” as having a total animal-based food value of, or

exceeding, 70% in the diet. I defined “herbivore” as having a total plant-based food value of, or exceeding, 70% in the diet. All taxa with values for both plant- and animal-based food less than 70% were categorised as “omnivores”. For the purposes of analysis (particularly for ancestral state reconstruction), these provided a more standardised comparative approach that facilitated comparisons between the extant and extinct clades. It also provides a useful reference point for comparison to many results from literature which apply similar criteria to dietary classification.

I also created a more complex set of dietary guilds for each major extant amniote lineage based on a priori cut-off values for the purposes of (a) comparison to results of previous studies and (b) investigating the taxonomic distribution of different dietary compositions in each major amniote lineage in a directly comparable manner. These guilds, however, are not for use in downstream analysis but rather for comparison with the guilds generated in the k-means cluster analysis. This helps to place the results of the current study in broader context. Following Pineda-Munoz and Alroy (2014), I classify a species as a specialist in a food type if that item accounts for upwards of 50% of its dietary composition, and a food type is ranked as “important” of it constitutes upwards of 20%. The dietary composition of a species is then expressed by which food type(s) accounts for more than 50% of the dietary composition, and which for more than 20% (e.g., a taxon with a dietary composition consistI ran the analyses using the third-order subdivisions (“Arth”, “Duro”, “Vert”, “PlantR”, “PlantO” for turtles and lizards; “Inv”, “Vland”, “Vfish”, “Fruit”, “Seed”, “Nect”, “PlantO” for birds and mammals).

3. Results

3.1. Principal components analysis (PCA)

Second order dietary classification

Turtles

The first three PCs explain 98.72% of the variance. PC1 (63.27% of the variance) displays the trade-off between Inv (which loads high on the positive axis) and PlantO (which loads high on the negative axis). PC1 also shows the general split between PlantT and AnimalT with Vert loading in the same direction as Inv and PlantR the same direction as PlantO. PC2 (22.39% of the variance) then shows the trade-offs between Inv and PlantO (both of which load positively) and Vert and PlantR (each of which load negatively). PC3 (13.06% of the variance) then separates the PlantR on the positive axis from Vert on the negative axis (see Figure 1).

Lizards

The first three PCs explain 98.16% of the variance. PC1 (87.54% of the variance) shows the division between Inv (which loads far positively) and all other food categories, with PlantR loading the furthest negatively. PC2 (6.47% of the variance) then shows the separation of Vert (loaded negatively) from all other categories, especially PlantR which loads the furthest from Vert. PC3 (4.15% of the variance) displays the separation of PlantO, which loads negatively, from all other food categories. On all three axes, PlantR loads inversely to the other categories (see Figure 2).

Birds

The first three PCs account for 98.79% of the variance. PC1 (72.77% of the variance) displays the separation of Inv from all other categories. Inv loads far on the positive axis, the others all load with negative values, with PlantR having the highest negative value. PC2 (20.32% of the variance) primarily separates Vtotal from PlantR on the negative and positive axes respectively. Inv loads close to PlantR on this principal component. PC3 (5.69% of the variance) shows the division of PlantO (loaded negatively) with all other food categories (see Figure 3).

Mammals

The first three PCs explain 98.63% of the variance. PC1 (54.80% of the variance) shows the separation of Inv (with a positive loading) from all other categories. PlantO loads the furthest from Inv, followed by PlantR, and then Vtotal. PC2 (31.76% of the variance) displays the split between PlantO (loaded positively) and PlantR (loaded negatively). Inv loads in the same direction as PlantO on this PC. PC3 (12.07% of the variance) shows the separation of Vtotal, on the negative axis, from all other categories. Inv, PlantR, and PlantO all have similar loading values on this PC (see Figure 4).

Third order dietary classification

Turtles

The first four components explain 99.3% of the variance in the data, taken collectively. The first principal component (51.5% of the variance) primarily separates taxa feeding on vegetative plant structures, which load negatively, from faunivorous animals. Feeders of invertebrate food sources other than terrestrial arthropods load strongly negatively on the second principal component (19.2% of the variance) primarily distinguishing them from feeders of terrestrial arthropods, which load positively. On the third principal component (15.6% of the variance), arthropod-feeding loads positively, reproductive plant structures load most strongly negatively. The fourth principal component (12.9% of the variance) primarily separates

vertivores, which load negatively, from other dietary groupings. In summary, the most important division in the dietary data for turtles is between folivory and faunivory as a whole (see Figure 5). The next most important divisions are different kinds of invertivores (a) from each other, and (b) from feeders of reproductive plant structures.

Lizards

The first four components explain 99.2% of the variance in the data, taken collectively. The first principal component (86.1% of the variance) separates taxa feeding on arthropods, which load very strongly positively, from those feeding on all other food types. Other faunivorous food sources load close to zero on the first principal component, while the plant-based food sources loaded negatively. The consumption of vertebrates and reproductive plant parts both load strongly (negatively and positively respectively) on the second principal component (6.5% of the variance). Feeding on vegetative plant material, and durophagy load strongly negatively on the third (4.1% of the variance), and fourth (2.5% of the variance) respectively. Ultimately, the most important division in the dietary data for lizards is that of arthropod-based diets from non-arthropod based diets (see Figure 6). The subsequent divisions in the data explain a far lower proportion of overall variance.

Birds

The first six principal components explain 99.3% of the variance in the bird dietary data. The first principal component (56.7% of the variance) discriminates invertivores, which load negatively, from all other dietary groups. Frugivores are the furthest separated from invertivores on this axis, with the highest positive loading. Frugivory negatively loads strongly on the second principal component (15.2% of the variance) and granivory loads positively. The third principal component (10.9% of the variance) discriminates several divisions in the data, the most important being granivores, with a strong negative loading, from taxa in all other dietary strategies,

especially nectarivores. The fourth component (8.7% of the variance) shows strong loadings for both vertivorous (negatively loaded) and nectarivorous (positively loaded) taxa. Piscivory and vegetative plant material load negatively on fifth component (4.5% of the variance) against other food sources which load positively. Subsequently on the sixth principal component (3.5%), vegetative plant material loads positively and fish loads negatively. As with lizards, the separation of invertivorous from non-invertivorous diets is the most important division in the dietary data for birds (see Figure 7). The next most important divisions are of different kinds of reproductive plant-based diets.

Mammals

The first six principal components explain 99.5% of the variance in the mammal dietary data. Taxa feeding on invertebrates and vegetative plant material each load strongly (positively and negatively respectively) on the first principal component (55.7% of the variance), while taxa feeding on other dietary items load very weakly (<|0.1|). The second principal component (24.6% of the variance) primarily separates taxa feeding on vegetative plant material, which load positively, from those feeding on fruit, which load negatively. The third component (10.0% of the variance) displays several divisions in data but the strongest loadings are for feeders of fruit, positively loaded, and terrestrial vertebrates, which load negatively. The fourth component (5.8% of the variance) primarily separates granivores, which load negatively from other dietary strategies. Nectarivory and piscivory load negatively on the fifth component (2.1% of the variance) separating these food sources from all others, and these two sets of taxa load strongly, and opposite one another, on the sixth component (1.4% of the variance). In summation, the most important divisions in the mammal dietary data are invertivores and folivores from all other dietary types (see Figure 8). The next most important divisions are the separation of the different herbivorous feeding strategies.

3.2. Correlation matrix

Second order dietary classification

The results were similar for all clades, with variation in specific values (see Figure 9; Tables 12-15). Invertebrates had the strongest negative correlations with plant material for all clades. For lizards and birds, the strongest negative correlation was between invertebrates and reproductive plant structures (see Figure 9). For turtles and mammals, it was between invertebrates and vegetative plant structures (see Figure 9).

Third order dietary classification

Turtles

All animal food types in turtles have a negative correlation with all plant food types (see Figure 10; Table 16). This is more pronounced for vegetative plant material (coefficients = -0.38 to -0.48) than for reproductive plant structures (coefficients = -0.23 to -0.30). Different kinds of animal- and plant-based foods have very weak correlation coefficients with each other. The correlation between vertebrate material and invertebrates other than terrestrial arthropods is very close to zero (0.013).

Lizards

Terrestrial arthropods show a negative correlation with all other food types in lizards (see Figure 10; Table 17). This anticorrelation is less pronounced with other animal-based food sources (least with other invertebrate material) and more pronounced with plant material (most with reproductive plant structures). Animal-based food types other than terrestrial arthropods have a very weak correlation with all plant-based food types. Vegetative and reproductive plant structures are positively correlated with each other in the compositions of lizard diets.

Birds

Most pairwise correlation coefficients between the percentages of different food types in the dietary composition of birds indicate no, or little, statistical relationship (coefficient <|0.2|; see Figure 10; Table 18). The only exceptions to this were negative correlations between invertebrate food sources and all other food sources barring fish (coefficient = -0.16). The strongest negative correlations with invertebrates are with seeds (coefficient = -0.38) and fruits (coefficient = -0.44), while the weakest is with terrestrial vertebrates (coefficient = -0.24).

Mammals

Correlations within different plant- and animal-based food sources were very weak (<|0.2|; see Figure 10; Table 19) but there are several negative correlations between animal- and plant-based food sources in the composition of mammal diets. Invertebrates are most negatively correlated with seed (coefficient = -0.31), fruit (coefficient = -0.34), and vegetative plant material (coefficient = -0.51). There is also a negative correlation between vegetative plant material and terrestrial vertebrates (coefficient = -0.24).

3.3. Cluster analysis

The number of maximum possible unique combinations of different food types in the dietary composition of an animal is 180 for turtles (see Figure 11), 354 for lizards (see Figure 12), 791 for birds, (see Figure 13), and 346 for mammals (see Figure 14). These values represent the maximum possible k-values for each respective dataset presented here.

Silhouette scores

Turtles. If the maximum value of k is capped at 10, the best possible silhouette score is 0.4072 at five clusters. This remains the highest possible silhouette score if

the maximum value of k is set to 20. If the maximum value of k is capped at 50, the highest silhouette score is instead 0.4642, at 39 clusters. If the maximum value of k is capped at 100, the best silhouette score is 0.5238 at 88 clusters. The maximum possible silhouette score for the turtle dataset is 0.5424 at 113 clusters. The silhouette score for k=2 is 0.3823, a difference of 0.1601 from the maximum possible score.

Lizards. If the maximum value of k is capped at 10, the best possible silhouette score is 0.9010 at 10 clusters. The highest possible silhouette score if the maximum value of k is set to 20 is 0.9026 at 11 clusters. If the maximum value of k is capped at 50, the highest silhouette score is 0.9267 at 50 clusters. If the maximum value of k is capped at 100, the best silhouette score is 0.9430 at 95 clusters. The maximum possible silhouette score for the lizard dataset is 0.9561 at 225 clusters. The silhouette score for k=2 is 0.8671, a difference of 0.089 from the maximum possible score.

Birds. If the maximum value of k is capped at 10, the best possible silhouette score is 0.5632 at 9 clusters. The highest possible silhouette score if the maximum value of k is set to 20 is 0.6082 at 18 clusters. If the maximum value of k is capped at 50, the highest silhouette score is 0.6320 at 44 clusters. If the maximum value of k is capped at 100, the best silhouette score is 0.6806 at 96 clusters. The maximum possible silhouette score for the bird dataset is 0.9682 at 785 clusters. The silhouette score for k=2 is 0.3823, a difference of 0.5859 from the maximum possible score.

Mammals. If the maximum value of k is capped at 10, the best possible silhouette score is 0.5586 at 10 clusters. The highest possible silhouette score if the maximum value of k is set to 19 is 0.5877 at 18 clusters. If the maximum value of k is capped at 50, the highest silhouette score is 0.6447 at 49 clusters. If the maximum value of k is capped at 100, the best silhouette score is 0.7561 at 98 clusters. The maximum possible silhouette score for the mammal dataset is 0.9805 at 344 clusters. The

silhouette score for k=2 is 0.4207, a difference of 0.5598 from the maximum possible score.

Elbow graph

Inspecting each elbow plot, it is evident that the point at which increasing the k-value no longer greatly reduced sum of square values within clusters is between 5 and 20 clusters. For the dietary datasets for all major amniote lineages, the WSS values are reduced by a single order of magnitude (from the maximum possible at a single cluster) between 10 and 20 clusters (see Figure 15). This indicates that adding additional clusters does not substantially increase information on diet variation those clusters contain. The biggest decreases in WSS values are between 1 and 5 clusters. The shape of the curve is very smooth and resembles the “elbow” heuristic very strongly for turtles, lizards, and mammals. The decrease in WSS values is less linear initially for birds though the point of infliction in the elbow graph begins to apply at the same stage.

DIETARY GUILDS FOR DOWNSTREAM ANALYSIS

For the purposes of downstream analysis, I determined that ten clusters is the most optimal for each major amniote lineage. I inspected the output from cluster analyses with k-values set at 5, 10, and 20 (see Tables 20-31). I chose to explore these values as they represent the range of k-values at which (a) the “elbow” curve appears and WSS is no longer substantially reduced by adding further clusters, and (b) the point at which silhouette scores begin to exceed 60% of the maximum value. The former does not reflect a hard rule but rather it is indicative, from inspecting the plots (see Figures 11-15) that the rate at which silhouette scores increase with higher k-values begins to slow. Furthermore, I seek to limit interpretations to clusters that add substantial information so as to avoid overfitting a very large number of only weakly informative clusters, which is also pragmatic for downstream analyses. I also compared the dietary guilds generated in the cluster analyses against the guilds I

generated using the a priori cut-off method of Pineda-Munoz and Alroy (2014). The a priori guilds were (a) very numerous (see Appendix A.2), and (b) included several dietary guilds with a single taxon. Pragmatically, these factors limit their usage in analyses as they would introduce (a) high model complexity, and (b) reduced statistical power. Nevertheless, the potential optimality of a much higher count of clusters provides interesting insight into the distribution of dietary variation among amniote species (see Chapter One, Discussion).

The guilds generated with a k-value of 5 revealed the most important large divisions in the input data but lacked sufficient detail. In particular, the complexity of generalist and omnivorous diets are obscured using a k-value of 5. The guilds generated with a k-value of 20 were complex and difficult to interpret in the context of broader analysis. The clusters generated with a k-value of 10 were very effective at demonstrating the wide range of dietary compositions of extant amniotes but are still easily interpreted. I therefore feel that dietary guilds representing clusters generated using k-means cluster analysis with a k-value of 10 will be the most appropriate for downstream analysis, particularly for estimating transition rates as this will be computationally challenging with a higher number of guilds. The guilds generated with a k-value of 20 will also be used for conducting analyses of variance in regard to body size, since this is a less-computationally intensive task.

Dietary guilds (k=10)

In interpreting the results of the k-means cluster analyses (k = 10), there are several factors to consider in describing the guilds recovered. I take the approach of naming these guilds according to the food categories that contribute most to their compositions. This classification system is ranked in accordance with the way each category is grouped and divided in the datasets. These names are not intended to represent a set of replacement names for previously hypothesized dietary groups (i.e., those of other authors), but are expedient handles for explanations of pooled diets among the clusters used in my downstream research in chapters 2 and 3.

Under normal circumstances, I applied the definitions ‘faunivory’ and ‘herbivory’ to the guilds for which more than 70% of the dietary composition of the guild comprised animal or plant material, respectively. Unless stated otherwise, a guild is omnivorous if neither animal nor plant material forms more than 70% of the dietary composition of the guild based on the centroid values of the untransformed percentages of each food source. I have chosen a value of 70% to match the criteria I use for the traditional guilds (see Chapter One, Methods). There are two instances (Guild 6 in lizards, and Guild 7 in mammals) where I waived this rule for reasons explained with their descriptive text (see Chapter One, Results).

I place particular emphasis on the second-order subdivisions when describing guilds in two contexts. Firstly, they are useful in describing the composition of generalist dietary guilds (e.g., “mixed herbivory with a predominant dietary composition of reproductive plant material”, and “predominantly carnivorous mixed faunivory”). Secondly, they provide a metric, consistent between the different datasets, for comparing guilds, particularly the results of further analyses that use the guilds as variables (e.g., “frugivory” and “nectarivory” are both guilds with a predominant dietary composition of reproductive plant material). I, therefore, primarily refer to the second-order categories when comparing sets of guilds with similar attributes. Wherever possible, I use the third-order categories when applying names to guilds.

These are most informative for further classifying a guild after a first-order classification (e.g., a “folivore” refers to a herbivore that primarily consumes vegetative plant material; a “piscivore” refers to a faunivore that primarily consumes fish). This is especially true of guilds composed overwhelmingly (>90%) of a single third-order category. Therefore, from the perspective of composition, the most important information is the primary first order food category, followed by either the primary second or third order food categories depending on how many subdivisions are present in a given guild’s dietary composition.

After which food types are the most represented, a guild can be further defined as either specialised or generalised. A dietary specialist, in this context, would be in a guild composed entirely, or overwhelmingly, of a single third order food category. A generalist, by contrast, would have a substantial (at least 10%) contribution from more than one third-order dietary subdivision. The division between generalist and

specialist isn't always easy to determine. The main reason for this is that the context of each lineage has a different effect on the spread of the data. The most obvious example is that of Guild 3 in lizards. This guild consists of 90% arthropod material and small amounts of each of the other categories (varying from taxon to taxon) combining to form the remaining 10%. By the standards of the other clades, this would be seen as a specialist guild. However, Guild 2 in lizards (which is, by a big margin, the most speciose) consists entirely of arthropod material. The most important division in the lizard dataset (as determined by the principal components analysis) is between arthropods and all other food categories. Guild 3 can (a) be reasonably defined as generalist in the context of the lizard data, and (b) be potentially informative for other hypothesis-testing exercises (see Chapters 2, 3).

Turtles

The clusters produced by the analysis, hereafter referred to as guilds, using a k-value of 10 can be summarized as follows:

Guild 1 (39 taxa/14.6%) diets are composed of a high proportion of vegetative plant parts with a minor input from each of the other food categories. As a guild, this represents "predominantly florivorous herbivory". This can be simplified as "**folivory s.l.**".

Guild 2 (34 taxa/12.7%) diets are composed predominantly of arthropods with substantial input from other invertebrate food sources as well as vertebrates with a smaller contribution from plant material. As a guild, this represents "predominantly insectivorous generalist faunivory". This can be simplified as "**mixed faunivory (pred. Arth)**".

Guild 3 (48 taxa/17.9%) diets are composed of approximately equal contributions from terrestrial arthropods, other invertebrate material, and both reproductive and vegetative plant material. There is only a very minor component of vertebrate material. As a guild, this represents "omnivory consisting of a variety of invertebrate and plant material". This can be simplified as "**omnivory**".

Guild 4 (24 taxa/9.0%) diets are composed of a predominant contribution of invertebrate material excluding terrestrial arthropods. Terrestrial arthropods then form the next largest contribution to the dietary composition, followed by components of vertebrates and plant material. As a guild this represents “predominantly durophagous generalist faunivory”. This can be simplified as “**mixed faunivory (pred. InvO)**”.

Guild 5 (21 taxa/7.8%) diets are composed mostly of reproductive plant structures with a substantial contribution of vegetative plant material and a very minor component of animal material. As a guild, this represents “generalist herbivory with a preference for reproductive plant material”. This can be simplified as “**mixed herbivory (pred. PlantR)**”.

Guild 6 (9 taxa/3.4%) diets consist almost exclusively of invertebrate material other than terrestrial arthropods. As a guild, this represents “invertivory specialising primarily in gastropods, molluscs, crustaceans, and other aquatic invertebrates”. This can be simplified as “**durophagy s.s.**”.

Guild 7 (17 taxa/6.3%) diets are composed almost exclusively of vegetative plant material. As a guild, this represents “herbivory specialised in vegetative plant structures”. This can be simplified as “**folivory s.s.**”.

Guild 8 (5 taxa/1.9%) diets are composed almost exclusively of terrestrial arthropod material. As a guild, this represents “invertivory specialising primarily in terrestrial tetrapods”. This can be simplified as “**insectivory s.s.**”.

Guild 9 (36 taxa/13.4%) diets are composed mostly of vegetative plant material with a substantial contribution of reproductive plant parts and a very minor component of animal material. As a guild, this represents “generalist herbivory with a preference for vegetative plant material”. This can be simplified as “**mixed herbivory (pred. PlantO)**”.

Guild 10 (35 taxa/13.1%) diets are composed predominant contribution of vertebrate material. Invertebrates other than terrestrial arthropods then form the next largest contribution to the dietary composition, followed by small components of arthropods

and plant material. As a guild this represents “predominantly durophagous generalist faunivory”. This can be simplified as “**mixed faunivory (pred. Vert)**”.

In summary, the turtle dataset can be reasonably divided into three herbivorous guilds, five faunivorous guilds, and a single omnivorous guild. Vertebrate feeding clusters least with other categories. Arthropod feeding, conversely, is most widespread among the guilds. To some extent, most turtles are generalist feeders. For example, the “mixed” faunivorous guilds, containing a mix of Arth and/or Duro and/or Vert are far more populated than the specialist insectivorous and durophagous guilds (see Table 21).

Lizards

The clusters produced by the analysis, hereafter referred to as guilds, using a k-value of 10, can be summarized as follows:

Guild 1 (53 taxa/1.0%) diets have a near-equal contribution of arthropods and vertebrates, with a small component of durophagy, and a very small component of reproductive plant structures. As a guild, this represents “generalist faunivory with a preference for both vertebrate and invertebrate food sources”. This can be simplified as “**mixed faunivory**”.

Guild 2 (4287 taxa/81.4%) diets are composed exclusively of arthropods. As a guild, this represents “specialist faunivory dominated by arthropod-feeding”. This can be simplified as “**insectivory sensu stricto (s.s.)**”.

Guild 3 (312 taxa/5.9%) diets are, by a wide margin, composed primarily of arthropods with minor contributions from the other food categories. As a guild, this represents “specialist faunivory dominated by arthropod-feeding but not exclusively so”. This can be simplified as “**insectivory sensu lato (s.l.)**”.

Guild 4 (27 taxa/0.5%) diets are mostly durophagous, with a significant arthropod input, and a smaller component of vertebrates. As a guild, this represents “semi-specialist faunivory with a preference for durophagy”. This can be simplified as “**durophagy sensu lato (s.l.)**”.

Guild 5 (18 taxa/0.3%) diets are largely composed of vertebrates, and has a minor arthropod component. As a guild, this represents “specialist faunivory with a preference for vertebrate carrion”. This can be simplified as “**carnivory**”.

Guild 6 (317 taxa/6.0%) diets have a large arthropod component, and a significant contribution of reproductive plant structures. As a guild, this represents “generalist omnivory dominated by arthropod-feeding with a substantial component of the diet supplemented with reproductive plant structures”. This can be simplified as “**insectivory-omnivory**”.

Guild 7 (67 taxa/1.3%) diets are primarily composed of reproductive plant parts, with a modest, but substantial, contribution of vegetative plant material. As a guild, this represents “mixed herbivory with a predominant dietary composition of reproductive plant structures”. This can be simplified as “**mixed herbivory (non-fibrous)**”.

Guild 8 (83 taxa/1.6%) diets are composed of approximately equal contributions of arthropods and reproductive plant structures, with smaller contributions from the other groups. As a guild this represents “generalist omnivory with a substantial contribution of both plant- and animal-based food sources”. This can be simplified as “**omnivory**”.

Guild 9 (86 taxa/1.6%) diets are composed of near-equal contributions of reproductive and vegetative plant parts with a noticeable contribution of arthropods as well. As a guild, this represents “generalist herbivory with a preference for both vegetative and reproductive plant structures”. This can be simplified as “**mixed herbivory**”.

Guild 10 (15 taxa/0.3%) diets are composed almost exclusively of vegetative plant structures, with no significant contribution of any other food source. As a guild, this

represents “specialist herbivory with a preference for vegetative plant structures”. This can be simplified as “**folivory**”.

An immediately obvious result is the overwhelming predominance of obligate insectivory in lizards (>80% of species). When accounting for the fact that Cluster 3 would be categorised as insectivory by most traditional definitions and the presence of insectivory-omnivory and durophagy; about 94% of lizards could justifiably be classified as “invertivores” (see Table 24, Figure 17). It should also be noted that the insectivore-omnivores include many (what are effectively) insectivorous taxa that opportunistically include nectar and/or tree sap in their diets (see ‘Gehyra protocol’ in Methods). Arthropod-feeding is most widespread in varying proportions among the different guilds and reproductive plant structures are also more frequent in generalist/mixed feeding strategies than vegetative structures. This is consistent with findings from other clades. Additionally, lizards include many guilds that are present universally such as insectivory, mixed herbivory, and mixed faunivory.

Birds

The clusters produced by the analysis using a k-value of 10, hereafter referred to as guilds, can be summarized as follows:

Guild 1 (343 taxa/3.5%) diets are almost entirely composed of fruit, with only minor contributions from the other sources. As a guild, this represents “specialised herbivory with a strong preference for fruit-feeding”. This can be simplified as “**frugivory**”.

Guild 2 (1237 taxa/12.4%) diets are mostly composed of fruit, with a large contribution of invertebrates. As a guild, this represents “omnivory with a preference for fruit”. This can be simplified as “**frugivory-omnivory**”.

Guild 3 (562 taxa/4.5%) diets are composed primarily of nectar, with a minor contribution of invertebrates. As a guild this represents “specialised herbivory, or predominantly-herbivorous omnivory, with a preference for a nectar”. This can be simplified as “**nectarivory**”.

Guild 4 (1404 taxa/14.0%) diets have approximately equal contributions from both invertebrates and seed with substantial components of fruit and vegetative plant material. As a guild, this represents “generalist omnivory with a predominant component of mixed plant material”. This can be simplified as “**omnivory**”.

Guild 5 (336 taxa/3.4%) diets are composed of a large contribution of fish, a significant contribution of invertebrates, and a smaller contribution of terrestrial vertebrates. As a guild, this represents “generalist faunivory with a preference for fish”. This can be simplified as “**piscivory sensu lato (s.l.)**”.

Guild 6 (2783 taxa/27.8%) diets are entirely composed of invertebrates. As a guild, this represents “specialist faunivory with a strong preference for invertebrate food sources”. This can be simplified as “**invertivory sensu strictu (s.s.)**”.

Guild 7 (370 taxa/3.7%) diets are mostly composed of terrestrial vertebrates with some input from invertebrates. As a guild, this represents “specialist faunivory with a preference for the terrestrial vertebrates”. This can be simplified as “**carnivory**”.

Guild 8 (246 taxa/2.5%) diets have a component of vegetative plant structures accounting for the largest share of dietary composition, with smaller contributions from seeds, invertebrates. As a guild, this represents “generalist herbivory with a preference for vegetative plant structures”. This can be simplified as “**mixed herbivory (pred. PlantO)**”.

Guild 9 (475 taxa/4.8%) diets are mostly composed of seed with a small contribution from invertebrates as well. As a guild, this represents “specialised herbivory with a preference for seeds and nuts”. This can be simplified as “**granivory**”.

Guild 10 (2232 taxa/22.3%) diets have a large invertebrate component with minor (though collectively important) contributions from the other food categories. As a guild, this represents “generalist faunivores or mixed-feeders with a strong bias towards invertebrate food sources”. This can be simplified as “**invertivory sensu lato (s.l.)**”.

In summary, the bird dataset can be reasonably divided into four herbivorous guilds, four faunivorous guilds, and a single omnivorous guild (see Table 27, Figure 18).

Vertebrate carrion-feeding clusters least with other categories. Invertebrate- and fruit-feeding, conversely, is most widespread among the guilds.

Mammals

The clusters produced by the analysis using a k-value of 10, which will hereafter be referred to as guilds, can be summarized as follows:

Guild 1 (441 taxa/8.4%) diets are composed of a near-equal contribution of terrestrial vertebrates, and invertebrates. There are also smaller components of other animal food sources as well as plant food sources. Taken together, there is a significant plant contribution. As a guild, this represents “generalist faunivory with a dietary composition of both vertebrate and invertebrate food sources”. This can be simplified as “**mixed faunivory**”.

Guild 2 (548 taxa/10.5%) diets are primarily comprised of invertebrates with the next largest input coming from terrestrial vertebrates with much smaller input from the other food categories. As a guild, this represents “generalist faunivory dominated by invertebrate-feeding with a meaningful non-invertebrate component”. This can be simplified as “**invertivory sensu lato (s.l.)**”.

Guild 3 (635 taxa/12.1%) diets are composed, overwhelmingly, of vegetative plant material with no significant contribution of any other food source. As a guild, this represents “specialist herbivory with a preference for vegetative plant structures”. This can be simplified as “**folivory**”.

Guild 4 (788 taxa/15.0%) diets have near-equal inputs from seed and fruit with substantial contributions from vegetative plant structures, and invertebrates. As a guild this represents “predominantly herbivorous generalist feeding dominated by reproductive plant structures”. This can be simplified as “**mixed herbivory with a preference for reproductive plant structures**”.

Guild 5 (78 taxa/1.5%) diets are composed primarily of fish, a significant invertebrate component, and an important contribution from terrestrial vertebrates. As a guild, this represents “generalist faunivory with a preference for fish”. This can be simplified as “**piscivory sensu lato (s.l.)**”.

Guild 6 (984 taxa/18.8%) diets have a predominant component of vegetative plant structures, with some input from seed, fruit, invertebrates, and nectar. As a guild this represents “predominantly herbivorous generalist feeding dominated by vegetative plant structures”. This can be simplified as “**mixed herbivory with a preference for vegetative plant structures**”.

Guild 7 (500 taxa/9.5%) diets have a large fruit component, with invertebrates constituting the next most-important contribution. There is also an input from nectar, and vegetative plant structures. As a guild, this represents “omnivory with a bias towards plant-based food sources”. This can be simplified as “true **omnivory**”.

Guild 8 (95 taxa/1.8%) diets are overwhelmingly dominated by terrestrial vertebrates with little input from other food categories. As a guild, this represents “specialist faunivory with a preference for the carrion of terrestrial vertebrates”. This can be simplified as “**carnivory**”.

Guild 9 (899 taxa/17.1%) diets are entirely composed of invertebrates. As a guild, this represents “specialist faunivory with a predominance of invertebrate food sources”. This can be simplified as “**invertivory sensu stricto (s.s.)**”.

Guild 10 (279 taxa/5.3%) diets have a very high fruit component, with only minor contributions from the other sources. As a guild, this represents “specialist herbivory with a strong preference for fruit-feeding”. This can be simplified as “**frugivory**”.

In summary, the mammal dataset can be reasonably divided into four herbivorous guilds, five faunivorous guilds, and a single omnivorous guild (see Tables 31; Figure 19). Vertebrate carrion-feeding clusters least with other categories. Invertebrates and all plant divisions are relatively widespread among the different guilds. Two unique features of mammals are (a) there are two mixed herbivorous guilds, and (b) omnivory has a far higher plant contribution than animal contribution. Predominantly

herbivorous guilds also comprise a higher proportion of taxa than predominantly faunivorous guilds.

4. Discussion

4.1. Overview

In all lineages, the optimal k-value as determined by silhouette score was very high (113 for turtles, 225 for lizards, 785 for birds, 344 for mammals). This indicates that there is a very high degree of overlap between the dietary compositions of different amniote taxa. Previous research exploring dietary classification has proposed relatively high numbers of dietary guilds (e.g., Lintulaakso et al. 2022 presented 100 dietary guilds in mammals). However, many studies applying discrete dietary classifications to broad biological and macroevolutionary questions use significantly fewer; either the three classical guilds (Espinoza et al., 2004; Price et al., 2012; Stephens & Wiens, 2003), or typically fewer than 10 more nuanced dietary guilds (Burin et al., 2016; R. Cooke et al., 2022; Reuter et al., 2023; Shipps et al., 2023). From a pragmatic perspective, these numbers of potential dietary categories predicted by the silhouette score are too high to be useful or interpretable in the context of currently available statistical analysis of diet evolution. Some of these diet clusters account for very few taxa — it is not uncommon for a cluster to account for less than 0.5% of the species of a clade when allowing k-values greater than 10. For the purposes of downstream analysis, this will reduce statistical power greatly. The same was true when I categorized the data according to the comprehensive a priori classification scheme of Pineda-Munoz and Alroy (2014), which allows up to 45 guilds in turtles, 51 guilds in lizards, 132 guilds in birds, and 99 guilds in mammals if applied to the percentile dietary data in the current study. My finding that dietary data fails to cluster optimally into a smaller, more manageable number of discrete clusters

in all major amniote lineages in the current study is consistent with the results and methodological suggestions of, for example, Wisniewski et al. (2023) and Grundler and Rabosky (2021) and suggests that real-life dietary variation is a complex, multivariate trait that cannot be neatly divided up discrete categories and may be best envisioned as having continuous, albeit highly uneven, quantitative distribution.

From the perspective of interpretability, following a k-value of between 10 and 20, the only outcome of increasing the number of guilds is the introduction of more finely-parsed omnivorous and generalist guilds. This apparent porosity of dividing lines between dietary guilds is expected in the face of extensive recent research indicating that a wide array of generalist feeding habits exist around specialist extremes, and that diet is best treated as a continuous rather than discrete variable (Grundler & Rabosky, 2021; Lintulaakso et al., 2023; Wisniewski et al., 2023), a position that I reassert here.

For the purposes of comparison between clades, and for use in downstream analysis, I will be primarily referring to the dietary guilds generated using a k-value of 10. These guilds are appropriate as they adequately capture the most important divisions in the dietary data for each clade while still representing a manageable number of dietary guilds for interpretive purposes. Dietary classification systems based on qualitative definitions or arbitrary cut-off values are not always best equipped to accurately represent diet in the context of macroevolutionary studies. I interpret the clusters obtained using a k-value of 10 as capturing the most important large-scale divisions in the broad spectrum of diet, and not as discrete, mutually exclusive clusters. The results can then be compared to those from existing studies that define dietary guilds differently so as to determine if the shift in definition causes a change in results.

4.2. Turtles

The consumption of fibrous plant material versus that of invertebrate material (taken collectively) is by far the biggest driver of variation of dietary composition patterns among turtles. This is followed by the division between insectivory and other forms of

invertivory (mostly durophagy). Turtles are overwhelmingly generalists if using the cut-off of 90% of dietary composition comprising of a single food source sensu Stephens and Wiens (2003). Under the 10-guild scheme, generalists account for 88.4% of turtle species. Under the 20-guild scheme, this only slightly decreases to 88.0%. If a more lenient cut-off of 60% is applied (Shipps et al., 2023) the proportion of generalist taxa drops to 52.1% and 48.0% respectively which is still high relative to other major amniote lineages (see Tables 20-31; Figures 15-19). Predominantly herbivorous guilds (42.1% of the total) are slightly more common than predominantly faunivorous guilds (40.0%), while a single omnivorous guild accounts for 17.9% of turtle taxa (see Table 21; Figure 16).

The sparsity of previous studies focused specifically on dietary classification in turtles provides a challenge in assessing this result in broader context. I found that a majority of turtle taxa coded as “mainland terrestrial” in the original dataset of Angielczyk et al. (2015) are either herbivorous (39 of 50 species; 78%) or omnivorous (7 of 50 species; 14%), consistent with the assessments of Ernst et al. (1989). There have also been studies suggesting that turtles tend towards dietary generalism more so than other ectothermic taxa of comparable body size (Luiselli, 2006; Luiselli et al., 2021). Some research has also suggested that evolutionary transitions into omnivory (the parameters of which often fit “generalism” sensu the current study) act as an evolutionary “sink” wherein speciation rates decline and extinction rates increase (Burin et al., 2016; Price et al., 2012). This, among other factors, could offer an explanation to the relative low species richness of Testudines relative to other clades of similar rank, and that a higher percentage of extant turtle taxa are at heightened risk of extinction than any other amniote lineage (Lovich et al., 2018). It is also possible that extant turtles represent a predominantly generalist subset of an ancestrally specialist clade. Testing this empirically is complicated by the limited knowledge of ancestral turtle diets in the fossil record (Foth et al., 2017). It should be noted that a dietary generalist may still be filling a distinct ecological niche such that it could be classified as a specialist in the broader sense (Loxdale et al., 2011). Given the unique morphology of turtles compared to other amniotes, I propose that this may offer an explanation to the high incidence of dietary generalism among turtles.

4.3. Lizards

Lizards are an exceptional lineage in that a single dietary guild (strict insectivory) accounts for a supermajority of taxa (81.4%; see Figure 17). Dietary variation in lizards is essentially an extreme version of the broader trend with the vast majority of variation of diet in lizards being explained by the separation of insectivory from several contained incidences of other dietary compositions. Following the 10-guild scheme, lizard taxa are overwhelmingly faunivorous (89.1% of taxa) and specialist (82.0% of taxa), and insectivory-omnivory (which is still >60% insectivorous) accounts for the largest share of generalist/omnivorous taxa (see Figure 17). Predominantly herbivorous lizard taxa are only 3.5% of the total (see Figure 17). These results are all consistent with expectations of previous research (Cooper Jr & Vitt, 2002; Meiri, 2010; Meiri, 2018; Pietczak & Vieira, 2017).

Hypotheses regarding the apparent dietary homogeneity among lizards basically sum to the idea that invertivory may simply be the optimal strategy for lizards given their anatomical and physiological constraints (Cooper Jr & Vitt, 2002; Pough, 1973). Evolutionary shifts towards omnivory or herbivory often constitute an opportunistic response to reduced abundance of insects in the environment (Herrel, 2007; Van Damme, 1999) and often involve minimal anatomical adaptation beyond lengthening of the short intestine (Cooper Jr & Vitt, 2002; O'Grady, 2006; O'Grady et al., 2005). Few lizards are specially adapted to a folivorous diet (Cooper Jr & Vitt, 2002) and thus are more likely to be omnivores or generalist herbivores that consume a blend of fibrous and non-fibrous plant material, likely supplemented with insects. This is evidenced in the current study by the positive correlation between fibrous and non-fibrous plant material (see Table 13). There is, therefore, a near-linear increase in intake in both kinds of plant material at the expense of the invertebrate component of the diet. Evolutionary shifts out of insectivory are also thought to drive increased body size (Herrel, Vanhooydonck, Joachim, et al., 2004; Meiri, 2010).

Previous research has shown that the dynamics of dietary composition are not consistent between different lizard families. Examples of this include the repeated

evolution of herbivory in small-bodied liolaemids (Espinoza et al., 2004; Ocampo et al., 2022), or the conspicuous overrepresentation of carnivory among varanids relative to other families (Pianka, 1995; Sweet & Pianka, 2003). Basically, certain lizard lineages and individual taxa, independently deviate from the, evidently evolutionary successful, “small insectivore” default design and explore novel morphologies (Meiri, 2018; Melstrom et al., 2021). This pattern, recovered in the current study, also mirrors the repeated evolution of other traits such as viviparity (Andrews & Mathies, 2000; Guillette, 1993), and limblessness (O'shea, 2021; Pianka & Vitt, 2003; Shine, 1986). It is also important to note that “insects” cover a wide range of taxa with unique material and nutritional properties (Allen, 1989; Bernard et al., 1997; Razeng & Watson, 2015; Sheine & Kay, 1977; Sheine & Kay, 1982). It may, then, be a misnomer to refer to most lizard taxa as being “specialist insectivores”. Future research on diet in lizards should seek to develop a more comprehensive dietary classification system for lizards that accommodates for the diversity of different kinds of insects as food sources.

4.4. Birds

The strongest driver of variance in dietary composition of birds, following the broader pattern, is invertivory. The next most important divisions are between the different types of reproductive plant material. Carnivory and, especially folivory, explain lower proportions of variance. The correlation matrices for birds indicated that most pairwise linear correlation coefficients between different food sources were very low other than between invertivory and the plant-based food sources (see Table 18). As with lizards, this is reflected in the dietary compositions of guilds, most of which contain at least a small component of invertebrates (see Table 18). Birds are mostly divided into specialist guilds which account for 31.3% of taxa at the 90% cut-off, but 73.6% of taxa at the 60% cut-off (see Tables 26-28). Collectively, reproductive plant structures provide a higher proportion of the average dietary composition of birds than in any other major amniote lineage, with an especially high incidence of granivory and nectarivory. The opposite is true of folivory, which is scarce among bird taxa (see Figure 18).

The results of the current study are expected given the existing consensus that most bird taxa are invertivorous with a diversity of alternative dietary niches in existence as well (Burin et al., 2016; Kissling et al., 2012; Kissling et al., 2014; Lopes et al., 2016). Previous research has demonstrated dietary specialization to be a predictor of high species richness among birds (Belmaker et al., 2012) and omnivory to act as an evolutionary sink (Burin et al., 2016). Bird lineages have also been shown as having a uniquely high incidence of phylogenetic trait conservatism on many anatomical features (Barnagaud et al., 2014; Duchêne & Cardillo, 2015), including features related to diet such as ceca size (Hunt et al., 2019). This could explain the apparent tendency towards dietary specialization in birds. A key finding in the current study is the apparent importance of generalist invertivory (invertivory s.l.) as a major division in overall dietary variation. Even at a k-value of 5, there is a distinction between “strict invertivory” (invertivory >90% of dietary composition) and “generalist invertivory” (invertivory 50-90% of dietary composition; see Tables 26-28). As will be explored in the following chapters, this distinction may have implications in the context of broader macroevolutionary studies.

4.5. Mammals

The strongest drivers of dietary variation in mammals are the relative consumption of invertebrates and fibrous plant material. Following the general pattern, most of the strongest linear correlations between food sources in mammals are between invertivory and different kinds of plant material (see Tables 11, 19; Figure 19). In contrast to birds, frugivory is a far more important driver of dietary variance than are granivory or nectarivory (see Figures 3, 4, 7, and 8). Mammals are unique among major amniote lineages in that a majority of taxa are herbivorous (51.2% under the 10-guild system).

Many mammals are dietary generalists (63.7% under the 10-guild system with a 90% cut-off; though only 33.0% at a cut-off of 60%). Dietary generalism in mammals is often expressed as mixed faunivory or mixed herbivory. Even under the more finely-parsed 20-guild system, omnivorous guilds with near-equal (i.e., both >40%) contributions of total plant and total animal material to the dietary composition are

rare and taxonomically depauperate (see Table 31). This is in agreement with the three “concentrations” of diets in nutritional terms described by Lintulaakso et al. (2023), wherein animal based food sources plotted together on a ternary plot, while fibrous and non-fibrous plant food-based diets were closer to each other than to the animal food sources. Another notable quirk of mammals is that there is a comparatively high negative linear correlation between fibrous plant material and terrestrial vertebrates as food sources (see Table 19). This is likely a function of large omnivorous carnivorans and suids consuming a combination of these food sources (Jiangzuo & Flynn, 2020; Sacco & Van Valkenburgh, 2004; Schley & Roper, 2003; Wu, 2022). It could also be indicative of the continuum between frugivory and browse folivory wherein forest-dwelling medium sized mammals consume combinations of fruit and leaves in an evolutionary gradient between “frugivore” and “browser” (Bodmer et al., 2006; Bodmer, 1989, 1990; Kunz & Ingalls, 1994).

The results of the current study broadly support previous hypotheses surrounding the dietary habits of mammals. It has been suggested that herbivory accounts for most biomass and highest alpha taxonomic diversity of mammals, and not of other major clades, because mammals have the largest body sizes among extant animal groups and constitute the bulk of the extant megafauna taxa (Asner et al., 2016; Klein et al., 2022). Klein et al. (2022) found that plant material similarly constituted most of the dietary compositions of extinct dinosaurs – a group which occupied the megafauna niche in the past. The relative abundance of herbivores among mammalian taxa is, therefore, attributable to this lineage dominating the herbivorous ecological niches while, as evidenced by the results for other clades, herbivory is otherwise quite rare among amniotes. The most common generalist diets in mammals were “invertebrate+non-fibrous plant”, “fibrous+ non-fibrous plant”, and “invertebrate+vertebrate”. This is consistent with the findings of Reuter et al. (2023) who demonstrated the evolutionary versatility of predominantly invertivorous omnivory, a matter that will be explored in greater detail in the coming chapters. Reuter et al. (2023) also provided a contradiction to the previous assertion that omnivory acts as an evolutionary “sink” in mammals (Price et al., 2012). The patterns of dietary generalism among mammals recovered in the current study are in agreement with the findings of Reuter et al. (2023).

4.6. Comparisons

The most important universal finding of the analyses of this chapter is that the biggest driver of variance in dietary compositions is the degree to which a taxon is invertivorous. The lines of evidence supporting these conclusions are (a) invertivory is the strongest predictor of dietary variance and has the strongest negative correlation with other food sources, and (b) that omnivorous and generalist dietary guilds typically include at least a small proportion of invertivory in their dietary compositions. All clades have at least two “levels” of invertivory (or insectivory in the case of turtles and lizards). This is not affected by the overall prevalence of invertivory as a percentage of total taxa in a given clade and this separation is already universally present at a k-value of 10, indicating its importance (see Figures 1-8, 20; Tables 21, 24, 27, 30). The most obvious points of divergence between the major amniote lineages relate to (a) the prevalence of folivory and its importance in driving variation in dietary composition, and (b) the extent to which taxa in different clades are either dietary specialists or dietary generalists. In both instances, there is a conspicuous similarity in the patterns between turtles and mammals, and between lizards and birds.

Folivory is common and constitutes an important driver of variance in the dietary compositions of turtles and mammals. By contrast, the feeding strategy is rare in lizards, and rarer still in birds. As mentioned previously, the high proportion of folivorous (and herbivorous more generally) taxa among mammals can be explained by the lineage having undergone an adaptive radiation into the “megafauna” role in Cenozoic ecosystems and thus should be expected to follow an exceptional pattern relative to other lineages (Klein et al., 2022). The overall scarcity of folivory in birds can possibly be explained by energetic constraints in flying animals imposed by body size (Kunz & Ingalls, 1994; Olsen, 2015). There are a few exceptions that have evolved adaptations to a folivorous diet, such as the Hoatzin (Grajal, 1995). The scarcity of herbivory in lizards could reflect (a) an adaptive constraint inherent to the lineage (Cooper Jr & Vitt, 2002), and/or (b) that they struggle to adapt to key herbivorous niches in the face of mammalian competition in a given ecosystem (Novosolov et al., 2018). This could explain, in part, why many obligate herbivorous lizards evolve in insular contexts (Van Damme, 1999). The fact that turtles mirror

mammals to some extent in the importance of high-fibre folivory may reflect the fact that they have adapted to the “macroherbivore” role in certain contexts such as marine (Goatley et al., 2012), and insular (Stoddart & Savy, 1983) ecosystems. Herbivorous turtle populations have also been shown to have a higher proportional impact on ecosystem biomass than lizards of comparable size and ecological nice (Iverson, 1982; Lovich et al., 2018). It should be noted (a) that while a high percentage of turtle taxa are folivorous, turtles are comparatively species-sparse clade, (b) that a majority of turtle taxa do consume some meaningful degree of invertebrate material in their dietary compositions, putting them at odds with mammals and in line with other diapsid lineages (lizards and birds), and (c) many turtles feed on aquatic vegetative material which may be seen as a separate dietary niche from terrestrial folivory, though similar from a digestive perspective (Bjorndal, 1985; Bloodgood et al., 2020; Demarco et al., 2022).

There is an immediately noticeable tendency towards generalism in turtles and mammals, and specialization in lizards and birds. As previously noted, it is important to contextualise this result. Firstly, an animal that consumes a mixed diet may perform a constrained ecological role if accounting for other factors such as locomotion, feeding/hunting style, and substrate among many others (Loxdale et al., 2011). Secondly, were the data to be more finely subdivided (e.g., the splitting of “invertebrates” into each order thereof), many “specialists” as defined by the current data would be reclassed as generalists. Nonetheless, the broader dietary categories used the current study are informative as they correlate with, and occasionally predict, important aspects of animal anatomy and physiology such as gut morphology (Battley & Piersma, 2005; Delsuc et al., 2014; Langer & Snipes, 1991; O'Grady, 2006; O'Grady et al., 2005; Sakaguchi, 2003; Song et al., 2020), and masticatory apparatus (Christiansen & Wroe, 2007; Melstrom, 2017; Melstrom et al., 2021; Shipps et al., 2023). Future research should look into comparative adaptive constraints between major amniote lineages in relation to the evolution of dietary generalism versus specialism.

Carnivory and, where applicable, piscivory were a consistently low drivers of variation in dietary composition. Furthermore, carnivorous guilds are less speciose than dietary guilds primarily composed by any other second-order subdivision of the

dietary data. This result is expected as the trophic pyramid, a long-standing central tenet of ecology, holds that plants, the lowest level, feed herbivores which, in turn, feed carnivores (Bodenheimer, 1938; Elton, 1927). The total biomass decreases each at each level of the trophic pyramid along with a decrease in available energy flow from the lower trophic levels (Lindeman, 1942). Per this model, the low number of carnivorous species (secondary consumers) are a result of this guild representing taxa at the highest trophic levels which are expected have lower species diversity (Begon & Townsend, 2021; Bodenheimer, 1938; Elton, 1927). This guild is conspicuously rare among lizards. As with herbivory, a contributing factor to this could be mammalian competition, which has an advantage in factors such as locomotion and metabolism, for macropredatory niches (Purwandana et al., 2016; Wilson & Parker, 2023).

4.7. Conclusions

I propose, based on the results of the current study, that the spectrum of diet could be represented with invertivory as the central point with two broad dietary gradients extending from it: one towards hypercarnivory, one towards high-fibre folivory. The “U-shaped” (or V-shaped) pattern I present also mirrors aspects of other hypotheses (which I will discuss further in the coming chapters) relating to diet in terms of evolutionary transitions (Amador & Giannini, 2021; Jiangzuo & Flynn, 2020; Reuter et al., 2023), and life history traits such as body size (M. Clauss et al., 2013; R. Cooke et al., 2022; Hiiemae, 2000), and mean body temperature (Clarke & O'Connor, 2014). In the context of the current study, invertivory serves as an anchor for the spectrum of diet in amniotes because (a) the separation of invertivory from other food sources is an important driver of variation in the dietary datasets of all major amniote lineages, and (b) it is the most widespread food source between different clusters and groups with other food sources very frequently. The different dietary guilds can be expressed, then, as gradients of invertivory. In a more philosophical sense, invertivory most likely represents the ancestral condition for Amniota and has been demonstrated as the ancestral condition of several major evolutionary radiations through deep time, including the initial evolutionary shifts into herbivory and omnivory (Melstrom et al., 2021; Modesto et al., 2009; Reuter et al.,

2023; Sues & Reisz, 1998; Wilson, 2013). The implication of this patterns is that they add some weight to the hypothesis that folivory and hypercarnivory represent derived, and extreme, conditions in amniotes (Sahney et al., 2010; Sues, 2000; Sues & Reisz, 1998).

The first biological gradient is between invertivory and carnivory. There is a high prevalence of mixed faunivory, involving both invertebrate and vertebrate material, in all major lineages of amniote (see Tables 20-31). This is likely a reflection of ecological availability of invertebrate food sources as a supplement to a vertebrate meat-based diet and the high rate of evolutionary shifts between invertivory and carnivory (Pollard & Puckett, 2021; Reuter et al., 2023; Rowe et al., 2016).The distinction between these groups of animals in terms of anatomical and physiological adaptation is not clear-cut (Christiansen & Wroe, 2007; Hume, 2003; Lintulaakso et al., 2023; Vézina, 1985). There are, however, conspicuous differences, especially in dentition and ecology, between insectivores, durophages, myrmecophages, piscivores, and hypercarnivores that provide points of distinction along this gradient (Clark et al., 2023; Hartstone-Rose & Steynder, 2013; Herrel et al., 2002; Lonnberg, 1903; McNab, 1984, 2000; Redford, 1987; Vézina, 1985). The primary factor separating invertivory from hypercarnivory is that of prey size relative to predator size, and energetics. Hypercarnivores, feeding on large vertebrates reach a larger body size than invertivores, mixed faunivores, and small vertebrate-feeders to successfully hunt their larger prey, which in turn provides increased energy and protein to sustain the larger body size (Carbone et al., 1999; De Cuyper et al., 2019).

The second biological gradient, between invertivory and folivory, is multifaceted. By far the most common constituents of omnivorous guilds recovered in the current study involve a combination of invertebrates and non-fibrous plant material, with a smaller contribution of vegetative plant matter (see Tables 20-31), consistent with findings from previous inquiries on the subject (Edwards et al., 2021; Herrel, Vanhooydonck, & Van Damme, 2004; Jiangzuo & Flynn, 2020; Lintulaakso et al., 2023; Reuter et al., 2023). A high rate of evolutionary transition between invertivory and omnivory has been demonstrated in several lineages (Amador & Giannini, 2021; Burin et al., 2016; Jiangzuo & Flynn, 2020; Reuter et al., 2023). Low-fiber plant food sources such as nectar and fruit provide an accessible source of readily available

energy to supplement an invertivorous diet (Edwards et al., 2021; McNab, 2014; Teixeira et al., 2013). Likewise, many ordinarily nectarivorous and frugivorous taxa incorporate their diets with invertebrates as a source of protein (Gartrell, 2000; Herrera, 1984), and many herbivorous or omnivorous taxa are invertivorous as juveniles and undergo an ontogenetic shift to a diet with a higher component plant material (Bouchard & Bjorndal, 2006; Howell et al., 2016; Silva et al., 2020).

There is also a high prevalence, in the current study (see Tables 20-31) and in others (Cork, 1996; Lintulaakso et al., 2023; Pineda-Munoz & Alroy, 2014; Reuter et al., 2023; Shipley et al., 2009; Verde Arregoitia & D'Elía, 2021), of mixed herbivorous guilds which incorporate both fibrous and non-fibrous plant material in their diets. Many herbivores in forested environments consume a combination of fibrous and non-fibrous plant material as a supplementary source of energy (Cork, 1996; Foley & Cork, 1992). It has also been hypothesized that the anatomical and physiological adaptations of granivorous or frugivorous diet serve to pre-adapt an animal to a strictly folivorous diet; to which the anatomical adaptations are far more extensive relative to any form of faunivory (Bodmer et al., 2006; Bodmer, 1990; Chivers, 1989; Chivers & Hladik, 1980; Kunz & Ingalls, 1994; Lambert, 1998; Rosenberger et al., 2011). The gradient between invertivory and folivory is, therefore, an accumulation of increased total carbohydrate material in the diet, and subsequently of increased fiber in the diet (Lintulaakso et al., 2023).

5. Limitations and future direction

I assembled the datasets I used in the current study with the primary goal of maximising taxonomic sample size. The structure and composition of the data I used are suitable for studies covering the breadth of this one. Given the limited quantity and quality of information practically obtainable, certain limitations are inevitable. Most of these relate to resolution of data and unavoidable error in measurement.

There are several different potential sources of dietary data in animals. These include qualitative or semi-quantitative methods such as observation of feeding or measurement of time spent feeding on different food sources. These are limited by

the fact that the observed actions of an animal feeding on a given set food sources is a poor indicator of the proportion each food source contributes to the total energy intake of a given animal (Garnick et al., 2018; McInnis et al., 1983; Pineda-Munoz & Alroy, 2014; Shrestha & Wegge, 2006). There are also quantitative field techniques including analysis of gut and faecal contents. While relative contributions of each food type are attainable this way, there are several shortcomings to the method. Firstly, different food items are digested at different rates and some food items (particularly softer materials like the flesh of fruits) are broken down quicker by digestive processes. An analysis of gut or, especially, faecal contents would, therefore, potentially be biased to less-digestible food sources (Balestrieri et al., 2011; Kohfeld & Harrison, 2000; Nielsen et al., 2018; Pineda-Munoz & Alroy, 2014). This bias is reduced in gut analysis over faecal analysis though far fewer studies use gut content analysis as it is a far more complex method (Balestrieri et al., 2011; Kohfeld & Harrison, 2000; Pineda-Munoz & Alroy, 2014). Furthermore, studies that do display gut content records present results as either relative volume of each food type, relative mass of each food type, or both. Mass is preferable as an indicator of dietary composition over volume since mass is a direct proxy for calorific energy content.

All methods of collecting and tracing the dietary composition of animals are limited in that a single observation or sample of observations cannot account for temporal variation in diet (a) seasonally, and (b) ontogenetically (Chatterji et al., 2022; Shahar et al., 2001). Studies that truly capture the dietary composition of an animal across its entire lifetime are very rare. Given that bias and generalisation are inevitable when collating a large pool of sources on dietary data, a high-quality approximation of diet is the best that is practically possible for a study aiming to answer a scientific question of such a wide breadth as the current study.

The EltonTraits database covers all extant taxa for birds and mammals. However, the percentage data are drawn largely from qualitive statements in the literature (Wilman et al., 2014). Additionally, the diets for many taxa are inferred based on the diets of congeneric taxa (Wilman et al., 2014). This method will, naturally, introduce some error as most data are inferred rather than observed. Some studies have demonstrated a discrepancy between dietary compositions of taxa in the EltonTraits

database and those acquired through quantitative methods (Gomes et al., 2022; Sebastián-González et al., 2023). However, there are no datasets of comparable size, to my knowledge, that cover such a wide taxonomic breadth of birds and mammals.

The datasets I collected for turtles and lizards are taxonomically wide and drawn mostly from primary literature sources. Particularly in the dataset for lizards, however, there are several instances where diets are inferred from those of closely related taxa. Additionally, it is important to note that both the turtle and lizard datasets are drawn from disparate sources (including mass, volumetric, observational, and other data; see Chapter One: Methods and Materials). As discussed in the Methods section, I have indicated (a) the source of the data, (b) the kind of data, and (c) my confidence in the data based on the sources it is drawn from. This will facilitate future, more-focused research that may require higher accuracy and/or precision in data used. The resolution of data currently available is appropriate for analysis in the context of the current study given that I seek to answer broad-scale questions.

6. Figures

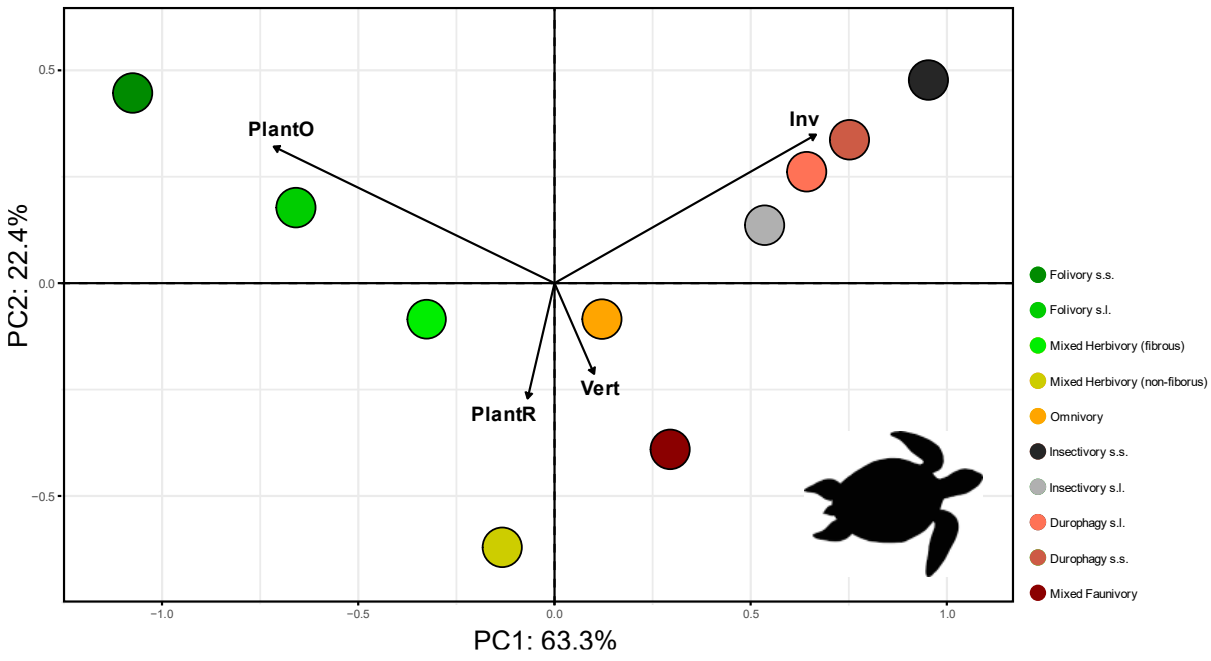


Figure 1: Principle Components Analysis (PCA) for turtles using the four second-order divisions in the dietary data. Circles represent centroid co-ordinates of dietary guilds recovered by the k-means cluster analysis (see Table 21). Abbreviations: Inv, invertebrates; Vert, vertebrate carrion; PlantR, reproductive plant structures; PlantO, vegetative plant structures.

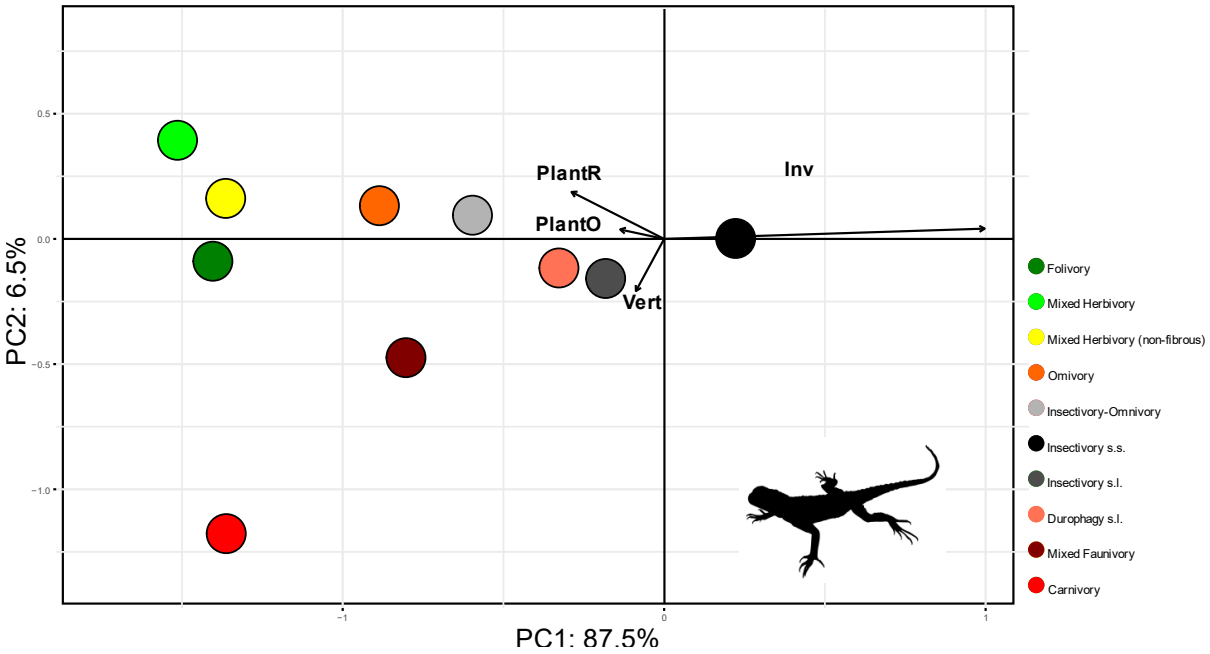


Figure 2: Principle Components Analysis (PCA) for lizards using the four second-order divisions in the dietary data. Circles represent centroid co-ordinates of dietary guilds recovered by the k-means cluster analysis (see Table 24). Abbreviations: Inv, invertebrates; Vert, vertebrate carrion; PlantR, reproductive plant structures; PlantO, vegetative plant structures.

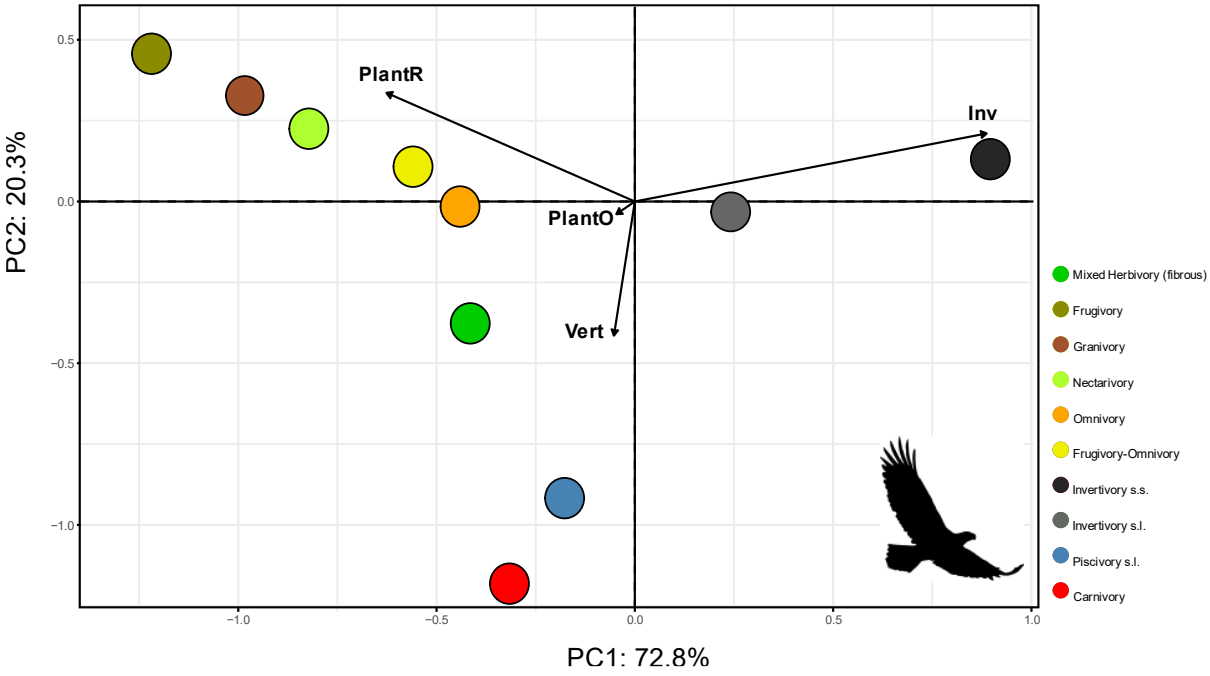


Figure 3: Principle Components Analysis (PCA) for birds using the four second-order divisions in the dietary data. Circles represent centroid co-ordinates of dietary guilds recovered by the k-means cluster analysis (see Table 27). Abbreviations: Inv, invertebrates; Vert, vertebrate carrion; PlantR, reproductive plant structures; PlantO, vegetative plant structures.

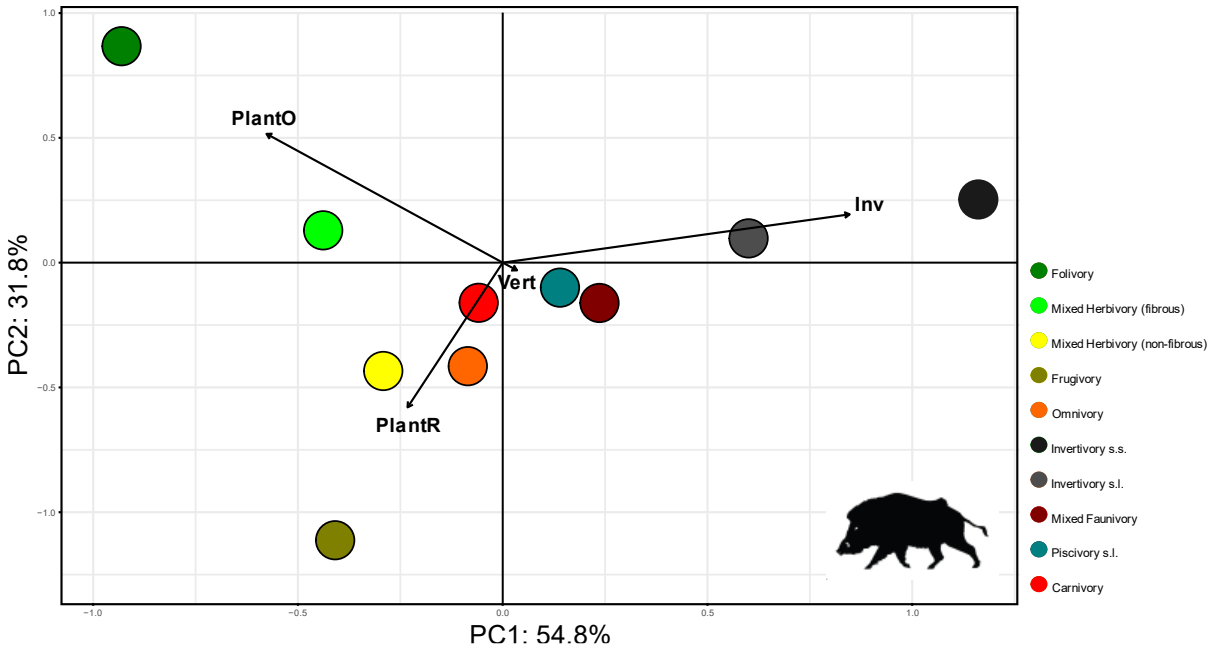


Figure 4: Principle Components Analysis (PCA) for mammals using the four second-order divisions in the dietary data. Circles represent centroid co-ordinates of dietary guilds recovered by the k-means cluster analysis (see Table 27). Abbreviations: Inv, invertebrates; Vert, vertebrate carrion; PlantR, reproductive plant structures; PlantO, vegetative plant structures.

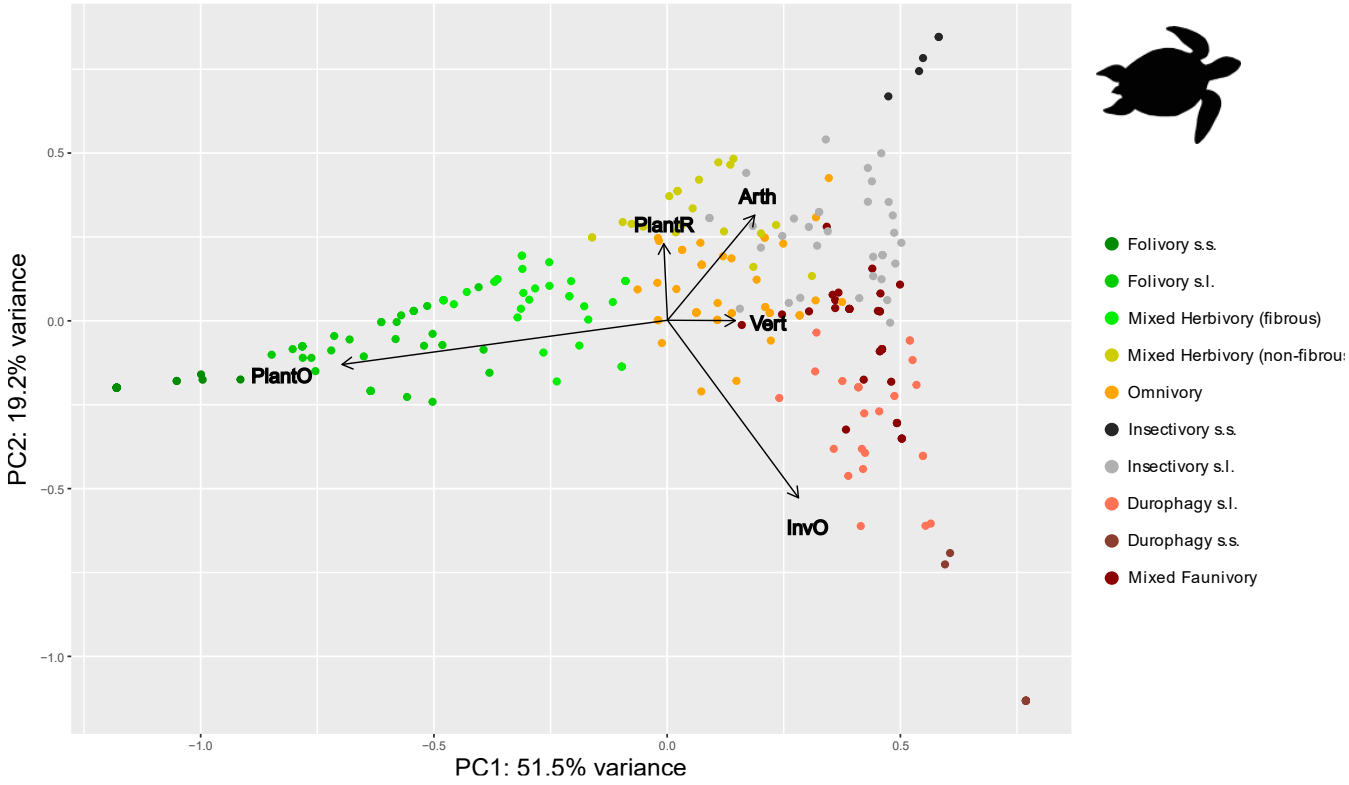


Figure 5: Principal components analysis (PCA) on third-order dietary categories in turtles, displaying the first two principal components. Points represent species. Arrows indicate loading direction of each variable on the axes of the principal components. Colour-coded by dietary guild recovered in k-means cluster analysis (k=10).

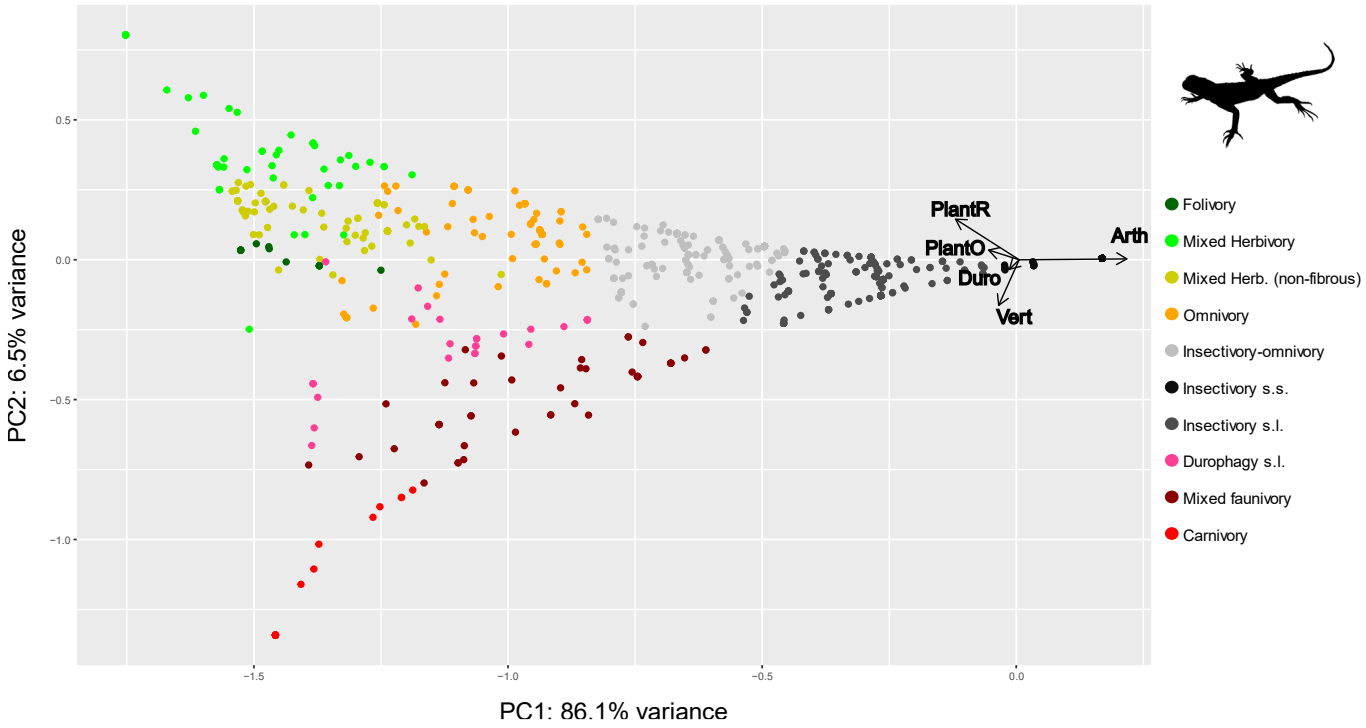


Figure 6: Principal components analysis (PCA) on third-order dietary categories in lizards, displaying the first two principal components. Points represent species. Arrows indicate loading direction of each variable on the axes of the principal components. Colour-coded by dietary guild recovered in k-means cluster analysis (k=10).

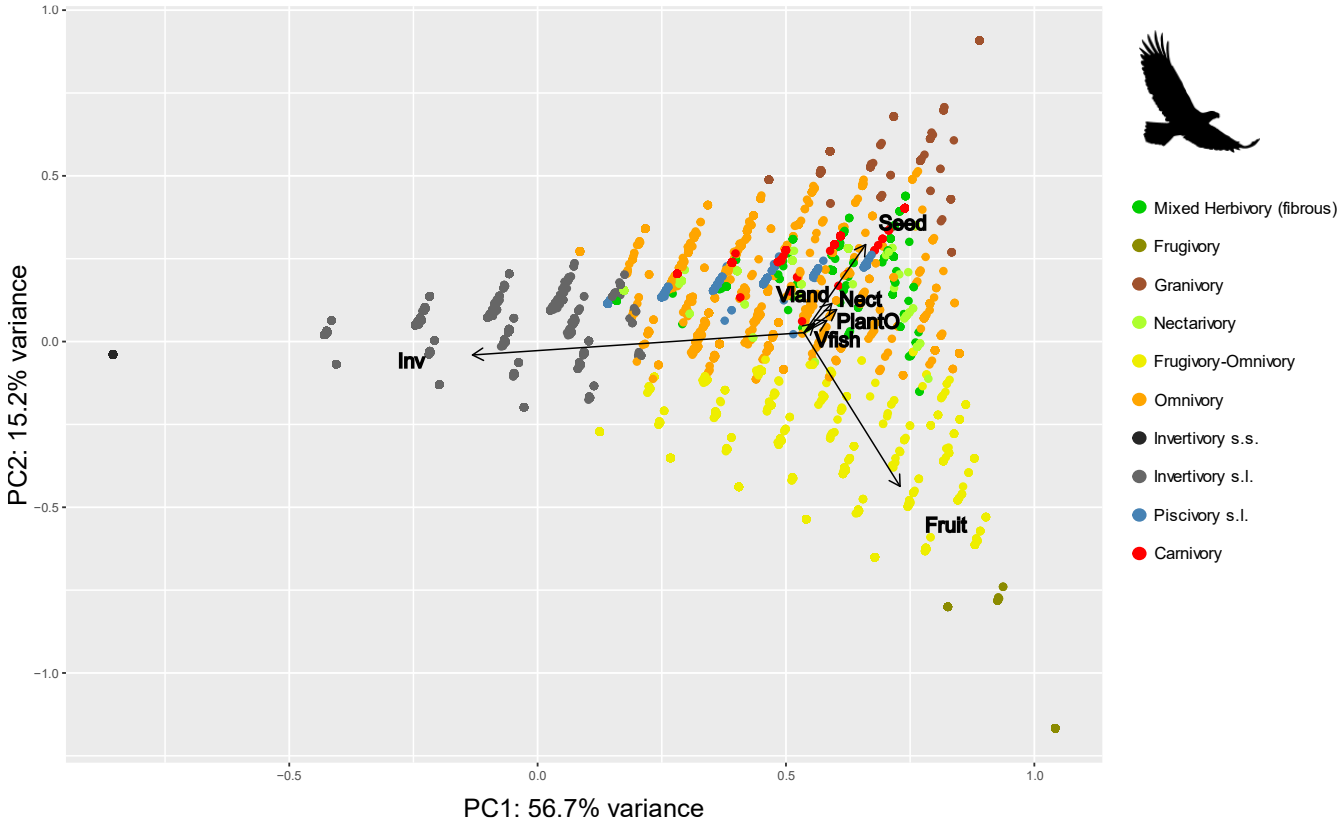


Figure 7: Principal components analysis (PCA) on third-order dietary categories in birds, displaying the first two principal components. Points represent species. Arrows indicate loading direction of each variable on the axes of the principal components. Colour-coded by dietary guild recovered in k-means cluster analysis (k=10).

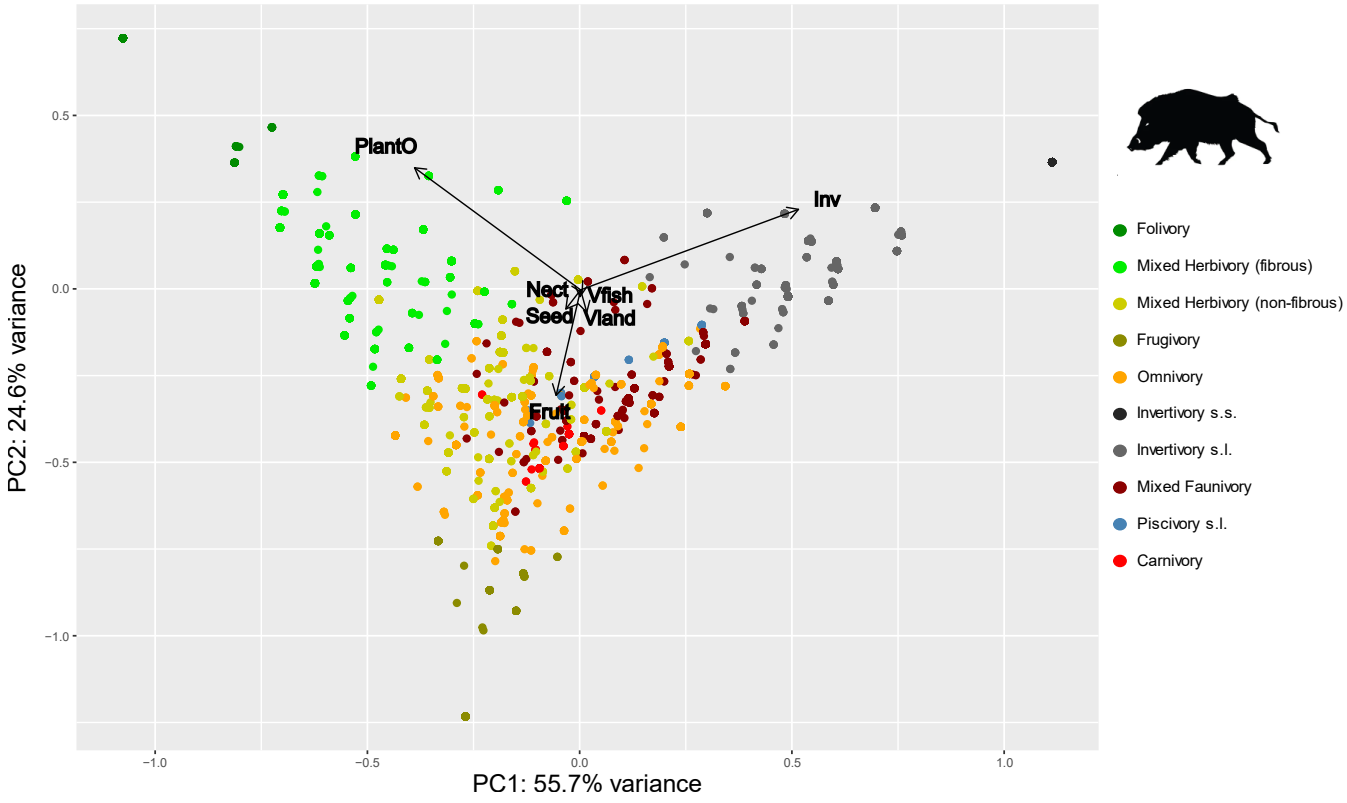


Figure 8: Principal components analysis (PCA) on third-order dietary categories in birds, displaying the first two principal components. Points represent species. Arrows indicate loading direction of each variable on the axes of the principal components. Colour-coded by dietary guild recovered in k-means cluster analysis (k=10).

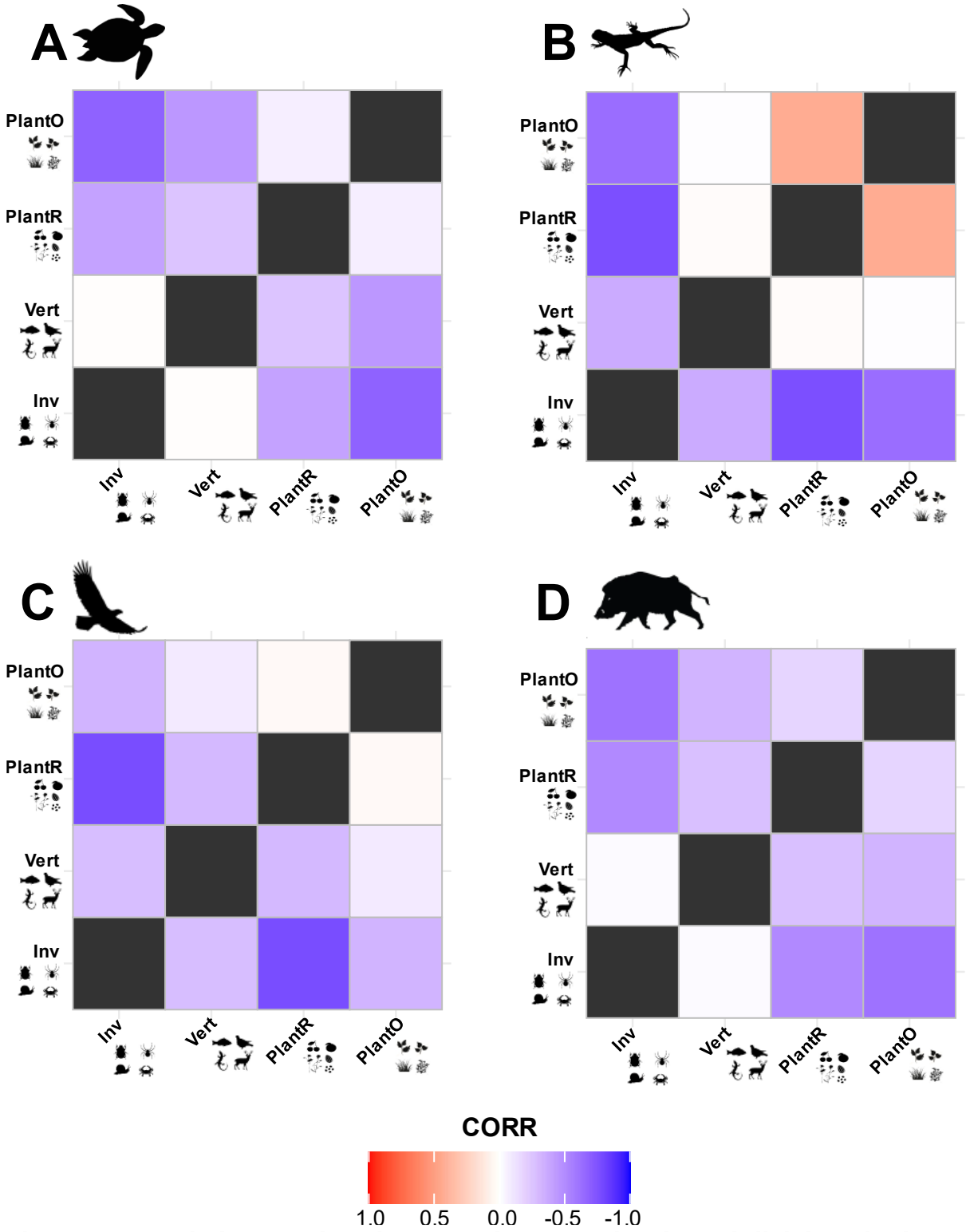


Figure 9: Correlation matrices between the second-order subdivisions in the dietary data (Inv, Vert, PlantR, PlantO) for turtles (A), lizards (B), birds (C), and mammals (D). Corr - correlation scale between two variables ranging from perfect correlation (1.0) to perfect negative correlation (-1.0).

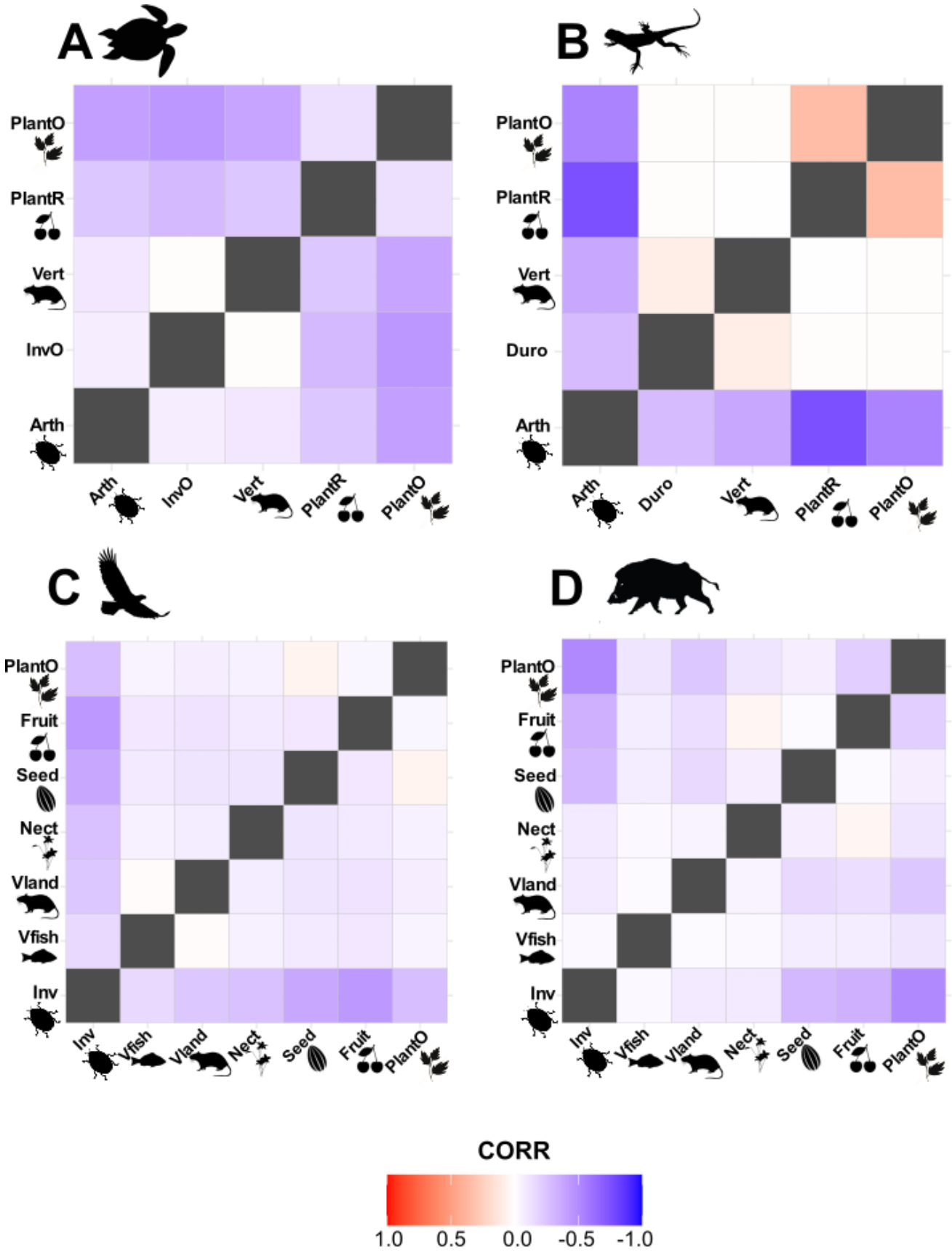


Figure 10: Correlation matrices between the third-order subdivisions in the dietary data (Inv, Vert, PlantR, PlantO) for turtles (A), lizards (B), birds (C), and

mammals (D). Corr - correlation scale between two variables ranging from perfect correlation (1.0) to perfect negative correlation (-1.0).

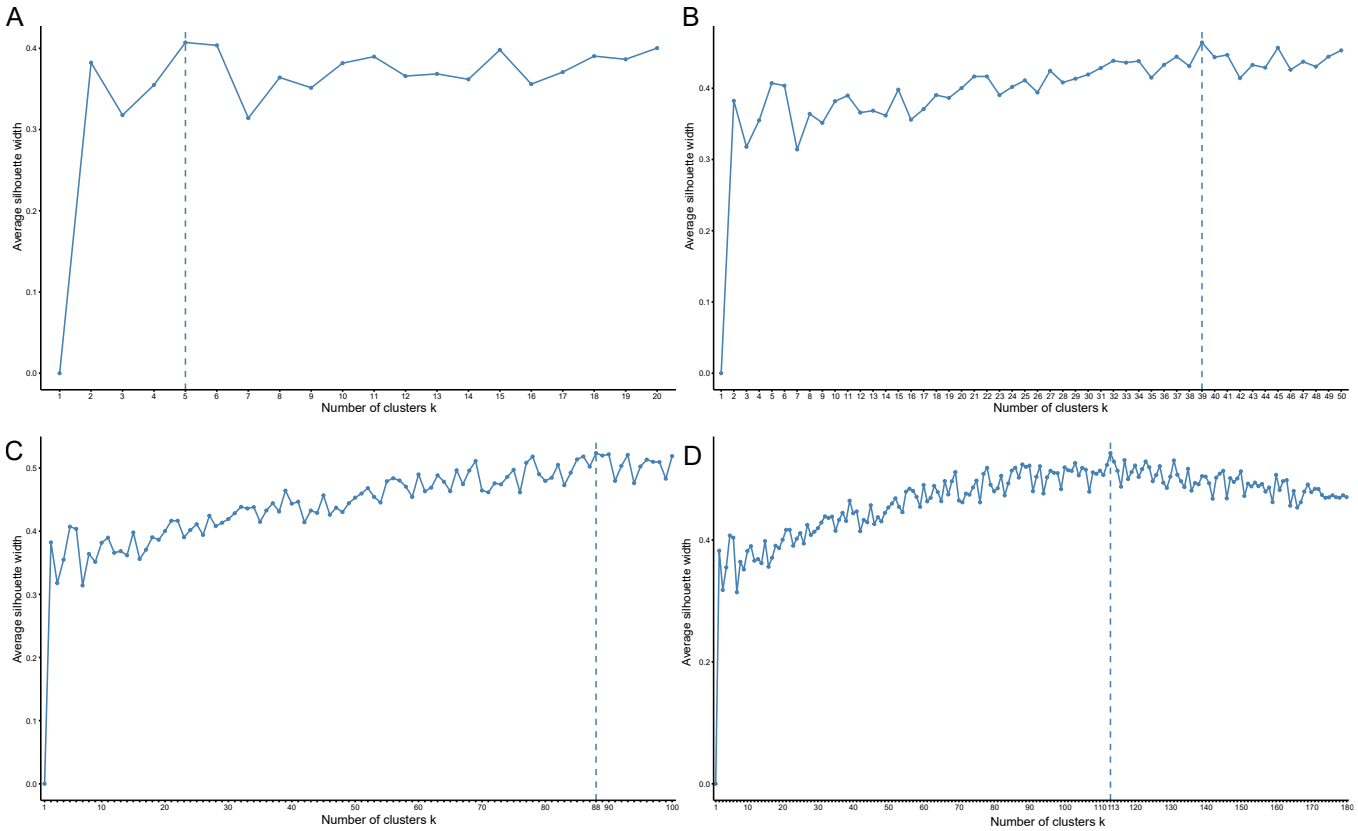


Figure 11: Silhouette scores of arcsine-transformed dietary data in turtles. Optimal number clusters shown when the k-value is set to (A) 20, (B) 50, (C) 100, and (D) 180 (k-max).

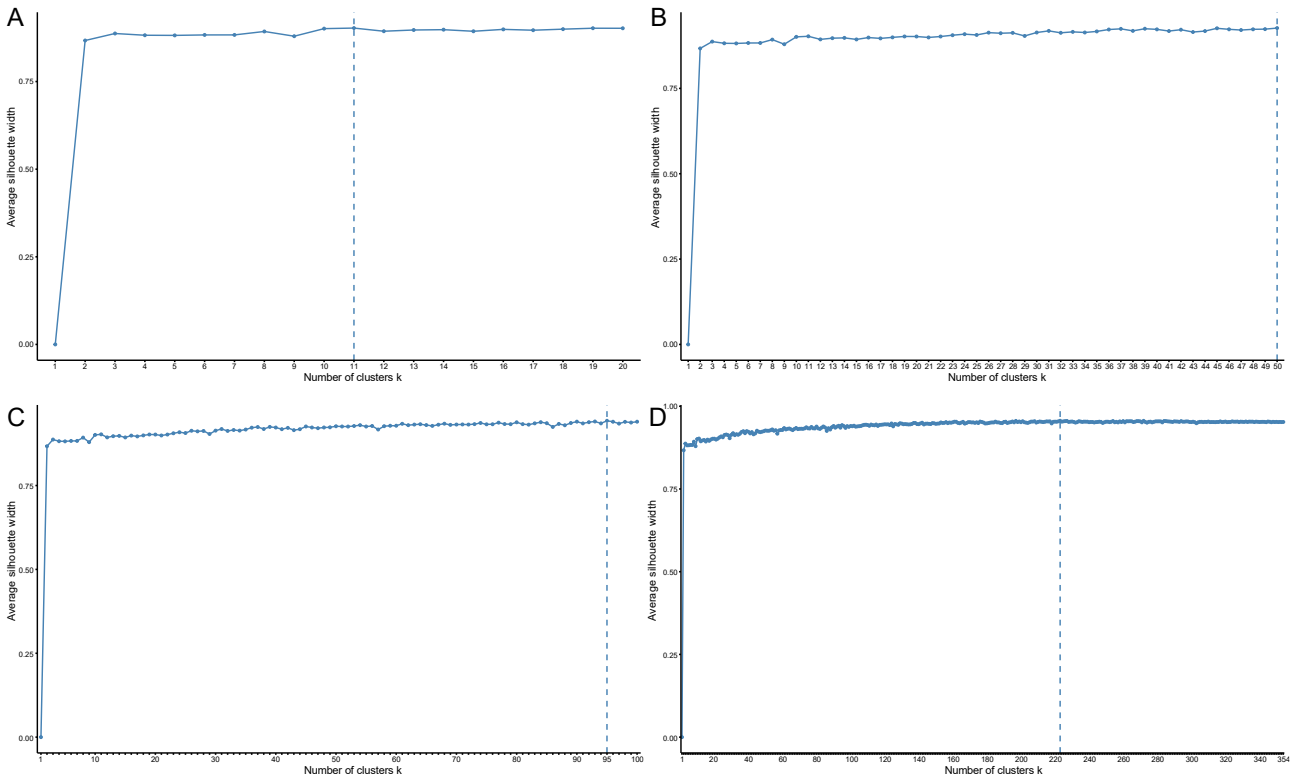


Figure 12: Silhouette scores of arcsine-transformed dietary data in lizards. Optimal number clusters shown when the k-value is set to (A) 20, (B) 50, (C) 100, and (D) 354 (k-max).

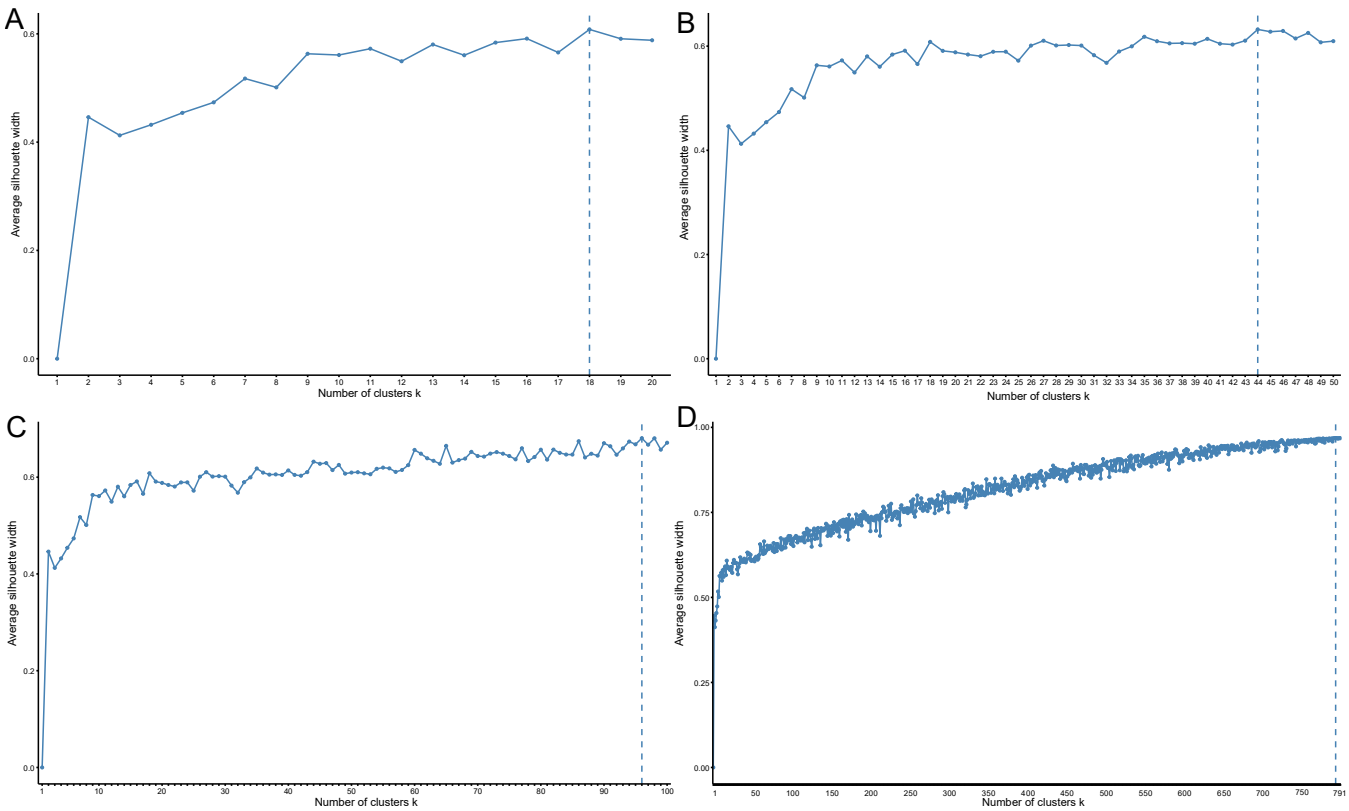


Figure 13: Silhouette scores of arcsine-transformed dietary data in birds. Optimal number clusters shown when the k-value is set to (A) 20, (B) 50, (C) 100, and (D) 791 (k-max).

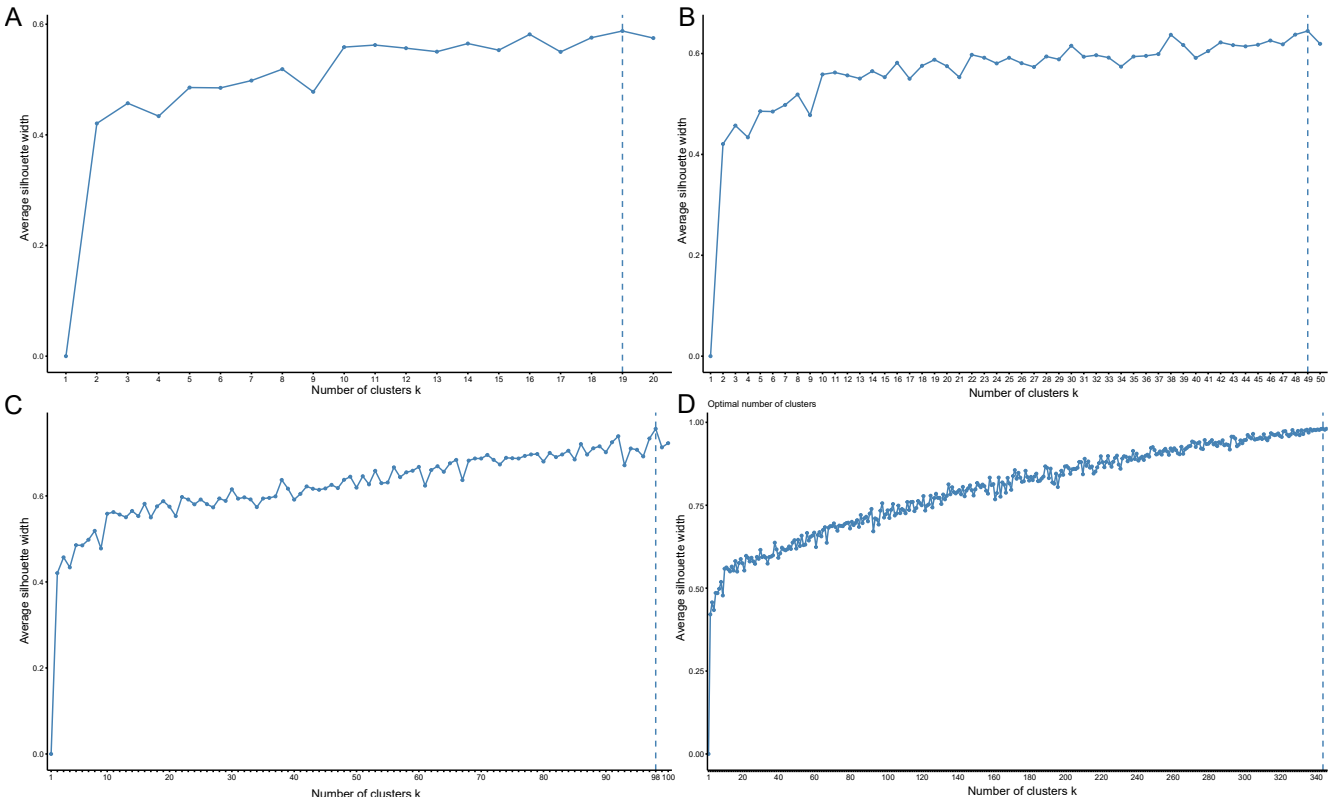


Figure 14: Silhouette scores of arcsine-transformed dietary data in mammals. Optimal number clusters shown when the k-value is set to (A) 20, (B) 50, (C) 100, and (D) 343 (k-max).

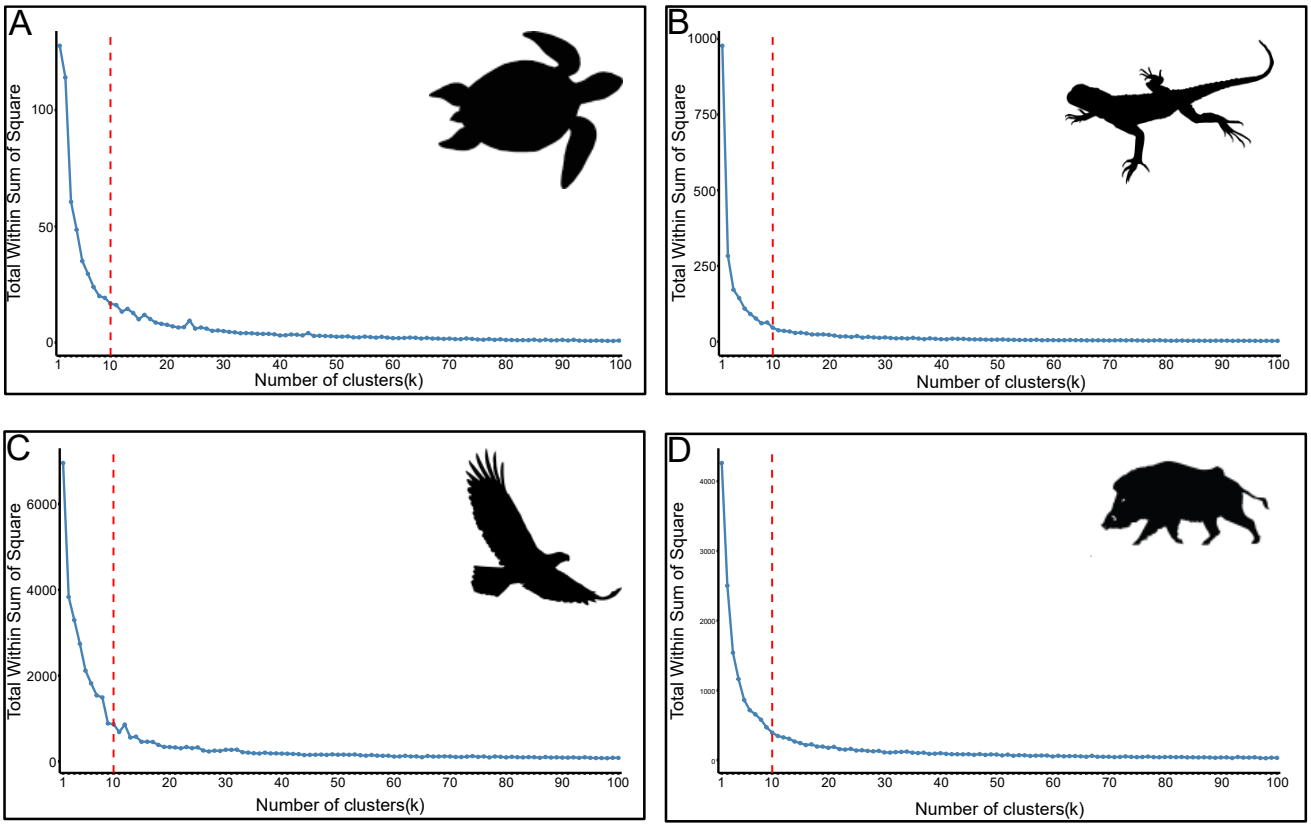


Figure 15: Elbow graphs plotting number of clusters (k-value) against within sum of squares (WSS) values per cluster for (A) turtles, (B) liards, (C) birds, and (D) mammals.

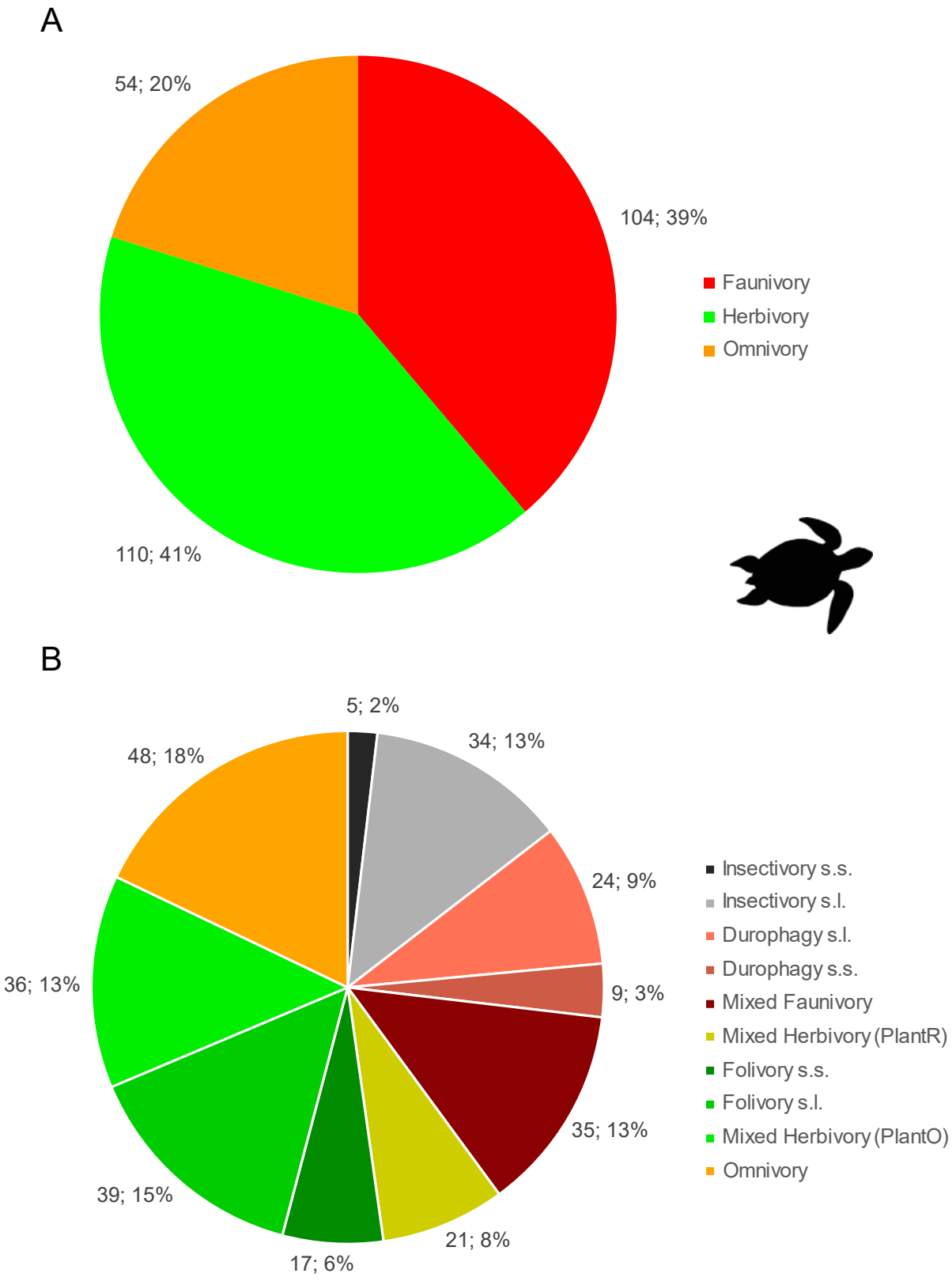


Figure 16: Numbers and percentages of all species of turtles in each (A) classical dietary guild, and (B) dietary guild recovered in the k-means cluster analysis. Abbreviations: Inv, invertebrates; Vert, vertebrate carrion; PlantR, reproductive plant structures; PlantO, vegetative plant structures; Mixed Herbivory

(V), mixed herbivory predominantly consisting of vegetative plant structures; Insectivory s.l., predominantly insectivorous mixed invertivory; Durophagy s.l., predominantly durophagous mixed invertivory; Mixed Herbivory (R), mixed herbivory predominantly consisting of reproductive plant structures; Durophagy s.s., "strict" durophagy; Insectivory s.s., "strict" insectivory; folivory s.l., mixed herbivory composed overwhelmingly but not exclusively of vegetative plant material; folviory s.s., “strict” folivory. N = 268.

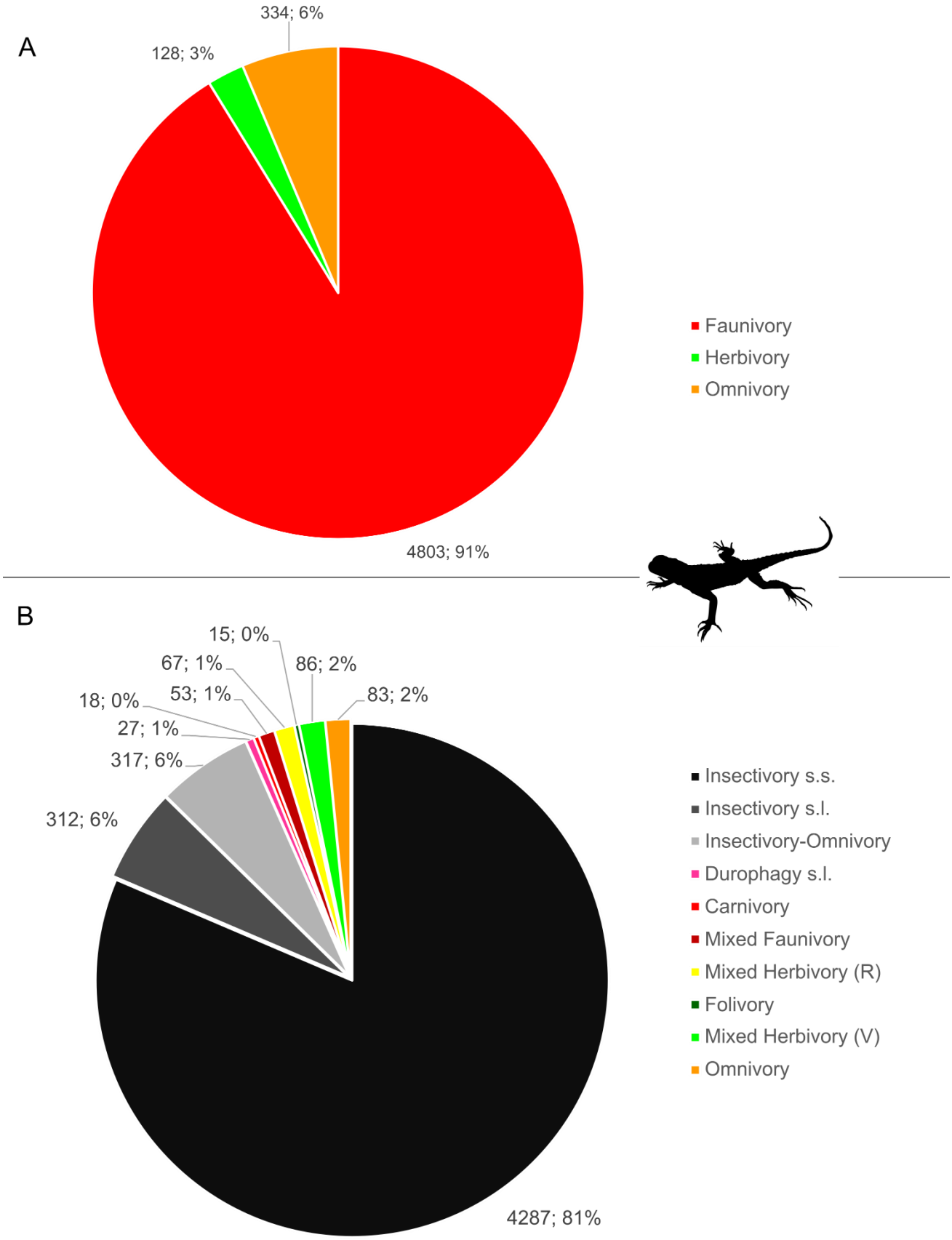


Figure 17: Numbers and percentages of all species of lizards in each (A) classical dietary guild, and (B) dietary guild recovered in the k-means cluster analysis. Abbreviations: Insectivory s.s., "strict" insectivory; Insectivory s.l., predominantly insectivorous mixed invertivory; Durophagy s.l., predominantly

durophagous mixed invertivory; Mixed Herbivory (V), mixed herbivory predominantly consisting of vegetative plant structures; Mixed Herbivory (R), mixed herbivory predominantly consisting of reproductive plant structures. N = 5265.

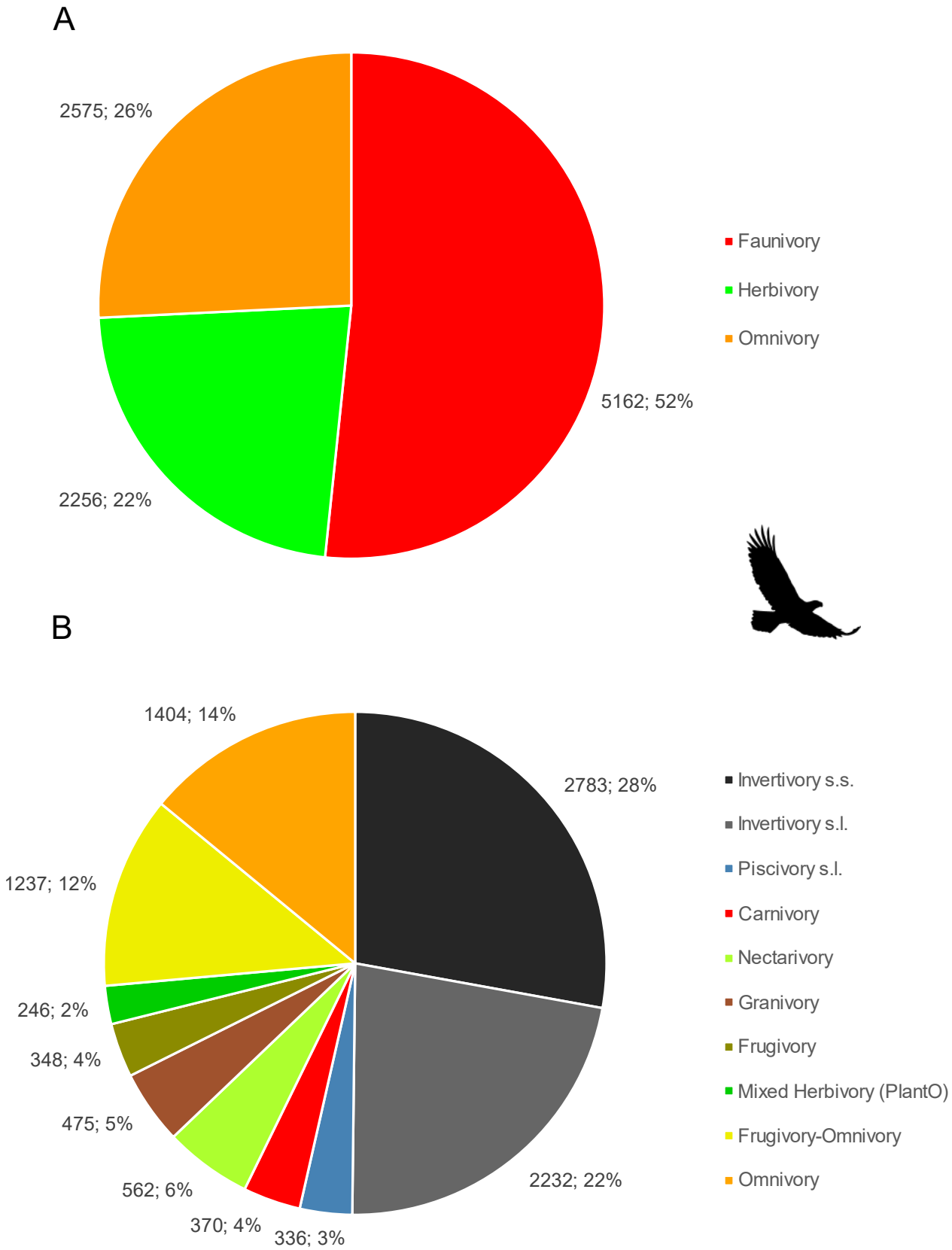


Figure 18: Numbers and percentages of all species of birds in each (A) classical dietary guild, and (B) dietary guild recovered in the k-means cluster analysis. Abbreviations: Inv, invertebrates; Vert, vertebrate carrion; PlantR - reproductive plant structures; PlantO, vegetative plant structures; Piscivory s.l.,

predominantly piscivorous dietary generalism; Invertivory s.s., "strict" invertivory; Invertivory s.l., predominantly invertivorous dietary generalism. N = 9993.

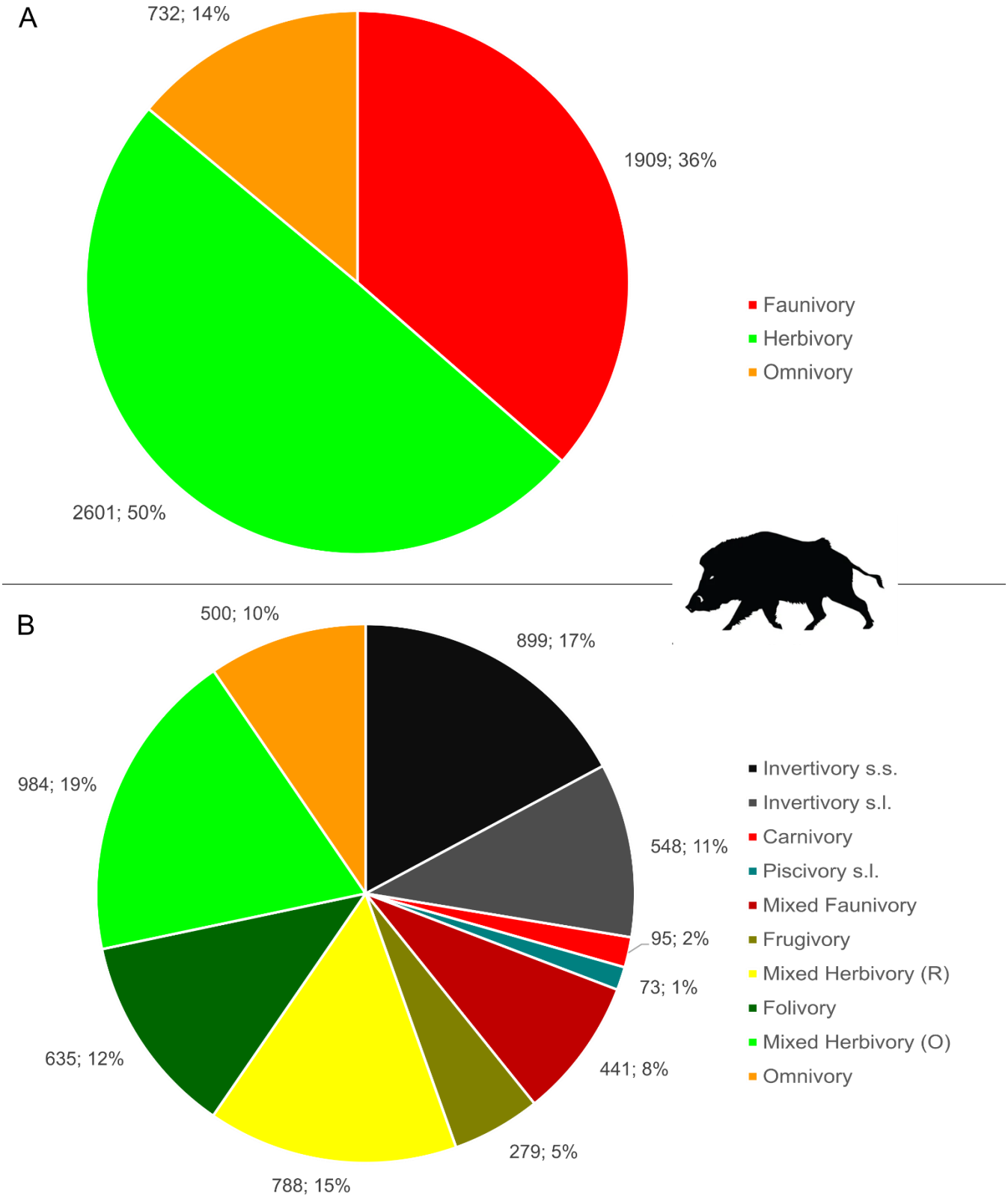


Figure 19: Numbers and percentages of all species of mammals in each (A) classical dietary guild, and (B) dietary guild recovered in the k-means cluster analysis. Abbreviations: Inv, invertebrates; Vert, vertebrate carrion; PlantR, reproductive plant structures; PlantO, vegetative plant structures; Invertivory s.l., predominantly invertivorous dietary generalism; Mixed Herbivory (R), mixed herbivory predominantly consisting of reproductive plant structures; Piscivory s.l., predominantly piscivorous dietary generalism; Mixed Herbivory (V), mixed herbivory

predominantly consisting of vegetative plant structures; Invertivory s.s., "strict" invertivory. N = 5242.

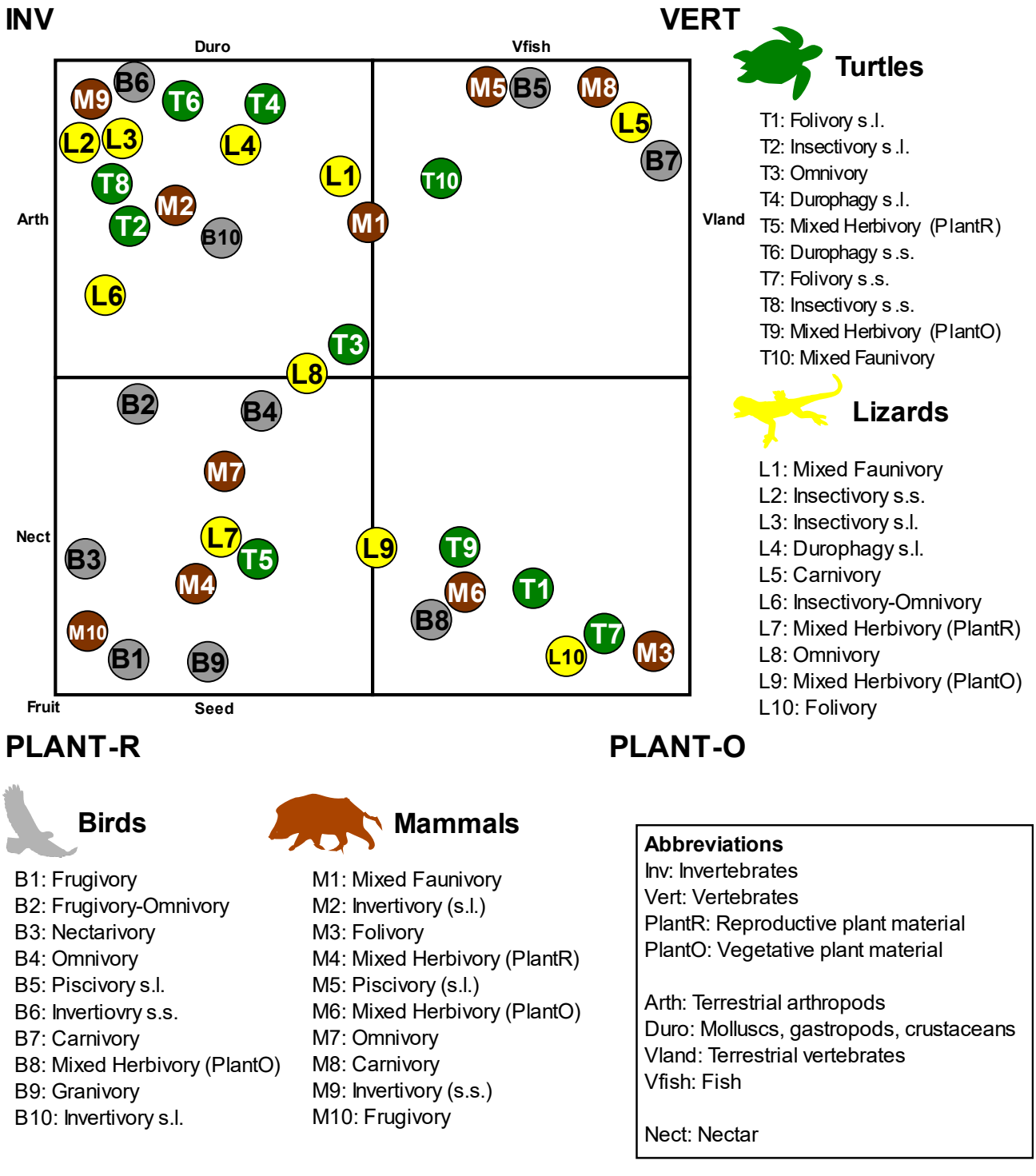


Figure 20: Schematic representation of where each dietary guild recovered in the cluster analysis for each clade fits in the dietary spectrum. The position of each guild is selected qualitatively based off of which food categories form each guild and in which relative proportions. The guilds are numbered by clade (T - turtle,

L - lizard, B - bird, M - mammal) and which cluster number they received as per the cluster analyses.

7. Tables

Table 1: Definitions of dietary guilds from selected sources. The first row indicates the lineage/clade, the second row indicates the literature source from which the definition originates.

	Tetrapods	**Tetrapods**	**Lizards**	**Lacertid lizards**	**Liolaemid lizards**	**Liolaemid lizards**	**Birds**	**Mammals**	**Rodents**	**Marsupials**	**Marsupials**
	Atwood et al. 2020	**Cooke et al. 2022**	**Meiri 2018**	**Van Damme 1999**	**Espinoza et al. 2004**	**Ocampo et al. 2022**	**Burin et al. 2015**	**Pineda-Munoz et al. 2016**	**Arregoitia and D'Elia 2020**	**Amador et al. 2021**	**Amador et al. 2021**
Faunivory	(Called "predator") Animal matter >80% of diet	NA	Animal matter >90% of diet	NA	NA	NA	NA	NA	Animal matter (except worms) >50% of diet	(Called "animalivory") Animal matter >50% of diet	NA
Carnivory	NA	Vertebrates >50% of diet					Terrestrial vertebrates >50% of diet	Vertebrates >50% of diet		NA	Vertebrates >50% of diet
Invertivory		Invertebrates >50% of diet	NA	Diet consists exclusively of insects	Plant matter <10% of diet	Plant matter <10% of diet	Invertebrates >50% of diet	Invertebrates >50% of diet	NA		Invertebrates >50% of diet
Insectivory		NA									

Vormivory				NA	NA	NA	NA	NA	Worms >50% of diet		NA
Piscivory							Fish >50% of diet		NA		
Omnivory	Both animal and plant matter >20% of diet each	Vertebrates, invertebrates, and plant matter each <50% of diet	Animal matter <90% of diet, plant matter <50% of diet	NA	Plant matter 10-50% of diet	Plant matter 10-75% of diet	No single food item >50% of diet	No food category accounts for greater than 50% of the dietary composition	No food category accounts for greater than 50% of the dietary composition	No food category >50% of diet	No food category >50% of diet
Herbivory	Plant matter >80% of diet	Plant matter >50% of diet	Plant matter >50% of diet	Any docemented intention consumption of plant matter	Plant matter >70% of diet	Plant matter >75% of diet	Fibrous plant matter >50% of diet	NA	NA	Plant matter >50% of diet	NA
Frugivory	NA	NA	NA	NA	NA	NA	Fruit >50% of diet	Fruit >50% of diet	Fruit >50% of diet	NA	Fruit >50% of diet
Granivory							Seed >50% of diet	Seed >50% of diet	Seed >50% of diet		Seed >50% of diet
Nectarivory							Nectar >50% of diet	NA	NA		Nectar >50% of diet

Fungivory							NA	Fungi >50% of diet	NA	(Called "mycophagy") Fungi >50% of diet	(Called "mycophagy") Fungi >50% of diet
Folivory								Fibrous plant matter >50% of diet	Fibrous plant material >50% of diet		NA
Browse herbivory								NA	NA	NA	Leaves >50% of diet
Grass herbivory											Grass >50% of diet
Gumivory								Gum/sap > 50% of diet			(Called "exudivory") Gum/sap >50% of diet
Specialist herbivory								NA	Diet consists of >50% any plant type not previously mentioned		NA

Table 2: Definitions of each food type included in the datasets for the purposes of downstream analysis. The final four columns indicate the datasets in which a given food type is included.

Food type	Definition	Turtles	Lizards	Birds	Mammals
AnimalT	Total animal material	YES	YES	YES	YES
Inv	Total invertebrates	YES	YES	YES	YES
Arth	Terrestrial arthropods	YES	YES	NO	NO
InvO	Mollusks, gastropods, and crustaceans	YES	YES	NO	NO
Vert	Total vertebrate meat	YES	YES	YES	YES
Vland	Terrestrial vertebrates	NO	NO	YES	YES
Vfish	Fish	NO	NO	YES	YES
PlantT	Total plant material	YES	YES	YES	YES
PlantR	Reproductive plant structures	YES	YES	YES	YES
Fruit	Fruit, pulses, flowers	NO	NO	YES	YES
Seed	Seeds, grains, nuts	NO	NO	YES	YES
Nect	Nectar, pollen, sap	NO	NO	YES	YES
PlantO	Vegetative plant material, fungi, algae	YES	YES	YES	YES

Table 3: Glossary of dietary guilds and definitions as used in the current study. “Overwhelmingly” in this context refers to a single food group contributing more than 80% of total dietary composition. “Significant” in this context refers to a single food group contributing more than 20% of total dietary composition.

Term	Definition
Specialist	Diet composed fully, or overwhelmingly of a single third-order food source category
Faunivory	Diet composed fully, or overwhelmingly, of animal-based food sources
Invertivory	Diet composed fully, or overwhelmingly, of invertebrates
Insectivory	Diet composed fully, or overwhelmingly, of terrestrial arthropods
Durophagy	Diet composed fully, or overwhelmingly, of gastropods, molluscs, and/or crustaceans
Carnivory	Diet composed fully, or overwhelmingly, of vertebrate meat
Piscivory	Diet composed fully, or overwhelmingly, of fish
Herbivory	Diet composed fully, or overwhelmingly, of plant material
Nectarivory	Diet composed fully, or overwhelmingly, of nectar and/or sap
Granivory	Diet composed fully, or overwhelmingly, of seeds and/or nuts
Frugivory	Diet composed fully, or overwhelmingly, of fruits and/or flowers
Folivory	Diet composed fully, or overwhelmingly, of vegetative plant material
Generalist	Diet composed of significant contributions of two or more food categories of any order level
Mixed faunivory	Faunivorous diet with significant contribution of both invertebrate and vertebrate material

Mixed herbivory	Herbivorous diet with significant contribution of both reproductive (non-fibrous) and vegetative (fibrous) plant material
Omnivory	Diet composed of significant contributions of both animal- and plant-based food sources

Table 4: Summary of the principal components analysis (PCA) on arcsine-transformed percentage data of each food type (second-order) in the diet for turtles.

	PC1	**PC2**	**PC3**	**PC4**
Proportion	63.27%	22.39%	13.06%	1.28%
Cumulative	63.27%	85.66%	98.72%	100.0%
Loadings				
Inv	0,676	0,595	0,113	0,419
Vert	0,102	-0,364	-0,743	0,552
PlantR	-0,070	-0,462	0,656	0,592
PlantO	-0,726	0,547	-0,063	0,411

Table 5: Summary of the principal components analysis (PCA) on arcsine-transformed percentage data of each food type (second-order) in the diet for lizards.

	PC1	**PC2**	**PC3**	**PC4**
Proportion	87.54%	6.47%	4.15%	1.84%
Cumulative	87.54%	94.01%	98.16%	100.0%
Loadings				

Inv	0,949	0,144	0,046	0,277
Vert	-0,084	-0,729	0,282	0,618
PlantR	-0,274	0,656	0,470	0,522
PlantO	-0,130	0,131	-0,835	0,518

Table 6: Summary of the principal components analysis (PCA) on arcsine-transformed percentage data of each food type (second-order) in the diet for birds.

	PC1	**PC2**	**PC3**	**PC4**
Proportion	72.77%	20.32%	5.69%	1.21%
Cumulative	72.77%	93.09%	98.79%	100.0%
Loadings				
Inv	0,815	0,366	0,272	0,357
Vert	-0,049	-0,721	0,524	0,450
PlantR	-0,576	0,584	0,394	0,415
PlantO	-0,043	-0,068	-0,704	0,706

Table 7: Summary of the principal components analysis (PCA) on arcsine-transformed percentage data of each food type (second-order) in the diet for mammals.

	PC1	**PC2**	**PC3**	**PC4**
Proportion	54.80%	31.76%	12.07%	1.37%
Cumulative	54.80%	86.56%	98.63%	100.0%
Loadings				
Inv	0,806	0,242	0,347	0,414

Vert	0,033	-0,038	-0,786	0,617
PlantR	-0,221	-0,724	0,419	0,501
PlantO	-0,549	0,645	0,294	0,444

Table 8: Summary of the principal components analysis (PCA) on arcsine-transformed percentage data of each food type (third-order) in the diet for turtles.

	PC1	**PC2**	**PC3**	**PC4**	**PC5**
Proportion	51.53%	19.20%	15.60%	12.94%	0.73%
Cumulative	51.53%	70.73%	86.33%	99.27%	100.00%
Loadings					
asin.Arth	0.237	0.468	0.701	0.153	0.458
asin.InvO	0.356	-0.791		0.284	0.399
asin.Vert	0.184		-0.186	-0.842	0.472
asin.PlantR		0.341	-0.656	0.432	0.517
asin.PlantO	-0.885	-0.197	0.191		0.376

Table 9: Summary of the principal components analysis (PCA) on arcsine-transformed percentage data of each food type (third-order) in the diet for lizards.

	PC1	**PC2**	**PC3**	**PC4**	**PC5**
Proportion	86.14%	6.51%	4.09%	2.50%	0.77%
Cumulative	86.14%	92.65%	96.73%	99.23%	100.0%
Loadings					
asin.Arth	0.947	0.135		0.135	0.257

asin.Duro		-0.150		-0.753	0.638
asin.Vert		-0.722	0.254	0.485	0.413
asin.PlantR	-0.133	0.154	-0.844	0.334	0.366
asin.PlantO	-0.277	0.643	0.468	0.261	0.473

Table 10: Summary of the principal components analysis (PCA) on arcsine-transformed percentage data of each food type (third-order) in the diet for birds.

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**
Proportion	56.65%	15.15%	10.85%	8.68%	4.51%	3.49%	0.66%
Cumulative	56.65%	71.80%	82.86%	91.34%	95.85%	99.34%	100.0%
Loadings							
asin.Inv	-0.936	-0.122	-0.113		0.131		0.280
asin.Vland		0.159	0.471	0.694	0.369		0.347
asin.Vfish					-0.459	-0.757	0.450
asin.Nect		0.126	0.451	-0.718	0.339		0.375
asin.Seed	0.174	0.481	-0.708		0.327		0.358
asin.Fruit	0.271	-0.841	-0.229		0.214		0.349
asin.PlantO					-0.606	0.644	0.457

Table 11: Summary of the principal components analysis (PCA) on arcsine-transformed percentage data of each food type (third-order) in the diet for mammals.

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**
Proportion	55.70%	24.58%	10.00%	5.75%	2.07%	1.43%	0.46%

Cumulative	55.70%	80.29%	90.28%	96.03%	98.11%	99.54%	100.0%
Loadings							
asin.Inv	0.791	0.440	0.275	0.101	0.185		0.245
asin.Vland		-0.122	-0.623	0.606	0.331		0.345
asin.Vfish					-0.587	0.652	0.477
asin.Fruit		-0.577	0.666	0.285	0.230		0.280
asin.Seed		-0.104	-0.159	-0.713	0.483		0.466
asin.Nect					-0.443	-0.754	0.483
asin.PlantO	-0.603	0.668	0.254	0.176	0.174		0.254

Table 12: Correlation matrix between the four second-order food sources (Inv, Vert, PlantR, and PlantO) in turtles. Values range from -1 to 1. A positive value indicates that the percentages of both food sources increase together in the dietary compositions of most taxa. A negative value indicates that the percentage of one food source increases in the dietary composition at the expense of the other in most taxa.

	Inv	**Vert**	**PlantR**	**PlantO**
Inv	1.000	0.008	-0.403	-0.684
Vert	0.008	1.000	-0.254	-0.448
PlantR	-0.403	-0.254	1.000	-0.069
PlantO	-0.684	-0.448	-0.069	1.000

Table 13: Correlation matrix between the four second-order food sources (Inv, Vert, PlantR, and PlantO) in lizards. Values range from -1 to 1. A positive value indicates that the percentages of both food sources increase together in the dietary compositions of most taxa. A negative value indicates that the percentage of one

food source increases in the dietary composition at the expense of the other in most taxa.

	Inv	**Vert**	**PlantR**	**PlantO**
Inv	1.000	-0.362	-0.758	-0.632
Vert	-0.362	1.000	0.018	-0.010
PlantR	-0.758	0.018	1.000	0.431
PlantO	-0.632	-0.010	0.431	1.000

Table 14: Correlation matrix between the four second-order food sources (Inv, Vert, PlantR, and PlantO) in birds. Values range from -1 to 1. A positive value indicates that the percentages of both food sources increase together in the dietary compositions of most taxa. A negative value indicates that the percentage of one food source increases in the dietary composition at the expense of the other in most taxa.

	Inv	**Vert**	**PlantR**	**PlantO**
Inv	1.000	-0.283	-0.767	-0.322
Vert	-0.283	1.000	-0.299	-0.093
PlantR	-0.767	-0.299	1.000	0.025
PlantO	-0.322	-0.093	0.025	1.000

Table 15: Correlation matrix between the four second-order food sources (Inv, Vert, PlantR, and PlantO) in mammals. Values range from -1 to 1. A positive value indicates that the percentages of both food sources increase together in the dietary compositions of most taxa. A negative value indicates that the percentage of one food source increases in the dietary composition at the expense of the other in most taxa.

	Inv	**Vert**	**PlantR**	**PlantO**
Inv	1.000	-0.022	-0.509	-0.606

Vert	-0.022	1.000	-0.269	-0.320
PlantR	-0.509	-0.269	1.000	-0.183
PlantO	-0.606	-0.320	-0.183	1.000

Table 16: Correlation matrix between the third-order food sources (Arth, InvO, Vert, PlantR, and PlantO) in turtles. Values range from -1 to 1. A positive value indicates that the percentages of both food sources increase together in the dietary compositions of most taxa. A negative value indicates that the percentage of one food source increases in the dietary composition at the expense of the other in most taxa.

	Arth	**InvO**	**Vert**	**PlantR**	**PlantO**
Arth	1,000	-0,065	-0,098	-0,241	-0,413
InvO	-0,065	1,000	0,013	-0,297	-0,451
Vert	-0,098	0,013	1,000	-0,236	-0,388
PlantR	-0,241	-0,297	-0,236	1,000	-0,127
PlantO	-0,413	-0,451	-0,388	-0,127	1,000

Table 17: Correlation matrix between the third-order food sources (Arth, Duro, Vert, PlantR, and PlantO) in lizards. Values range from -1 to 1. A positive value indicates that the percentages of both food sources increase together in the dietary compositions of most taxa. A negative value indicates that the percentage of one food source increases in the dietary composition at the expense of the other in most taxa.

	Arth	**Duro**	**Vert**	**PlantO**	**PlantR**
Arth	1.000	-0.294	-0.385	-0.543	-0.762
Duro	-0.294	1.000	0.086	0.008	0.008
Vert	-0.385	0.086	1.000	-0.011	0.008

PlantO	-0.543	0.008	-0.011	1.000	0.352
PlantR	-0.762	0.008	0.008	0.352	1.000

Table 18: Correlation matrix between the third-order food sources (Inv, Vfish, Vland, Nect, Seed, Fruit, and PlantO) in birds. Values range from -1 to 1. A positive value indicates that the percentages of both food sources increase together in the dietary compositions of most taxa. A negative value indicates that the percentage of one food source increases in the dietary composition at the expense of the other in most taxa.

	Inv	**Vfish**	**Vland**	**Nect**	**Seed**	**Fruit**	**PlantO**
Inv	1.000	-0.159	-0.237	-0.269	-0.379	-0.441	-0.280
Vfish	-0.159	1.000	0.018	-0.059	-0.086	-0.104	-0.049
Vland	-0.237	0.018	1.000	-0.080	-0.111	-0.123	-0.068
Nect	-0.269	-0.059	-0.080	1.000	-0.112	-0.095	-0.059
Seed	-0.379	-0.086	-0.111	-0.112	1.000	-0.097	0.062
Fruit	-0.441	-0.104	-0.123	-0.095	-0.097	1.000	-0.037
PlantO	-0.280	-0.049	-0.068	-0.059	0.062	-0.037	1.000

Table 19: Correlation matrix between the third-order food sources (Inv, Vfish, Vland, Nect, Seed, Fruit, and PlantO) in mammals. Values range from -1 to 1. A positive value indicates that the percentages of both food sources increase together in the dietary compositions of most taxa. A negative value indicates that the percentage of one food source increases in the dietary composition at the expense of the other in most taxa.

	Inv	**Vfish**	**Vland**	**Nect**	**Seed**	**Fruit**	**PlantO**
Inv	1,000	-0,032	-0,093	-0,090	-0,315	-0,342	-0,511
Vfish	-0,032	1,000	-0,016	-0,025	-0,083	-0,079	-0,108
Vland	-0,093	-0,016	1,000	-0,048	-0,159	-0,140	-0,243

Nect	-0,090	-0,025	-0,048	1,000	-0,073	0,046	-0,107
Seed	-0,315	-0,083	-0,159	-0,073	1,000	-0,025	-0,070
Fruit	-0,342	-0,079	-0,140	0,046	-0,025	1,000	-0,209
PlantO	-0,511	-0,108	-0,243	-0,107	-0,070	-0,209	1,000

Table 20: Average percentages of each third-order dietary per dietary guild recovered in the cluster analysis (k=5) for turtles. The final two columns represent the total number of species in the guild, and the percentage of species in the clade.

Guild	Arth	Duro	Vert	PlantR	PlantO	COUNT	PERCENT
1	8,58	27,83	57,14	3,36	3,11	**36**	**0,134**
2	47,71	24,79	8,84	6,27	12,41	**73**	**0,272**
3	7,28	84,67	2,78	1,17	4,11	**18**	**0,067**
4	9,73	12,04	4,03	44,31	30,03	**67**	**0,250**
5	4,69	4,12	1,58	7,47	82,27	**74**	**0,276**
Grand Total	**18,37**	**20,33**	**11,71**	**15,38**	**34,30**	**268**	**1,000**

Table 21: Average percentages of each third-order dietary per dietary guild recovered in the cluster analysis (k=10) for turtles. The final two columns represent the total number of species in the guild, and the percentage of species in the clade.

Guild	Arth	Duro	Vert	PlantR	PlantO	COUNT	PERCENT
1	3,08	5,00	1,79	6,95	82,92	**39**	**0,146**
2	56,94	18,21	11,29	4,38	9,24	**34**	**0,127**
3	23,25	20,81	7,00	23,71	25,02	**48**	**0,179**
4	24,08	59,46	7,00	1,67	7,83	**24**	**0,090**
5	2,52	4,33	3,33	70,29	19,52	**21**	**0,078**
6	1,11	97,33	0,67	0,67	0,22	**9**	**0,034**
7	0,00	0,47	0,12	0,00	99,41	**17**	**0,063**
8	97,40	0,20	0,20	2,20	0,00	**5**	**0,019**
9	8,69	8,00	2,22	25,28	56,92	**36**	**0,134**
10	8,83	26,97	57,77	3,46	2,97	**35**	**0,131**
Grand Total	**18,37**	**20,33**	**11,71**	**15,38**	**34,30**	**268**	**1,000**

Table 22: Average percentages of each third-order dietary per dietary guild recovered in the cluster analysis (k=20) for turtles. The final two columns

represent the total number of species in the guild, and the percentage of species in the clade.

Guild	Arth	Duro	Vert	PlantR	PlantO	COUNT	PERCENT
1	0,00	0,25	0,13	0,00	99,63	**16**	**0,060**
2	3,00	0,73	2,00	55,82	40,27	**11**	**0,041**
3	6,09	10,18	6,18	2,91	74,64	**11**	**0,041**
4	97,40	0,20	0,20	2,20	0,00	**5**	**0,019**
5	33,25	12,00	10,38	36,88	6,25	**8**	**0,030**
6	1,00	4,70	0,96	4,39	88,52	**23**	**0,086**
7	34,79	51,14	4,57	2,86	6,64	**14**	**0,052**
8	2,10	50,80	44,20	0,80	2,20	**10**	**0,037**
9	0,67	0,33	1,00	27,20	70,80	**15**	**0,056**
10	1,50	6,00	3,43	76,07	13,00	**14**	**0,052**
11	11,91	74,91	4,55	1,91	6,73	**11**	**0,041**
12	6,00	17,33	4,33	29,67	42,67	**15**	**0,056**
13	28,50	26,63	11,17	10,29	23,42	**24**	**0,090**
14	0,00	100,00	0,00	0,00	0,00	**7**	**0,026**
15	23,42	7,25	1,67	7,67	61,67	**12**	**0,045**
16	65,26	16,05	5,63	2,37	10,79	**19**	**0,071**
17	2,75	3,50	93,75	0,00	0,00	**4**	**0,015**
18	7,94	20,63	61,25	5,81	4,38	**16**	**0,060**
19	22,26	17,37	0,37	30,26	29,74	**19**	**0,071**
20	37,14	22,64	35,71	2,14	2,36	**14**	**0,052**
Grand Total	**18,37**	**20,33**	**11,71**	**15,38**	**34,30**	**268**	**1,000**

Table 23: Average percentages of each third-order dietary per dietary guild recovered in the cluster analysis (k=5) for lizards. The final two columns represent the total number of species in the guild, and the percentage of species in the clade.

Guild	Arth	Duro	Vert	PlantR	PlantO	COUNT	PERCENT
1	99,99	0,00	0,00	0,00	0,00	**4296**	**0,816**
2	11,24	1,36	1,61	49,88	32,57	**191**	**0,036**
3	62,56	4,70	5,00	24,25	3,53	**365**	**0,069**
4	16,61	15,50	66,63	1,30	0,17	**46**	**0,009**
5	86,83	2,07	4,86	5,24	0,95	**367**	**0,070**
Grand Total	**92,53**	**0,66**	**1,33**	**3,87**	**1,50**	**5265**	**1,000**

Table 24: Average percentages of each third-order dietary per dietary guild recovered in the cluster analysis (k=10) for lizards. The final two columns

represent the total number of species in the guild, and the percentage of species in the clade.

Guild	Arth	Duro	Vert	PlantR	PlantO	COUNT	PERCENT
1	46,30	5,96	44,64	1,98	0,25	**53**	**0,010**
2	100,00	0,00	0,00	0,00	0,00	**4287**	**0,814**
3	88,58	2,31	5,68	2,51	0,86	**312**	**0,059**
4	25,74	61,96	6,19	2,41	3,70	**27**	**0,005**
5	5,89	0,39	93,72	0,00	0,00	**18**	**0,003**
6	71,06	1,39	1,61	24,01	2,14	**317**	**0,060**
7	7,71	0,68	2,26	74,89	14,45	**66**	**0,013**
8	41,10	2,27	2,94	36,54	9,99	**84**	**0,016**
9	12,06	0,63	1,09	43,51	42,37	**86**	**0,016**
10	4,60	0,00	0,00	3,20	92,20	**15**	**0,003**
Grand Total	**92,53**	**0,66**	**1,33**	**3,87**	**1,50**	**5265**	**1,000**

Table 25: Average percentages of each third-order dietary per dietary guild recovered in the cluster analysis (k=20) for lizards. The final two columns represent the total number of species in the guild, and the percentage of species in the clade.

Guild	Arth	Duro	Vert	PlantR	PlantO	COUNT	PERCENT
1	1,08	0,42	98,50	0,00	0,00	**12**	**0,002**
2	81,34	7,79	7,87	1,34	1,57	**53**	**0,100**
3	80,73	0,17	1,16	17,18	0,71	**93**	**0,018**
4	69,31	0,47	1,43	28,60	0,17	**191**	**0,036**
5	3,05	0,22	1,00	67,85	27,88	**41**	**0,008**
6	47,23	0,59	2,77	48,05	1,51	**39**	**0,007**
7	57,00	1,73	38,36	1,36	0,15	**33**	**0,006**
8	0,00	100,00	0,00	0,00	0,00	**3**	**0,000**
9	99,86	0,00	0,02	0,00	0,00	**4293**	**0,815**
10	30,00	54,15	5,85	5,38	4,62	**26**	**0,005**
11	23,14	1,39	4,03	39,08	28,50	**36**	**0,007**
12	21,50	1,54	2,88	70,88	3,21	**24**	**0,005**
13	90,53	1,32	5,59	1,91	0,60	**236**	**0,045**
14	70,32	0,19	1,94	13,16	15,84	**31**	**0,006**
15	4,60	0,00	0,00	3,20	92,20	**15**	**0,003**
16	50,70	1,03	0,92	25,81	22,22	**37**	**0,007**
17	5,10	0,52	0,06	44,02	50,31	**48**	**0,009**
18	62,17	21,78	8,56	7,50	0,00	**18**	**0,003**
19	22,24	10,64	62,40	4,40	0,32	**25**	**0,005**
20	2,55	0,27	0,00	96,73	0,45	**11**	**0,002**
Grand Total	**92,53**	**0,66**	**1,33**	**3,87**	**1,50**	**5265**	**1,000**

Table 26: Average percentages of each third-order dietary per dietary guild recovered in the cluster analysis (k=5) for birds. The final two columns represent the total number of species in the guild, and the percentage of species in the clade.

Guild	Inv	Vland	Vfish	Fruit	Seed	Nect	PlantO	COUNT	PERCENT
1	17,84	0,03	0,00	3,00	0,19	77,52	1,41	**580**	**0,058**
2	98,67	0,43	0,11	0,45	0,18	0,07	0,09	**3210**	**0,321**
3	52,02	14,28	7,06	13,92	7,01	2,72	3,00	**3766**	**0,377**
4	15,92	0,48	0,07	11,18	52,83	0,99	18,53	**1470**	**0,147**
5	12,74	1,04	0,02	78,76	2,78	1,33	3,32	**967**	**0,097**
Grand Total	**55,91**	**5,69**	**2,71**	**14,83**	**10,75**	**5,82**	**4,29**	**9993**	**1,00**

Table 27: Average percentages of each third-order dietary per dietary guild recovered in the cluster analysis (k=10) for birds. The final two columns represent the total number of species in the guild, and the percentage of species in the clade.

Guild	Inv	Vland	Vfish	Fruit	Seed	Nect	PlantO	COUNT	PERCENT
1	1,52	0,06	0,00	97,96	0,09	0,06	0,32	**348**	**0,035**
2	31,35	1,85	0,04	55,63	3,14	4,64	3,34	**1237**	**0,124**
3	18,36	0,04	0,00	2,03	0,16	78,52	0,89	**562**	**0,056**
4	30,32	3,75	0,69	17,46	34,12	2,36	11,29	**1404**	**0,140**
5	26,10	10,21	63,07	0,18	0,09	0,00	0,36	**336**	**0,034**
6	100,00	0,00	0,00	0,00	0,00	0,00	0,00	**2783**	**0,278**
7	12,35	85,46	1,73	0,27	0,08	0,03	0,08	**370**	**0,037**
8	10,98	0,69	0,41	4,31	12,72	1,46	69,43	**246**	**0,025**
9	9,54	0,21	0,00	1,54	85,96	0,34	2,42	**475**	**0,048**
10	75,10	6,26	1,84	7,92	5,15	1,98	1,75	**2232**	**0,223**
Grand Total	**55,91**	**5,69**	**2,71**	**14,83**	**10,75**	**5,82**	**4,29**	**9993**	**1,00**

Table 28: Average percentages of each third-order dietary per dietary guild recovered in the cluster analysis (k=20) for birds. The final two columns represent the total number of species in the guild, and the percentage of species in the clade.

Guild	Inv	Vland	Vfish	Fruit	Seed	Nect	PlantO	COUNT	PERCENT
1	0,00	0,00	0,00	100,00	0,00	0,00	0,00	**277**	**0,028**
2	46,52	1,40	0,03	48,29	1,18	1,60	0,98	**601**	**0,060**
3	83,41	3,60	1,04	5,96	4,07	0,73	1,18	**1254**	**0,125**
4	39,29	48,11	4,26	3,61	2,64	0,34	1,76	**296**	**0,030**
5	15,86	0,48	0,00	3,05	72,97	0,91	6,73	**394**	**0,039**
6	50,37	0,70	0,10	0,37	45,45	0,50	2,51	**299**	**0,030**
7	66,40	5,92	1,64	12,40	7,63	2,98	3,03	**801**	**0,080**

8	5,58	0,15	0,00	41,96	36,82	1,69	13,80	**337**	**0,034**
9	6,28	92,64	1,05	0,04	0,00	0,00	0,00	**277**	**0,028**
10	1,93	0,00	0,00	1,40	0,70	0,00	95,96	**57**	**0,006**
11	43,06	0,22	0,00	1,48	1,04	52,84	1,37	**183**	**0,018**
12	14,90	1,78	0,04	74,82	2,60	1,56	4,30	**500**	**0,050**
13	41,01	12,63	45,25	0,23	0,32	0,00	0,55	**217**	**0,022**
14	0,00	0,00	0,00	0,00	100,00	0,00	0,00	**179**	**0,018**
15	9,23	0,00	0,00	0,64	0,00	89,87	0,27	**377**	**0,038**
16	13,82	3,49	82,24	0,00	0,00	0,00	0,46	**152**	**0,015**
17	100,00	0,00	0,00	0,00	0,00	0,00	0,00	**2783**	**0,278**
18	15,59	1,32	0,46	7,40	19,29	1,46	54,48	**281**	**0,028**
19	26,18	1,35	0,05	29,76	2,75	35,56	4,35	**207**	**0,021**
20	35,26	3,05	0,67	21,61	27,79	1,19	10,42	**521**	**0,052**
Grand Total	**55,91**	**5,69**	**2,71**	**14,83**	**10,75**	**5,82**	**4,29**	**9993**	**1,00**

Table 29: Average percentages of each third-order dietary per dietary guild recovered in the cluster analysis (k=5) for mammals. The final two columns represent the total number of species in the guild, and the percentage of species in the clade.

Guild	Inv	Vland	Vfish	Fruit	Seed	Nect	PlantO	COUNT	PERCENT
1	12,54	2,11	0,02	21,85	24,04	3,02	36,27	**1853**	**0,353**
2	49,75	29,96	6,23	6,78	2,97	1,48	2,83	**1230**	**0,235**
3	98,95	0,27	0,08	0,21	0,02	0	0,48	**1005**	**0,192**
4	0,61	0,06	0	2,11	2,65	0	94,57	**838**	**0,160**
5	2,97	0,7	0	90,79	0,22	2,18	3,13	**316**	**0,060**
Grand Total	**35,35**	**7,88**	**1,49**	**15,17**	**9,63**	**1,55**	**28,88**	**5242**	**1,000**

Table 30: Average percentages of each third-order dietary per dietary guild recovered in the cluster analysis (k=10) for mammals. The final two columns represent the total number of species in the guild, and the percentage of species in the clade.

Guild	Inv	Vland	Vfish	Fruit	Seed	Nect	PlantO	COUNT	PERCENT
1	38,72	48,28	1,89	6,03	2,65	0,05	2,38	**441**	**0,084**
2	77,72	11,17	2,94	2,34	0,49	0,2	5,15	**548**	**0,105**
3	0,17	0,02	0	0,46	0,13	0	99,23	**635**	**0,121**
4	13,82	1,62	0	21,09	41,8	0,29	21,37	**788**	**0,150**
5	28,36	1,1	70,55	0	0	0	0	**73**	**0,014**
6	9,82	1,39	0	12,77	14,04	0,18	61,79	**984**	**0,188**
7	24,38	4,3	0,16	39,74	4,44	13,88	12,5	**500**	**0,095**
8	2,84	94,21	1,16	1,16	0	0,21	0,42	**95**	**0,018**

9	100	0	0	0	0	0	0	**899**	**0,171**
10	2,01	0,18	0	93,55	0	2,15	2,11	**279**	**0,053**
Grand Total	**35,35**	**7,88**	**1,49**	**15,17**	**9,63**	**1,55**	**28,88**	**5242**	**1,000**

Table 31: Average percentages of each third-order dietary per dietary guild recovered in the cluster analysis (k=10) for mammals. The final two columns represent the total number of species in the guild, and the percentage of species in the clade.

Guild	Inv	Vland	Vfish	Fruit	Seed	Nect	PlantO	COUNT	PERCENT
1	0	0	0	0	0	0	100	**586**	**0,112**
2	1,31	0,46	0	40,51	45,6	0,29	11,83	**175**	**0,033**
3	19,24	1,95	0	21,49	30,41	0,39	25,97	**538**	**0,103**
4	28,36	1,1	70,55	0	0	0	0	**73**	**0,014**
5	0	0	0	100	0	0	0	**180**	**0,034**
6	2,66	2,95	0	43,58	2,72	0,52	47,57	**173**	**0,033**
7	2,84	94,21	1,16	1,16	0	0,21	0,42	**95**	**0,018**
8	73,61	23,7	0,65	0,65	0	0,09	1,3	**230**	**0,044**
9	47,6	51,12	0,56	0,15	0	0	0,56	**267**	**0,051**
10	8,08	0	0	2,05	78,9	0	10,96	**73**	**0,014**
11	18,49	5,29	0,34	49,41	2,18	2,18	22,1	**119**	**0,023**
12	100	0	0	0	0	0	0	**899**	**0,171**
13	2,61	1,01	0	11,56	9,37	0,22	75,24	**506**	**0,097**
14	22,23	45,24	3,07	16,31	7,68	0,3	5,18	**168**	**0,032**
15	50,99	6,25	3,65	22,14	12,97	2,08	1,93	**192**	**0,037**
16	2,22	0	0	3,89	0	93,89	0	**18**	**0,003**
17	22,08	1,51	0	32,83	1,04	41,6	0,94	**106**	**0,020**
18	17,59	1,59	0	2,53	25,88	0,02	52,39	**415**	**0,079**
19	6,91	1,62	0	78,6	0,51	5,07	7,28	**136**	**0,026**
20	82,39	1,88	3,31	2,9	0,78	0,31	8,43	**293**	**0,056**
Grand Total	**35,35**	**7,88**	**1,49**	**15,17**	**9,63**	**1,55**	**28,88**	**5242**	**1,000**

CHAPTER TWO

1. Introduction

The common ancestor of all extant amniotes was almost certainly faunivorous (Sues, 2000; Sues & Reisz, 1998), and most likely invertivorous (Modesto et al., 2009). The earliest evolutionary shifts in diet are hypothesized as being from invertivory to carnivory (Sahney et al., 2010). The earliest transitions towards herbivory occurred in the late Carboniferous and early Permian (Brocklehurst, 2016; Reisz & Frobisch, 2014; Sues & Reisz, 1998), occurring independently five times (Sues & Reisz, 1998). By the mid-to-late Permian, the spread of taxa across ecological niches approximately resembled those of the modern day, including the primary trophic levels of “faunviore”, “omnivore”, and “herbivore” being composed by functionally similar taxa to those occupying these roles in contemporary ecosystems (Benton, 2012; Olson, 1966; Zavada & Mentis, 1992). It has been hypothesized that the earliest herbivores evolved in early amniotes from faunivorous ancestors via an omnivorous intermediate stage (Paul M. Barrett, 2014; Sahney et al., 2010; Sues, 2000; Sues & Reisz, 1998). A hypothesized vector for the adoption of cellulytic microorganisms into the gut microbiomes of early herbivorous tetrapod taxa may have been by way of detritivorous forbears foraging in decomposing plant debris (Hotton et al., 1997). Furthermore, most early herbivorous clades have insectivorous sister taxa, suggesting insectivory to be a likely ancestral state for herbivorous clades rather than carnivory (Sues & Reisz, 1998).

Several focused investigations into evolutionary transitions in diet in fossil lineages demonstrate that shifts from faunivory to herbivory occurred in multiple intermediate steps rather than discrete events. For example, while not testing evolutionary transitions explicitly, Mann et al. (2023) suggested the bulbous dentition of a new taxon of edaphosaurid (*Melanedaphodon hovaneci*), to represent an omnivorous (primarily granivorous or durophagous) intermediate between an insectivorous early-branching condition and the high-fiber folivory of the late-branching *Edaphosaurus*. Another example looking at dental morphology, the herbivorous Traversodontidae, a speciose group of Triassic gomphodont cynodonts, diverged from an omnivorous

sister clade (Trirachodontidae) within a clade that was ancestrally faunivorous (Hendrickx et al., 2020). The herbivorous lineage diversified greatly in this example, while the omnivorous sister clade was composed of few taxa and went extinct relatively quickly (Hendrickx et al., 2020). Paul M. Barrett (2014) found a tendency for herbivorous dinosaur clades to diverge from omnivorous sister taxa rather than from faunivorous ancestors directly. L. E. Zanno and P. J. Makovicky (2011) demonstrated that morphological characters associated with herbivory evolve sequentially in lineages where herbivory evolves from a faunivorous ancestral condition. This is suggestive of an omnivorous intermediate stage between faunivory and herbivory.

Reconstructing diets of fossil taxa is, in most cases, based on indirect inference rather than direct data, and there is room for such inferences to be inaccurate (Casey & Post, 2011; Hopkins et al., 2022). For example, a complicating factor in understanding evolutionary transitions between dietary strategies in fossil amniotes is that, at least in reptiles, there is little anatomical adaptation to dental, cranial, or skeletal structures needed to transition from faunivory to generalist omnivory (Cooper Jr & Vitt, 2002; Dearing, 1993; Hotton et al., 1997; Sues & Reisz, 1998). This adds difficulty in confidently assigning dietary categories to fossil taxa, making it difficult to distinguish omnivores from faunivores among early branching amniotes. This has led to some studies employing a herbivore-faunivore binary system when examining the fossil record (Barrett, 1998). This limited precision in dietary classification of extinct taxa presents a challenge in effectively comparing and contrasting patterns in evolutionary transition between dietary guilds in extinct clades.

Given that the inclusion of more precise dietary classification systems has a profound impact on evolutionary hypotheses surrounding the evolution of diet in extant taxa, the use of diet as a simple binary character may not be suitable for testing these hypotheses in the fossil record. Analytical techniques for reconstructing diet of fossil organisms, aside from inferences from craniodental characters, include tooth wear analysis (Calandra et al., 2016; DeSantis, 2016; Miller & Pittman, 2021; Ungar & Williamson, 2000), stable isotopes (Casey & Post, 2011; Miller & Pittman,

2021; Schoeninger & DeNiro, 1982), and tooth complexity studies (Evans & Pineda-Munoz, 2018; Melstrom, 2017). Going forward, these methods may provide a more accurate, detailed understanding of the dietary strategies of extinct organisms and better facilitate investigation into evolutionary transitions in diet in fossil clades.

Another important step in inferring how diet has evolved through deep time in the fossil record is investigating the pace and tempo of evolutionary transitions between dietary guilds in extant taxa. Extant amniotes present a large sample size, and a wide diversity of dietary strategies and dietary compositions. The relatively recent efforts to understand the phylogenetic relationships of crown amniote clades presents an ideal opportunity for analysing dietary transitions in a robust phylogenetic framework. Given that dietary diversity evolves relatively early in the amniote tree, the patterns of dietary transitions and the commonalities between these patterns among different living amniote clades might serve as a model for how we expect diets to have evolved over deep time.

A “classical” assumption about transitions in dietary strategy is that there should be high transition rates into omnivorous or generalist guilds from specialist herbivorous and faunivorous guilds which are historically thought to have higher rates of speciation (Burin et al., 2016; Futuyma & Moreno, 1988; Price et al., 2012). More intuitively, it is unlikely that a radical shift in dietary composition (i.e., from strict faunivory directly to strict herbivory) would constitute a discrete evolutionary event due to the need to evolve anatomical and physiological requirements for processing and extracting nutrients from plant material. Omnivory would, therefore, serve as a transitional stage between a faunivorous ancestor and a herbivorous descendent (Hotton et al., 1997; Reuter et al., 2023; Sues & Reisz, 1998). To this end, under an equal rates model of character evolution, with an equal number of independent origins of both faunivory and herbivory; one would expect the rate of transition into omnivory to be double that into either specialized guild. Given that faunivory represents the most likely ancestral condition of amniotes (Modesto et al., 2009; Sues & Reisz, 1998), the earliest iteration of this model would be “faunivory → omnivory → herbivory” (see Figure 21). Following the establishment of the different ecological niches over time, this evolutionary pathway for dietary changes within

lineages would, ultimately, be an ordered “faunivory ← → omnivory ← → herbivory” model.

Omnivory has been suggested in both mammals (Price et al., 2012), and birds (Burin et al., 2016) to constitute an “evolutionary sink”. This means that transition rates were higher into omnivory from other guilds than the inverse. Omnivory is an evolutionary “sink” because rates of extinction are higher, and rates of speciation are lower. Omnivory was also found to serve as an intermediate phase between different character states in birds (Burin et al., 2016). Transition rates directly between faunivorous and herbivorous guilds, however, were far lower, as would be expected under the ordered model detailed above. Therefore, while transitions out of omnivory are uncommon, they typically coincide with an increase in rates of speciation. As a result of the interplay between evolutionary transitions, speciation, and extinction, omnivory is relatively rare compared with more specialised feeding strategies despite a higher rate of transition in than out. Similar results have also been reported in emydid turtles (Stephens & Wiens, 2003) and muroid rodents (Rowe et al., 2016).

Recent research has scrutinized these narratives and added some more nuance in certain clades. Omnivorous liolaemid lizards, a group known for “unconventional” macroevolutionary patterns in regards to diet (Espinoza et al., 2004), have been shown to have higher rates of diversification and out-transition (Ocampo et al., 2022). In noctilionoid bats (Rojas et al., 2018) and ruminants (Cantalapiedra et al., 2014), generalist herbivores have been shown to have higher rates of diversification than specialist herbivores feeding on only a single type of plant material. This distinction between “omnivory” and “generalism” is important as the change in definition can shift the narrative in relation to evolutionary transitions.

More broadly in mammals, Reuter et al. (2023) demonstrated that transitions to herbivorous feeding strategies often originated from omnivory that includes a component of invertebrate material rather than omnivory composed of other combinations of food types. Transitions from invertivore-omnivore ancestors to herbivorous descendant clades constitute the origin of many major evolutionary radiation events (Reuter et al., 2023). Regardless of phylogenetic diversification, the authors concluded that certain omnivorous and generalist strategies play an important role as transitional stages between more specialized feeding strategies.

Vertivory (carnivory sensu the current study) was shown to transition from, and to, invertivory and mixed faunivory as faunivory is often understood as an ecophysiological gradient between invertivory and carnivory, separated primarily by size of prey (Amador & Giannini, 2021; Carbone et al., 1999; De Cuyper et al., 2019; Reuter et al., 2023; Van Valen, 1969; Vézina, 1985). Unsurprisingly, transitions between herbivory and carnivory are rare as adaptations to oral and gut processing anatomy are very divergent between the two feeding strategies (Button & Zanno, 2020; Christiansen, 2007; Da Silva et al., 2016; López-Aguirre et al., 2022; Monteiro & Nogueira, 2011). Hypercarnivory has also been shown to function as an evolutionary "ratchet" in which lineages tend to become more anatomically and ecologically specialized for a diet of large vertebrate prey in carnivoran mammals (Sacco & Van Valkenburgh, 2004; Van Valkenburgh et al., 2004). Were these findings to be universal to all amniotes, the model of evolutionary transitions I present above could be further refined to "carnivory ← → mixed faunivory ← → invertivory ← → omnivory ← → herbivory".

Numerous studies have suggested that granivory may represent a transitional stage between frugivory and folivory in mammals (Bodmer, 1989; Lambert, 1998; Rosenberger et al., 2011). Seed-eating requires more extensive adaptive modifications to the teeth and gut than does frugivory (Lambert 1998). Many of these adaptations, such as longer food retention times and increased gut surface-area, result in adaptations for granivorous feeding strategies serving as pre-adaptation to a folivorous diet. Bodmer (1989) suggests that the gut-processing mechanisms of modern folivorous artiodactyls originated from adaptations to overcome seed defensive mechanisms in a granivorous ancestor. Kunz and Ingalls (1994) suggests that the evolution of frugivory served as a pre-adaptation for folivory in bats. Folivory is rare in birds but also tends to evolve from an intermediate phase involving consumption of reproductive plant parts, rather than from faunivory directly (Olsen, 2015). From the perspective of evolutionary transitions, there is little work on the evolution of folivory in lepidosaurs though folivorous lizards show more extensive modification to their teeth and guts than do lizards feeding on other kinds of plant material (Cooper Jr & Vitt, 2002). It should be noted that, in terms of oral processing, folivorous lizards have evolved dentition for shearing leaves rather than crushing them (Throckmorton, 1976). It is unlikely that adaptation to seed-eating, which is

exceedingly rare in lizards (Nagy & Shemanski, 2009), would convey any benefit to this process. Studies asserting the “seed-to-leaf” hypothesis do so from the perspective of anatomical adaptation rather than explicit modelling of evolutionary transitions. It is not clear from the existing literature if this evolutionary pathway is reversible. This hypothesis for the evolution of folivory implies an ordered model wherein frugivory → granivory → folivory. If incorporated into the model I present in previous paragraphs, the final iteration of the expanded hypothetical model of evolutionary transitions between dietary strategies is “carnivory ← → mixed faunivory ← → invertivory ← → omnivory ← → granivory/frugivory ← → folivory” (see Figure 22).

The primary limitation of much of the existing research into evolutionary transitions between dietary guilds lies in how those guilds are defined. Some studies deploy the classical three guild system or a similar “specialist faunivore/herbivore” versus “generalist” approach (Price et al., 2012; Stephens & Wiens, 2003; Van Damme, 1999). Amador and Giannini (2021) provide a prime example of how interpretations of evolutionary dynamics can change markedly based on the parameters used to study them in a study on diet evolution in marsupials. In this study, an evolutionary transition model using a simplified dietary classification system (four guilds) revealed a relatively high frequency of evolutionary transitions from “animalivory” (faunivory sensu the current study) and herbivory. A comparative analysis using a more complex dietary classification system (ten guilds) revealed that these transitions were between insectivory and specifically frugivory and browse-herbivory (Amador & Giannini, 2021).

Burin et al. (2016), examining birds, defined “omnivore” as any taxon in which no single food source (between terrestrial vertebrates, fish, invertebrates, vegetative plant material, fruit, seeds, and nectar; third-order subdivisions sensu the current study) composed greater than 50% of the dietary composition. As stated earlier, the study found omnivory to constitute an evolutionary sink in birds with rates of transition into the guild exceeded those out of the guild. While this may well be true of omnivory as defined by that study, it may not hold true for specific generalist sub-guilds with dietary compositions consisting of different combinations of the different

food sources. For example, a taxon with a dietary composition of 55% invertebrate material, and 45% plant matter would be counted as a specialist invertivore under this classification scheme though such a taxon would likely have a higher probability of originating an evolutionary shift towards specialised herbivory than would a taxon consuming a diet composed entirely of invertebrates.

Reuter et al. (2023), examining mammals, defined guilds as a composite of whichever food sources (between invertebrates, vertebrates, non-fibrous plant material, and fibrous plant material; second-order subdivisions sensu the current study) are included in the dietary composition. This allowed for far more nuance in interpreting evolutionary transitions between dietary guilds and demonstrated the results of Amador and Giannini (2021) to be broadly generalizable across Mammalia. However, the study (a) did not account for different kinds of non-fibrous plant material which require substantially different anatomical and physiological adaptations to consume, and (b) did not account for relative proportions of each food type in the dietary composition. The former was not a limiting factor in the context of the study, but it inhibits the ability to test hypotheses of the evolution of different kinds of herbivory such as the “seed-to-leaf” pathway mentioned earlier. The latter may result in the importance of certain food types being over- or understated which could bear implications on the interpretation of results from an anatomical and ecophysiological standpoint.

In this chapter, I present models of the evolutionary transition rates between the dietary guilds I recovered in the k-means cluster analysis (k=10) in each major amniote lineage. I do this to test if the hypothetical model I developed based off of previous studies and assumptions based on anatomical and physiological constraints (“carnivory ← → mixed faunivory ← → invertivory ← → omnivory ← → granivory/frugivory ← → folivory”) is generalizable across all major amniote lineages. I also compare the findings of this analysis to other investigations into evolutionary transitions between dietary guilds that deployed complex classification systems (Amador & Giannini, 2021; Burin et al., 2016; Reuter et al., 2023). The novel contribution of the current study is that the dietary guilds are defined such that there is a more nuanced division of omnivorous and generalist guilds. This change in

categorization may well reveal new insights as to (a) whether omnivory acts as an evolutionary sink with higher rates of transition in than out, and (b) the role of omnivorous and generalist guilds in facilitating evolutionary transitions between more specialised guilds. As discussed in Chapter One, diet is best expressed as a continuous variable or a spectrum rather than a set of discrete variables. However, I present transition rates between the k-means dietary guilds as representing shifts through areas of the broader dietary spectrum rather than transitions between confined, mutually-exclusive biological traits. Finally, I perform a supplementary set of analyses using the "classical" dietary guilds to compare and contrast results between dietary classification systems, as well as to compare patterns between extant amniote lineages and two extinct clades (non-mammalian synapsids, and non-avian theropods).

2. Methods and Materials

2.1. Data collection

I used the dietary guilds generated by the cluster analysis (k=10) for each major extant amniote lineage. I also used the "classical" dietary guilds to draw comparisons between patterns in evolutionary transitions between the dietary classification systems. I also collected dietary data for two extinct amniote lineages: non-mammalian synapsids, and non-avian theropods. Analysis on these extinct taxa facilitates comparison of evolutionary trends through deep time.

I used the dataset of Hellert et al. (2022) for extinct non-mammalian synapsids. The complete dataset includes some therian taxa which I removed. Hellert et al. (2022) categorised each taxon as "faunivore", "omnivore", or "herbivore" based on primary literature sources, first-hand observations of dental morphology, and inference from a taxon's closest evolutionary relatives and assignments recorded in the palaeobiological database (PBDB) and associated literature references (Peters & McClennen, 2016). This dataset uses jaw length (measured from anterior end of the

dentary to the articular facet for the jaw) as a proxy for body mass (Hellert et al. 2022).

I reduced the Dinosauria body mass dataset of Benson et al. (2017) to include only non-avian theropods (138 taxa after modification). This dataset includes body mass data for each taxon derived from multiple proxy measurements. Using PBDB (Peters & McClennen, 2016) and associated literature references, I assigned each non-avian theropod to “faunivory”, “omnivory”, or “herbivory” based on written statements expressing these classifications. Regarding both fossil clades, there were some instances where a more precise dietary guild has been suggested in the literature (e.g., “piscivore” or “insectivore”). For consistency with categories used in non-mammalian synapsids, and to acknowledge that we lack detailed dietary data for fossil species, I limit extinct taxa to the three classical dietary categories. This occasionally necessitated reducing dietary precision – for example in spinosaurids where multiple lines of evidence suggest they are piscivores (Amiot et al., 2010; Charig & Milner, 1997; Cuff & Rayfield, 2013; Gimsa et al., 2016), I considered them faunivores for comparability.

2.2. Phylogeny

For each clade, I selected appropriate phylogenies suitable for performing all necessary analyses in a phylogenetic framework. I chose topologies from recent large phylogenetic analyses that are widely used in the scientific literature for macroevolutionary studies. Where necessary (see Appendices A.3., A.4., A.5.), I altered trees to be fully dichotomous and ultrametric using the R functions “make2di”, and “chronos” from the ‘ape’ package (Paradis et al., 2004). In numerous instances, either data are incomplete for certain taxa that are present in the phylogenies, or taxa for which I have complete data do not match the species names the phylogenies (or vice versa). In these cases, where there were excess tips in a phylogeny not in the dataset, I used the “drop.tip” function in the ‘ape’ package (Paradis et al. 2004) in R to prune the phylogeny down to match the dataset without altering the underlying topological structure of the tree. I deleted any taxa present in

the dataset but not in the phylogenies using the “match” base function in R (R Core Team & Team, 2022). When fitting evolutionary rates models, it is advisable to use, at minimum, 1000 random topologies from a given phylogenetic study to fully account for phylogenetic uncertainty with a high degree of precision (Rubolini et al., 2015). Unfortunately, time restraints limited to me to less topological variation than I would have preferred. To compensate, I selected two phylogenies constructed from different backbone topologies wherever possible in order to maximise differences between the phylogenetic topologies. Substantially different results from each topology would be indicative of the possibility that further exploration across multiple topologies could change the outcomes of the research. There were no substantive differences in the transition rates recovered for any given lineage between phylogenetic topologies. I, therefore, conclude that the results recovered provide an accurate overview of the broad patterns.

For turtles, I chose the time-calibrated consensus tree of R. C. Thomson et al. (2021). This study uses molecular data from 591 turtle specimens representing 279 living species (80% of the total 348) and 90 genera (98% of the 92 total). The tree was built using Bayesian phylogenetic analysis in Mr Bayes v3.2 (Ronquist et al., 2012). After altering the tree to match taxa with complete dietary data, the final tree for all analyses contains 268 tips.

For lizards, I opted to use two differing higher-level squamate topologies. First, I use the time-calibrated consensus tree of Tonini et al. (2016). This study uses Phylogenetic Assembly with Soft Taxonomic InferenceS (PASTIS) (Jetz et al., 2012; Thomas et al., 2013) to create a fully-sampled phylogeny of 9754 squamate taxa (100% of the recognised taxa at the time). Pruned down to non-serpentine squamates (i.e. ‘lizards’) with complete dietary data, the final tree from the topology of Tonini et al. (2016) includes 5265 tips. I excluded Serpentes from the dataset since there is substantially less dietary variation among snakes than among other amniotes, being a nearly entirely faunivorous group with some variation in prey preferences (Colston et al., 2010). I also used the topology of Pyron and Burbrink (2014) which, in turn, is based on the molecular phylogeny of Pyron et al. (2013). This study uses a supermatrix approach to create a phylogeny of 4161 species of squamates. I performed only a single iteration of each topology on account of

limitations on computational time. Pruned down to non-serpentine squamates with complete dietary data, the final tree from the topology of Pyron et al. (2013) includes 2343 tips.

For birds, I chose to use the time-calibrated trees from Jetz et al. (2012). This study constructed fully sampled trees of the 9993 species of bird recognised at the time. In creating the trees, the authors constrained the “deeper level relationships” using topologies of Hackett et al. (2008) and Ericson et al. (2006) as backbone phylogenies. The authors then built on these backbones using molecular data for 6663 bird species and subsequently added the remaining taxa (without molecular data available) using taxonomic data from literature sources (Jetz et al., 2012) for a total of 9993 species. For each of my analyses, I used a single random topology from each backbone phylogeny. For the topologies from both backbones, the final tree matched to taxa with complete dietary data contains all 9993 tips, while the tree matched to taxa with complete dietary and body size data is reduced slightly to 9783 tips.

I selected the time-calibrated trees devised by Upham et al. (2019) for mammals. This study created tree-sets from 5911 extant and extinct mammalian taxa. The authors first created ML trees from 4098 taxa with molecular data available. These served as backbone trees (often referred to in-text as “DNA-only trees”) for the final tree construction. The study uses two backbones: one for a node-dating analysis and one for a fossil birth-death analysis (“tip-dating”). The authors then built the full trees on these backbones using taxonomic information to add the remaining 1813 taxa without molecular data. For my analyses, I first used one random tree from each of the “complete” (“constrained topology”) trees.

For synapsids, I opted to use the time-calibrated metatree of Hellert et al. (2022). The study included 2128 taxa of extinct synapsids (ranging Carboniferous through Eocene in age). This study constructed a metatree as per the protocol of Lloyd et al. (2016). Given the size of the dataset used, I had to prune the tree down significantly to fit the data for analysis. Because of the structure of the tree I implemented, only a single topology analysis was done for the synapsid group. A potential solution for this

in future research may be enforcing random topological re-arrangements on the tree or adopting a supertree approach instead. Pruned down to non-mammalian taxa with complete dietary and body size data, the final tree has 404 tips.

I used the Dinosauria phylogeny from Benson et al. 2014 for the non-avian theropod dataset. This phylogeny includes 657 dinosaur taxa. It has been used for macroevolutionary studies in both its original publication and in Benson et al. (2017). As was the case with the non-mammalian synapsids, the final tree used for analysis is significantly pruned down to fit the dataset. The final tree, matching non-avian theropod taxa with complete dietary and body mass data, has 138 tips.

2.3. Evolutionary transition rates

I fitted a series of Mk models (Yang et al., 1995) to each topology for each clade to calculate rates of transition between dietary guilds. I performed these analyses using the dietary guilds recovered in the k-means cluster analysis as discrete states (k=10). I chose the guilds generated using a k-value of ten because they sufficiently capture dietary complexity for the purposes of this analysis but not to the point that fitting and interpreting the model would become overly complex. For each analysis, I tested three different models: equal rates – “ER”; symmetrical rates – “SYM”; and all rates different – “ARD” (Felsenstein, 1985; Felsenstein & Churchill, 1996). I evaluated which model was the best fit by means of AICc weights.

I used the fitMk function in the R package “phytools” (Revell, 2012). The output from this analysis is the transition rate matrix between the dietary guilds as character states. This approach generates a probability of each character state being represented at each ancestral node given its distribution at the tips of the tree under a given topology. I repeat these models using the traditional dietary guilds (faunivory, omnivory, and herbivory). This allows me to compare the results of these analyses using the cluster analysis-generated guilds to results using a simpler, more standardised approach on the same data. This was useful for comparing each clade, not only to each other, but to many literature sources as well. Since the data for the non-mammalian synapsids and non-avian theropods is exclusively in this format,

conducting these analyses on the extant taxa was necessary to facilitate comparison.

3. Results

3.1. Turtles

K-means guilds

The symmetrical ("SYM) model fit the best to the data in terms of AIC weights. This was true of the guilds recovered in the k-means cluster analysis, as well as the classical dietary guilds.

There were transition rates higher than zero between Guild 3 (omnivory) and all other guilds except Guild 7 (folivory s.s.). The highest transition rate between Guild 3 (omnivory) and another guild was with Guild 9 (predominantly folivorous mixed herbivory) (1.030, see Table 35; Figure 23). However, transition rates between Guild 3 (omnivory) and the other herbivorous guilds (Guilds 1, 5, and 7) were low (See Table 35; Figure 23). Transition rates between Guild 3 (omnivory) and the mixed faunivorous guilds were high (Guilds 2, 4, and 10; see Table 35; Figure 23), but low between Guild 3 (omnivory) and the specialised invertivorous guilds (Guilds 6, and 8).

Transition rates between all herbivorous guilds and Guilds 6 (durophagy s.s.), 8 (insectivory s.s.), and 10 (predominantly carnivorous mixed faunivory) were zero. The highest transition rates between faunivorous and herbivorous guilds were between Guild 1 (folivory s.l.) and Guilds 2 (predominantly insectivorous mixed faunivory) and 4 (predominantly durophagous mixed faunivory).

Transition rates between the predominantly folivorous guilds (Guilds 1, 7, and 9) were all high (see Table 35; Figure 23). The transition rate between Guild 5 (mixed herbivory composed predominantly of reproductive plant parts) and Guild 9

(predominantly folivorous mixed herbivory) were high (1.233) though much lower between Guild 5 (mixed herbivory composed predominantly of reproductive plant parts) and the other folivorous guilds with a higher component of vegetative plant material (see Table 35; Figure 23). There were high rates of transition between the different faunivorous guilds (see Table 35; Figure 23). Two exceptions were the transition rates between Guild 10 (predominantly carnivorous mixed faunivory) and Guild 8 (insectivory s.s.) (0.026); and the transition rate between Guilds 6 (durophagy s.s.) and 8 (insectivory s.s.) was zero.

Traditional guilds

Transition rates between omnivory and both faunivory and herbivory, were higher than rates between faunivory and herbivory directly. For the SYM model, the transition rate between faunivory and herbivory is the lowest (6.27). Transition rates between omnivory and faunivory (19.881), and omnivory and herbivory (19.775) are nearly identical.

3.2. Lizards

K-means guilds

The log likelihood and AIC values was highest for the “all rates different” (ARD) model for both topologies. In terms of AIC weights, the ARD model fared the best for both typologies and for the analyses using both the k-means cluster generated guilds and the classical dietary guilds (Pyron & Burbrink, 2014; Pyron et al., 2013; Tonini et al., 2016).

Tonini et al. (2016) topology

Transition rates into Guild 8 (omnivory) were higher than transition rates out of Guild 8 (omnivory). Other than the predominantly carnivorous guilds, there were transition rates greater than zero in at least one direction between Guild 8 (omnivory) and at least one guild characterised by each other second-order subdivision of the dietary data (see Table 36; Figure 24). The predominantly insectivorous guilds had far higher overall rates of transition into Guild 8 (omnivory) than the inverse. Guild 6 (insectivory-omnivory) transitioned into Guild 8 (omnivory) at three times the rate of the inverse (0.003; and 0.001 respectively). The mixed herbivorous guilds (Guilds 7, and 9) transitioned into Guild 8 (omnivory) at a higher rate than Guild 10 (folivory).

Transition rates (taken collectively) from the faunivorous guilds to the herbivorous guilds were slightly higher than the inverse. The rates of transition from the predominantly invertivorous (especially insectivorous) mixed faunivory to the herbivorous guilds were higher than those from the carnivorous or durophagous guilds. The mixed herbivorous guilds (Guilds 7 and 9) had higher transition rates into the invertivorous guilds compared to Guild 10 (folivory). The guild reflecting a diet composed predominantly of reproductive plant parts (Guild 7) had higher rates of transition from faunivorous guilds than to them (see Table 40). The inverse was true for the guilds composed primarily of vegetative plant structures (Guilds 9, and 10).

Transition rates within the faunivorous and herbivorous guilds were higher than between them (see Table 36; Figure 24). Transition rates into the specialised guilds were generally higher than rates out of them. Transition rates within the herbivorous

guilds showed a distinct pattern. Guild 7 (reproductive plant part-dominant mixed herbivory) had higher transition rates into the other herbivorous guilds than the inverse. Guild 10 (folivory) had in-transition rates greater than zero from all other herbivorous guilds but none into the other herbivorous guilds (see Table 36; Figure 24). Guild 9 (vegetative plant part-dominant mixed herbivory) filled an intermediate position with approximately equal total rates of transition into and out of the other herbivorous guilds (see Table 36; Figure 24). There was a similar pattern for the faunivorous guilds. There were higher rates of transition into Guild 2 (insectivory s.s.) from the other faunivorous guilds than the inverse. The opposite was true for Guilds 3 (isectivory s.l.) and 6 (insectivory-omnivory). There was a relatively high (0,003) transition rate from Guild 1 (mixed faunivory) to Guild 5 (carnivory). There were no other transition rates greater than 0,001 involving Guild 5 (carnivory) and the other faunivorous guilds. There were also higher rates of transition from the other faunivorous guilds into Guild 4 (durophagy s.l.) than out of it (see Table 36; Figure 24).

Pyron et al. (2013) topology

Rates of transition out of Guild 8 (omnivory) were generally lower than transition rates into the guild. The highest transition rates into Guild 8 (omnivory) were from Guilds 6 (insectivory-omnivory; 0.005), 9 (mixed herbivory; 0.004), and 7 (mixed herbivory composed primarily of reproductive plant structures; 0.002). Transition rates between Guild 8 (omnivory) and Guilds 1 (mixed faunivory), 4 (durophagy s.l.), 5 (carnivory), and 10 (folivory) were zero or close to zero.

Transition rates directly between herbivorous and faunivorous guilds were generally low. The highest transition rates were between invertivorous (Guilds 2, 3, and 6) and mixed herbivorous guilds (Guilds 7, and 9) (see Table 37; Figure 25). Transition rates from herbivorous guilds to invertivorous guilds were generally higher than the inverse. There was also a conspicuous transition rate of 0.001 from Guild 4 (durophagy s.l.) to 10 (folivory). Most other faunivore-herbivore transitions involved insectivory and mixed herbivory.

Transition rates into Guild 10 (folivory) from the other herbivorous guilds were higher than rates out of the guild. The highest rates of transition into folivory were from Guilds 9 (mixed herbivory) followed by 7 (mixed herbivory composed primarily of reproductive plant structures). The transition rate from Guild 7 (mixed herbivory composed primarily of reproductive plant structures) to Guild 9 (mixed herbivory) (0.017) was more than three times higher than the inverse (0.005). Transition rates into Guilds 4 (durophagy s.l.) and 5 (carnivory) were highest from Guild 1 (mixed faunivory). Reverse transition rates back into Guild 1 (mixed faunivory) were lower (see Table 37; Figure 25). The highest rate of transition into Guild 1 (mixed faunivory) was from Guild 3 (insectivory s.l.). Transition rates into Guilds 2 (insectivory s.s.) and 3 (insectivory s.l.) were higher than the inverse in all instances.

Traditional guilds

When replicating the ancestral state reconstruction analyses using the traditional categories, the results are more consistent between topologies than they were when using the guilds generated by the k-means cluster analysis. There were, however,

some important differences. In terms of AIC weights, the “symmetrical” (SYM) model scores the highest for the topology of Tonini et al. (2016). The “all rates different” (ARD) model was the best fit for the topology of Pyron et al. (2013).

Tonini et al. (2016) topology

The transition rate between faunivory and herbivory is zero, or very close to zero. The transition rate between herbivory and omnivory is higher (0.006) than between faunivory and omnivory (0.002).

Pyron et al. (2013) topology

The transition rate from faunivory to herbivory was a low 0.055, while it was zero in the opposite direction. Faunivory transitioned into omnivory at a rate far lower (0.534) than the inverse (8.782). Conversely, the transition rate from herbivory to omnivory (6.732) was far higher than from omnivory to herbivory (0.945).

3.3. Birds

K-means guilds

The “all rates different” (ARD) model was the best fit to backbone topology of Ericson (2006), while the “symmetrical rates” (SYM) model was the best fit to the backbone topology of Hackett (2008).

Ericson et al. (2006) topology

Transition rates were generally higher into Guild 4 (omnivory) than out of the guild. The highest rates of transition into Guild 4 (omnivory) were from Guilds 9 (granivory; 0.095) 2 (frugivory-omnivory; 0.063), and 8 (predominantly folivorous mixed herbivory; 0.055). In each case, rates of transition in the opposite direction were lower (see Table 38; Figure 26). There was a relatively high rate of transition from Guild 4 (omnivory) to Guild 10 (invertivory s.l.; 0.020). Transition rates, in both directions, between Guild 4 (omnivory) and Guilds 3 (nectarivory), and 5 (pisicivory s.l.) were low (See Table 38; Figure 26). Transition rates between Guild 4 (omnivory) and Guilds 1 (frugivory), 6 (invertivory s.s.), and 7 (carnivory) were at, or close to, zero (see Table 38; Figure 26).

Transition rates between faunivorous and herbivorous guilds were generally low (see TABLE). The most conspicuous were from Guild 1 (frugivory) to Guilds 10 (invertivory s.l.; 0.288), and 6 (invertivory s.s.; 0.076). Transitions in the opposite direction were lower.

Transitions within herbivorous guilds followed a simple pattern. Guild 9 (granivory) transitioned into Guild 8 (mixed herbivory) at a higher rate than the inverse (see Table 38; Figure 26). Guild 2 (frugivory-omnivory) transitioned into Guild 1 (frugivory) at a higher rate than the inverse (see Table 38; Figure 26). Transition rates between the specialised herbivorous guilds (Guilds 1, 3, and 9) were at, or near, zero. Transitions to, and from, Guild 3 (nectarivory) were almost mostly to, and from, Guilds 2 (frugivory-omnivory), and 4 (omnivory) rather than from other mostly

herbivorous guilds (see Table). Within the faunivorous guilds, rates of transition between Guilds 5 (piscivory s.l.) and 7 (carnivory) were high in both directions but both guilds showed higher rates of transition into Guild 10 (invertivory s.l.) than the inverse. The transition rate from Guild 10 (invertivory s.l.) into Guild 6 (invertivory s.s.) was slightly higher than in the opposite direction (see Table 38; Figure 26). Transition rates between Guild 6 (invertivory s.s.) and Guilds 5 (piscivory s.l.) and 7 (carnivory) were at, or near, zero (see Table 38; Figure 26).

Hackett et al. (2008) topology

Transition rates involving Guild 4 (omnivory) were highest with other generalist guilds, including Guilds 10 (invertivory s.l.; 0.023), 2 (frugivory-omnivory; 0.018), and 8 (mixed herbivory; 0.010). Transition rates between Guild 4 (omnivory) and the more specialised guilds were far lower except for Guild 9 (granivory; 0.015).

Transition rates between faunivorous and herbivorous guilds were very low. The only such transition rates >0.001 were between Guild 10 (invertivory s.l.) and Guilds 2 (frugivory-omnivory; 0.015) and 3 (nectarivory; 0.001).

The highest herbivore-to-herbivore transition rate was between Guilds 1 (frugivory) and 2 (frugivory-omnivory) (0.293). The transition rate between Guilds 8 (mixed herbivory) and 9 (granivory) (0.004) was higher than between either guild and any other herbivorous guild. Transition rates between the specialised herbivorous guilds (Guilds 1, 3, and 9) were low (see Table 39; Figure 27). The highest transition rate within the faunivorous guilds was between Guilds 6 (invertivory s.s.) and 10 (invertivory s.l.) (0.037). Transition rates were relatively high between Guild 10

(invertivory s.l.) and both Guilds 5 (piscivory s.l.; 0.012) and 7 (carnivory; 0.004). The latter two guilds also displayed a relatively high transition rate with each other (0.003) but neither with Guild 6 (invertivory s.s.).

Traditional guilds

For both backbone topologies (Jetz et al., 2012), the best-fitting model was the “all-rates different” (ARD) model. The only difference between the two topologies is that herbivory transitions into omnivory at a lower rate than the inverse using the topology of Ericson et al. (2006), while the opposite is true for the topology of Hackett et al. (2008).

Ericson et al. (2006) topology

Rates of transition directly between faunivory and herbivory were near zero. Omnivory transitioned into faunivory at a far higher rate (0.027) than the inverse (0.006). By contrast, the herbivory transitioned into omnivory at a slightly higher rate (0.021) than the inverse (0.020).

Hackett et al. (2008) topology

The rate at which herbivory and faunivory transition into each other is close-to-zero. Transition rates out of omnivory are higher than into the guild in relation to both faunivory (0.026; against 0.007) and herbivory (0.020; against 0.017).

3.4. Mammals

K-means guilds

The “all rates different” (ARD) model was the best fit on both mammal topologies (Upham et al., 2019) for the Mk analysis. In general, the herbivorous and faunivorous guilds transitioned to, and from, Guild 7 (omnivory) at a higher rate than they transitioned into each other. Furthermore, the highest rates of transition are within the different herbivorous and faunivorous guilds rather than between them.

Tip-dating topology

Overall, transition rates out of Guild 7 (omnivory) were higher than rates of transition into the guild. There were rates of transition greater than zero out of Guild 7 (omnivory) to every other guild other than Guilds 6 (predominantly folivorous mixed herbivory) and 9 (invertivory s.s.). Conversely, the transition rates into Guild 7 (omnivory) from Guilds 2 (invertivory s.l.), 3 (folivory), 6 (vegetative plant part-dominant mixed herbivory), and 10 (frugivory), were all zero. Transition rates from the carnivorus guilds into Guild 7 (omnivory), and vice versa, were higher than for the insectivorous guilds (see Table 40; Figure 28). By a wide margin, the highest rates of transition, in both directions, between Guild 7 (omnivory) and the herbivorous guilds is with Guild 4 (reproductive plant part-dominant mixed herbivory).

Transition rates from the faunivorous to herbivorous guilds are, in total, higher than the inverse. Collectively, transition rates from the herbivorous guilds were higher into

the predominantly invertivorous guilds (Guilds 1, 2, and 9) than into the carnivorous guilds (see Table 40; Figure 28). Transition rates from the herbivorous guilds, composed predominantly of reproductive plant structures, to the faunivorous guilds were all zero (see Table 40; Figure 28). The highest transition rates between faunivorous and herbivorous guilds involve the Guild 6 (predominantly folivorous mixed herbivory).

Rates of transition into the mixed herbivorous guilds (Guilds 4, and 6) from the other herbivorous guilds were lower than the inverse, on average. The only transition rate above zero between Guild 4 (reproductive plant part-dominant mixed herbivory) and the other herbivorous guilds is to Guild 6 (vegetative plant part-dominant mixed herbivory). There are relatively high transition rates from Guild 6 (vegetative plant part-dominant mixed herbivory) to Guilds 3 (folivory) and 10 (frugivory), while the inverses were low or zero (see Table 40; Figure 28). There are low transition rates, in both directions, between Guild 3 (folivory) and Guild 10 (frugivory).

The highest transition rate between the faunivorous guilds is from Guild 9 (invertivory s.s.) to Guild 1 (mixed faunivory). The highest transition rate into Guild 5 (piscivory s.l.) is from Guild 8 (carnivory). All other rates of transition between Guild 5 (piscivory s.l.) and the other faunivorous guilds are relatively low (see Table 40; Figure 28). The highest transition rate into Guild 8 (carnivory) from other faunivorous guilds is from Guild 2 (inveritovory s.l.) with realtively high rates from the other faunivorous guilds as well. Rates of transition out of Guild 8 (carnivory) were all rather low (see Table 40; Figure 28). Transition rates between the invertivorous guilds were low in all directions. Both invertivorous guilds were characterised by low rates of in-transition and higher rates of out-transition.

Node-dating topology

There were transition rates greater than zero from Guild 7 (omnivory) to every other guild other than Guilds 6 (vegetative plant part-dominant mixed herbivory) and 9 (invertivory s.s.). Into Guild 7 (omnivory), there were transition rates exceeding zero from all other guilds except Guilds 2 (invertivory s.l.), 6 (vegetative plant part-dominant mixed herbivory), and 10 (frugivory). Overall, transition rates from Guild 7 (omnivory) to the faunivorous guilds were approximately equal to transition rates in the opposite direction, though with variation between the specific guilds. Transition rates between the carnivorous guilds and Guild 7 (omnivory) were, on average, higher than between Guild 7 (omnivory) and the insectivorous guilds. Guild 9 (invertivory s.s.) had a low transition rate into Guild 7 (omnivory), while opposite rate was zero (see Table 41; Figure 29). In both directions, the transition rates between Guild 7 (omnivory) and Guild 4 (reproductive plant part-dominant mixed herbivory) is the highest of any herbivorous guild. The transition rates between Guilds 3 (folivory) and 10 (frugivory) and Guild 7 (omnivory) are very low in comparison.

Transition rates from the faunivorous to herbivorous guilds are, on average, higher than the inverse. In general, the carnivorous guilds (Guilds 1, 5, and 8), had higher cumulative transition rates into the herbivorous guilds than the invertivorous guilds (Guilds 2, and 9). In particular, there was a high transition rate to Guild 3 (folivory) from Guild 1 (mixed faunivory) (0.014). There were no transition rates greater than zero between Guild 2 (invertivory s.l.) and any of the herbivorous guilds. Rates of transition from the predominantly folivorous guilds (Guilds 3, and 6) to the faunivorous guilds were far higher than from the herbivorous guilds with a

predominant dietary composition of reproductive plant structures (Guilds 4, and 10). In the inverse direction, however, there was a more even spread of transition rates greater than zero into the different herbivorous guilds. Guild 4 (reproductive plant part-dominant mixed herbivory) had, by far, the lowest rates of transition with the faunivorous guilds in any direction (see Table 41; Figure 29).

All transition rates between Guild 4 (reproductive plant part-dominant mixed herbivory) and the other herbivorous guilds were at zero. By contrast, the transition rates between Guild 6 (vegetative plant part-dominant mixed herbivory) and the other herbivorous guilds were relatively high (see Table 41; Figure 29). On average, transition rates into Guild 3 (folivory) from the other herbivorous guilds were far higher than the inverse. In particular, the transition rate from Guild 6 (vegetative plant part-dominant mixed herbivory) to Guild 3 (folivory) was a relatively high 0.043, while the inverse was very low (0.001). By contrast, the transition rate from Guild 6 (vegetative plant part-dominant mixed herbivory) to Guild 10 (frugivory) was relatively high (0.009) while the inverse was zero (see Table 41; Figure 29).

The single highest transition rate within the faunivorous guilds is from Guild 9 (invertivory s.s.) to Guild 1 (mixed faunivory) (0.046). All transition rates above zero into Guild 5 (piscivory s.l.) are from the other carnivorous guilds (see Table 41; Figure 29). Transition rates are, in general, higher into Guild 8 (carnivory) from the other faunivorous guilds (including the invertivorous guilds) than the inverse. The invertivorous guilds showed generally low transition rates in all directions and their transition rates with each other were lower than with the carnivorous guilds (see Table 41; Figure 29).

Traditional guilds

The two mammal topologies produced very consistent results between the two backbone topologies for transition rates and numbers between the traditional dietary guilds in mammals. The specifics differ between the topologies but the general patterns are the same. For both topologies, the “all rates different” (ARD) model was the best fit.

Tip-dating backbone topology

The transition rate from faunivory to herbivory was zero while the inverse was very low (0.002). Faunivory transitioned to omnivory at a much lower rate (0.004) than the inverse (0.016). The transition rate from herbivory to omnivory (0.006) was also much lower than the inverse (0.026).

Node-dating topology

Herbivory transitioned to faunivory at a very low rate (0.001) while the rate in the opposite direction was zero. Transition rates out of omnivory to faunivory (0.016) and herbivory (0.021) were far higher than the inverse (0.004, and 0.005 respectively). These results match those of the tip-dating backbone topology.

3.5. Early-branching synapsids

Traditional guilds

The “symmetrical” (SYM) model was the best-fitting for the Mk analysis.

The transition rate between herbivory and faunivory was low (0.003). The transition rate between omnivory and faunivory was only slightly higher (0.004). By far, the highest transition rate was between omnivory and herbivory (0.009).

3.6. Non-avian theropods

Traditional guilds

The “all rates different” (ARD) model was the best-fitting model.

The transition rate from herbivory to faunivory was zero, but faunivory transitioned into herbivory at a low rate (0.001). The transition rate from omnivory to faunivory (0.036) was higher than the inverse (0.004) by a wide margin. The transition rate from herbivory to omnivory was zero, while the transition rate from omnivory into herbivory (0.017) was relatively high.

3.7. Summary across lineages

Net transition rates out of omnivorous guilds generally exceeded rates of transition into them on topologies where the “all rates different” model was the best fit. In all amniote lineages, the highest transition rates into, and out of, omnivorous guilds were from other generalist guilds (e.g., mixed herbivory, invertivory s.l.). Other than in mammals, transition rates between omnivorous guilds and specialised folivory and carnivory were low. By contrast, transition rates between omnivorous guilds and guilds composed predominantly of invertebrates and reproductive plant material (e.g., nectarivory and granivory in birds) were relatively high.

Transition rates directly between predominantly faunivorous guilds and predominantly herbivorous guilds were low in comparison to other sets of transition rates. In general, transition rates from faunivorous guilds into herbivorous guilds exceeded the inverse. Most such transitions were between generalist guilds composed primarily of invertebrate material and reproductive plant material (e.g., invertivory s.l. and mixed herbivory composed primarily of reproductive plant structures).

Transition rates between different herbivorous guilds followed a distinct pattern. Firstly, the highest transition rates were between different mixed, or generalist, herbivorous guilds. Transition rates directly between specialist herbivorous guilds (e.g., folivory and frugivory) were consistently low. Secondly, transition rates into specialised folivory from mixed herbivory generally exceeded rates in the opposite direction. Finally, transition rates between guilds that contain substantial contributions of both fibrous plant material and seed (e.g., mixed herbivory and granivory in birds) were generally high.

Mirroring patterns in transition rates between different herbivorous guilds, direct transition rates between specialised faunivorous guilds (e.g., invertivory s.s. to carnivory) are low. Transitions between strict invertivory and strict carnivory typically happen by way of a mixed faunivorous intermediate. Transition rates into strict invertivorous guilds tend to be higher than those out of them into mixed faunivorous guilds. The opposite is true of strict carnivorous guilds.

4. Discussion

The most important results of the current study in the context of transitions between dietary guilds in amniote evolution are (a) the role of dietary generalism in evolutionary pathways between dietary guilds, and (b) the dynamics of evolutionary transitions into and out of specialist dietary guilds (especially invertivory and folivory). The results I present in this chapter support some of the existing hypotheses surrounding evolutionary transitions between dietary guilds and refute others.

The results of the analyses using the classical dietary guilds match the patterns expected under the "faunivory ← → omnivory ← → herbivory" model (see Figures 30-38). Transition rates directly between faunivory and herbivory are low-to-zero. Both faunivory and herbivory transition to, and from, omnivory relatively high rates. The results of the analyses on the k-means cluster generated guilds shift this narrative somewhat. The final hypothetical model I presented ("carnivory ← → mixed faunivory ← → invertivory ← → omnivory ← → granivory/frugivory ← → folivory") is matched by the results of the current study but with important considerations introduced by the way in which dietary guilds are defined.

The results of the current study do not support the notion that omnivory constitutes an evolutionary "sink" as has previously been asserted (Burin et al., 2016; Price et al., 2012). Transition rates into the omnivorous guilds (k-means generated) across amniotes, were higher than out of the guild, but by a smaller margin than would be expected under the evolutionary sink hypothesis (Burin et al., 2016; Price et al., 2012). However, many of the generalist guilds (e.g., mixed herbivory), which would have been considered omnivorous by the definitions used in other studies, showed higher rates of out-transition. This demonstrates the importance of dietary

classification criteria, since some generalist guilds may be evolutionary sinks (from the perspective of the tempo and polarity of transition rates), while others are certainly not. An important nuance is that there is a high rate of transition, in both directions, between omnivorous guilds and both generalist invertivorous guilds (e.g., invertivory s.l.) and generalist herbivorous guilds (e.g., mixed herbivory). Transition rates between specialist guilds (e.g., invertivory-carnivory or frugivory-folivory) were generally low across amniote lineages. This would be expected given that the taxa in these guilds would likely possess anatomical and physiological apparatus more specialized to their dietary strategies. It would, therefore, be “harder” for these taxa to undergo an evolutionary shift to an alternative dietary strategy. As such, transition pathways into, and out of, specialist guilds are often via similarly-composed generalist guilds (e.g., mixed faunivory-carnivory or mixed herbivory-folivory). The results of the current study then do not indicate the broad generalist dietary space (encompassing omnivorous and generalist guilds) as an evolutionary sink, but as an evolutionary complex transitional space, providing pathways between more specialized spaces on the dietary spectrum.

The results of the current study demonstrate (a) that invertivory is an evolutionarily versatile as a trait, and (b) that average transition rates towards invertivory are higher than away from invertivory. Consistent with previous studies (Burin et al., 2016; Reuter et al., 2023) on evolutionary transitions, transition rates into specialised invertivory were higher than out of the guild in most analyses. The opposite is true of carnivory and piscivory which tend to have higher rates of transition into mixed faunivorous and invertivorous guilds than the inverse. This same phenomenon was reported in mammals by Reuter et al. (2023) who reported that smaller-bodied carnivorous taxa incorporate invertebrate material in their diet as it is a more

abundant food source than vertebrate meat, explaining a high rate of transition from carnivory to invertivory. Large-bodied hypercarnivory may well be an evolutionary "ratchet" (Van Valkenburgh et al., 2004) after a certain stage of anatomical and behavioral adaptation to the feeding strategy though this is not likely true of carnivory in small-bodied predators that feed primarily on small-bodied prey.

It is difficult to ascertain whether high rates of transition into invertivory are a constant throughout deep time since reconstruction of ancestral dietary states is limited by gaps in evidence from the fossil record (Cantalapiedra et al., 2014; Hou et al., 2004; Miller et al., 2022; Mueller et al., 2018; Wang et al., 2023; Zhonghe & Fucheng, 2004). It is often assumed that invertivory represents the ancestral condition of amniotes (Modesto et al., 2009), and of the stem groups of mammals, archosaurs, and lepidosaurs, though this is not certain (Mueller et al., 2018). Invertivory has been proposed to represent the ancestral condition of the crown groups of mammals (Gill et al., 2014; Reuter et al., 2023), and squamates (Cooper Jr & Vitt, 2002; Glaudas et al., 2019). Piscivory (Brusatte et al., 2015), and granivory (Larson et al., 2016; Miller & Pittman, 2021) have been proposed as the ancestral condition of crown birds based off of interpretations of fossil evidence. These inferences are restricted to the ancestors of extant crown-group birds. A more thorough analysis of Mesozoic avian taxa would likely reveal a different result since the earliest bird radiation includes forms occupying a wide variety of dietary niches (Hou et al., 2004; Wang et al., 2023; Zhonghe & Fucheng, 2004). Evidence from, for example, the Upper Jurassic Yanliao and Lower Cretaceous Jehol Biota indicate that early stem bird taxa already displayed several specialized dietary niches such as durophagy, granivory, and herbivory based on preserved stomach contents (O'Connor, 2019; O'Connor & Zhou, 2020; Zhonghe, 2006; Zhonghe & Fucheng,

2004; Zhou, 2014). There is a possibility that the ancestral bird was invertivorous since invertivorous birds have been shown to occupy the widest functional morphospace (Miller & Pittman, 2021; Miller et al., 2022). Testing this empirically would require fossil evidence preceding the earliest radiation of birds into multiple specialised dietary guilds. Aquatic carnivory has been posited as the ancestral condition of extant turtles (Natchev et al., 2015). Given that strict carnivory is rare among extant turtles (only 4 taxa sensu this study see Table 22), it is plausible that this ancestral turtle may have consumed invertebrate material as well. Accepting invertivory as representing the ancient ancestral condition of Amniota, the results of the current study would suggest that there have been many transitions out of invertivory and many more back into invertivory, each in the order of thousands.

It is expected that there would be a high rate of transition between invertivory and both carnivory and omnivory. Invertivory and faunivory represent a dietary gradient most demarcated by prey size relative to body size of the predator (Carbone et al., 1999; De Cuyper et al., 2019; Van Valen, 1969). It has long been hypothesized that early transitions into omnivory and herbivory originated from insectivorous clades (Sues & Reisz, 1998), and that omnivory often involves a combination of invertebrate and reproductive plant material (Reuter et al., 2023). It has also been shown that anatomical adaptations to invertebrate consumption in some lineages provide a selective advantage for the evolution of, for example, frugivorous (Herrera, 1984) birds, and herbivorous/omnivorous primates (Redford et al., 1984), and bears (Jiangzuo & Flynn, 2020).

Regardless of the directionality, the results of the current study support those of Reuter et al. (2023) in that there is (a) a pattern of evolutionary transition towards

invertivory, and (b) that omnivory with a substantial invertebrate component acts as the origin of evolutionary transitions into several other dietary guilds. Given the wide availability of invertebrates as a food source (M. Clauss et al., 2013; Reuter et al., 2023), and the relative “ease” of evolutionary transition towards invertivorous or partly-invertivorous diets (Melstrom et al., 2021), it is entirely plausible that these guilds represents a generalised or “default” condition for all amniotes. Hence, there is a high (re)evolutionary rate of transition into them. The notion that small, invertivorous and omnivorous taxa are the origin of major evolutionary radiations throughout deep time is not a new one (Grossnickle, 2020; Hellert et al., 2022; Reuter et al., 2023; Wilson, 2013) and is supported by the patterns in evolutionary transition rates revealed in the current study.

Another previous hypothesis supported by the results of the current study is the “seed-to-leaf” hypothesis on the evolution of folivory (Bodmer, 1989; Lambert, 1998; Rosenberger et al., 2011). In both birds and mammals, there were high rates of transition between guilds with a high component of vegetative plant material and mixed herbivorous guilds, especially guilds with a high component of seed (see Figures 33-36). Rates of transition directly between folivorous guilds and omnivorous/faunivorous guilds were low. Specialist herbivorous dietary guilds composed of reproductive plant structures (nectarivory, granivory, frugivory) are more likely to evolve from omnivory without an additional mixed herbivorous intermediate step, As evidenced by a high transition rate between omnivory and specialised non-fibrous herbivorous guilds. This is a result of these food sources requiring less extensive anatomical and physiological adaptation from an invertivorous/omnivorous ancestral state for these guilds to evolve than folivory (Ayala-Berdon & Schondube, 2011; Jordano, 2000; Schondube et al., 2001).

The consistently low rates of transition out of folivory suggest that high-fibre herbivory (such as that of a buffalo) may present as much of an evolutionary "rachet" as hypercarnivory (such as that of a lion), in each case explained by the high degree of morphological specialisation required by these guilds (Bodmer, 1989; Christiansen & Wroe, 2007; Edwards, 1995; Herrel et al., 2002; Santana et al., 2010). That rates of transition into folivory are highest, while highest out of carnivory may reflect the high abundance of fibrous plant material in many terrestrial ecosystems relative to vertebrate food material (M. Clauss et al., 2013; Hiiemae, 2000). This may place an ecological selective pressure towards the evolution of folivory. The high energetic cost and associated risks of acquiring energy from large-bodied vertebrate prey may drive a high rate of transition towards invertivory and mixed faunivory in smaller faunivorous taxa (Reuter et al., 2023).

The results of the current study broadly match the patterns expected under the model I presented in the introduction ("carnivory ← → mixed faunivory ← → invertivory ← → omnivory ← → granivory/frugivory ← → folivory") except that "omnivory" covers several gradations of dietary generalism. The best representation of the model I propose based on the results of analysis would be "Carnivory ← → mixed faunivory ← → invertivory s.l. ← → omnivory ← → mixed herbivory ← → folivory" (see Figure 49). In this instance, the evolution of invertivory, frugivory, granivory, and nectarivory "skips" the generalist herbivorous/faunivorous step so the model presents as "invertivory s.s. ← → invertivory s.l. ← → omnivory ← → nectarivory/granivory/frugivory". Depending on interpretations of ancestral character estimation, it would be prudent to anchor this model with invertivory at the middle, with hypercarnivory and folivory representing extreme ends. Evolutionary transitions occur along this two-pronged continuum centered at invertivory, with carnivory and

folivory representing the extremes of each gradient. There is a high rate of evolutionary transition “down” the faunivorous gradient towards invertivory, and “up” the herbivorous gradient towards folivory.

5. Limitations and future direction

The patterns in evolutionary transitions in diet in the fossil lineages in the current study match those in extant taxa using the classical dietary classification system. In the context of extending the principles of evolutionary transitions between dietary transitions into studies through deep time, it would be prudent for future research to attempt more precise dietary classification to fossil taxa using methods such as microwear analysis (Gill et al., 2014; Melstrom, 2017), and isotopic analysis (Casey & Post, 2011; Miller et al., 2022). It is clear, from the analysis I present in this chapter, that the way diet is classified and defined has a measurable impact on the interpretation of results of studies relating to the macroevolutionary dynamics of diet (see Figures 39-48). Given that the results between extinct and extant taxa match when analysing the classical dietary guilds, it is reasonable to expect that the patterns revealed by the more nuanced dietary guilds would be transferrable through deep time. In particular, it would be instructive to examine the central role of invertivory in driving evolutionary radiations in extinct amniotes. This is because of (a) the status of invertivory as the most probable ancestral condition of all amniotes and many major amniote lineages, and (b) because certain aspects of the evolution of herbivory recovered in the current study may not replicate in extinct ecosystems that lack flowering plants or grasses (Janis et al., 2002; Saarinen, 2019; Tiffney, 2004; Wing & Sues, 1992).

Data precision is also a limitation on the current study in regards to the study of fossil taxa. The Paleobiology Database (PBDB) is a large online database containing stratigraphic and palaeobiological data for fossil taxa (Marshall et al., 2018; Uhen et al., 2023). Ecological data, such as diet, are inputted individually for each taxa by the contributor(s) who create and edit that taxon's entry and data for higher taxonomic ranks are applied to all taxa within those ranks unless specifically edited otherwise

(Uhen et al., 2023). Traditionally, diet in extinct animals have been inferred from proxies such dental and cranio-mandibular morphology, where the masticatory apparatus of herbivores is thought to be adapted for grinding and crushing, and that of carnivores for slicing and piercing (Barrett & Rayfield, 2006; Button & Zanno, 2020; Farlow, 1976; Hotton et al., 1997; Marshall, 2009; Van Valkenburgh & Molnar, 2002; Lindsay E Zanno & Peter J Makovicky, 2011). All entries are backed with citations however the criteria by which the diet of a taxon is determined may not be consistent from entry-to-entry. Furthermore, some entries may contain more precise dietary characterizations (e.g., piscivore, or insectivore) and others only broader classifications (i.e., “herbivore”, “omnivore”, “carnivore”). This does impose limitations on collecting these kinds of data from PBDB for analyses requiring high-resolution data.

Mammals are unique among major amniote lineages in that there is a relatively high transition rate between guilds with a high proportion of fibrous plant material and guilds with a high percentage of vertebrate meat in the dietary composition. In particular, there is a high transition rate observed between mixed faunivory and folivory. This contradicts the pattern observed in other lineages in the current study, and in recent research on mammals (Amador & Giannini, 2021; Reuter et al., 2023). This can be explained by the relative rarity of carnivory and mixed faunivory compared to the relative abundance of folivory among mammalian taxa. It also possible that the Mk models may have interpreted the ancestors at deep nodes of, for example, Artiodactlya, Carnivora, and/or Marsupialia as being carnivorous or mixed faunivorous. The common ancestors of obligate faunivorous and herbivorous mammalian lineages, such as cetaceans and ruminants (Wu, 2022), have been interpreted as being broadly faunivorous in the past. A low number of evolutionary

transition events in phylogenetic history may translate to a high rate given the probabilities based on distributions of the different guilds among living taxa. Finally, it important to consider that mixed faunivory is still a generalist and partially invertivorous guild. It is likely that any such transitions are occurring between small-bodied, generalist taxa rather than large hypercarnivores and specialised folivores (Reuter et al., 2023). Future work should include additional ecologically informative variables, such as body size, to truly unwrap the dynamics of evolutionary transitions between dietary guilds.

One limitation of the current study is that only a single approach to transition rate modelling is used. Future investigations comparing transition rates in diet between major amniote lineages should incorporate multiple models of testing evolutionary transition rates such as ‘multiple state speciation and extinction’ (FitzJohn, 2012), and reversible jump MCMC (Pagel & Meade, 2006); Reuter et al. (2023). It is possible that these different approaches may reveal a different narrative to the one I present here. The different approaches did subtly alter the results of (Reuter et al., 2023). It would also be informative to explore estimations of raw numbers of transitions between dietary guilds following Amador and Giannini (2021) since there may be a disconnect between rates of transition and numbers of transition.

6. Figures

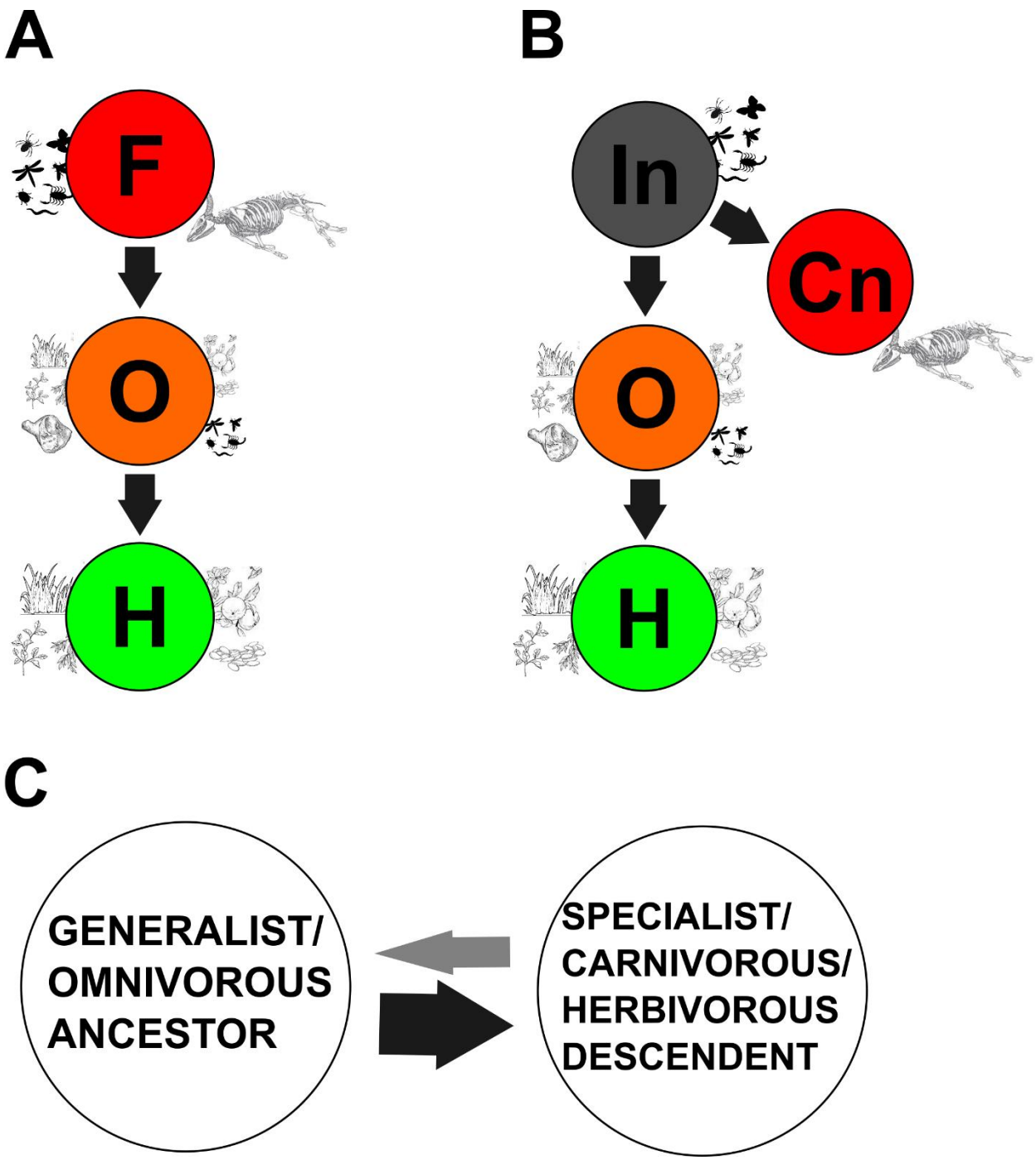


Figure 21: Simplified schematic illustrations of some of the "classical" evolutionary hypotheses about the evolution of diet in tetrapods. A; herbivory evolves from a faunivorous ancestral condition via an omnivorous intermediate stage. B; omnivory and, by extension, herbivory more frequently evolves from invertivorous ancestors rather than carnivorous ancestors. C; transition rates from omnivory and generalist dietary strategies to specialised faunivorous and herbivorous feeding strategies are higher than the inverse. Abbreviations: F -

faunivory, O - omnivory, H - herbivory, In - invertivory, Cn - carnivory. Darker, thicker arrows represent higher transition rates compared to lighter, thinner arrows.

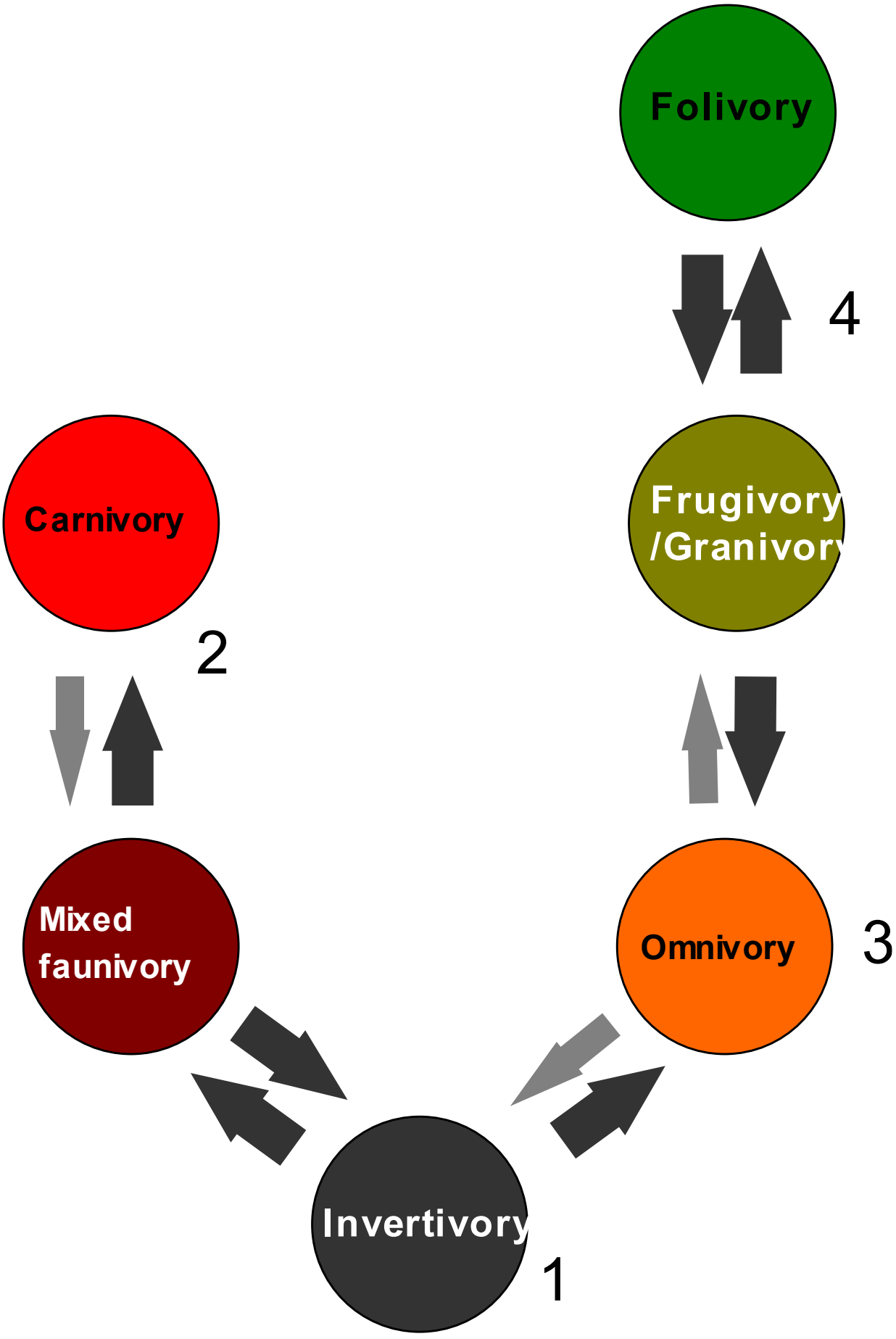

Folivory
4
Carnivory
Frugivory
/Granivory
2
Mixed
faunivory
Omnivory
3
Invertivory
1

Figure 22: Simplified schematic overview of the "null" model of expectations of the rate and tempo of evolutionary transitions between dietary guilds based on a synthesis of previous hypotheses. 1 - Invertivory as the ancestral amniote condition (e.g., Modesto et al. 2009); 2 - high transition rate into hypercarnivory which represents an "evolutionary rachet" (Van Valkenburgh et al. 2004); 3 - high transition rate into omnivory as an "evolutionary sink" (Price et al. 2012; Burin et al. 2016); 4 - "seed-to-leaf" evolutionary pathway from granivory/frugivory to folivory (e.g., Rosenberger 2011; Bodmer et al. 2006).

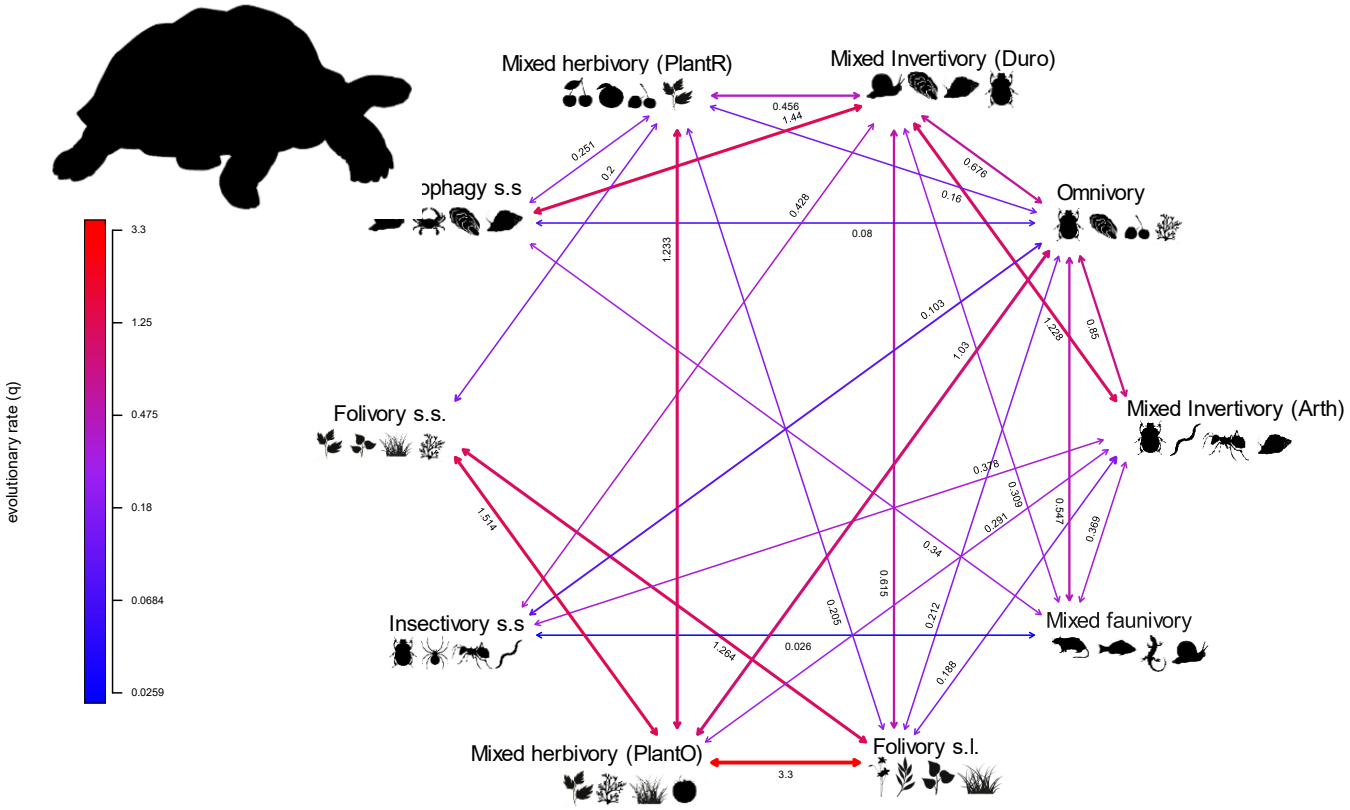


Figure 23: Evolutionary rates of transition between the k-means cluster dietary guilds in turtles as per the results of the Mk analysis ("fitMk" function), "symmetrical" (SYM) model. Abbreviations: Arth - arthropods (and other invertebrates not accounted for by durophagy), Duro - durophagy (gastropods, mollusks, crustaceans), PlantR - reproductive plant structures, PlantO - vegetative plant structures (as well as algae and fungi).

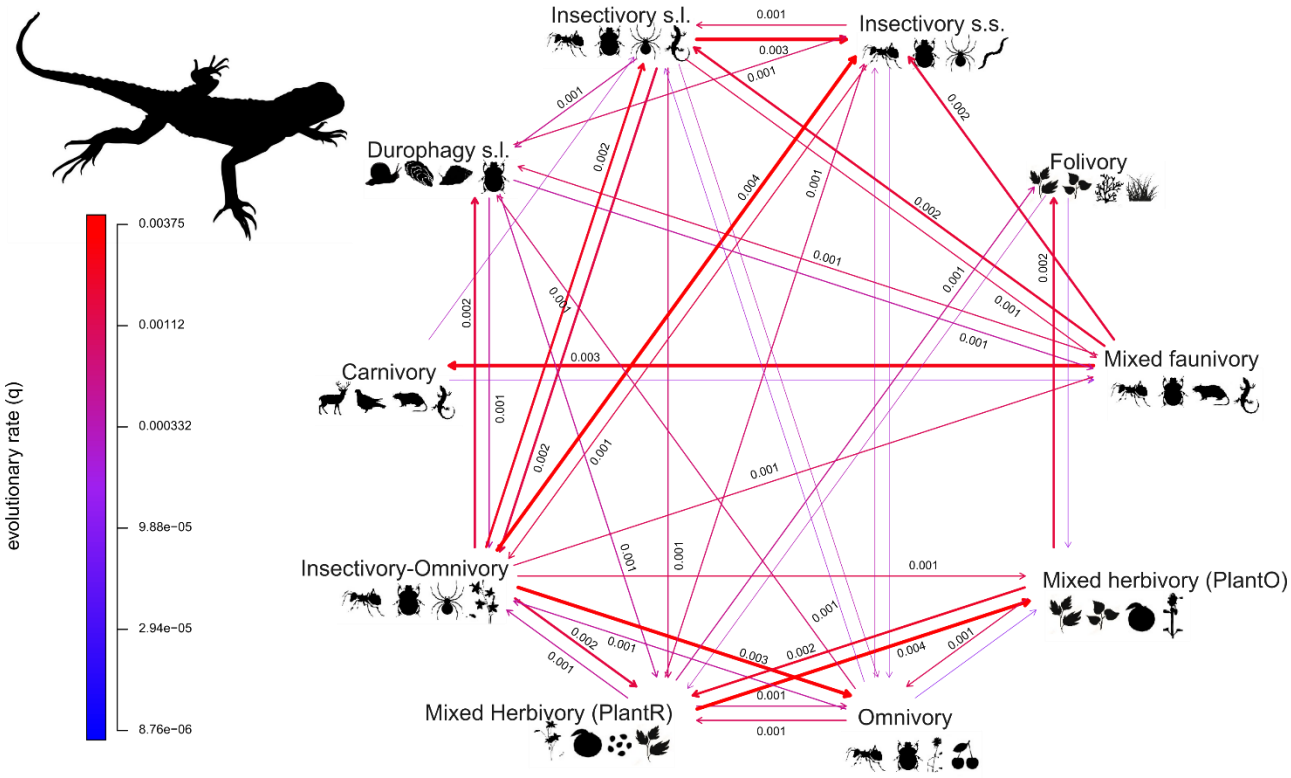


Figure 24: Rates of evolutionary transition between dietary guilds (k-means cluster analysis) in lizards (topology of Tonini et al. 2016) recovered by the Mk marginal maximum likelihood analysis ("all rates different" model - ARD). Direction of arrows indicates "from state - to state". Full set of transition rates in TABLE. Only transition rates >0.001 are shown. Abbreviations: PlantO, vegetative plant structures; PlantR, reproductive plant structures.

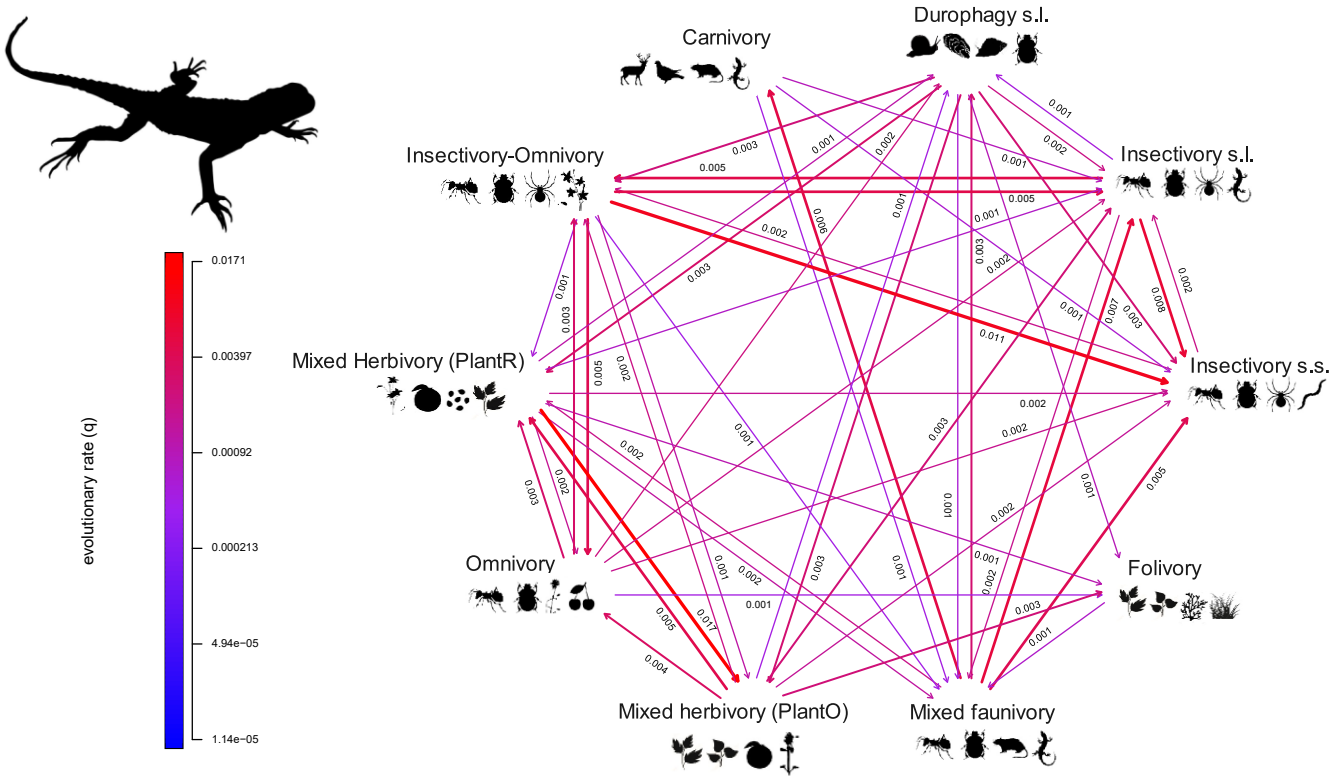


Figure 25: Rates of evolutionary transition between dietary guilds (k-means cluster analysis) in lizards (topology of Pyron et al. 2014) recovered by the Mk marginal maximum likelihood analysis ("all rates different" model - ARD). Direction of arrows indicates "from state - to state". Abbreviations: PlantO, vegetative plant structures; PlantR, reproductive plant structures.

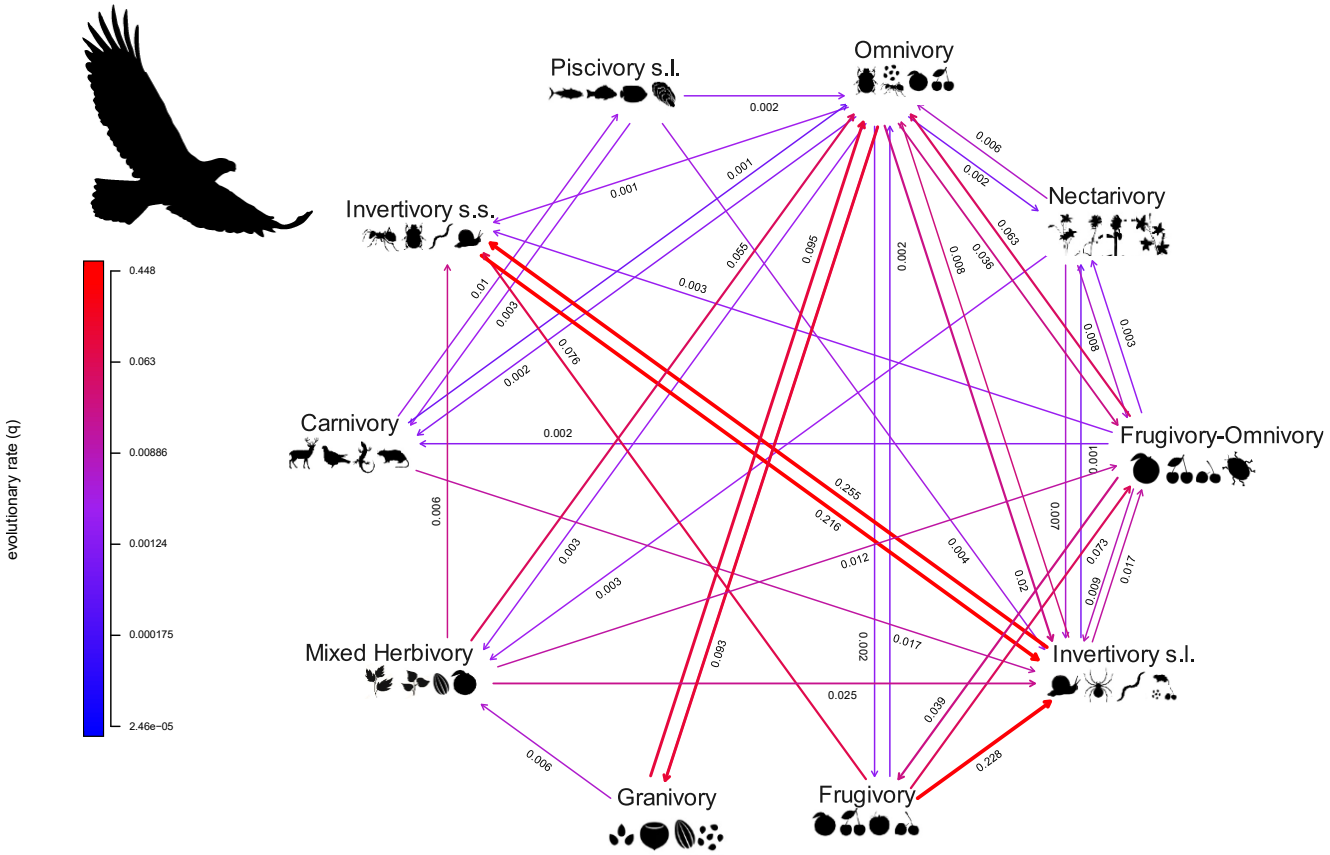


Figure 26: Rates of evolutionary transition between dietary guilds (k-means cluster analysis) in birds (backbone topology of Ericson et al. 2006) recovered by the Mk marginal maximum likelihood analysis ("all rates different" model - ARD). Only transition rates >0.001 are shown. Direction of arrows indicates "from state - to state".

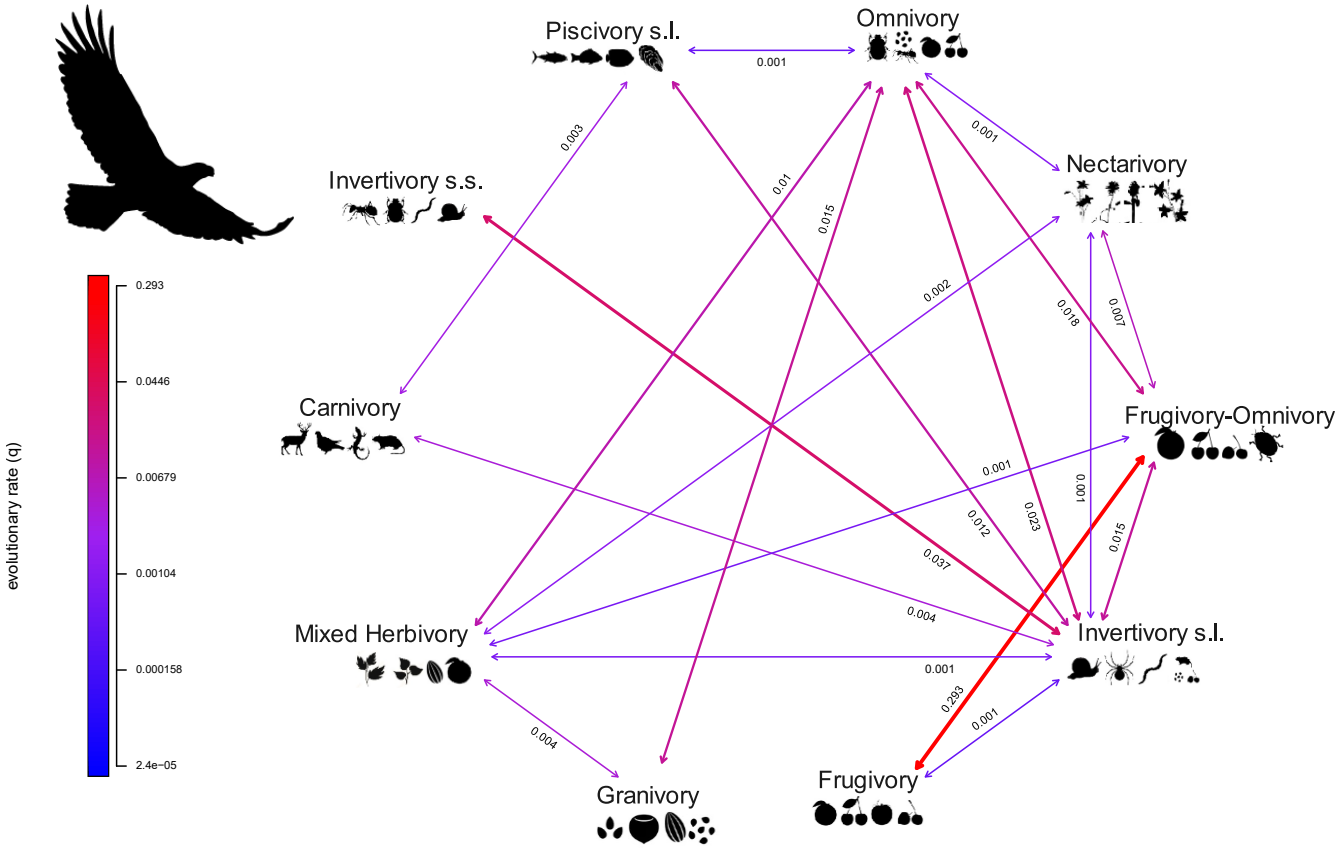


Figure 27: Rates of evolutionary transition between dietary guilds (k-means cluster analysis) in birds (backbone topology of Hackett et al. 2008) recovered by the Mk marginal maximum likelihood analysis ("all rates different" model - ARD). Only transition rates >0.001 are shown. Direction of arrows indicates "from state - to state".

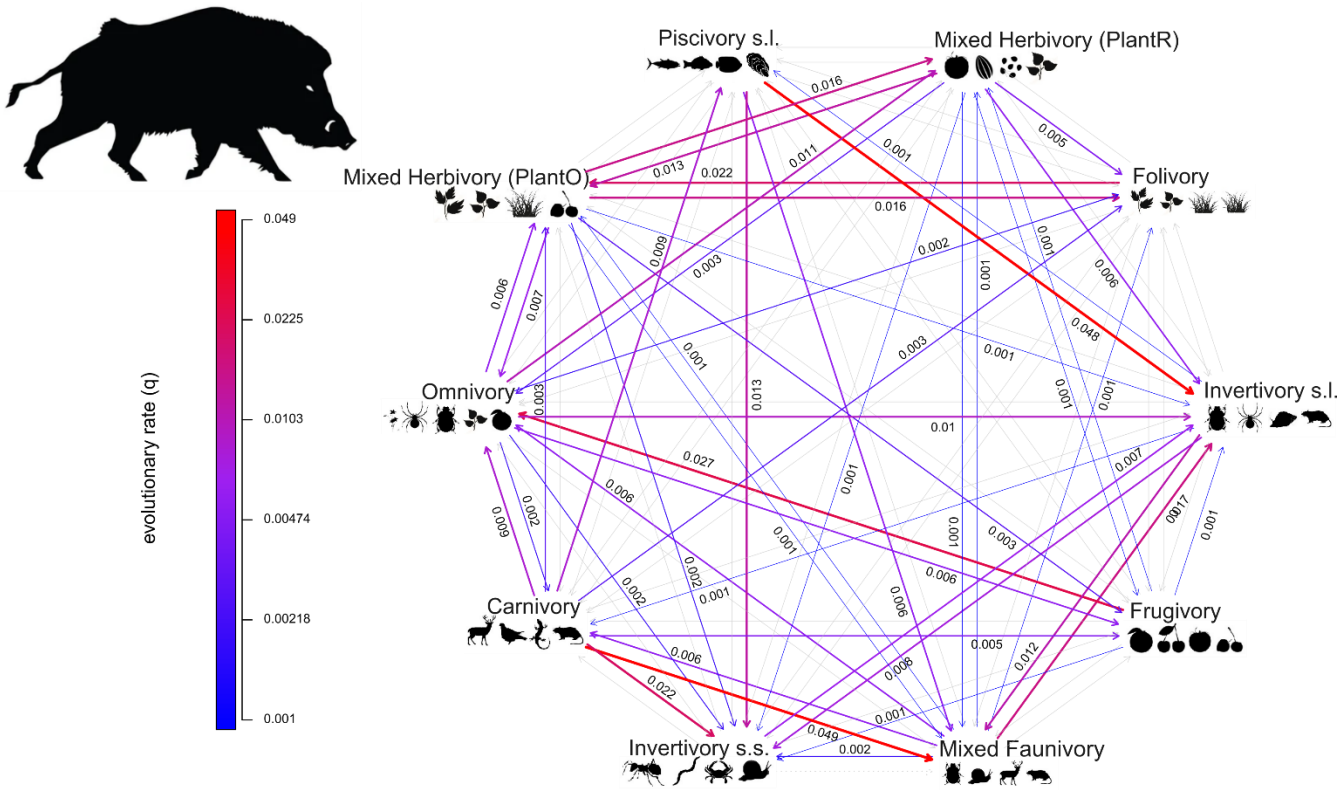


Figure 28: Rates of evolutionary transition between dietary guilds (k-means cluster analysis) in mammals (tip-dating backbone topology) recovered by the Mk marginal maximum likelihood analysis ("all rates different" model - ARD). Only transition rates >0.001 are shown. Direction of arrows indicates "from state - to state". Abbreviations: PlantO, vegetative plant structures; PlantR, reproductive plant structures.

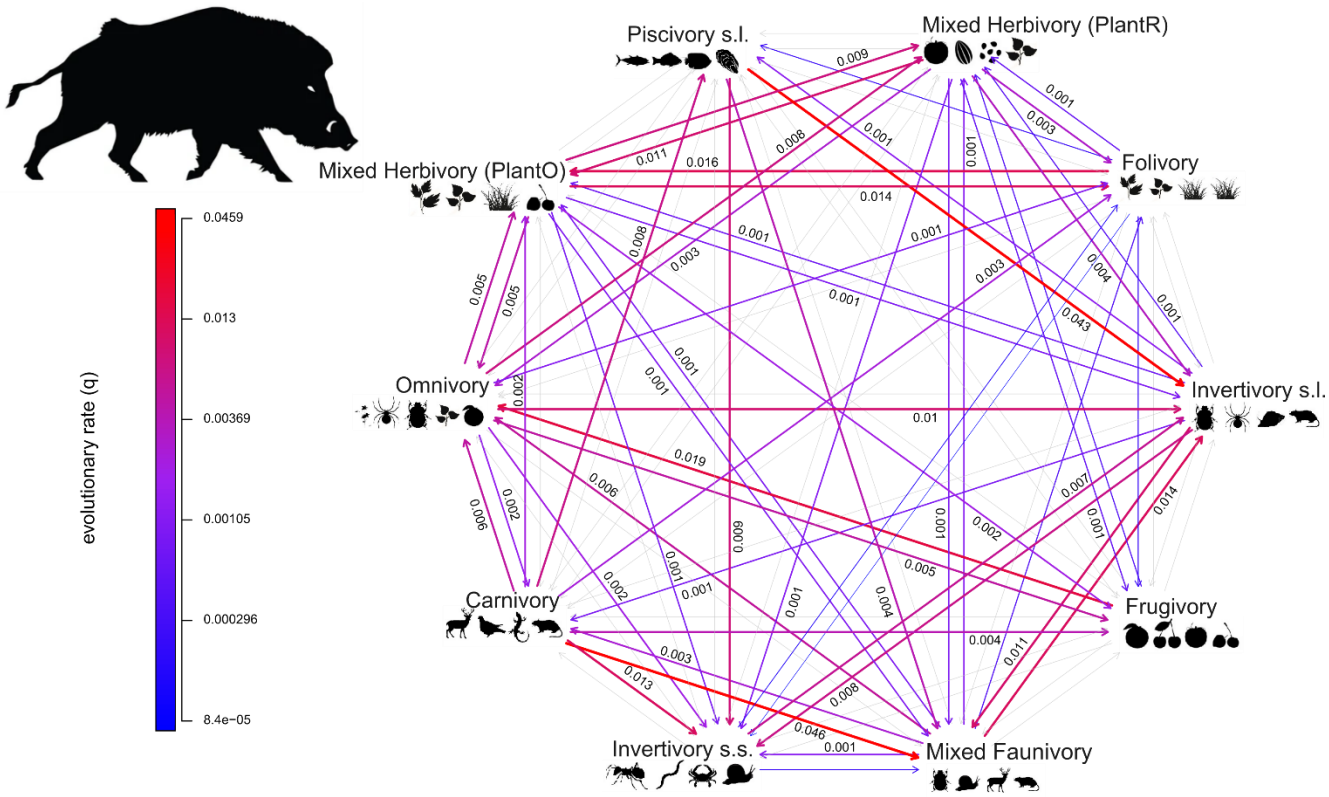


Figure 29: Rates of evolutionary between dietary guilds (k-means cluster analysis) in mammals (node-dating backbone topology) recovered by the Mk marginal maximum likelihood analysis ("all rates different" model - ARD). Only transition rates >0.001 are shown. Direction of arrows indicates "from state - to state". Abbreviations: PlantO, vegetative plant structures; PlantR, reproductive plant structures.

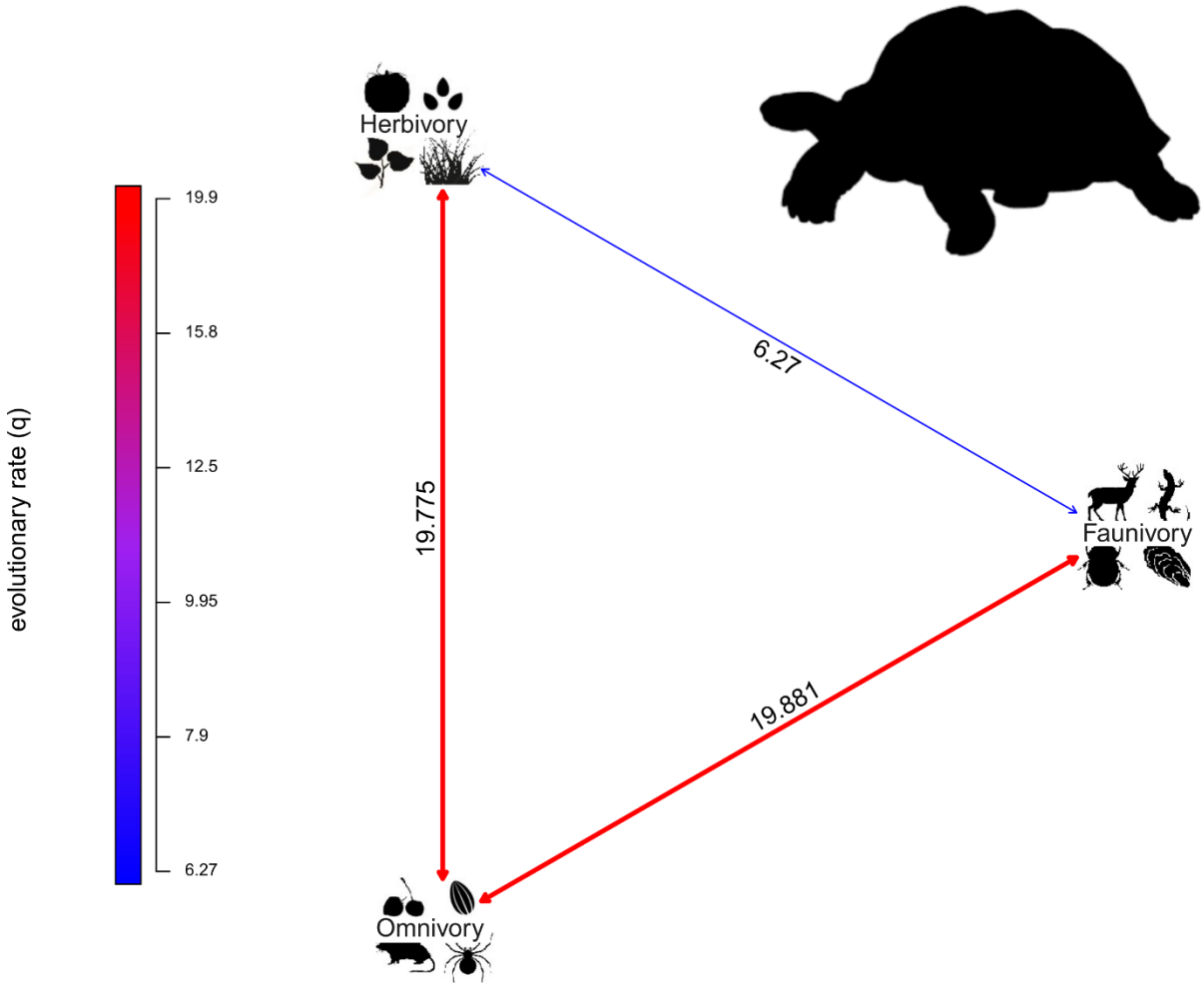


Figure 30: Evolutionary rates of transition between the classical dietary guilds in turtles as per the results of the Mk analysis ("fitMk" function), "symmetrical" (SYM) model. Numbers on the lines indicate evolutionary transition rates.

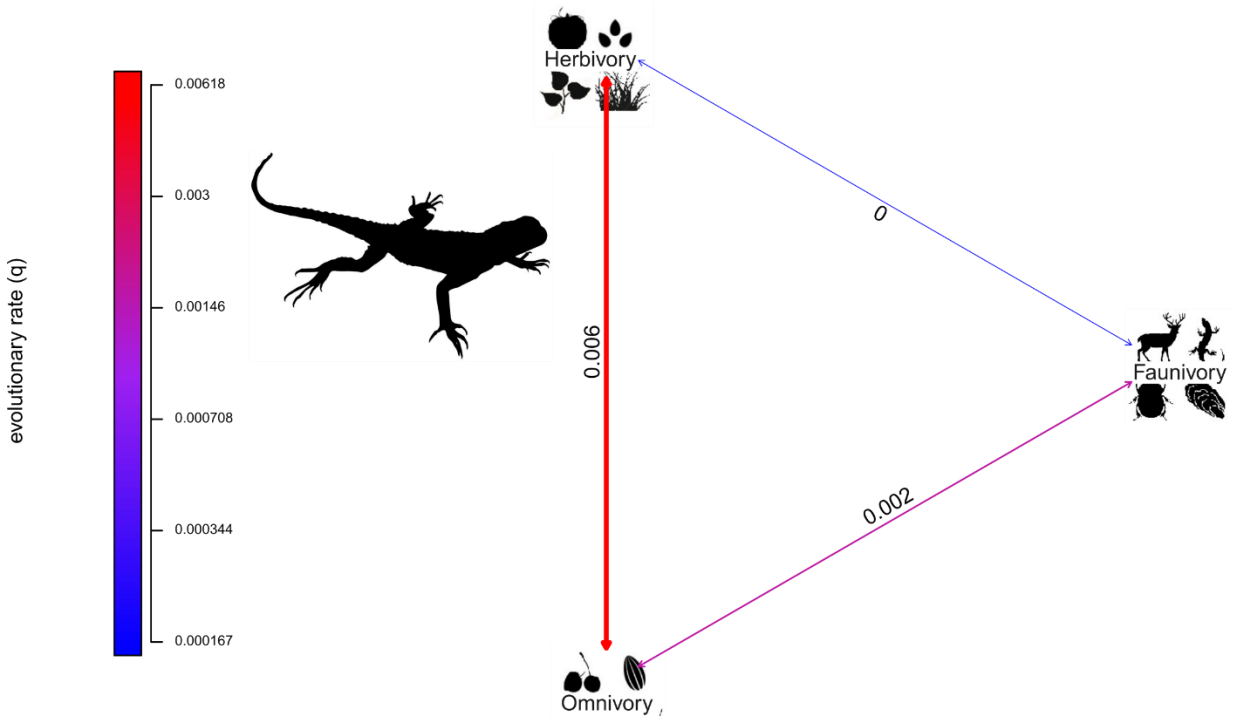


Figure 31: Evolutionary transition rates between the classical dietary guilds in lizards (topology of Tonini et al. 2016) as per the results of the Mk analysis ("fitMk" function), "symmetrical" (SYM) model. Direction of arrows indicates "from state - to state".

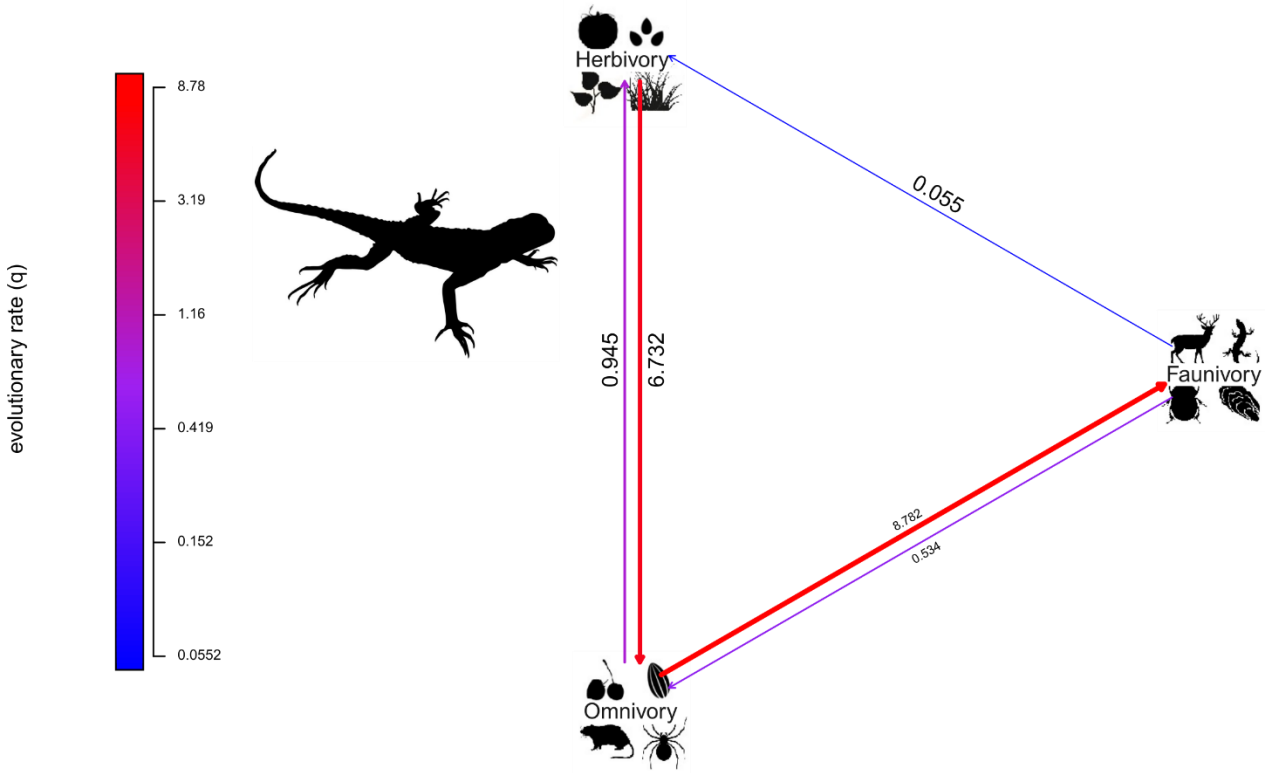


Figure 32: Evolutionary transition rates between the classical dietary guilds in lizards (topology of Pyron et al. 2013) as per the results of the Mk analysis ("fitMk" function), "all rates different" (ARD) model. Direction of arrows indicates "from state - to state".

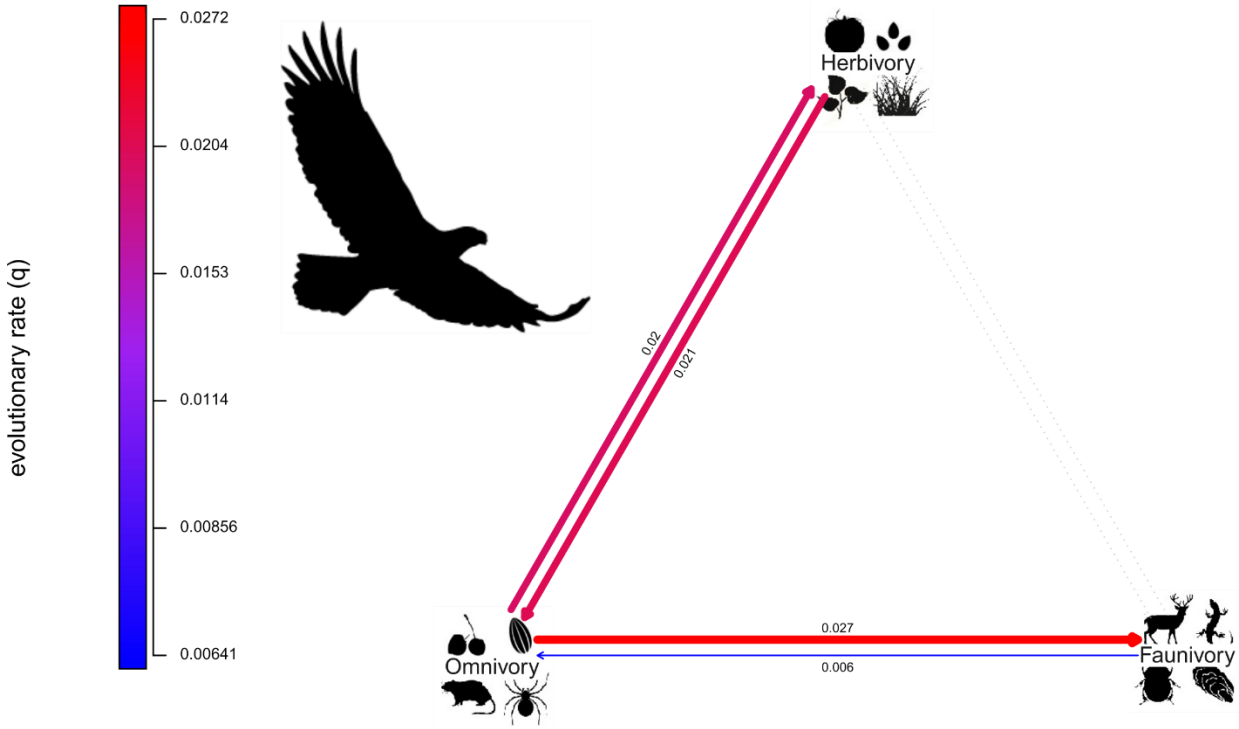


Figure 33: Evolutionary rates of transition between the classical dietary guilds in birds (topology of Ericson et al. 2006) as per the results of the Mk analysis ("fitMk" function), "all rates different" (ARD) model. Direction of arrows indicates "from state - to state".

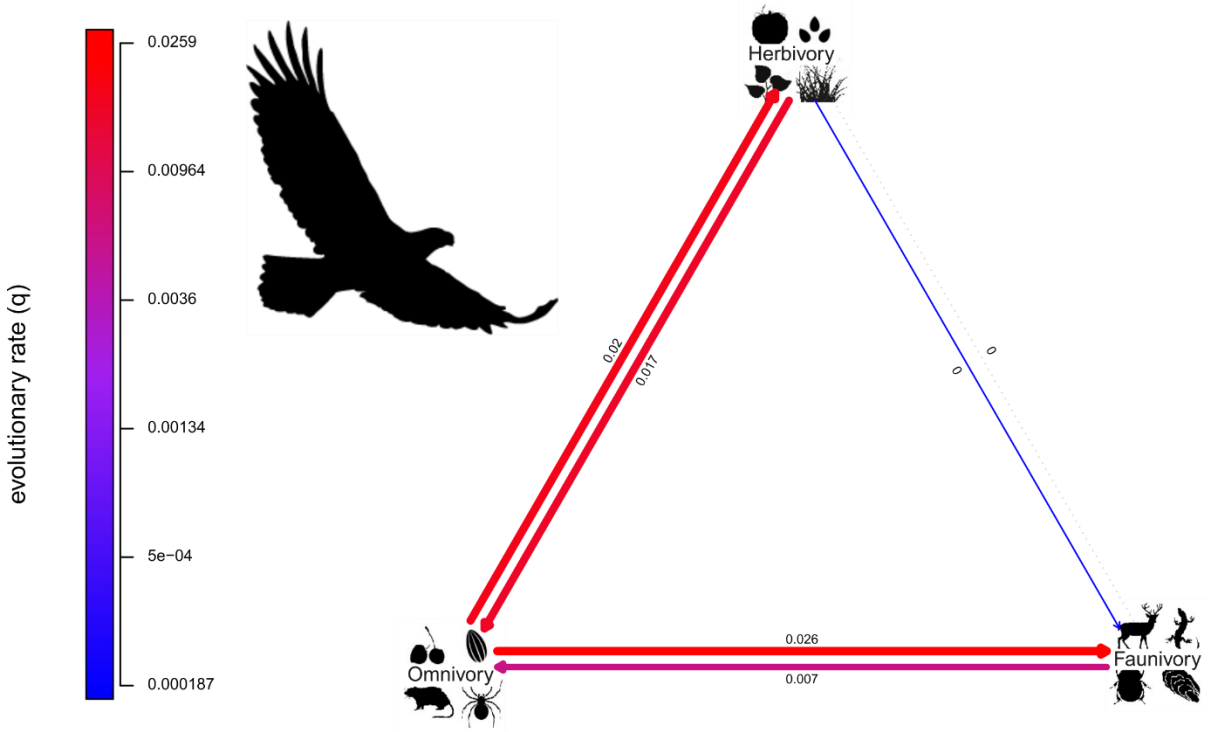


Figure 34: Evolutionary rates of transition between the classical dietary guilds in birds (topology of Hackett et al. 2008) as per the results of the Mk analysis ("fitMk" function), "all rates different" (ARD) model. Direction of arrows indicates "from state - to state".

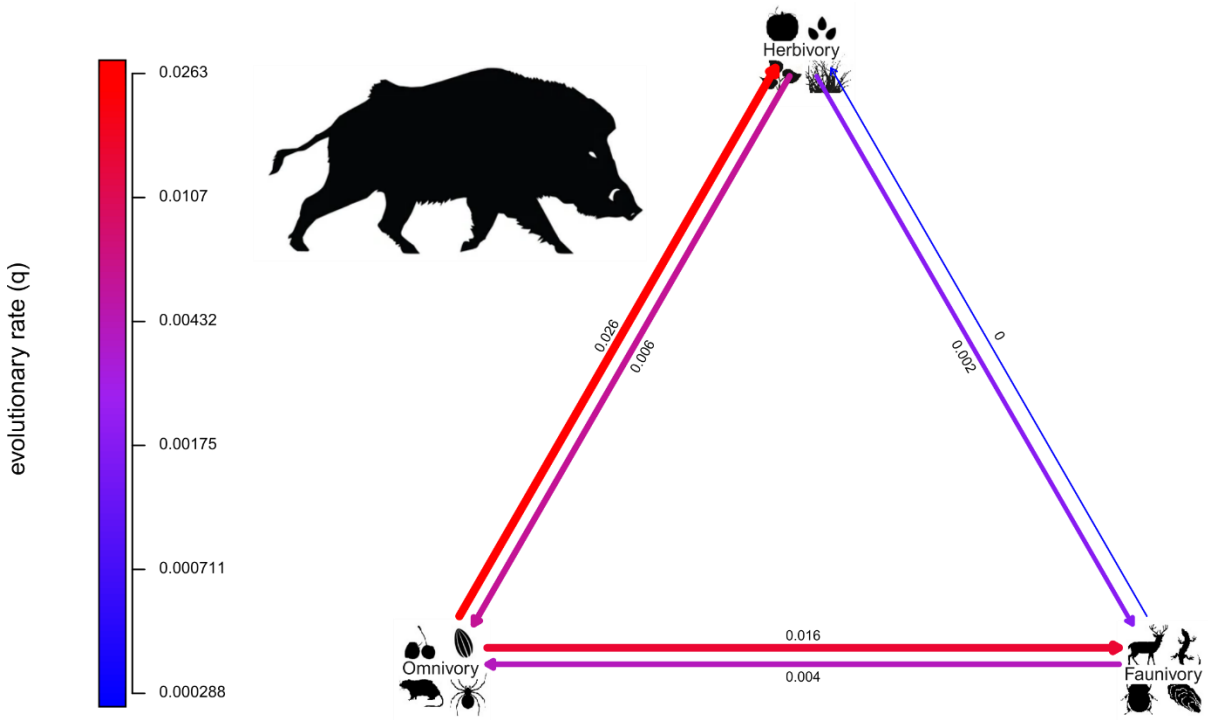


Figure 35: Evolutionary rates of transition between the classical dietary guilds in mammals (tip-dating backbone topology) as per the results of the Mk analysis ("fitMk" function), "all rates different" (ARD) model. Direction of arrows indicates "from state - to state".

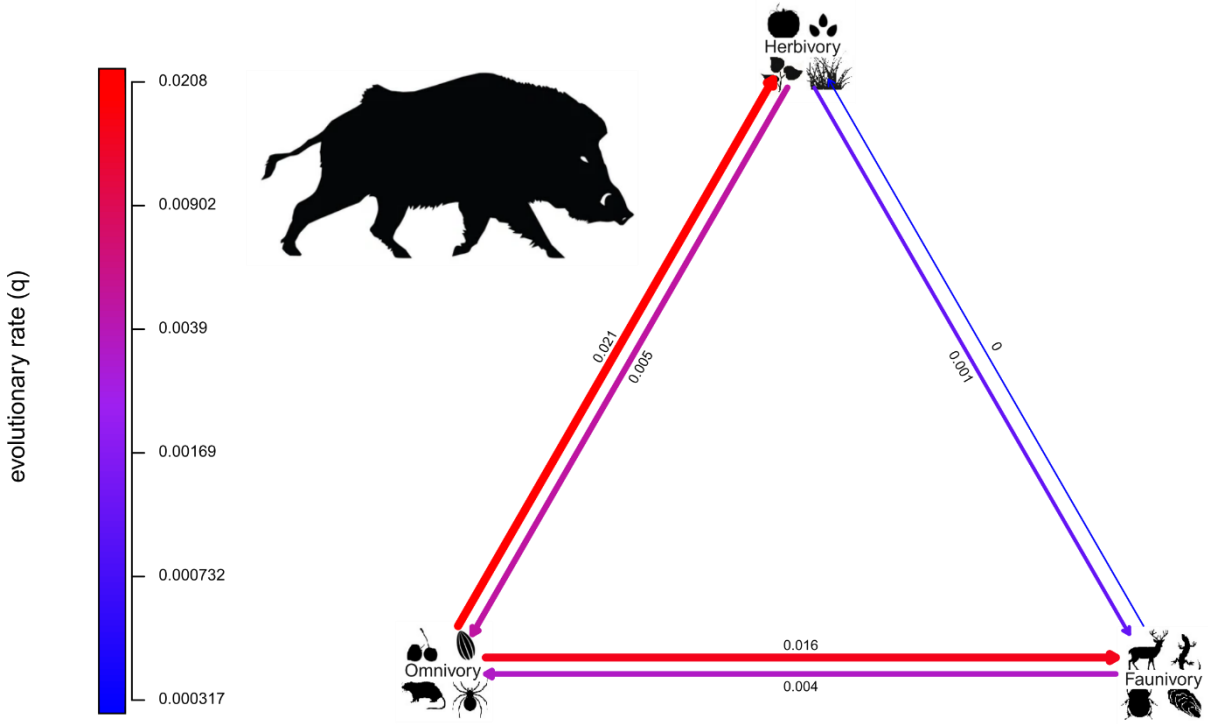


Figure 36: Evolutionary rates of transition between the classical dietary guilds in mammals (node-dating backbone topology) as per the results of the Mk analysis ("fitMk" function), "all rates different" (ARD) model. Direction of arrows indicates "from state - to state".

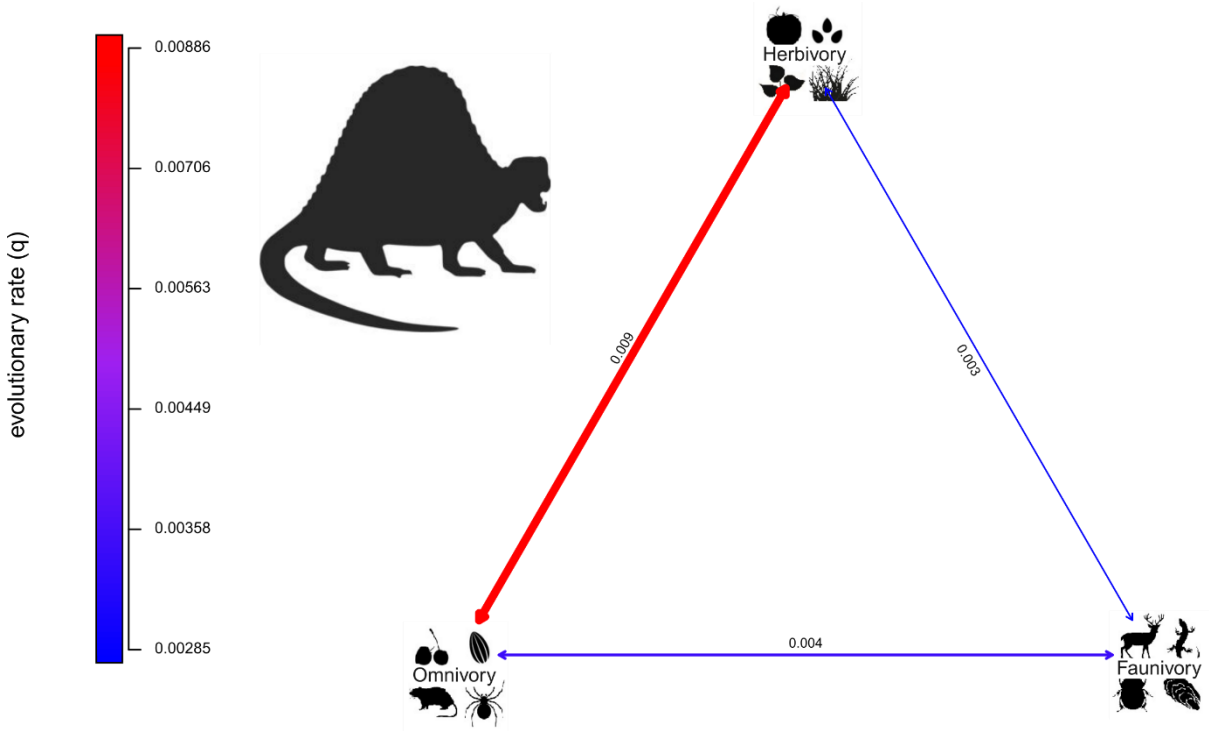


Figure 37: Evolutionary rates of transition between the classical dietary guilds in non-mammalian synapsids as per the results of the Mk analysis ("fitMk" function), "all rates different" (ARD) model. Direction of arrows indicates "from state - to state".

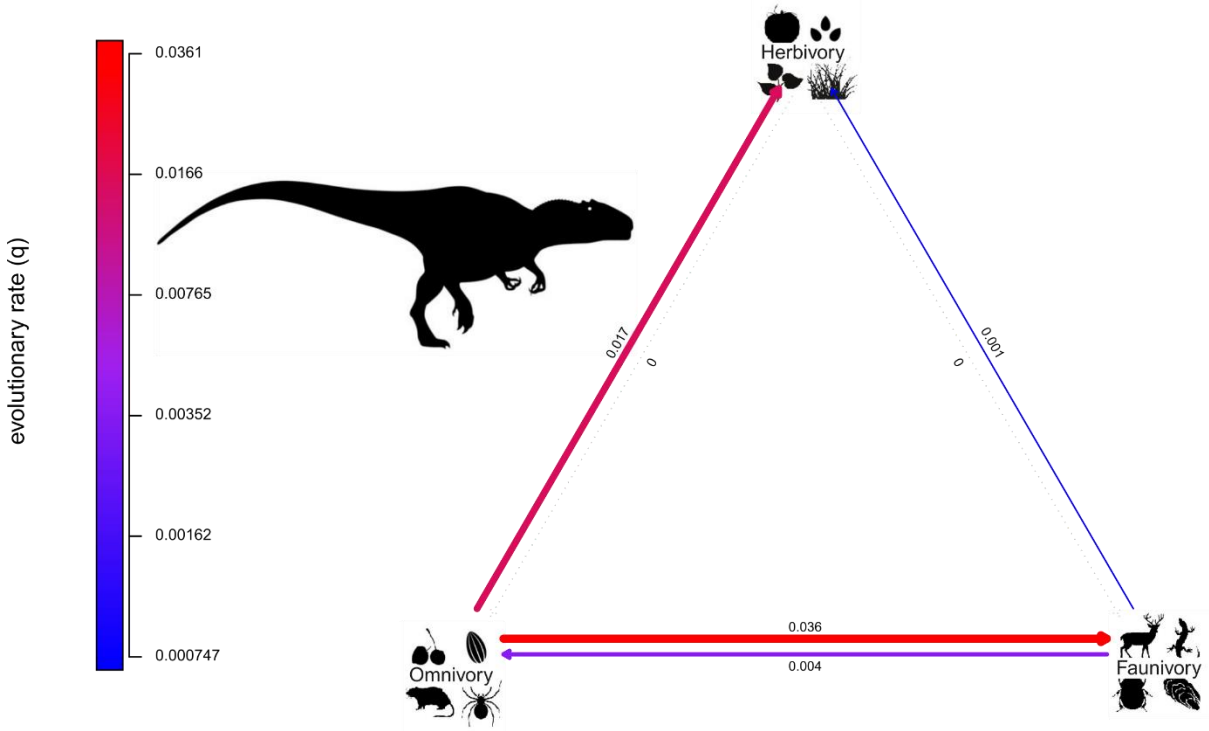


Figure 38: Evolutionary rates of transition between the classical dietary guilds in non-avian theropods as per the results of the Mk analysis ("fitMk" function), "all rates different" (ARD) model. Direction of arrows indicates "from state - to state".

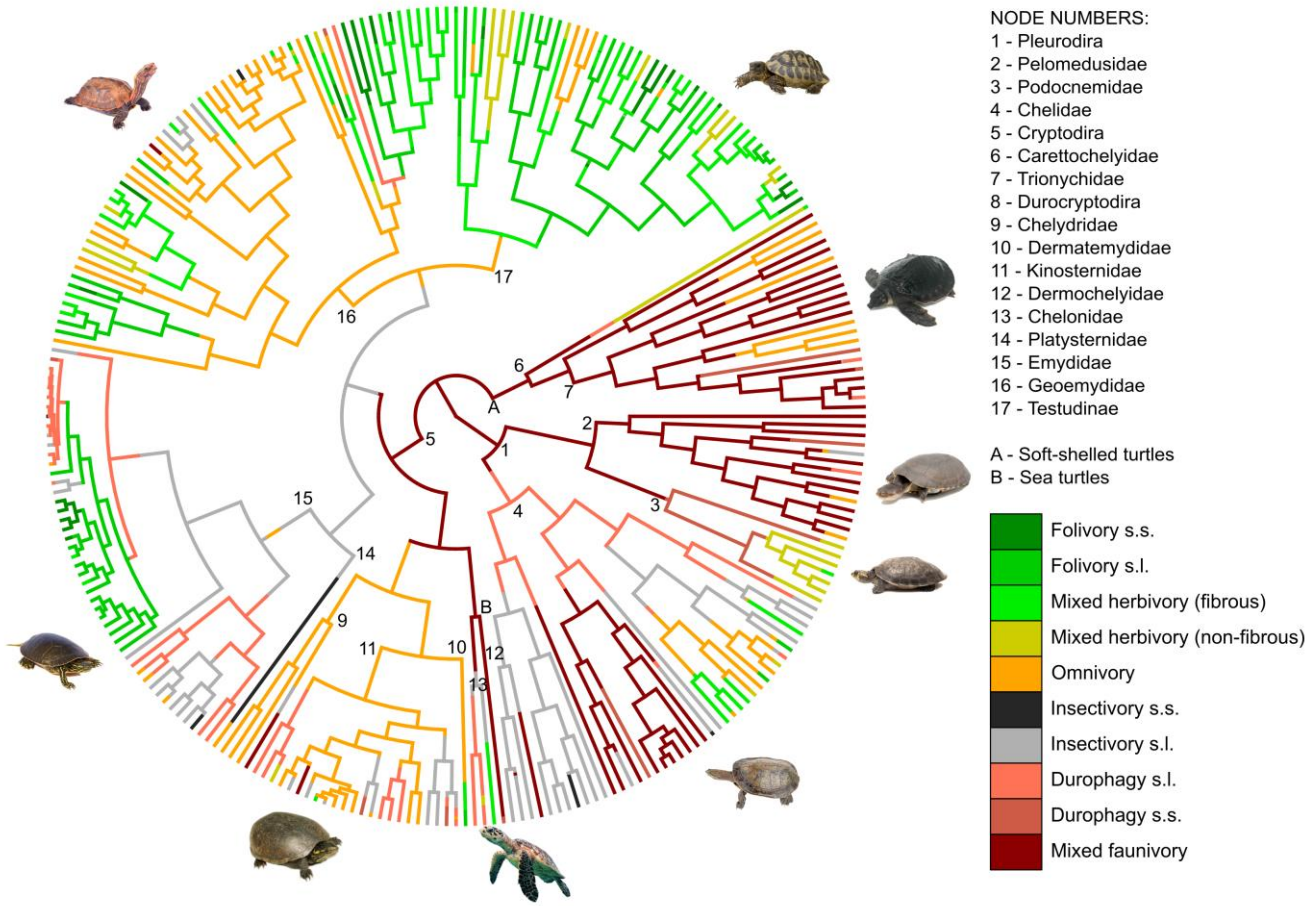


Figure 39: Turtle phylogeny (Thomson et al. 2021) with branches coloured by the dietary guild (recovered in the k-means cluster analysis) with the highest probability of representing the ancestral condition at each node, taken from a single random simulation of stochastic character mapping analysis conducted for the purposes of visualization ("symmetrical" model - SYM).

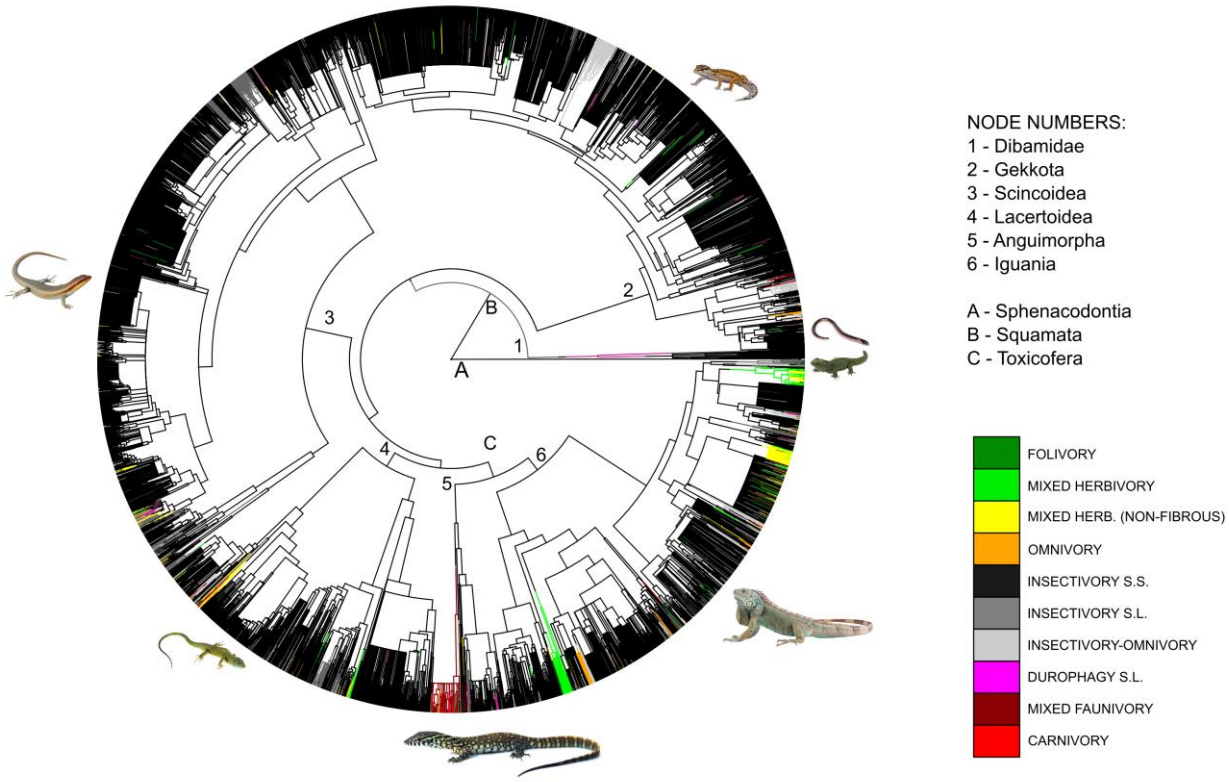


Figure 40: Lizard phylogeny (Tonini et al. 2016) with branches coloured by the dietary guild (recovered in the k-means cluster analysis) with the highest probability of representing the ancestral condition at each node, taken from a single random simulation of stochastic character mapping analysis conducted for the purposes of visualization ("all rates different" model - ARD).

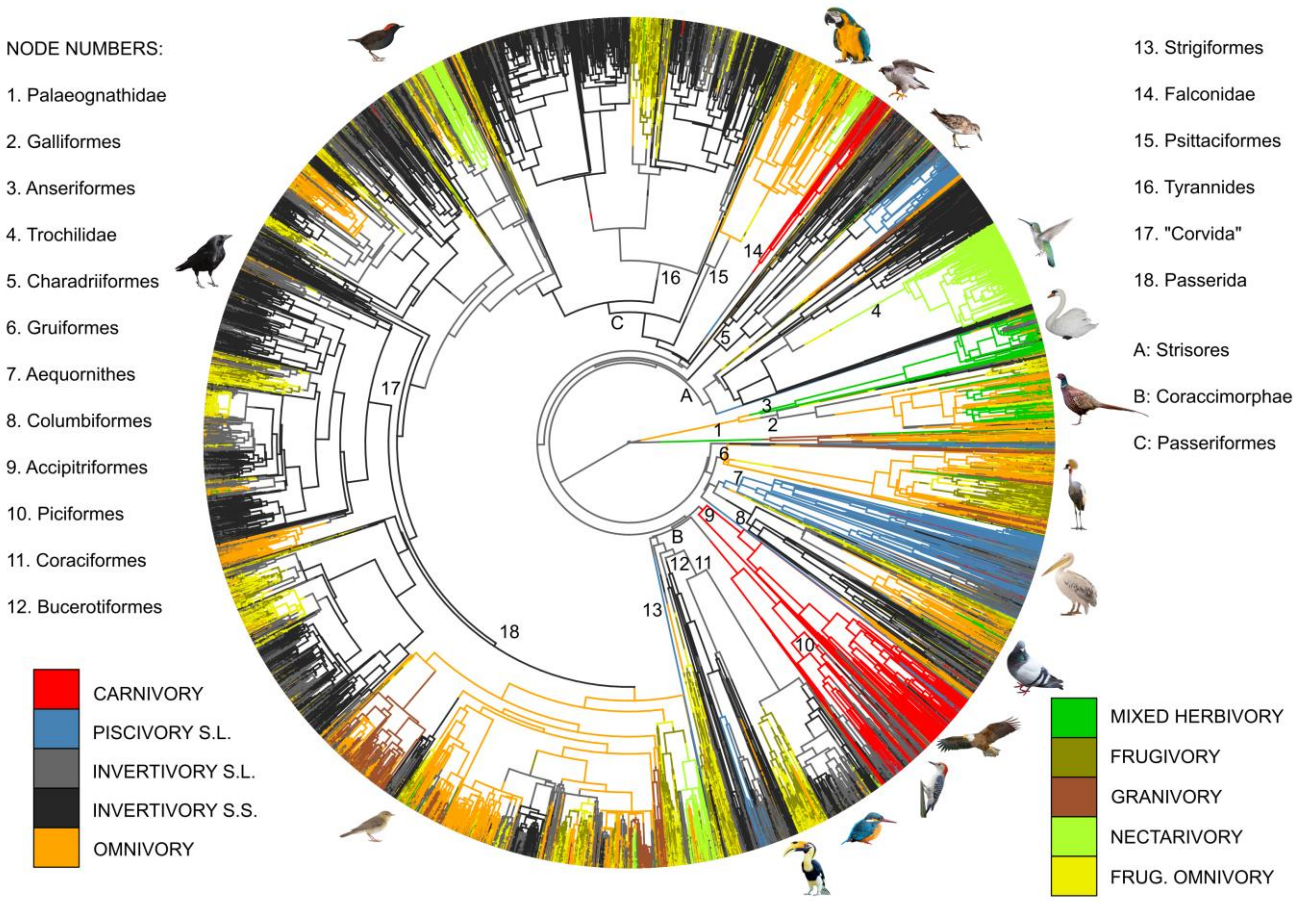


Figure 41: Bird phylogeny (Hackett et al. 2008) with branches coloured by the dietary guild (recovered in the k-means cluster analysis) with the highest probability of representing the ancestral condition at each node, taken from a single random simulation of stochastic character mapping analysis conducted for the purposes of visualization ("symmetrical" model - SYM).

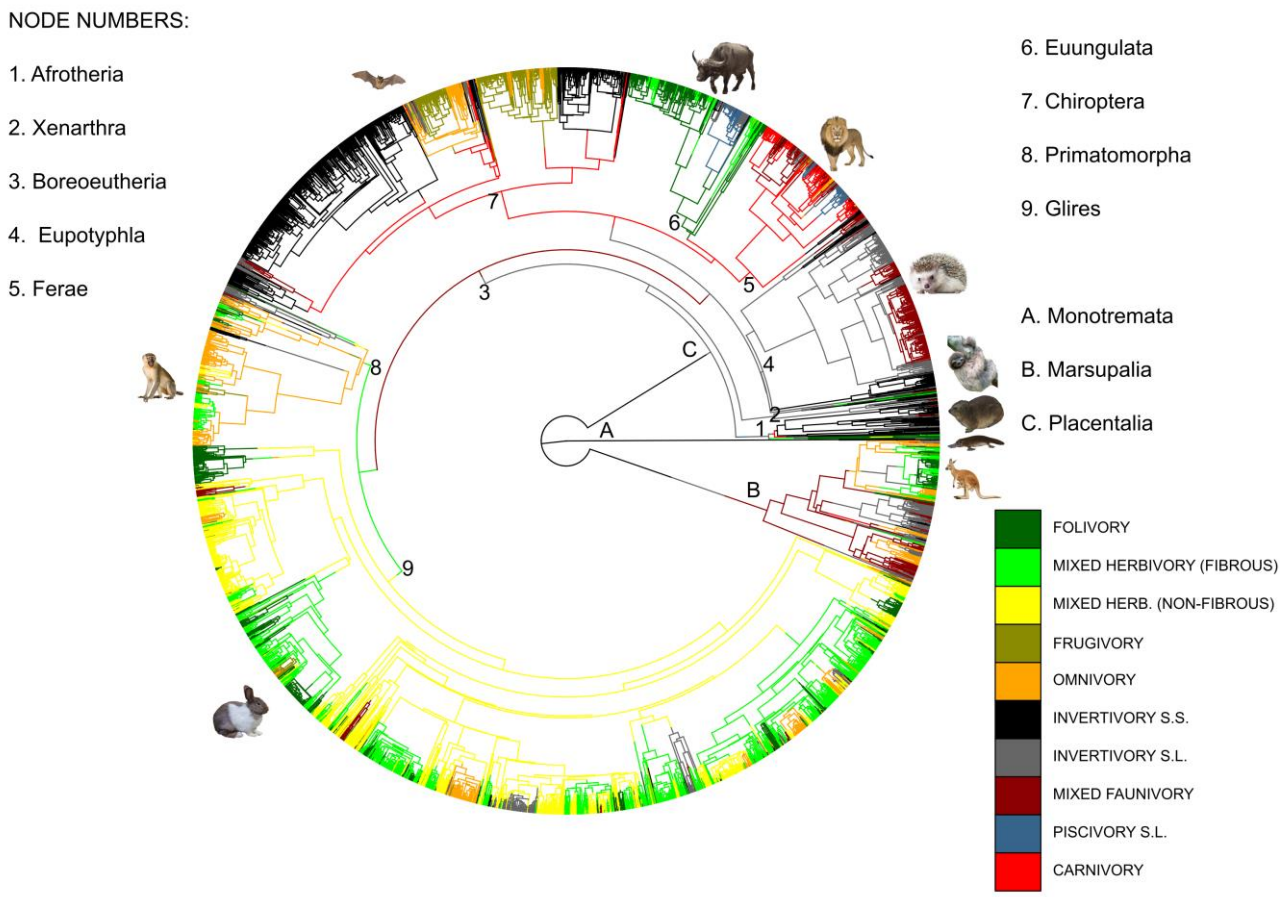


Figure 42: Mammal phylogeny (node-dating backbone topology; Upham et al. 2019) with branches coloured by the dietary guild (recovered in the k-means cluster analysis) with the highest probability of representing the ancestral condition at each node, taken from a single random simulation of stochastic character mapping analysis conducted for the purposes of visualization ("all rates different" model - ARD).

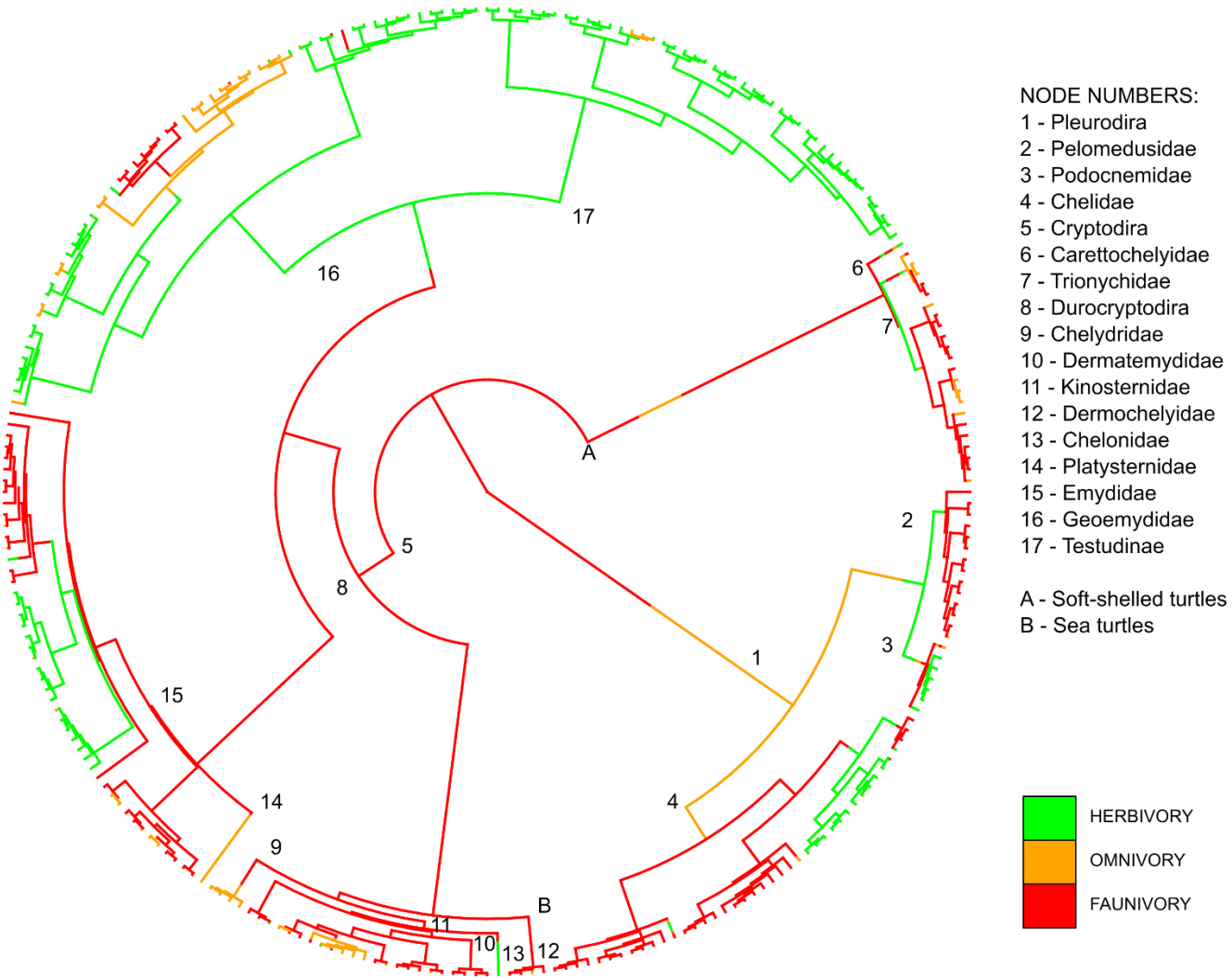


Figure 43: Turtle phylogeny (Thomson et al. 2021) with branches coloured by the classical dietary guild with the highest probability of representing the ancestral condition at each node, taken from a single random simulation of the stochastic character mapping analysis ("symmetrical" model - SYM).

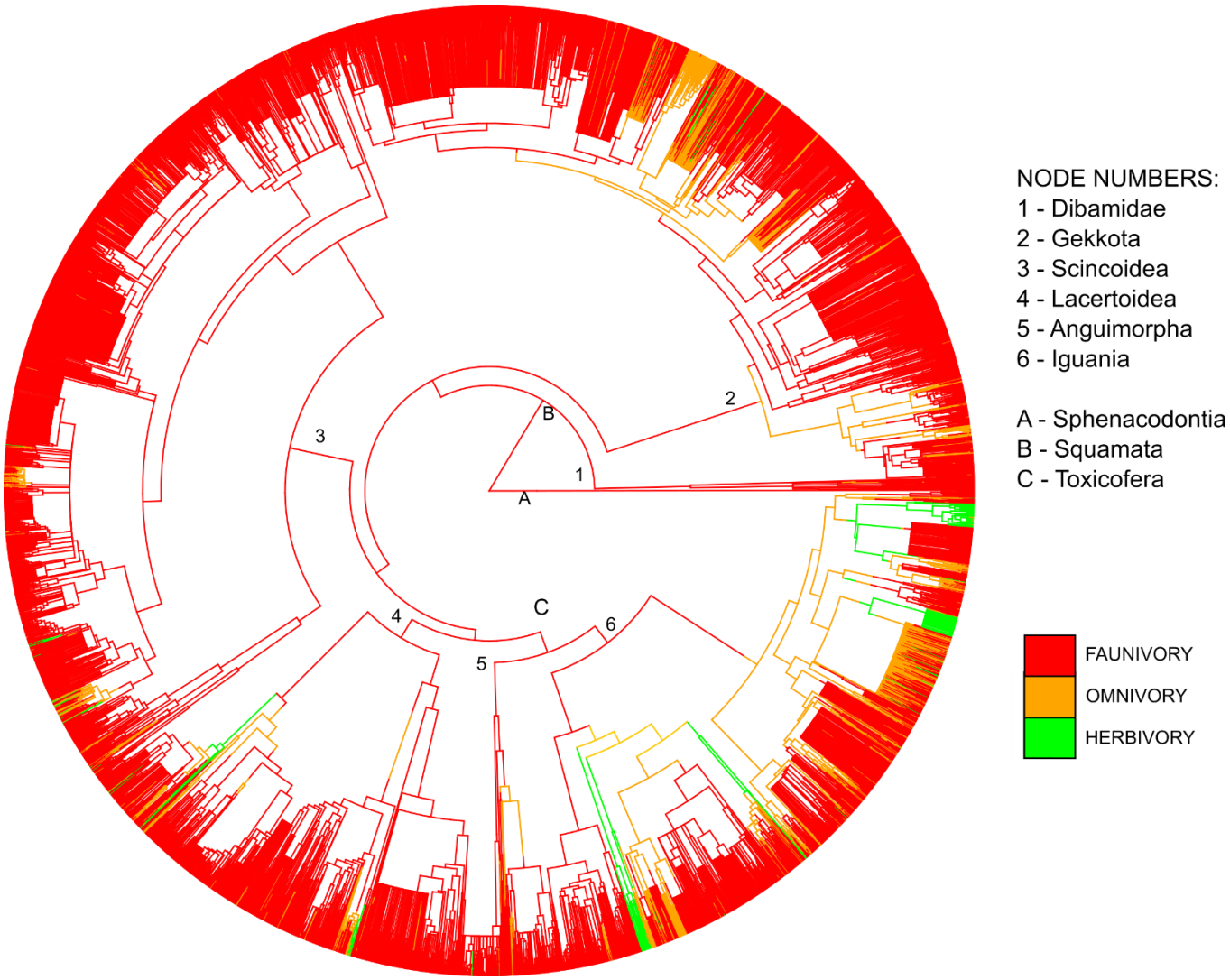


Figure 44: Lizard phylogeny (Tonini et al. 2016) with branches coloured by the classical dietary guild with the highest probability of representing the ancestral condition at each node, taken from a single random simulation of the stochastic character mapping analysis ("all rates different" model - ARD).

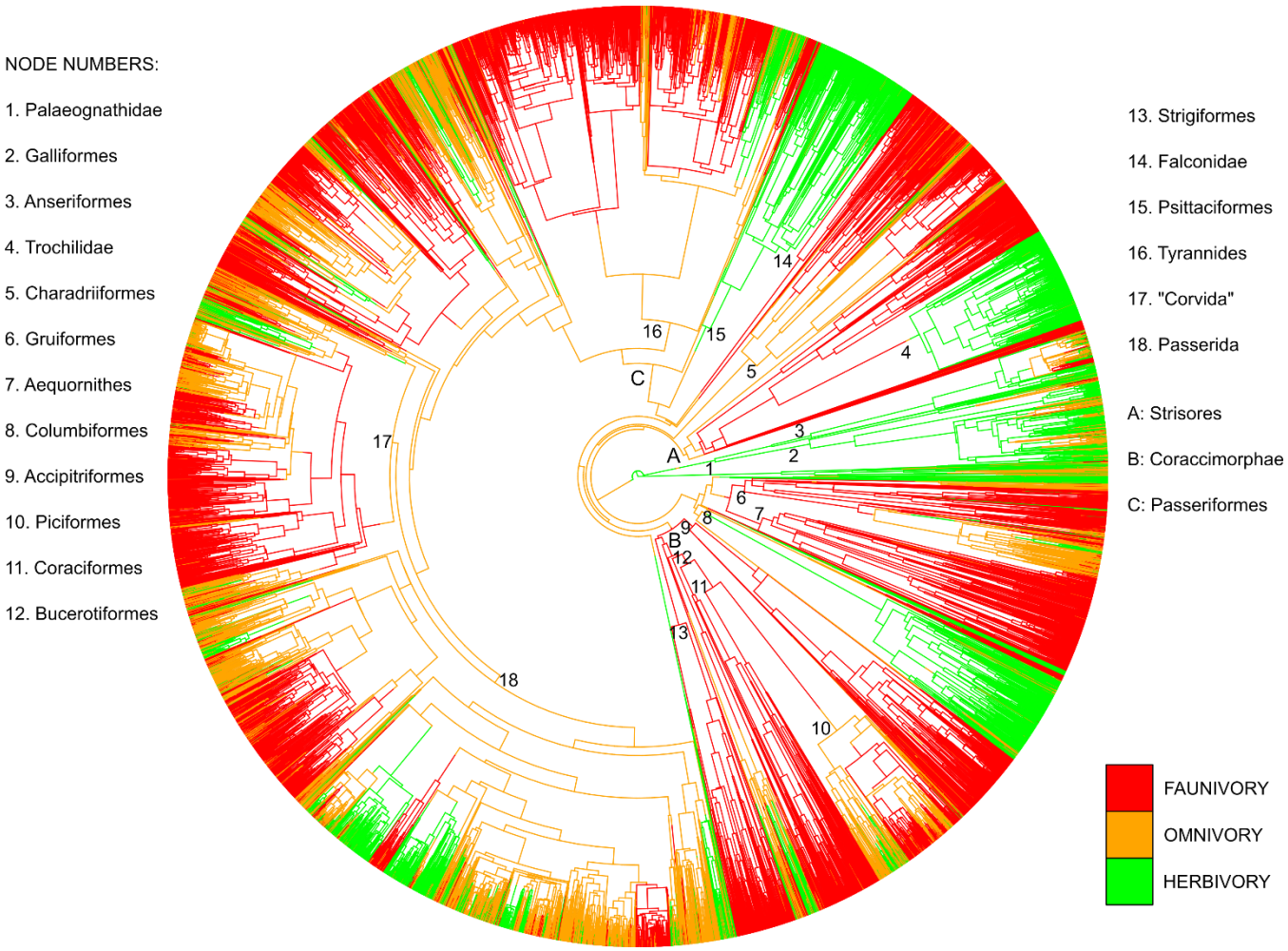


Figure 45: Bird phylogeny (Hackett et al. 2008) with branches coloured by the classical dietary guild the highest probability of representing the ancestral condition at each node, taken from a single random simulation of the stochastic character mapping analysis ("all rates different" model - ARD).

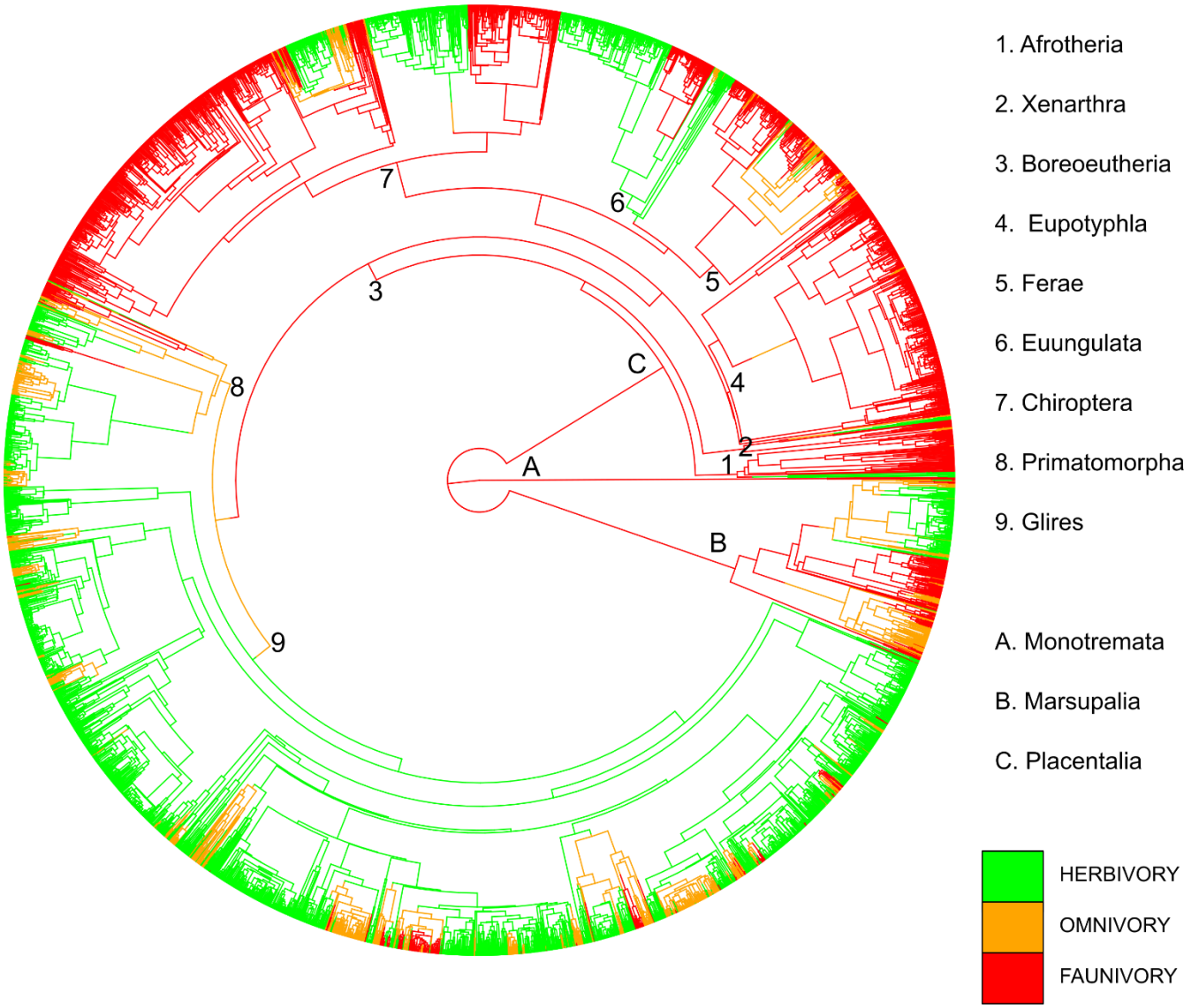


Figure 46: Mammal phylogeny (node-dating backbone topology; Upham et al. 2019) with branches coloured by the classical dietary guild with the highest probability of representing the ancestral condition at each node, taken from a single random simulation of the stochastic character mapping analysis ("all rates different" model - ARD).

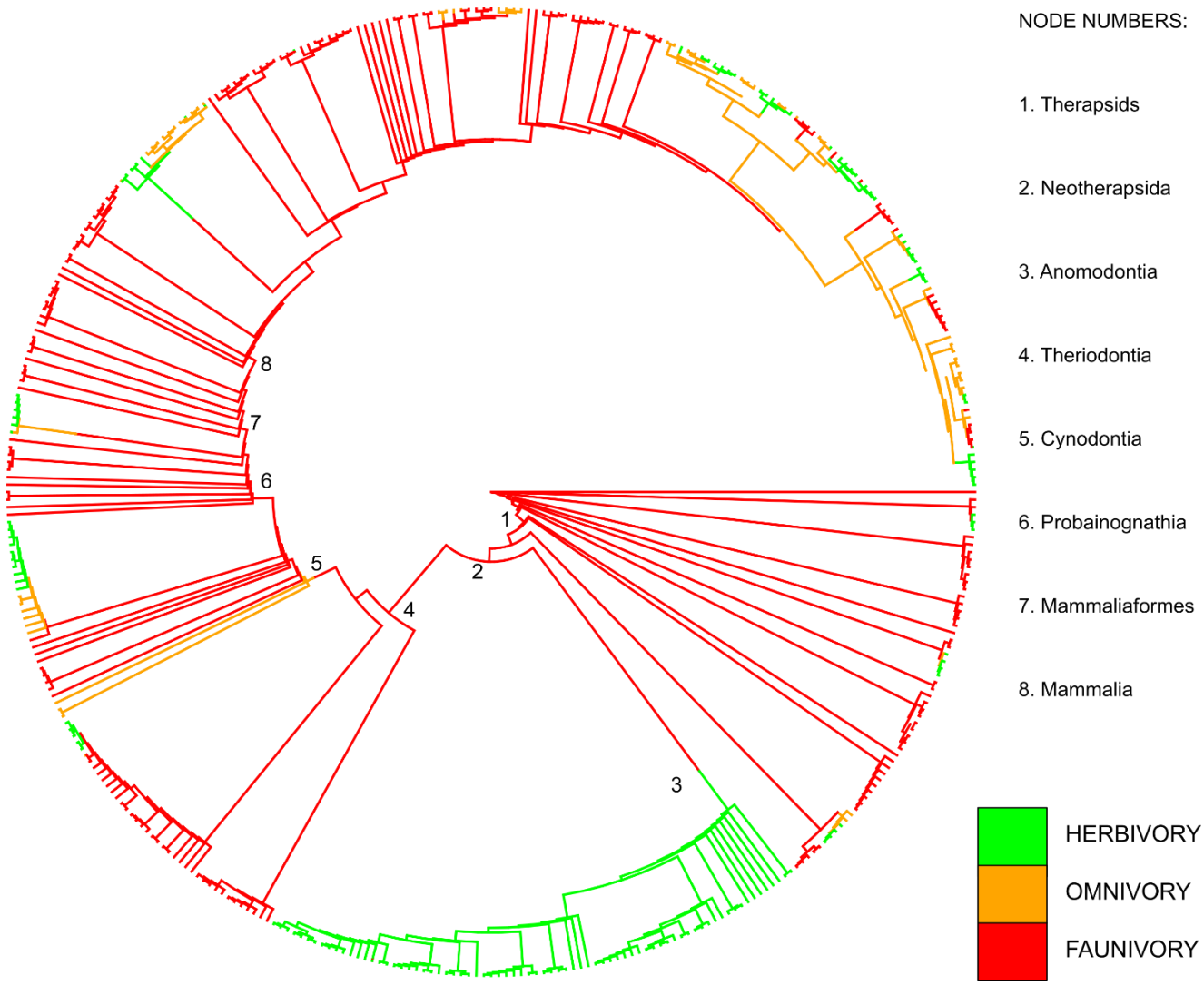


Figure 47: Synapsid phylogeny (Hellert et al. 2022) with branches coloured by the classical dietary guild with the highest probability of representing the ancestral condition at each node, taken from a single random simulation of the stochastic character mapping analysis ("all rates different" model - ARD).

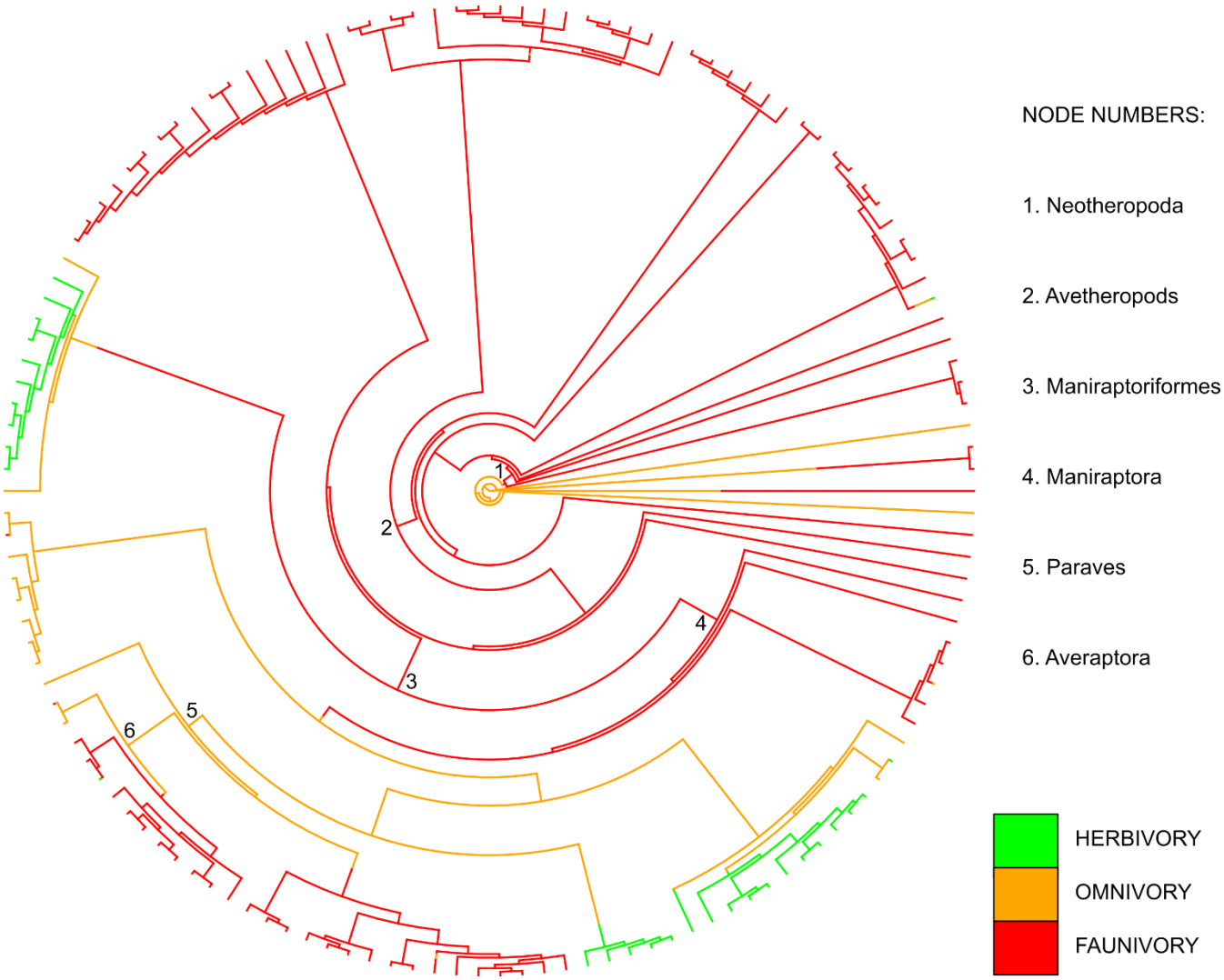


Figure 48: Theropod phylogeny (Benson et al. 2018) with branches coloured by the classical dietary guild with the highest probability of representing the ancestral condition at each node, taken from a single random simulation of the stochastic character mapping analysis ("all rates different" model - ARD).

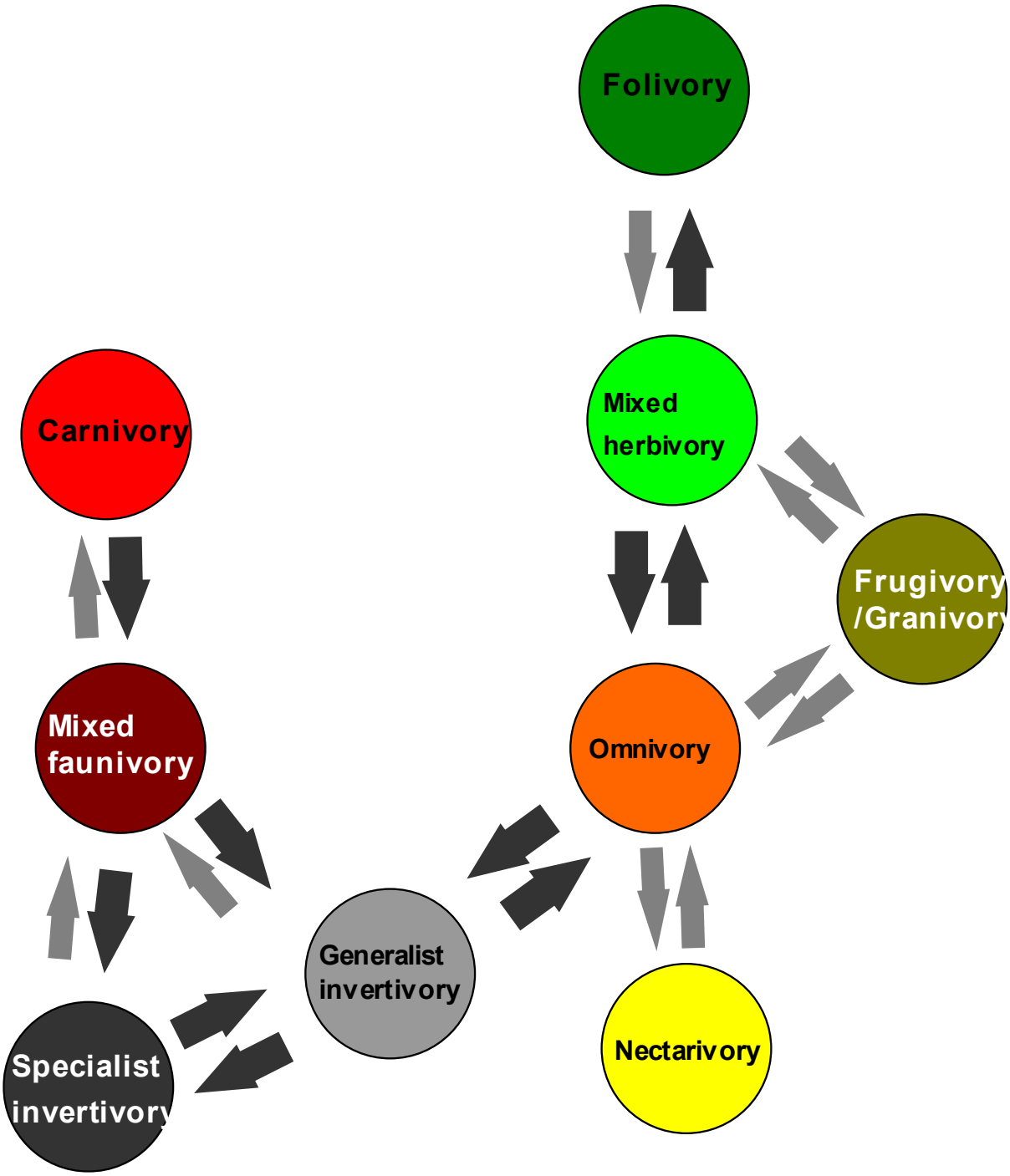


Figure 49: Simplified schematic overview of the pattern of dietary evolution proposed in this study. Darker, thicker arrows indicate higher transition rates; lighter, thinner arrows indicate lower transition rates. The arrow weighting is an approximation across all four major amniote lineages in this study (turtles, lizards, birds, and mammals) and does not represent a set of real numerical values.

7. Tables

Table 32: Summary of key findings from selected studies analysing evolutionary transitions between dietary strategies.

Lineage	Dietary Guilds	Key findings	Additional notes	Reference
Emydid turtles	"Specialist" (more than 90% animal or plant matter); "Generalist" (less than 90% animal or plant matter)	At least double the number of transitions from generalist to specialist than the inverse.	Dietary shifts often co-occur with changes in habitat.	Stephen and Wiens 2003
Lacertid lizards	"Insectivorous" (diet exclusively consists of arthropod and other animal material); "Herbivorous" (any intentional consumption of plant material)	Almost double the number of evolutionary shifts from insectivory to herbivory than the inverse.	Dietary shifts often co-occur with changes in habitat, specifically between island and mainland habitats.	Van Damme 1999
Liolaemid	"Insectivore" (diet consists of <10% plant matter); "Omnivore" (diet consists of 10-50% plant matter); "Herbivore" (diet consists of >70% plant matter)	The clade is ancestrally insectivorous. Herbivory evolves independently multiple times, often via an omnivorous transitional stage.	Herbivory evolves at a much faster rate in liolaemid lizards than in other squamates, and is not associated with changes in body size.	Espinoza et al. 2004

Liolaemid lizards	"Insectivory" (diet consists of <10% plant matter); "Omnivory" (diet consists of 10-75% plant matter); "Herbivory" (diet consists of >75% plant matter)	The clade is ancestrally insectivorous. Herbivory evolves independently multiple times, often via an omnivorous transitional stage.	There are high transition rates out of omnivory into the more specialist guilds and vice versa. This contradicts the idea that omnivory is an "evolutionary sink" (Price et al. 2012; Burin et al. 2016).	Ocampo et al. 2022
Anseriform	"Herbivory index" (percentage of diet composed of plant matter as a continuous trait)	Five independent origins of herbivory (diet consisting of >80% plant material) in Anseriformes.	Corrected for the effects of phylogeny, there is no relationship between herbivory and body size.	Olsen 2015
Birds	"Omnivore" (no dietary item constituted more than 50% of the animal's diet; all other guilds were assigned if a given dietary item accounted for over 50% of the animal's diet); "Carnivory" (vertebrate carrion >50%); "Frugivory" (fruit >50%); "Granivory" (seed >50%); "Herbivory" (vegetative plant material >50%); "Insectivory" (invertebrates >50%); "Nectarivory" (nectar >50%); "Piscivory" (fish >50%)	Transition rates into omnivory were higher than out of the guild in all directions.	Omnivory is an "evolutionary sink" with low speciation and high extinction rates. Complimenting the results of Price et al. (2012) for mammals.	Burin et al. 2016
Phyllostomid bats	"Frugivory" (diet "mostly" consists of fruit); "Animalivory" (diet "mostly" consists of animal flesh); "Nectarivory" (diet "mostly" consists of nectar); "Sanguivory" (diet "mostly" consists of animal blood)	The clade is ancestrally animalivorous. Sanguivory, frugivory and nectarivory evolve from animalivorous ancestors. Nectarivory and frugivory evolve together.	Study primarily investigating relationship between dietary and morphometric data, rather than evolutionary transitions.	Monteiro and Nogueira 2011

Phyllostomid bats	"Frugivory" (diet "mostly" consists of fruit); "Insectivory" (diet "mostly" consists of insects); "Carnivory" (diet "mostly" consists of vertebrate carrion); "Nectarivory" (diet "mostly" consists of nectar); "Sanguivory" (diet "mostly" consists of animal blood)	The clade is ancestrally Insectivorous. Carnivory, sanguivory, frugivory and nectarivory evolve from insectivorous ancestors. Nectarivory and frugivory evolve together.	Study primarily investigating relationship between dietary and morphometric data, rather than evolutionary transitions.	Monteiro and Nogueira 2011
Mammals	"Carnivore" (diet primarily consists of animal material); "Herbivore" (diet primarily consists of plant material); "Omnivore" (neither plant nor animal material is the dominant dietary item)	The clade is ancestrally carnivorous. Herbivory evolves independently multiple times via omnivory.	Omnivory is an "evolutionary sink" with low speciation and high extinction rates. Complimenting the results of Burin et al. (2016) for birds.	Price et al. 2012
Murid rodents	"Carnivore" (diet consists "almost entirely" of animal material); "Herbivore" (diet consists "almost entirely" of animal material); "Omnivore" (diet consists of a qualitative mix of plant and animal material)	The clade is ancestrally omnivorous (though with a carnivorous outgroup). Carnivory and herbivory evolve independently multiple times.	There is a relationship between evolutionary shifts in dietary strategy and habitat shifts.	Rowe et al. 2016
Marsupials	"Animalivory" (diet composed mostly of animal material); "Herbivory" (diet composed mostly of plant material); "Mycophagy" (diet composed mostly of fungi); "Omnivory" (no single dominant dietary item)	The clade is ancestrally animalivorous. Animalivory transitions directly into an ancestrally-herbivorous clade wherein omnivory and mycophagy evolve independently multiple times.	Mycophagy exclusively evolves from herbivory, while omnivory evolves from both herbivory and animalivory	Amador and Giannini 2021

Marsupials	"Insectivory" (diet composed mostly of arthropods); "Carnivory" (diet composed mostly of vertebrate carrion); "Grass herbivory" (diet composed mostly of grasses, rushes, forbs etc.); "Browse herbivory" (diet composed mostly of leaves); "Frugivory" (diet composed mostly of fruit); "Nectarivory" (diet composed mostly of nectar); "Exudivory" (diet composed mostly of exudates); "Granivory" (diet composed mostly of seeds); "Mycophagy" (diet composed mostly of fungi); "Omnivory" (no single dominant dietary item)	The clade is ancestrally insectivorous. Insectivory transitions directly into an ancestrally-(browse) herbivorous clade wherein omnivory and other non-animalivorous guilds evolve independently multiple times.	There were several evolutionary shifts towards carnivory as opposed to only one shift towards browse herbivory. Omnivory is typically a derived character trait.	Amador and Giannini 2021
Dinosaur				Barrett 1998

Table 33: AIC scores and weights for each Mk model (ER – "equal rates", SYM – "symmetrical rates", ARD – "all rates different") using guilds generated in the k-means cluster analysis as discrete characters.

Model	ER		SYM		ARD	
AIC	Score	Weight	Score	Weight	Score	Weight
Turtles	1019.45	0.0	987.87	1.0	1038.03	0.0
Lizards (Tonini et al. 2016)	6693.37	0.0	5804.45	0.0	4828.12	1.0
Lizards (Pyron et al. 2014)	4164.16	0.0	3624.03	0.0	3588.98	1.0
Birds (Ericson et al. 2006; Jetz et al. 2012)	27797.72	0.0	24989.58	0.0	23829.91	1.0
Birds (Hackett et al. 2008; Jetz et al. 2012)	27787.90	0.0	23353.45	1.0	24357.89	0.0
Mammals (tip-dating; Upham et al. 2019)	6986.78	0.0	6120.27	0.0	5994.28	1.0
Mammals (node-dating; Upham et al. 2019)	6914.05	0.0	6102.09	0.0	5981.49	1.0

Table 34: AIC scores and weights for each Mk model (ER – "equal rates", SYM – "symmetrical rates", ARD – "all rates different") using classical dietary guilds as discrete characters.

Model	ER	SYM	ARD

AIC	Score	Weight	Score	Weight	Score	Weight
Turtles (Thomson et al. 2021)	407.06	0.02	399.69	0.913	405.00	0.064
Lizards (Tonini et al. 2016)	2705.85	0.0	2537.51	1.0	3585.56	0.0
Lizards (Pyron et al. 2014)	1713.87	0.0	1599.20	0.0	1492.51	1.0
Birds (Ericson et al. 2006; Jetz et al. 2012)	11468.65	0.0	10427.80	0.0	9993.33	1.0
Birds (Hackett et al. 2008; Jetz et al. 2012)	11374.86	0.0	10348.61	0.0	10166.16	1.0
Mammals (tip-dating; Upham et al. 2019)	2527.41	0.0	2450.83	0.0	2379.08	1.0
Mammals (node-dating; Upham et al. 2019)	2523.26	0.0	2454.52	0.0	2389.57	1.0

Early-branching synapsids (Hellert et al. 2022)	370.77	0.232	368.38	0.768	390.56	0.0
Non-avian theropods (Benson et al. 2014)	154.52	0.045	149.81	0.477	149.81	0.477

Table 35: Transition rates between dietary guilds (k-means) in turtles using the "fitMk" function; "symmetrical" (SYM) model. Transition rates are from character state in the first column to the column headers. Key: 1 – folivory s.l., 2 – insectivory s.l., 3 – omnivory, 4 – durophag s.l., 5 – mixed herbivory (predominantly reproductive), 6 – durophagy s.s., 7 – folivory s.s., 8 – insectivory s.s., 9 – mixed herbivory (predominantly vegetative), 10 – mixed faunivory.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
1	NA	0,000	0,188	0,212	0,615	0,205	0,000	1,264	0,000	3,300
2	0,000	NA	0,369	0,547	0,309	0,000	0,340	0,000	0,026	0,000
3	0,188	0,369	NA	0,850	1,228	0,000	0,000	0,000	0,378	0,291
4	0,212	0,547	0,850	NA	0,676	0,160	0,080	0,000	0,103	1,030
5	0,615	0,309	1,228	0,676	NA	0,456	1,440	0,000	0,428	0,000

6	0,205	0,000	0,000	0,160	0,456	NA	0,251	0,200	0,000	1,233
7	0,000	0,340	0,000	0,080	1,440	0,251	NA	0,000	0,000	0,000
8	1,264	0,000	0,000	0,000	0,000	0,200	0,000	NA	0,000	1,514
9	0,000	0,026	0,378	0,103	0,428	0,000	0,000	0,000	NA	0,000
10	3,300	0,000	0,291	1,030	0,000	1,233	0,000	1,514	0,000	NA

Table 36: Transition rates between dietary guilds (k-means) in lizards (topology of Tonini et al. 2016) using the "fitMk" function; "all rates different" (ARD) model. Transition rates are from character state in the first column to the column headers. Key: 1 – mixed faunivory, 2 – insectivory s.s., 3 – insectivory s.l., 4 – durophagy s.l., 5 – carnivory, 6 – insectivory-omnivory, 7 – mixed herbivory (predominantly reproductive), 8 – omnivory, 9 – mixed herbivory (predominantly vegetative), 10 – folivory.

	1	**10**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	NA	0.000	0.002	0.002	0.001	0.003	0.000	0.001	0.000	0.001
10	0.004	NA	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
2	0.000	0.000	NA	0.001	0.000	0.000	0.001	0.000	0.000	0.000
3	0.001	0.000	0.003	NA	0.001	0.000	0.002	0.001	0.000	0.000
4	0.001	0.000	0.001	0.000	NA	0.000	0.001	0.001	0.000	0.001
5	0.000	0.000	0.000	0.000	0.000	NA	0.000	0.000	0.000	0.000

6	0.001	0.000	0.004	0.002	0.002	0.000	NA	0.002	0.003	0.001
7	0.000	0.001	0.001	0.000	0.000	0.001	0.001	NA	0.001	0.004
8	0.000	0.000	0.000	0.000	0.001	0.000	0.001	0.001	NA	0.000
9	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.002	0.001	NA

Table 37: Transition rates between dietary guilds (k-means) in lizards (topology of Pyron et al. 2014) in the sensitivity analysis using the "fitMk" function; "all rates different" (ARD) model. Transition rates are from character state in the first column to the column headers. Key: 1 – mixed faunivory, 2 – insectivory s.s., 3 – insectivory s.l., 4 – durophagy s.l., 5 – carnivory, 6 – insectivory-omnivory, 7 – mixed herbivory (predominantly reproductive), 8 – omnivory, 9 – mixed herbivory (predominantly vegetative), 10 – folivory.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
1	NA	0	0.005	0.007	0.003	0.006	0	0.002	0	0
2	0.001	NA	0	0	0	0	0	0	0	0
3	0	0	NA	0.002	0	0	0.002	0	0	0
4	0.002	0	0.008	NA	0.001	0	0.005	0	0	0
5	0.001	0.001	0.003	0.002	NA	0	0.003	0.003	0	0.003
6	0.001	0	0.001	0.001	0	NA	0	0	0	0

7	0.001	0	0.011	0.005	0	0	NA	0.001	0.005	0.001
8	0.002	0.001	0.002	0.001	0.001	0	0	NA	0.002	0.017
9	0	0.001	0.002	0.002	0.002	0	0.003	0.003	NA	0
10	0	0.003	0.002	0.003	0.001	0	0.002	0.005	0.004	NA

Table 38: Transition rates between dietary guilds (k-means) in birds (backbone topology of Ericson et al. 2006) using the "fitMk" function; "all rates different" (ARD) model. Transition rates are from character state in the first column to the column headers. Key: 1 – frugivory, 2 – frugivory-omnivory, 3 – nectarivory, 4 – omnivory, 5 – piscivory s.l., 6 – invertivory s.s., 7 – carnivory, 8 – mixed herbivory (predominantly vegetative), 9 – granivory, 10 – invertivory s.l.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
1	NA	0,228	0,073	0,000	0,000	0,000	0,076	0,000	0,000	0,000
2	0,000	NA	0,012	0,000	0,008	0,000	0,255	0,001	0,000	0,000
3	0,039	0,009	NA	0,001	0,063	0,000	0,000	0,000	0,000	0,000
4	0,000	0,007	0,013	NA	0,006	0,000	0,001	0,000	0,003	0,000
5	0,003	0,020	0,036	0,002	NA	0,000	0,001	0,000	0,010	0,092
6	0,000	0,056	0,000	0,000	0,002	NA	0,000	0,003	0,000	0,000
7	0,000	0,216	0,000	0,000	0,000	0,000	NA	0,000	0,000	0,000
8	0,000	0,023	0,000	0,000	0,001	0,010	0,000	NA	0,000	0,000
9	0,000	0,030	0,012	0,000	0,055	0,000	0,006	0,000	NA	0,000
10	0,000	0,004	0,012	0,000	0,095	0,000	0,001	0,000	0,006	NA

Table 39: Transition rates between dietary guilds (k-means) in birds (backbone topology of Hackett et al. 2008) using the "fitMk" function; "symmetrical" (SYM) model. Transition rates are from character state in the first column to the column headers. Key: 1 – frugivory, 2 – frugivory-omnivory, 3 – nectarivory, 4 – omnivory, 5 – piscivory s.l., 6 – invertivory s.s., 7 – carnivory, 8 – mixed herbivory (predominantly vegetative), 9 – granivory, 10 – invertivory s.l.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	NA	0.000	0.000	0.000	0.008	0.000	0.000	0.014	0.000
2	0.000	NA	0.046	0.000	0.000	0.000	0.000	0.004	0.104
3	0.000	0.099	NA	0.000	0.000	0.000	0.000	0.004	0.023
4	0.000	0.000	0.000	NA	0.000	0.000	0.000	0.000	0.336
5	0.003	0.000	0.000	0.000	NA	0.000	0.000	0.023	0.002
6	0.000	0.000	0.000	0.000	0.001	NA	0.000	0.338	0.000
7	0.001	0.000	0.056	0.000	0.000	0.000	NA	0.000	0.001
8	0.001	0.000	0.000	0.002	0.000	0.499	0.000	NA	0.033
9	0.001	0.000	0.007	0.219	0.000	0.067	0.005	0.011	NA

Table 40: Transition rates between dietary guilds (k-means) in mammals (tip-dating backbone topology) using the "fitMk" function; "all rates different" (ARD) model. Transition rates are from character state in the first column to the column headers. Key: 1 – mixed faunivory, 2 – invertivory s.l., 3 – folivory, 4 – mixed herbivory (predominantly reproductive), 5 – piscivory s.l., 6 – mixed herbivory (predominantly vegetative), 7 – omnivory, 8 – carnivory, 9 – invertivory s.s., 10 – frugivory.

	1		**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
1	NA		0.000	0.017	0.001	0.001	0.000	0.001	0.006	0.006	0.002
2	0.000		NA	0.001	0.000	0.001	0.000	0.000	0.027	0.000	0.001

3	0.012		0.000	NA	0.000	0.000	0.001	0.000	0.000	0.001	0.008
4	0.000		0.000	0.000	NA	0.000	0.000	0.022	0.000	0.000	0.000
5	0.001		0.001	0.006	0.005	NA	0.000	0.013	0.003	0.000	0.001
6	0.006		0.000	0.048	0.000	0.000	NA	0.000	0.000	0.000	0.013
7	0.001		0.003	0.001	0.016	0.016	0.000	NA	0.007	0.000	0.002
8	0.000		0.006	0.010	0.002	0.011	0.000	0.006	NA	0.002	0.002
9	0.049		0.005	0.000	0.003	0.000	0.009	0.003	0.009	NA	0.022
10	0.000		0.000	0.007	0.000	0.000	0.000	0.000	0.000	0.000	NA

Table 41: Transition rates between dietary guilds (k-means) in mammals (node-dating backbone topology) using the "fitMk" function; "all rates different" (ARD) model. Transition rates are from character state in the first column to the column headers. Key: 1 – mixed faunivory, 2 – invertivory s.l., 3 – folivory, 4 – mixed herbivory (predominantly reproductive), 5 – piscivory s.l., 6 – mixed herbivory (predominantly vegetative), 7 – omnivory, 8 – carnivory, 9 – invertivory s.s., 10 – frugivory.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
1	NA	0.000	0.014	0.000	0.001	0.000	0.001	0.006	0.003	0.001
2	0.000	NA	0.000	0.000	0.000	0.000	0.000	0.019	0.000	0.000
3	0.011	0.000	NA	0.000	0.001	0.001	0.001	0.000	0.001	0.008
4	0.000	0.000	0.000	NA	0.001	0.000	0.016	0.000	0.000	0.000
5	0.001	0.001	0.004	0.003	NA	0.000	0.011	0.003	0.000	0.001
6	0.004	0.000	0.043	0.000	0.000	NA	0.000	0.000	0.000	0.009
7	0.001	0.002	0.001	0.014	0.009	0.000	NA	0.005	0.000	0.001
8	0.000	0.005	0.010	0.001	0.008	0.000	0.005	NA	0.002	0.002
9	0.046	0.004	0.000	0.003	0.000	0.008	0.002	0.006	NA	0.013
10	0.000	0.000	0.007	0.000	0.000	0.000	0.000	0.000	0.000	NA

Table 42: Transition rates ("fitMk" function) between classical dietary guilds in all major amniote lineages included in the current study. The brackets indicate the best-fitting model (SYM – "symmetrical" model, ARD – "all rates different" model) based on AIC weights. Key: F – faunivory, O – omnivory, H – herbivory.

	Turtles (SYM)	**Lizards - Tonini (SYM)**	**Lizards - Pyron (ARD)**	**Birds - Ericson (ARD)**	**Birds - Hackett (ARD)**	**Mammals - TD (ARD)**	**Mammals - ND (ARD)**	**Synapsids (SYM)**	**Theropods (ARD)**
F>H	6.270	0.000	0.055	0.000	0.000	0.000	0.000	0.003	0.001
H>F	6.270	0.000	0.000	0.000	0.000	0.002	0.001	0.003	0.000
F>O	19.881	0.002	0.534	0.006	0.007	0.004	0.004	0.004	0.004
O>F	19.881	0.002	8.782	0.027	0.026	0.016	0.016	0.004	0.036
H>O	19.775	0.006	6.732	0.021	0.017	0.006	0.005	0.009	0.000
O>H	19.775	0.006	0.945	0.020	0.020	0.026	0.021	0.009	0.017

CHAPTER THREE

1. Introduction

Researchers have long noted a conspicuous association between diet and body size in amniotes (Benavidez et al., 2018; Byrne, 1940; Clauss et al., 2003; M. Clauss et al., 2013; Colbert, 1949; Rob Cooke et al., 2022; Demment & Van Soest, 1985; Jenkins, 1981). Scientific inquiries have proposed optimal body size ranges for different dietary guilds (Case, 1979; Price & Hopkins, 2015). Furthermore, body size is often presented as a predictor of diet along with, or alongside, other ecological variables such as habitat use (Mittelbach, 1981), home range size (Gittleman & Harvey, 1982; McNab, 1963; Perry & Garland Jr, 2002; Slavenko et al., 2016; Tucker et al., 2014), population abundance and density (LaBarbera, 1989; White et al., 2007), and locomotory style (Lintulaakso & Kovarovic, 2016; Warren & Crompton, 1998). Several studies have attempted to investigate this relationship from an ecophysiological (Belovsky, 1997; Carbone et al., 1999; Case, 1979; Clauss et al., 2007; M. Clauss et al., 2013; Franz et al., 2011; Fritz et al., 2012; Pough, 1973; Sander et al., 2011), and evolutionary (Espinoza et al., 2004; Meiri, 2008; Olsen, 2015; Price & Hopkins, 2015; Zanno & Makovicky, 2013) perspective.

The current scientific consensus holds that that folivores (diet composed primarily of vegetative plant material) and hypercarnivores (diet composed primarily of large vertebrates) tend to larger body size ranges than their evolutionary relatives with other feeding strategies, while invertivores and nectarivores tend to the lowest body size ranges (Carbone et al., 1999; M. Clauss et al., 2013; Rob Cooke et al., 2022; Hiiemae, 2000; Miller & Pittman, 2021; Miller et al., 2022; Pigot et al., 2020; Pineda-Munoz et al., 2016; Pough, 1973). Omnivores and taxa feeding on diets composed of fruit, seeds, and small vertebrates occupy intermediate positions (Marcus Clauss, Patrick Steuer, et al., 2013; Hiiemae, 2000; Miller & Pittman, 2021; Miller et al., 2022; Reuter et al., 2023). Exceptions to the extremes of this “rule” are (a) large

invertivores (e.g., myrmecophagous mammals; Carbone et al., 1999; McNab, 2000), and (b) small folivores (e.g., arboreal mammalian browsers such as the koala and sloth, and the small folivorous bird *Phytotoma rara*; Cork & Folley, 1996; Bakker & Kelt, 2000; Lopez-Calleja & Bozinovic 2000).

Some studies have even demonstrated specific optimal body mass ranges for different dietary guilds. For example, Pineda-Munoz et al. (2016) found that mammals >30kg are usually hypercarnivorous or folivorous, those under 1 kg are mostly invertivores, granivores and omnivores, the intermediate range is composed primarily of frugivorous forms. Pough (1973) showed that herbivorous lizards in the families Agamidae, Gerrhosauridae, Iguanidae, and Scincidae, had larger body masses (>300 g) than did their invertivorous cogeners. The study also found an ontogenetic shift wherein individuals from herbivorous lizard species were insectivorous until reaching 50-300g in body mass. A study by Miller et al. (2022) provides a set of optimal body size ranges between different dietary guilds for birds. The study finds an optimal body mass cut-off wherein most carnivores exceed 450g, and most invertivores are smaller than 300g. They report a similar cut-off between herbivorous strategies where herbivores weighing more than 400g are assumed to be folivores or frugivores, and birds below 250g assumed to be nectarivores or granivores. Carbone (1999) found that, due to energy requirements at larger body masses, carnivorans tend, with a few exceptions, to transition from small prey (<50% of the predator's body mass) to larger prey (>50% of the predator's body mass) at a body mass of ~21.5 kg. Smaller prey in this context refers primarily to invertebrates but also small-bodied vertebrates.

There is some disagreement as to (a) the mechanism driving the pattern of optimal body size distribution between dietary guilds, and (b) the extent to which the pattern is actually statistically significant, especially when accounting for shared evolutionary history (i.e. phylogenetic autocorrelation; Felsenstein 1985). Candidate explanations fall into two broad categories: physiological explanations and ecological explanations.

A classical physiological hypothesis is that large body size in folivorous taxa facilitates larger gut capacity and allows a higher intake of lower quality high-fibre food material (the “digestive efficiency” hypothesis or the “Jarman-Bell Principle”; Bell, 1971; Belovsky, 1997; Jarman, 1968). Smaller animals have faster metabolic rates relative to body size than larger animals and must therefore consume more digestible food sources to meet their metabolic demands (M. Clauss et al., 2013; Geist, 1974). It is thus expected under the digestive efficiency hypothesis that there would be a strong statistical relationship between consumption of low-quality food (such as leaves, in folivores) and large body mass. Since this relationship would be informed by biological principles rather than phylogenetic history, it should remain statistically significant when corrected for non-independence of variables introduced by underlying phylogenetic structure. However, it often does not remain significant, in studies where this has been tested (Langer & Clauss, 2018; Steiner et al., 2022). Furthermore, important mechanistic aspects of this hypothesis do not stand up to scrutiny when tested empirically in living animals. In particular, numerous studies have shown that there is no statistically-informed association between body mass and measures of digestive efficiency, such as rate of food intake or food retention time in the gut in squamates (Franz et al., 2011), birds (Fritz et al., 2012) or mammals (Clauss et al., 2007; M. Clauss et al., 2013).

Ecological hypotheses propose that the relationship between dietary composition and body size is the result of energy availability, accessibility, and abundance (in terms of bioavailability of energy) of a given food type in the natural environment rather than the digestibility of that food type (the “abundance packet-size hypothesis” following Olsen, 2015; Case, 1979; Hiiemae, 2000; M. Clauss et al., 2013). The “abundance packet-size” hypothesis seeks to explain the same broad patterns of body size variation between dietary guilds as the digestive efficiency hypothesis, but suggests that the underlying cause is the physical distribution of food availability within ecosystems, rather than the digestive properties of those food types (Clauss et al. 2013). Under this hypothesis, the correlation between herbivory, especially on fibrous vegetative material, and body mass can be explained by the fact that plant material constitutes are far greater proportion of total biomass in an ecosystem and, therefore, a more abundant source of energy. This hypothesis also suggests that carnivorous clades with larger body sizes will evolve to favor large vertebrate prey.

This is because energy and dietary protein is more readily available in large amounts, relative to time spent on hunting, in larger vertebrate prey than in smaller invertebrates (Carbone et al., 1999; Marcus Clauss, Patrick Steuer, et al., 2013; De Cuyper et al., 2019). Large body size in the extremes of folivory and hypercarnivory is supported by a high availability of carbohydrates and protein respectively (M. Clauss et al., 2013; Hiiemae, 2000). The “abundance-packet size” hypothesis thus predicts a far weaker correlation between body size and diet than the digestive efficiency hypothesis (M. Clauss et al., 2013). Since the dietary composition is not directly influencing the variance in body mass, a core expectation of the “abundance-packet size” is considerable overlap in body size ranges between dietary guilds.

Regardless of the proposed underlying mechanism, folivores and hypercarnivores generally attain the largest body size averages and invertivores the smallest body size averages among extant amniotes (Atwood et al., 2020; Carbone et al., 1999; M. Clauss et al., 2013; Rob Cooke et al., 2022; De Cuyper et al., 2019; Hiiemae, 2000; Meiri, 2008; Meiri, 2010; Pineda-Munoz et al., 2016). Studies of clades of lower taxonomic rank (e.g., liolaemid lizards and anseriform birds) have demonstrated exceptions to this trend at statistically significant levels. A shortcoming of studies in smaller groups is that there may be a lack of statistical power to test general patterns. This is because a smaller clade may lack sufficient independent origins of large body size and/or diverse feeding strategies to adequately test trait associations statistically. The precise cause-effect relationship between diet and body size is also not clear. Some research suggests that changes in diet drive changes in body size, or, conversely, that changes in body size facilitate dietary transitions (see Table 43). Because the relationship between diet and body size may be influenced by the underlying phylogenetic non-independence of data points of the taxa they evolve in, these hypotheses should be tested using phylogenetic comparative methods (Felsenstein 1985). However, many of the examples reviewed above did not use such methods. Numerous studies have also suggested that any conflation between body size distribution in amniotes and dietary strategy may be the result of an additional variable or variables altogether.

The purpose of this chapter is (a) to statistically investigate the strength of the effect, if any, of dietary composition on body size across most living amniotes, and (b) to

compare the relationship between body size and different classification systems of diet and resolutions of dietary data. I extend parts of this study to the fossil record by comparing body size between classical dietary guilds in two fossil groups (non-mammalian synapsids and non-avian theropods). Due to the limitations on classifying dietary strategy in extinct organisms, this is the only way to test these hypotheses in extinct taxa. I take a comparative approach on extant clades by comparing findings of both classical dietary guilds and more complex dietary guilds recovered in the k-means cluster analysis. This will be informative as to how the classification of diet may impact palaeontological research on the evolution of diet and body size in the fossil record.

2. Methods and Materials

2.1. Data preparation

In this chapter, I evaluated the statistical relationship between body size and diet expressed both as percentage of diet composed of different food sources, and discrete dietary guilds. I used the same data sources listed in Chapter 1, and the same phylogenetic topologies listed in Chapter 2 for all analyses. For the purposes of this exercise, I excluded cetaceans, sirenians, and pinnipeds from the mammal dataset, penguins from the bird dataset, and sea turtles from the turtle dataset due to the large body sizes of these animals, attributable to vastly different environmental (and physical) pressures and biological adaptations associated with habitual locomotion in an aquatic medium, and inhabiting a marine environment (Campione & Evans, 2012). I discuss any impact these taxa may have on results where appropriate. Aside from semi-aquatic taxa, there were still outliers in regards to large body size, such as *Pelochelys cantorii* for turtles, *Varanus komodoensis* for lizards, *Struthio camelus* for birds, and *Loxodonta africana* for mammals. However, I included these taxa as data points in this study because they represent important instances of their respective dietary strategies evolving in terrestrial ecological contexts, and are, therefore, comparable to the remaining taxa in their respective datasets.

2.2. Linear regression

I conducted ordinary (i.e., non-phylogenetic) linear models regressing logBM against each arcsine-transformed percentage variable using the ‘lm’ function in the ‘stats’ package in R (R Core Team & Team, 2022). The purpose of this was to evaluate the existence of a face-value correlation between body size and the proportions of different food sources in an animal’s dietary composition, agnostic to the potential causes of the correlation (e.g. such a correlation could result only from phylogenetic structure, see below). These ordinary linear regression models examine the relationship between body mass and different food types as independent factors within the taxa under investigation. These simple linear models provide insights into the associations between variables. They also provide important points of comparison to results from the literature. However, they fail to account for the underlying phylogenetic structure of the dataset, which introduces non-independence

to the data comparisons. This is because each of the traits have an unequal covariance structure due to the fact that pairs of species have different durations of shared evolutionary history, depending on the recency of their common ancestor. Therefore, treating these observations as independent (or as having equal covariances) could result in overestimating the significance of certain relationships, and artificially inflating statistical significance (Felsenstein, 1985; Grafen, 1989).

My primary analyses therefore use phylogenetic comparative methods, that account for underlying phylogenetic structure. This allows an evaluation of the correlation between changes in diet and body mass along evolving lineages, and whether the correlation is robust when corrected for phylogenetic autocorrelation. To do this, I would prefer to use phylogenetic generalised least squares regressions (pGLS; Grafen 1989). However, in exploratory analyses, I found these analyses were prohibitively time-consuming for my larger datasets. Most prominently in birds (9993 species), a single model had failed to converge following a day running. Given the number of variables being tested across all major amniote lineages and each topology, it would be prohibitively time-consuming to adopt this approach. Therefore, I instead used ordinary least squares regression of phylogenetic independent contrasts (PICs; Felsenstein 1985), as a computationally rapid an analytically equivalent (Blomberg et al.2012) approach to this problem. I discuss shortcomings and limitations in interpretation of this method, as well as ways it might be preferred to pGLS, in the discussion section.

I calculated phylogenetic independent contrasts (PICs; Felsenstein 1985) for log body mass (logBM, or proxy thereof) and the arcsine-transformed percentages of each food category in the diet for each clade using the ‘pic’ function in the ‘ape’ package in R (Paradis, 2012; Paradis et al., 2019; Paradis et al., 2004). I then performed a set of linear regression models using the ‘lm’ function in R. I performed the linear regressions on the PICs for logBM against the PICs for each arcsine-transformed proportional dietary variable to assess the linear relationship between diet and body size corrected for the effects of phylogeny. I used the formula “lm(logBM.pic~Diet.pic-1)” since regressions on PICs must be forced through the origin to ensure the assumption of phylogenetic independence of the variables (Garland Jr et al., 1992). This approach allows for an assessment of the association

between body mass and diet, while accommodating the underlying phylogenetic relationships between the data points. Linear regression on PICs has been demonstrated to produce identical results to the phylogenetic generalised least squares (PGLS) regression on large datasets (Blomberg et al., 2012) when assuming Brownian motion in trait evolution.

2.3. Correlation analysis

Diagnostic plots of the residuals of most of the linear models (both ordinary, and on PICs) revealed violations of the assumptions of a linear model (see Chapter Three, Results). While theoretical considerations, particularly related to sample size, still allow for meaningful interpretation of these results (albeit with caution), additional steps were needed to assess the relationship between body size and diet as a series of continuous variables. I performed two series of non-parametric tests on the data; Spearman's rank correlation, and Kendall's rank correlation. The purpose of this was to assess if these, more appropriate, statistical tests (given the distribution of residuals in the linear models) provided alternate interpretations of the nature of correlation between body mass and percentage of each food type in the diet.

The value of non-parametric ranked correlation tests is in their ability to assess the statistical relationship between body mass and each dietary category, while being robust to the non-normal distribution of data and violations of some linear model assumptions. These tests determine the presence or absence of a monotonic relationship between the variables in question. A caveat, however, is that correlation tests do not provide a measure of potential predictive power of one variable over another. Therefore, I consider the results of these tests in conjunction with the results of linear regression models. While non-parametric tests do not have the capacity to "confirm" the results of linear models, they do offer additional lines of support for the inferred relationship between variables.

I calculated the correlation coefficients (Spearman's rho, and Kendall's tau) between the logBM and each proportional dietary variable (arcsine-transformed percentages of each dietary category), as well as on the PICs of those respective variables. I

calculated both correlation coefficients using the ‘cor.test’ function of the ‘stats’ package of R (Revell, 2012). The purpose of this was to assess the strength and direction of the monotonic relationship, if any, between body mass and the proportion of each food type in the diet, both without considering phylogenetic covariance and corrected for phylogenetic structure.

2.4. Analyses of variance

The use of percentage values of different food sources are limited by the fact that the percentages (and transformations thereof) of each food category represent the consumption of that food category as an independent phenomenon rather than of diet composition in a holistic sense. Multiple regression would not be appropriate for this since the different variables adding to 100% would introduce collinearity to the predictor variables, potentially impacting on the interpretability of the results of the regression. Therefore, I assessed the variation in body size between the dietary guilds generated in the k-means cluster analyses (k=10) for each major amniote lineage (see Chapter One, Methods). A statistically significant ANOVA model is indicative that the mean values of body size in one or more dietary guilds are distinguishable. The statistical significance of pairwise p-values between the individual guilds is an indicator of whether any two dietary guilds are likely to come from populations with differing mean body size values. A statistically significant ANOVA model wherein the pairwise p-values between most guilds are statistically significant would, therefore, indicate that different dietary strategies have differing body size optima. For the purposes of comparison, I also use the classical dietary guilds as predictor groups. This was also prudent as the fossil clades are limited to the classical dietary guilds (being the only measure of diet available for those clades in lieu of proportional data).

First, I performed linear models with logBM as the dependent variable and the guilds as a categorical predictor to run diagnostic tests on the data. Diagnostic plots revealed many of the same short-comings that arose with the linear models between body mass and the continuous dietary variables. The parametric ANOVA tests are robust to modest violations of parametric assumptions (especially normal distribution

of residuals) on data sets with larger sample sizes (Montgomery, 2017). There is, therefore, meaningful interpretive value in the results of the parametric ANOVA tests, with the caveat that the assumption of residual normality (and any others) is violated by the data presented here.

I first performed one-way analysis of variance (ANOVA) tests to statistically compare the differences in mean body size between the different guilds. I performed the ANOVAs using both the k-means cluster generated guilds and the classical guilds as predictors. I used the ‘aov’ function in the ‘stats’ package (R Core Team & Team, 2022) in R to perform the ANOVAs. I then use the ‘TukeyHSD’ function in the ‘stats’ package in R to perform post-hoc pairwise comparisons between the different guilds.

To correct for non-independence of data caused by the underlying phylogenetic structure of the datasets, my primary analysis is a set of phylogenetic ANOVAs using the ‘phylANOVA’ function in the R package ‘phytools’ (Revell, 2012). For each phylogenetic ANOVA, I set the number of simulations to 1000, and I apply the Holm method of adjusting the p-value (Holm, 1979). I also performed phylogenetic ANOVA on the guilds generated with k-values of 5 and 20 to investigate if the result changes as further complexity is introduced to the dietary classification system used.

3. Results

3.1. Turtles

Linear models

The ordinary linear models regressing log-transformed carapace length (log-CL) against the arcsine-transformed percentage data for invertebrates other than terrestrial arthropods, vegetative plant structures, and total animal material were non-significant (p-value >0.05). The models that reached statistical significance tended to very low effect sizes and R-squared values (see Table 44). Two dietary arcsine-percentages had a statistically significant negative impact on log-CL; arthropods (slope = -0.267; p-value = 0.000; R^2 = 0.09), and total invertebrate material (slope = -0.146; p-value = 0.000; R^2 = 0.07). Three dietary arcsine-percentages had a statistically significant positive impact on log-CL; vertebrates (slope = 0.169; p-value = 0.006; R^2 = 0.03), reproductive plant structures (slope = 0.145; p-value = 0.019; R^2 = 0.02), and plant material collectively (slope = 0.074; p-value = 0.004; R^2 = 0.03).

The phylogenetic linear models regressing the PICs of log-CL against those of the arcsine-transformed percentage data for total animal material, total invertebrate material, arthropods, vertebrates, and reproductive plant structures were non-significant (p-value >0.05). The effect sizes and R-squared values were consistently low (see Table 45). The dietary PIC of proportional consumption of invertebrates other than terrestrial arthropods had a statistically significant negative impact on the PIC of log-CL (slope = -0.063; p-value = 0.017; R^2 = 0.018). The PICs of two dietary arcsine-percentages had a statistically significant positive impact on the PIC of log-CL: total plant material (slope = 0.077; p-value = 0.013; R^2 = 0.020), and vegetative plant structures (slope = 0.074; p-value = 0.029; R^2 = 0.014).

Non-parametric correlation tests

The ordinary Spearman's correlation tests found a non-significant (p-value >0.05) correlation between log-CL and arcsine-transformed percentage data for durophagy (p-value = 0.053), and both reproductive (p-value = 0.237) and vegetative (p-value = 0.452) plant structures. The correlations that reached statistical significance tended to low correlation coefficients (see Table 46). Three dietary arcsine-percentages had a statistically significant negative correlation with log-CL: arthropods (Spearman's rho = -0.422; p-value = 0.005), total invertebrate material (Spearman's rho = -0.305; p-value = 0.000), and total animal material (Spearman's rho = -0.171; p-value = 0.005). Two dietary arcsine-percentages had a statistically significant positive correlation with log-CL: vertebrates (Spearman's rho = 0.148; p-value = 0.016), and total plant material (Spearman's rho = 0.156; p-value = 0.011).

The Spearman's correlation tests on PIC values found a non-significant (p-value >0.05) correlation between the PIC of log-CL and those of arcsine-transformed percentage data for all food categories except for arthropods. The correlations that reached statistical significance tended to low correlation coefficients (see Table 46). Only one dietary PIC had a statistically significant negative correlation with the PIC of log-CL: arthropods (Spearman's rho = -0.125; p-value = 0.003).

The ordinary Kendall's correlation tests found a non-significant (p-value >0.05) correlation between log-CL and arcsine-transformed percentage data for both reproductive (p-value = 0.277), and vegetative (p-value = 0.518) plant structures. The correlations that reached statistical significance tended to low correlation coefficients (see Table 47). Four dietary arcsine-percentages had a statistically significant negative correlation with log-CL: arthropods (Kendall's tau = -0.304; p-value = 0.000), total invertebrate material (Kendall's tau = -0.212; p-value = 0.000), total animal material (Kendall's tau = -0.118; p-value = 0.006), and durophagy (Kendall's tau = -0.087; p-value = 0.045). Only one dietary arcsine-percentage had a statistically significant positive correlation with log-CL: total plant material (Kendall's tau = 0.028; p-value = 0.014).

The Kendall's correlation tests on PIC values found a non-significant (p-value >0.05) correlation between the PIC of log-CL and those of arcsine-transformed percentage

data for all food categories except arthropods (see Table 47). Only one dietary arcsine-percentage had a statistically significant negative correlation with log-CL: arthropods (Kendall's tau = -0.125; p-value = 0.003).

Guild comparisons

The ordinary ANOVA comparing mean log-CL between the dietary guilds recovered by the k-means cluster analysis in turtles reached statistical significance (p-value = <0.001, see Table 48). The Tukey post-hoc test showed that 10 pairwise comparisons were statistically significant (p-value = <0.05; see Table 49). The mean log-CL for Guild 10 (mixed faunivory) was greater than those of Guilds 2 (predominantly insectivorous mixed invertivory), 3 (omnivory), and 4 (predominantly durophagous mixed invertivory). The mean log-CL for Guild 5 (mixed herbivory composed primarily of reproductive plant structures) was greater than those of Guilds 2 (predominantly insectivorous mixed invertivory), and 3 (omnivory). The value of these differences did not exceed 0.25 (see Table 49). The mean log-CL values of both Guilds 1 (folivory) and 9 (mixed herbivory composed primarily of vegetative plant structures) were greater than those of Guilds 2 (predominantly insectivorous mixed invertivory), and 3 (omnivory). The value of these differences did not exceed 0.25 (see Table 49).

The phylogenetic ANOVA comparing mean log-CL between the dietary guilds recovered by the k-means cluster analysis in turtles did not reach statistical significance (p-value = >0.05) using either the guilds generated using a k-value of 5 or 10. The phylogenetic ANOVA using the guilds generated with a k-value of 20 was statistically significant (p-value = 0.038). The post-hoc test showed all pairwise p-values for all phylogenetic ANOVA to be non-significant (see Tables 48, 51-54).

The ordinary ANOVA comparing median log-CL between the classical dietary guilds reached statistical significance (p-value = <0.001). The Tukey post-hoc test showed that, with statistical significance, the mean log-CL for herbivory was greater than those of omnivory and, by a smaller margin, faunivory. The value of these

differences did not exceed 0.2 (see Table 49). The pairwise comparison between faunivory and omnivory was not statistically significant.

The phylogenetic ANOVA comparing mean log-CL between the classical dietary guilds in turtles did not reach statistical significance (p-value = >0.05). The post-hoc test showed all pairwise p-values to be >0.05 (see Table 55).

3.2. Lizards

Linear models

The ordinary linear models regressing log-SVL against the arcsine-transformed percentage data for all food types were significant (p-value >0.05; see Table 58). The models tended to low effect sizes and R-squared values. Three dietary arcsine-percentages had a statistically significant negative impact on log-SVL: arthropods (slope = -0.274; p-value = 0.000; R^2 = 0.02), total invertebrate material (slope = -0.262; p-value = 0.000; R^2 = 0.02), and total animal material (slope = -0.219; p-value = 0.000; R^2 = 0.01). Five dietary arcsine-percentages had a statistically significant positive impact on log-SVL: vertebrates (slope = 0.721; p-value = 0.000; R^2 = 0.03), durophagy (slope = 0.655; p-value = 0.000; R^2 = <0.01), vegetative plant structures (slope = 0.611; p-value = 0.000; R^2 = <0.01), reproductive plant structures (slope = 0.452; p-value = 0.000; R^2 = 0.01), and plant material collectively (slope = 0.334; p-value = 0.000; R^2 = 0.02).

The phylogenetic linear models, using the topology of Tonini et al. (2016), regressing the PICs of log-SVL against those of the arcsine-transformed percentage data were significant for all food types, except vegetative plant structures (p-value = 0.420; see Table 59). The models tended to low effect sizes and R-squared values. Three dietary PICs had a statistically significant negative impact on the PIC of log-SVL: total invertebrate material (slope = -0.071; p-value = 0.000; R^2 = 0.02), arthropods (slope = -0.065; p-value = 0.000; R^2 = 0.02), and total animal material (slope = -0.059; p-value = 0.000; R^2 = 0.01). Four dietary PICs had a statistically significant positive impact on the PIC of log-SVL: total plant material (slope = 0.101; p-value =

0.000; R^2 = 0.01), reproductive plant structures (slope = 0.094; p-value = 0.000; R^2 = 0.01), durophagy (slope = 0.070; p-value = 0.011; R^2 = <0.01), and vertebrates (slope = 0.056; p-value = 0.017; R^2 = <0.01).

The phylogenetic linear models regressing the PICs of log-SVL against those of the arcsine-transformed percentage data, using the topology of Pyron et al. (2013), were significant for all food types, except arthropods (p-value = 0.147), durophagy (p-value = 0.914), and vertebrates (p-value = 0.058). The models tended to low effect sizes and R-squared values. Two dietary PICs had a statistically significant negative impact on the PIC of log-SVL: total invertebrate material (slope = -0.056; p-value = 0.000; R^2 = 0.02), and total animal material (slope = -0.051; p-value = 0.000; R^2 = 0.01). Three dietary PICs had a statistically significant positive impact on the PIC of log-SVL: vegetative plant structures (slope = 0.126; p-value = 0.000; R^2 = <0.01), total plant material (slope = 0.084; p-value = 0.000; R^2 = 0.02), reproductive plant structures (slope = 0.047; p-value = 0.004; R^2 = <0.01).

Non-parametric correlation tests

The ordinary Spearman's correlation tests found a non-significant (p-value >0.05; see Table 60) correlation between log-SVL and arcsine-transformed percentage data for all food types. The correlations tended to low correlation coefficients. Three dietary arcsine-percentages had a statistically significant negative correlation with log-SVL: total invertebrate material (Spearman's rho = -0.360; p-value = 0.000), arthropods (Spearman's rho = -0.348; p-value = 0.000), and total animal material (Spearman's rho = -0.261; p-value = 0.000). Five dietary arcsine-percentages had a statistically significant positive correlation with log-SVL: vertebrates (Spearman's rho = 0.282; p-value = 0.000), total plant material (Spearman's rho = 0.262; p-value = 0.000), reproductive plant structures (Spearman's rho = 0.241; p-value = 0.000), vegetative plant structures (Spearman's rho = 0.240; p-value = 0.000), and durophagy (Spearman's rho = 0.163; p-value = 0.000).

The Spearman's correlation tests on PIC values, using the topology of Tonini et al. (2016), found a significant (p-value <0.05; see Table 60) correlation between the PIC

of log-SVL and those of arcsine-transformed percentage data for all food categories. The correlations that reached statistical significance tended to low correlation coefficients. Three dietary PIC had a statistically significant negative correlation with the PIC of log-CL: arthropods (Spearman's rho = -0.152; p-value = 0.000), total invertebrates (Spearman's rho = -0.144; p-value = 0.000), and total animal material (Spearman's rho = -0.115; p-value = 0.000). Five dietary PICs had a statistically significant positive correlation with that of log-SVL: vertebrates (Spearman's rho = 0.136; p-value = 0.000), total plant material (Spearman's rho = 0.135; p-value = 0.000), reproductive plant structures (Spearman's rho = 0.120; p-value = 0.000), vegetative plant structures (Spearman's rho = 0.084; p-value = 0.000), and durophagy (Spearman's rho = 0.071; p-value = 0.000).

The Spearman's correlation tests on PIC values, using the topology of Pyron et al. (2013), found a significant (p-value <0.05; see Table 97) correlation between the PIC of log-SVL and those of arcsine-transformed percentage data for all food categories except arthropods (p-value = 0.965) and durophagy (p-value = 0.819). The correlations that reached statistical significance tended to low correlation coefficients. Two dietary PICs had a statistically significant negative correlation with the PIC of log-SVL: total invertebrates (Spearman's rho = -0.190; p-value = 0.000), and total animal material (Spearman's rho = -0.150; p-value = 0.000). Four dietary PICs had a statistically significant positive correlation with log-SVL: total plant material (Spearman's rho = 0.159; p-value = 0.000), vertebrates (Spearman's rho = 0.145; p-value = 0.000), reproductive plant structures (Spearman's rho = 0.141; p-value = 0.000), and vegetative plant structures (Spearman's rho = 0.107; p-value = 0.000).

The ordinary Kendall's correlation tests found a significant (p-value <0.05; see Table 61) correlation between log-SVL and arcsine-transformed percentage data for all food types. The correlations tended to low correlation coefficients. Three dietary arcsine-percentages had a statistically significant negative correlation with log-SVL: total invertebrate material (Kendall's tau = -0.284; p-value = 0.000), arthropods (Kendall's tau = -0.277; p-value = 0.000), and total animal material (Kendall's tau = -0.209; p-value = 0.000). Five dietary arcsine-percentages had a statistically

significant positive correlation with log-SVL: vertebrates (Kendall's tau = 0.229; p-value = 0.000), total plant material (Kendall's tau = 0.210; p-value = 0.000), vegetative plant structures (Kendall's tau = 0.195; p-value = 0.000), reproductive plant structures (Kendall's tau = 0.193; p-value = 0.000), and durophagy (Kendall's tau = 0.132; p-value = 0.000).

The Kendall's correlation tests on PIC values, using the topology of Tonini et al. (2016), found a significant (p-value <0.05; see Table 61) correlation between the PIC of log-SVL and those of arcsine-transformed percentage data for all food categories. The correlations that reached statistical significance tended to low correlation coefficients. Three dietary PIC had a statistically significant negative correlation with the PIC of log-SVL: arthropods (Kendall's tau = -0.111; p-value = 0.000), total invertebrates (Kendall's tau = -0.105; p-value = 0.000), and total animal material (Kendall's tau = -0.084; p-value = 0.000). Five dietary arcsine PICs had a statistically significant positive correlation with that of log-SVL: vertebrates (Kendall's tau = 0.108; p-value = 0.000), total plant material (Kendall's tau = 0.104; p-value = 0.000), reproductive plant structures (Kendall's tau = 0.093; p-value = 0.000), vegetative plant structures (Kendall's tau = 0.067; p-value = 0.000), and durophagy (Kendall's tau = 0.057; p-value = 0.000).

The Kendall's correlation tests on PIC values, using the topology of Pyron et al. (2013), found a significant (p-value <0.05; see Table 61) correlation between the PIC of log-SVL and those of arcsine-transformed percentage data for all food categories except arthropods (p-value = 0.974) and durophagy (p-value = 0.822). The correlations that reached statistical significance tended to low correlation coefficients. Two dietary PICs had a statistically significant negative correlation with the PIC of log-SVL: total invertebrates (Kendall's tau = -0.138; p-value = 0.000), and total animal material (Kendall's tau = -0.109; p-value = 0.000). Four dietary PICs had a statistically significant positive correlation with log-SVL: total plant material (Kendall's tau = 0.120; p-value = 0.000), vertebrates (Kendall's tau = 0.113; p-value = 0.000), reproductive plant structures (Kendall's tau = 0.107; p-value = 0.000), and vegetative plant structures (Kendall's tau = 0.083; p-value = 0.000).

Dietary Guild comparisons

The ordinary ANOVA comparing mean log-SVL between the dietary guilds recovered by the k-means cluster analysis in lizards reached statistical significance (p-value = <0.001; see Table 62). The Tukey post-hoc test showed several statistically significant pairwise comparisons (see Table 63). The mean log-SVL of Guild 2 (insectivory s.s.) was significantly smaller than those of all other guilds. In ranked order of size of that difference (largest to smallest): Guild 5 (carnivory), Guild 1 (mixed faunivory), Guild 10 (folivory), Guild 4 (predominantly durophagous mixed invertivory), Guild 7 (mixed herbivory composed primarily of reproductive plant structures), Guild 9 (mixed herbivory), Guild 8 (omnivory), Guild 3 (insectivory s.l.), and, finally, Guild 6 (insectivory-omnivory). The mean log-SVL of Guild 6 (insectivory-omnivory) is significantly smaller than those of (in ranked order): Guilds 5 (carnivory), 1 (mixed faunivory), 10 (folivory), 7 (mixed herbivory composed primarily of reproductive plant structures), and Guild 3 (insectivory s.l.). The mean log-SVLs for Guilds 4 (predominantly durophagous mixed invertivory) and 10 (folivory) are statistically higher than those of the insectivorous guilds (Guilds 2, 3, and 6), and Guild 8 (omnivory). The mean log-SVL for Guild 8 (omnivory) is significantly smaller than those of all guilds except the insectivorous guilds (Guilds 2, 3, and 6). The mean log-SVLs of Guilds 1 (mixed faunivory) and 5 (carnivory) are significantly higher than those of all other guilds except for each other, and Guild 10 (folivory).

The phylogenetic ANOVA comparing mean log-SVL between the dietary guilds recovered by the k-means cluster analysis in lizards (k = 10), using the topology of Tonini et al. (2016), was statistically significant (p-value = 0.001; see Table 62). The pairwise p-values revealed by the post-hoc test to be statistically significant, followed a different pattern than those of the non-phylogenetic ANOVA. Corrected for the non-independence in the data introduced by underlying phylogenetic structure, the mean log-SVL of Guild 2 (insectivory s.s.) was smaller than that of (in ranked order of pairwise t-value): Guilds 1 (mixed faunivory), 9 (mixed herbivory composed primarily of vegetative plant structures), 5 (carnivory), 7 (mixed herbivory composed primarily of reproductive plant structures), 4 (predominantly durophagous mixed invertivory), and 10 (folivory). The mean log-SVL of Guild 4 (predominantly durophagous mixed

invertivory) was greater than that of Guilds 2 (insectivory s.s.), and 3 (insectivory s.l.). The mean log-SVL of Guild 7 (mixed herbivory composed primarily of reproductive plant structures) was greater than that of the insectivorous guilds (Guilds 2, 3, and 6), and Guild 8 (omnivory).

The phylogenetic ANOVA comparing mean log-SVL between the dietary guilds recovered by the k-means cluster analysis in lizards with k-values of 5 and 20, using the topology of Tonini et al. (2016), were both statistically significant (p-value = 0.001; see Tables 66-68). Several pairwise p-values between guilds generated using a k-value of 5 are statistically significant. Corrected for the non-independence in the data introduced by underlying phylogenetic structure, the mean log-SVL of Guild 1 (strict insectivory, see Table 23) was significantly smaller than all other guilds. Corrected for the non-independence in the data introduced by underlying phylogenetic structure, the mean log-SVL of Guilds 2 (herbivory; taken generally, see Table 23) and 4 (non-insectivorous faunivory, see Table 23) are significantly larger those of Guilds 3 (omnivory; taken generally, see Table 23) and 5 (insectivory sensu lato, see Table 23). All pairwise p-values using the guilds generated with a k-value of 20 were non-significant.

The phylogenetic ANOVA comparing mean log-SVL between the dietary guilds recovered by the k-means cluster analysis in lizards, using the topology of Pyron et al. (2013), was statistically significant (p-value = 0.001; see Table 62). The pairwise p-values revealed by the post-hoc test to be statistically significant, followed a similar that of the phylogenetic ANOVA using the topology of Tonini et al. (2016). Corrected for the non-independence in the data introduced by underlying phylogenetic structure, the mean log-SVL of Guild 2 (insectivory s.s.) was smaller than that of (in ranked order): Guilds 4 (predominantly durophagous mixed invertivory), 9 (mixed herbivory composed primarily of vegetative plant structures), 7 (mixed herbivory composed primarily of reproductive plant structures), 5 (carnivory), and 10 (folivory). The mean log-SVL values of Guilds 7 (mixed herbivory composed primarily of reproductive plant structures), and 10 (folivory) are greater than those of the insectivorous guilds (Guilds 2, 3, and 6), and Guild 8 (omnivory). The mean log-SVL of Guild 5 (carnivory) is greater than that of the insectivorous guilds (Guilds 2, 3, and

6), while the mean log-SVL of Guild 4 (predominantly durophagous mixed invertivory) is greater than that of Guilds 2 (insectivory s.s.) and 3 (insectivory s.l.).

The phylogenetic ANOVA comparing mean log-SVL between the dietary guilds recovered by the k-means cluster analysis in lizards with k-values of 5 and 20, using the topology of Pyron et al. (2013), were both statistically significant (p-value = 0.001; see Table 62). Several pairwise p-values between guilds generated using a k-value of 5 are statistically significant. Corrected for the non-independence in the data introduced by underlying phylogenetic structure, the mean log-SVL of Guild 1 (strict insectivory, see Table 23) was significantly smaller than all other guilds. The mean log-SVL of Guilds 2 (herbivory; taken generally, see Table 23) and 4 (non-insectivorous faunivory, see Table 23) are significantly larger those of Guilds 3 (omnivory; taken generally, see Table 23) and 5 (insectivory sensu lato, see Table 23). All pairwise p-values using the guilds generated with a k-value of 20 were non-significant.

The ordinary ANOVA comparing mean log-SVL between the classical dietary guilds reached statistical significance (p-value = <0.001; see Table 62). The Tukey post-hoc test showed that all pairwise comparisons between the classical guilds were statistically significant (see Table 101). The mean log-SVL for herbivory was greater than those of omnivory and, by a greater margin, faunivory. The mean log-SVL for omnivory was statistically greater than that of faunivory.

The phylogenetic ANOVA comparing mean log-SVL between the classical dietary guilds in lizards, using the topology of Tonini et al. (2016), was statistically significant (p-value = 0.001). The post-hoc test revealed that the only pairwise p-value not to reach statistical significance was between faunivory and omnivory (p-value = 0.116). Corrected for the non-independence in the data introduced by underlying phylogenetic structure, the mean log-SVL of herbivory was greater than those of faunivory, and, to a lesser extent, omnivory.

The phylogenetic ANOVA comparing mean log-SVL between the classical dietary guilds in lizards, using the topology of Pyron et al. (2013), was statistically significant

(p-value = 0.001; see Table 62). The results followed an identical pattern to the phylogenetic ANOVA using the topology of Tonini et al. (2016). The post-hoc test revealed that the only pairwise p-value not to reach statistical significance was between faunivory and omnivory (p-value = 0.116). Corrected for the non-independence in the data introduced by underlying phylogenetic structure, the mean log-SVL of herbivory was greater than those of faunivory, and, to a lesser extent, omnivory.

3.3. Birds

Linear models

The ordinary linear models regressing log-BM against the arcsine-transformed percentage data for seeds (p-value = 0.360) was non-significant (p-value >0.05; see Table 76). The remaining models, that reached statistical significance, tended to low effect sizes and R-squared values. Four dietary arcsine-percentages had a statistically significant negative impact on log-BM: nectar (slope = -0.887; p-value = 0.000; R^2 = 0.10), total invertebrate material (slope = -0.42; p-value = 0.000; R^2 = 0.13), total reproductive plant structures (slope = -0.07; p-value = 0.000; R^2 = <0.01), and total animal material (slope = -0.03; p-value = 0.004; R^2 = <0.01). Six dietary arcsine-percentages had a statistically significant positive impact on log-BM: fish (slope = 1.42; p-value = 0.000; R^2 = 0.10), vegetative plant material (slope = 1.28; p-value = 0.000; R^2 = 0.09), total vertebrate material (slope = 1.16; p-value = 0.000; R^2 = 0.24), terrestrial vertebrates (slope = 1.11; p-value = 0.000; R^2 = 0.15), fruit (slope = 0.31; p-value = 0.000; R^2 = 0.02), and total plant material (slope = 0.10; p-value = 0.000; R^2 = <0.01).

The phylogenetic linear models regressing the PICs of log-BM against those of the arcsine-transformed percentage data, using the backbone topology of Ericson et al. (2006), were significant for all food types, except nectar (p-value = 0.536; see Table 78). The models had varying effect sizes, though many had high R-squared values. Four dietary PICs had a statistically significant negative impact on the PIC of log-BM: total invertebrate material (slope = -0.974; p-value=0.000; R^2 = 0.35), total vertebrate

material (slope = -0.748; p-value=0.000; R^2 = 0.904), fish (slope = -0.674; p-value=0.000; R^2 = 0.927), and total animal material (slope = -0.295; p-value=0.000; R^2 = 0.913). Six dietary PICs had a statistically significant positive correlations on the PIC of log-BM: terrestrial vertebrates (slope = 2.207; p-value=0.000; R^2 = 0.90), seed (slope = 1.18; p-value=0.000; R^2 = 0.79), fruit (slope = 1.13; p-value=0.000; R^2 = 0.76), total plant material (slope = 0.633; p-value=0.000; R^2 = 0.87), reproductive plant structures (slope = 0.612; p-value=0.000; R^2 = 0.84), vegetative plant structures (slope = 0.115; p-value = 0.001; R^2 = <0.01).

The phylogenetic linear models, using the backbone topology of Hackett et al. (2008), regressing the PICs of log-BM against those of the arcsine-transformed percentage data were significant for all food types, except nectar (p-value = 0.272). The models tended to low effect sizes and R-squared values. The results were mostly different than those of the phylogenetic linear models using the topology of Ericson et al. (2006). Particularly in this instance, and as mentioned in the Methods section, these results should be interpreted in the context of the distributions of the residuals of the linear models violating several assumptions of linear regression. Six dietary PICs had a statistically significant negative impact on the PIC of log-BM: fish (slope = -0.324; p-value = 0.000; R^2 = 0.18), total vertebrate material (slope = -0.295; p-value = 0.000; R^2 = <0.01), seed (slope = -0.124; p-value = 0.000; R^2 = 0.01), total reproductive plant material (slope = -0.083; p-value = 0.000; R^2 = 0.01), total plant material (slope = -0.059; p-value = 0.000; R^2 = <0.01), and fruit (slope = -0.041; p-value = 0.000; R^2 = <0.01). Four dietary PICs had a statistically significant positive impact on the PIC of log-BM: total invertebrate material (slope = 0.176; p-value = 0.000; R^2 = 0.16), vegetative plant structures (slope = 0.089; p-value = 0.000; R^2 = <0.01), terrestrial vertebrates (slope = 0.079; p-value = 0.000; R^2 = <0.01), total animal material (slope = 0.041; p-value = 0.000; R^2 = <0.01).

Non-parametric correlation tests

The ordinary Spearman's correlation tests found a significant (p-value <0.05; see Table 79) correlation between log-BM and arcsine-transformed percentage data for all food types. The correlations tended to low correlation coefficients. Four dietary

arcsine-percentages had a statistically significant negative correlation with log-BM: invertebrates (Spearman's rho = -0.340; p-value = 0.000), nectar (Spearman's rho = -0.293; p-value = 0.000), total animal material (Spearman's rho = -0.054; p-value = 0.000), total reproductive plant material (Spearman's rho = -0.029; p-value = 0.005). Seven dietary arcsine-percentages had a statistically significant positive correlation with log-BM: total vertebrate material (Spearman's rho = 0.480; p-value = 0.000), terrestrial vertebrates (Spearman's rho = 0.404; p-value = 0.000), fish (Spearman's rho = 0.320; p-value = 0.000), vegetative plant structures (Spearman's rho = 0.240; p-value = 0.000), fruit (Spearman's rho = 0.170; p-value = 0.000), seeds (Spearman's rho = 0.082; p-value = 0.000), and total plant material (Spearman's rho = 0.054; p-value = 0.000).

The Spearman's correlation tests on PIC values, using the topology of Ericson et al. (2006), found a significant (p-value <0.05; see Table 79) correlation between the PIC of log-BM and those of arcsine-transformed percentage data for all food categories except seed (p-value = 0.189), total reproductive plant material (p-value = 0.670), and nectar (p-value = 0.920). The correlations that reached statistical significance tended to low correlation coefficients. Two dietary PICs had a statistically significant negative correlation with the PIC of log-BM: invertebrates (Spearman's rho = -0.094; p-value = 0.000), and total animal material (Spearman's rho = -0.035; p-value = 0.001). Six dietary PICs had a statistically significant positive correlation with the PIC of log-BM: total vertebrate material (Spearman's rho = 0.146; p-value = 0.000), terrestrial vertebrates (Spearman's rho = 0.139; p-value = 0.000), fruit (Spearman's rho = 0.043; p-value = 0.000), total plant material (Spearman's rho = 0.031; p-value = 0.002), vegetative plant structures (Spearman's rho = 0.029; p-value = 0.004), and fish (Spearman's rho = 0.024; p-value = 0.000).

The Spearman's correlation tests on PIC values, using the topology of Hackett et al. (2008), found a significant (p-value <0.05; see Table 79) correlation between the PIC of log-BM and those of arcsine-transformed percentage data for all food categories except seed (p-value = 0.189), total reproductive plant material (p-value = 0.828), and nectar (p-value = 0.245). The correlations that reached statistical significance tended to low correlation coefficients. Two dietary PICs had a statistically significant negative correlation with the PIC of log-BM: invertebrates (Spearman's rho = -0.098;

p-value = 0.000), and total animal material (Spearman's rho = -0.034; p-value = 0.001). Six dietary PICs had a statistically significant positive correlation with the PIC of log-BM: total vertebrate material (Spearman's rho = 0.153; p-value = 0.000), terrestrial vertebrates (Spearman's rho = 0.136; p-value = 0.000), fish (Spearman's rho = 0.050; p-value = 0.000), fruit (Spearman's rho = 0.041; p-value = 0.000), vegetative plant structures (Spearman's rho = 0.029; p-value = 0.004), total plant material (Spearman's rho = 0.027; p-value = 0.008).

The ordinary Kendall's correlation tests found a significant (p-value <0.05; see Table 80) correlation between log-BM and arcsine-transformed percentage data for all food types. The correlations tended to low correlation coefficients. Four dietary arcsine-percentages had a statistically significant negative correlation with log-BM: invertebrates (Kendall's tau = -0.250; p-value = 0.000), nectar (Kendall's tau = -0.237; p-value = 0.000), total animal material (Kendall's tau = -0.040; p-value = 0.000), total reproductive plant material (Kendall's tau = -0.020; p-value = 0.007). Seven dietary arcsine-percentages had a statistically significant positive correlation with log-BM: total vertebrate material (Kendall's tau = 0.385; p-value = 0.000), terrestrial vertebrates (Kendall's tau = 0.325; p-value = 0.000), fish (Kendall's tau = 0.258; p-value = 0.000), vegetative plant structures (Kendall's tau = 0.192; p-value = 0.000), fruit (Kendall's tau = 0.133; p-value = 0.000), seeds (Kendall's tau = 0.062; p-value = 0.000), and total plant material (Kendall's tau = 0.040; p-value = 0.000).

The Kendall's correlation tests on PIC values, using the topology of Ericson et al. (2006), found a significant (p-value <0.05; see Table 80) correlation between the PIC of log-BM and those of arcsine-transformed percentage data for all food categories except seed (p-value = 0.181), total reproductive plant material (p-value = 0.669), and nectar (p-value = 0.914). The correlations that reached statistical significance tended to low correlation coefficients. Two dietary PICs had a statistically significant negative correlation with the PIC of log-BM: invertebrates (Kendall's tau = -0.066; p-value = 0.000), and total animal material (Kendall's tau = -0.025; p-value = 0.000). Six dietary PICs had a statistically significant positive correlation with the PIC of log-BM: total vertebrate material (Kendall's tau = 0.112; p-value = 0.000), terrestrial vertebrates (Kendall's tau = 0.107; p-value = 0.000), fruit (Kendall's tau = 0.031; p-

value = 0.000), vegetative plant structures (Kendall's tau = 0.022; p-value = 0.003), total plant material (Kendall's tau = 0.022; p-value = 0.002), and fish (Kendall's tau = 0.019; p-value = 0.000).

The Kendall's correlation tests on PIC values, using the topology of Hackett et al. (2008), found a significant (p-value <0.05; se Table 80) correlation between the PIC of log-BM and those of arcsine-transformed percentage data for all food categories except seed (p-value = 0.188), total reproductive plant material (p-value = 0.819), and nectar (p-value = 0.245). The correlations that reached statistical significance tended to low correlation coefficients. Two dietary PICs had a statistically significant negative correlation with the PIC of log-BM: invertebrates (Kendall's tau = -0.069; p-value = 0.000), and total animal material (Kendall's tau = -0.024; p-value = 0.001). Six dietary PICs had a statistically significant positive correlation with the PIC of log-BM: total vertebrate material (Kendall's tau = 0.117; p-value = 0.000), terrestrial vertebrates (Kendall's tau = 0.105; p-value = 0.000), fish (Kendall's tau = 0.040; p-value = 0.000), fruit (Kendall's tau = 0.030; p-value = 0.000), vegetative plant structures (Kendall's tau = 0.022; p-value = 0.004), and total plant material (Kendall's tau = 0.019; p-value = 0.007).

Guild comparisons

The ordinary ANOVA comparing mean log-BM between the dietary guilds recovered by the k-means cluster analysis (k=10) in birds reached statistical significance (p-value = <0.001; see Table 81). The Tukey post-hoc test showed the only pairwise comparisons not to reach statistical significance were between Guilds 8 (mixed herbivory) and 5 (piscivory s.l.); Guilds 9 (granivory) and 6 (invertivory s.s.); Guilds 8 (mixed herbivory) and 7 (carnivory); and between Guilds 7 (carnivory) and 5 (piscivory s.l.). The mean log-BM values for Guilds 3 (mixed herbivory), 7 (carnivory) and 5 (piscivory s.l.) were higher than for all other guilds though not significantly different from each other. In ranked order: Guild 3 (nectarivory), Guild 6 (invertivory s.s.), Guild 9 (granivory), Guild 10 (invertivory s.l.), Guild 4 (omnivory), and Guild 1 (frugivory). Guild 1 (frugivory) had the next highest mean log-BM after the three largest guilds (Guilds 3, 5, and 7). The guilds with the lowest mean log-BM values

are Guilds 6 (invertivory s.s.), and 3 (nectarivory). The mean log-BM of Guild 7 (nectarivory) being lower than that of Guild 6 (invertivory s.s.).

The phylogenetic ANOVA comparing mean log-BM between the dietary guilds recovered by the k-means cluster analysis (k=10) in birds, using the topology of Ericson et al. (2006), was statistically significant (p-value = 0.001; see Table 81). The pairwise p-values revealed by the post-hoc test to be statistically significant, revealed the same general set of patterns as the ordinary ANOVA. Corrected for the non-independence of data introduced by underlying phylogenetic structure, the mean log-BM of Guild 7 (carnivory) is greater than that of (in ranked order): Guilds 3 (nectarivory), and 6 (invertivory s.s.). The mean log-BM of Guild 5 (piscivory s.l.) is greater than that of (in ranked order): Guilds 3 (nectarivory), 6 (invertivory s.s.), and 10 (invertivory s.l.). The mean log-BM of Guild 8 (mixed herbivory) is only greater than that of Guild 3 (nectarivory). In addition to the latter three Guilds, the mean log-BM of Guild 6 (invertivory s.s.) was, corrected for the non-independence of data introduced by underlying phylogenetic structure, statistically smaller than those of (in ranked order): Guilds 10 (invertivory s.l.), 2 (frugivory-omnivory), and 4 (omnivory).

The phylogenetic ANOVA comparing mean log-BM between the dietary guilds recovered by the k-means cluster analysis in birds with k-values of 5 and 20, using the backbone topology of Ericson et al. (2006), were both statistically significant (p-value = 0.001; see Table 81). Few pairwise p-values between guilds generated using a k-value of 5 are statistically significant. Corrected for the non-independence in the data introduced by underlying phylogenetic structure, the mean log-BM of Guild 2 (strict insectivory; see Table 26) was significantly smaller than that of Guilds 3 (mixed faunivory), and 5 (frugivory). All pairwise p-values using the guilds generated with a k-value of 20 were non-significant.

The phylogenetic ANOVA comparing mean log-BM between the dietary guilds recovered by the k-means cluster analysis (k=10) in birds, using the topology of Hackett et al. (2008), was statistically significant (p-value = 0.001). The pairwise p-values revealed by the post-hoc test to be statistically significant, revealed the same general set of patterns as the ordinary ANOVA. Corrected for the non-independence of data introduced by underlying phylogenetic structure, the mean log-BM of Guild 7 (carnivory) is greater than that of (in ranked order): Guilds 3 (nectarivory), 6

(invertivory s.s.), and 9 (granivory). The mean log-BM of Guild 5 (piscivory s.l.) is greater than that of (in ranked order): Guilds 3 (nectarivory), 6 (invertivory s.s.), 10 (invertivory s.l.), and 9 (granivory). The mean log-BM of Guild 8 (mixed herbivory) is only greater than that of Guild 3 (nectarivory). In addition to the latter three Guilds, the mean log-BM of Guild 6 (invertivory s.s.) was, corrected for the non-independence of data introduced by underlying phylogenetic structure, statistically smaller than those of (in ranked order): Guilds 10 (invertivory s.l.), 2 (frugivory-omnivory), 4 (omnivory), and 1 (frugivory).

The phylogenetic ANOVA comparing mean log-BM between the dietary guilds recovered by the k-means cluster analysis in birds with k-values of 5 and 20, using the backbone topology of Hackett et al. (2008), were both statistically significant (p-value = 0.001; see Table 81). Few pairwise p-values between guilds generated using a k-value of 5 are statistically significant. Corrected for the non-independence in the data introduced by underlying phylogenetic structure, the mean log-BM of Guild 2 (strict insectivory; see Table 26) was significantly smaller than that of Guilds 3 (mixed faunivory), and 5 (frugivory). All pairwise p-values using the guilds generated with a k-value of 20 were non-significant.

The ordinary ANOVA comparing median log-BM between the classical dietary guilds reached statistical significance (p-value = <0.001; see Table 81). The Tukey post-hoc test showed that only the pairwise comparison between faunivory and omnivory was non-significant (p-value = >0.05). The mean log-BM for herbivory was greater than those of omnivory and, by a slightly lesser margin, faunivory.

The phylogenetic ANOVA comparing mean log-BM between the classical dietary guilds in birds, using the topology of Ericson et al. (2006), was not statistically significant (p-value = 0.918). The post-hoc test revealed the all pairwise p-values to be non-significant (p-value = 1.0).

The phylogenetic ANOVA comparing mean log-BM between the classical dietary guilds in birds, using the topology of Hackett et al. (2008), was not statistically significant (p-value = 0.906). The post-hoc test revealed the all pairwise p-values to

be non-significant (p-value = 1.0). This result is consistent with the results of the phylogenetic ANOVA using the topology of Ericson et al. (2006).

3.4. Mammals

Linear models

The ordinary linear models regressing log-BM against the arcsine-transformed percentage data for nectar (p-value=0.090) was non-significant (p-value >0.05; see Table 96). The models that reached statistical significance tended to low effect sizes and R-squared values. Three dietary arcsine-percentages had a statistically significant negative impact on log-BM: total invertebrate material (slope = -0.96; p-value = 0.000; R^2 = 0.24), total animal material (slope = -0.69; p-value = 0.000; R^2 = <0.17), and seed (slope = -0.48; p-value = 0.000; R^2 = <0.01). Seven dietary arcsine-percentages had a statistically significant positive impact on log-BM: fish (slope = 3.01; p-value = 0.000; R^2 = 0.04), vegetative plant material (slope = 0.97; p-value = 0.000; R^2 = 0.20), total plant material (slope = 0.73; p-value = 0.000; R^2 = 0.18), total vertebrate material (slope = 0.55; p-value = 0.000; R^2 = 0.02), fruit (slope = 0.33; p-value = 0.000; R^2 = 0.01), terrestrial vertebrates (slope = 0.29; p-value = 0.000; R^2 = <0.01), and total reproductive plant material (slope = 0.09; p-value = 0.013; R^2 = <0.01).

The phylogenetic linear models, using the tip-dating backbone topology, regressing the PICs of log-BM against those of the arcsine-transformed percentage data were significant for all food types, except nectar (p-value = 0.332; see Table 97), total animal material (p-value = 0.988), fish (p-value = 0.079) and seed (p-value = 0.495). The models tended to low effect sizes and R-squared values. Three dietary PICs had a statistically significant negative impact on the PIC of log-BM: total reproductive plant material (slope = -0.193; p-value = 0.000; R^2 = <0.01), total invertebrates (slope = -0.176; p-value = 0.000; R^2 = <0.01), fruit (slope = -0.128; p-value = 0.000; R^2 = 0.18). Five dietary PICs had a statistically significant positive impact on the PIC of log-BM: vegetative plant structures (slope = 0.207; p-value = 0.000; R^2 = 0.01), total vertebrate material (slope = 0.203; p-value = 0.000; R^2 = <0.01), terrestrial

vertebrates (slope = 0.154; p-value = 0.000; R^2 = <0.01), and total plant material (slope = 0.150; p-value = 0.000; R^2 = <0.01).

The phylogenetic linear models, using the node-dating backbone topology, regressing the PICs of log-BM against those of the arcsine-transformed percentage data were significant for all food types, except fruit (p-value = 0.876), total animal material (p-value = 0.880), total plant material (p-value = 0.688), and nectar (p-value = 0.736). The models tended to low effect sizes and R-squared values. Three dietary PICs had a statistically significant negative impact on the PIC of log-BM: total seed (slope = -0.652; p-value = 0.000; R^2 = 0.02), total reproductive plant material (slope = -0.231; p-value = 0.000; R^2 = <0.01), and total invertebrates (slope = -0.082; p-value = 0.001; R^2 = <0.01). Three dietary PICs had a statistically significant positive impact on the PIC of log-BM: vegetative plant structures (slope = 0.176; p-value = 0.000; <R^2 = 0.01), total vertebrate material (slope = 0.203; p-value = 0.000; R^2 = <0.01), and terrestrial vertebrates (slope = 0.062; p-value = 0.013; R^2 = <0.01).

Non-parametric correlation tests

The ordinary Spearman's correlation tests found a significant (p-value <0.05; see Table 99) correlation between log-BM and arcsine-transformed percentage data for all food types except nectar (p-value = 0.790) and total vertebrate material (p-value = 0.872). The correlations tended to low correlation coefficients. Three dietary arcsine-percentages had a statistically significant negative correlation with log-BM: invertebrates (Spearman's rho = -0.594; p-value = 0.000), animal material (Spearman's rho = -0.519; p-value = 0.000), and terrestrial vertebrates (Spearman's rho = -0.031; p-value = 0 027). Six dietary arcsine-percentages had a statistically significant positive correlation with log-BM: total plant material (Spearman's rho = 0.520; p-value = 0.000), vegetative plant structures (Spearman's rho = 0.483; p-value = 0.000), fruit (Spearman's rho = 0.295; p-value = 0.000), total reproductive plant material (Spearman's rho = 0.212; p-value = 0.000), fish (Spearman's rho = 0.145; p-value = 0.000), and seed (Spearman's rho = 0.041; p-value = 0.003).

The Spearman's correlation tests on PIC values, using the tip-dating backbone topology, found a significant (p-value <0.05; see Table 99) correlation between the PIC of log-BM and those of arcsine-transformed percentage data for all food categories except total reproductive plant material (p-value = 0.668), nectar (p-value = 0.226), and fruit (p-value = 0142). The correlations that reached statistical significance tended to low correlation coefficients. Three dietary PICs had a statistically significant negative correlation with the PIC of log-BM: invertebrates (Spearman's rho = -0.103; p-value = 0.000), total animal material (Spearman's rho = -0.048; p-value = 0.001), and seed (Spearman's rho = -0.028; p-value = 0.046). Five dietary PICs had a statistically significant positive correlation with the PIC of log-BM: total vertebrate material (Spearman's rho = 0.060; p-value = 0.000), total plant material (Spearman's rho = 0.052; p-value = 0.000), vegetative plant structures (Spearman's rho = 0.045; p-value = 0.001), fish (Spearman's rho = 0.041; p-value = 0.003), and terrestrial vertebrates (Spearman's rho = 0.037; p-value = 0.000).

The Spearman's correlation tests on PIC values, using the node-dating backbone topology, found a significant (p-value <0.05; see Table 99) correlation between the PIC of log-BM and those of arcsine-transformed percentage data for all food categories except total reproductive plant material, nectar (p-value = 0.163), fruit (p-value = 0.140), and total vertebrate material (p-value = 0.522). The correlations that reached statistical significance tended to low correlation coefficients. Three dietary PICs had a statistically significant negative correlation with the PIC of log-BM: invertebrates (Spearman's rho = -0.105; p-value = 0.000), total animal material (Spearman's rho = -0.055; p-value = 0.000), and seed (Spearman's rho = -0.034; p-value = 0.015). Four dietary PICs had a statistically significant positive correlation with the PIC of log-BM: total plant material (Spearman's rho = 0.066; p-value = 0.000), vegetative plant structures (Spearman's rho = 0.053; p-value = 0.000), fish (Spearman's rho = 0.040; p-value = 0.004), and total vertebrate material (Spearman's rho = 0.039; p-value = 0.005).

The ordinary Kendall's correlation test found a significant (p-value <0.05; see Table 100) correlation between log-BM and arcsine-transformed percentage data for all food types except nectar (p-value = 0.790), and total vertebrate material (p-value =

0.872). The correlations tended to low correlation coefficients. Three dietary arcsine-percentages had a statistically significant negative correlation with log-BM: invertebrates (Kendall's tau = -0.446; p-value = 0.000), animal material (Kendall's tau = -0.396; p-value = 0.000), and terrestrial vertebrates (Kendall's tau = -0.024; p-value = 0.027). Six dietary arcsine-percentages had a statistically significant positive correlation with log-BM: total plant material (Kendall's tau = 0.397; p-value = 0.000), vegetative plant structures (Kendall's tau = 0.365; p-value = 0.000), fruit (Kendall's tau = 0.224; p-value = 0.000), total reproductive plant material (Kendall's tau = 0.152; p-value = 0.000), fish (Kendall's tau = 0.118; p-value = 0.000), and seed (Kendall's tau = 0.030; p-value = 0.003).

The Kendall's correlation tests on PIC values, using the tip-dating backbone topology, found a significant (p-value <0.05; see Table 100) correlation between the PIC of log-BM and those of arcsine-transformed percentage data for all food categories except total reproductive plant material (p-value = 0.665), nectar (p-value = 0.225), and fruit (p-value = 0.138). The correlations that reached statistical significance tended to low correlation coefficients. Three dietary PICs had a statistically significant negative correlation with the PIC of log-BM: invertebrates (Kendall's tau = -0.078; p-value = 0.000), total animal material (Kendall's tau = -0.036; p-value = 0.000), and seed (Kendall's tau = -0.022; p-value = 0.044). Five dietary PICs had a statistically significant positive correlation with the PIC of log-BM: total vertebrate material (Kendall's tau = 0.047; p-value = 0.000), total plant material (Kendall's tau = 0.039; p-value = 0.000), vegetative plant structures (Kendall's tau = 0.035; p-value = 0.001), fish (Kendall's tau = 0.033; p-value = 0.003), and terrestrial vertebrates (Kendall's tau = 0.029; p-value = 0.007).

The Kendall's correlation tests on PIC values, using the node-dating backbone topology, found a significant (p-value <0.05; see Table 100) correlation between the PIC of log-BM and those of arcsine-transformed percentage data for all food categories except total reproductive plant material (p-value = 0.532), nectar (p-value = 0.163), fruit (p-value = 0.130), and terrestrial vertebrates (p-value = 0.063). The correlations that reached statistical significance tended to low correlation coefficients. Three dietary PICs had a statistically significant negative correlation with the PIC of log-BM: invertebrates (Kendall's tau = -0.080; p-value = 0.000), total

animal material (Kendall's tau = -0.041; p-value = 0.000), and seed (Kendall's tau = -0.026; p-value = 0.015). Four dietary PICs had a statistically significant positive correlation with the PIC of log-BM: total plant material (Kendall's tau = 0.050; p-value = 0.000), vegetative plant structures (Kendall's tau = 0.040; p-value = 0.000), fish (Kendall's tau = 0.033; p-value = 0.004), and total vertebrate material (Kendall's tau = 0.031; p-value = 0.005).

Guild comparisons

The ordinary ANOVA comparing mean log-BM between the dietary guilds recovered by the k-means cluster analysis in mammals reached statistical significance (p-value = <0.001; see Table 101). The Tukey post-hoc test showed the only pairwise comparisons not to reach statistical significance were between Guilds 4 (mixed herbivory composed primarily of reproductive plant parts) and 10 (frugivory), Guilds 6 (mixed herbivory composed primarily of vegetative plant parts) and 7 (omnivory), Guilds 3 (folivory) and 8 (carnivory), and between Guilds 7 (omnivory) and 10 (frugivory). The mean log-BM values for Guild 5 (piscivory s.l.) was significantly greater than those of all other guilds, except Guild 8 (carnivory), (in ranked ascending order): Guild 9 (invertivory s.s.), Guild 2 (invertivory s.l.), Guild 1 (mixed faunivory), Guild 4 (mixed herbivory composed primarily of reproductive plant parts), Guild 10 (frugivory), Guild 7 (omnivory), Guild 6 (mixed herbivory composed primarily of vegetative plant parts), and Guild 3 (folivory). The mean log-BM values of Guilds 3 (folivory), and 8 (carnivory) are larger than those of all guilds except Guilds 5 (piscivory s.l.), and each other, following the same ranked order as the pairwise comparisons between Guild 5 (piscivory s.l.) and the other guilds. While Guilds 5 (piscivory s.l.), 8 (carnivory), and 3 (folivory) represented the guilds with the highest mean log-BM values, the invertivorous guilds (Guilds 2, and 9), and Guild 1 (mixed faunivory) had the lowest. The mean log-BM value of Guild 9 (invertivory s.s.) was lower than those of all other guilds (in ranked order from largest to smallest): Guilds 8 (carnivory), 5 (piscivory s.l.), 3 (folviory), 6 (mixed herbivory composed primarily of vegetative plant parts), 7 (omnivory), 10 (frugivory), 4 (mixed herbivory composed primarily of reproductive plant parts), 1 (mixed faunivory), and 9 (invertivory s.l.). The

latter ranked order of guilds is reflective of the overall sequence of the mean log-BM of the dietary guilds recovered by the k-means cluster analysis in mammals.

The phylogenetic ANOVA comparing mean log-BM between the dietary guilds recovered by the k-means cluster analysis (k=10) in mammals, using the tip-dating backbone topology, was statistically significant (p-value = 0.036). The majority of pairwise p-values, revealed by the post-hoc test, were not statistically significant (p-value = >0.05). Corrected for the non-independence of data points introduced by underlying phylogenetic structure of the data, the mean log-BM of Guild 3 (folivory) was greater than that of Guild 2 (invertivory s.l.). All other pairwise comparisons were not statistically significant (see Table 104).

The phylogenetic ANOVA, using the tip-dating backbone topology, comparing mean log-BM between the dietary guilds recovered by the k-means cluster analysis in mammals with a k-value of 5 fell short of statistical significance (p-value = 0.058). The phylogenetic ANOVA comparing mean log-BM between the dietary guilds recovered by the k-means cluster analysis in mammals with a k-value of 20, was statistically significant (p-value = 0.018; see Table 101). Few pairwise p-values between guilds generated using a k-value of 5 are statistically significant. Corrected for the non-independence in the data introduced by underlying phylogenetic structure, the mean log-BM of Guild 4 (folivory, see Table 26) was significantly larger than those of Guilds 2 (mixed faunivory, see Table 26), and 3 (strict invertivory, see Table 26). All pairwise p-values using the guilds generated with a k-value of 20 are non-significant.

The phylogenetic ANOVA comparing mean log-BM between the dietary guilds recovered by the k-means cluster analysis (k=10) in mammals, using the node-dating backbone topology, was statistically significant (p-value = 0.029; see Table 101). The majority of pairwise p-values revealed by the post-hoc test were not statistically significant (p-value = >0.05). Corrected for the non-independence of data points introduced by underlying phylogenetic structure of the data, the mean log-BM of Guild 3 (folivory) was greater than those of Guilds 9 (invertivory s.s), and 2 (invertivory s.l.). All other pairwise comparisons were not statistically significant.

The phylogenetic ANOVA, using the tip-dating backbone topology, comparing mean log-BM between the dietary guilds recovered by the k-means cluster analysis in mammals with k-values of 5 and 20 were both statistically significant (see Table 101). Few pairwise p-values between guilds generated using a k-value of 5 are statistically significant. Corrected for the non-independence in the data introduced by underlying phylogenetic structure, the mean log-BM of Guild 4 (folivory, see Table 26) was significantly larger than those of Guilds 2 (mixed faunivory, Table 26), and 3 (strict invertivory, Table 26). All pairwise p-values using the guilds generated with a k-value of 20 are non-significant.

The ordinary ANOVA comparing median log-BM between the classical dietary guilds reached statistical significance (p-value = <0.001; see Table 101). The Tukey post-hoc test showed that the pairwise comparisons between all guilds were significant (p-value = >0.05). The mean log-BM for herbivory was greater than those of faunivory and, by a lesser margin, omnivory (see Table 103). The mean log-BM for omnivory was larger than that of faunivory.

The phylogenetic ANOVA comparing mean log-BM between the classical dietary guilds in mammals, using the tip-dating backbone topology, was not statistically significant (p-value = 0.096; see Table 101). The post-hoc test revealed the all pairwise p-values to be non-significant (p-value = >0.05).

The phylogenetic ANOVA comparing mean log-BM between the classical dietary guilds in mammals, using the node-dating backbone topology, was not statistically significant (p-value = 0.114; see Table 101). The post-hoc test revealed the all pairwise p-values to be non-significant (p-value = >0.05).

3.5. Early-branching synapsids

Guild comparisons

The ordinary ANOVA comparing mean log-dentary length (hereafter referred to as log-BM) between the classical dietary guilds in non-mammalian synapsids reached statistical significance (p-value = <0.001; see Table 116). The Tukey post-hoc test showed that only the pairwise comparison between faunivory and omnivory was not statistically significant (p-value = >0.05; see Table 117). The average log-BM of herbivory was larger than that of omnivory, and, to a lesser extent, faunivory.

The phylogenetic ANOVA comparing mean log-BM between the classical dietary guilds in non-mammalian synapsids was not statistically significant (p-value = 0.177); see Table 151. The post-hoc test revealed the all pairwise p-values to be non-significant (p-value = >0.05; see Table 118).

3.6. Non-avian theropods

Guild comparisons

The non-phylogenetic ANOVA comparing mean log-BM between the classical dietary guilds in non-avian theropods reached statistical significance (p-value = <0.001; see Table 119). The Tukey post-hoc test showed that only the pairwise comparison between faunivory and herbivory was not statistically significant (p-value = >0.05; see table 120). The average log-BM of omnivory was smaller than that of faunivory, and, to a slightly lesser extent, herbivory.

The phylogenetic ANOVA comparing mean log-BM between the classical dietary guilds in non-avian theropods was not statistically significant (p-value = 0.29; see Table 157). The post-hoc test revealed the all pairwise p-values to be non-significant (p-value = >0.05; see Table 121).

3.7. Model diagnostics

Diagnostic plots on the linear models showed that residuals strayed from normality. Varying from clade to clade, Q-Q plots of the residuals demonstrated either kurtosis

or (typically right) skewness. The residuals on all diagnostic plots, similarly, showed some stray from homoscedasticity and linearity. In all cases this effect was not extreme but still immediately noticeable. These issues were present in all clades but less pronounced for the turtle dataset. This can likely be explained by (a) the smaller sample size, and (b) the smaller range in body size among turtles.

Diagnostic plots of the linear regressions of the PICs revealed several short-comings, consistent across each clade. Q-Q plots indicated a modest kurtosis in the spread of the residuals on most linear models. The residuals of some models also showed limited skewness. There were also consistent violations of linearity and homoscedasticity. These were largely the result of phylogenetic outliers (i.e., taxa with extreme PIC values but not necessarily extreme trait values). There was a tendency for residuals to cluster in a central point on plots of residuals against fitted values with high-leverage outliers. I opted not to perform a process of systematic outlier exclusion for two reasons. Firstly, it is an extremely time-intensive task, especially given the sizes of the datasets and the number of variables being used. Secondly, these are “phylogenetic outliers” in terms of their PIC values, not the values of the biological traits used to calculate the PIC values. The nodes representing these outliers contain taxa for which there is no basis to exclude on empirical or biological grounds. The data presented by these taxa are informative to the objectives of this study and, particularly in the smaller turtle dataset, their exclusion could negatively impact the interpretive value of the results. I, therefore, decided to complement the parametric analyses with non-parametric correlation tests and I further discuss alternative methods in the discussion section.

3.8. Overview: percentile dietary data

The linear regression models showed that individual dietary categories typically had very weak effects on body size within a clade, even when the correlation was statistically significant. This indicates that overall variation in face-value species body size distributions is large compared to the component of variation that is correlated with diet. When corrected for the non-independence introduced by underlying phylogenetic structure of the data (through regression of PIC values), these effect

sizes are smaller still, suggesting that correlations of evolutionary changes in body size to evolutionary changes of diet are typically very weak or absent. Nonetheless, there were several important patterns evident across the major amniote lineages.

The proportion of invertebrate material in the diet had a negative statistical relationship with body mass in almost every analysis in all major amniote lineages (see Figures 50-61). By contrast, there was a near-universal positive correlation between vertebrate carnivory and body mass. Importantly, this dichotomy between vertebrate- and invertebrate-feeding in relation to body mass was significant when analysing PICs. This indicates that evolutionary transitions from carnivorous to invertivorous diets correlated with evolutionary decreases in body size and that increasing the proportion of vertebrate material to a faunivorous diet drove an evolutionary increase in body size. In turtles and lizards, the proportion of the diet comprised of arthropods had a stronger negative effect on body mass as opposed to durophagy (which, in lizards, had a positive correlation with snout-vent length). This implies that the correlation between invertivory and lower body mass is contingent on the specific type of invertebrates being consumed. In birds, the phylogenetic linear models showed a negative correlation between fish consumption and body mass. These models were confounded by several taxa in the clade Charadriiformes. Charadriiformes, a generally small-bodied clade, evolve piscivory independently multiple times and many are invertivorous (Smith & Clarke, 2015). The PIC values for the clade had a strong leverage effect on the residuals of the PIC regression models in birds resulting in high heteroscedasticity in the linear models. However, the non-parametric correlation tests confirmed a weak positive monotonic relationship between body mass and proportion of fish in the diet in birds.

The contrast between the different subdivisions of plant material was less evident than between vertebrates and invertebrates. Only in mammals did the proportion of vegetative plant material in the diet have a stronger positive statistical correlation with body mass than did the proportion of reproductive plant material. In turtles, the proportion of plant material in general is a poor predictor of body size. In lizards and birds, the percentage of the diet comprised of vegetative plant structures was associated with higher body mass in the non-phylogenetic analyses. However, the PICs of reproductive plant structures, particularly fruit, had a slightly stronger

statistical association with increased body mass than did vegetative plant structures in lizards and birds (see Tables 60-61, 79-80). This indicates that the addition of non-fibrous plant material to the diet predicts a stronger positive scaling in body mass relative to evolutionary relatives (which consumed less, or no, non-fibrous plant material) than does the addition of vegetative plant matter to the diet. This result is particularly informative in the context of evolutionary transitions between dietary guilds (see the discussion for this chapter, and General Thesis conclusion). In birds, nectar consumption correlated with lower body mass in ordinary analyses, though not in phylogenetic analyses. In mammals, all analyses comparing proportional nectar consumption to body mass were not statistically significant. This indicates that nectarivory (which is common in birds but rare in other major amniote lineages) is correlated with decreased body mass but that these two variables are phylogenetically coupled. As such, it is possible that (a) nectarivory drives small body size but has only evolved in select, completely-nectarivorous clades, (b) that an extrinsic selection pressure or adaptive constraint is driving the evolution of both variables, and/or (c) that nectarivores evolve from small-bodied ancestors and retain this trait and so there isn't a significant negative scaling relationship between the PIC values for nectar consumption and body mass. Ultimately, there is insufficient evidence to support any clear hierarchy of the association between the proportion of different kinds of plant material in an animal's dietary composition and body mass across the major amniote lineages.

3.9. Overview: dietary guilds

K-means guilds

The distribution of mean body mass between guilds, if not accounting for non-independence of data points introduced by the underlying phylogenetic structure of the data, reveals a distinct pattern. The comparisons of mean body mass between guilds reveal that there is a statistically significant difference in mean body size between certain guilds wherein carnivores and folivores tend to the highest body masses, and invertivores and nectarivores the lowest (see Figures 62-66). This pattern follows the U-shaped curve in body size distribution recovered by Rob Cooke

et al. (2022). The intermediate body size ranges are filled by omnivores, mixed faunivores, mixed herbivores, frugivores, and granivores. The differences in mean body mass between the guilds occupying the intermediate body size ranges are often not statistically significant in a phylogenetic framework.

When corrected for the non-independence of datapoints introduced by phylogeny, the U-shaped curve is only statistically significant at the extremes of diet and body size (folivory and carnivory versus invertivory and nectarivory) and results differ between clades. This is indicative of overlap in the ranges of body size values between the intermediate guilds. The most important evolutionary shifts accompanied by an increase in body size are, therefore, shifts out of invertivory, and shifts into carnivory or folivory. Birds demonstrate the U-shaped curve in body size distribution (Rob Cooke et al., 2022) more strongly than any other clade. Lizards show a strong division in body mass between insectivores and non-insectivores with carnivores and herbivores occupying the largest body size classes. In both lizards and birds, the differences in mean body mass between the extreme points (carnivory and folivory versus invertivory and nectarivory) are statistically significant in both the ordinary and phylogenetic analyses of variance. Also in lizards, the mean body masses of many of the intermediate guilds (e.g., mixed herbivory and mixed faunivory) are significantly higher than that of strict insectivory when corrected for underlying phylogenetic structure. In a clade that is >80% insectivorous with multiple independent origins of both carnivory and herbivory, this further highlights the predictive power of an evolutionary shift out of insectivory on an increase in body mass. Body mass distribution among mammals also displays the U-shaped pattern but only the difference in mean body mass is between folivory, on the larger extreme, and invertivory, on the smaller extreme, is statistically significant when correcting for the non-independence of the data introduced by phylogeny (see Tables 51, 65, 67, 84, 86, 104, 106). The difference in body mass between carnivores and invertivores in mammals was not statistically significant in the phylogenetic ANOVA. In the case of turtles, which repeat the same pattern in body size distribution superficially, phylogenetic ANOVA results reveal all pairwise p-values between feeding guilds to be non-significant.

Folivory is one dietary extreme on the U-shaped curve correlated with larger body size. In lizards, phylogenetic ANOVA pairwise p-values show that all herbivorous guilds (including mixed herbivory consisting primarily of reproductive plant structures) have significantly larger mean SVL values than the insectivorous guilds, though not of the other guilds. The mean body size values between the different herbivorous guilds in turtles and lizards (see Figure 68) do not differ significantly. In birds and mammals, mean body mass values of folivory, and predominantly folivorous mixed herbivory, are significantly larger than all other guilds, except carnivory and piscivory, in the ordinary ANOVA tests. The mean body masses of folivores are only significantly larger than invertivores when correcting for non-independence of the data introduced by underlying phylogenetic structure. It is important to note that birds lack a strictly folivorous guild and most taxa in the mixed herbivorous guild (including the largest representative; *Struthio camelus*) consume a mix of vegetative and reproductive plant material. Even accounting for those considerations, the mean and maximum values of body mass in both birds and mammals are dominated by herbivores with a predominance of vegetative plant material in the dietary composition is higher than those of most other guilds.

Folviores are excluded from the lowest body size classes in all major amniote lineages, except in turtles. Herbivores are among the largest reptiles, though the largest body sizes in both lizards and turtles belong to carnivores and mixed faunivores (see Figures 62-69). There are also no substantial differences in body size between different herbivorous guilds in the reptilian clades. In birds, mean folivore (more accurately, mixed herbivore) body sizes do not differ greatly from those of carnivores and only large flightless herbivorous birds (like the 111 kg ostrich) are substantially larger than the largest flighted carnivorous birds (e.g., *Vulture gryphus* at 11.3 kg, which is heavier than the largest flighted herbivore: the 11.1 kg *Cygnus buccinator*). The upper size limits of folivores are higher than other guilds in mammals by substantial margins (see Table 130). and large mammals from open habitats (such as elephants, rhinos, hippos, and large artiodactyls; each exceeding one metric tonne of body mass) dominate the upper body mass range for folivores. The smallest folivorous lizard species (*Dipsosaurus dorsalis*, and some *Ctensaura* species) have SVL measurements in the 150-200 mm range. These are larger than the mean SVL for lizards (108 mm), and more than double the lower size

bound for mixed herbivores. Small birds (such as finches in the genus *Pyrrhula*) and mammals (such as bats in the genus *Chiropodomys*, and rodents in the genus *Calomys*) also fit into their clades' respective folivorous guilds at body masses under 30g. While these taxa are in the lower echelons of body mass in those clades, they are far higher than the lower bounds for other dietary guilds. Taken together, these lines of evidence suggest that folivores occupy the largest body size ranges of amniotes but overlap extensively with the body size ranges of other non-insectivorous dietary guilds.

All major lineages of amniotes show a tendency towards large body size in carnivores and piscivores, which constitute the opposite extreme of the U-shaped curve to folivory. However, the mean body mass values of carnivorous/piscivorous guilds only were significantly higher than those of invertivores in phylogenetic analyses of variance in lizards and birds. This indicates that evolutionary shifts into carnivory are a weaker indicator of increased body mass in turtles and mammals than in lizards and birds. Indeed, carnivore body mass values reach the upper limits of body mass in all major amniote lineages except mammals. The largest turtle is *Pelochelys cantorii*, a mixed faunivore with a CL value of 2000 mm; more than 50% larger than the largest herbivore (*Chelonoidis porter*; 1300 mm). Most of the largest lizard taxa (SVL > 700 mm) are all carnivorous and mixed faunivorous varanids (including *V. komodoensis*, and *V. salvator* which can reach snout-vent lengths exceeding 1000 mm). To place the growth potential of carnivorous lizards into perspective, *Varanus komodoensis* has a maximum recorded SVL of 1570 mm. This is more than double that of the largest herbivorous lizard (766 mmm), which is also a varanid (*Varanus bitatawa*). The largest carnivorous flighted birds are scavengers (e.g., *Vultur gryphus*; 11 236 g) and piscivores (e.g., *Pelecanus crispus*; 9 512 g). Among mammals, the largest terrestrial carnivores are bears (e.g., *Ursus maritimus*; 388 750 g). In all clades, except turtles, the smallest carnivores and piscivores are larger than the smallest representatives of most other guilds. The smallest carnivorous lizard is *Varanus primordius* (120 mm; above the mean SVL for all lizards). The smallest mammalian carnivores were sanguivorous vampire bats (e.g., *Diphylla ecaudata*; 29 g), the piscivorous water shrew (*Nectogale elegans*; 32.5 g), and small mustelids (e.g., *Mustela nivalis*; 104 g). The smallest vertebrate-feeding birds were small, piscivorous coraciiforms which weighed under 20g in some

instances (e.g., *Choloceryle aenea*; 14 g). Importantly, carnivores represent the upper body size limits of turtles, lizards, and flighted birds. Therefore, carnivory is correlated with large body size to, at least, the same extent as folivory in all major amniote lineages other than mammals.

The most statistically robust result of this study is the correlation between small body size and an invertivorous diet. In all major amniote lineages, the strictly invertivorous guild had the lowest mean body size (except for birds where that of nectarivory was smaller; see Figures 62-69). In all clades, the generalist invertivorous guilds had higher mean body size values (often by a multiple) than the strictly invertivorous guilds. In all clades, except turtles, there was a statistically significant difference in mean body mass between the strictly invertivorous guild and at least one other guild in both the ordinary and phylogenetic analyses of variance. Aside from comparison of mean values, the upper and lower size bounds of invertivores were substantially lower than those of other guilds for each clade. These lines of evidence indicate (a) that there is a lower upper-body size limit on invertivores (especially insectivores) than other dietary guilds, and (b) that evolutionary shifts into invertivory consistently correlate with a decrease in body size.

There is a sharp division in body size in reptiles between insectivorous and non-insectivorous reptiles. In turtles, the insectivorous guilds had, by a wide margin, the lowest maximum carapace length values which were less than half those of mixed faunivores, herbivores, and omnivores (see Table 124). The durophagous guilds showed also slightly larger body size maxima in turtles (see Table 124). In lizards, insectivory s.s. had, with statistical significance in a phylogenetic context, a lower mean SVL than all other guilds. When not correcting for non-independence of the data introduced by phylogeny, this even held true for the comparison between insectivory s.s. and insectivory s.l. Taxa in the latter only incorporate a small percentage (often <10%) of non-arthropod material into their dietary compositions. Nearly all of the largest strictly insectivorous lizards are legless amphisbaenians, which can attain snout-vent lengths of up to 810 mm. If amphisbaenians and other families composed entirely of legless forms (Cordylidae, Pygopodidae, and Dibamidae) are excluded, the mean snout-vent length for insectivory s.s. drops from 92 mm to 80 mm and the largest taxon is the varanid *Varanus exanthematicus* (750

mm). This value is still among the highest for lizards, however. The contrast in body size values between strict insectivores and other guilds in lizards was far greater at the lower bounds. The smallest lizard species pertaining to insectivory s.l. (*Cricosaura typica*; 40 mm) has an SVL value more than double that of the smallest strict insectivore (*Sphaerodactylus elasmorhynchus*; 17 mm). The gap between the smallest strict insectivore and the smallest insectivore-omnivore (*Lygodactylus decaryi*; 27 mm) is more modest. The minimum SVL values for all other guilds were more than triple that of insectivory s.s.

Body size distribution among the invertivorous guilds in endothermic clades followed much the same pattern as the reptiles. The highest body masses reached by strict insectivores among birds and mammals were the semi-aquatic *Eudyptes sclateri* (5889 g) and *Lobodon carcinophaga* (225 000 g) respectively. The next-largest strictly invertivorous birds were oceanic pelecaniforms, like *Thaumatibis gigantea* (3 515 g), and anseriiforms, like *Tachyeres brachypterus* (3 450 g). The largest invertivorous terrestrial mammals were myrmecophages such as *Orycteropus afer* (52 350 g), *Smutsia gigantea* (33 000 g), and *Myrmecophaga tridactyla* (22 333 g). The smallest invertivorous birds and mammals weighed under 5 g (see Tables 128, 130). In birds and mammals, there is a measurable difference in the lower bounds of body weight between invertivores and other guilds, though it is not as extreme as the difference in the upper bounds of body mass.

There was considerable overlap in body size distribution between the guilds occupying the intermediate space between insectivory/nectarivory and folivory/carnivory. The mean body mass measures of generalist invertivores, omnivores, durophages, and granivores tended towards the smaller end of the body size scale. By contrast, frugivores and mixed herbivores tended towards the larger end of the spectrum. These divisions were weakest in reptiles where there was little difference between ranges in body size between different herbivorous guilds (see Figures 62-69). The contrast was clearest in birds where most taxa are sorted into specialised guilds (see Figure 66). The biggest differences were in the upper bounds of body size. Frugivores, omnivores, and mixed herbivores are capable of attaining relatively high body sizes in all guilds (see Figure 66). The limit on maximum body size in granivores and durophages is lower (see Figure 66).

Classical Guilds

The classical dietary guilds provide a weak explanation of variation in body size when compared to the guilds recovered in the k-means cluster analysis. Other than in lizards, the phylogenetic ANOVAs comparing the classical dietary guilds were not statistically significant in any major amniote lineage included in the current study. This indicates that, corrected for phylogenetic non-independence of datapoints, the differences in body mass between the classical dietary guilds are not significant. The classical dietary guilds provide a poor explanatory variable of body mass variation in comparison to the more complex dietary guilds recovered in the k-means cluster analysis.

Comparisons between the classical dietary guilds revealed two sets of patterns across the extant and extinct alike. In lizards, birds, and non-mammalian synapsids, mean body masses of herbivores were larger than those of faunivores. Omnivory typically held an intermediate position though many pairwise p-values between omnivory and faunivory were not statistically significant. Omnivores had the lowest mean body mass values of the classical dietary guilds in turtles, mammals, and non-avian theropods. Most faunivorous lizard and bird taxa are invertivorous. Several lines of evidence presented in the current study indicate that invertivory is a reliable predictor of small body size. Faunivorous lizards and birds are, therefore, smaller than their omnivorous and herbivorous counterparts. Carnivores and mixed faunivores constitute a larger share of faunivorous taxa in turtles and mammals (see Figures 16-19). Lack of precise dietary data for the fossil taxa makes this distinction impossible to tell with a high degree of certainty. However, many Mesozoic carnivorous theropods were the largest in their ecosystems, making them comparable to extant mammalian carnivores in terrestrial ecosystems (Van Valkenburgh & Molnar, 2002).

4. Discussion

4.1. Overview

The results of the current study do not support an intrinsic link between diet and body mass in major amniote lineages. Corrected for underlying phylogenetic structure, the only consistent pattern between the major lineages of amniotes is that strict invertivores are constrained to the lowest body size classes (see Figures 61-69). Nectarivores also have very low mean body sizes, though this dietary guild is largely confined to birds (see Figures 16-19). Furthermore, the proportion of any singular dietary constituent within an organism's diet has a weak effect on body mass within all major amniote lineages (see Figures 50-61). Combined, these lines of evidence contradict the digestive efficiency hypothesis that correlations detected between diet and body size are likely attributable to factors beyond the inherent biological attributes of food sources that constitute the dietary composition themselves.

The ordinary models did reveal a clearer pattern, however. In general; piscivory, carnivory, and folivory are associated with larger body size. The intermediate ranges of body mass are occupied by mixed herbivory, frugivory, granivory, mixed faunivory, durophagy, and various iterations of omnivory. The smallest body size values are those of invertivores and nectarivores. This pattern is broadly consistent with existing hypotheses on the relationship between diet and body mass (Case, 1979; M. Clauss et al., 2013; R. Cooke et al., 2022; Hiiemae, 2000; Miller & Pittman, 2021; Pough, 1973). However, many of these studies did not utilize phylogenetic comparative methods. The results of the current study reveal a high degree of overlap between these intermediate guilds and, across all major amniote lineages, that pairwise p-values of differences in body mass between guilds, other than between the highest (carnivory, folivory) and smallest extremes of the distribution (insectivory, nectarivory), are seldom significant when corrected for non-independence of data points introduced by underlying phylogenetic structure.

4.2. "Abundance-packet size" hypothesis versus "digestive efficiency" hypothesis

The "abundance-packet size" states that the association between body mass and consumption of a given food source is based on abundance and energy readily available from that food source in the surrounding ecosystem, rather considerations related to the digestive efficiency of the dietary item in and of itself (M. Clauss et al., 2013; Hiiemae, 2000). This contrasts with the "digestive physiology" hypothesis, wherein large body size (especially in folivores) evolves as part of a set of physiological adaptations to a diet consisting of lower-quality food sources (M. Clauss et al., 2013). The distribution of body sizes I recover between guilds, particularly at the extremes of the distribution curve, is consistent with the pattern expected under the "abundance-packet size" hypothesis to explain the link between body size and diet (Clauss et al. 2013; see Figure 70). Animals feeding on large vertebrates and vegetative plant matter are expected to reach the largest body sizes under this hypothesis due to the relative ease of acquiring large quantities of energy from those food sources in the natural environment (M. Clauss et al., 2013; Hiiemae, 2000). Conversely, insectivores and nectarivores are expected to occupy the lowest body size ranges under this hypothesis. because most terrestrial invertebrate food sources are abundant but packaged in discrete, widely dispersed packages making them a reliable and constant supply of energy but not one that can be successfully exploited to provide sufficient energy to sustain large body masses (Carbone et al., 1999; M. Clauss et al., 2013; Hiiemae, 2000). The strong limitations on body size in nectarivory can be explained by the capacity for a flowering plant to produce sufficient nectar to support the energetic needs of a larger pollinator and maintain mechanisms to protect it from competition against the plants "preferred" pollinator (Brown et al., 1978; Feinsinger, 1987; Gartrell, 2000). Other dietary guilds (e.g., granivores, frugivores, and omnivores) then occupy the medium body size ranges.

The digestive efficiency hypothesis would predict (a) that proportion of diet composed of each food source would have a large effect on body size values, (b) the ability to confidently discriminate between mean body sizes of different dietary

guilds, and (c) specifically that fibrous plant material consumption (a surrogate for digestive efficiency) would be a strong predictor of large body size (Bell, 1971; Clauss et al., 2007; M. Clauss et al., 2013; Dudley & Vermeij, 1992; Jarman, 1968). A substantial degree of overlap in the relationship between body size and diet is expected following the “abundance-packet size” hypothesis (M. Clauss et al., 2013). A smaller animal can sustain a diet of lower-quality food material insofar as it is able to meet its caloric demands (M. Clauss et al., 2013). Several outlier taxa have body sizes that contradict expectations given the kinds of food sources in their dietary compositions under the “digestive physiology hypothesis” (e.g., small folivores or large invertivores). The causal relationship between diet and body size, therefore, is very weak despite a superficial pattern in the distribution of body size values between dietary guilds.

The results of the current study provide several lines of evidence that support the “abundance-packet size” hypothesis. Broadly, the linear models, correlation tests, and ANOVA indicate that an animal’s dietary composition has little predictive power over body mass (see Figures 50-61). The only exception, in all major amniote lineages is that invertivory has a negative statistical association with body size (see Figures 62-69). Carnivory, relative to invertivory, correlates to a larger body size in all major amniote lineages except turtles. This distinction is expected under the “abundance-packet size” hypothesis since larger body size in hypercarnivores is driven by the higher energy available in large vertebrate prey (Carbone et al., 1999; De Cuyper et al., 2019). Furthermore, the association between folivory and large body size only statistically significant in mammals when tested in a phylogenetic framework and increasing herbivory in the diet has a very modest effect on body mass (see Tables 98-110). The digestive efficiency hypothesis predicts that folivory (the consumption of low-digestibility food sources) should drive large body size (Bell, 1971; Belovsky, 1997; Jarman, 1968). In lineages other than mammals, which are exceptional as they include the terrestrial megafauna taxa (Klein et al., 2022), the difference in mean body size between folivores and non-fibrous herbivores is not statistically significant in a phylogenetic framework. The largest folivores are dependent on fibrous plant material since they lose the ability to be selective with food source at the maximum body size limits (M. Clauss et al., 2013). This is particularly true for grass-feeding grazers, including the mammalian megafauna,

which rely on gut processing of fibrous plant material (Bodmer et al., 2006; Clauss et al., 2003; M. Clauss et al., 2013). Combined, these lines of evidence refute a causal relationship between large body size and the intrinsic properties of any given food type from a digestive efficiency perspective. I propose that the “abundance-packet size” hypothesis (M. Clauss et al., 2013; Hiiemae, 2000) offers a more plausible explanation for the limited correlation between diet and body size.

4.3. Invertivory-carnivory trade-off

Dietary guilds composed of vertebrate meat have the highest mean body sizes of the respective dietary guilds each in turtles, lizards, and birds. Among faunivores, those consume an increasing proportion of invertebrate material see a decrease in body size (see Figure 68). The dichotomy in faunivory between small-bodied invertivores and large-bodied carnivores has been documented in several studies (Carbone et al., 1999; De Cuyper et al., 2019; Miller et al., 2022; Reuter et al., 2023). This dichotomy typically explained in terms of energy quantity in larger prey, and higher energy intake in larger predators, rather than digestive efficiency trade-offs between invertebrates and vertebrate carrion (Carbone et al., 1999; M. Clauss et al., 2013; De Cuyper et al., 2019; Hedenström & Rosén, 2001; Marti et al., 1993; Vézina, 1985). The trade-off in body size between invertivory and carnivory is, therefore, consistent with patterns expected under the “abundance-packet size” hypothesis, though not necessarily with the digestive efficiency hypothesis.

The energetic trade-off between consumption of invertebrates and vertebrates is attributable to the caloric and protein content readily available in the carcass of a single large-bodied vertebrate as a prey option. This content is low in invertivorous diets relative to the number of individual invertebrates that would need to be found, captured and eaten to provide the same content as a large vertebrate. A large predator would, therefore, expend a prohibitively excessive amount of energy foraging on an invertebrate-dominant diet (Marcus Clauss, Patrick Steuer, et al., 2013; De Cuyper et al., 2019; Sebastián-González et al., 2023; Vézina, 1985). There is evidence for differential biological adaptation between invertivory and carnivory in

terms of oral (Christiansen & Wroe, 2007; Christiansen, 2007; Morales-García et al., 2021), and gut (Hume, 2003) processing between invertivores and carnivores. However, the demarcation between invertivory and carnivory in terms of anatomical adaptation is not abrupt (Van Valen, 1969), many carnivores supplement their diets with invertebrate material (Koike et al., 2012), and some carnivorous taxa are invertivorous in the earlier stages of their ontogeny (Purwandana et al., 2016; Tucker et al., 1996). The most fundamental difference between large- and small-bodied faunivores documented in the literature is that larger carnivores take larger (vertebrate) prey relative to their body sizes, supplying larger quantities of energy and cover larger home ranges to acquire that prey (Carbone et al., 1999; De Cuyper et al., 2019; McNab, 1963, 1978, 2000; Vézina, 1985). The evolution of large body size in carnivores is, therefore, driven by energy availability in the environment rather than different innate properties of vertebrate material to invertebrate material.

There are several examples of large-bodied invertivores in the datasets I use in the current study (Angielczyk et al., 2015; Meiri, 2018; Wilman et al., 2014), though there are explanations for these exceptions that uphold the “abundance-packet size” hypothesis. In turtles, durophages are larger than insectivores. Lindeman (2016) found that species of the turtle genus *Graptemys* which fed primarily on large molluscs had larger body sizes than their non-molluscivorous congeners. This study was limited to a single genus but it is intuitive that aquatic gastropods and molluscs (anchored to the substrate) would provide large quantities of energy relative to energy expended in foraging, than would hunting more agile and spatially dispersed insects. In lizards, the largest insectivores are legless forms (which have longer snout-vent-lengths because of unique locomotory and substrate adaptations; Meiri 2010) and members of Varanidae (a clade which tends to large body size regardless of dietary guild; Pianka 1995). In birds and mammals, the largest invertivorous taxa feed on marine invertebrates. Additionally, in mammals, myrmecophagous taxa reach the largest body sizes among terrestrial invertivores. Both marine invertebrates and social insects provide large concentrated sources of energy and thus facilitate the evolution of larger body size (R. Cooke et al., 2022; McNab, 1984, 2000). All mammalian invertivores that exceed the 21.5 kg threshold of Carbone et al. (1999), at which faunivores transition to feeding on prey with larger body sizes than the predator, are either myrmecophages (e.g., *Myrmecophaga tridactyla*; 22.33

kg) or marine forms (e.g., *Balaeonoptera musculosus*; 19900 kg). Myrmecophagy has also been demonstrated to correlate with increased SVL in lizards (Cavalcanti et al., 2023). The intermediate range occupied by mixed faunivores in lizards and mammals, and some generalist invertivorous in birds, further illustrate that there is a degree of overlap in body size ranges between invertivores and carnivores that is expected under the “abundance-packet size” hypothesis (M. Clauss et al., 2013; Hiiemae, 2000).

Prey size, and predator-prey size ratio, has been repeatedly demonstrated to be correlated with body mass in mammalian and avian predators (Barton & HOUSTON, 1993; Carbone et al., 1999; De Cuyper et al., 2019; Hedenström & Rosén, 2001; Jaksic, 1983). Body size in terrestrial predators is also constrained by the speed, stealth and endurance needed to effectively hunt (Gittleman, 1985, 2013; Gittleman & Harvey, 1982; Taylor, 1989). Flighted birds are further limited by the need to effectively seek, chase, and hunt the prey, and lift it off the ground (ANDERSSON & NORBERG, 1981; Dudley & Vermeij, 1992; Masman & Klaassen, 1987; Miller et al., 2022). In lieu of specialised adaptations to an aquatic or semi-aquatic lifestyle, a terrestrial piscivorous mammal can be assigned to the same class of predators as those that take small, terrestrial vertebrate prey. This would explain why fully terrestrial mammalian piscivores tend to body sizes below 10 kg (e.g., *Prionailurus planiceps*; 6 750 g, *Genetta piscivore*; 1 648 g). The largest flighted bird is a scavenger (*Vultur gryphus*) which is far less constrained by the need to hunt and carry its prey but would benefit from larger body size owing to the need to store more body fat and travel wide distances (Houston, 1974a, 1974b; Moleón et al., 2014; Ruxton & Houston, 2004). The only imposition on a scavenging bird is the need to maintain powered flight which is energetically costly at large body sizes: hence, vultures are large and move by static soaring (Dudley & Vermeij, 1992; Masman & Klaassen, 1987). Actively predatory birds are further constrained by the requirements for speed and manoeuvrability while hunting. There is no reason to assume, *prima facie*, that feeding on fish would impose a different constraint on bird body size than feeding on small terrestrial vertebrates. Hence, carnivorous and piscivorous birds have similar mean body masses.

4.4. The spectrum of herbivory

The data collected here do not provide strong support for a central tenet of the digestive efficiency hypothesis: that the evolution of folivory selects for larger body size on the basis of digestive efficiency (Bell, 1971; Belovsky, 1997; Jarman, 1968). Statistical analyses in the current study reveal a very high degree of overlap in body size classes between different herbivorous guilds. The ordinary analyses of variance revealed that folivores have the largest average body mass values, followed by mixed herbivores, frugivores, granivores, and, finally, nectarivores. This pattern is expected under the U-shaped curve in body mass distribution (Rob Cooke et al., 2022) and the “abundance-packet size” hypothesis (M. Clauss et al., 2013; Hiiemae, 2000). This distribution of body mass values was most evident in birds where a high proportion of taxa belong to specialised herbivorous guilds (such as nectarivory and granivory, which are not present in the other clades). It was also evident in mammals where the upper-limit of body masses of terrestrial folivores were the highest of any taxa included in the current study. It was less evident in the reptilian clades where more taxa are mixed herbivores than folivores and mean body sizes between these guilds do not differ significantly. This result is not unexpected since mammals occupy the “megafauna” role in contemporary terrestrial ecosystems and thus the niche of “very large bodied folivore” is filled mostly by mammalian taxa, as it was by non-avian dinosaurs in the Mesozoic (Klein et al., 2022). The upper limit on body size in mammalian folivores is therefore higher than in other clades but there is still significant overlap between folivory and other herbivorous guilds, as is expected under the “abundance-packet size” hypothesis (Clauss et al., 2007; M. Clauss et al., 2013).

The phylogenetic analyses showed that much of the variation in body mass between different herbivorous dietary strategies was not statistically significant when accounting for non-independence of the data introduced by underlying phylogenetic structure. The phylogenetic analyses of variance showed that the mean body mass values of all herbivorous guilds in lizards, predominantly folivorous mixed herbivory in birds, and folivory in mammals were significantly higher than the invertivorous guilds but not the other herbivorous guilds, when accounting for phylogenetic non-independence of data. In the case of birds, the only significant pairwise p-value

between two herbivorous guilds was between mixed herbivory and nectarivory (see Tables 84, 86). The phylogenetic linear models and correlation tests, however, showed that percentage of vegetative plant material in the dietary composition showed only a very weak correlation with body size. In the case of lizards and birds, the percentage of reproductive plant structures, particularly fruit in the case of birds, in the diet had a stronger positive correlation to body mass than did vegetative plant structures. The results of chapter two (see Figure 49) and previous studies (Amador & Giannini, 2021; Herrel, Vanhooydonck, Joachim, et al., 2004; Reuter et al., 2023) indicate that most evolutionary transitions from faunivory to omnivory/herbivory are between insectivorous taxa and taxa that consume substantial proportions of non-fibrous plant material in their dietary composition. The higher correlation co-efficient values for PICs of reproductive plant material could then be indicative of increased body mass following an evolutionary shift out of invertivory.

Given the high rate of transition between folivorous guilds and guilds composed primarily of reproductive plants recovered in Chapter Two (see Chapter Two, Results) and hypothesized by previous work (Bodmer, 1989; Kunz & Ingalls, 1994; Lambert, 1998; Rosenberger et al., 2011) the results of the phylogenetic tests provide a particularly strong line of evidence against the digestive efficiency hypothesis. Given the phylogenetic proximity of these feeding strategies, the digestive efficiency hypothesis should predict that a difference in body size between animals consuming (less digestible) vegetative plant material and (more digestible) reproductive plant structures (particularly seeds and fruit) would remain significant in phylogenetically corrected tests. That this is not the case contradicts the notion that adaptations to low digestive efficiency of fibrous plant material drives the evolution of large body size. In mammals, the correlation coefficients and regression slopes were almost equal, though those for vegetative plant material were marginally higher (see Figure 59, 61). The exceptional result in mammals can be explained by the megaherbivores. It is hypothesised that the forebears of large mammalian grazers were mixed herbivores (Bodmer et al., 2006; Bodmer, 1989, 1990; Kunz & Ingalls, 1994; Rosenberger et al., 2011). Increased folivory in mammalian lineages would, therefore, drive a shift to increased body size when accompanied by a shift to an open environment. This conclusion is an inference and would need to be tested empirically.

The percentage of vertebrates in the dietary composition had a stronger correlation with increased body mass in the phylogenetic correlation tests and linear models than did vegetative plant material in turtles, lizards, and birds. Furthermore, differences in this effect between vegetative and reproductive plant material were less pronounced than was the analogous distinction between vertebrates and invertebrates. This is instructive since no previous study has claimed that the difference in body size between invertivores and carnivores is driven by adaptations to digestive efficiency (Carbone et al., 1999; De Cuyper et al., 2019; Gittleman, 2013; McNab, 2000; Tucker et al., 2016; Vézina, 1985). Since the physiological requirements for carnivory and invertivory are essentially identical (Hume, 2003; Schondube et al., 2001; Van Valen, 1969), the difference in body size ranges between the two guilds is driven by available in energy in prey source relative to energy expended acquiring it (Carbone et al., 1999; De Cuyper et al., 2019). This is significant, as the results of the current study demonstrate, in a phylogenetic framework as evolutionary shifts into carnivory typically originate from invertivorous ancestors.

The “abundance-packet size” hypothesis holds that the largest body size classes of amniotes are restricted to folivory because (a) fibrous plant material is the most abundant food source in most terrestrial environments, and (b) the ability to be selective with choice of food source is constrained to lower body sizes (M. Clauss et al., 2013; Owen-Smith, 1988). This is evidenced by the fact that the upper bounds of body size for folivores is substantially higher than for other herbivorous guilds in birds and mammals (see Figure 66). However, there is a high degree of overlap in body size ranges between different herbivorous guilds at the small and medium body size classes (see Figure 66). The overlap in body size between herbivorous guilds is consistent across size classes in turtles and lizards. Herbivorous lizards are typically only found in insular environments, free of mammalian competition (Cooper Jr & Vitt, 2002; Head et al., 2013; Zimmerman & Tracy, 1989). With limits on terrestrial non-avian reptile body mass imposed by factors like thermoregulation (Zimmerman & Tracy, 1989) and sprawling locomotion (Pianka, 1995), herbivorous lizards are unable to effectively compete with mammals for the niche of terrestrial megaherbivore. Folivorous and mixed herbivorous lizards, therefore, may have

similar body size ranges because folivorous lizards are excluded from the larger size classes of amniotes by ecological competition and/or other, unrelated factors.

The distribution of body mass values between different herbivorous guilds in mammals supports the “abundance-packet size” hypothesis (M. Clauss et al., 2013; Hiiemae, 2000) from a perspective of energy availability. Folivorous mammals from grassland and savannah habitats (e.g., *Loxodonta africana*, *Hippopotamus amphibius*, *Bos taurus*, and *Giraffa camelopardalis*) are the largest extant terrestrial amniotes (Onstein et al., 2022; Owen-Smith, 1988). Mixed herbivores from similar habitats (e.g., *Rhinoceros unicornis*; 1 602 333 kg) also reach the upper echelons of the body mass ranges of Amniota. Folivorous grazers in open environments consume a widely abundant food source (grass) and are able to ingest large amounts due to adaptations to gut-processing. Herbivores that rely on oral-processing mechanisms are constrained in body size by higher foraging times needed to ingest similar amounts of energy as gut-processors (Bodmer et al., 2006; Clauss et al., 2003). Mammals at body sizes close to the mean for the clade are often frugivores and are primarily found in forested environments where fruit is plentiful year round (Bodmer et al., 2006; Pineda-Munoz et al., 2016). Several small and average-sized arboreal mammals from densely-wooded habitats have also evolved folivory, and many adopt a mixed herbivorous approach (Cork, 1996; Foley & Cork, 1992; Liu et al., 2020; McNab, 1978; Pauli et al., 2016). There is, therefore, a substantial overlap in body size distributions between different herbivorous guilds in mammals except at the upper end of the body size range, which is occupied by large folivores subsisting on a widely available food source and are able to consume it in large quantities (Bodmer et al., 2006; Bodmer, 1990; M. Clauss et al., 2013; Hiiemae, 2000).

The patterns in body size distribution between herbivorous guilds seen in mammals is mirrored in birds. The largest bird taxa are flightless birds which include partially folivorous forms (e.g., *Struthio camelus*), as well as frugivorous and omnivorous taxa (e.g., Casuariiformes). Among flighted birds, partially folivorous anseriiforms (e.g., *Cygnus buccinator*) still reach higher body mass values than the largest flying frugivores (e.g., *Crax rubra*). The mean body mass for granivorous birds is substantially lower than for mixed herbivores/semifolivores and frugivores (see

table). This could be attributed to (a) smaller food size of seeds compared with fruits and leaves (Miller & Pittman, 2021; Miller et al., 2022), and (b) the fact that granivory often evolves in desert ecosystems where food sources are often scarce (Brown et al., 1979; Reichman, 1979). It should be noted that the difference in mean body mass between frugivory and granivory is not statistically significant when correcting for underlying phylogenetic non-independence of the data (see Tables 84, 86). There is substantial overlap in body mass between mixed herbivorous/partially folivorous, frugivorous, and granivorous birds at the small- and mean size ranges among birds (see Figure 66). Furthermore, several small, flighted birds do evolve folivory (López-Calleja, 2000). As with mammals, there is substantial overlap in body size distributions between different herbivorous guilds except at the upper size limits. Folivores reach the largest body sizes but are not excluded from the smaller body size classes.

Birds are the only major amniote lineage to clearly demonstrate the dichotomy between the two extremes of herbivory in relation to body size: folivory versus nectarivory. The ordinary ANOVA do show a strong separation of body size between the herbivorous guilds in birds (ranked nectarivory < granivory < frugivory < mixed herbivory). However, the only difference to be statistically significant in the phylogenetic analysis is between nectarivory and mixed herbivory. Previous research on birds has shown that differences in measures of the digestive tract between dietary guilds are not significantly different when corrected for underlying phylogenetic non-independence (Duque-Correa et al., 2022). It has also been suggested that the size difference between granivorous and frugivorous birds can be explained by the size (and therefore energy content) of food taken (Miller & Pittman, 2022). It is possible, therefore, that body size, like gastrointestinal morphology, is conserved in specific bird clades, which tend to evolve eating habits to best suit the energy requirements for their body sizes rather than diet driving body size evolution directly. The correlation between nectarivory and small body size, like the correlation between insectivory and small body size, is robust to phylogenetic comparative methods. Nectarivorous birds have significantly lower minimum, maximum, and mean body mass values than any other guild in birds (see Figure 64). Unlike invertivores, which are small on average but include numerous large-bodied taxa,

the largest nectarivorous bird species (*Chalcopsitta duivenbodei*) weighs only 218 g. This is lower than the mean body size for all birds (250 g; see Table 127).

The relationship between small body size and nectarivory is consistent with the "abundance-packet size" hypothesis (M. Clauss et al., 2013; Hiiemae, 2000). Nectar is an extremely high-quality energy source (Ayala-Berdon & Schondube, 2011; Brown et al., 1978; Gartrell, 2000; Teixeira et al., 2013). Many plant species have evolved a symbiotic relationship with nectarivores which act as pollinating agents (Feinsinger, 1987; Fleming et al., 2009; Hansen et al., 2006; Olesen & Valido, 2003). Nectarivorous birds are, as such, selective feeders. The "abundance-packet size" hypothesis predicts that small-bodied taxa are able to be selective due to lower energy requirements, which enables a preference for highly digestible food sources like nectar (M. Clauss et al., 2013). Larger nectarivores are able to travel further and are, thus, more effective pollinators than their smaller counterparts (Brown et al., 1978). However, producing sufficient nectar and defending it from competitor nectarivores is an energetically costly process for plants. Therefore, nectarivores are constrained to lower body size classes by the fact that it would be biologically unfeasible for plants to produce the quantities of nectar needed to sustain larger body sizes in their pollinating agents (Brown et al., 1978). This size constraint is further enhanced by the fact that nectarivores expend large amounts of energy in the process of extracting their food source from the flower (Wolf et al., 1975; Wolf et al., 1972). Nectarivory is, therefore, a model example of animals being constrained to smaller body size by a selective-feeding dietary strategy on a highly-nutritious food source that is only available in small packages, taken in several bouts of feeding.

4.5. Limitations

In the current study, I present the results of phylogenetically-corrected and ordinary linear models, correlation tests, and analyses of variance. Given that residual errors in models using taxonomic units as datapoints may not be independently and identically distributed due to underlying phylogenetic structure, it often recommended that such models be limited to only phylogenetically-corrected methods (Freckleton,

2009). It is, however, informative to compare ordinary and phylogenetically-corrected results since a relationship that is significant in an ordinary or generalised linear model but not in a phylogenetic model may simply indicate that a functional association between two variables is real but phylogenetically clustered (Carbone et al., 2014; Marcus Clauss, Marie T Dittmann, et al., 2013; Clauss et al., 2014).

For the purposes of the current study, which boasts a very broad taxonomic/phylogenetic coverage, a relationship that is significant in an ordinary model but not in a phylogenetic model provides sufficient evidence to indicate that a superficial relationship may be better explained by phylogeny or other extrinsic factors. Aside from the “abundance-packet size” hypothesis, which I consider to be the most plausible explanation of the results within the scope of this study, it also entirely possible that lineage-specific constraints, independent of diet, impact body size. For example, the results of the current study strongly refute the idea of a relationship between diet and body size in turtles when correcting for underlying phylogenetic structure. This is consistent with the limited existing research on the topic (Herrel et al., 2002), and it has been previously proposed that body size in turtles is the result of adaptive constraints independent of diet and other commonly-assumed correlate variables (Farina et al., 2023). Future research could focus on empirically testing whether the association between diet and body size across Amniota is best explained by ecological considerations, extrinsic factors in phylogenetic history, an intrinsic association involving other co-variates, or a combination of the above. Such a study would deploy similar methods to those used in the current study but will require the incorporation of additional explanatory variables (e.g., habitat, substrate, and a myriad of physiological and anatomical indicators).

A major limitation of interpreting the results of the statistical tests used in the current study lies in the spread of residuals in the data. I address these concerns here by deploying non-parametric alternatives to ordinary linear regression. I chose correlation tests over phylogenetic generalized least squares (PGLS) modelling here because regression models assume precision in the measurement of the predictor variable (Sokal & Rohlf, 1995). Given the breadth of this study, such well-parsed data are currently impossible for a variable such as percentage of diet composed of

different food types. I, therefore, judged non-parametric correlation tests to be a more appropriate method of testing the relationship between diet and body size using the data currently available. This is particularly true of the bird and mammal datasets wherein the percentage dietary data are parsed in intervals of 10% (Wilman et al., 2014). Going forward, I propose the exploration of alternative techniques to answering this question with data parsed in this manner, such as robust phylogenetic regression (Adams et al., 2022).

5. Conclusion: lessons for the fossil record

Results from the ANOVA analyses conducted on the two fossil clades included in this study (non-mammalian synapsids, and non-avian theropods) are, effectively,

inconclusive. Uncorrected for the non-independence of data points introduced by phylogeny, the mean body mass of herbivorous non-mammalian synapsids was larger than that of both faunivores and omnivores to a similar extent statistically. In non-avian theropods, the mean body masses of both herbivores and faunivores were larger than those of omnivores. Correcting for non-independence of data points introduced by underlying phylogenetic structure of the data using phylogenetic ANOVA, the body size differences between these guilds were not statistically significant in either group of fossil taxa. It is possible that the lowest body sizes were among omnivores because the sample includes a high proportion of hypercarnivores and folivores due to preservation bias for larger taxa, though this is not demonstrable empirically due to the taxa being assigned to dietary guilds based on different criteria depending on the source publication (Uhen et al., 2023). It is difficult to assign precise dietary guilds to fossil taxa is inferred from indirect evidence in dental and skeletal morphology rather than direct observation (Casey & Post, 2011; Hopkins et al., 2022; Miller & Pittman, 2021; Ungar & Williamson, 2000).

The more comprehensive analysis of diet and body size in the extant taxa in this study, when compared to the more limited study using classical dietary guilds, reveals that the classical dietary guilds do not sufficiently explain the relationship between diet and body mass. I also conclude that, even when accounting for the many subtleties of dietary classification, diet is simply a poor predictor of variations in body mass among amniotes. Previous research has offered the evolution of herbivory as having a potential causal effect on increased body size in Palaeozoic tetrapods (Reisz & Frobisch, 2014), and the exceptional gigantism in sauropod dinosaurs (Paul M Barrett, 2014; Farlow, 1987; Sander et al., 2011). It should be noted that these studies do discuss alternate factors influencing body size beyond the physiological requirements of herbivory. Equally, several studies have cast doubt on the notion that diet and body size are intrinsically linked in fossil taxa (Brocklehurst, 2016; Brocklehurst et al., 2017; M. Clauss et al., 2013; Zanno & Makovicky, 2013). These studies all deploy the classical dietary guilds as predictor variables. To my knowledge, there is currently no large-scale study on the evolution of diet and body size in fossil taxa that utilizes dietary guilds other than “faunivore”, “herbivore”, and “omnivore”. Based on the results of the current study I believe that future studies on the macroevolution of body size on extinct amniote lineages should

not include diet as singular predictor variable of body size evolution in amniotes through deep time, but rather contextualize diet within other extrinsic factors such as ecological opportunism. One potential enhancement to such studies would be the widespread inclusion of invertivory as a dietary variable (alongside the classical dietary guilds). Placed in a phylogenetic framework, the only consistent correlation between diet and body mass across major amniote lineages is that between invertivory (specifically feeding on non-social insects) and small body mass, specifically a lower maximum body size relative to other dietary guilds. I believe that the inclusion of "invertivory" as a dietary guild in a broad dataset of extinct taxa may prove informative in macroevolutionary studies on body size through deep time. The application of continuous dietary metrics such as multi-proxy stable isotopes (Casey & Post, 2011; Davis & Pineda Munoz, 2016; DeNiro & Epstein, 1981; Schoeninger & DeNiro, 1982; Struck et al., 2002) may also better refine guild discrimination in extinct taxa which could allow future research to more accurately replicate research on extant taxa in extinct lineages.

In the current study, I conclude that diet, defined in the classical sense, is a poor predictor of body size in two extinct lineages and four extant lineages (covering a majority of modern terrestrial amniote taxa). I propose the following recommendations to palaeobiological investigations into body size and diet evolution going forward: (a) diet should not be a priori regarded as a determinant of, or correlate to, body size in extinct taxa but rather considered in conjunction with other variables including extrinsic factors, and (b) investigations into the association between diet and body size are better suited to evolutionary shifts away from invertivory towards carnivory (and, in some cases, towards omnivory and herbivory) rather than comparisons between herbivores and carnivores. It is also crucial to consider the effect of the underlying phylogenetic structure of the data as this can significantly alter the interpretation of results. More specifically, following the work of M. Clauss et al. (2013), there is a need to empirically test role of ecological opportunism in relation to the distribution of caloric energy between different food sources more widely in extinct clades.

6. Figures

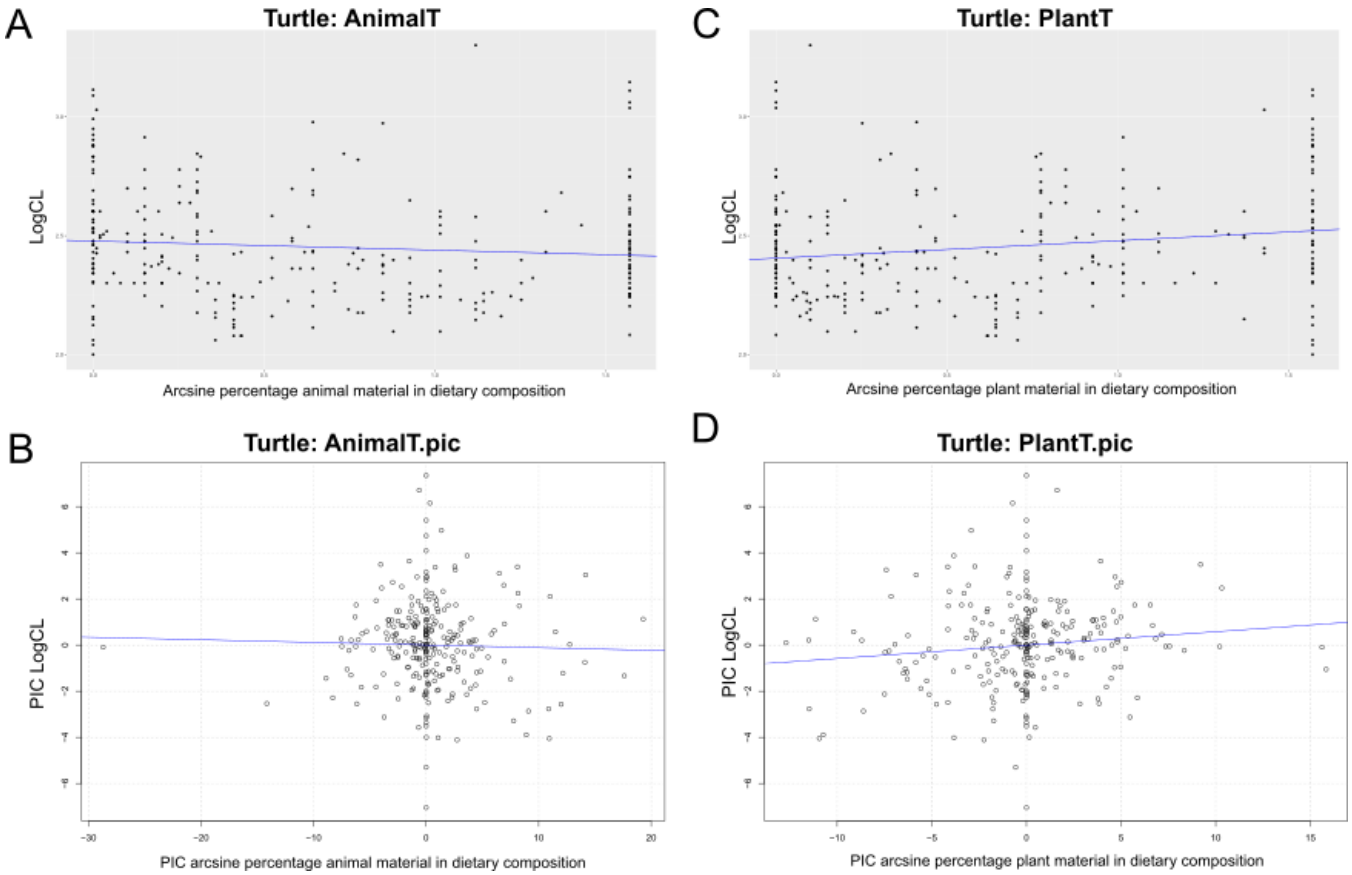


Figure 50: Ordinary, and phylogenetic linear models between log-carapace length (logCL), and arcsine-percentage of total animal (A, B), and total plant (C, D) material in the dietary compositions of turtle taxa. Abbreviations: **AnimalT**, percentage of total animal material in the diet; **PlantT**, percentage of total plant material in the diet; **PIC**, phylogenetic independent contrasts.

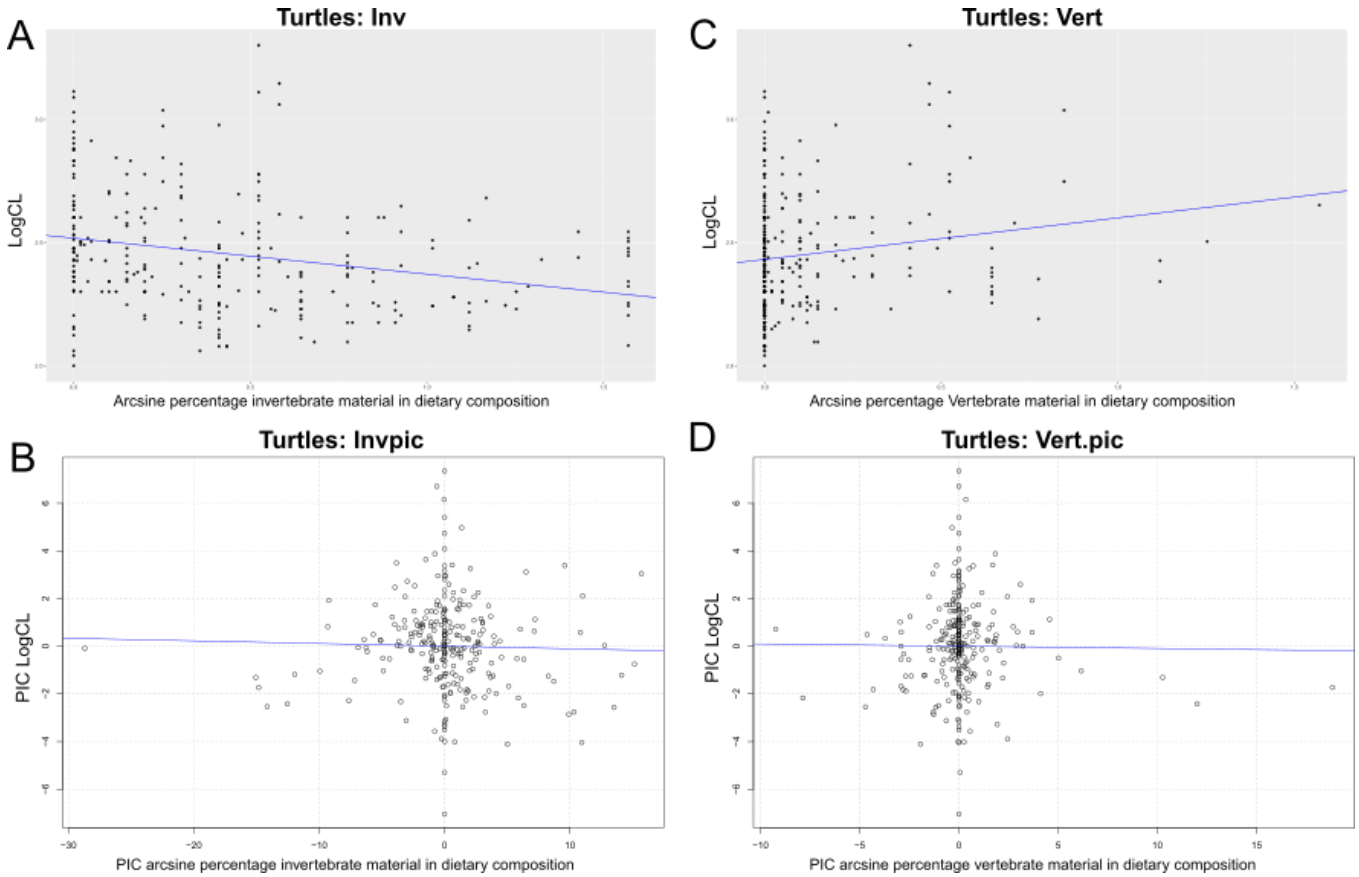


Figure 51: Ordinary, and phylogenetic linear models between log-carapace length (logCL), and arcsine-percentage of total invertebrate (A, B), and total vertebrate (C, D) material in the dietary compositions of turtle taxa. **Abbreviations**: **Inv**, percentage of total invertebrate material in the diet; **Vert**, percentage of total vertebrate material in the diet; **PIC**, phylogenetic independent contrasts.

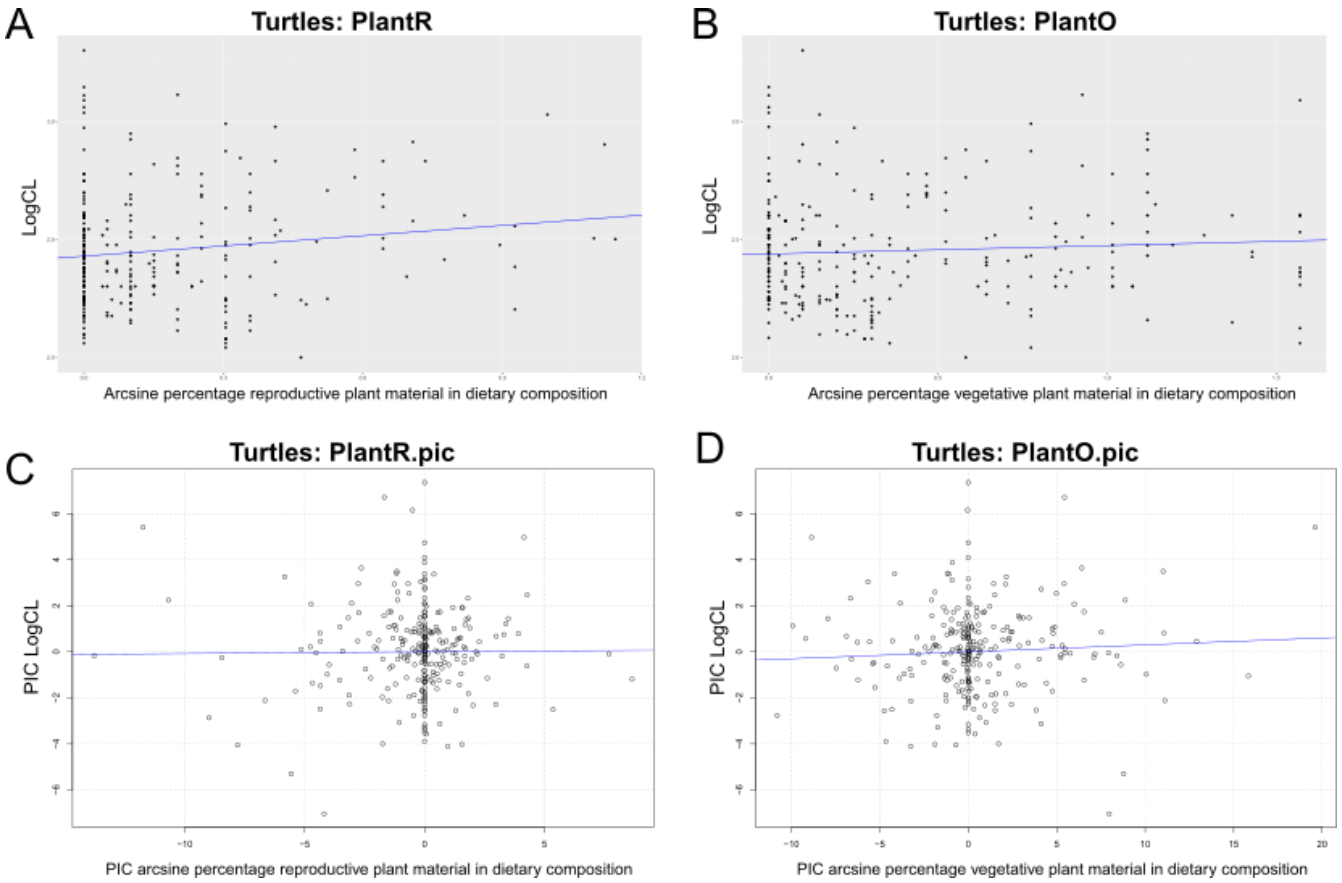


Figure 52: Ordinary, and phylogenetic linear models between log-carapace length (logCL), and arcsine-percentage of total reproductive (A, B), and total vegetative (C, D) material in the dietary compositions of turtle taxa.
Abbreviations: **PlantR**, percentage of total reproductive plant material in the diet; **PlantO**, percentage of total vegetative plant material in the diet; **PIC**, phylogenetic independent contrasts.

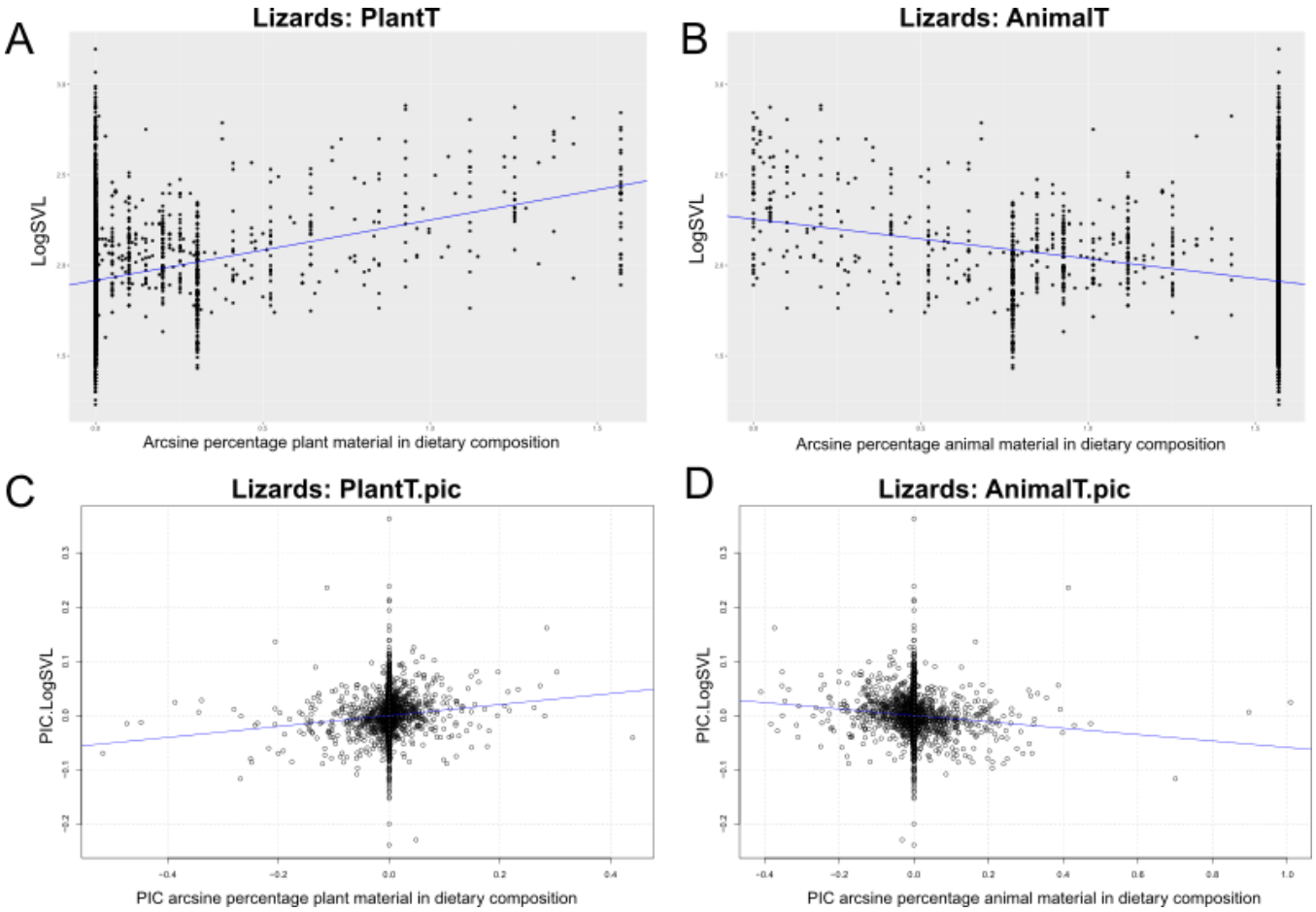


Figure 53: Ordinary, and phylogenetic (topology of Tonini et al. 2016) linear models between log-snout-vent length (logSVL), and arcsine-percentage of total animal (A, B), and total plant (C, D) material in the dietary compositions of lizard taxa. Abbreviations: **AnimalT**, percentage of total animal material in the diet; **PlantT**, percentage of total plant material in the diet; **PIC**, phylogenetic independent contrasts.

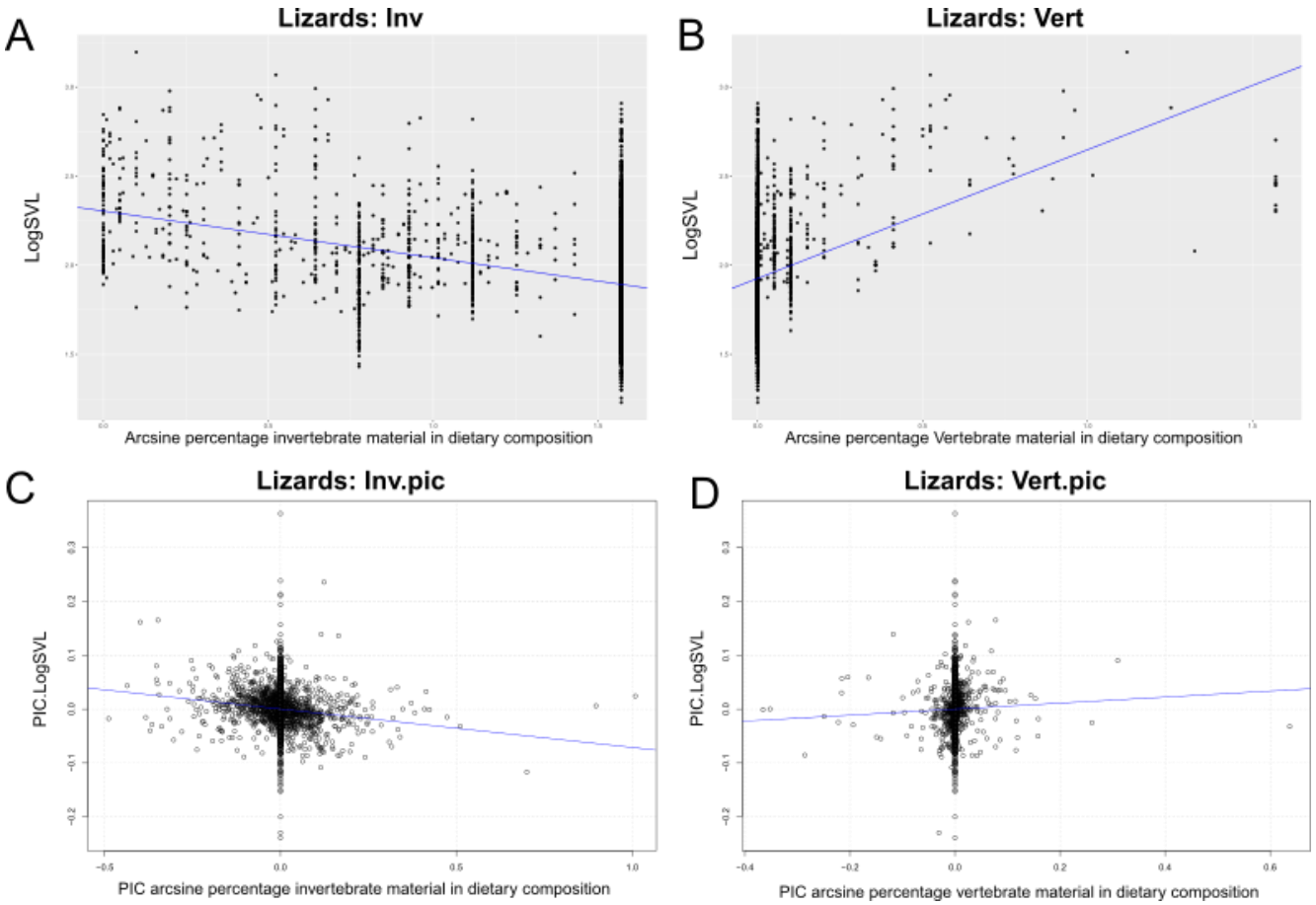


Figure 54: Ordinary, and phylogenetic (topology of Tonini et al. 2016) linear models between log-snout-vent length (logSVL), and arcsine-percentage of total invertebrate (A, B), and total vertebrate (C, D) material in the dietary compositions of lizard taxa. Abbreviations: **Inv**, percentage of total invertebrate material in the diet; **Vert**, percentage of total vertebrate material in the diet; **PIC**, phylogenetic independent contrasts.

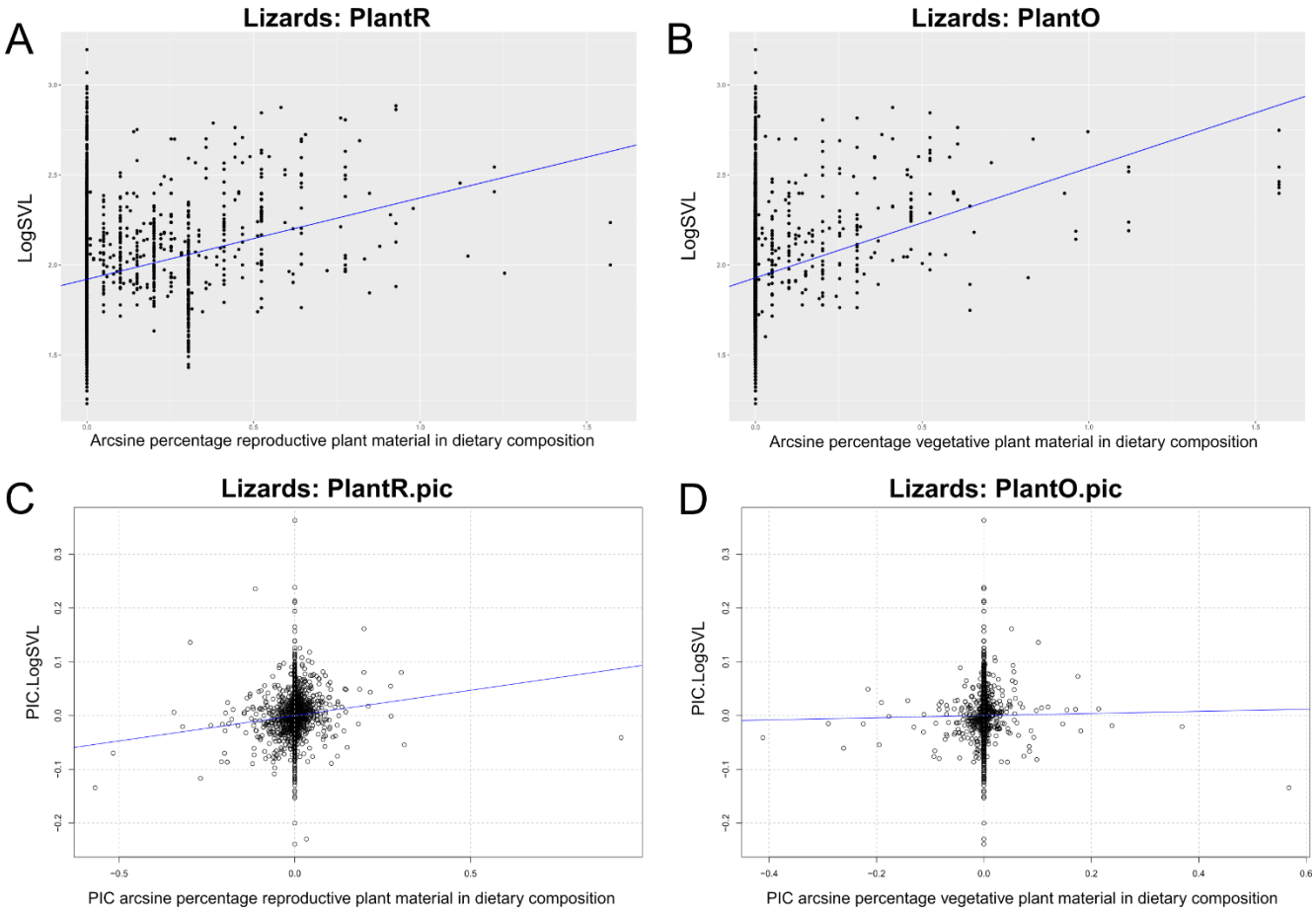


Figure 55: Ordinary, and phylogenetic (topology of Tonini et al. 2016) linear models between log-carapace length (logCL), and arcsine-percentage of total reproductive (A, B), and total vegetative (C, D) material in the dietary compositions of lizard taxa. Abbreviations: **PlantR**, percentage of total reproductive plant material in the diet; **PlantO**, percentage of total vegetative plant material in the diet; **PIC**, phylogenetic independent contrasts.

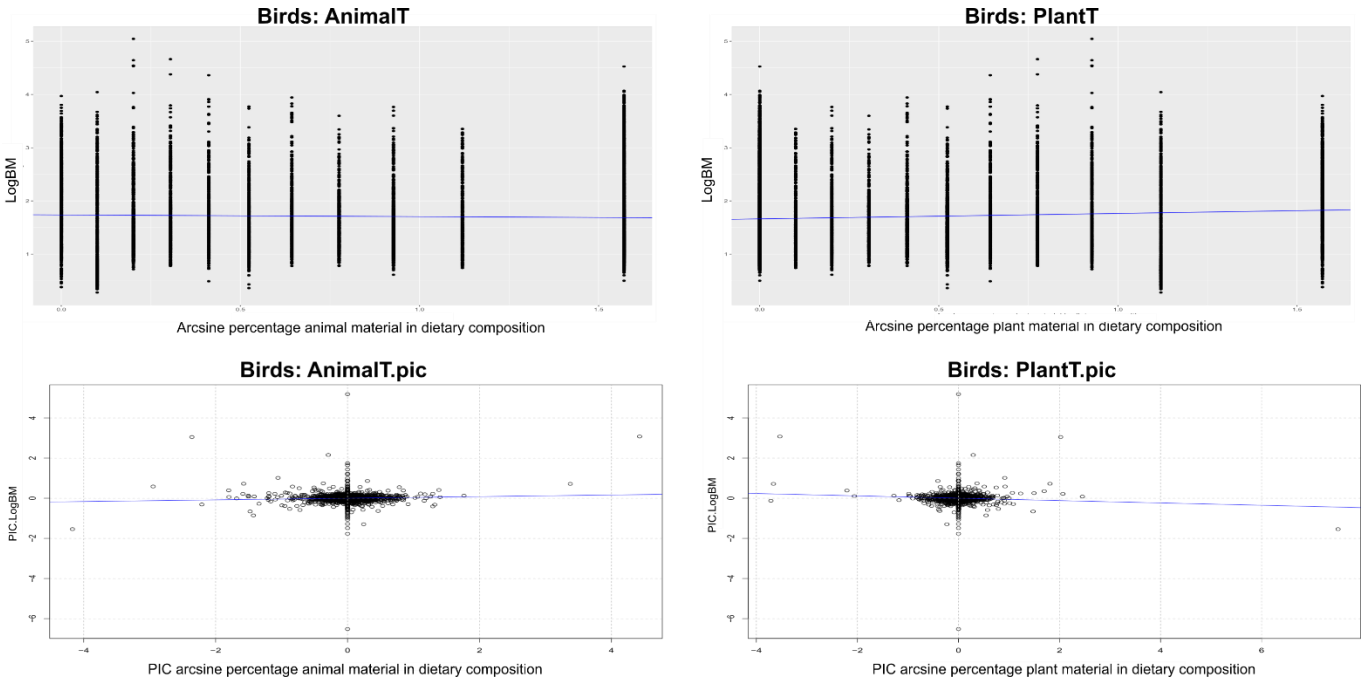


Figure 56: Ordinary, and phylogenetic (backbone topology of Hackett et al. 2008) linear models between log-body mass (logBM), and arcsine-percentage of total animal (A, B), and total plant (C, D) material in the dietary compositions of bird taxa. Abbreviations: **AnimalT**, percentage of total animal material in the diet; **PlantT**, percentage of total plant material in the diet; **PIC**, phylogenetic independent contrasts.

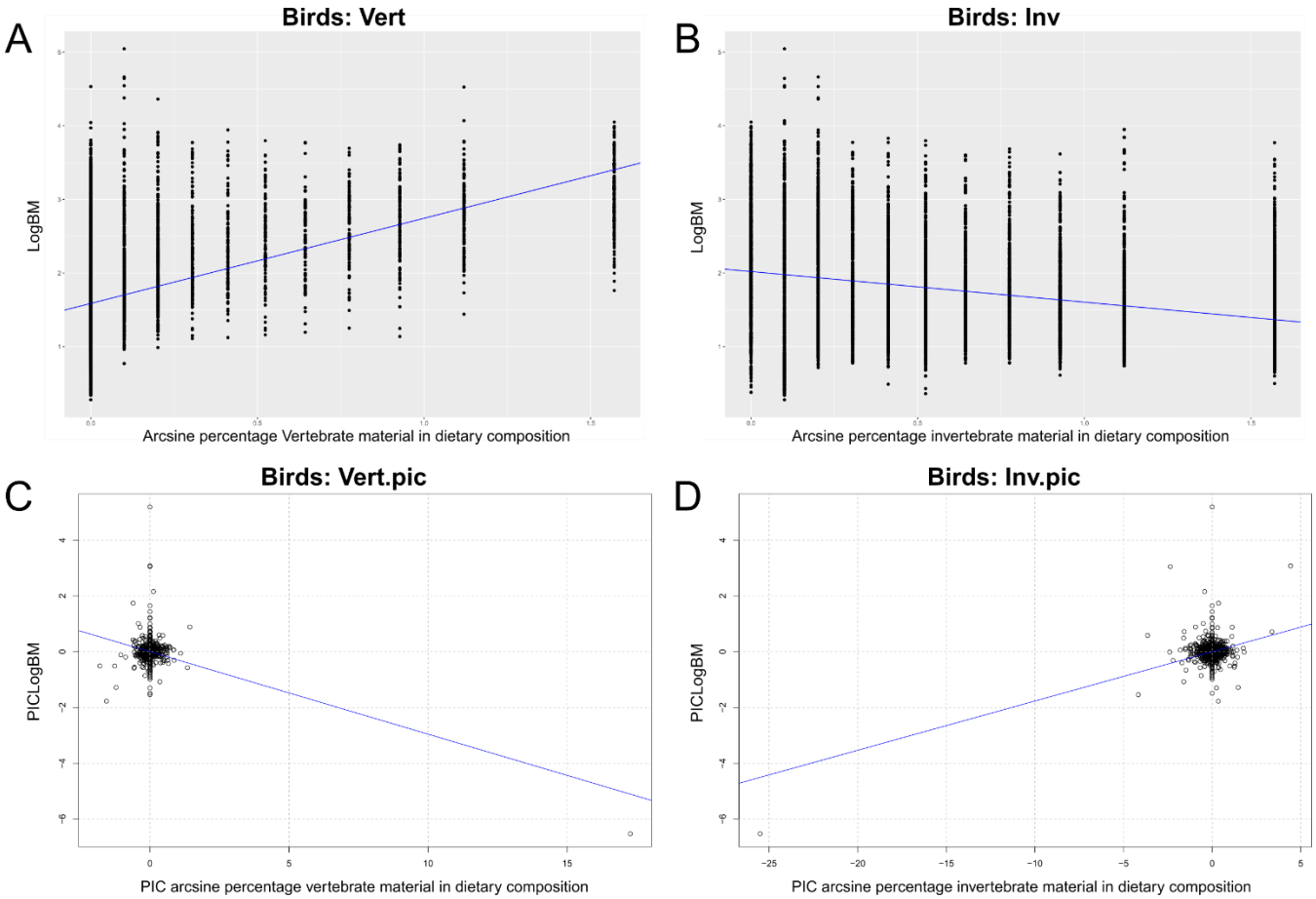


Figure 57: Ordinary, and phylogenetic (backbone topology of Hackett et al. 2008) linear models between log-body mass (logBM), and arcsine-percentage of total invertebrate (A, B), and total vertebrate (C, D) material in the dietary compositions of bird taxa. Abbreviations: **Inv**, percentage of total invertebrate material in the diet; **Vert**, percentage of total vertebrate material in the diet; **PIC**, phylogenetic independent contrasts.

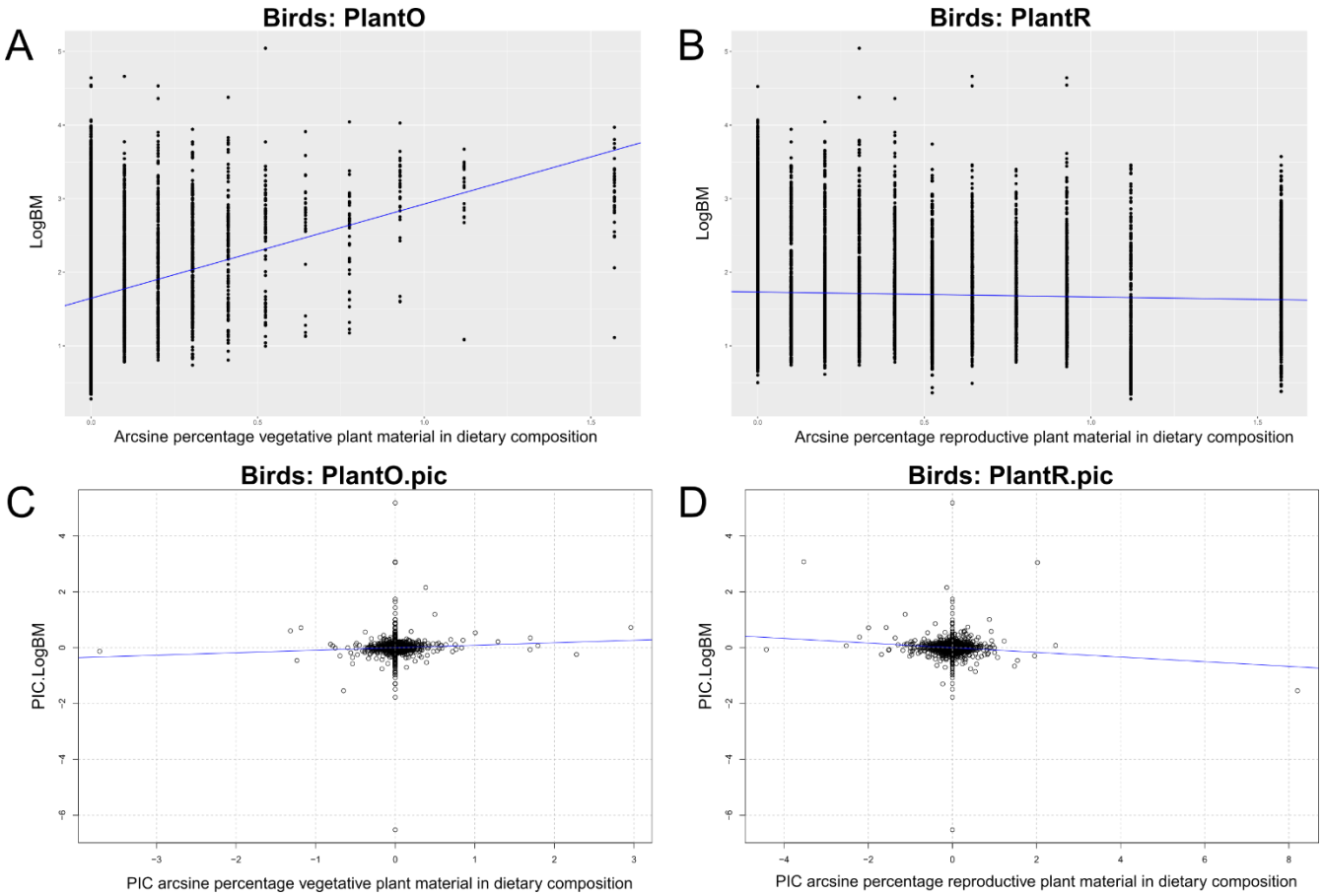


Figure 58: Ordinary, and phylogenetic (backbone topology of Hackett et al. 2008) linear models between log-body mass (logBM), and arcsine-percentage of total reproductive (A, B), and total vegetative (C, D) material in the dietary compositions of bird taxa. Abbreviations: **PlantR**, percentage of total reproductive plant material in the diet; **PlantO**, percentage of total vegetative plant material in the diet; **PIC**, phylogenetic independent contrasts.

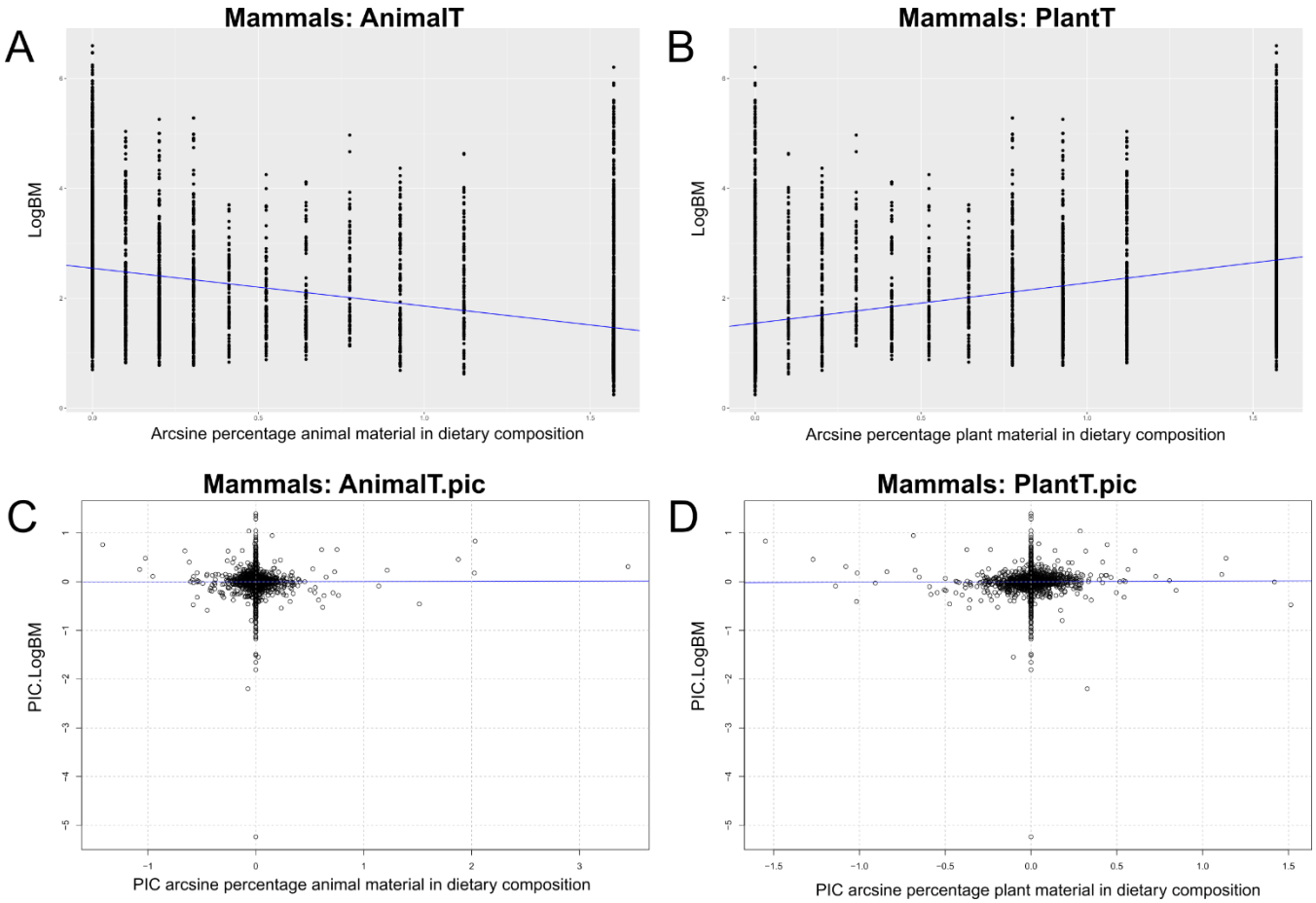


Figure 59: Ordinary, and phylogenetic (node-dating backbone topology of Upham et al. 2019) linear models between log-body mass (logBM), and arcsine-percentage of total animal (A, B), and total plant (C, D) material in the dietary compositions of mammal taxa. Abbreviations: **AnimalT**, percentage of total animal material in the diet; **PlantT**, percentage of total plant material in the diet; **PIC**, phylogenetic independent contrasts.

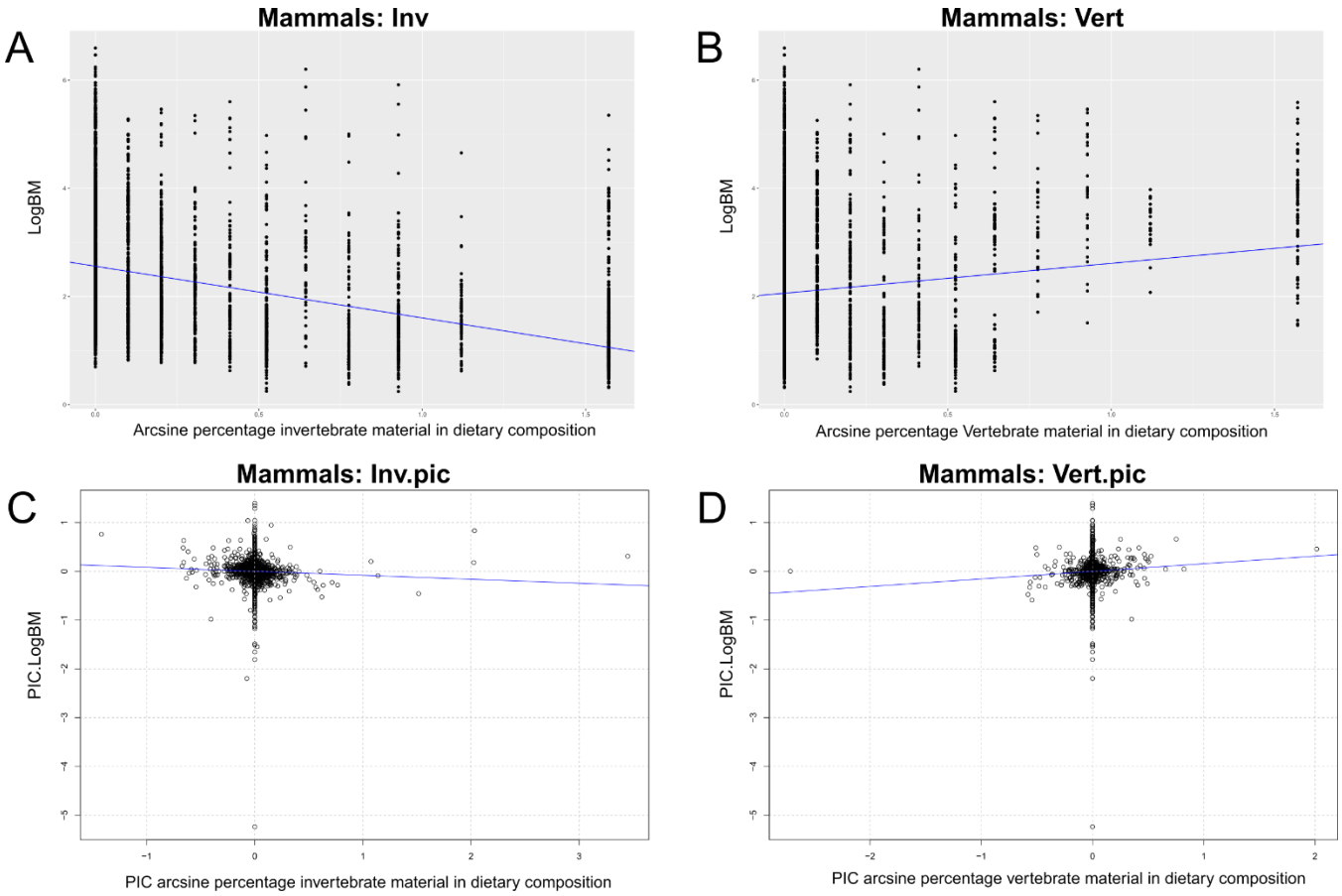


Figure 60: Ordinary, and phylogenetic (node-dating backbone topology of Upham et al. 2019) linear models between log-body mass (logBM), and arcsine-percentage of total invertebrate (A, B), and total vertebrate (C, D) material in the dietary compositions of bird taxa. Abbreviations: **Inv**, percentage of total invertebrate material in the diet; **Vert**, percentage of total vertebrate material in the diet; **PIC**, phylogenetic independent contrasts.

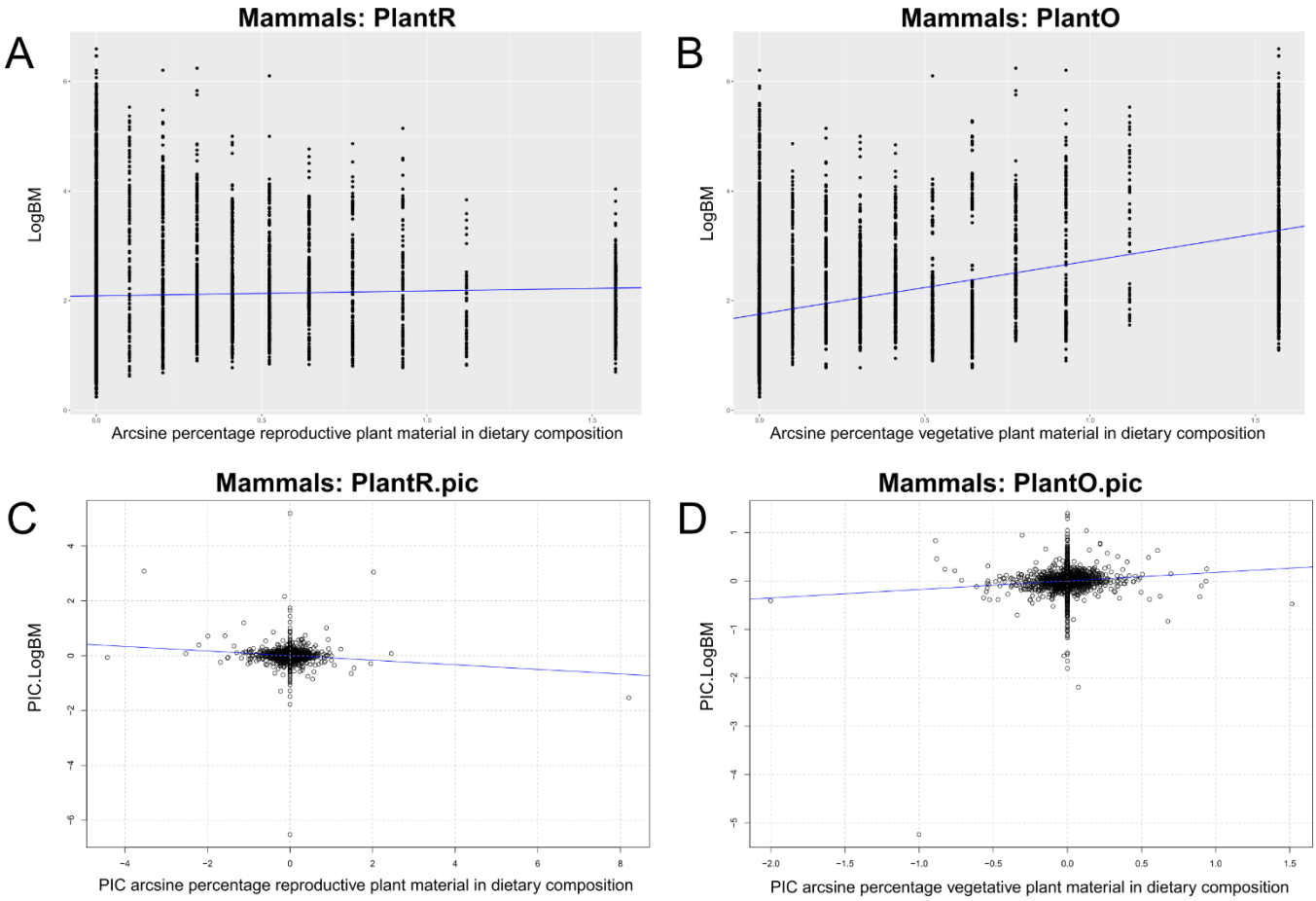
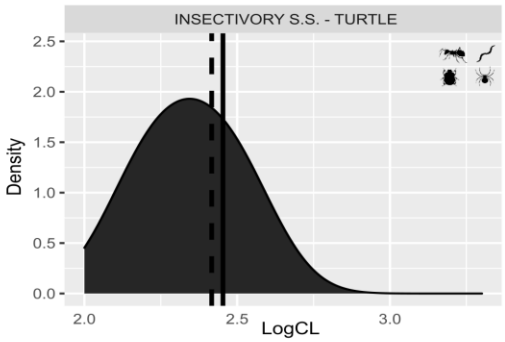
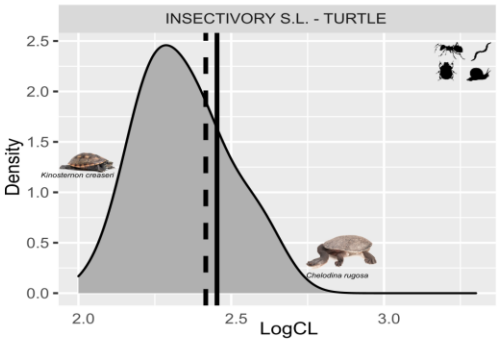
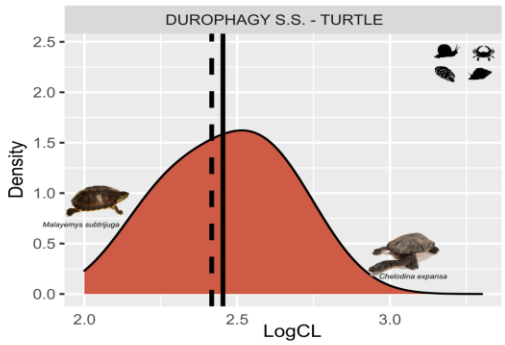
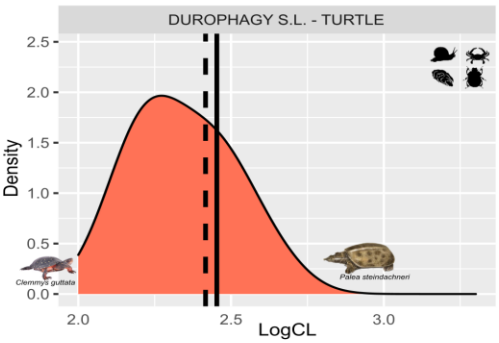


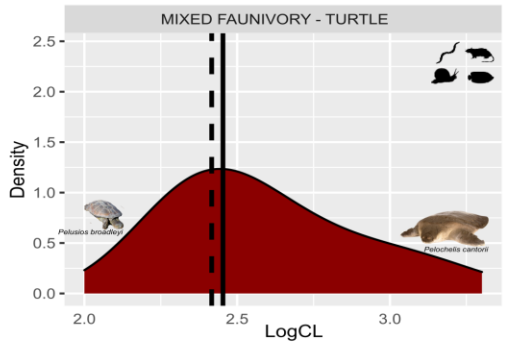
Figure 61: Ordinary, and phylogenetic (node-dating backbone topology of Upham et al. 2019) linear models between log-body mass (logBM), and arcsine-percentage of total reproductive (A, B), and total vegetative (C, D) material in the dietary compositions of bird taxa. Abbreviations: **PlantR**, percentage of total reproductive plant material in the diet; **PlantO**, percentage of total vegetative plant material in the diet; **PIC**, phylogenetic independent contrasts.

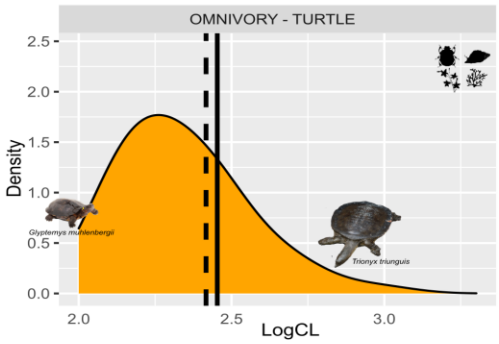

INSECTIVORY S.S. - TURTLE
Density
LogCL

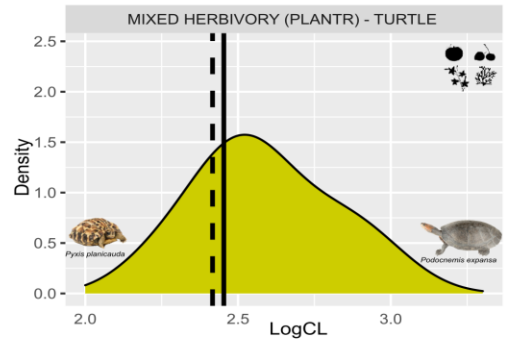

INSECTIVORY S.L. - TURTLE
Kinosternon creaseri
Chelodina rugosa
Density
LogCL

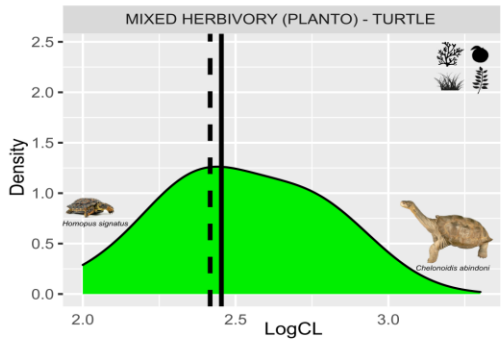

DUROPHAGY S.S. - TURTLE
Malayemys subtrijuga
Chelodina expansa
Density
LogCL

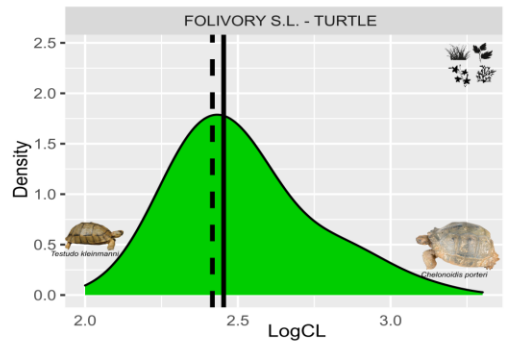

DUROPHAGY S.L. - TURTLE
Clemmys guttata
Palea steindachneri
Density
LogCL


MIXED FAUNIVORY - TURTLE
Pelusios broadleyi
Pelochelis cantorii
Density
LogCL


OMNIVORY - TURTLE
Glyptemys muhlenbergii
Trionyx triunguis
Density
LogCL


MIXED HERBIVORY (PLANTR) - TURTLE
Pyxis planicauda
Podocnemis expansa
Density
LogCL


MIXED HERBIVORY (PLANTO) - TURTLE
Homopus signatus
Chelonoidis abingdoni
Density
LogCL


FOLIVORY S.L. - TURTLE
Testudo kleinmanni
Chelonoidis porteri
Density
LogCL

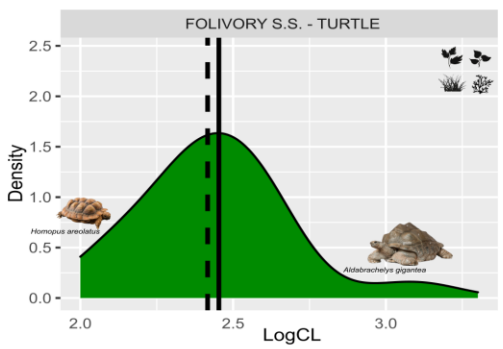

FOLIVORY S.S. - TURTLE
Homopus areolatus
Aldabrachelys gigantea
Density
LogCL

Figure 62: Density plots of log-carapace length (logCL) values in each guild recovered by the k-means cluster analysis in turtles. The solid line represents the mean body mass for all turtlesin the dataset, and the dotted line represents the median body mass of all turtles in the dataset. Smallest and largest representative of each guild are scaled according to logCL.

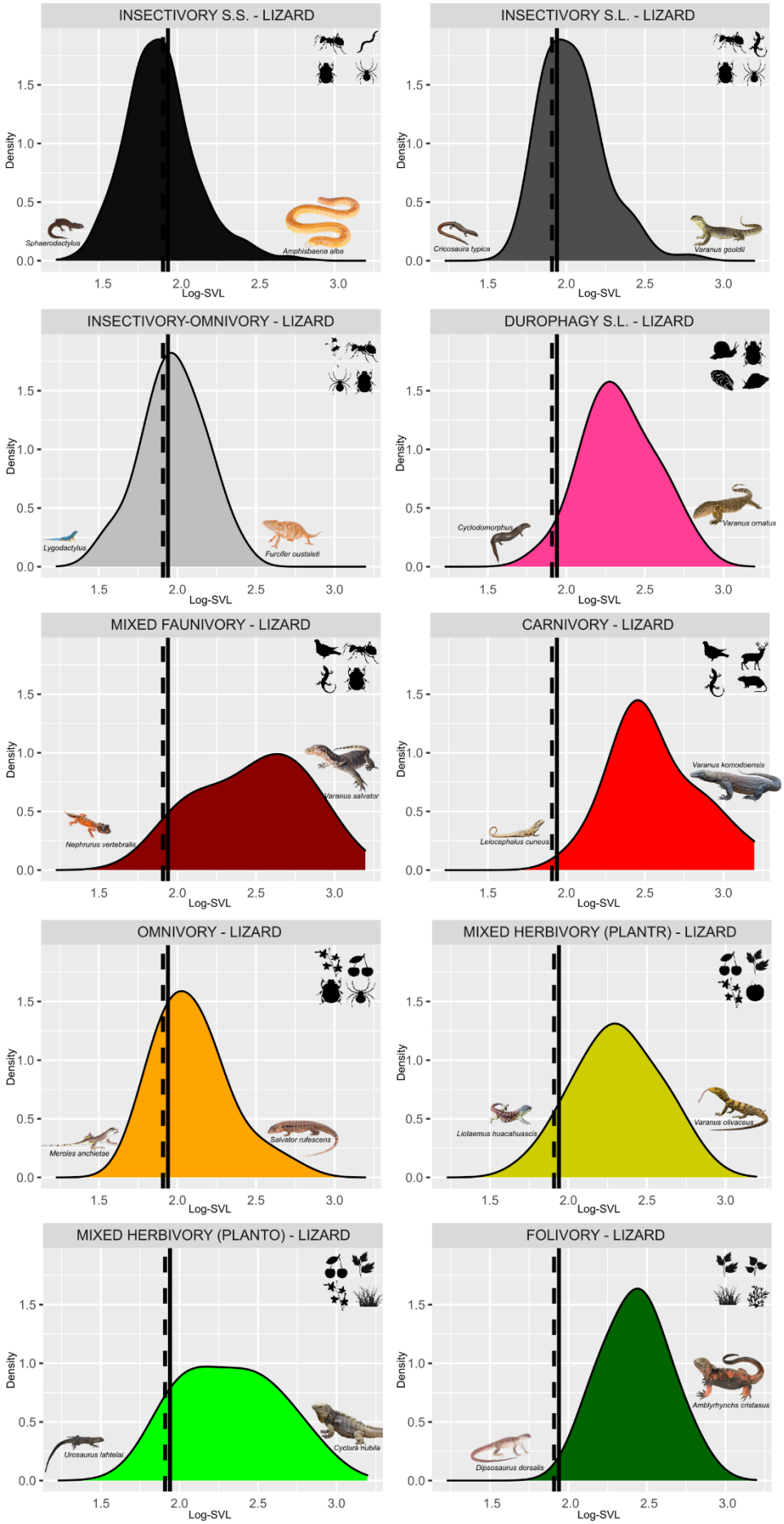

INSECTIVORY S.S. - LIZARD
Sphaerodactylus
Amphisbaena alba
INSECTIVORY S.L. - LIZARD
Cricosaura typica
Varanus gouldii
INSECTIVORY-OMNIVORY - LIZARD
Lygodactylus
Furcifer oustaleti
DUROPHAGY S.L. - LIZARD
Cyclodomorphus
Varanus ornatus
MIXED FAUNIVORY - LIZARD
Nephrurus vertebralis
Varanus salvator
CARNIVORY - LIZARD
Leiocephalus cuneus
Varanus komodoensis
OMNIVORY - LIZARD
Meroles anchietae
Salvator rufescens
MIXED HERBIVORY (PLANTR) - LIZARD
Liolaemus huacahuasicus
Varanus olivaceus
MIXED HERBIVORY (PLANTO) - LIZARD
Urosaurus lahtelai
Cyclura nubila
FOLIVORY - LIZARD
Dipsosaurus dorsalis
Amblyrhynchs cristatus
Density
Log-SVL
0.0
0.5
1.0
1.5
2.0
2.5
3.0

Figure 63: Density plots of log-snout-vent length (logSVL) values in each guild recovered by the k-means cluster analysis in lizards. The solid line represents the mean body mass for all lizards in the dataset, and the dotted line represents the median body mass of all lizards in the dataset. Smallest and largest representatives of each guild are scaled according to logSVL.

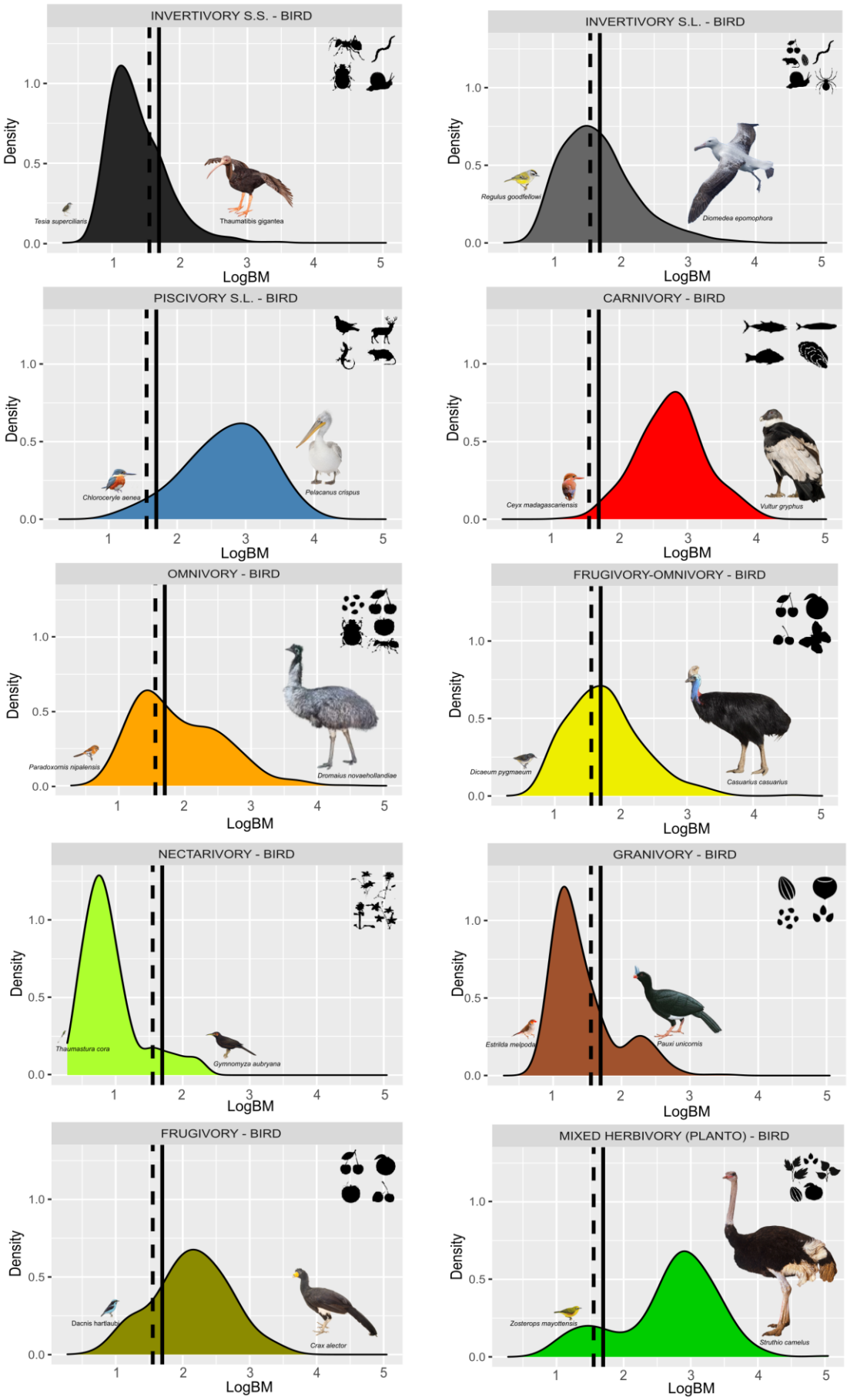

INVERTIVORY S.S. - BIRD
Tesia superciliaris
Thaumatibis gigantea
INVERTIVORY S.L. - BIRD
Regulus goodfellowi
Diomedea epomophora
PISCIVORY S.L. - BIRD
Chloroceryle aenea
Pelacanus crispus
CARNIVORY - BIRD
Ceyx madagascariensis
Vultur gryphus
OMNIVORY - BIRD
Paradoxornis nipalensis
Dromaius novaehollandiae
FRUGIVORY-OMNIVORY - BIRD
Dicaeum pygmaeum
Casuarius casuarius
NECTARIVORY - BIRD
Thaumastura cora
Gymnomyza aubryana
GRANIVORY - BIRD
Estrilda melpoda
Pauxi unicornis
FRUGIVORY - BIRD
Dacnis hartlaubi
Crax alector
MIXED HERBIVORY (PLANTO) - BIRD
Zosterops mayottensis
Struthio camelus
Density
LogBM

Figure 64: Density plots of log-body mass (logBM) values in each guild recovered by the k-means cluster analysis in birds. The solid line represents the mean body mass for all birdsin the dataset, and the dotted line represents the median body mass of all birds in the dataset. Smallest and largest representatives of each guild are scaled according to logBM.

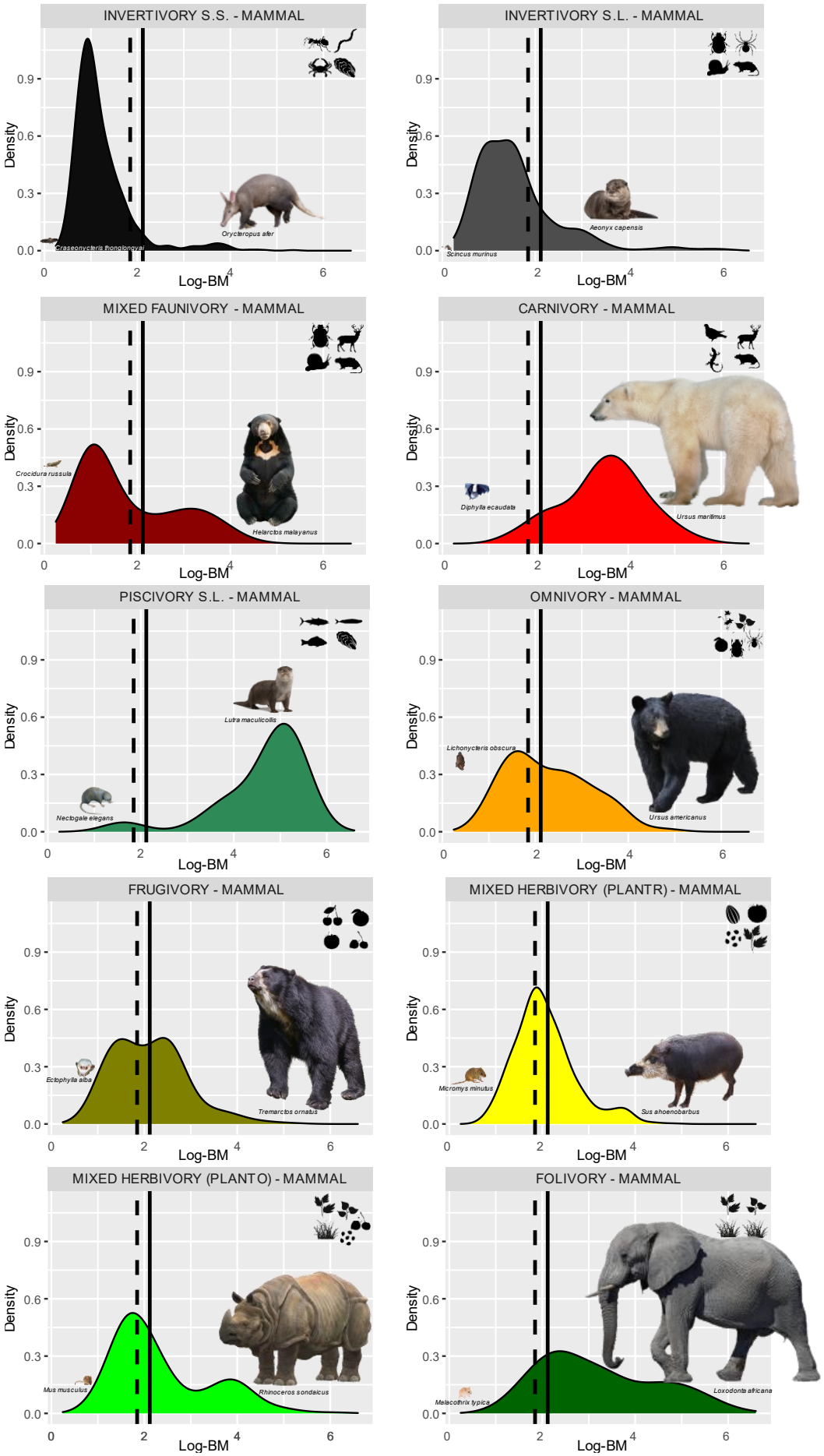

INVERTIVORY S.S. - MAMMAL
Orycteropus afer
Craseonycteris thonglongyai
INVERTIVORY S.L. - MAMMAL
Aeonyx capensis
Scincus murinus
MIXED FAUNIVORY - MAMMAL
Helarctos malayanus
Crocidura russula
CARNIVORY - MAMMAL
Ursus maritimus
Diphylla ecaudata
PISCIVORY S.L. - MAMMAL
Lutra maculicollis
Nectogale elegans
OMNIVORY - MAMMAL
Ursus americanus
Lichonycteris obscura
FRUGIVORY - MAMMAL
Tremarctos ornatus
Ectophylla alba
MIXED HERBIVORY (PLANTR) - MAMMAL
Sus ahoenobarbus
Micromys minutus
MIXED HERBIVORY (PLANTO) - MAMMAL
Rhinoceros sondaicus
Mus musculus
FOLIVORY - MAMMAL
Loxodonta africana
Melacothrix typica
Density
Log-BM

Figure 65: Density plots of log-body mass (logBM) values in each guild recovered by the k-means cluster analysis in mammals. The solid line represents the mean body mass for all mammals in the dataset, and the dotted line represents the median body mass of all mammals in the dataset. Smallest and largest representatives of each guild are scaled according to logBM.

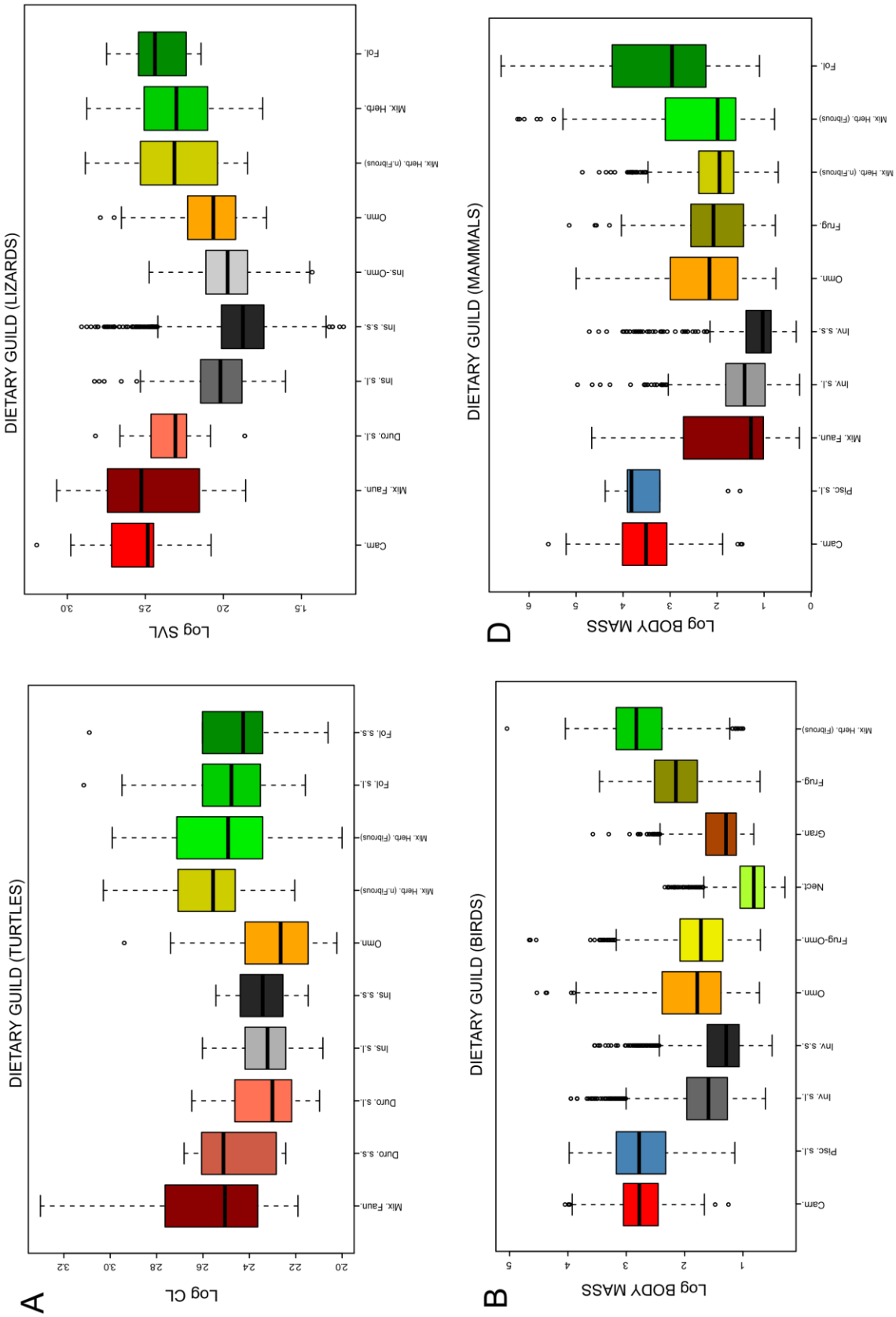


Figure 66: Box-and-whisker plots of body size distribution between the dietary guilds (k-value = 10) in each major amniote lineage.

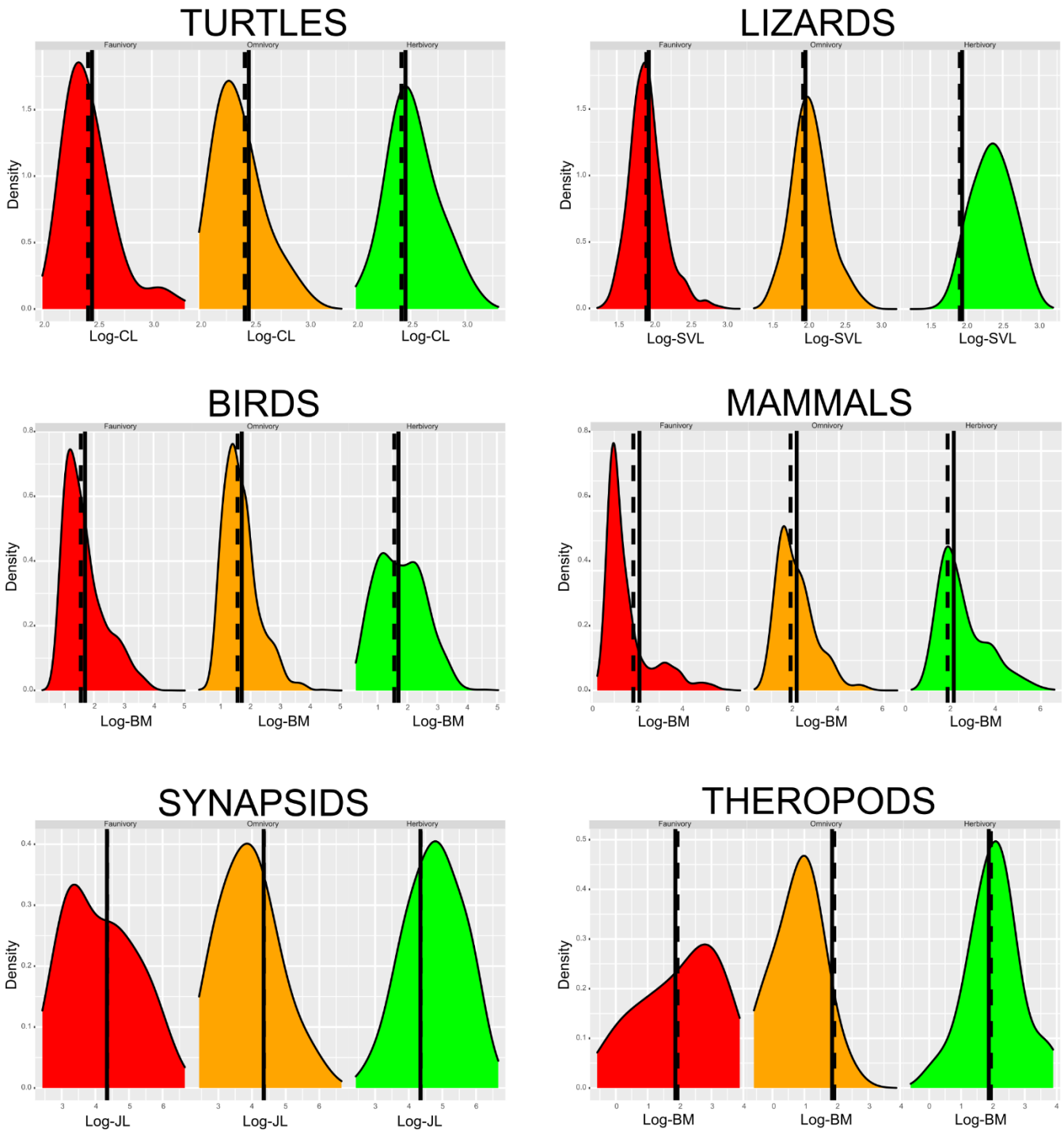


Figure 67: Density plots of log-transformed body mass (or proxy thereof; LogBM) in the classical dietary guilds in each extant, and extinct, clade in this study (red - faunivory; orange - omnivory, green - herbivory). "Synapsids" is short for non-mammalian synapsids, and "theropods" for non-avian theropods. Solid lines represent the mean body mass of all taxa in a given clade; dotted lines represent the median body mass of all taxa in a given clade. Abbreviations: CL, carapace length; SVL, snout-vent length; BM, body mass; JL, jaw length.

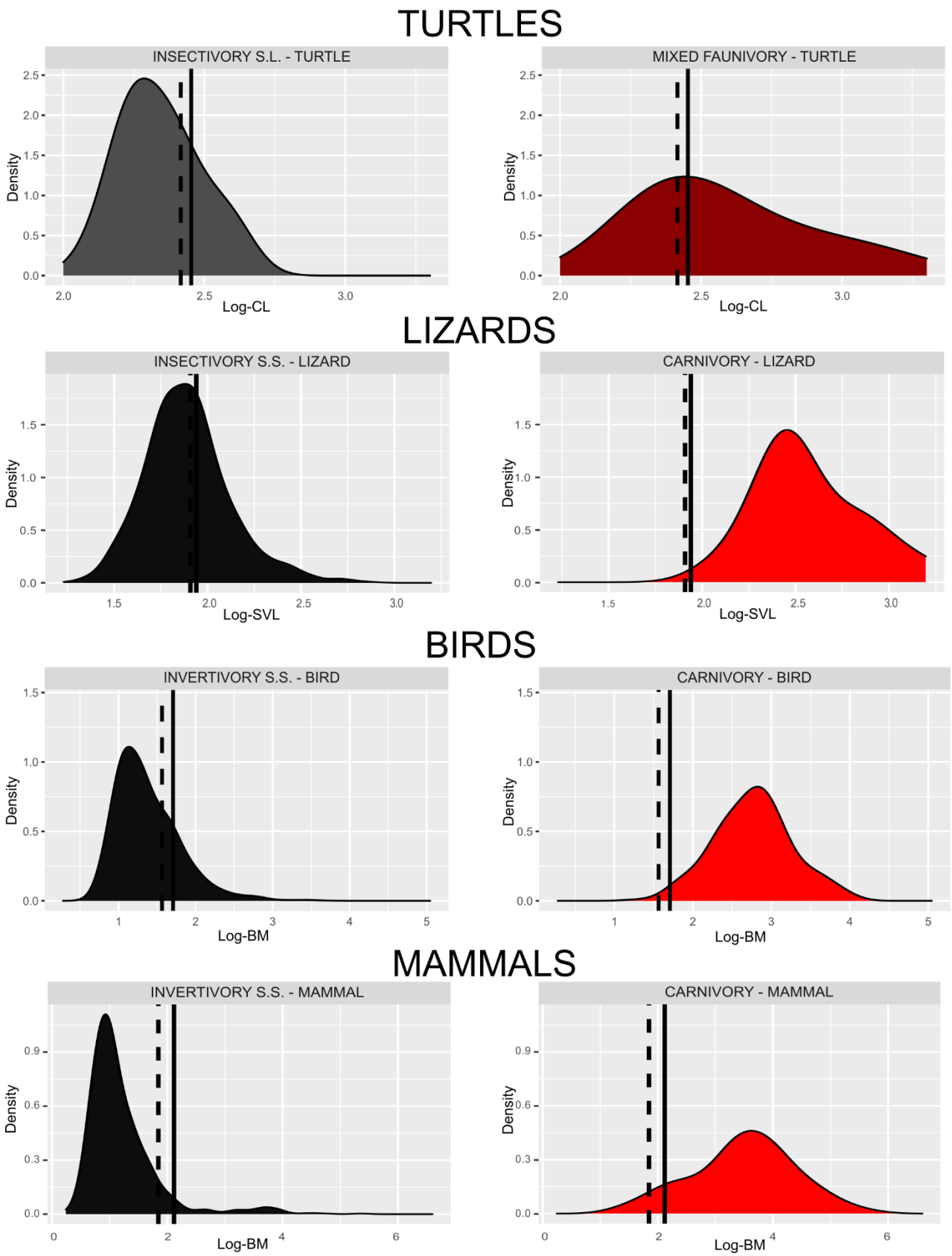


Figure 68: Comparison between density plots of log-transformed body mass (or proxy thereof) values in cognate invertivorous (black) and carnivorous (red) guilds in (A) turtles, (B) lizards, (C) birds, and (D) mammals. The solid line represents the mean body mass value in each respective clade. The dotted line represents the median body mass value in each respective clade. For turtles, the

mixed invertivorous (predominantly insectivorous) guild is shown as the strictly insectivorous guild in turtles has a low sample size, and the mixed faunivorous guild is shown as the k-means cluster analysis did not recover a strictly carnivorous guild in turtles. Abbreviations: CL, carapace length; SVL, snout-vent length; BM, body mass.

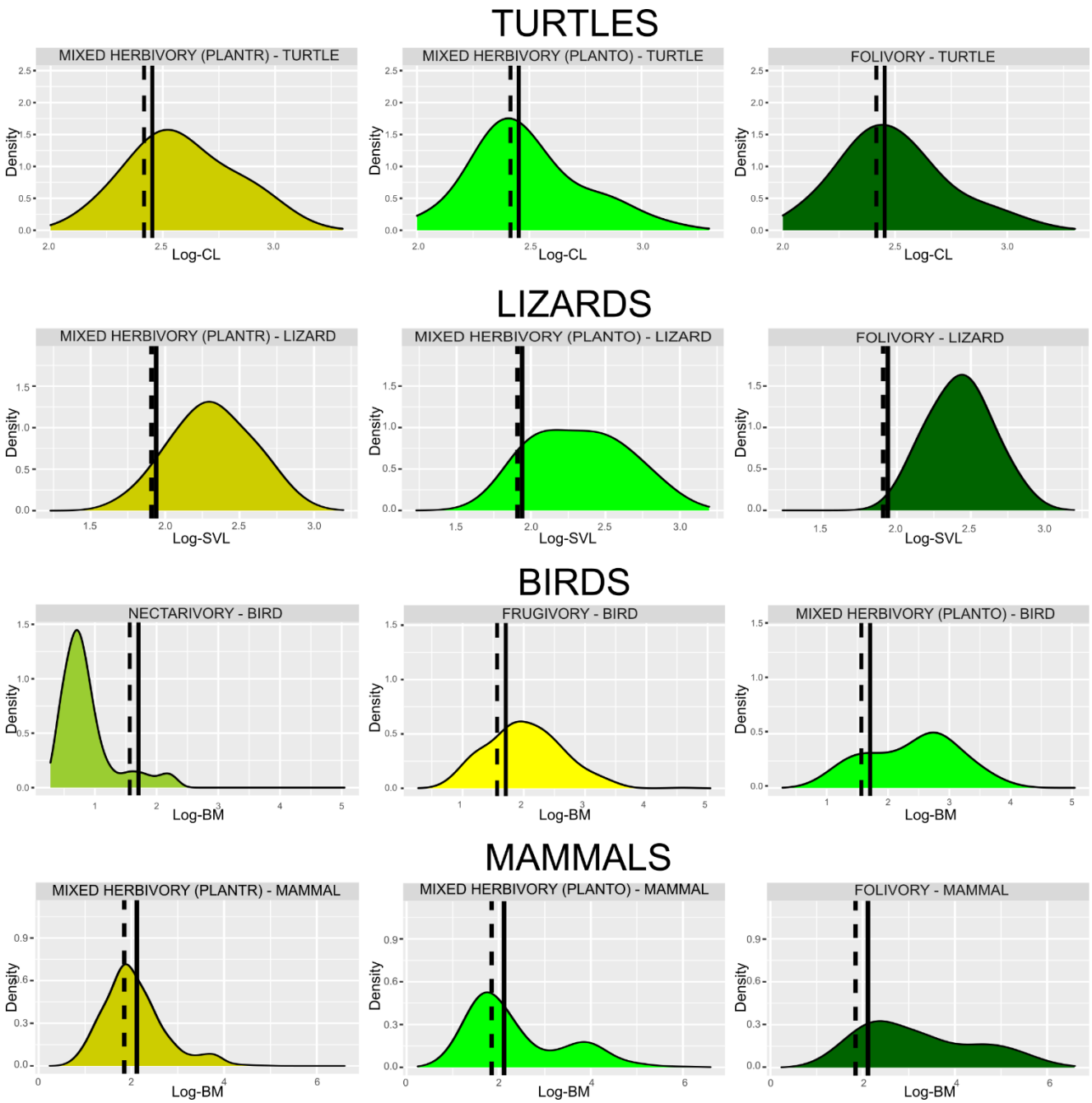


Figure 69: Comparison between density plots of log-transformed body mass (or proxy thereof) values in selected herbivorous guilds. The primary purpose of this figure is to illustrate the differences between herbivorous guilds composed of reproductive versus vegetative plant structures. The solid line represents the mean body mass value in each respective clade. The dotted line represents the median body mass value in each respective clade. For turtles, lizards, and mammal; mixed herbivory with a predominance of reproductive plant structures (dark yellow), mixed

herbivory with a predominance of vegetative plant structures (light green), and folivory (dark green). Since the results of the k-means cluster analysis generated more specialist than generalist guilds in birds; nectarivory (yellow-green), frugivory (light yellow), and mixed herbivory with a predominance of vegetative plant parts (light green) are shown. Abbreviations: CL, carapace length; SVL, snout-vent length; BM, body mass.

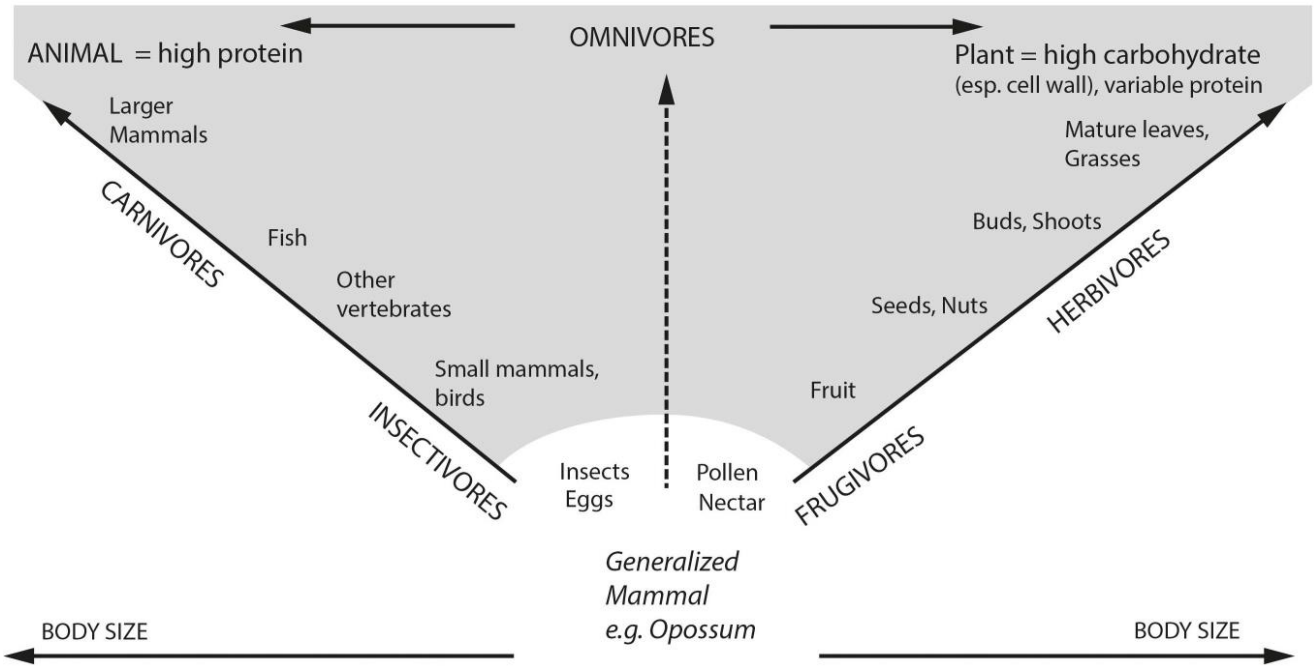


Figure 70: Expected patterns in body size distribution relative to dietary composition based on ecological availability of energy from different food sources ("abundance packet size" hypothesis as per Olsen 2015). Adapted from Claus et al. 2013.

7. Tables

Table 43: Summary of key findings from selected studies analysing the relationship between diet and body size.

Lineage	Dietary Guilds	Key findings	Additional notes	Reference
Mammals, birds,	"Herbivore" (>50% plant material in the diet), "Invertivore" (>50% invertebrates in the diet), "Carnivore" (>50% vertebrates in the diet), "Omnivore" (no dominant dietary component)	U-shaped relationship between diet and body size where herbivores and carnivores (the two extremes) have larger body sizes, while omnivores and invertivores are smaller on average	Results not corrected for phylogeny	Cooke et al. (2022)
Testudines	"Biters" (durophages or large-vertebrate carnivores), "Omnivores" (diet composed of both plants and invertebrates), "Herbivores" (diet composed primarily of plant material), "Insectivores" (diet composed of arthropods and other small invertebrates), "Piscivores" (diet composed of fish)	No significant difference in carapace length or body mass between groups	Biters had signifcantly greater head height and bite force than other groups	Herrel et al. 2002
Podocnemid	Percentage of total volume of diet composed of (a) total plant material, and (b) fibrous plant material	No significant relationship between increased plant consumption and body mass	No "obvious evolutionary trend" between diet, body size, and habitat in the clade	Eisemberg et al. 2016

Non-serpentine	"Carnivore" (diet primarily consists of animal material); "Herbivore" (diet primarily consists of plant material); "Omnivore" (neither plant nor animal material is the dominant dietary item)	Lizards with larger body sizes were more likely to be herbivores than omnivores or carnivores	Larger lizards were more likely to be insular or aquatic/semi-aquatic	Meiri 2018
Lacertid lizards	"Insectivorous" (diet exclusively consists of arthropod and other animal material); "Herbivorous" (any intentional consumption of plant material)	Herbivorous lacertids "tend to be larger" than their insectivorous counterparts	Transition to an island habitat facilitates transitions to herbivory. No significant difference in body size between mainland and insular populations	Van Damme 1999
Polychrotid	Percentage of diet composed of fruit (above 5% indicates "intentional herbivory")	Mean snout-vent-length (SVL) increases with increased fruit consumption	Relationship between frugivory and large body size is independent of insularity	Herrel et al. 2004
Liolaemid	"Insectivore" (diet consists of <10% plant matter); "Omnivore" (diet consists of 10-50% plant matter); "Herbivore" (diet consists of >70% plant matter)	Herbivorous liolaemid lizards retain ancestral small body size, in contrast to herbivorous lizards from other clades	There is a correlation between the evolution of herbivory and shifts to cool-climates	Espinoza et al. 2004
Anseriform	"Herbivory index" (percentage of diet composed of plant matter as a continuous trait)	No significant correlation between the evolution of herbivory and large body size	There is a positive correlation between herbivory index unadjusted for phylogeny but not when taking the effects of phylogeny into account	Olsen 2015

Mammals	"Carnivore" (diet primarily consists of animal material); "Herbivore" (diet primarily consists of plant material); "Omnivore" (neither plant nor animal material is the dominant dietary item)	Herbivores are the largest group, followed by herbivores then carnivores. Evolutionary shifts in diet are almost always accompanied by changes in body mass.	Flying mammals (bats) follow the same rule as terrestrial mammals but marine mammals do not	Price and Hopkins 2015
Mammals	"Carnivore" (diet primarily consists of vertebrate material); "Frugivore" (diet primarily consists of fruit); "Fungivore" (diet consists primarily of fungi), "Granivore" (diet consists primarily of seeds); "Gumnivore" (diet consists primarily of worms and similar invertebrates); "Herbivore" (diet consists primarily of fibrous plant material); "Insectivore" (diet consists primarily of arthropods); "Generalist" (no dietary item dominant)	The smallest mammals tended to insectivory and granivory, the largest to carnivory and herbivory, frugivory and other guilds occupied the medium body size ranges	There was a very wide range of body size among herbivores, while carnivores were clusted around a smaller body size range	Pineda-Munoz et al. 2016
Mammal	Animals were classified into 15 distinct guilds based on the combination (presence or absence) of the following four food categories in their diets: invertebrates, vertebrates, fibrous plant material, non-fibrous plant material	Omnivores that included vertebrate carrion in their diets were significantly larger than other kinds of generalist feeders	If grouped by kind of plant material, body sizes did not differ between guilds	Reuter et al. 2023
Captorhinids	"Carnivore" (diet primarily consists of animal material); "Herbivore" (diet primarily consists of plant material)	Shift to large body size preceded evolution of herbivory		Brocklehurst 2016

Carboniferous	"Carnivore" (diet primarily consists of animal material); "Herbivore" (diet primarily consists of plant material)	There was a tendency towards large body size in both carnivores and herbivores	Brockleh urst and Brink 2017
Theropod	"Carnivore" (diet primarily consists of animal material); "Herbivore" (diet primarily consists of plant material)	No evidence of directional evolution of large body size in herbivorous clades	Zanno and Makovicky

Table 44: Results of ordinary linear models regressing the arcsine-transformed percentage values of each food type against log-transformed values of carapace length in turtles. Abbreviations: **Std.error**, standard error. N = 264.

Model	Estimate	Std.error	Statistic	p-value	R^2
Animal (total)	-0.038	0.026	-1.485	0.139	0.008
Invertebrates (total)	-0.146	0.033	-4.443	0.000	0.070
Arthropods	-0.267	0.052	-5.186	0.000	0.093
Durophagy	-0.032	0.049	-0.652	0.515	0.002
Vertebrates	0.169	0.061	2.762	0.006	0.028
Plant (total)	0.074	0.025	2.893	0.004	0.031
Plant (fibrous)	0.036	0.033	1.093	0.276	0.005
Plant (non-fibrous)	0.145	0.062	2.355	0.019	0.021

Table 45: Results of phylogenetic linear models regressing the PICs of arcsine-transformed percentage values (topology of Thomson et al. 2021) of each food type against the PIC of log-transformed values carapace length in turtles. Abbreviations: **Std.error**, standard error. N = 264.

Model	Estimate	Std.error	Statistic	p-value	R^2
Animal (total)	-0.015	0.024	-0.618	0.537	0.001
Invertebrates (total)	-0.025	0.025	-0.998	0.319	0.001
Arthropods	0.029	0.022	1.343	0.180	0.001
Durophagy	-0.06	0.026	-2.409	0.017	0.000
Vertebrates	0.10	0.077	1.325	0.186	0.000
Plant (total)	0.077	0.031	2.513	0.013	0.014
Plant (fibrous)	0.074	0.034	-0.597	0.551	0.004
Plant (non-fibrous)	-0.033	0.055	2.192	0.029	0.000

Table 46: Results of Spearman's rank-correlation tests correlating the arcsine-transformed percentage values of each food type against log-transformed values of carapace length in turtles. The "Phylogenetic" column refers to correlation tests done on the PICs of those variables (topology of Thomson et al. 2021). N = 264.

Variable	Phylogenetic	Ordinary

	Correlation (rho)	p-value	Correlation (rho)	p-value
Animal (total)	-0.046	0.455	-0.171	0.005
Invertebrates (total)	-0.095	0.123	-0.305	0.000
Arthropods	-0.185	0.003	-0.422	0.000
Durophagy	0.026	0.676	-0.119	0.053
Vertebrates	0.035	0.572	0.148	0.016
Plant (total)	0.101	0.102	0.156	0.011
Plant (fibrous)	0.007	0.909	0.046	0.452
Plant (non-fibrous)	0.005	0.938	0.073	0.237

Table 47: Results of Kendall's rank-correlation tests correlating the arcsine-transformed percentage values of each food type against log-transformed values of carapace length in turtles. The "Phylogenetic" column refers to correlation tests done on the PICs of those variables (topology of Thomson et al. 2021). N = 264.

Variable	Phylogenetic		Ordinary	
	Correlation (tau)	p-value	Correlation (tau)	p-value
Animal (total)	-0.032	0.442	-0.118	0.006
Invertebrates (total)	-0.063	0.128	-0.212	0.000
Arthropods	-0.125	0.003	-0.304	0.000
Durophagy	0.021	0.614	-0.087	0.045
Vertebrates	0.028	0.514	0.110	0.016
Plant (total)	0.069	0.100	0.106	0.014
Plant (fibrous)	0.004	0.887	0.028	0.518
Plant (non-fibrous)	0.006	0.932	0.049	0.277

Table 48: Results of ANOVA analyses comparing mean log-transformed carapace length between the dietary guilds recovered in the k-means cluster analysis, and the classical dietary guilds in turtles. Abbreviations: **phy**, phylogenetic ANOVA; **Df**, degrees of freedom; **Sum Sq**, sum of square distances; **Mean Sq**, mean square distances. N = 264.

	Df	Sum Sq	Mean Sq	F-value	P-value
K = 10	9	2.671	0.297	6.202	0.001
-Residuals	254	12.153	0.048	NA	NA

Classical guilds	2	1.006	0.503	9.498	0.000
-Residuals	261	13.818	0.053	NA	NA
K = 5 (phy)	4	1.492	0.373	7.244	0.316
-Residuals		13.332	0.051	NA	NA
K = 10 (phy)	9	2.671	0.297	6.202	0.119
-Residuals		12.153	0.048	NA	NA
K = 20 (phy)	9	4.555	0.240	5.696	0.038
-Residuals		10.269	0.042	NA	NA
Classical (phy)	2	1.00	0.05	9.50	0.366
-Residuals	261	13.82	0.05	NA	NA

Table 49: Posthoc pairwise comparisons from the ordinary ANOVA between mean log-transformed carapace length between the dietary guilds recovered in the k-means cluster analysis in turtles. Abbreviations: **diff**, group mean difference; **lwr**, lower range of group mean difference; **upr**, upper range of group mean difference; **p adj**, adjusted p-value. **Guild numbers**: **1**, folivory s.l. (n = 39); **2**, insectivory s.l. (n = 34); **3**, omnivory (n = 48); **4**, durophagy s.l. (n = 24); **5**, mixed herbivory composed primarily of reproductive plant parts (n = 21); **6**, durophagy s.s. (n = 9); **7**, folivory s.s. (n = 17); **8**, insectivory s.s. (n = 5); **9**, mixed herbivory composed primarily of reproductive plant parts (n = 36); **10**, mixed faunivory (n = 35).

	diff	**lwr**	**upr**	**p adj**
10-1	0,074	-0,089	0,237	0,909
2-1	-0,170	-0,334	-0,006	0,035
3-1	-0,175	-0,326	-0,025	0,009
4-1	-0,172	-0,359	0,014	0,096
5-1	0,072	-0,117	0,261	0,969
6-1	-0,049	-0,320	0,222	1,000
7-1	-0,073	-0,276	0,130	0,979
8-1	-0,169	-0,501	0,162	0,832
9-1	0,005	-0,158	0,167	1,000
2-10	-0,244	-0,412	-0,076	0,000
3-10	-0,249	-0,404	-0,094	0,000
4-10	-0,246	-0,436	-0,056	0,002
5-10	-0,002	-0,194	0,191	1,000
6-10	-0,123	-0,396	0,151	0,916
7-10	-0,147	-0,353	0,059	0,410
8-10	-0,243	-0,577	0,091	0,376
9-10	-0,069	-0,236	0,098	0,947
3-2	-0,005	-0,162	0,151	1,000
4-2	-0,003	-0,194	0,188	1,000

5-2	0,242	0,048	0,436	0,003
6-2	0,121	-0,153	0,395	0,924
7-2	0,097	-0,111	0,304	0,896
8-2	0,000	-0,334	0,335	1,000
9-2	0,174	0,006	0,343	0,035
4-3	0,003	-0,177	0,183	1,000
5-3	0,248	0,065	0,430	0,001
6-3	0,126	-0,140	0,393	0,886
7-3	0,102	-0,095	0,299	0,819
8-3	0,006	-0,322	0,334	1,000
9-3	0,180	0,025	0,335	0,010
5-4	0,245	0,032	0,458	0,011
6-4	0,124	-0,165	0,412	0,936
7-4	0,099	-0,126	0,325	0,924
8-4	0,003	-0,343	0,349	1,000
9-4	0,177	-0,013	0,367	0,092
6-5	-0,121	-0,411	0,169	0,945
7-5	-0,145	-0,373	0,083	0,574
8-5	-0,242	-0,589	0,106	0,446
9-5	-0,068	-0,260	0,125	0,982
7-6	-0,024	-0,324	0,275	1,000
8-6	-0,120	-0,519	0,278	0,994
9-6	0,053	-0,220	0,327	1,000
8-7	-0,096	-0,451	0,259	0,997
9-7	0,078	-0,129	0,284	0,972
9-8	0,174	-0,160	0,508	0,815

Table 50: Posthoc pairwise comparisons from the ordinary ANOVA between mean log-transformed carapace length between the classical dietary guilds (faunivory, n = 101; omnivory, n = 53; herbivory = 110) in turtles.
Abbreviations: **diff**, group mean difference; **lwr**, lower range of group mean difference; **upr**, upper range of group mean difference; **p adj**, adjusted p-value.

	diff	**lwr**	**upr**	**p adj**
Herbivory-Faunivory	0.094	0.020	0.169	0.009
Omnivory-Faunivory	-0.063	-0.155	0.029	0.239
Omnivory-Herbivory	-0.158	-0.248	-0.067	0.000

Table 51: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed carapace length between the dietary guilds recovered in the k-means cluster analysis in turtles (k=10). Guild numbers: **1**, folivory s.l. (n = 39); **2**, insectivory s.l. (n = 34); **3**, omnivory (n = 48); **4**,

durophagy s.l. (n = 24); **5**, mixed herbivory composed primarily of reproductive plant parts (n = 21); **6**, durophagy s.s. (n = 9); **7**, folivory s.s. (n = 17); **8**, insectivory s.s. (n = 5); **9**, mixed herbivory composed primarily of reproductive plant parts (n = 36); **10**, mixed faunivory (n = 35).

	1	**10**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	1	1	1	1	1	1	1	1	1	1
10	1	1	1	1	1	1	1	1	1	1
2	1	1	1	1	1	1	1	1	1	1
3	1	1	1	1	1	0.836	1	1	1	0.72
4	1	1	1	1	1	1	1	1	1	1
5	1	1	1	0.836	1	1	1	1	1	1
6	1	1	1	1	1	1	1	1	1	1
7	1	1	1	1	1	1	1	1	1	1
8	1	1	1	1	1	1	1	1	1	1
9	1	1	1	0.72	1	1	1	1	1	1

Table 52: Posthoc pairwise t-values from the phylogenetic ANOVA comparisons between mean log-transformed carapace length between the dietary guilds recovered in the k-means cluster analysis in turtles. Guild numbers: **1**, folivory s.l. (n = 39); **2**, insectivory s.l. (n = 34); **3**, omnivory (n = 48); **4**, durophagy s.l. (n = 24); **5**, mixed herbivory composed primarily of reproductive plant parts (n = 21); **6**, durophagy s.s. (n = 9); **7**, folivory s.s. (n = 17); **8**, insectivory s.s. (n = 5); **9**, mixed herbivory composed primarily of reproductive plant parts (n = 36); **10**, mixed faunivory (n = 35).

	1	**10**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	0,000	-1,452	3,308	3,717	2,956	-1,220	0,576	1,149	1,630	-0,090
10	1,452	0,000	4,628	5,127	4,140	0,029	1,433	2,274	2,326	1,327
2	-3,308	-4,628	0,000	0,112	0,044	-3,987	-1,407	-1,489	-0,004	-3,311
3	-3,717	-5,127	-0,112	0,000	-0,051	-4,325	-1,513	-1,656	-0,058	-3,699
4	-2,956	-4,140	-0,044	0,051	0,000	-3,666	-1,368	-1,407	-0,028	-2,974
5	1,220	-0,029	3,987	4,325	3,666	0,000	1,333	2,036	2,219	1,121
6	-0,576	-1,433	1,407	1,513	1,368	-1,333	0,000	0,258	0,966	-0,624
7	-1,149	-2,274	1,489	1,656	1,407	-2,036	-0,258	0,000	0,865	-1,201
8	-1,630	-2,326	0,004	0,058	0,028	-2,219	-0,966	-0,865	0,000	-1,663
9	0,090	-1,327	3,311	3,699	2,974	-1,121	0,624	1,201	1,663	0,000

Table 53: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed carapace length between the dietary guilds recovered in the k-means cluster analysis in turtles (k = 5). See Table 20 for details of each guild.

	1	**2**	**3**	**4**	**5**
1	1.0	0.45	1.0	1.0	1.0
2	0.45	1.0	1.0	1.0	1.0
3	1.0	1.0	1.0	1.0	1.0
4	1.0	1.0	1.0	1.0	1.0
5	1.0	1.0	1.0	1.0	1.0

Table 54: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed carapace length between the dietary guilds recovered in the k-means cluster analysis in turtles (k = 20). See Table 21 for details of each guild.

	1	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**2**	**20**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
10	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.56	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
11	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
12	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.19	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
13	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.93	1.00
14	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
15	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
16	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.93	1.00
17	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
18	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

19	1.00	0.56	1.00	0.19	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.19	0.56
2	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
20	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
3	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
4	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
5	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
6	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
7	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.56	1.00
8	1.00	1.00	1.00	1.00	0.93	1.00	1.00	0.93	1.00	1.00	0.19	1.00	1.00	1.00	1.00	1.00	1.00	0.56	1.00	1.00
9	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.56	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Table 55: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed carapace length between the classical dietary guilds (faunivory, n = 101; omnivory, n = 53; herbivory = 110) in turtles.

	Faunivory	**Herbivory**	**Omnivory**
Faunivory	NA	1.000	1.000
Herbivory	1.000	NA	0.165
Omnivory	1.000	0.165	NA

Table 56: Posthoc pairwise t-values from the phylogenetic ANOVA comparisons between mean log-transformed carapace length between the classical dietary guilds (faunivory, n = 101; omnivory, n = 53; herbivory = 110) in turtles.

	Faunivory	**Herbivory**	**Omnivory**

Faunivory	NA	-2.979	1.620
Herbivory	2.979	NA	4.099
Omnivory	-1.620	-4.099	NA

Table 57: Results of ordinary linear models regressing the arcsine-transformed percentage values of each food type against log-transformed values of snout-vent length in lizards. Abbreviations: **Std.error**, standard error. N = 4001.

Model	Estimate	Std.error	Statistic	p-value	R^2
Animal (total)	-0.219	0.012	-18.655	0.000	0.080
Invertebrates (total)	-0.262	0.009	-27.683	0.000	0.161
Arthropods	-0.274	0.010	-28.856	0.000	0.172
Durophagy	0.655	0.061	10.658	0.000	0.028
Vertebrates	0.721	0.037	19.757	0.000	0.089
Plant (total)	0.334	0.017	19.339	0.000	0.086
Plant (fibrous)	0.611	0.038	15.909	0.000	0.060
Plant (non-fibrous)	0.452	0.030	15.302	0.000	0.055

Table 58: Results of phylogenetic linear models regressing the PICs of arcsine-transformed percentage values of each food type against the PIC of log-transformed values snout-vent length in lizards (topology of Tonini et al. 2016). Abbreviations: **Std.error**, standard error. N = 4001.

Model	Estimate	Std.error	Statistic	p-value	R^2
Animal (total)	-0.059	0.008	-6.955	0.000	0.012
Invertebrates (total)	-0.071	0.008	-9.147	0.000	0.020
Arthropods	-0.065	0.007	-8.649	0.000	0.018
Durophagy	0.070	0.027	2.550	0.011	0.002
Vertebrates	0.056	0.024	2.379	0.017	0.001
Plant (total)	0.101	0.014	7.348	0.000	0.013
Plant (fibrous)	0.020	0.025	0.806	0.420	0.000
Plant (non-fibrous)	0.094	0.015	6.373	0.000	0.010

Table 59: Results of phylogenetic linear models regressing the PICs of arcsine-transformed percentage values of each food type against the PIC of log-transformed values snout-vent length in lizards (topology of Pyron et al. 2014). Abbreviations: **Std.error**, standard error. N = 1997.

Model	Estimate	Std.error	Statistic	p-value	R^2
Animal (total)	-0.051	0.009	-5.423	0.000	0.015
Invertebrates (total)	-0.056	0.009	-6.488	0.000	0.021
Arthropods	-0.009	0.006	-1.450	0.147	0.001
Durophagy	0.004	0.034	0.108	0.914	0.000
Vertebrates	0.049	0.026	1.897	0.058	0.002
Plant (total)	0.084	0.015	5.482	0.000	0.015
Plant (fibrous)	0.126	0.031	4.096	0.000	0.008
Plant (non-fibrous)	0.047	0.016	2.895	0.004	0.004

Table 60: Results of Spearman's rank-correlation tests correlating the arcsine-transformed percentage values of each food type against log-transformed values of snout-vent length in lizards. The first two columns refer to correlation tests done on the PICs of those variables, generated using the phylogenies of Tonini et al. (2016; n = 4001), and Pyron et al. (2013; n = 1997).

Variable	Tonini et al. 2016		Pyron et al. 2013		Ordinary	
	Correlation (rho)	p-value	Correlation (rho)	p-value	Correlation (rho)	p-value
Animal (total)	-0.115	0.000	-0.150	0.000	-0.261	0.000
Invertebrates (total)	-0.144	0.000	-0.190	0.000	-0.360	0.000
Arthropods	-0.152	0.000	-0.001	0.965	-0.348	0.000
Durophagy	0.071	0.000	-0.005	0.819	0.163	0.000
Vertebrates	0.136	0.000	0.145	0.000	0.282	0.000
Plant (total)	0.135	0.000	0.159	0.000	0.262	0.000
Plant (fibrous)	0.084	0.000	0.107	0.000	0.240	0.000
Plant (non-fibrous)	0.120	0.000	0.141	0.000	0.241	0.000

Table 61: Results of Kendall's rank-correlation tests correlating the arcsine-transformed percentage values of each food type against log-transformed values of snout-vent length in lizards. The first two columns refer to correlation

tests done on the PICs of those variables, generated using the phylogenies of Tonini et al. (2016; n = 4001), and Pyron et al. (2013; n = 1997).

Variable	Tonini et al. 2016		Pyron et al. 2013		Ordinary	
	Correlation (tau)	p-value	Correlation (tau)	p-value	Correlation (tau)	p-value
Animal (total)	-0.084	0.000	-0.109	0.000	-0.209	0.000
Invertebrates (total)	-0.105	0.000	-0.138	0.000	-0.284	0.000
Arthropods	-0.111	0.000	-0.001	0.974	-0.277	0.000
Durophagy	0.057	0.000	-0.004	0.822	0.132	0.000
Vertebrates	0.108	0.000	0.113	0.000	0.229	0.000
Plant (total)	0.104	0.000	0.120	0.000	0.210	0.000
Plant (fibrous)	0.067	0.000	0.083	0.000	0.195	0.000
Plant (non-fibrous)	0.093	0.000	0.107	0.000	0.193	0.000

Table 62: Results of ANOVA analyses comparing mean log-transformed snout-vent length between the dietary guilds recovered in the k-means cluster analysis, and the classical dietary guilds in lizards. Abbreviations: **Df**, degrees of freedom; **Sum Sq**, sum of square distances; **Mean Sq**, mean square distances. N = 4001.

	Df	Sum Sq	Mean Sq	F-value	P-value
K=10	9	57.350	6.372	119.814	0.000
-Residuals	3991	212.258	0.053	NA	NA
Classical guilds	2	19.748	9.874	157.990	0.000
-Residuals	3998	249.860	0.062	NA	NA
K=5 (Tonini)	4	50.832	12.708	232.114	0.001
Residuals		218.776	0.055	NA	NA
K=10 (Tonini)	9	57.35	6.37	119.81	<0.01
Residuals	3991	212.26	0.05	NA	NA
K=20 (Tonini)	19	60.9117	3.206	61.15	0.001
Residuals		208.696	0.052	NA	NA
Classical (Tonini)	2	19.75	9.87	157.99	<0.01
Residuals	3998	249.86	0.06	NA	NA
K=5 (Pyron)	4	33.936	8.484	167.881	0.001

Residuals		100.615	0.050	NA	NA
K=10 (Pyron)	9	37.06	4.12	83.88	<0.01
Residuals	3991	97.49	0.05	NA	NA
K=20 (Pyron)	19	39.32	2.081	43.269	0.001
Residuals		95.018	0.048	NA	NA
Classical (Pyron)	2	11.65	5.83	94.50	NA
Residuals	3998	122.90	0.06	NA	NA

Table 63: Posthoc pairwise comparisons from the ordinary ANOVA between mean log-transformed snout-vent length between the dietary guilds recovered in the k-means cluster analysis in lizards. Abbreviations: **diff**, group mean difference; **lwr**, lower range of group mean difference; **upr**, upper range of group mean difference; **p adj**, adjusted p-value. **Guild numbers**: **1**, mixed faunivory (n = 52); 2, insectivory (sensu stricto; n = 3 156); **3**, insectivory (sensu lato; n = 278); **4**, predominantly durophagous mixed invertivory (n = 22); **5**, carnivory (n = 17); **6**, insectivory-omnivory (n = 272); **7**, mixed herbivory comprised primarily of reproductive plant structures (n = 41); **8**, omnivory (n = 72); **9**, mixed herbivory (n = 77); **10**, folivory (n = 14).

	diff	**lwr**	**upr**	**p adj**
10-1	-0.053	-0.273	0.167	0.999
2-1	-0.588	-0.690	-0.486	0.000
3-1	-0.440	-0.550	-0.330	0.000
4-1	-0.139	-0.325	0.047	0.345
5-1	0.090	-0.114	0.294	0.930
6-1	-0.507	-0.618	-0.397	0.000
7-1	-0.160	-0.312	-0.007	0.032
8-1	-0.386	-0.518	-0.253	0.000
9-1	-0.169	-0.300	-0.038	0.002
2-10	-0.535	-0.730	-0.339	0.000
3-10	-0.387	-0.587	-0.187	0.000
4-10	-0.086	-0.335	0.164	0.986
5-10	0.143	-0.121	0.406	0.786
6-10	-0.454	-0.654	-0.254	0.000
7-10	-0.106	-0.332	0.120	0.896
8-10	-0.332	-0.546	-0.119	0.000

9-10	-0.115	-0.328	0.097	0.783
3-2	0.148	0.102	0.194	0.000
4-2	0.449	0.293	0.605	0.000
5-2	0.678	0.500	0.855	0.000
6-2	0.081	0.035	0.127	0.000
7-2	0.428	0.314	0.543	0.000
8-2	0.202	0.115	0.289	0.000
9-2	0.419	0.335	0.503	0.000
4-3	0.301	0.139	0.462	0.000
5-3	0.530	0.347	0.712	0.000
6-3	-0.067	-0.130	-0.005	0.022
7-3	0.280	0.158	0.402	0.000
8-3	0.054	-0.042	0.151	0.748
9-3	0.271	0.177	0.365	0.000
5-4	0.229	-0.007	0.464	0.066
6-4	-0.368	-0.530	-0.206	0.000
7-4	-0.021	-0.214	0.172	1.000
8-4	-0.247	-0.424	-0.069	0.000
9-4	-0.030	-0.206	0.147	1.000
6-5	-0.597	-0.779	-0.414	0.000
7-5	-0.249	-0.460	-0.039	0.007
8-5	-0.475	-0.672	-0.278	0.000
9-5	-0.258	-0.454	-0.063	0.001
7-6	0.348	0.225	0.470	0.000
8-6	0.122	0.025	0.218	0.003
9-6	0.339	0.244	0.433	0.000
8-7	-0.226	-0.369	-0.083	0.000
9-7	-0.009	-0.150	0.132	1.000
9-8	0.217	0.097	0.337	0.000

Table 64: Posthoc pairwise comparisons from the ordinary ANOVA between mean log-transformed snout-vent length between the classical dietary guilds (faunivory, n = 3 623; omnivory, n = 280; herbivory, n = 98) in lizards.

Abbreviations: **diff**, group mean difference; **lwr**, lower range of group mean difference; **upr**, upper range of group mean difference; **p adj**, adjusted p-value.

	diff	lwr	upr	p adj
Herbivory-Faunivory	0.437	0.377	0.497	0.000
Omnivory-Faunivory	0.088	0.051	0.124	0.000
Omnivory-Herbivory	-0.349	-0.418	-0.281	0.000

Table 65: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed snout-vent length between the dietary guilds recovered in the k-means cluster analysis (k=10) in lizards (topology of Tonini et al. 2016). Guild numbers: **1**, mixed faunivory (n = 52); 2, insectivory (sensu strictu; n = 3 156); **3**, insectivory (sensu lato; n = 278); **4**, predominantly durophagous mixed invertivory (n = 22); **5**, carnivory (n = 17); **6**, insectivory-omnivory (n = 272); **7**, mixed herbivory comprised primarily of reproductive plant structures (n = 41); **8**, omnivory (n = 72); **9**, mixed herbivory (n = 77); **10**, folivory (n = 14).

	1	10	2	3	4	5	6	7	8	9
1	NA	1.000	0.045	0.322	1.000	0.969	0.174	1.000	0.720	1.000
10	1.000	NA	0.045	0.070	1.000	1.000	0.070	1.000	0.128	1.000
2	0.045	0.045	NA	0.288	0.045	0.045	1.000	0.045	0.234	0.045
3	0.322	0.070	0.288	NA	0.045	0.196	1.000	0.045	1.000	0.275
4	1.000	1.000	0.045	0.045	NA	1.000	0.128	1.000	0.550	1.000
5	0.969	1.000	0.045	0.196	1.000	NA	0.099	1.000	0.550	1.000
6	0.174	0.070	1.000	1.000	0.128	0.099	NA	0.045	1.000	0.196
7	1.000	1.000	0.045	0.045	1.000	1.000	0.045	NA	0.045	1.000
8	0.720	0.128	0.234	1.000	0.550	0.550	1.000	0.045	NA	0.128
9	1.000	1.000	0.045	0.275	1.000	1.000	0.196	1.000	0.128	NA

Table 66: Posthoc pairwise t-values from the phylogenetic ANOVA comparisons between mean log-transformed snout-vent length between the dietary guilds recovered in the k-means cluster analysis (k=10) in lizards (topology of Tonini et al. 2016). Guild numbers: **1**, mixed faunivory (n = 52); 2, insectivory (sensu strictu; n = 3 156); **3**, insectivory (sensu lato; n = 278); **4**, predominantly durophagous mixed invertivory (n = 22); **5**, carnivory (n = 17); **6**, insectivory-omnivory (n = 272); **7**, mixed herbivory comprised primarily of

reproductive plant structures (n = 41); **8**, omnivory (n = 72); **9**, mixed herbivory (n = 77); **10**, folivory (n = 14).

	1	**10**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	NA	0.77	18.23	12.62	2.37	-1.39	14.53	3.31	9.19	4.07
10	-0.77	NA	8.66	6.12	1.09	-1.72	7.18	1.49	4.93	1.72
2	-18.23	-8.66	NA	-10.27	-9.10	-12.08	-5.53	-11.82	-7.36	-15.76
3	-12.62	-6.12	10.27	NA	-5.89	-9.19	3.43	-7.26	-1.78	-9.13
4	-2.37	-1.09	9.10	5.89	NA	-3.07	7.20	0.34	4.39	0.53
5	1.39	1.72	12.08	9.19	3.07	NA	10.35	3.75	7.64	4.18
6	-14.53	-7.18	5.53	-3.43	-7.20	-10.35	NA	-9.00	-3.98	-11.37
7	-3.31	-1.49	11.82	7.26	-0.34	-3.75	9.00	NA	5.01	0.20
8	-9.19	-4.93	7.36	1.78	-4.39	-7.64	3.98	-5.01	NA	-5.74
9	-4.07	-1.72	15.76	9.13	-0.53	-4.18	11.37	-0.20	5.74	NA

Table 67: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed snout-vent length between the dietary guilds recovered in the k-means cluster analysis (k=10) in lizards (topology of Pyron et al. 2013). Guild numbers: **1**, mixed faunivory (n = 42); 2, insectivory (sensu strictu; n = 1 447); **3**, insectivory (sensu lato; n = 177); **4**, predominantly durophagous mixed invertivory (n = 12); **5**, carnivory (n = 10); **6**, insectivory-omnivory (n = 180); **7**, mixed herbivory comprised primarily of reproductive plant structures (n = 28); **8**, omnivory (n = 43); **9**, mixed herbivory (n = 54); **10**, folivory (n = 4).

	1	**10**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	NA	1.000	0.062	0.104	1.000	0.062	0.084	1.000	0.792	1.000
10	1.000	NA	0.045	0.045	1.000	1.000	0.045	1.000	0.045	0.722
2	0.062	0.045	NA	0.504	0.045	0.045	1.000	0.045	0.138	0.045
3	0.104	0.045	0.504	NA	0.045	0.045	1.000	0.045	1.000	0.154
4	1.000	1.000	0.045	0.045	NA	1.000	0.104	1.000	0.504	1.000
5	0.062	1.000	0.045	0.045	1.000	NA	0.045	1.000	0.062	1.000
6	0.084	0.045	1.000	1.000	0.104	0.045	NA	0.045	1.000	0.104
7	1.000	1.000	0.045	0.045	1.000	1.000	0.045	NA	0.045	1.000
8	0.792	0.045	0.138	1.000	0.504	0.062	1.000	0.045	NA	0.084
9	1.000	0.722	0.045	0.154	1.000	1.000	0.104	1.000	0.084	NA

Table 68: Posthoc pairwise t-values from the phylogenetic ANOVA comparisons between mean log-transformed snout-vent length between the dietary guilds recovered in the k-means cluster analysis (k=10) in lizards (topology of Pyron et al. 2013). Guild numbers: **1**, mixed faunivory (n = 42); 2, insectivory (sensu strictu; n = 1 447); **3**, insectivory (sensu lato; n = 177); **4**, predominantly durophagous mixed invertivory (n = 12); **5**, carnivory (n = 10); **6**, insectivory-omnivory (n = 180); **7**, mixed herbivory comprised primarily of reproductive plant structures (n = 28); **8**, omnivory (n = 43); **9**, mixed herbivory (n = 54); **10**, folivory (n = 4).

	1	**10**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	NA	-0.35	16.48	11.21	2.02	-2.55	13.09	2.24	7.64	3.23
10	0.35	NA	5.46	4.12	1.46	-1.21	4.73	1.36	3.50	1.62
2	-16.48	-5.46	NA	-8.14	-6.52	-10.86	-4.42	-10.52	-5.84	-13.65
3	-11.21	-4.12	8.14	NA	-4.17	-8.62	2.93	-6.69	-1.52	-8.01
4	-2.02	-1.46	6.52	4.17	NA	-3.63	5.21	-0.34	3.02	0.00
5	2.55	1.21	10.86	8.62	3.63	NA	9.57	3.91	7.24	4.52
6	-13.09	-4.73	4.42	-2.93	-5.21	-9.57	NA	-8.23	-3.33	-10.05
7	-2.24	-1.36	10.52	6.69	0.34	-3.91	8.23	NA	4.54	0.50
8	-7.64	-3.50	5.84	1.52	-3.02	-7.24	3.33	-4.54	NA	-4.83
9	-3.23	-1.62	13.65	8.01	0.00	-4.52	10.05	-0.50	4.83	NA

Table 69: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed snout-vent length between the dietary guilds recovered in the k-means cluster analysis (k=5) in lizards (topology of Tonini et al. 2016). See Table 23 for details of the guilds.

	1	**2**	**3**	**4**	**5**
1	1	0.01	0.02	0.01	0.024
2	0.01	1	0.024	0.258	0.012
3	0.02	0.024	1	0.01	0.985
4	0.01	0.258	0.01	1	0.01
5	0.024	0.012	0.985	0.01	1

Table 70: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed snout-vent length between the

dietary guilds recovered in the k-means cluster analysis (k=20) in lizards (topology of Tonini et al. 2016). See Table 25 for details of the guilds.

	1	10	11	12	13	14	15	16	17	18	19	2	20	3	4	5	6	7	8	9
1	1	1	1	0.81	1	0.676	1	1	1	1	1	0.936	1	1	1	0.676	1	1	0.676	1
10	1	1	1	1	1	1	1	1	1	0.364	1	0.81	1	1	1	0.676	1	1	0.81	1
11	1	1	1	1	1	1	1	1	1	0.364	1	1	1	1	1	1	1	1	1	1
12	0.81	1	1	1	1	1	1	1	1	0.364	1	1	0.364	1	0.364	1	1	1	1	1
13	1	1	1	1	1	1	1	1	1	0.81	1	1	1	1	1	1	1	1	1	1
14	0.676	1	1	1	1	1	1	1	1	0.19	1	1	1	1	0.81	1	1	1	1	1
15	1	1	1	1	1	1	1	1	1	0.19	1	1	1	1	1	1	1	1	1	1
16	1	1	1	1	1	1	1	1	1	0.364	1	1	0.525	1	0.81	1	1	1	1	1
17	1	1	1	1	1	1	1	1	1	0.19	1	1	1	1	1	1	1	1	1	1
18	1	0.364	0.364	0.364	0.81	0.19	0.19	0.364	0.19	1	1	0.19	1	0.525	1	0.19	1	0.364	0.19	0.676
19	1	1	1	1	1	1	1	1	1	1	1	0.936	1	1	1	1	1	1	1	1
2	0.936	0.81	1	1	1	1	1	1	1	0.19	0.936	1	0.19	1	0.19	1	1	1	1	1
20	1	1	1	0.364	1	1	1	0.525	1	1	1	0.19	1	0.676	1	0.525	1	1	0.936	0.936
3	1	1	1	1	1	1	1	1	1	0.525	1	1	0.676	1	0.676	1	1	1	1	1
4	1	1	1	0.364	1	0.81	1	0.81	1	1	1	0.19	1	0.676	1	0.525	1	0.936	0.525	1
5	0.676	0.676	1	1	1	1	1	1	1	0.19	1	1	0.525	1	0.525	1	1	1	1	0.525
6	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
7	1	1	1	1	1	1	1	1	1	0.364	1	1	1	1	0.936	1	1	1	1	1
8	0.676	0.81	1	1	1	1	1	1	1	0.19	1	1	0.936	1	0.525	1	1	1	1	1
9	1	1	1	1	1	1	1	1	1	0.676	1	1	0.936	1	1	0.525	1	1	1	1

Table 71: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed snout-vent length between the dietary guilds recovered in the k-means cluster analysis (k=5) in lizards (topology of Pyron et al. 2014). See Table 23 for details of the guilds.

	1	2	3	4	5
1	**1**	**0.01**	**0.01**	**0.01**	**0.015**
2	**0.01**	**1**	**0.016**	**0.116**	**0.021**
3	**0.01**	**0.016**	**1**	**0.01**	**0.857**
4	**0.01**	**0.116**	**0.01**	**1**	**0.01**
5	**0.015**	**0.021**	**0.857**	**0.01**	**1**

Table 72: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed snout-vent length between the classical dietary guilds (faunivory, n = 3 623; omnivory, n = 280; herbivory, n = 98) in lizards (topology of Tonini et al. 2016).

	Faunivory	Herbivory	Omnivory
Faunivory	NA	0.003	0.116
Herbivory	0.003	NA	0.004
Omnivory	0.116	0.004	NA

Table 73: Posthoc pairwise t-values from the phylogenetic ANOVA comparisons between mean log-transformed snout-vent length between the classical dietary guilds (faunivory, n = 3 623; omnivory, n = 280; herbivory, n = 98) in lizards (topology of Tonini et al. 2016).

	Faunivory	Herbivory	Omnivory
Faunivory	NA	-17.081	-5.658
Herbivory	17.081	NA	11.909
Omnivory	5.658	-11.909	NA

Table 74: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed snout-vent length between the

classical dietary guilds (faunivory, n = 1 758; omnivory, n = 175; herbivory, n = 64) in lizards (topology of Pyron et al. 2013).

	Faunivory	**Herbivory**	**Omnivory**
Faunivory	NA	0.003	0.349
Herbivory	0.003	NA	0.003
Omnivory	0.349	0.003	NA

Table 75: Posthoc pairwise t-values from the phylogenetic ANOVA comparisons between mean log-transformed snout-vent length between the classical dietary guilds (faunivory, n = 1 758; omnivory, n = 175; herbivory, n = 64) in lizards (topology of Pyron et al. 2013).

	Faunivory	**Herbivory**	**Omnivory**
Faunivory	NA	-13.574	-2.965
Herbivory	13.574	NA	10.332
Omnivory	2.965	-10.332	NA

Table 76: Results of ordinary linear models regressing the arcsine-transformed percentage values of each food type against log-transformed values of body mass in birds. Abbreviations: **Std.error**, standard error. N = 9783.

Model	**Estimate**	**Std.error**	**Statistic**	**p-value**	**R^2**
Animal (total)	-0.032	0.011	-2.876	0.004	0.001
Invertebrates (total)	-0.416	0.011	-37.885	0.000	0.128
Vertebrates (total)	1.157	0.021	56.209	0.000	0.244
Terrestrial	1.114	0.027	41.479	0.000	0.150
Fish	1.419	0.043	32.801	0.000	0.099
Plant (total)	0.103	0.013	7.729	0.000	0.006
Plant (fibrous)	1.281	0.042	30.492	0.000	0.087
Plant (non-fibrous)	-0.067	0.015	-4.465	0.000	0.002
Fruit	0.313	0.021	15.203	0.000	0.023
Seed	-0.024	0.026	-0.916	0.360	0.000
Nectar	-0.887	0.028	-31.982	0.000	0.095

Table 77: Results of phylogenetic linear models regressing the PICs of arcsine-transformed percentage values of each food type against the PIC of log-transformed values of body mass in birds (backbone topology of Hackett et al. 2008). Abbreviations: **Std.error**, standard error. N = 9783.

Model	Estimate	Std.error	Statistic	p-value	R^2
Animal (total)	0.041	0.008	4.883	0.000	0.002
Invertebrates (total)	0.176	0.004	42.552	0.000	0.156
Vertebrates (total)	-0.295	0.007	-42.803	0.000	0.158
Terrestrial	0.079	0.019	4.112	0.000	0.002
Fish	-0.324	0.007	-45.967	0.000	0.178
Plant (total)	-0.059	0.009	-6.732	0.000	0.005
Plant (fibrous)	0.089	0.016	5.490	0.000	0.003
Plant (non-fibrous)	-0.083	0.008	-10.108	0.000	0.010
Fruit	-0.041	0.010	-3.952	0.000	0.002
Seed	-0.124	0.012	-10.642	0.000	0.011
Nectar	0.030	0.027	1.098	0.272	0.000

Table 78: Results of phylogenetic linear models regressing the PICs of arcsine-transformed percentage values of each food type against the PIC of log-transformed values of body mass in birds (backbone topology of Ericson et al. 2006). Abbreviations: **Std.error**, standard error. N = 9783.

Model	Estimate	Std.error	Statistic	p-value	R^2
Animal (total)	-0.295	0.001	-320.801	0.000	0.913
Invertebrates (total)	-0.974	0.014	-71.924	0.000	0.346
Vertebrates (total)	-0.748	0.002	-303.342	0.000	0.904
Terrestrial	2.207	0.011	197.848	0.000	0.800
Fish	-0.674	0.002	-352.444	0.000	0.927
Plant (total)	0.633	0.002	255.979	0.000	0.870
Plant (fibrous)	0.115	0.046	2.513	0.012	0.001
Plant (non-fibrous)	0.612	0.003	224.628	0.000	0.838
Fruit	1.134	0.006	174.742	0.000	0.757
Seed	1.183	0.006	193.689	0.000	0.793
Nectar	-0.035	0.056	-0.619	0.536	0.000

Table 79: Results of Spearman's rank-correlation tests correlating the arcsine-transformed percentage values of each food type against log-transformed values of body mass in birds. The first two columns refer to correlation tests done on the PICs of those variables, generated using the phylogenies of Hackett et al. (2008), and Ericson et al. (2006). N = 9783.

Variable	Hackett et al. 2008		Ericson et al. 2006		Ordinary	
	Correlation (rho)	p-value	Correlation (rho)	p-value	Correlation (rho)	p-value
Animal (total)	-0.034	0.001	-0.035	0.001	-0.054	0.000
Invertebrates (total)	-0.098	0.000	-0.094	0.000	-0.340	0.000
Vertebrates (total)	0.153	0.000	0.146	0.000	0.480	0.000
Terrestrial	0.136	0.000	0.139	0.000	0.404	0.000
Fish	0.050	0.000	-0.094	0.000	0.320	0.000
Plant (total)	0.027	0.008	0.031	0.002	0.054	0.000
Plant (fibrous)	0.029	0.004	0.029	0.004	0.240	0.000
Plant (non-fibrous)	0.002	0.828	0.004	0.670	-0.029	0.005
Fruit	0.041	0.000	0.043	0.000	0.170	0.000
Seed	-0.013	0.189	-0.013	0.189	0.082	0.000
Nectar	-0.012	0.245	0.001	0.920	-0.293	0.000

Table 80: Results of Kendell's rank-correlation tests correlating the arcsine-transformed percentage values of each food type against log-transformed values of body mass in birds. The first two columns refer to correlation tests done on the PICs of those variables, generated using the phylogenies of Hackett et al. (2008), and Ericson et al. (2006). N = 9783.

Variable	Hackett et al. 2008		Ericson et al. 2006		Ordinary	
	Correlation (tau)	p-value	Correlation (tau)	p-value	Correlation (tau)	p-value
Animal (total)	-0.024	0.001	-0.025	0.000	-0.040	0.000
Invertebrates (total)	-0.069	0.000	-0.066	0.000	-0.250	0.000
Vertebrates (total)	0.117	0.000	0.112	0.000	0.385	0.000
Terrestrial	0.105	0.000	0.107	0.000	0.325	0.000
Fish	0.040	0.000	-0.066	0.000	0.258	0.000
Plant (total)	0.019	0.007	0.022	0.002	0.040	0.000

Plant (fibrous)	0.022	0.004	0.022	0.003	0.192	0.000
Plant (non-fibrous)	0.002	0.819	0.003	0.669	-0.020	0.007
Fruit	0.030	0.000	0.031	0.000	0.133	0.000
Seed	-0.010	0.188	-0.010	0.181	0.062	0.000
Nectar	-0.009	0.245	0.001	0.914	-0.237	0.000

Table 81: Results of ordinary ANOVA analyses comparing mean log-transformed body mass between the guilds recovered in the k-means cluster analysis, and the classical dietary guilds in birds. Abbreviations: **Df**, degrees of freedom; **Sum Sq**, sum of square distances; **Mean Sq**, mean square distances; **Eta Sq**, eta squared. N = 9783.

	Df	**Sum Sq**	**Mean Sq**	**F-value**	**P-value**
K=10	9	1786	198.45	699.8	0.000
-Residuals	9965	2826	0.28	NA	NA
Classical guilds	2	13.092	6.546	13.865	0.000
-Residuals	9780	4617.404	0.472	NA	NA
K=5 (Ericson)	4	900.552	225.138	604.760	0.001
-Residuals		3711.599	0.372	NA	NA
K=10 (Ericson)	9	1786.088	198.454	699.771	0.001
-Residuals		2826.063	0.284	NA	NA
K=20 (Ericson)	19	2060.010	108.422	422.914	0.001
-Residuals		2552.141	0.256	NA	NA
Classical (Ericson)	2	13.09	6.55	13.86	0.918
-Residuals	9780	4617.40	0.47	NA	NA
K=5 (Hackett)	4	900.552	225.138	604.760	0.001
-Residuals		3711.599	0.372	NA	NA
K=10 (Hackett)	9	1786.088	198.454	699.771	0.001
-Residuals		2826.063	0.284	NA	NA
K=20 (Hackett)	19	2060.010	108.422	422.914	0.001
-Residuals		2552.141	0.256	NA	NA
Classical (Hackett)	2	13.09	6.55	13.86	0.906

-Residuals	9780	4617.40	0.47	NA	NA

Table 82: Posthoc pairwise comparisons from the ordinary ANOVA between mean log-transformed body mass between the dietary guilds recovered in the k-means cluster analysis (k=10) in birds. Abbreviations: **diff**, group mean difference; **lwr**, lower range of group mean difference; **upr**, upper range of group mean difference; **p adj**, adjusted p-value. **Guild numbers**: **1**, frugivory (n = 348); **2**, frugivory-omnivory (n = 1237); **3**, nectarivory (n = 562); **4**, omnivory (n = 1404); **5**, piscivory (sensu lato; n = 336); **6**, invertivory (sensu stricto; n = 2 783); **7**, carnivory (n = 370); **8**, mixed herbivory (n = 246); **9**, granivory (n = 475); **10**, invertivory (sensu lato; n = 2232).

	diff	**lwr**	**upr**	**p adj**
10-1	-0,452	-0,549	-0,355	0
2-1	-0,363	-0,466	-0,261	0
3-1	-1,204	-1,319	-1,089	0
4-1	-0,229	-0,330	-0,128	0
5-1	0,599	0,469	0,729	0
6-1	-0,751	-0,847	-0,655	0
7-1	0,641	0,515	0,766	0
8-1	0,549	0,409	0,690	0
9-1	-0,680	-0,798	-0,561	0
2-10	0,089	0,029	0,148	0
3-10	-0,752	-0,832	-0,673	0
4-10	0,223	0,165	0,280	0
5-10	1,051	0,951	1,151	0
6-10	-0,299	-0,347	-0,251	0
7-10	1,093	0,998	1,187	0
8-10	1,001	0,888	1,115	0
9-10	-0,227	-0,313	-0,142	0
3-2	-0,841	-0,926	-0,755	0
4-2	0,134	0,069	0,200	0
5-2	0,962	0,857	1,067	0
6-2	-0,388	-0,445	-0,330	0
7-2	1,004	0,904	1,104	0

8-2	0,913	0,795	1,030	0
9-2	-0,316	-0,407	-0,225	0
4-3	0,975	0,891	1,059	0
5-3	1,803	1,686	1,920	0
6-3	0,453	0,375	0,531	0
7-3	1,845	1,732	1,958	0
8-3	1,753	1,625	1,882	0
9-3	0,525	0,420	0,630	0
5-4	0,828	0,724	0,932	0
6-4	-0,522	-0,577	-0,467	0
7-4	0,870	0,771	0,968	0
8-4	0,778	0,662	0,895	0
9-4	-0,450	-0,540	-0,361	0
6-5	-1,350	-1,449	-1,251	0
7-5	0,042	-0,086	0,170	0.99
8-5	-0,050	-0,192	0,093	0.985
9-5	-1,278	-1,399	-1,157	0
7-6	1,392	1,299	1,485	0
8-6	1,301	1,188	1,413	0
9-6	0,072	-0,012	0,155	0.168
8-7	-0,091	-0,230	0,047	0.538
9-7	-1,320	-1,437	-1,203	0
9-8	-1,229	-1,361	-1,096	0

Table 83: Posthoc pairwise comparisons from the ordinary ANOVA between mean log-transformed body mass between the classical dietary guilds (faunivory, n = 5 127; omnivory, n = 2 480; herbivory, n = 2 176) in birds. Abbreviations: **diff**, group mean difference; **lwr**, lower range of group mean difference; **upr**, upper range of group mean difference; **p adj**, adjusted p-value.

	diff	**lwr**	**upr**	**p adj**
Herbivory-Faunivory	0.084	0.042	0.125	0.000
Omnivory-Faunivory	-0.011	-0.051	0.028	0.784
Omnivory-Herbivory	-0.095	-0.142	-0.047	0.000

Table 84: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the dietary guilds recovered in the k-means cluster analysis (k=10) in birds (backbone topology of Ericson et al. 2006). Guild numbers: **1**, frugivory (n = 348); **2**, frugivory-omnivory (n = 1237); **3**, nectarivory (n = 562); **4**, omnivory (n = 1404); **5**, piscivory (sensu lato; n = 336); **6**, invertivory (sensu stricto; n = 2 783); **7**, carnivory (n = 370); **8**, mixed herbivory (n = 246); **9**, granivory (n = 475); **10**, invertivory (sensu lato; n = 2232).

	1	**10**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	1	0.799	1	0.045	1	1	0.093	1	1	0.242
10	0.799	1	1	0.468	1	0.045	0.045	0.093	0.108	1
2	1	1	1	0.304	1	0.093	0.045	0.207	0.175	1
3	0.045	0.468	0.304	1	0.093	0.045	1	0.045	0.045	1
4	1	1	1	0.093	1	0.192	0.045	0.252	0.252	0.108
5	1	0.045	0.093	0.045	0.192	1	0.045	1	1	0.07
6	0.093	0.045	0.045	1	0.045	0.045	1	0.045	0.07	1
7	1	0.093	0.207	0.045	0.252	1	0.045	1	1	0.07
8	1	0.108	0.175	0.045	0.252	1	0.07	1	1	0.07
9	0.242	1	1	1	0.108	0.07	1	0.07	0.07	1

Table 85: Posthoc pairwise t-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the dietary guilds recovered in the k-means cluster analysis (k=10) in birds (backbone topology of Ericson et al. 2006). Guild numbers: **1**, frugivory (n = 348); **2**, frugivory-omnivory (n = 1237); **3**, nectarivory (n = 562); **4**, omnivory (n = 1404); **5**, piscivory (sensu lato; n = 336); **6**, invertivory (sensu stricto; n = 2 783); **7**, carnivory (n = 370); **8**, mixed herbivory (n = 246); **9**, granivory (n = 475); **10**, invertivory (sensu lato; n = 2232).

	1	**10**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	0,000	14,726	11,249	33,151	7,188	-14,587	24,810	-16,109	-12,382	18,083
10	-14,726	0,000	-4,690	29,918	-12,279	-33,273	19,753	-36,546	-27,984	8,450
2	-11,249	4,690	0,000	31,035	-6,466	-29,023	21,307	-31,820	-24,551	10,994

3	-33,151	-29,918	-31,035	0,000	-36,680	-48,631	-18,393	-51,745	-43,071	-15,809
4	-7,188	12,279	6,466	36,680	0,000	-25,289	29,945	-27,950	-21,149	15,930
5	14,587	33,273	29,023	48,631	25,289	0,000	43,304	-1,035	1,101	33,374
6	-24,810	-19,753	-21,307	18,393	-29,945	-43,304	0,000	-47,232	-36,714	-2,714
7	16,109	36,546	31,820	51,745	27,950	1,035	47,232	0,000	2,086	35,750
8	12,382	27,984	24,551	43,071	21,149	-1,101	36,714	-2,086	0,000	29,374
9	-18,083	-8,450	-10,994	15,809	-15,930	-33,374	2,714	-35,750	-29,374	0,000

Table 86: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the dietary guilds recovered in the k-means cluster analysis (k=10) in birds (backbone topology of Hackett et al. 2008). Guild numbers: **1**, frugivory (n = 348); **2**, frugivory-omnivory (n = 1237); **3**, nectarivory (n = 562); **4**, omnivory (n = 1404); **5**, piscivory (sensu lato; n = 336); **6**, invertivory (sensu stricto; n = 2 783); **7**, carnivory (n = 370); **8**, mixed herbivory (n = 246); **9**, granivory (n = 475); **10**, invertivory (sensu lato; n = 2232).

	1	**10**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	1	0.714	1	0.068	1	0.915	0.045	0.915	1	0.207
10	0.714	1	1	0.576	0.8	0.045	0.045	0.068	0.192	1
2	1	1	1	0.4	1	0.068	0.068	0.182	0.399	1
3	0.068	0.576	0.4	1	0.162	0.045	1	0.045	0.045	1
4	1	0.8	1	0.162	1	0.112	0.045	0.264	0.418	0.087
5	0.915	0.045	0.068	0.045	0.112	1	0.045	1	1	0.045
6	0.045	0.045	0.068	1	0.045	0.045	1	0.045	0.068	1
7	0.915	0.068	0.182	0.045	0.264	1	0.045	1	1	0.045
8	1	0.192	0.399	0.045	0.418	1	0.068	1	1	0.182
9	0.207	1	1	1	0.087	0.045	1	0.045	0.182	1

Table 87: Posthoc pairwise t-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the dietary guilds recovered in the k-means cluster analysis (k=10) in birds (backbone topology of Hackett et al. 2008). Guild numbers: **1**, frugivory (n = 348); **2**, frugivory-omnivory (n = 1237); **3**, nectarivory (n = 562); **4**, omnivory (n = 1404); **5**,

piscivory (sensu lato; n = 336); **6**, invertivory (sensu stricto; n = 2 783); **7**, carnivory (n = 370); **8**, mixed herbivory (n = 246); **9**, granivory (n = 475); **10**, invertivory (sensu lato; n = 2232).

	1	**10**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	0,00	14,73	11,25	33,15	7,19	-14,59	24,81	-16,11	-12,38	18,08
10	-14,73	0,00	-4,69	29,92	-12,28	-33,27	19,75	-36,55	-27,98	8,45
2	-11,25	4,69	0,00	31,04	-6,47	-29,02	21,31	-31,82	-24,55	10,99
3	-33,15	-29,92	-31,04	0,00	-36,68	-48,63	-18,39	-51,75	-43,07	-15,81
4	-7,19	12,28	6,47	36,68	0,00	-25,29	29,94	-27,95	-21,15	15,93
5	14,59	33,27	29,02	48,63	25,29	0,00	43,30	-1,03	1,10	33,37
6	-24,81	-19,75	-21,31	18,39	-29,94	-43,30	0,00	-47,23	-36,71	-2,71
7	16,11	36,55	31,82	51,75	27,95	1,03	47,23	0,00	2,09	35,75
8	12,38	27,98	24,55	43,07	21,15	-1,10	36,71	-2,09	0,00	29,37
9	-18,08	-8,45	-10,99	15,81	-15,93	-33,37	2,71	-35,75	-29,37	0,00

Table 88: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the dietary guilds recovered in the k-means cluster analysis (k=5) in birds (backbone topology of Ericson et al. 2006). See Table 26 for details of guilds.

	1	**2**	**3**	**4**	**5**
1	1	0.908	0.084	0.12	0.056
2	0.908	1	0.01	0.14	0.01
3	0.084	0.01	1	1	1
4	0.12	0.14	1	1	1
5	0.056	0.01	1	1	1

Table 89: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the dietary

guilds recovered in the k-means cluster analysis (k=20) in birds (backbone topology of Ericson et al. 2006). See Table 28 for details of guilds.

	1	10	11	12	13	14	15	16	17	18	19	2	20	3	4	5	6	7	8	9
1	1	1	0.696	1	1	1	0.585	1	0.488	1	1	1	1	1	1	1	1	1	1	1
10	1	1	0.19	0.488	1	0.19	0.19	1	0.19	0.19	0.19	0.19	0.19	0.19	1	0.19	0.19	0.19	1	1
11	0.696	0.19	1	0.19	0.19	1	1	0.19	1	0.19	1	1	0.19	1	0.19	1	1	0.488	0.963	0.19
12	1	0.488	0.19	1	1	1	1	0.88	0.19	1	0.488	0.798	1	0.27	1	0.88	1	1	1	1
13	1	1	0.19	1	1	0.372	0.19	1	0.19	1	0.27	0.798	1	0.19	1	0.27	0.19	0.27	1	1
14	1	0.19	1	1	0.372	1	1	0.19	1	0.19	1	1	0.488	1	0.27	1	1	1	1	0.19
15	0.585	0.19	1	1	0.19	1	1	0.19	1	0.19	1	1	1	1	0.19	1	1	1	0.696	0.19
16	1	1	0.19	0.88	1	0.19	0.19	1	0.19	1	0.19	0.19	0.963	0.19	1	0.19	0.19	0.19	1	1
17	0.488	0.19	1	0.19	0.19	1	1	0.19	1	0.19	1	1	0.19	0.19	0.19	1	1	0.19	1	0.19
18	1	0.19	0.19	1	1	0.19	0.19	1	0.19	1	0.27	0.798	1	0.372	1	0.19	0.27	0.798	1	1
19	1	0.19	1	0.488	0.27	1	1	0.19	1	0.27	1	1	0.88	1	0.19	1	1	1	1	0.19
2	1	0.19	1	0.798	0.798	1	1	0.19	1	0.798	1	1	1	1	0.19	1	1	1	1	0.27
20	1	0.19	0.19	1	1	0.488	1	0.963	0.19	1	0.88	1	1	1	1	0.27	0.27	1	1	1
3	1	0.19	1	0.27	0.19	1	1	0.19	0.19	0.372	1	1	1	1	0.19	1	1	1	1	0.19
4	1	1	0.19	1	1	0.27	0.19	1	0.19	1	0.19	0.19	1	0.19	1	0.19	0.19	0.19	1	1
5	1	0.19	1	0.88	0.27	1	1	0.19	1	0.19	1	1	0.27	1	0.19	1	1	1	1	0.19
6	1	0.19	1	1	0.19	1	1	0.19	1	0.27	1	1	0.27	1	0.19	1	1	1	1	0.19

7	1	0.19	0.488	1	0.27	1	1	0.19	0.19	0.798	1	1	1	1	0.19	1	1	1	1	0.27
8	1	1	0.963	1	1	1	0.696	1	1	1	1	1	1	1	1	1	1	1	1	1
9	1	1	0.19	1	1	0.19	0.19	1	0.19	1	0.19	0.27	1	0.19	1	0.19	0.19	0.27	1	1

Table 90: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the dietary guilds recovered in the k-means cluster analysis (k=5) in birds (backbone topology of Hackett et al. 2008). See Table 26 for details of guilds.

	1	**2**	**3**	**4**	**5**
1	1	0.892	0.056	0.066	0.018
2	0.892	1	0.01	0.195	0.018
3	0.056	0.01	1	1	1
4	0.066	0.195	1	1	1
5	0.018	0.018	1	1	1

Table 91: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the dietary

guilds recovered in the k-means cluster analysis (k=20) in birds (backbone topology of Hackett et al. 2008). See Table 28 for details of guilds.

	1	10	11	12	13	14	15	16	17	18	19	2	20	3	4	5	6	7	8	9
1	1	1	0.508	1	1	1	0.805	1	0.19	1	1	1	1	1	1	1	1	1	1	1
10	1	1	0.19	1	1	0.19	0.19	1	0.19	0.19	0.19	0.19	0.6	0.19	1	0.19	0.19	0.272	1	1
11	0.508	0.19	1	0.19	0.19	1	1	0.19	1	0.19	1	1	0.19	1	0.19	1	1	0.508	0.6	0.19
12	1	1	0.19	1	1	1	1	0.805	0.19	1	1	0.508	1	0.272	1	0.696	1	1	1	0.904
13	1	1	0.19	1	1	0.19	0.19	1	0.19	1	0.272	0.6	1	0.19	1	0.19	0.272	0.19	1	1
14	1	0.19	1	1	0.19	1	1	0.19	1	0.508	1	1	1	1	0.19	1	1	1	1	0.19
15	0.805	0.19	1	1	0.19	1	1	0.19	1	0.272	1	1	1	1	0.19	1	1	1	1	0.19
16	1	1	0.19	0.805	1	0.19	0.19	1	0.19	1	0.19	0.272	1	0.19	1	0.19	0.19	0.19	1	1
17	0.19	0.19	1	0.19	0.19	1	1	0.19	1	0.19	1	1	0.508	0.19	0.19	1	1	0.19	1	0.19
18	1	0.19	0.19	1	1	0.508	0.272	1	0.19	1	0.39	1	1	0.6	1	0.508	0.39	1	1	1
19	1	0.19	1	1	0.272	1	1	0.19	1	0.39	1	1	1	1	0.19	1	1	1	1	0.19
2	1	0.19	1	0.508	0.6	1	1	0.272	1	1	1	1	1	1	0.19	1	1	1	1	0.19
20	1	0.6	0.19	1	1	1	1	1	0.508	1	1	1	1	1	1	0.39	0.508	1	1	1
3	1	0.19	1	0.272	0.19	1	1	0.19	0.19	0.6	1	1	1	1	0.19	1	1	1	1	0.19
4	1	1	0.19	1	1	0.19	0.19	1	0.19	1	0.19	0.19	1	0.19	1	0.19	0.19	0.19	1	1

5	1	0.19	1	0.696	0.19	1	1	0.19	1	0.508	1	1	0.39	1	0.19	1	1	1	1	0.19
6	1	0.19	1	1	0.272	1	1	0.19	1	0.39	1	1	0.508	1	0.19	1	1	1	1	0.19
7	1	0.272	0.508	1	0.19	1	1	0.19	0.19	1	1	1	1	1	0.19	1	1	1	1	0.19
8	1	1	0.6	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
9	1	1	0.19	0.904	1	0.19	0.19	1	0.19	1	0.19	0.19	1	0.19	1	0.19	0.19	0.19	1	1

Table 92: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the classical dietary guilds (faunivory, n = 5 127; omnivory, n = 2 480; herbivory, n = 2 176) in birds (topology of Hackett et al. 2008).

	Faunivory	**Herbivory**	**Omnivory**
Faunivory	NA	1.00	1.00
Herbivory	1.00	NA	1.00
Omnivory	1.00	1.00	NA

Table 93: Posthoc pairwise t-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the classical dietary guilds (faunivory, n = 5 127; omnivory, n = 2 480; herbivory, n = 2 176) in birds (topology of Hackett et al. 2008).

	Faunivory	**Herbivory**	**Omnivory**
Faunivory	NA	-4.756	0.665
Herbivory	4.756	NA	4.697
Omnivory	-0.665	-4.697	NA

Table 94: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the classical

dietary guilds (faunivory, n = 5 127; omnivory, n = 2 480; herbivory, n = 2 176) in birds (topology of Ericson et al. 2006).

	Faunivory	**Herbivory**	**Omnivory**
Faunivory	NA	1.000	1.000
Herbivory	1.000	NA	0.165
Omnivory	1.000	0.165	NA

Table 95: Posthoc pairwise t-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the classical dietary guilds (faunivory, n = 5 127; omnivory, n = 2 480; herbivory, n = 2 176) in birds (topology of Ericson et al. 2006).

	Faunivory	**Herbivory**	**Omnivory**
Faunivory	NA	-2.979	1.620
Herbivory	2.979	NA	4.099
Omnivory	-1.620	-4.099	NA

Table 96: Results of ordinary linear models regressing the arcsine-transformed percentage values of each food type against log-transformed values of body mass in mammals. Abbreviations: **Std.error**, standard error. N = 5159.

Model	**Estimate**	**Std.error**	**Statistic**	**p-value**	**R^2**
Animal (total)	-0.688	0.021	-32.318	0.000	0.168
Invertebrates (total)	-0.955	0.024	-40.357	0.000	0.240
Vertebrates (total)	0.552	0.061	9.018	0.000	0.016
Terrestrial	0.290	0.067	4.359	0.000	0.004
Fish	3.010	0.200	15.024	0.000	0.042
Plant (total)	0.732	0.022	33.828	0.000	0.182
Plant (fibrous)	0.974	0.027	35.747	0.000	0.199
Plant (non-fibrous)	0.090	0.036	2.490	0.013	0.001
Fruit	0.331	0.046	7.135	0.000	0.010
Seed	-0.478	0.084	-5.697	0.000	0.006
Nectar	-0.249	0.147	-1.696	0.090	0.001

Table 97: Results of phylogenetic linear models regressing the PICs of arcsine-transformed percentage values of each food type against the PIC of log-transformed values of body mass in birds (tip-dating backbone topology of Upham et al. 2019). Abbreviations: **Std.error**, standard error. N = 5159.

Model	Estimate	Std.error	Statistic	p-value	R^2
Animal (total)	-0.001	0.034	-0.016	0.988	0.000
Invertebrates (total)	-0.176	0.037	-4.779	0.000	0.004
Vertebrates (total)	0.203	0.043	4.727	0.000	0.004
Terrestrial	0.154	0.044	3.540	0.000	0.002
Fish	0.193	0.110	1.756	0.079	0.001
Plant (total)	0.150	0.030	4.920	0.000	0.005
Plant (fibrous)	0.207	0.027	7.617	0.000	0.011
Plant (non-fibrous)	-0.193	0.028	-6.869	0.000	0.009
Fruit	-0.128	0.026	-4.852	0.000	0.005
Seed	0.041	0.060	0.683	0.495	0.000
Nectar	-0.096	0.099	-0.971	0.332	0.000

Table 98: Results of phylogenetic linear models regressing the PICs of arcsine-transformed percentage values of each food type against the PIC of log-transformed values of body mass in birds (node-dating backbone topology of Upham et al. 2019). Abbreviations: **Std.error**, standard error. N = 5159.

Model	Estimate	Std.error	Statistic	p-value	R^2
Animal (total)	0.004	0.024	0.151	0.880	0.000
Invertebrates (total)	-0.082	0.025	-3.199	0.001	0.002
Vertebrates (total)	0.156	0.035	4.396	0.000	0.004
Terrestrial	0.062	0.025	2.475	0.013	0.001
Fish	-0.082	0.025	-3.199	0.001	0.002
Plant (total)	0.011	0.028	0.402	0.688	0.000
Plant (fibrous)	0.176	0.029	6.121	0.000	0.007
Plant (non-fibrous)	-0.231	0.034	-6.795	0.000	0.009
Fruit	-0.006	0.041	-0.156	0.876	0.000
Seed	-0.652	0.064	-10.230	0.000	0.020
Nectar	0.025	0.075	0.338	0.736	0.000

Table 99: Results of Spearman's rank-correlation tests correlating the arcsine-transformed percentage values of each food type against log-transformed values of body mass in birds. The first two columns refer to correlation tests done on the PICs of those variables, generated using the tip-dating, and node-dating topologies of Upham et al. (2019). N = 5159.

Variable	Tip-dating backbone		Node-dating backbone		Ordinary	
	Correlation (rho)	p-value	Correlation (rho)	p-value	Correlation (rho)	p-value
Animal (total)	-0.048	0.001	-0.055	0.000	-0.519	0.000
Invertebrates (total)	-0.103	0.000	-0.105	0.000	-0.594	0.000
Vertebrates (total)	0.060	0.000	0.039	0.005	0.002	0.872
Terrestrial	0.037	0.007	0.026	0.062	-0.031	0.027
Fish	0.041	0.003	0.040	0.004	0.145	0.000
Plant (total)	0.052	0.000	0.066	0.000	0.520	0.000
Plant (fibrous)	0.045	0.001	0.053	0.000	0.483	0.000
Plant (non-fibrous)	-0.006	0.668	-0.009	0.522	0.212	0.000
Fruit	0.020	0.142	0.021	0.140	0.295	0.000
Seed	-0.028	0.046	-0.034	0.015	0.041	0.003
Nectar	-0.017	0.226	-0.019	0.163	0.004	0.790

Table 100: Results of Kendall's rank-correlation tests correlating the arcsine-transformed percentage values of each food type against log-transformed values of body mass in birds. The first two columns refer to correlation tests done on the PICs of those variables, generated using the tip-dating, and node-dating topologies of Upham et al. 2019. N = 5159.

Variable	Tip-dating backbone		Node-dating backbone		Ordinary	
	Correlation (tau)	p-value	Correlation (tau)	p-value	Correlation (tau)	p-value
Animal (total)	-0.036	0.000	-0.041	0,000	-0,396	0,000
Invertebrates (total)	-0.078	0.000	-0.080	0,000	-0,446	0,000
Vertebrates (total)	0.047	0.000	0.031	0,005	0,001	0,952
Terrestrial	0.029	0.007	0.020	0,063	-0,024	0,024
Fish	0.033	0.003	0.033	0,004	0,118	0,000
Plant (total)	0.039	0.000	0.050	0,000	0,397	0,000

Plant (fibrous)	0.035	0.001	0.040	0,000	0,365	0,000
Plant (non-fibrous)	-0.005	0.665	-0.007	0,532	0,152	0,000
Fruit	0.016	0.138	0.016	0,130	0,224	0,000
Seed	-0.022	0.044	-0.026	0,015	0,030	0,005
Nectar	-0.014	0.225	-0.016	0,163	0,003	0,803

Table 101: Results of ordinary ANOVA analyses comparing mean log-transformed body mass between the dietary guilds recovered in the k-means cluster analysis, and the classical dietary guilds in mammals. Abbreviations: **TD**, tip-dating backbone topology; **ND**, node-dating backbone topology; **Df**, degrees of freedom; **Sum Sq**, sum of square distances; **Mean Sq**, mean square distances; **Eta Sq**, eta squared. N = 5159.

	Df	**Sum Sq**	**Mean Sq**	**F-value**	**P-value**
K=10	9	2182.046	242.450	290.089	0.000
-Residuals	5149	4303.407	0.836	NA	NA
Classical guilds	2	936.513	468.257	435.098	0.000
-Residuals	5156	5548.939	1.076	NA	NA
K=5 (TD)	4	1600.749	400.187	455.930	0.058
-Residuals		4486.119	0.878	NA	NA
K=10 (TD)	9	2182.05	242.45	290.09	0.035
-Residuals	5149	4303.41	0.84	NA	NA
K=20 (TD)	19	2497.929	131.470	186.677	0.018
-Residuals		3588.938	0.704	NA	NA
Classical (TD)	2	936.51	468.26	435.10	0.096
-Residuals	5156	5548.94	1.08	NA	NA
K=5 (ND)	4	1600.749	400.187	455.930	0.058
-Residuals		4486.119	0.878	NA	NA
K=10 (ND)	9	2182.05	242.45	290.09	0.029
-Residuals	5149	4303.41	0.84	NA	NA
K=20 (ND)	19	2497.929	131.470	186.677	0.018
-Residuals		3588.938	0.704	NA	NA
Classical (ND)	2	936.51	468.26	435.10	0.114
-Residuals	5156	5548.94	1.08	NA	NA

Table 102: Posthoc pairwise comparisons from the ordinary ANOVA between mean log-transformed body mass between the dietary guilds recovered in the k-means cluster analysis in mammals. Abbreviations: **diff**, group mean difference; **lwr**, lower range of group mean difference; **upr**, upper range of group mean difference; **p adj**, adjusted p-value. **Guild numbers**: **1**, mixed faunivory (n = 440); **2**, invertivory (sensu lato; 513); **3**, folivory (n = 635); **4**, mixed herbivory comprised primarily of reproductive plant structures (n = 788); **5**, piscivory (sensu lato; n = 36); **6**, mixed herbivory comprised primarily of vegetative plant structures (n = 984); **7**, omnivory (n = 500); **8**, carnivory (n = 95); **9**, invertivory (sensu stricto; n = 889); **10**, frugivory (n = 279).

	diff	**lwr**	**upr**	**p adj**
10-1	0.299	0.077	0.520	0.001
2-1	-0.216	-0.404	-0.028	0.010
3-1	1.423	1.244	1.603	0.000
4-1	0.259	0.087	0.431	0.000
5-1	2.827	2.326	3.329	0.000
6-1	0.563	0.397	0.729	0.000
7-1	0.483	0.294	0.672	0.000
8-1	1.681	1.354	2.008	0.000
9-1	-0.592	-0.761	-0.424	0.000
2-10	-0.515	-0.730	-0.300	0.000
3-10	1.125	0.917	1.333	0.000
4-10	-0.040	-0.241	0.162	1.000
5-10	2.529	2.016	3.041	0.000
6-10	0.264	0.068	0.461	0.001
7-10	0.184	-0.032	0.400	0.176
8-10	1.382	1.038	1.726	0.000
9-10	-0.891	-1.090	-0.692	0.000
3-2	1.640	1.468	1.811	0.000
4-2	0.475	0.311	0.640	0.000
5-2	3.044	2.545	3.543	0.000
6-2	0.779	0.622	0.937	0.000
7-2	0.699	0.517	0.881	0.000
8-2	1.897	1.574	2.220	0.000
9-2	-0.376	-0.537	-0.216	0.000

4-3	-1.164	-1.319	-1.010	0.000
5-3	1.404	0.908	1.900	0.000
6-3	-0.860	-1.007	-0.713	0.000
7-3	-0.941	-1.114	-0.768	0.000
8-3	0.257	-0.061	0.576	0.237
9-3	-2.016	-2.166	-1.865	0.000
5-4	2.568	2.075	3.061	0.000
6-4	0.304	0.166	0.442	0.000
7-4	0.224	0.058	0.389	0.001
8-4	1.422	1.107	1.736	0.000
9-4	-0.851	-0.993	-0.710	0.000
6-5	-2.264	-2.755	-1.773	0.000
7-5	-2.345	-2.844	-1.845	0.000
8-5	-1.147	-1.713	-0.580	0.000
9-5	-3.420	-3.912	-2.928	0.000
7-6	-0.080	-0.239	0.078	0.847
8-6	1.118	0.807	1.429	0.000
9-6	-1.156	-1.289	-1.022	0.000
8-7	1.198	0.874	1.522	0.000
9-7	-1.075	-1.237	-0.913	0.000
9-8	-2.273	-2.586	-1.961	0.000

Table 103: Posthoc pairwise comparisons from the ordinary ANOVA between mean log-transformed body mass between the classical dietary guilds (faunivory, n = 1826; omnivory, n = 732; herbivory, n = 2601) in mammals. Abbreviations: **diff**, group mean difference; **lwr**, lower range of group mean difference; **upr**, upper range of group mean difference; **p adj**, adjusted p-value.

	diff	**lwr**	**upr**	**p adj**
Herbivory-Faunivory	0.934	0.860	1.008	0.000
Omnivory-Faunivory	0.526	0.420	0.633	0.000
Omnivory-Herbivory	-0.408	-0.510	-0.306	0.000

Table 104: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the dietary guilds recovered in the k-means cluster analysis in mammals (tip-dating backbone topology of Upham et al. 2019). Guild numbers: **1**, mixed faunivory (n = 440); **2**, invertivory (sensu lato; 513); **3**, folivory (n = 635); **4**, mixed herbivory comprised primarily of reproductive plant structures (n = 788); **5**, piscivory (sensu lato; n = 36); **6**, mixed herbivory comprised primarily of vegetative plant structures (n = 984); **7**, omnivory (n = 500); **8**, carnivory (n = 95); **9**, invertivory (sensu stricto; n = 889); **10**, frugivory (n = 279).

	1	**10**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	NA	1.000	1.000	0.465	1.000	0.084	1.000	1.000	0.416	1.000
10	1.000	NA	1.000	1.000	1.000	0.156	1.000	1.000	1.000	1.000
2	1.000	1.000	NA	0.045	1.000	0.045	1.000	1.000	0.315	1.000
3	0.465	1.000	0.045	NA	0.266	1.000	0.266	0.396	1.000	0.123
4	1.000	1.000	1.000	0.266	NA	0.374	1.000	1.000	1.000	1.000
5	0.084	0.156	0.045	1.000	0.374	NA	0.465	0.266	0.812	0.045
6	1.000	1.000	1.000	0.266	1.000	0.465	NA	1.000	1.000	1.000
7	1.000	1.000	1.000	0.396	1.000	0.266	1.000	NA	1.000	1.000
8	0.416	1.000	0.315	1.000	1.000	0.812	1.000	1.000	NA	0.123
9	1.000	1.000	1.000	0.123	1.000	0.045	1.000	1.000	0.123	NA

Table 105: Posthoc pairwise t-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the dietary guilds recovered in the k-means cluster analysis in mammals (tip-dating backbone topology of Upham et al. 2019). Guild numbers: **1**, mixed faunivory (n = 440); **2**, invertivory (sensu lato; 513); **3**, folivory (n = 635); **4**, mixed herbivory comprised primarily of reproductive plant structures (n = 788); **5**, piscivory (sensu lato; n = 36); **6**, mixed herbivory comprised primarily of vegetative plant structures (n = 984); **7**, omnivory (n = 500); **8**, carnivory (n = 95); **9**, invertivory (sensu stricto; n = 889); **10**, frugivory (n = 279).

	1	**10**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	NA	-4.27	3.64	-25.10	-4.76	-17.84	-10.74	-8.08	-16.25	11.11
10	4.27	NA	7.57	-17.13	0.62	-15.62	-4.27	-2.69	-12.73	14.20
2	-3.64	-7.57	NA	-30.21	-9.17	-19.31	-15.66	-12.17	-18.58	7.42
3	25.10	17.13	30.21	NA	23.88	-8.96	18.49	17.21	-2.56	42.44
4	4.76	-0.62	9.17	-23.88	NA	-16.48	-6.96	-4.28	-14.32	19.04
5	17.84	15.62	19.31	8.96	16.48	NA	14.60	14.86	6.41	22.00

6	10.74	4.27	15.66	-18.49	6.96	-14.60	NA	1.60	-11.38	27.32
7	8.08	2.69	12.17	-17.21	4.28	-14.86	-1.60	NA	-11.71	21.04
8	16.25	12.73	18.58	2.56	14.32	-6.41	11.38	11.71	NA	23.04
9	-11.11	-14.20	-7.42	-42.44	-19.04	-22.00	-27.32	-21.04	-23.04	NA

Table 106: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the dietary guilds recovered in the k-means cluster analysis in mammals (node-dating backbone topology of Upham et al. 2019). Guild numbers: **1**, mixed faunivory (n = 440); **2**, invertivory (sensu lato; 513); **3**, folivory (n = 635); **4**, mixed herbivory comprised primarily of reproductive plant structures (n = 788); **5**, piscivory (sensu lato; n = 36); **6**, mixed herbivory comprised primarily of vegetative plant structures (n = 984); **7**, omnivory (n = 500); **8**, carnivory (n = 95); **9**, invertivory (sensu stricto; n = 889); **10**, frugivory (n = 279).

	1	**10**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	NA	1.000	1.000	0.228	1.000	0.045	1.000	1.000	0.496	1.000
10	1.000	NA	1.000	1.000	1.000	0.252	1.000	1.000	1.000	1.000
2	1.000	1.000	NA	0.045	1.000	0.045	1.000	1.000	0.252	1.000
3	0.228	1.000	0.045	NA	0.117	1.000	0.080	0.480	1.000	0.045
4	1.000	1.000	1.000	0.117	NA	0.306	1.000	1.000	1.000	1.000
5	0.045	0.252	0.045	1.000	0.306	NA	0.754	0.396	0.720	0.045
6	1.000	1.000	1.000	0.080	1.000	0.754	NA	1.000	1.000	1.000
7	1.000	1.000	1.000	0.480	1.000	0.396	1.000	NA	1.000	1.000
8	0.496	1.000	0.252	1.000	1.000	0.720	1.000	1.000	NA	0.228
9	1.000	1.000	1.000	0.045	1.000	0.045	1.000	1.000	0.228	NA

Table 107: Posthoc pairwise t-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the dietary guilds recovered in the k-means cluster analysis in mammals (node-dating backbone topology of Upham et al. 2019). Guild numbers: **1**, mixed faunivory (n = 440); **2**, invertivory (sensu lato; 513); **3**, folivory (n = 635); **4**, mixed herbivory comprised primarily of reproductive plant structures (n = 788); **5**, piscivory (sensu lato; n = 36); **6**, mixed herbivory comprised primarily of vegetative plant structures (n = 984); **7**, omnivory (n = 500); **8**, carnivory (n = 95); **9**, invertivory (sensu stricto; n = 889); **10**, frugivory (n = 279).

	1	**10**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**

1	NA	-4.27	3.64	-25.10	-4.76	-17.84	-10.74	-8.08	-16.25	11.11
10	4.27	NA	7.57	-17.13	0.62	-15.62	-4.27	-2.69	-12.73	14.20
2	-3.64	-7.57	NA	-30.21	-9.17	-19.31	-15.66	-12.17	-18.58	7.42
3	25.10	17.13	30.21	NA	23.88	-8.96	18.49	17.21	-2.56	42.44
4	4.76	-0.62	9.17	-23.88	NA	-16.48	-6.96	-4.28	-14.32	19.04
5	17.84	15.62	19.31	8.96	16.48	NA	14.60	14.86	6.41	22.00
6	10.74	4.27	15.66	-18.49	6.96	-14.60	NA	1.60	-11.38	27.32
7	8.08	2.69	12.17	-17.21	4.28	-14.86	-1.60	NA	-11.71	21.04
8	16.25	12.73	18.58	2.56	14.32	-6.41	11.38	11.71	NA	23.04
9	-11.11	-14.20	-7.42	-42.44	-19.04	-22.00	-27.32	-21.04	-23.04	NA

Table 108: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the dietary guilds recovered in the k-means cluster analysis (k=5) in mammals (tip-dating backbone topology of Upham et al. 2019). See Table 29 for details of guilds.

	1	**2**	**3**	**4**	**5**
1	1	1	0.978	0.064	1
2	1	1	1	0.03	1
3	0.978	1	1	0.03	0.203
4	0.064	0.03	0.03	1	0.978
5	1	1	0.203	0.978	1

Table 109: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the dietary guilds recovered in the k-means cluster analysis (k=20) in mammals (tip-dating backbone topology of Upham et al. 2019). See Table 31 for details of guilds.

	1	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**2**	**20**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	1	0.19	1	0.372	1	1	0.728	1	1	0.905	1	1	0.19	1	1	1	1	1	0.552	1
10	0.19	1	1	1	0.905	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
11	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

12	0.372	1	1	1	1	1	1	1	1	1	1	1	1	1	0.905	1	1	0.552	1	1
13	1	0.905	1	1	1	1	1	1	1	1	1	1	0.19	1	1	1	1	1	1	1
14	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
15	0.728	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
16	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
17	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
18	0.905	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
19	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
20	0.19	1	1	1	0.19	1	1	1	1	1	1	1	1	1	1	1	0.19	1	1	1
3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
4	1	1	1	0.905	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0.905	1
5	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
6	1	1	1	1	1	1	1	1	1	1	1	1	0.19	1	1	1	1	1	0.905	1
7	1	1	1	0.552	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0.372	1
8	0.552	1	1	1	1	1	1	1	1	1	1	1	1	1	0.905	1	0.905	0.372	1	1
9	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 110: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the dietary guilds recovered in the k-means cluster analysis (k=5) in mammals (tip-dating backbone topology of Upham et al. 2019). See Table 29 for details of guilds.

	1	**2**	**3**	**4**	**5**
1	1	1	0.99	0.072	1
2	1	1	1	0.036	1
3	0.99	1	1	0.01	0.273

4	0.072	0.036	0.01	1	0.99
5	1	1	0.273	0.99	1

Table 111: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the dietary guilds recovered in the k-means cluster analysis (k=20) in mammals (node-dating backbone topology of Upham et al. 2019). See Table 31 for details of guilds.

	1	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**2**	**20**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	1	0.19	1	0.19	1	1	0.724	1	1	0.19	1	1	0.19	1	1	1	1	1	0.37	1
10	0.19	1	1	1	0.724	1	1	1	1	1	1	1	1	1	1	1	0.37	1	1	1
11	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
12	0.19	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0.89	1	1
13	1	0.724	1	1	1	1	1	1	1	1	1	1	0.19	1	1	1	1	1	1	1
14	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
15	0.724	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
16	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
17	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
18	0.19	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
19	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
20	0.19	1	1	1	0.19	1	1	1	1	1	1	1	1	1	1	1	0.37	1	1	1
3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
4	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0.546	1
5	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
6	1	0.37	1	1	1	1	1	1	1	1	1	1	0.37	1	1	1	1	1	0.724	1
7	1	1	1	0.89	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
8	0.37	1	1	1	1	1	1	1	1	1	1	1	1	1	0.546	1	0.724	1	1	1
9	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 112: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the classical dietary guilds (faunivory, n = 1826; omnivory, n = 732; herbivory, n = 2601) in mammals (tip-dating backbone topology of Upham et al. 2019).

	Faunivory	**Herbivory**	**Omnivory**
Faunivory	NA	0.201	0.360
Herbivory	0.201	NA	0.201
Omnivory	0.360	0.201	NA

Table 113: Posthoc pairwise t-values from the phylogenetic ANOVA comparisons between mean log-transformed snout-vent length between the classical dietary guilds (faunivory, n = 1826; omnivory, n = 732; herbivory, n = 2601) in mammals (tip-dating backbone topology of Upham et al. 2019).

	Faunivory	**Herbivory**	**Omnivory**
Faunivory	NA	-29.494	-11.596
Herbivory	29.494	NA	9.398
Omnivory	11.596	-9.398	NA

Table 114: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the classical dietary guilds (faunivory, n = 1826; omnivory, n = 732; herbivory, n = 2601) in mammals (node-dating backbone topology of Upham et al. 2019).

	Faunivory	**Herbivory**	**Omnivory**
Faunivory	NA	0.20	0.39
Herbivory	0.20	NA	0.20
Omnivory	0.39	0.20	NA

Table 115: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the classical dietary guilds (faunivory, n = 1826; omnivory, n = 732; herbivory, n = 2601) in mammals (node-dating backbone topology of Upham et al. 2019).

	Faunivory	**Herbivory**	**Omnivory**

Faunivory	NA	-29.494	-11.596
Herbivory	29.494	NA	9.398
Omnivory	11.596	-9.398	NA

Table 116: Results of ANOVA analyses comparing mean log-transformed jaw length between the classical dietary guilds in early-branching synapsids. Abbreviations: **Df**, degrees of freedom; **Sum Sq**, sum of square distances; **Mean Sq**, mean square distances. N = 404.

	Df	**Sum Sq**	**Mean Sq**	**F-value**	**P-value**
Ordinary	2	42.550	21.275	24.366	0.000
-Residuals	401	350.130	0.873	NA	NA
Phylogenetic	2	42.550	21.275	24.366	0.177
-Residuals	401	350.130	0.873	NA	NA

Table 117: Posthoc pairwise comparisons from the ordinary ANOVA between mean log-transformed jaw length between the classical dietary guilds (faunivory, n = 204; omnivory, n = 53; herbivory, n = 147) in early-branching synapsids. Abbreviations: **diff**, group mean difference; **lwr**, lower range of group mean difference; **upr**, upper range of group mean difference; **p adj**, adjusted p-value.

	diff	**lwr**	**upr**	**p adj**
Herbivory-Faunivory	0.598	0.361	0.836	0.000
Omnivory-Faunivory	-0.259	-0.598	0.080	0.172
Omnivory-Herbivory	-0.857	-1.209	-0.505	0.000

Table 118: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed jaw length between the classical dietary guilds (faunivory, n = 204; omnivory, n = 53; herbivory, n = 147) in early-branching synapsids.

	Faunivory	**Herbivory**	**Omnivory**
Faunivory	NA	0.471	0.633
Herbivory	0.471	NA	0.471

Omnivory	0.633	0.471	NA

Table 119: Posthoc pairwise t-values from the phylogenetic ANOVA comparisons between mean log-transformed jaw length between the classical dietary guilds (faunivory, n = 204; omnivory, n = 53; herbivory, n = 147) in early-branching synapsids.

	Faunivory	**Herbivory**	**Omnivory**
Faunivory	NA	-5.920	1.797
Herbivory	5.920	NA	5.726
Omnivory	-1.797	-5.726	NA

Table 120: Results of ANOVA analyses comparing mean log-transformed body mass between the classical dietary guilds in non-avian theropods. **Abbreviations**: **Df**, degrees of freedom; **Sum Sq**, sum of square distances; **Mean Sq**, mean square distances. N = 138.

	Df	**Sum Sq**	**Mean Sq**	**F-value**	**P-value**
Ordinary	2	21.360	10.680	8.924	0.000
-Residuals	135	161.558	1.197	NA	NA
Phylogenetic	2	21.360	10.680	8.924	0.290
-Residuals	135	161.558	1.197	NA	NA

Table 121: Posthoc pairwise comparisons from the ordinary ANOVA between mean log-transformed body mass between the classical dietary guilds (faunivory, 93; omnivory, 16; herbivory, 29) in non-avian theropods. **Abbreviations**: **diff**, group mean difference; **lwr**, lower range of group mean difference; **upr**, upper range of group mean difference; **p adj**, adjusted p-value.

	diff	**lwr**	**upr**	**p adj**
Herbivory-Faunivory	0.034	-0.517	0.586	0.988
Omnivory-Faunivory	-1.220	-1.922	-0.518	0.000
Omnivory-Herbivory	-1.254	-2.062	-0.447	0.001

Table 122: Posthoc pairwise p-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the classical dietary guilds (faunivory, 93; omnivory, 16; herbivory, 29) in non-avian theropods.

	Faunivory	**Herbivory**	**Omnivory**
Faunivory	NA	0.971	0.159
Herbivory	0.971	NA	0.220
Omnivory	0.159	0.220	NA

Table 123: Posthoc pairwise t-values from the phylogenetic ANOVA comparisons between mean log-transformed body mass between the classical dietary guilds (faunivory, 93; omnivory, 16; herbivory, 29) in non-avian theropods.

	Faunivory	**Herbivory**	**Omnivory**
Faunivory	NA	-0.148	4.120
Herbivory	0.148	NA	3.682
Omnivory	-4.120	-3.682	NA

Table 124: Dietary guilds in turtles (recovered by the k-means cluster analysis) by minimum, maximum, and mean carapace length (CL) in millimetres. Arranged from highest to lowest mean value.

Guild	**N**	**Minimum CL**	**Maximum CL**	**Mean CL**
Mixed Faunivory	**35**	155	2000	499.8
Mixed Herbivory (PlantR)	**21**	160	1070	439.5
Mixed Herbivory (PlantO)	**36**	100	980	385
Folivory s.l.	**39**	144	1300	376.9
Folivory s.s.	**17**	115	1230	327
Durophagy s.s.	**9**	175	480	313.3
Omnivory	**48**	115	950	247.5
Durophagy s.l.	**24**	125	445	234

Insectivory s.l.	**34**	121	400	233
Insectivory s.s.	**5**	140	350	233
TOTAL	**264**	**100**	**2000**	**337.3**

Table 125: Classical dietary guilds in turtles by minimum, maximum, and mean carapace length (CL) in millimetres. Arranged from highest to lowest mean value.

Guild	N	Minimum CL	Maximum CL	Mean CL
Herbivory	**110**	100	1300	384.5
Faunivory	**101**	121	2000	323.6
Omnivory	**53**	115	950	265.8
TOTAL	**264**	**100**	**2000**	**337**

Table 126: Dietary guilds in lizards (recovered by the k-means cluster analysis) by minimum, maximum, and mean snout-vent length (SVL) in millimetres. Arranged from highest to lowest mean value.

Guild	N	Minimum SVL	Maximum SVL	Mean SVL
Carnivory	**17**	120	1570	463.9
Mixed Faunivory	**52**	72	1170	389.4
Folivory	**14**	139	560	292.9
Mixed Herbivory (PlantR)	**41**	70	766	264.8
Durophagy s.l.	**22**	73	660	251.9
Mixed Herbivory (PlantO)	**77**	56	750	244.4
Omnivory	**72**	53	614	147.2
Insectivory s.l.	**278**	40	670	124.8
Insectivory-Omnivory	**272**	27	299	105
Insectivory s.s.	**3156**	17	810	92
TOTAL	**4001**	**17**	**1570**	**107.9**

Table 127: Classical dietary guilds in lizards by minimum, maximum, and mean snout-vent length (SVL) in millimetres. Arranged from highest to lowest mean value.

Guild	N	Minimum SVL	Maximum SVL	Mean SVL
Herbivory	**98**	58	766	274.6
Omnivory	**280**	27	614	122.6
Faunivory	**3623**	17	1570	102.2
TOTAL	**4001**	**17**	**1570**	**107.9**

Table 128: Dietary guilds in birds (recovered by the k-means cluster analysis) by minimum, maximum, and mean body mass (BM) in grams. Arranged from highest to lowest mean value.

Guild	N	Minimum BM	Maximum BM	Mean BM
Mixed Herbivory (PlantO)	**246**	9,9	111000,0	1595,5
Piscivory s.l.	**326**	13,8	9512,1	1123,8
Carnivory	**370**	17,7	11236,1	1109,6
Omnivory	**1404**	5,2	34093,3	345,7
Frugivory	**348**	5,1	2872,0	290,8
Frugivory-Omnivory	**1237**	5,0	46073,9	254,1
Invertivory s.l.	**2225**	4,1	8905,6	151,8
Granivory	**475**	6,5	3743,2	69,7
Invertivory s.s.	**2782**	3,2	3515,0	49,7
Nectarivory	**562**	1,9	218,0	17,4
TOTAL	**9975**	**1,9**	**111000,0**	**259,6**

Table 129: Classical dietary guilds in birds by minimum, maximum, and mean body mass (BM) in grams. Arranged from highest to lowest mean value.

Guild	N	Minimum BM	Maximum BM	Mean BM
Herbivory	**2176**	1.9	111000	376.8
Faunivory	**5127**	3.2	33569.3	262
Omnivory	**2480**	2.3	46073.9	212.6
TOTAL	**9783**	**1.9**	**111000**	**275**

Table 130: Dietary guilds in mammals (recovered by the k-means cluster analysis) by minimum, maximum, and mean body mass (BM) in grams. Arranged from highest to lowest mean value.

Guild	N	Minimum BM	Maximum BM	Mean BM
Piscivory s.l.	**36**	32.5	400000	112234.9
Folivory	**635**	13.4	3940034	59291.4
Carnivory	**95**	29.3	388750.4	17041.7
Mixed Herbivory (PlantO)	**984**	6	1750000	10473.3
Invertivory s.l.	**513**	1.8	1600000	8698.2
Omnivory	**500**	5.6	99949.4	1849.8
Frugivory	**279**	5.8	140000.6	1363.3
Mixed Faunivory	**440**	1.8	46500	1036.2
Mixed Herbivory (PlantR)	**788**	5	73569.7	654.8
Invertivory s.s.	**889**	2.1	225000	543.5
TOTAL	**5159**	**1.8**	**3940034**	**11792.5**

Table 131: Classical dietary guilds in mammals by minimum, maximum, and mean body mass (BM) in grams. Arranged from highest to lowest mean value.

Guild	N	Minimum BM	Maximum BM	Mean BM
Herbivory	**2601**	5	3940034	18637.45
Faunivory	**1826**	1.75	1600000	5904.44
Omnivory	**732**	6	190792.3	2158.699
TOTAL	**5159**	**1.8**	**3940034**	**11792.5**

Table 132: Classical dietary guilds in early-branching synapsids by minimum, maximum, and mean jaw length (JL) in millimetres. Arranged from highest to lowest mean value.

Guild	N	Minimum JL	Maximum JL	Mean JL
Herbivory	**147**	14.34	781.30	160.05
Faunivory	**204**	11.30	636.36	108.40
Omnivory	**53**	12.85	379.21	71.95

TOTAL	**404**	**11.30**	**781.30**	**122.41**

Table 133: Classical dietary guilds in non-avian theropods by minimum, maximum, and mean body mass (BM) in kilograms. Arranged from highest to lowest mean value.

Guild	N	Minimum BM	Maximum BM	Mean BM
Faunivory	**93**	0,36	7693,7	832,15
Herbivory	**29**	1,27	7328,2	616,85
Omnivory	**16**	0,26	155,77	19,176
TOTAL	**138**	**0,26**	**7393,7**	**692,65**

THESIS CONCLUSION

1. Chapter One: Overview

In Chapter One, I assembled new datasets of the dietary compositions (by percentage of each food type) of turtles and lizards, and analysed these alongside existing data for birds and mammals (Wilman et al., 2014) to determine patterns in the distributions of dietary compositions among major amniote lineages. I performed principal component analyses, correlation tests, and cluster analyses on proportional data detailing the percentages of different food categories in the dietary composition of extant turtles, lizards, birds and mammals. The most important results of these analyses were (a) the proportional consumption of invertebrate material is the single most important driver of variation in amniote diet, and it co-occurs with many other food types and forms the backbone of omnivorous and generalist guilds, and (b) variation in dietary composition among amniotes is complex, and unevenly distributed in multivariate diet space. This presents difficulty in summarising all variation in dietary data using a manageable number of well-separated clusters. This potentially suggests that future research could investigate analysis of dietary composition as a continuous trait. Nevertheless, a substantial number of species are divided among a smaller number (10) of biologically informative dietary clusters that can pragmatically be treated as discrete categories for the purposes of analysis that capture the most important natural divisions in the data, as opposed to relying on a priori cut-off values for defining dietary guilds.

Many other aspects of the distribution of dietary composition differs between groups. Except for mammals, most taxa in all major amniote lineages are either faunivorous or omnivorous. Most turtle and mammal species adhere to generalist dietary strategies with a significant contribution of at least two second-order food groups (invertebrates, vertebrates, reproductive plant matter, and vegetative plant matter). Most lizards and birds are dietary specialists. Lizard taxa are divided between the insectivorous majority of species, and several different guilds consisting of different combinations and proportions of non-arthropod material. Most bird species are

sorted into specialist guilds with only three generalist guilds (omnivory, frugivory-omnivory, and invertivory s.l.) accounting for relatively high proportions of bird taxa.

Most taxa across the major amniote lineages incorporate some degree of invertebrate material into their diets. Each lineage has one “strict” invertivorous guild, and one predominantly invertivorous guild. Invertebrates cluster with many other food categories and form part of most mixed and generalist guilds (omnivory, mixed faunivory, and mixed herbivory to a lesser extent). All major amniote lineages include a mixed faunivorous guild combining invertebrate and vertebrate matter. Both birds and mammals include a piscivorous guild with predominant contribution of fish, and a substantial contribution of invertebrates to the dietary composition. This is indicative of faunivory existing on a spectrum between invertivory and carnivory, with many faunivores consuming both kinds of animal-based food types. Invertebrates (more specifically, terrestrial arthropods) form a substantial part of the dietary composition of the omnivorous guilds in all major amniote lineages and are a minor part of some mixed herbivorous guilds as well. Vertebrate meat, by contrast, is usually only paired with invertebrate material in mixed faunivorous guilds. The same is true, in turtles and lizards, for durophagous material (molluscs, gastropods, crustaceans), which tend to cluster alongside other invertebrate food sources.

All major amniote lineages possess, at least, one mixed herbivorous guild combining reproductive and vegetative plant structures. In all clades except birds, the numbers of species in these mixed herbivorous guilds far exceed those in specialised herbivorous guilds. Birds are also exceptional in that they lack a specialised folivorous guild, and have distinct granivorous and nectarivorous guilds. Both birds and mammals have specialised frugivorous guilds but turtles and lizards are limited to mixed herbivorous guilds with a predominance of reproductive plant material in their dietary compositions. Reproductive plant structures form larger components of the omnivorous guilds than do vegetative structures. However, in contrast to vertebrate meat, vegetative material is still an important part of the omnivorous guilds, except in birds.

2. Chapter Two: Overview

In Chapter Two, I used maximum likelihood Mk models to determine rates of evolutionary transition between dietary guilds in major lineages of extant and some extinct amniotes. The purpose of this exercise was to gain an understanding of the tempo and directionality of evolutionary transitions between the different dietary guilds. Evolutionary transitions between the classical dietary guilds follow the pattern: faunivory → omnivory → herbivory. Using the more nuanced dietary guilds recovered in the k-means cluster analysis (see Chapter One, Methods), the fully or partially invertivorous guilds were the most evolutionary plastic feeding strategies. The pattern of evolutionary transition here is: invertivory → generalist/omnivorous intermediate stage(s) → carnivorous or specialist herbivorous descendent. The evolutionary pathways revealed by both the classical dietary guilds and those recovered in the k-means cluster analysis are reversible at all stages. However, transition rates into specialised folivorous and invertivorous guilds are broadly higher than rates out of them, while the inverse is true for other specialised dietary guilds.

Invertivory evolves from, and gives rise to, a multitude of generalist guilds with varying dietary compositions (e.g., omnivory, mixed herbivory, mixed faunivory). Other dietary guilds composed primarily of a single food type (carnivory, piscivory, folivory, frugivory, granivory, and nectarivory) typically evolve from a generalist guild that incorporates a substantial component of the primary food type in the dietary composition of the specialist guild (e.g., mixed faunivory → carnivory). Turtles and mammals, with large numbers of species in generalist guilds, did not show a consistent pattern. Lizards, where most taxa are obligate insectivores, showed multiple independent origins of the evolution of dietary strategies incorporating non-arthropod food material. Birds, where a higher proportion of species fit into an array of specialist guilds, show several phylogenetically clustered instances of the evolution of different guilds.

3. Chapter Three: Overview

In Chapter Three I investigated the statistical relationship between diet and body mass in extant and some extinct amniotes. While there is a pattern evident in how

body mass values are distributed between dietary guilds, dietary composition is a weak statistical predictor of body mass. The effect is weaker still when accounting for underlying phylogenetic structure, which is essential to evaluate whether the face-value correlations between the diets and body sizes of species result from a close co-evolutionary relationship between diet and body size. This indicates that evolutionary changes in diet and evolutionary changes in body size are either weakly correlated or uncorrelated. These results vary between dietary guilds and between major amniote lineages.

Given the weak or absent relationships between dietary guilds and body mass when accounting for phylogenetic structure, and the weak predictive power of any given food type in the dietary composition, I propose that a strong and direct functional relationship between diet and body size, as expected under “digestive efficiency” hypothesis is absent. Instead, I propose that extrinsic factors, such as total energy availability from a given food source in an environmental context as outlined by Hiiemae (2000) and M. Clauss et al. (2013), or the “abundance-packet size” hypothesis offers a more plausible explanation of the correlation between dietary guild and body size recovered in the ordinary analysis.

Comparisons of mean body mass values between dietary guilds revealed a pattern in which insectivores and nectarivores tended to the lowest body sizes, and carnivores, piscivores, and folivores tended to the largest. The intermediate levels of body size distribution were occupied by omnivores, mixed herbivores, mixed faunivores, generalist invertivores, frugivores, granivores, and durophages. This pattern approximates the U-shaped curve in body size distribution between dietary strategies as described by Rob Cooke et al. (2022). The use of phylogenetic comparative methods revealed that this pattern is not generally statistically significant when accounting for non-independence in the data introduced by underlying phylogenetic structure except between the extremes (large carnivores and folivores, small invertivores and nectarivores). Given that this pattern was consistent across all major amniote lineages, the correlations between diet and body mass are, therefore, unlikely to reflect a direct physiological link between the two variables.

There were some differences in these results between the major amniote lineages. In turtles, the statistical evidence of any relationship between diet and body size is very weak in a phylogenetic context. The association between larger body size and a non-insectivorous diet was stronger in lizards than in other groups. Corrected for the underlying phylogenetic structure, the association between increased consumption of reproductive plant material (specifically fruit) and increased body size was slightly stronger than that of vegetative plant material in lizards and birds. The difference in body size between folivores and other herbivorous guilds was most evident mammals while it was minimal in the other major amniote lineages. The correlation between insectivory and small body size was, therefore, universal, while the dietary guilds that had the strongest evolutionary correlation with large body size varied between major amniote lineages.

4. The current study: leading contributions

This research has yielded a series of pioneering contributions that advance our understanding of the macroevolution of diet in amniotes. Firstly, I provide comprehensive insights into the dietary compositions of major extant amniote lineages. Through rigorous analysis, I investigate the rate, tempo, and directionality of evolutionary transitions between different dietary guilds and explore the statistical relationship between diet and body size. Furthermore, I extend these analyses to the fossil record, uncovering invaluable insights into the deep past. The pursuit of these investigations necessitated another novel contribution: the creation of datasets containing detailed, percentage-based information about the diets of the vast majority of extant species of turtles and lizards.

The most important finding across all of my analyses is the critical role invertivory plays in structuring amniote dietary variation, transition, and macroevolution. I find that invertebrates are the most common food type to be consumed in all extant amniote lineages in this study. Invertebrates also form an important component of generalist and omnivorous guilds. Similarly, invertivorous feeding strategies are the most evolutionary plastic. There is a high number of evolutionary transitions between

invertivorous guilds, and several omnivorous, faunivorous, and herbivorous guilds. The evolution of non-invertivorous dietary guilds is, therefore, often accompanied the evolution of increased body size class.

5. Final synthesis

In the first chapter of this thesis, I propose that diet in amniotes is best understood as a spectrum split into two biological gradients; one between invertivory and carnivory, and one between invertivory and folivory. These gradients are reflected in the divisions of data and in the dietary compositions of the guilds recovered in the cluster analysis. I propose that omnivory forms part of a broader spectrum of generalist feeding guilds (along with generalist invertivory, mixed faunivory, and mixed herbivory) that facilitate the evolution of specialised forms of faunivory and carnivory. This pattern is mirrored in chapter two by the tempo, and directionality of evolutionary transition rates between dietary guilds, and in chapter three with the distribution of body size values in a phylogenetic framework. The interplay between these findings can be explained from a perspective of ecology and energetics.

From invertivore to carnivore and back again

Invertivory is the most probable ancestral condition of amniotes (Modesto et al., 2009; Sahney et al., 2010; Sues, 2000; Sues & Reisz, 1998). Evolutionary shifts to carnivory were likely the earliest transitions out of invertivory in deep time (Sahney et al., 2010). The transition from invertivory to carnivory is biologically “easy” in the sense that it requires minimal adaptations to oral and gut processing (Christiansen & Wroe, 2007; Hume, 2003; Morales-García et al., 2021; Schondube et al., 2001; Stevens & Hume, 2004; Van Valen, 1969). In all major amniote lineages, invertivorous guilds account for a higher percentage of species than mixed faunivorous guilds which, in turn, account for a higher percentage of species than carnivorous guilds. Furthermore, in the current study, evolutionary transition rates

from guilds incorporating higher proportions of vertebrate material in the dietary composition to more invertivorous guilds were higher than the inverse.

The invertivory → mixed faunivory → carnivory biological and evolutionary gradient is mirrored by an increase in body mass corresponding with increased carnivory in the dietary composition. Larger mammalian faunivores (above ~21.5 kg) have been shown to take prey with higher body masses than themselves (Carbone et al., 1999; De Cuyper et al., 2019; Vézina, 1985). This is expected under the "abundance-packet size" hypothesis since large bodied vertebrate prey provides a larger, more concentrated source of energy to sustain the large body size of hypercarnviores. Digestive properties are similar between invertebrate and vertebrate food sources, and most anatomical differences between invertivory and carnivory are in oral processing apparatus (Christiansen & Wroe, 2007; Van Valen, 1969). Given the high abundance of invertebrates in the natural environment; it is not surprising that smaller carnivorous taxa may incorporate invertebrate material into their diets opportunistically in times when their preferred vertebrate food sources become scarce (Reuter et al., 2023). This could explain an evolutionary tendency towards invertivory along this evolutionary gradient. Only after a carnivorous taxon reaches a certain body size class, is there an evolutionary point of infliction in which evolutionary reversion to an invertivorous diet becomes impossible (Van Valkenburgh et al., 2004).

The road to folivory: an extra evolutionary step

The earliest evolutionary shifts to herbivory in deep time are often hypothesized to have originated from invertivorous lineages (Grossnickle et al., 2019; Hellert et al., 2022; Melstrom & Irmis, 2019; Sues & Reisz, 1998). The opportunistic feeding on plant material in invertivorous taxa (Cooper Jr & Vitt, 2002; Edwards et al., 2021; Herrel, Vanhooydonck, & Van Damme, 2004; Rex et al., 2010) lays the foundation for future of evolution of herbivory. The addition of plant material to an invertivorous diet, and the subsequent evolution of specialised herbivory, necessitates substantial changes to oral and gut processing anatomy (P. D. Edwards et al., 2020; German et al., 2010; German et al., 2015; Kohl et al., 2016; Morales-García et al., 2021;

O'Grady, 2006; O'Grady et al., 2005; Schondube et al., 2001; Sues, 2000; Sues & Reisz, 1998; Weishampel & Norman, 1989).

The addition of reproductive plant structures (e.g., nectar and fruit) to an ancestrally invertivorous diet requires less extensive anatomical adaptation than does the introduction of vegetative plant structures. Hence, many taxa are able to incorporate nectar and fruit into an ordinarily invertivorous diet with changes to digestive enzyme activity and gut symbiotes but little anatomical change (Cooper Jr & Vitt, 2002; Gartrell, 2000; O'Grady et al., 2005; Schondube et al., 2001). This explains the model of evolutionary transition I recover of: invertivory → omnivory → nectarivory/granivory/frugivory. This pattern is also reflected in the frequent clustering of, and high negative correlations between, invertebrate food sources and reproductive plant structures in the dietary compositions of many amniote taxa (see Tables 20-31).

The digestive systems of frugivorous and granivorous taxa possess anatomical and physiological characteristics that lie partway between those of folivorous taxa and those of faunivorous (invertivorous) taxa (Bodmer et al., 2006; Bodmer, 1989, 1990; Chivers, 1989; Chivers & Hladik, 1980; Kunz & Ingalls, 1994; Lambert, 1998; Rosenberger et al., 2011). This explains why folivory evolves through an additional step of the model as: invertivory → omnivory → mixed herbivory → folivory. The gradient between invertivory and folivory through generalist intermediate steps differs from the analogous evolution of carnivory in the following ways: (a) folviory is taxonomically far more abundant than carnivory in some lineages, especially in mammals, (b) it is not uncommon for a substantial proportion of fibrous plant material to be included alongside invertebrate material in omnivorous diets, and (c) transition rates into folivory tend to exceed those in the opposite direction (see Figures 23-26).

There is an increase in body size along the gradient between invertivory and folivory. However, only the extreme ends of this body size curve are statistically significant when accounting for underlying phylogenetic non-independence of the data, and the proportion of fibrous plant material in the dietary composition has a very minimal statistical impact on body size. This is expected under the “abundance-packet size” hypothesis since vegetative plant material is an abundant source of energy in most terrestrial environments, supporting larger body (M. Clauss et al., 2013; Hiiemae,

2000). Strict folivores are present at the same small and intermediate size ranges as other herbivorous guilds (Cork, 1996; Duque-Márquez et al., 2019; Foley & Cork, 1992; Liu et al., 2020; Pauli et al., 2016). However, the largest body size values are attained by grazers in open habitats (Bodmer et al., 2006; Bodmer, 1990; Clauss et al., 2003; Pineda-Munoz et al., 2016). The results I present in Chapter Three uphold these hypotheses.

Evolutionary transitions from specialist feeding guilds into omnivory, or other generalist feeding guilds, are often driven by ecological necessity due to limited availability of a taxon's preferred food source in the environment (Burin et al., 2016; M. Clauss et al., 2013; Reuter et al., 2023; Rex et al., 2010). This might explain why transition rates are, on average, higher into folivory, and out of carnivory, in relation to mixed herbivory and mixed faunivory respectively. Fibrous plant material, especially grass, provides a far larger pool of biomass than large vertebrates. Hypercarnivory also comes with high competition and physical risk and high energy expenditure in the process of hunting (McNab, 2000, 2010; Van Valkenburgh, 2007). It is, therefore, consistent with the "abundance-packet size" hypothesis that there would be a high rate of transition from carnivory to invertivory, while rates of transition would be higher towards folivory. From the perspective of energetics, a small bodied carnivore or mixed faunivore would have an incentive to transition to a diet of invertebrates which are an abundant source of energy suitably packaged for small-bodied taxa. By contrast, the abundance of fibrous plant material in the environment could provide a selection pressure towards increased folivory over time.

6. Going forward

The spectrum of diet: the next phase in research

I propose that the interplay between the spread of food items in dietary guilds, the evolutionary transitions between guilds, and body size can be explained in the context of functional ecology and extinction risk. In as much as omnivory has been shown to act an evolutionary sink (Burin et al., 2016; Price et al., 2012), large

folivores, carnivores and piscivores have also been shown to be the most susceptible to extinction among major extant amniote lineages (Atwood et al., 2020; Richards et al., 2021; Van Valkenburgh et al., 2004). Omnivores, invertivores, nectarivores, and granivores have the lowest risk of extinction (Atwood et al., 2020). Dietary specialization, in general, has been shown to be a predictor of increased vulnerability to extinction in, for example, extant primates (Kamilar & Paciulli, 2008), and bats (Boyles & Storm, 2007). In the fossil record, studies of mass extinction events (such as across the Cretaceous-Palaeogene (K/Pg) boundary) show that the largest carnviores and herbivores are most at risk during mass extinction events, while small invertivores and omnivores fare better (Wilson, 2013).

Beyond dietary considerations, large-bodied taxa have been shown to be the most vulnerable to extinction (Maurer et al., 1992; Pimm et al., 1988). The distribution of indices of extinction risk between dietary guilds (Atwood et al., 2020) follows the U-shaped curve in body size distribution between guilds (Rob Cooke et al., 2022) I recovered in the current study. Evolutionary shifts in dietary strategy, from an invertivorous ancestral condition also follow this curve (to mutually-exclusive extremes of carnivory and folivory). The highest rates of evolutionary transitions between dietary guilds involved guilds associated with the small- and medium body size classes (e.g., invertivory, and omnivory). The largest carnivorous and herbivorous taxa are “locked out” of these transitions, rendering them more vulnerable to extinction (M. Clauss et al., 2013; Reuter et al., 2023; Van Valkenburgh et al., 2004). Furthermore, at least in modern ecosystems and throughout the Mesozoic, a single lineage (mammals and non-avian dinosaurs respectively) have dominated the “megafauna” ecological niche on a global scale, including the largest folivorous taxa (Klein et al., 2022).

Going forward, I would propose an explicit test of (a) the strength of the evolutionary “trend” towards different feeding guilds through deep time, (b) the relation of these patterns to patterns of extinction, and (c) the incorporation of other functional ecophysiological variables such as substrate and locomotion. The aim would be to test of shifts in body size co-evolve with shifts in both broad dietary strategy and degree of dietary generalism or specialisation along both biological and evolutionary gradients of the dietary spectrum. The diet-body size model I present here would be

supported if there were limited, and frequently reversed, shifts from invertivory to carnivory, and an increase in total-clade folivory over time. The value of incorporating additional variables would be to assess whether additional adaptive constraints in certain amniote lineages provide an advantage or disadvantage to filling certain ecological niches, defined as the interplay between diet and functional morphology.

Another improvement to this line of research would be the incorporation of data on ontogenetic dietary variation. Most ontogenetic shifts in diet are out of invertivory in the juvenile stage. These includes shifts to omnivory and (mostly non-fibrous) herbivory in lizards (Durtsche, 2000; Mautz & Nagy, 1987; Mitchell & Eichholz, 2020; Pough, 1973; Van Leeuwen et al., 2011), and birds (Foster, 1978; Lopes et al., 2016; Poulin et al., 1994), and shifts to carnivory or durophagy in varanid lizards (Lonnberg, 1903; Purwandana et al., 2016; Rieppel & Labhardt, 1979; Winkler et al., 2019), and crocodilians (Tucker et al., 1996). Such ontogenetic changes in diet have also been hypothesized in the fossil record. Examples of this include a shift from invertivory to herbivory in the Triassic cynodont *Exaeretodon argentinus* (Wynd et al., 2022), and to carnivory/piscivory in the maniraptoran *Deinonychus antirrhopus* (Frederickson et al., 2020) and the stem bird *Confuciusornis sanctus* (Marugan-Lobon & Chiappe, 2022). The incorporation of ontogenetic dietary data into the goals and objectives of the current study could include (a) changes in the most important drivers of variance in dietary data between juvenile amniotes and their mature counterparts across the amniote tree, (b) investigating ancestral dietary transition rates and reconstructing ancestral dietary states via linking ontogeny and phylogeny (Cau, 2024; Fink, 1982; Gould et al., 1977; Northcutt, 1990), (c) further investigating the relationship between diet and body size since shifts out of invertivory usually occur after the animal attains a certain body size class during development, and (d) further developing understanding of dietary ecology in fossil ecosystems.

There is a need for data collection on subdivisions between different kinds of invertebrate material in the dietary compositions of the major lineages of amniotes, especially birds and mammals. My analyses on turtles and lizards strongly suggest that there is biological and evolutionary significance to the division between insectivory and durophagy, in regards to evolutionary transitions and body size.

Molluscs, gastropods and crustaceans are common contributions to the dietary compositions of birds and mammals (Allen, 2004; Buchanan et al., 2006; McLaughlin et al., 2022; Quaintenne et al., 2010; Schley & Roper, 2003; Tseng & Flynn, 2018; Tseng et al., 2017; E. Varennes et al., 2015; É. Varennes et al., 2015; Zhang et al., 2019). It would be informative to investigate whether the same macroevolutionary patterns seen in durophagy in turtles and lizards are transferable to any other major amniote lineages. It would also be of use to future macroevolutionary studies to collate data on the percentages of social insects (ants and termites), and marine invertebrates in the dietary compositions of amniote species. These classes of invertebrates provide a far larger package of energy than most other invertebrate food sources and their consumption is, thus, associated with larger body size (R. Cooke et al., 2022; Delsuc et al., 2014; McNab, 1984, 2000; Redford, 1987; Werth, 2007). Combined, I believe these enhancements to data resolution would prove particularly helpful in studies relating to macroevolution and ecology.

I would like to have explored evolutionary transitions using alternate methods, such as Bayesian modelling (Bouckaert et al., 2014; Drummond & Rambaut, 2007; Drummond et al., 2012). It would useful to compare results across several different approaches. Unfortunately, constraints on time prohibited a more expansive approach to analysing evolutionary transitions and ancestral state reconstruction.

I would also like to have incorporated analysis on rates of speciation and extinction in relation to diet. In passing, I used the software Bayesian Analysis of Macroevolutionary Mixtures (Rabosky, 2014; Rabosky et al., 2014) to test for shifts in species diversification on the turtle phylogeny (Robert C Thomson et al., 2021). I do not formally present the results in the current study but there was a shift to increased species diversity on the node ancestral to Geoemydidae and Testudinae. This clade includes most herbivorous turtle taxa. I believe that a more thorough investigation of differential rates of speciation and extinction between dietary guilds may assist in answering such questions as the macroevolutionary position of omnivory as a transitory state or an evolutionary sink following the work of Price et al. (2012) and Burin et al. (2016).

The analyses between diet and body size could be greatly complemented by: (a) Hansen models seeking evolutionary optima for different guilds (Butler & King, 2004;

Khabbazian et al., 2016), and (b) placing the relationship between diet and body size into an evolutionary context by exploring alternative avenues to test for correlated trait evolution (Caetano & Harmon, 2019; Pagel & Meade, 2006; Pagel et al., 2004). Other methods that may reinforce the statistical strength of the conclusions I draw include robust phylogenetic regression (Adams et al., 2022; Uyeda et al., 2018). This may help overcome the statistical challenges associated with non-normal distribution of residual values in the regression models as outlined in Chapter Three (Methods, 2.1. Linear regression). I do partially address this issue with the non-parametric correlation tests. However, I believe regression to be a more powerful statistical tool, for the purposes of the specific macroevolutionary questions I am attempting to answer, owing to the capacity to calculate proportion of variance in the dependent variable explained by the independent variable (Fowler et al., 2013).

Both the analyses on evolutionary transitions, and the phylogenetic linear models, correlation tests and analyses of variance may have benefitted from the use of multiple topologies of each tree to account for phylogenetic uncertainty (Rubolini et al., 2015). However, I do not believe that the use of alternative topologies would have impacted on my results significantly as to warrant this as a major consideration. Topological variation in the trees I use are mostly limited to minor variation of sister taxon relationships within genera or, to a lesser extent, families (Ericson et al., 2006; Hackett et al., 2008; Jetz et al., 2012; Pyron et al., 2013; Robert C Thomson et al., 2021; Tonini et al., 2016; Upham et al., 2019). A few of the deepest nodes are unresolved in some instances as well. An example of this is the disagreement of the phylogenetic placement of Xenarthra, Afrotheria, and Boreoeutheria; three major lineages of mammals (Upham et al., 2019). However, the constituents of the major clades (e.g., families, orders and superorders) are largely consistent between topologies. Since most variation in dietary strategy is at this resolution (see Figures 43-46), I have no reason to believe that running the analyses I used in the current study on multiple iterations of the phylogenies of each major lineage would produce a substantially different result. The most obvious example of this is the case of birds. Dietary guilds are very phylogenetically clustered in this lineage (see Figure 35). The precise set of evolutionary relationships of species in, for example, the overwhelmingly nectarivorous Trochilidae (see Figure 45) may differ between topologies. However, it is highly unlikely that an optimal iteration of the bird tree

would nest several taxa from the mostly carnivorous Accipitriformes within Trochilidae. Short of a major revision of phylogenetic relationships at all nodes of any major lineage of amniotes, I do not believe that the results I present in this thesis would change drastically from the introduction of alternative phylogenetic hypotheses.

Additionally, alpha taxonomy constitutes an imperfect unit of measurement for testing the correlation between diet and body size. I suggest it would be more appropriate to explore an approach that accounts for alternative metrics of measuring body size distribution such as number of individual organisms or total biomass. This would allow an examination at species level and assess, in a granular way, whether small dietary differences are changing the phenotype. To refer to a percentage of a clade belonging to a given dietary guild, from the perspective of alpha taxonomy (percentage of species), discounts the evolutionary success of said dietary guild that would be captured by referring to the total biomass of a clade that dietary guild accounts for. For example, a clade with a certain diet and body size class may be more speciose than a sister clade with a different diet and body class. This would likely be caused by completely unrelated, or tangentially related, factors. This may artificially inflate a given range of body size values for a given dietary guild. I believe, therefore, that the total biomass of each dietary guild, as demonstrated by Klein et al. (2022), is a more informative unit of measurement for assessing the biological and ecological success of each dietary guild than is alpha taxonomy alone.

In light of the “abundance-packet size” hypothesis (M. Clauss et al., 2013; Hiiemae, 2000), I also propose an overall in the way dietary composition data are collected. The masses and volumes of different food items in the dietary composition of an animal do not account for essential information regarding the value of the food from the perspective of energy availability. Other metrics that I believe should be considered include: (a) the contribution of each food source to total caloric content of an animal’s diet, and (b) spatial distribution and nutrient density of each food source in the natural environment. A dietary guild can then be assessed by the total energy that can feasibly be extracted from the food sources that compose it. This approach could also benefit other studies relating to the macroevolutionary dynamics of other

life history traits in amniotes. Collecting the data necessary for such an undertaking may prove challenging.

LIST OF APPENDICES

Appendix A.1. Terminology: Summary of important terms used throughout the main text and their meanings.

Appendix A.2. Excel spreadsheets containing dietary guilds generated using the recommendations of Pineda-Munoz et al (2014) divided between guilds generated by the k-means cluster analysis (k=5, 10, and 20) for each major amniote lineage.

Appendix A.3. Turtle_dataset: Complete dietary and body size data for turtles. The dataset is modified from the dataset of Angielczyk et al. (2015). See Chapter One (2.2. Data collection: turtles) for an explanation of each column.

Appendix A.4. Lizard_dataset: Complete dietary and body size data for lizards. The dataset is modified from the dataset of Meiri (2018). See Chapter One (2.3. Data collection: lizards) for an explanation of each column.

Appendix A.5. Theropod_dataset: Complete dietary and body size data for non-avian theropod dinosaurs. See Chapter One (2.1. Data collection: overview) for an explanation of each column.

Appendix A.6. BirdFuncDat_edited: Data set of all extant birds from the EltonTraits database (Wilman et al., 2014). See Chapter One (2.1. Data collection: overview), and the "MetaData" file from the EltonTraits database (Wilman et al., 2014) for an explanation of each column. The following columns were not present in the original dataset:

- Diet.AnimalT: Summed total values of the columns "Diet.Inv", "Diet.Vend", "Diet.Vect", "Diet.Vfish", "Diet.Vunk", and "Diet.Scav".
- Diet.PlantT: Summed total values of the columns "Diet.Fruit", "Diet.Seed", "Diet.Nect", and "Diet.PlantO".
- Diet.Vland: Summed total values of the columns "Diet.Inv", "Diet.Vend", "Diet.Vect", "Diet.Vunk", and "Diet.Scav".
- Diet.PlantR: Summed total values of the columns "Diet.Fruit", "Diet.Seed", and "Diet.Nect".

- LogBM: Log-transformed values from the column “BodyMass.Value”. This transformation was completed using Microsoft Excel.

Appendix A.7. MamFuncDat_edited: Data set of all extant mammals from the EltonTraits database (Wilman et al., 2014). See Chapter One (2.1. Data collection: overview), and the “MetaData” file from the EltonTraits database (Wilman et al., 2014) for an explanation of each column. The following columns were not present in the original dataset:

- Diet.AnimalT: Summed total values of the columns “Diet.Inv”, “Diet.Vend”, “Diet.Vect”, “Diet.Vfish”, “Diet.Vunk”, and “Diet.Scav”.
- Diet.PlantT: Summed total values of the columns “Diet.Fruit”, “Diet.Seed”, “Diet.Nect”, and “Diet.PlantO”.
- Diet.Vland: Summed total values of the columns “Diet.Inv”, “Diet.Vend”, “Diet.Vect”, “Diet.Vunk”, and “Diet.Scav”.
- Diet.PlantR: Summed total values of the columns “Diet.Fruit”, “Diet.Seed”, and “Diet.Nect”.
- LogBM: Log-transformed values from the column “BodyMass.Value”. This transformation was completed using Microsoft Excel.

Appendix A.8. Theropod_tree: Phylogenetic tree of non-avian theropods (Newick format) pruned down from the original topology of Benson et al. (2014) to include only taxa included the dataset for non-avian theropod dinosaurs (Appendix A.7.).

Appendix A.9. Turtle_dataset_references: List of primary literature sources for turtle dietary data.

Appendix A.10. Lizard_dataset_references: List of primary literature sources for lizard dietary data.

Appendix A.11. Theropod_dataset_references: List of primary literature sources for non-avian theropod dietary data.

Appendix A.12. Full R-script for all analyses ordered sequentially by chapter.

A.1. TERMINOLOGY

Here I present a list of important terms that I employ when making qualified statements about dietary guilds and the food sources that compose them. It should be noted that these terms are to facilitate the process of writing and communicating vital information in a condensed, accessible manner. I do not propose any of these terms to represent formal scientific definitions. As such, I explain the rationale for each of their uses.

Terminology related to subdivision of dietary categories:

- First-order: This refers to total plant and animal material in the dietary composition of a given taxon. The first-order percentile dietary categories are “AnimalT” and “PlantT”. The classical dietary guilds (faunivory, omnivory, and herbivory) are also based on first order subdivisions of dietary data. The classical dietary guilds are also called “supraclassifications” in contexts when dietary guilds recovered in the k-means cluster analysis are aggregated into a classical dietary guild based on the primary first-order subdivision in the dietary composition of the guild. A guild recovered in the k-means cluster analysis can also be referred to as “herbivorous” or “faunivorous” if more than 70% of the dietary composition of that guild is composed of plant- or animal-material respectively (e.g., “folivory” and “frugivory” are both herbivorous guilds).
- Second-order: This refers to the primary subdivisions of animal- and plant-based food material. These are invertebrates and vertebrates, and reproductive/non-fibrous and vegetative/fibrous plant structures respectively. The second-order percentile dietary categories are “Inv”, “Vert”, “PlantR”, and “PlantO”. I heavily reference second-order subdivisions of dietary data throughout the main text as they are consistent between the different datasets.
- Third-order: This refers to the most granular sub-divisions of animal- and plant-based food material. The third-order percentile dietary categories are “Arth”, “Duro”, “Vland”, “Vfish”, “Fruit”, “Seed”, and “Nect” (see Table 2 for definitions). I used these variables to generate the dietary guilds in the k-

means cluster analysis (see Chapter One, 2.4. Data ordination and visualization).

Terminology related to the categorization of different dietary guilds:

- Specialist: Any dietary guild overwhelmingly (>95%) composed by a single food source (third-order). I often refer to specialist guilds as “strict” in text (e.g., “strict folivory”) or appendage their titles with “s.s.” (sensu stricto).
- Generalist: Any dietary guild not overwhelmingly (>95%) composed by a single food source (third-order). I often appendage the titles of generalist guilds with “s.l.” (sensu lato).
- Mixed: A particular kind of generalist guild wherein a single first-order category accounts for >85% of the dietary composition, but two third-order categories each contribute >20% (e.g., “mixed faunivory”, and “mixed herbivory”).

A.9. TURTLE DATASET: REFERENCES

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A.10. LIZARD DATASET: REFERENCES

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