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Functional traits are phenotypic characteristics that contribute to fitness of species in dynamic and changing environments. In mammals, both categorical and continuous (e.g., quantitative) functional traits have been extensively utilized as proxies for diet, locomotion, and other aspects of species ecology, but there has been less focus on measurements of soft tissues. This is particularly true for the digestive system, which varies in size and complexity across Class Mammalia and plays a major role in the energetics of species. The overarching goal of my research was to guide more effective utilization of gastrointestinal (GI) morphology as a functional trait in small mammals. I therefore explored GI variation in relation to environment at two levels of biological organization. First, I examined how GI tracts (lengths and masses of four GI sections) varied within a population of deer mice (*Peromyscus maniculatus*) over the course of an entire year (2021) in the Southern Appalachian Mountains of North Carolina, USA. My objective was to demonstrate how seasonality, dietary quality, and reproductive activity impact GI morphological variation, providing insight into the plasticity and potential function of this soft tissue trait. Second, I applied this same set of traits to small mammal communities throughout the Appalachians, specifically assessing the effectiveness of GI morphology in distinguishing dietary groups as well as in driving community-level trait change across a major latitudinal and seasonality gradient. I also compared GI traits to established craniodental traits for both purposes. Overall, my work provides substantial new soft tissue trait data at both the intraspecific and interspecific levels and paves the way for more expansive use of GI traits in future studies to understand community assembly, individual and population health, and response to environmental change at population and community levels.

GUT CHECK: EXPLORING GASTROINTESTINAL MORPHOLOGY AS A CONTINUOUS FUNCTIONAL TRAIT IN APPALACHIAN SMALL MAMMAL COMMUNITIES

by

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Dr. Bryan McLean
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DEDICATION

This thesis is dedicated to Carol L. Poulos and Daniel K. Chapman. Words will never express how grateful I am for your constant and unwavering love and support, but I hope this is a good start.

APPROVAL PAGE

This thesis written by Olivia Scout Chapman has been approved by the following committee of the Faculty of The Graduate School at The University of North Carolina at Greensboro.

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CHAPTER I: INTRODUCTION

Functional traits are physical or behavioral attributes that influence the ability of a species to persist and successfully reproduce in specific ecosystem contexts (Kohli and Rowe 2019; Gallagher et al. 2020). For this reason, trait-based approaches have become central to our ability to understand community assembly and species- and community-level response to environmental change. Despite substantial research on mammalian ecomorphology and physiology over the past century, most functional traits currently used for the purpose of detecting change response in mammals are categorical, such as a species' diet guild and habitat preference. These categorizations overlook the more detailed variation that exists in key morphological and life history properties of species, which can often be measured on continuous scales to yield clearer links between phenotypic variation and fitness outcomes, and thus to understand global change responses in a more nuanced way (Laureto, Cianciaruso, and Samia 2015; Kohli and Rowe 2019).

The gastrointestinal (GI) tract is a soft tissue associated with the digestive system that has high functional significance both within and among mammal species. It is well known that mammalian GI morphology varies significantly with type and quality of diet (Schieck and Millar 1985; Naya 2008), with size and complexity being in general inversely correlated with dietary quality. Further, GI morphology can vary intraspecifically, both seasonally and with breeding activity (Derting and Hornung 2003; Naya et al. 2008a), suggesting it is especially fine-tuned to energetic requirements of individuals within their local environments. However, GI traits are far less commonly measured than other phenotypic traits such as craniodental proportions, the latter of which are predictive of diet in mammals but may also be more evolutionarily constrained over short timescales (Samuels 2009; Verde Arregoitia and D'Elía 2021).

The purpose of the first chapter of my research was to perform an in-depth examination of the gastrointestinal morphology of the North American deer mouse (*Peromyscus maniculatus*) in the Southern Appalachian Mountains of North Carolina, in order to demonstrate how GI morphological changes throughout an entire year correspond to seasonality (and, thus, dietary quality) as well as reproductive activity. This portion of my work also sought to refine our understanding of GI tract function and guide effective use of gastrointestinal morphology (a rarely-measured soft tissue trait in mammals) as a functional trait in small mammals.

The purpose of the second chapter of my research was to perform a trait-based ecological analysis of small mammal communities along the entire Appalachian Mountains biome to quantify patterns of GI and craniodental variation along a major latitudinal and climate gradient. This community-level approach was designed to compare how the traits correspond to established dietary guilds, provide insight on the importance of each trait set in small mammal community assembly, and establish critical baselines to study how environmental change (including climate change and habitat fragmentation) may impact small mammals across an entire ecosystem in the future.

CHAPTER II: SEASONAL AND SEX-SPECIFIC CHANGES IN THE GASTROINTESTINAL TRACTS OF *PEROMYSCUS MANICULATUS*

INTRODUCTION

FUNCTIONAL TRAITS IN SMALL MAMMAL RESEARCH

Functional traits are defined as the physical or behavioral attributes that influence the ability of a species to persist in specific community and ecosystem contexts (Kohli and Rowe 2019; Gallagher et al. 2020). Some common functional traits are continuous metrics, such as body mass and body length, but most functional traits currently used by researchers in mammalian ecological and evolutionary research are categorical, such as a species' diet guild or habitat guild (Kohli and Rowe 2019; Verde Arregoitia and D'Elía 2021). These categorizations tend to overlook the more detailed intraspecific variation that exists in the key morphological, behavioral, and life history properties of species (Parins-Fukuchi 2017; Kohli and Rowe 2019), which may mediate fitness in dynamic and changing environments. One likely reason for this shortcoming is that continuous traits are harder to obtain and often require intensive field sampling efforts or measurement of existing material (e.g., museum specimens; Kohli and Rowe 2019) across environmental gradients in order to refine exact functional roles. Nevertheless, for mammals and many other groups, it is increasingly important to develop a stronger focus on using continuous measurements as functional traits, as they facilitate more precise functional characterizations and improve our ability to monitor and detect global change response (Laureto et al. 2015; Parins-Fukuchi 2017; Kissling et al. 2019; Kohli and Rowe 2019).

FUNCTIONAL SIGNIFICANCE OF THE GASTROINTESTINAL TRACT

Changing climate and land use contexts are impacting the abundance and quality of food available to vertebrates in different regions and times of the year (Ayres 1993; Schradin and Pillay 2006; Mayor et al. 2017; Soares et al. 2019). The changing phenology of peak resource availability can cause some vertebrates to have a reproductive mismatch with resource peaks, leading to negative fitness consequences such as increased infant mortality (Post and Forchhammer 2007). Even for mobile species that can emigrate to more favorable conditions, however, alteration of diets in response to spatial or temporal variation in resource availability is often an important behavioral adjustment.

Morphological and physiological measurements of the gastrointestinal (hereafter, GI) tract may be important functional traits to consider both within and among species in changing environmental contexts (Naya et al. 2007; Naya et al. 2008b). For example, it is well known that GI morphology varies significantly across mammals with type and quality of diet (Chivers and Hladick 1980; Schieck and Millar 1985; Naya 2008). Herbivores, and in particular large ruminants, often have relatively larger and more complex digestive systems with larger numbers of compartments (Dehority 2002). Even in small mammals, herbivores tend to have a larger cecum and a longer and heavier large intestine, which is useful for processing poor-quality plant material, while omnivores and granivores have smaller ceca and a lighter large intestine (Schieck and Millar 1985). Further, GI morphology can also vary seasonally and with breeding activity (Derting and Hornung 2003; Naya et al. 2007; Naya 2008; Naya et al. 2008a; Naya et al. 2008b), suggesting it is also fine-tuned to energetic requirements and local environments.

Currently, there is a need to refine understanding of phenotypic plasticity of different GI traits in wild mammal species in the context of changing energy demands, although some studies have tested these ideas in the lab (Derting and Austin 1998; Hammond et al. 1999; Naya 2008). Small herbivorous mammals inhabiting higher latitudes tend to have access to lower quality diets during the winter due to inhibited plant growth, but also an increased energy demand due to costs of thermoregulation (Hammond and Wunder 1995; Korslund and Steen 2006). One way to compensate for this relatively higher energy requirement is to maximize the amount of time that available food is in the GI tract, which can maximize the nutrients absorbed (Hammond and Wunder 1995; Koteja 1995). Gut mass significantly increased during winter in populations of both *Peromyscus leucopus* and *Microtus pennsylvanicus* (Derting and Noakes 1995), and another study of *M. pennsylvanicus* demonstrated increases in both the weight and dry mass of the small intestine and the cecum with increased energetic demands (Derting and Bogue 1993). Populations of *Microtus ochrogaster* that were kept at cold temperatures also showed an increase in the length and mass of the cecum along with an increase in the total GI tract length (Gross et al. 1985). Hammond and Wunder (1995) demonstrated that when two species of rodents (*M. ochrogaster* and *Dicrostonyx groenlandicus*) were acclimated to lower temperatures in the lab, both species GI tracts increased in length. There was also an increase in the amount of digesta present in the GI tract when both species were acclimated to cold (Hammond and Wunder 1995). In *Peromyscus maniculatus* populations kept in semi-natural conditions, the dry mass of the small intestine was heavier in cold-acclimated mice than in warm-acclimated mice (Hammond et al. 2001). Importantly, the level of plasticity in the GI tract is also known to vary with latitude and altitude, with the small intestine being more plastic at higher latitudes and altitudes, potentially due to the more severe climatic fluctuation (Hammond et al. 2001; Naya et al. 2008a).

Reproduction can likewise have an exceptionally large effect on individual-level GI morphology (Millar and Norrie 1990; Derting and Noakes 1995; Derting and Hornung 2003; Naya et al. 2007), due to the increased energy demands associated with gestation and lactation during this period (Hammond 1997; Naya 2008; Naya et al. 2008b; Speakman 2008). A study on *P. leucopus* found that all of the GI organs of lactating females were heavier than the same organs from adult males (Derting and Hornung 2003). These effects decreased as the pups were eventually weaned, suggesting that these changes are reversible and heavily correlated with breeding status (Cripps and Williams 1975; Hammond 1997; Derting and Hornung 2003). In a laboratory study of albino rats, lactation likewise resulted in an increase in the wet and dry mass of the stomach as well as an increase in the length and mass of the small intestine (Cripps and Williams 1975). However, pregnancy itself did not cause any change in the stomach masses or length of the small intestine (Cripps and Williams 1975), consistent with lactation being the more energetically demanding activity (Speakman 2008). A laboratory study of *Microtus pinetorum* also found that lactation resulted in a significant increase in the length of the stomach and small intestine (Derting and Austin 1998), and a study of *Octodon degus* found that lactating females had longer ceca and greater overall gut mass than the control females (Naya et al. 2008b). Although the lactating *O. degus* females had shorter small intestines, they were thinner than the small intestines of the control females (Naya et al. 2008b), suggesting the trade-off still exists in this case. Finally, a study on a wild population of *P. maniculatus* found that GI tract size was greatest in lactating females, although the largest difference between lactating females and non-reproductively active males was only 12% (Millar and Norrie 1990).

CURRENT KNOWLEDGE GAPS

While the above studies suggest that internal organs like the GI tract whose roles are well-understood have high potential in functional trait studies, the rapid postmortem degradation of most soft tissues means that they are best obtained from fluid-preserved museum specimens or through intensive new field sampling. Unfortunately, the vast majority of small mammal specimens in natural history collections are preserved as skins and skeletons, with soft internal tissues often disposed of (Quay 1974; Greiman et al. 2018). Of a total of 2.3 million small mammal specimens stored between the 10 largest mammal archives in North America, only around 500,000 of them are fluid-preserved with GI tracts or organs (Greiman et al. 2018). Moreover, even when specimens are fluid-preserved, tissue shrinkage changes the morphology and leads to inaccurate measurements (Kingston 2018). This occurs regardless of the solution used to preserve tissues, although different solutions and concentrations may result in different degrees of shrinkage (Kingston 2018). Although this shrinkage may be predictable, correcting for it can still introduce bias (Kingston 2018). As a result of these factors, new measurements on fresh material are essential for describing intraspecific variation in GI morphology across the diversity of small mammals in the wild and how these are shaped by both extrinsic and intrinsic factors.

The purpose of my first chapter was to clarify how GI tract morphology (a rarely-measured soft tissue trait) changes with season and reproduction within a single species, thus guiding its more effective utilization as a functional trait in small mammals. Specifically, I examined these drivers of variation in GI trait morphology in populations of the North American deer mouse (*Peromyscus maniculatus*) in the Southern Appalachian Mountains of North Carolina, USA. I used a year-long field sampling campaign to document patterns of variation in lengths and masses of different GI sections, and attempted to link this variation to variables of body size, sex, and reproductive condition (pregnancy or lactation in females, maintenance of scrotal testes in males), and their interactions.

METHODS

FIELD SAMPLING

I sampled *P. maniculatus* at five plots in the Nantahala and Pisgah National Forests in western North Carolina (Table II.1) monthly in 2021. During each trapping event, at least five adult *P. maniculatus* were collected using Sherman live traps (with the exception of only two adult individuals collected in July and December). Trapping locations rotated among plots each month in order to avoid inducing local population decreases or other demographic effects; typically, I targeted three plots each month. Traps were baited with dilute vanilla extract, set at dusk, and checked at dawn the following morning. The non-edible bait ensured that any stomach contents or fecal pellets collected were a true representation of the individual's natural diet. All animals were euthanized in the field following approved protocols (UNCG IACUC #20-008) and recommendations of the American Society of Mammalogists Animal Care and Use Committee (Sikes et al. 2016). Immediately after euthanization, the GI tract was removed from each individual and frozen at -20° Celsius until processing (a maximum of two weeks). All individuals were preserved as voucher specimens in the UNC Greensboro mammal collection, with standard external measurements, multiple tissue samples, and full necropsy data including age, sex, and internal and external reproductive condition. Pregnancy or lactation (for females), and maintenance of scrotal testes (for males) were each considered evidence of reproductive activity.

Table II.1. Characteristics of the Five Plots Sampled, Including County, National Forest, Latitude, Longitude, and Elevation (m). The Maximum Distance Between Any Two Plots Was 5.97 km

Plot	County	National Forest	Latitude, Longitude	Elevation (m)
1	Transylvania	Pisgah	35.25335, -82.91935	1122
2	Transylvania	Pisgah	35.27768, -82.91628	1398
3	Jackson	Nantahala	35.26771, -82.98082	1116
4	Jackson	Nantahala	35.27771, -82.97295	1114
5	Jackson	Nantahala	35.25959, -82.95141	1234

GASTROINTESTINAL TRACT PROCESSING AND MORPHOMETRICS

Each GI tract was processed by thawing and then separating into four constituent sections; stomach, cecum, small intestine, and large intestine. Each section was cleared of any fat and connective tissue, placed into a petri dish with a small amount of physiological saline (to prevent desiccation), and subjected to three measurements: length, wet mass, and dry mass. Lengths were obtained to the nearest millimeter using a flexible measuring tape after gently extending each section. For curved sections (i.e., stomach and cecum), the measurement of the outer curve was used as the length measurement. To obtain wet mass, I emptied each section by cutting it open lengthwise and rinsing with physiological saline. A microscope slide was then used to gently scrape out any remaining contents. Each section was blotted to remove excess fluid and weighed to the nearest milligram using a Torbal AGZN120 Analytical Balance. Any stomach contents, cecal contents, and/ or fecal pellets were collected and frozen. To obtain dry mass, each section was dried at 57º Celsius to a constant mass (approximately 24 hours for all sections). Dried small intestines were archived as tissue samples with each voucher specimen.

For each section of the GI tract, I calculated mean length, wet mass, and dry mass across all individuals in the dataset (Table II.2), as well as for individuals within each month. All analyses in which individuals were binned by month or season were performed on both the raw and the scaled measurements. To scale lengths, raw values were divided by the head-body length of each individual (total length minus tail length). To scale masses, the cubic root of the raw values were divided by the head-body length of an individual (to prevent scaling a linear measure by a volumetric measure).

TESTING THE EFFECTS OF SEX, REPRODUCTION, AND SEASON

I first tested the effects of season, sex, and breeding condition on GI traits using a three-way analysis of variance (ANOVA) on the scaled measurements. Seasons (Winter, Spring, Summer and Fall) were delineated according to the winter solstice, spring equinox, summer solstice, and fall equinox. The distributions of the scaled lengths and scaled wet masses were both right-skewed so they were log10 transformed prior to analysis. However, there was no difference in the significance of the results between the transformed and untransformed data. The distribution of the dry masses appeared normal, so the dry mass data was not transformed. I ran separate ANOVAs for the scaled total length, scaled wet mass, and scaled dry mass. I also incorporated a sex x breeding interaction in my tests to account for sex-specific differences in the effect of breeding on trait variation.

To visualize annual change in scaled GI traits, I conducted polynomial linear regressions that predicted GI traits as a function of Julian day as well as the above variables. Regressions were only run if GI traits showed season as being significant in the three-way ANOVA. I also ran a regression for total GI tract length or mass (all sections summed). For each regression, I evaluated models that used a second-, third-, and fourth-order polynomial and compared these models section-wise using Akaike information criterion (AIC) scores. All analyses were conducted in R v4.0.2.

RESULTS

FIELD SAMPLING RESULTS

A total of 3,913 trap nights resulted in a total of 122 *P. maniculatus* captured (3.12% trap success). Of those individuals, 89 were collected as vouchers and the GI tracts measured. A total of 79 individual adult *P. maniculatus* were included in the analyses after excluding juveniles and sub-adults. Each month was represented by a mean of 6.58 mice, with a range of 2 (July and December) to 11 (January).

Table II.2. Mean Values for Six Measurements Taken on Adult *Peromyscus maniculatus* Gastrointestinal Tracts in This Study

Gastrointestinal section	Length (mm)	Scaled length	Wet mass (g)	Scaled wet mass	Dry mass (g)	Scaled dry mass
Stomach	32.304	0.395	0.259	0.008	0.055	0.005
Cecum	38.97	0.478	0.118	0.006	0.017	0.003
Small intestine	302.064	3.696	0.327	0.008	0.058	0.005
Large intestine	86.544	1.056	0.014	0.006	0.018	0.003
Total	459.636	5.626	0.809	0.011	0.148	0.006

GASTROINTESTINAL VARIATION WITH SEX, REPRODUCTION, AND SEASON

RESULTS

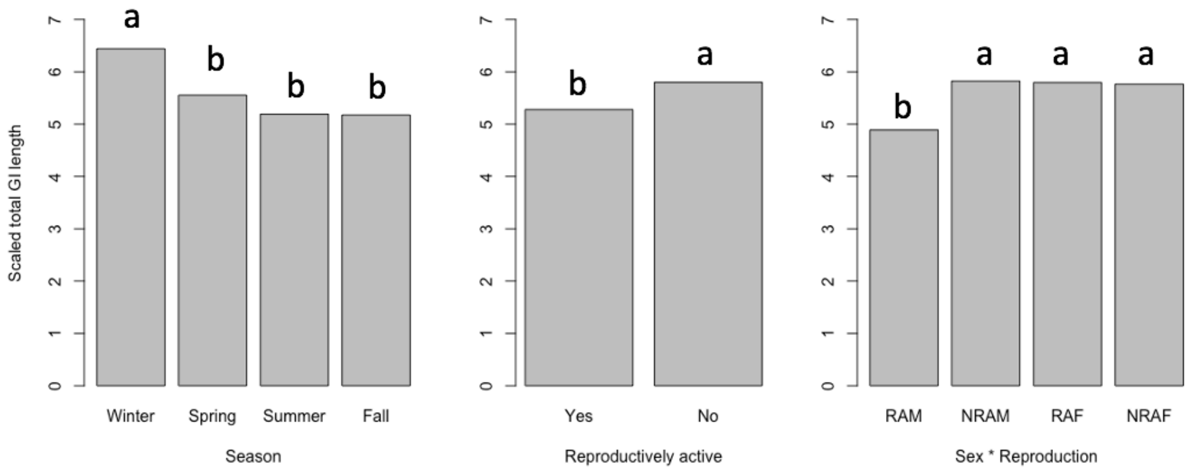
Season (Winter, Spring, Summer, or Fall) had a significant impact on GI length (P << 0.01) and wet mass (P << 0.01), but not dry mass (Table II.3). GI tracts were relatively longer and heavier in the winter than they were in the summer (Figure II.1). Sex did not have a significant effect on any trait, and reproduction only had a significant effect on GI length (P << 0.01) and wet mass (P < 0.05; Table II.3). However, all three traits (scaled total GI length, wet mass, and dry mass) displayed a significant sex x reproduction interaction (P < 0.05 for all; Table II.3). Reproductively active males had relatively shorter and lighter GI tracts than non-reproductively active males, while the difference between reproductively active females and non-reproductively active females was not significant (Figure II.1).

Table II.3. Results of Analysis of Variance Tests Relating Scaled Gastrointestinal Length, Wet Mass, and Dry Mass to Sex and Reproductive Condition

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Scaled total GI length					
Sex	2	0.00799	0.00399	1.661	0.197535
Reproductively active	1	0.03004	0.03004	12.493	0.000734 ***
Season	3	0.10364	0.03455	14.367	2.27e-07 ***
Sex:Reproductively active	1	0.01866	0.01866	7.759	0.006896 **
Residuals	69	0.16591	0.00240		
Scaled total GI wet mass					
Sex	2	0.00089	0.000446	0.325	0.723755
Reproductively active	1	0.00609	0.006092	4.441	0.038674 *
Season	3	0.02757	0.009190	6.698	0.000486 ***
Sex:Reproductively active	1	0.00832	0.008324	6.067	0.016232 *
Residuals	70	0.09603	0.001372		
Scaled total GI dry mass					
Sex	2	4.440e-07	2.219e-07	0.870	0.4234

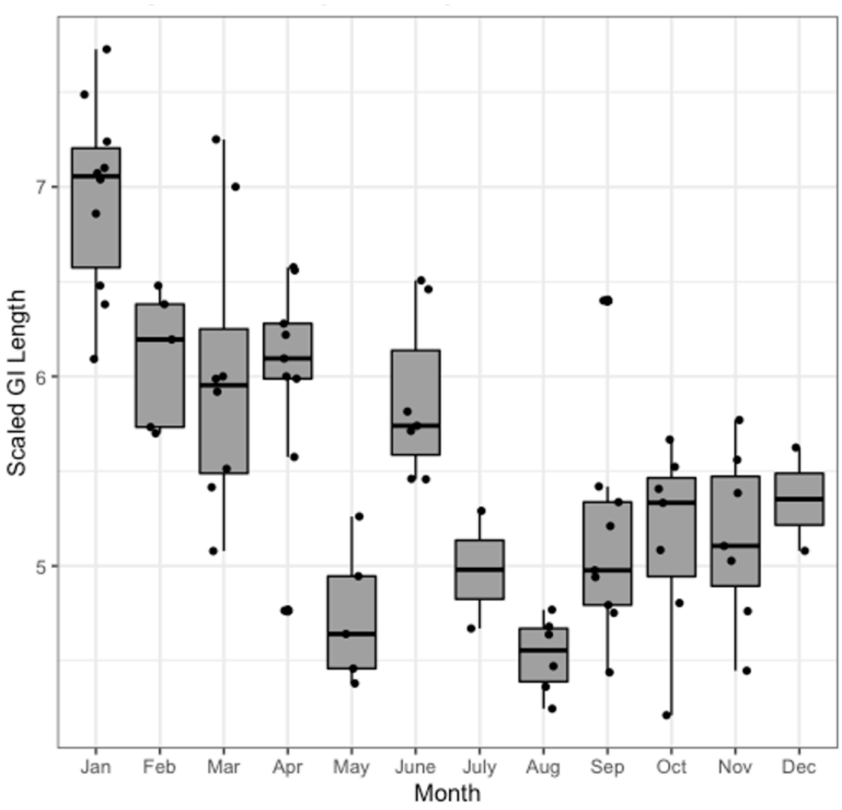
Reproductively active	1	2.730e-07	2.729e-07	1.070	0.3044
Season	3	6.010e-07	2.004e-07	0.786	0.5058
Sex:Reproductively active	1	1.481e-06	1.481e-06	5.809	0.0186 *
Residuals	70	1.785e-05	2.550e-07		

Figure II.1. The Effects of Season, Reproductive Activity, and the Interaction Between Sex and Reproductive Activity on the Scaled Total Gastrointestinal Length. Different Letters Represent a Significant Difference. "RAM" is Reproductively Active Males, "NRAM" is Non-Reproductively Active Males, "RAF" is Reproductively Active Females, and "NRAF" is Non-Reproductively Active Females.



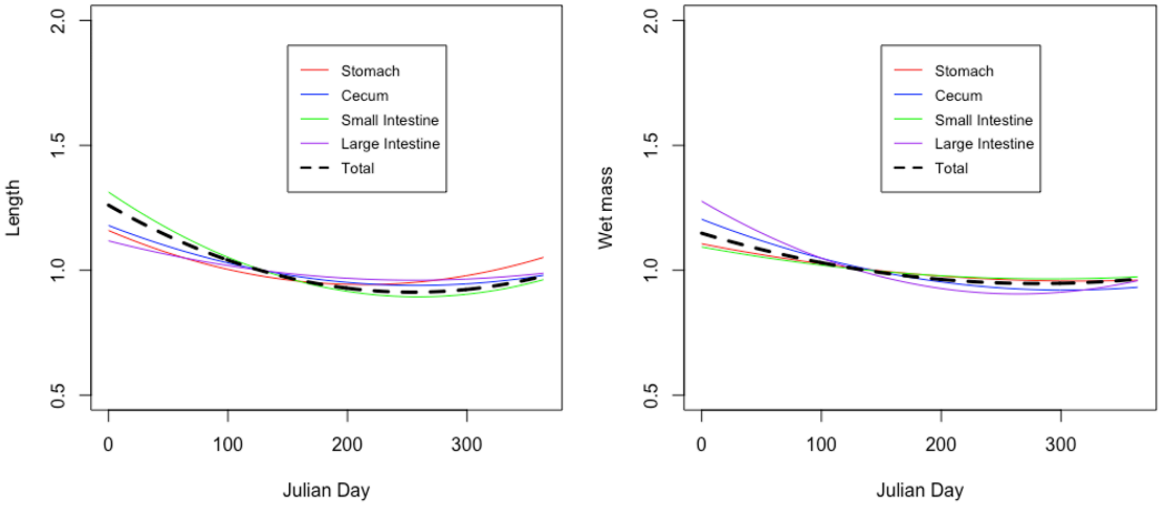
Scaled GI length varied over the course of the year (Figure II.2) such that January mice had the longest GI tracts and lengths decreased into the summer, before rising again in the fall and the beginning of winter. The largest average scaled GI length was in January (6.95), while the lowest average scaled GI length occurred in August (4.53), which is a decrease of approximately 35%. As with length, the largest average scaled GI wet mass occurred in January (0.0128), while the lowest average scaled GI wet mass occurred in August (0.0106), a decrease of approximately 18% (Figure A.1). The scaled dry masses stayed relatively constant throughout the year, with the heaviest average scaled dry mass occurring in June (0.0066) and the lowest average scaled dry mass occurring in September (0.0061), a change of approximately 8% (Figure A.2).

Figure II.2. Boxplots Depicting Monthly Differences in Scaled Gastrointestinal Tract Length



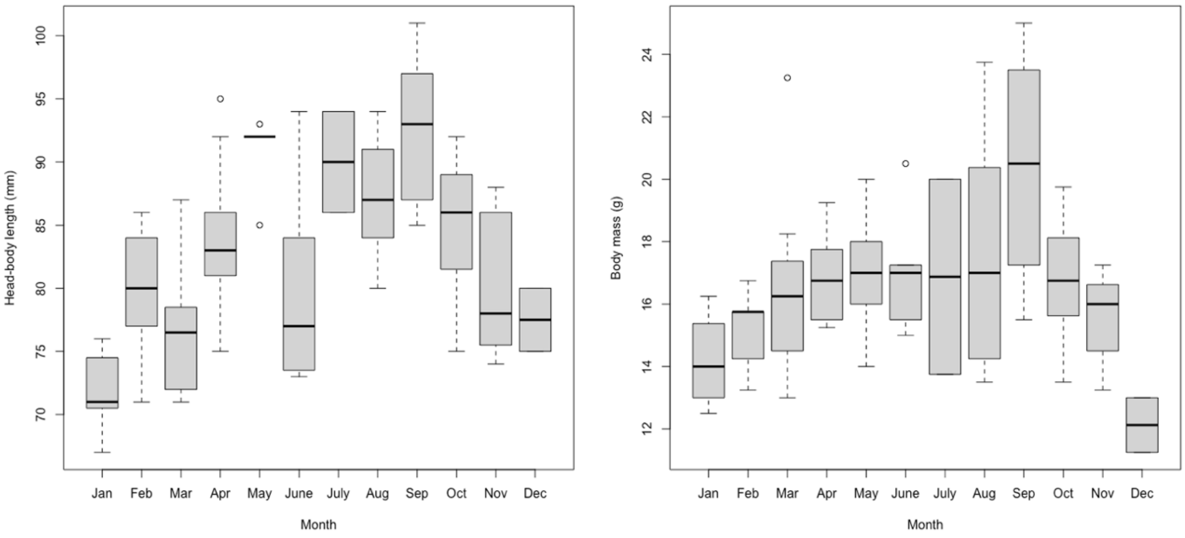
I ran polynomial linear regressions for GI traits on which season had a significant effect on, i.e., scaled length and scaled wet mass. The best fitting model for all traits was the second order polynomial (Table A.1). The small intestine was most variable over the year, as well as the total GI length (Figure II.3). Because the small intestine makes up a majority of the total GI length, changes in the small intestine appear to be driving the changes in the total GI tract. The wet masses of the cecum and the large intestine were the most variable over the year (Figure II.3).

Figure II.3. Top-Ranking Polynomial Regressions of Scaled Length (Left) and Wet Mass (Right) of Gastrointestinal Tract Sections. Separate Regressions Were Evaluated for Each Section (Stomach, Small and Large Intestines, and Cecum) and the Total Scaled Gastrointestinal Length



Finally, there was also a clear annual pattern in body size (head-body lengths and masses) of mice collected for this study. The head-body lengths were lowest in the winter and increased into the summer and fall, before decreasing again in the beginning of winter (Figure II.4). The body masses displayed a similar pattern, with the lowest average body masses occurring in December and January and the largest average body mass occurring in September (Figure II.4). Thus, focusing my analyses on scaled traits was essential in this research.

Figure II.4. Boxplots Depicting Monthly Differences in Body Mass and Head-Body Length of Adult *Peromyscus maniculatus* Used in This Study



DISCUSSION

SEASONAL GASTROINTESTINAL VARIATION AND THE CLIMATIC VARIABILITY HYPOTHESIS

Peromyscus maniculatus has one of the largest ranges of any North American mammal (Kurta 1995) and is suggested to be the most common small mammal in North America (McLean et al. 2019), being both widespread and abundant in many habitats. My sites were located in a highly seasonal, high-elevation part of North Carolina. Temperatures regularly dropped below freezing during the winter sampling sessions with occasional snowpack. However, it is important to note that my results may not be representative of all *P. maniculatus* populations, particularly ones that occur in more seasonal areas, which are exposed to different energetic demands and may also display very different breeding phonologies and levels of investment per reproductive bout (McLean et al. 2019; McLean and Guralnick 2021).

The climatic variability hypothesis (CVH) states that, due to the increase in climatic fluctuation at higher latitudes, individuals living in these areas should exhibit increased phenotypic flexibility (Naya 2008; Naya et al. 2008a; Molina-Montenegro and Naya 2012). This increased phenotypic flexibility should in turn allow phenotypically flexible populations to thrive and become more widely distributed throughout those habitats (Naya et al. 2008a). Naya et al. (2008a) evaluated the CVH as applied to small intestine length in rodents. They found that the length of the small intestine was indeed more plastic at higher latitudes and as the number of habitats occupied by those species increased (Naya et al. 2008a). A 2010 study of field mice in Chile also showed that the plasticity of the GI tract was larger in mice from higher latitudes (Bozinovic et al. 2010). My results are consistent with the expectation that *P. maniculatus* populations in relatively seasonal areas exhibit measurable plasticity in their GI tracts, which should be greater than in populations living at lower latitudes. The monthly average scaled lengths of the GI tracts in the mice I collected had a maximum change of approximately 35%, while the monthly average scaled lengths of the small intestine also showed a maximum change of 35%. Future studies should focus on conducting similar studies on levels of plasticity in the morphology of the GI tracts in wild populations located in less seasonal areas, in order to further test the CVH in this species.

EFFECTS OF SEX AND REPRODUCTIVE ACTIVITY

Reproductive activity was a significant effect on the scaled length and wet mass of the GI tract, as well as lengths and masses of most of the constituent sections, while sex was not. There was also a strong interaction between the two terms. While there was not a significant difference in the length and wet mass of reproductively active and non-reproductive females, reproductively active males had shorter and lighter GI tracts than non-reproductive males. These results were contrary to my hypothesis that reproductive activity results in longer GI tracts due to an increased energetic demand, especially in females. However, most of the reproductively active mice were captured in the spring and summer months (80% for females and 85.72% for males). Therefore, since season itself has a significant impact on GI morphology, it is difficult to tease apart these two factors. It is possible that the lack of a difference between reproductive and non-reproductive females actually does reflect the expected trend of increased GI length and mass in the former; absent the demands of reproduction, spring and summer individuals would be expected to have detectably shorter and lighter GI tracts. Another difficulty in parsing these effects was that only two females classified as reproductively active were lactating. Previous studies found that lactation represents the biggest increase in energetic demand during female reproduction (Cripps and Williams 1975, Speakman 2008), so an increase in the number of lactating females collected may have shown the expected trend.

COMPARING LENGTH VERSUS MASS TRAITS

Total length of the GI tract was more variable than the total wet mass and total dry mass, indicating that the length trait may be a more responsive trait than either of the mass traits to energetic demands encountered by mice in my study region. The wet mass showed a similar trend as the length measurements, reaching a maximum in summer months, although the maximum percent change in the monthly averages was lower (18% for wet mass versus 35% for length). The dry mass did not change significantly throughout the year, only showing a maximum change of 8% between months, suggesting that changes in amount of mucosa or cellular architecture are likely driving the wet mass changes. Further, it is important to note that wet mass of the cecum and the large intestine appeared to have the most dramatic changes, while the wet mass of the stomach and small intestine appeared relatively unchanged throughout the year.

A study on *M. pennsylvanicus* and *P. leucopus* found that the wet and dry masses of the stomach, cecum, and small intestine significantly increased in the winter, although there was no change in length (Derting and Noakes 1995). The increase in the wet mass of the small intestine was mainly attributed to an increase in mucosa (Derting and Noakes 1995), which is heavily involved in the absorption of nutrients (Jankowski et al. 1994; Doherty and Charman 2002). It is possible that there was no significant change in the total dry mass due to the removal of the mucosa during processing. However, contrary to my results, but consistent with the results of Derting and Noakes (1995), a study of wild *P. leucopus* showed that the dry mass of the cecum and the total GI tract dry mass was significantly higher in the winter and spring than in summer and fall.

The finding that lengths of the GI tracts in the *P. maniculatus* in this study were more variable than the wet or dry masses suggests that the length trait may be more indicative of changing diet and/or energetic demands. However, future studies should still continue to focus on both the length and the mass of the GI trait, particularly because my results may not be representative of other populations and species.

PEROMYSCUS MANICULATUS BODY SIZE THROUGHOUT THE YEAR

The clear trend in body size throughout the year suggests that it is essential to utilize a relativized metric of GI morphology. Individuals tended to be heavier in the summer months and lighter in the winter months, and the head-body lengths likewise increased into the summer and fall before decreasing into the winter months. The body size increase over the course of spring and summer could be due to the early-year cohort reaching maturation, given that adult mice continue to grow throughout their life (Myers and Master 1983). The summer increase could additionally be driven by older, overwintered adults being in better condition in the growing season versus the winter. Conversely, the decrease in the average head-body length starting in October may reflect weaning of the fall cohort and their recruitment into the population. It has been shown in the lab that cold exposure causes house mice (*Mus musculus*) to gain weight (Barnett 1965), but scarce resources in the winter months may cause weight loss in wild small mammal populations (Iverson and Turner 1974; Cameron and Spencer 1983; Lima et al. 1997). Maintaining a larger body mass in the colder months results in an increased energetic demand, so weight loss may be an adaptive response in wild small mammals (Iverson and Turner 1974).

Demographic changes occurring naturally throughout a year stand to bias trait-based inferences in wild populations since many traits do not exhibit true isometry with body size. However, the body size changes I observed are not likely to be driving seasonal and sex-specific patterns I found. It has been shown in lab mice that the intestine grows disproportionally faster than the body in young mice, but levels off as the mouse matures (O'Connor 1966). However, this would generate a trend opposite of what I observed and so it is unlikely that demography is driving seasonal patterns in GI length. The arrival of new cohorts throughout the year may have been responsible for some of the month-to-month trends seen in the GI morphology, such as the significant jump from May to June (potentially reflecting recruitment). It has been suggested that the ontogeny of the GI tract is not consistent as an individual grows, and certain organs may grow disproportionally than the rest of the body (Munn et al. 2021), so individual age, population demography, and ontogenetic trajectories of different soft tissues are critical factors to consider when applying similar methods to other species.

CONCLUSION

In this chapter, I showed that the GI tract in a population of *P. maniculatus* in western North Carolina varied significantly with diet quality and energetic demand. I found significant effects of reproduction on the length and wet mass of the GI tract, and these effects were sex-specific. This work provides evidence for the functional role of the GI tract and supports the use of this trait in more widespread community ecological studies. Continuous functional traits in small mammal research are lacking, especially from soft tissues. Thus, the observation that the GI tract responds to changes in energetic demand at the individual level suggests this underutilized soft tissue trait has the potential to be used as an effective continuous functional trait in many additional systems.

CHAPTER III: EVALUATING THE EFFECTIVENESS OF GASTROINTESTINAL MORPHOLOGY AS A CONTINUOUS FUNCTIONAL TRAIT IN APPALACHIAN SMALL MAMMAL COMMUNITIES

INTRODUCTION

SMALL MAMMAL COMMUNITIES IN THE FACE OF GLOBAL CHANGE

The average temperature of the globe has increased by roughly 1°C over the past 125 years and is expected to continue to increase (Root et al. 2003; IPCC 2021). Climate change has had a profound impact on some small mammal populations, such as range shifts (Moritz et al. 2008), species loss (Blois et al. 2010), changing demographics (Ozgul et al. 2010; Hoffman and Sgrò 2011) and the introduction and increased prevalence of vector-borne diseases (Garcia-Solache and Casadevall 2010). Simultaneously, habitat loss and fragmentation constantly change the spatial context within which mammals must survive, grow, and reproduce (Crooks et al. 2017). Both sets of changes require improved understanding of the ecological processes by which communities are assembled, and the phenotypic traits by which individuals maximize their fitness within explicit environmental and community contexts.

Small mammal communities are often structured by competition for food resources, and therefore many mammals possess morphological or behavioral traits that allow them to exploit the food resources available in a given area. Herbivorous small mammals existing in syntopy commonly partition resources by using different types of habitats and feeding on different plant species, or different parts of the same plant species (Bodmer 1990). In North American deserts, small mammal community composition is biased towards granivores, which tend to make up a majority of small mammal species (Brown 1973; Brown and Lieberman 1973; Brown et al.

1979; Morton 1979; Heske et al. 1994; Kelt et al. 1996) given that seeds are often plentiful in desert ecosystems. Indeed, the diversity of granivorous small mammals in western North America is closely correlated with annual precipitation, which can be used to predict seed abundance (Brown 1973). However, even among these granivores, successful coexistence is mediated by variation in morphological or behavioral traits that facilitate feeding on seeds of different sizes, or, foraging in separate areas (Brown and Lieberman 1973; Jezkova et al. 2011).

CURRENT RESEARCH ON MAMMALIAN DIETARY ECOLOGY

Because small mammals can be secretive and difficult to monitor with respect to dietary preferences and behavior, mammalian dietary ecology studies typically rely on qualitative (e.g., diet guilds) or, more rarely, quantitative and continuous (e.g., percent composition animal/plant matter in the diet, morphological proportions of the feeding apparatus) traits as proxies for dietary preference. Among the latter, craniodental traits such as measurements of the cranium, mandible and toothrow, and relative size of attachment sites for chewing musculature are common and can accurately predict the diet of many rodents and other species (Verde Arregoitia et al. 2017; Kohli and Rowe 2019; Samuels 2009; Martin et al. 2016). Tooth size and shape are also especially important for predicting diet because these traits directly relate to mastication (Ungar 2014). Carnivores tend to have large canines and sharp carnassials which aid in slicing meat (Meiri et al. 2005), herbivorous mammals tend to have flat occlusal surfaces of the teeth for grinding fibrous plant material, and omnivores tend to have large canines but flattened molars. One study demonstrated that a combination of 30 different cranial and dental morphometrics can be used to classify rodents as carnivores, herbivores, omnivores, or insectivores; this study was 98.11% accurate at classifying 318 individual animals into their respective dietary guilds (Samuels 2009). More recently, a set of eight linear measurements was shown to predict diet in small mammals of the Great Basin, USA, with 75% of 32 species being classifiable (Kohli and Rowe 2019).

Unfortunately, craniodental measurements are rarely perfectly representative of diet and can thus result in misclassification into dietary guilds (Kohli and Rowe 2019). This is primarily because some species accomplish different feeding behaviors with the same skull or tooth shapes, especially dietary generalists which make a living by their ability to acquire and process resources opportunistically. In addition, craniodental proportions may be structurally constrained on ecological timescales. Both factors mean that craniodental proportions may not reflect the actual diets of species, or reflect short-term dietary shifts that are potentially important for structuring mammal communities. For example, a study on African grazers found that although craniodental anatomy differed significantly among bovid species, differences in the stable carbon composition within the grazing species were not significantly correlated with craniodental anatomy (Codron et al. 2008). This indicated that although obligate grazers and facultative browsers do have measurable differences in craniodental anatomy, these differences did not reflect the large variation that was seen in their diets (Codron et al. 2008).

GASTROINTESTINAL MORPHOLOGY AMONG SMALL MAMMAL SPECIES

Given its intimate relationship to individual diet, the gastrointestinal (hereafter, GI) tract has the potential to be used as a continuous functional trait in mammalian ecological research (Naya et al. 2008b). It is well known that mammalian carnivores tend to have relatively unspecialized GI tracts, a result of their high-quality diets, while GI tracts of herbivores are typically more complex and often contain special structures or chambers that aid in processing low-quality diets with high fiber content. Even among small mammals, differences in GI tract morphology exist among dietary guilds, with small herbivores (e.g., voles, lemmings, rabbits) having longer and more complex GI tracts relative to their body sizes than small omnivores and granivores (e.g., mice, rats, squirrels; Schieck and Millar 1985), including relatively larger large intestines and ceca (Schieck and Millar 1985). As with larger mammals, these differences aid in breaking down plant material and processing high fiber diets (Schieck and Millar 1985). Another study focused on six rodent species (one strict herbivore, four omnivores, and one granivore) found that the strict herbivore had the longest large intestine and cecum when compared to the other species (Wang et al. 2003). However, GI measurements for any species are hard to capture *in situ* and thus require measurements on freshly euthanized specimens. These traits are also difficult to obtain from museum specimens since a majority are stored as skins and skeletons (Quay 1974; Greiman et al. 2018; Kohli and Rowe 2019). Even for specimens that are fluid-preserved, fixatives often cause tissue shrinkage and render the measurements of many soft tissues inaccurate (Kingston 2018). The result is a significant knowledge gap about GI morphology across mammalian species diversity.

The purpose of this chapter was to a) quantify gastrointestinal and craniodental morphology in small mammal species of the Appalachian Mountains of eastern North America; b) compare utility of these two trait types in accurately predicting dietary guild; and c) assess how each trait type relates to small mammal community assembly across a major latitudinal and environmental gradient. My community-level approach seeks to provide answers on the utility of GI traits in contributing to small mammal community assembly and to provide critical baseline information about how environmental change (including climate change and habitat fragmentation) may impact small mammal communities in this ecosystem in the future.

METHODS

COMPILING APPALACHIAN SMALL MAMMAL COMMUNITY DATASETS

The Appalachian Mountains cordillera spans 13 states and is an area of elevated mammal diversity, including a mixture of high and low elevation species, making it an ideal place to examine community assembly processes. To compile small mammal community datasets from across the region, I conducted a literature search for any small mammal census effort performed at sites in and around states spanned by the Appalachians. I also accessed small mammal trapping data generated by the National Ecological Observatory Network (NEON, https://www.neonscience.org/) and Long Term Ecological Research Networks (LTER). Community datasets from NEON sites were compiled by downloading latest and provisional releases for small mammal trapping data from the NEON data portal (*https://www.neonscience.org/data*; accessed 7 February 2022) for all sites falling within the region of interest. I used custom R scripts to parse NEON trapping records, harvest information on captured individuals and identities, identify unique individuals (from ear tag IDs), and write records to a community (site-by-species) matrix that represented either a) total captures, or b) total individuals. Scripts for harvesting NEON small mammal community data from these raw data products are available via GitHub (*https://github.com/bryansmclean/traits-v-space*).

My spatial and elevational thresholds for further inclusion of community datasets were intentionally broad so that sites spanned a large enough environmental gradient to explore community differences; the sites I compiled that were furthest from the main Appalachians cordillera were in Indiana, others were along the foothills of the Appalachians in several states, but several were at higher elevations of the core Appalachians. My methodological thresholds for dataset inclusion were that they were resulted from a) a minimum of 2,000 trap nights, with a minimum of two separate types of traps used (e.g., Sherman live traps and pitfall traps) or, alternatively, b) a minimum of 10,000 trap nights with use of a single trap type. These thresholds helped ensure that entire small mammal communities were well-sampled. For two sites (LTER2 and LTER3), the number of trap nights was not available, but these were included because LTER2 used a previously published species list (dating back to 1758) and trapping effort at LTER3 spanned 20 years (1979-1999); in each case I was confident that sufficient effort was given to sampling the entire small mammal community.

Finally, for every community dataset, I compiled a comprehensive list of small (defined as less than 300 grams) mammal species and concatenated these into a combined presence-absence matrix. I also recorded species abundances whenever possible, and used them to calculate proportional representations of species in each community. For two NEON sites (BART and HARV), identifications for some *Peromyscus* mice were ambiguous (e.g., individuals listed as "*Peromyscus leucopus/ maniculatus*"); in these cases, I assigned uncertain individuals to species according to the proportion of known *P. leucopus* and *P. maniculatus* at each site. The number of *Peromyscus* individuals without firm identifications was relatively low and ranged from 9%, to 17% of all *Peromyscus* individuals.

COMMUNITY COMPOSITION

To visualize community differences across the broad environmental gradient represented by sites, I performed non-metric multi-dimensional scaling (NMDS) analysis. Prior to this analysis, I dropped species that made up less than 0.1% of the total number of individuals (for sites where abundances were available) to avoid bias from species that are rare (or, rarely captured) across communities. To visualize potential latitudinal differences among communities, I also assigned sites to three latitudinal bins; high (44.14- 41.12 degrees), medium (41.11 – 38.084 degrees), or low (38.083- 35.05 degrees).

GASTROINTESTINAL TRAIT MEASUREMENTS

I obtained fresh or freshly-frozen GI tracts from each species in my combined community dataset from my own targeted field work in North Carolina, or from ongoing projects of museum curators (Virginia Museum of Natural History) and other mammal biologists (State University of New York College of Environmental Science and Forestry, Miami University of Ohio). I also obtained a large number of GI tracts from the NEON Biorepository (*https://biorepo.neonscience.org/*) from individuals that were primarily incidental capture mortalities at NEON sampling sites. I limited measurements to adult individuals; all specimens were aged based on external morphological features. Wherever possible, I also selected specimens for measurement from within my region of interest, but several individuals were measured from states outside the focal region. I also minimized the number of reproductively active specimens measured, particularly reproductive females. Frozen GI tracts were processed by thawing and separating into four constituent sections; stomach, cecum, small intestine, and large intestine. For species without a cecum (here, shrews and moles), I separated the tract into two sections, stomach and intestine, since it was not possible to further differentiate between the small and large intestine based on gross morphology. Each section was cleared of any fat and connective tissue and placed into a petri dish with a small amount of physiological saline (to prevent desiccation), and three measurements were taken: length, wet mass, and dry mass. Lengths were obtained by gently extending each section and measuring to the nearest millimeter using a flexible measuring tape. For curved sections (i.e., stomach and cecum), the length of the outer curve was used as the length measurement. Wet mass was obtained by first emptying each section by cutting the organ open lengthwise and rinsing with physiological saline. A microscope slide was then used to gently scrape out any remaining contents, and each section was blotted to remove excess fluid and weighed to the nearest milligram using a Torbal AGZN120 Analytical Balance. Any stomach contents, cecal contents, and fecal pellets were collected and frozen. Dry mass for GI sections was obtained by first drying at 57º Celsius to a constant mass (approximately 24 hours for all sections) and weighing to the nearest milligram. Dried small intestines from mammal specimens housed at UNC Greensboro were archived with each voucher specimen. Finally, I also obtained five standard external measurements for each mammal specimen (total, tail, hindfoot, and ear lengths; mass).

For each species, I calculated mean length, wet mass, and dry mass for each GI tract section (Table III.2). In addition, I scaled GI tract measurements by metrics of body mass to obtain relativized measures of GI tract proportions. GI section lengths were scaled by individual head-body lengths (i.e., total length minus the tail length) and GI masses were scaled by first transforming using a cube root and then scaling by the head-body length of an individual (thus ensuring that the scalar was of the same dimensionality as the GI measurement).

Although I generated substantial new GI trait data for most species in the combined dataset, 10 species were not available for measurement. For those species, I imputed total GI length data using PhyloPars (*https://www.ibi.vu.nl/programs/phylopars/*). I first created a phylogeny of all species in my dataset by pruning a phylogenetic tree created by Upham et al. (2019) to contain only the focal species. I then created a feature matrix of all sampled small mammal species that included species averages for GI tract lengths and head-body lengths, which allowed me to model the evolutionary allometry between GI length and body size as part of the imputation process. The average head-body length of specimens was used, except for the few species from which GI measurements came from other published sources; for the latter I used the average head-body length published in the PanTHERIA database (Jones et al. 2009). PanTHERIA did not contain the head-body length for the Allegheny woodrat (*Neotoma magister*), so I used the average of female and male head-body lengths listed by Castleberry et al. (2006). The imputed total GI lengths were scaled by the head-body length from the feature matrix prior to subsequent analysis.

CRANIODENTAL TRAIT MEASUREMENTS

I generated new craniodental measurements for species in my dataset by measuring specimens in museum collections. I measured five adult skulls for each of 31 species (with the exception of *Glaucomys sabrinus,* for which only two specimens were measured). For each skull, electronic calipers (Mitutoyo, Kanagawa, Japan) accurate to a hundredth of a millimeter were used to take eight individual measurements of the skull, mandible, and teeth under a dissection scope (upper incisor width and depth, lower incisor width, upper cheek teeth row length and width, rostrum length and width, and jaw level length). These linear measurements were previously shown by Kohli and Rowe (2019) to predict a species diet and are described fully in that study. The craniodental measurements were obtained from skulls provided by two natural history collections; the North Carolina Museum of Natural Sciences and the University of Michigan Museum of Zoology. I did not measure skulls for three additional species that were rare in my dataset (*Oryzomys palustris, Peromyscus gossypinus*, and *Rattus rattus*); instead, I imputed all eight traits using the same procedure as above for GI length, including head-body length in the feature matrix. I did not scale any craniodental measurements by body size because the eight measurements are functionally defined and unlikely to exhibit strong allometry.

COMPARING GASTROINTESTINAL MORPHOLOGY AMONG DIETARY GUILDS

Prior to assessing classification accuracy into dietary guilds based on either trait type, I visualized trait distributions by plotting allometries of total GI length and some GI sections. I performed this exploration step because my study contains many species for which GI measurements have never been reported.

Finally, Schiek and Millar (1985) previously suggested that total GI length was a poorer predictor of diet than some constituent sections, especially the small and large intestines. I therefore also compared individual GI sections among dietary guilds by re-plotting allometries for each section (stomach, cecum, small intestine, and large intestine) after dropping species lacking a cecum.

COMPARING THE EFFECTIVENESS OF GASTROINTESTINAL AND CRANIODENTAL TRAITS

Each small mammal species was assigned to a dietary guild as specified in the MammalDIET dataset created by Kissling et al. (2014). I used linear discriminant analyses (LDA) with jackknife cross validation in R v4.0.2 on both final trait sets (scaled GI measurements and raw craniodental measurements) to test whether there were differences in dietary classification accuracy. I first ran an LDA on all eight craniodental traits from 31 measured species and compared this to an LDA of nine GI traits from 24 measured species. The nine GI traits were lengths, wet masses, and dry masses of three sections (stomach, cecum, and intestine). I did not differentiate between the small and large intestine for species without a cecum, and for species with a cecum, the intestine was defined as the small intestine plus the large intestine. For species lacking ceca, the length, wet mass, and dry mass of the cecum was included as 0. Three dietary guilds (carnivore, omnivore, and herbivore) were represented in each ordination above. To achieve a more direct comparison between the trait types, I also down sampled the craniodental data matrix to the same 24 species contained in the GI matrix used here.

The above comparisons provide a taxonomically broad assessment of trait performance in dietary classification, but they omit some GI traits (specifically, length and masses of the cecum) that cannot be measured on many carnivorous small mammals lacking a cecum (shrews and moles). Therefore, to achieve a more detailed assessment of classification accuracy based on all GI traits, I performed additional LDAs limited to herbivore and omnivore dietary guilds (dropping all carnivores, as well as the omnivorous Eastern mole, *Scalopus aquaticus*, which lacks a cecum). This ordination contained 16 species with a full matrix of 12 GI traits. I compared classification accuracy to another craniodental LDA based on all eight craniodental traits, but down sampled to these same 16 species.

ENVIRONMENTAL REGRESSIONS

To explore the potential functional relationship between GI and craniodental traits and the environment, and how these traits may structure small mammal communities, I performed regressions of community trait indices on climate variables that are likely to correlate with the timing and magnitude of primary and secondary productivity. I obtained paired climate data for each site from the WorldClim 2.1 database (Fick and Hijmans 2017). Specifically, I downloaded all available bioclimatic variables at five arc-minute spatial resolution and used tools in QGIS 3.10 to extract long-term Annual Mean Temperature (MAT), Temperature Seasonality (standard deviation x 100) (TS), Annual Precipitation (MAP), and Precipitation Seasonality (coefficient of variation) (PS) values for each community using coordinates given in original data sources.

Finally, I also performed similar regressions using the latitude of each site as the dependent variable.

I performed two types of trait x environment regressions: those employing the community mean trait value and those that also incorporated species abundances in the form of community weighted means. For GI-based regressions, I used the scaled GI tract length for all species in each community. For craniodental-based regressions, I used scores on linear discriminant axes one and two from the classification LDAs above (based on all eight craniodental traits); I did this because no single craniodental trait alone is expected to be indicative of diet. I used the “weighted.mean” function in R in order to create a community weighted mean for each trait type. Regressions using community means (i.e., based on the presence-absence data) included all 21 sites, while regressions using community weighted means were only possible for 14 sites. I ran regressions of latitude and TS for the community mean and community weighted means of the craniodental LDA scores. All regressions were performed using the lm() function in R.

RESULTS

SCOPE OF THE SMALL MAMMAL COMMUNITIES

A total of 21 small mammal communities across eastern North America were included in my analysis, spanning 10 different states (Figure III.1; Table III.1). A total of 34 small mammal species were present across these combined communities (Figure III.2).

Figure III.1. Map of Northeastern North America Showing Locations of 21 Small Mammal Communities Analyzed in This Study

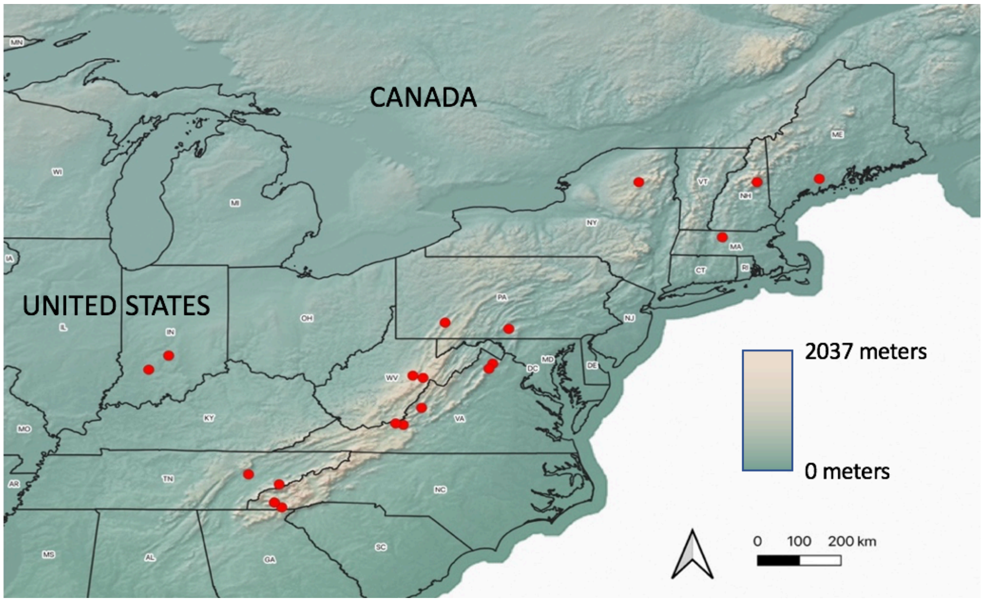
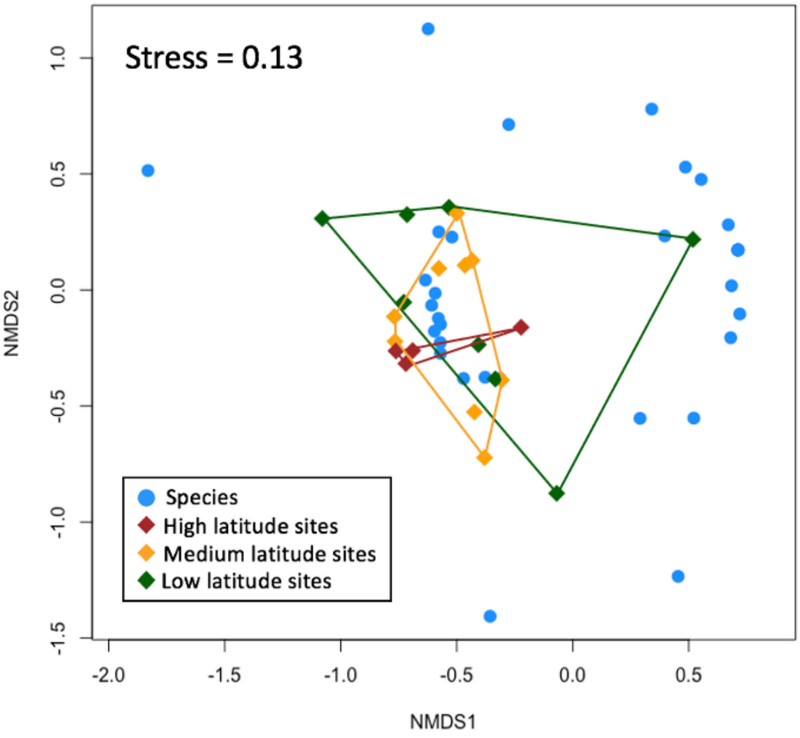


Table III.1. Characteristics of 21 Small Mammal Datasets Utilized for This Study, Including Details of Location, Trapping Effort, and Data Attribution

Site	State	Coordinates	Trap nights	Reference
LTER1	New York	44.0618, -74.3073	16,000	Demers, 2018
LTER2	North Carolina	35.0516, -79.2601	Unknown	Coweeta LTER, 2016
LTER3	Pennsylvania	40.1707, -79.2601	Unknown	Merritt, 2019
VIRG1	Virginia	37.8086, -79.8611	31,464	Mitchell et al., 1997
NC1	North Carolina	35.1855, -83.6241	23,336	Ford et al., 1999
VIRG2	Virginia	37.3371, -80.3256	18,144	Francl and Small, 2013
WV1	West Virginia	38.6405, -79.8245	24,693	Francl and Castleberry, 2004
WV2	West Virginia	38.7016, -80.0838	13,696	Kaminski et al., 2007
NC2	North Carolina	35.1855, -83.6241	13,838	Ford et al., 2000
PENN1	Pennsylvania	39.9965, -77.6319	2,443	Stewart et al., 2008
HOLT	Maine	44.1540, -69.6959	114,457	Wood et al., 2016
ILL1	Illinois	39.2558, -86.3248	27,972	Kellner et al., 2013
ILL2	Illinois	39.2558, -86.3248	23,205	Nelson et al., 2019

ILL3	Illinois	38.8667, -86.8333	6,781	Urban and Swihart, 2011
BART	New Hampshire	44.0639, -71.2874	36,652	NEON, 2022
BLAN	Virginia	39.0337, -78.0418	27,521	NEON, 2022
GRSM	Tennessee	35.6890, -83.5020	29,565	NEON, 2022
HARV	Massachusetts	42.5369, -72.1727	66,375	NEON, 2022
MLBS	Virginia	37.3783, -80.5248	19,901	NEON, 2022
ORNL	Tennessee	35.9641, -84.2826	57,611	NEON, 2022
SCBI	Virginia	38.8929, -78.1394	57,020	NEON, 2022

Figure III.2. Nonmetric Multidimensional Scaling Plots of 21 Small Mammal Communities Used in This Study and Their Species. The Sites are Color Coded by Latitude Bin, With High Latitude Sites Red, Medium Latitude Sites Orange, and Low Latitude Sites Green



RESULTING DATASET OF GASTROINTESTINAL TRAITS

Out of 34 small mammal species in the combined community dataset, I obtained GI tract measurements for 24 of them (70.59%). Numbers of GI tracts measured per species ranged from one (*Cryptotis parva*, *Neotoma floridana*, *Ochrotomys nuttalli*, *Rattus norvegicus*, *Scalopus aquaticus*) to 101 (*P. maniculatus*), with a median of 4.5 GI tracts per species. For species possessing a cecum, 12 GI traits were consistently obtained (length, wet mass, dry mass of four sections; Table III.2), while six GI traits were obtained for those lacking a cecum (length, wet mass, dry mass of two sections; Table III.2). I successfully imputed total GI tract length for the 10 species for which no GI tracts were available.

Table III.2. Means and Sample Sizes for Raw Gastrointestinal Measurements Taken on 24 Species in This Study. Three Measurements ("L", Length; "WM", Wet Mass; "DM", Dry Mass) are Listed for Each Section (Stomach, Cecum, Small and Large Intestines). Species That Do Not Possess a Cecum are Marked by an Asterisk, and for Those Species the Total Combined Measurements for Small and Large Intestines are Listed in the Small Intestine Field

Species	Stomach			Cecum		
	L	WM	DM	L	WM	DM
BLBR*	26.154	0.100	0.022	-	-	-
COCR*	57.333	0.343	0.058	-	-	-
CRPA*	15.000	0.027	0.006	-	-	-
GLSA	87.333	1.023	0.229	85.500	0.800	0.138
GLVO	43.000	0.561	0.090	63.600	0.441	0.058
MIPE	37.500	0.342	0.080	124.071	0.430	0.069
MIPI	43.5	0.257	0.062	75.75	0.197	0.033
MUMU	25.000	0.076	0.020	24.500	0.029	0.006
MYGA	42.077	0.245	0.054	78.231	0.323	0.051
NAIN	35.636	0.158	0.036	47.400	0.063	0.011
NEFL	98.000	2.978	0.720	145.000	2.208	0.353
OCNU	27.000	0.246	0.046	48.000	0.139	0.023
PELE	39.486	0.296	0.061	44.417	0.126	0.019
PEMA	32.830	0.267	0.057	39.290	0.121	0.018
RANO	68.000	1.493	0.322	70.000	0.595	0.096
SCAQ*	57.000	0.829	0.163	-	-	-

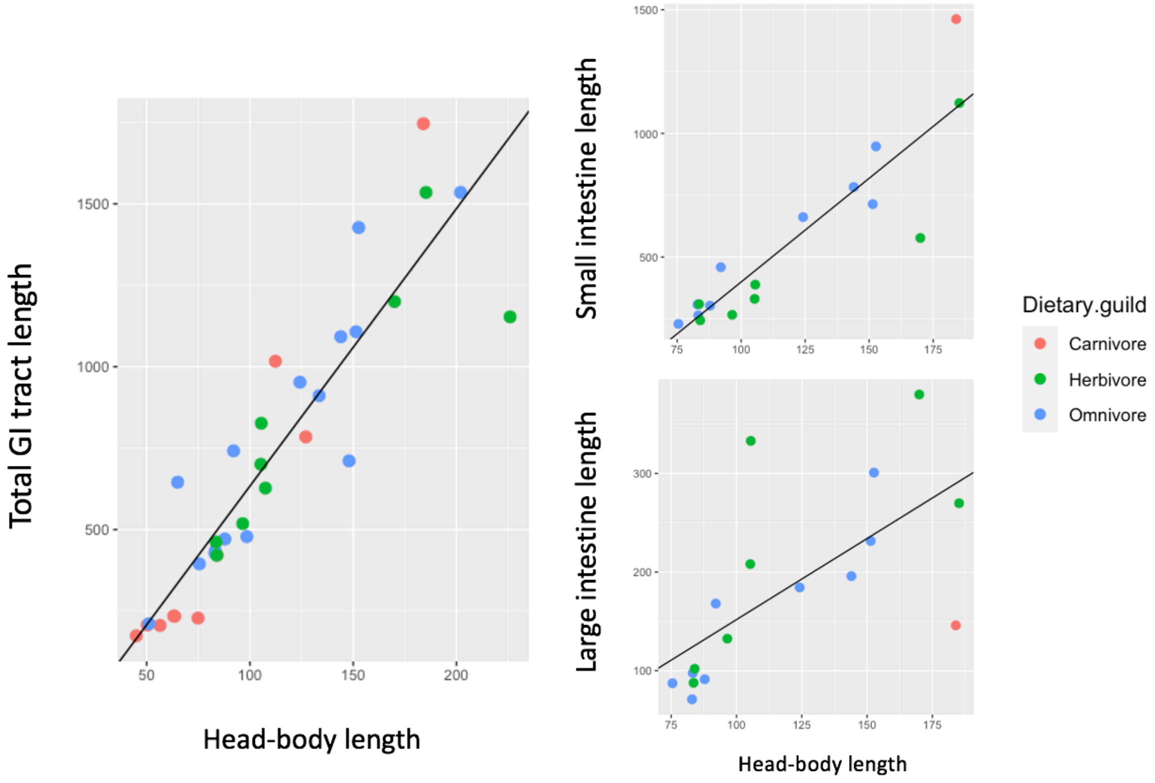
SIHI	62.600	0.873	0.172	99.000	0.766	0.129
SOCI*	15.000	0.038	0.006	-	-	-
SOFU*	18.778	0.058	0.012	-	-	-
SOHO*	15.250	0.025	0.004	-	-	-
SYCO	31.000	0.206	0.040	79.000	0.172	0.028
TAHU	60.750	1.124	0.230	81.750	0.631	0.127
TAST	45.154	0.518	0.105	68.077	0.305	0.049
ZAHU	36.000	0.010	0.023	33.333	0.053	0.010

Species	Small intestine			Large intestine			Sample size
	L	WM	DM	L	WM	DM	
BLBR*	395.654	0.442	0.071	-	-	-	26
COCR*	959.333	0.943	0.032	-	-	-	3
CRPA*	159.000	0.099	0.017	-	-	-	1
GLSA	947.500	1.764	0.316	300.833	0.848	0.153	6
GLVO	661.400	1.126	0.161	184.400	0.307	0.054	5
MIPE	330.857	0.818	0.150	208.071	0.335	0.059	14
MIPI	266.5	0.392	0.058	132.5	0.150	0.024	4
MUMU	308.000	0.384	0.095	71.000	0.064	0.012	3
MYGA	458.750	0.580	0.100	168.077	0.182	0.032	13
NAIN	263.818	0.372	0.072	97.636	0.098	0.018	11
NEFL	577.000	1.704	0.313	380.000	1.104	0.269	1
OCNU	244.000	0.365	0.066	102.000	0.077	0.014	1
PELE	303.514	0.284	0.049	91.333	0.102	0.017	37
PEMA	309.740	0.352	0.062	87.657	0.108	0.018	101
RANO	1462.000	5.152	1.106	146.000	0.709	0.140	1
SCAQ*	654.000	1.027	0.173	-	-	-	1
SIHI	714.000	1.711	0.314	231.600	0.597	0.108	5
SOCI*	187.946	0.148	0.023	-	-	-	37
SOFU*	215.111	0.211	0.035	-	-	-	9
SOHO*	191.750	0.189	0.033	-	-	-	4
SYCO	388.500	0.590	0.119	333.000	0.416	0.080	2
TAHU	1122.750	3.282	0.642	269.750	0.858	0.190	4
TAST	782.923	1.741	0.310	195.923	0.402	0.092	13
ZAHU	229.750	0.423	0.089	87.250	0.097	0.020	4

GASTROINTESTINAL MORPHOLOGY AMONG DIETARY GUILDS

The plot of average total GI tract lengths versus the average head-body length of 24 species did not show any dietary guild-specific patterns (Figure III.3; left). However, stronger patters were present when examining just the 17 species possessing a cecum. In the small intestine allometry, the only carnivore, 28.57% of the herbivores, and 88.89% of the omnivores fell on or above the line (Figure III.2; top right); this confirms that carnivores and a majority of omnivores have relatively longer small intestines than the herbivores. In the large intestine allometry, 42.86% of herbivores and 22.22% of omnivores fell on or above the line, while the only carnivore fell below the line (Figure III.3; bottom right). This indicates the opposite effect; specifically, that the herbivores tend to have relatively longer large intestines than omnivores and carnivores. An allometry of cecum length showed a similar pattern as the large intestine but weaker, with 57.14% of herbivores and 33.33% of omnivores falling on or above the line, and the only carnivore falling below the line (figure not shown).

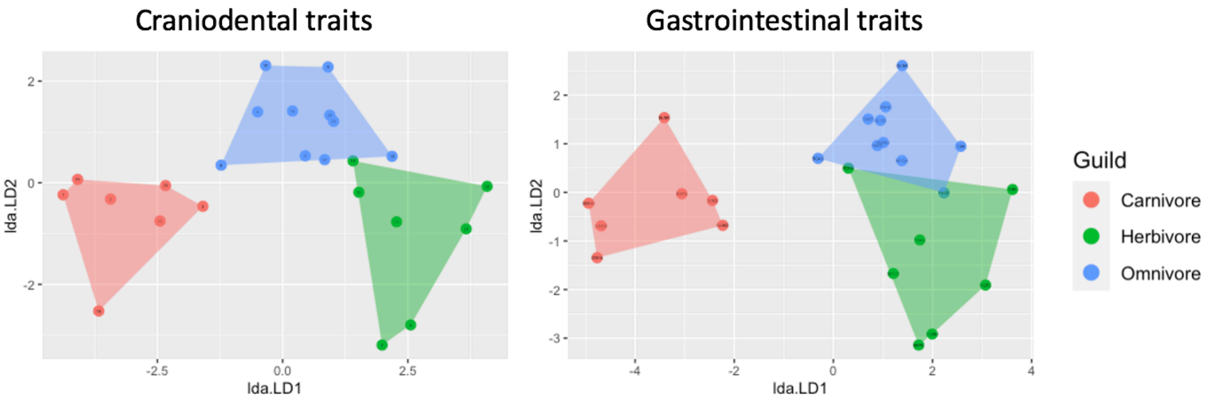
Figure III.3. Allometries of Total Gastrointestinal Tracts from 24 Small Mammal Species Representing Three Dietary Guilds (Left). Also Presented are Allometries of Small Intestine Lengths (Top Right) and Large Intestine Lengths (Bottom Right).



COMPARISON OF GASTROINTESTINAL AND CRANIODENTAL TRAITS

The craniodental LDA containing all 31 species had a 70.97% accuracy in predicting dietary guild. The omnivores were most accurately classified (75%), followed by the carnivores (70%) and herbivores (66.67%). Similarly, the GI LDA containing all 24 species (but only nine GI traits) was 70.83% accurate at predicting dietary guilds (Figure III.4). The carnivores were most accurately classified (85.71%), followed by omnivores (70%) and herbivores (54.14%; Table III.3). To achieve a more direct comparison, I performed a reduced craniodental LDA of the same 24 species for which GI traits existed and found 66.67% accuracy in predicting dietary guild (Figure III.4). The omnivores were most accurately classified at 90%, followed by carnivores (71.43%) and herbivores (28.57%, Table III.3).

Figure III.4. Linear Discriminant Analysis of 24 Small Mammal Species from Three Dietary Guilds Based on Craniodental (N = 8) and Gastrointestinal (N = 9) Traits



The classifications above do not make use of all GI traits measured, since some species do not possess a cecum and I did not differentiate the small and large intestine in shrews and moles. After removing these species, the same classification routine leveraged all 12 GI traits instead of only nine and was 87.5% accurate at predicting whether a species was an herbivore or an omnivore (16 species total; Figure III.5). The omnivores were most accurately classified at 88.89%, while the herbivores were 85.71% accurately predicted (Table III.3). However, a reduced craniodental LDA of these same 16 non-carnivorous species was less successful at predicting dietary guild (81.25%), with herbivores being most accurate at 85.71% and omnivores 77.78% accurate (Figure III.5; Table III.3).

Figure III.5. Linear Discriminant Analysis of 16 Small Mammal Species from Two Non-Carnivore Dietary Guilds Based on Craniodental (N = 8) and Gastrointestinal (N = 12) Traits

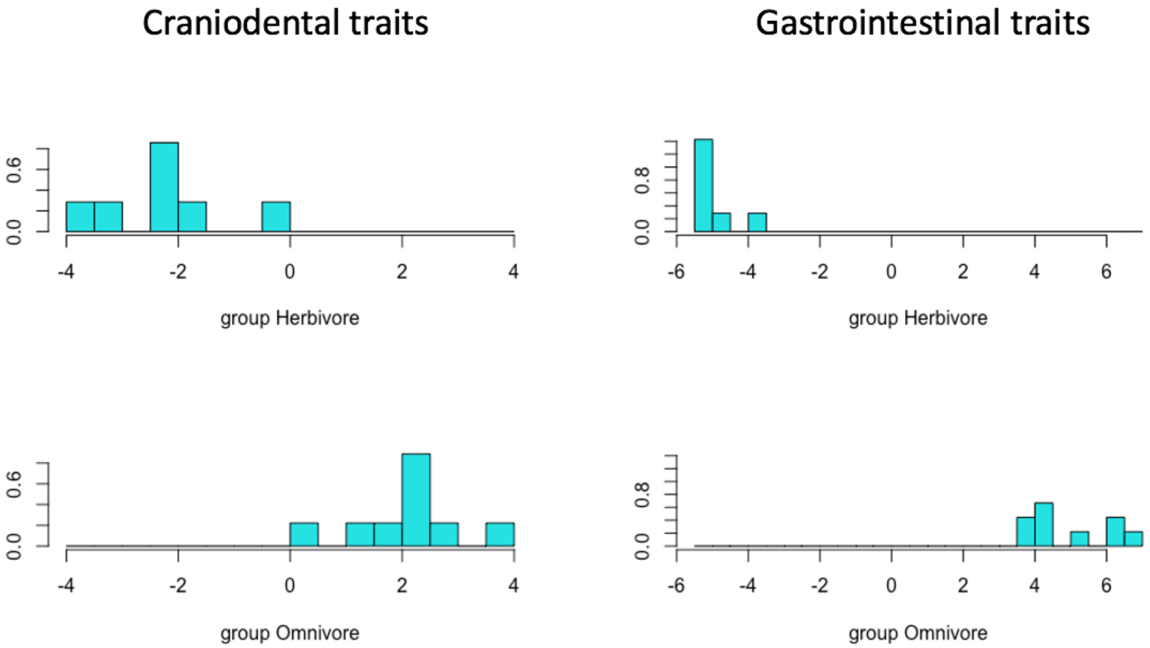


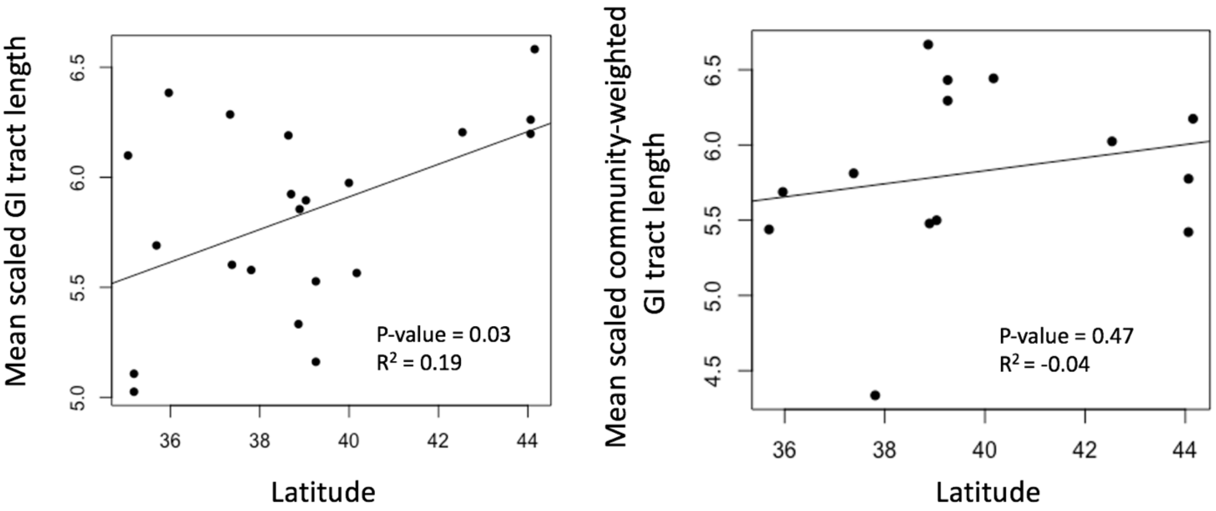
Table III.3. Classification Accuracy for Small Mammal Species to Dietary Guilds Using Gastrointestinal and Craniodental Traits. Numbers in Parentheses Represent the Total Accurate Classifications and Total Species Per Analysis.

LDA	Carnivore	Herbivore	Omnivore
Gastrointestinal LDA (3 guilds, 24 species)	85.71% (6/7)	57.14% (4/7)	70% (7/10)
Craniodental LDA (3 guilds, 24 species)	71.43% (5/7)	28.57% (2/7)	90% (9/10)
Gastrointestinal LDA (2 guilds, 16 species)	-	85.71% (6/7)	88.88% (8/9)
Craniodental LDA (2 guilds, 16 species)	-	85.71% (6/7)	77.78% (7/9)

RESULTS OF ENVIRONMETAL REGRESSIONS

The regression of the community mean GI lengths against latitude was positive and significant (P = 0.03), indicating that communities at higher latitudes have longer relative mean GI tract lengths than those at lower latitudes (Figure III.6, Table III.4). The same regression based on community weighted means was not significant (P = 0.47).

Figure III.6. Regressions of Community Mean (Left) and Community-Weighted Mean (Right) Scaled Total Gastrointestinal Tract Length Versus Latitude



The regression of the community scaled total GI tract length against TS for all 21 sites was not significant (P = 0.14; Figure B.1, Table III.4). The regressions of community scaled total GI length against MAT and PS were each weakly significant (P = 0.08; Figure B.1, Table III.4), but the same regression against MAP was not significant (P = 0.19; Figure B.2, Table III.4).

Considering community-weighted mean trait values, a regression of scaled total GI tract length against TS of 14 sites was not significant (P = 0.14; Figure B.1, Table III.4). Neither the regression of the community-weighted scaled total GI tract length against MAT (P = 0.80) or PS (P = 0.14) was significant (Figure B.2, Table III.4). The regression of the community-weighted scaled total GI tract length against MAP was likewise not significant (P = 0.68; Figure B.2, Table III.4).

Finally, none of the complimentary regressions using craniodental traits showed any patterns. The regressions of the community mean and community-weighted mean scores from linear discriminant axis one of the LDA containing eight craniodental measurements of all 34 species against latitude, TS, MAT, PS, and MAP were not significant (Table B.1). Likewise, the regressions of the community mean and community weighted mean scores from linear discriminant axis two of the LDA containing eight craniodental measurements of all 34 species against latitude, TS, MAT, PS, and MAP were not significant (Table B.1).

Table III.4. Summary of Separate Linear Regressions Relating Community Measures of Gastrointestinal Length to Environmental Variables and Latitude

Regression	Slope estimate	R^2	P-value
Community mean			
Latitude	0.07	0.19	0.03
Temperature seasonality	0.00	0.07	0.14
Annual mean temperature	-0.07	0.11	0.08
Precipitation seasonality	-0.05	0.11	0.08
Annual mean precipitation	0.00	0.04	0.19
Community-weighted mean			
Latitude	0.04	-0.04	0.47
Temperature seasonality	0.00	0.11	0.14
Annual mean temperature	-0.02	-0.08	0.80
Precipitation seasonality	0.07	0.11	0.14
Annual mean precipitation	0.00	-0.07	0.68

DISCUSSION

Developing an improved understanding of the ecological processes by which communities are assembled, and the phenotypic traits by which individuals maximize their fitness in these contexts, is critical for advancing ecological knowledge and achieving biodiversity conservation. Small mammal communities around the world have been studied intensively with respect to dietary resource partitioning, but the ways in which researchers capture these partitioning schemes are typically limited to coarse categorical descriptors. The morphology of the GI tract has the potential to be used as a continuous functional trait in mammalian ecology (Naya et al. 2008b), but it is underutilized in part because GI measurements are hard to capture *in situ* (thus requiring freshly euthanized specimens) and can rarely be obtained from specimens that are fluid-preserved due to tissue shrinkage in fixatives. The purpose of this chapter was to a) quantify gastrointestinal and craniodental morphology in small mammals of the Appalachian Mountains of eastern North America; b) compare utility of these two trait types in accurately predicting dietary guild; and c) assess how each trait type may relate to small mammal community assembly across a major latitudinal and environmental gradient.

DIFFERENCES IN GASTROINTESTINAL MORPHOLOGY AMONG DIETARY GUILDS

The gastrointestinal tract is a structure that plays a central role in energy acquisition and individual health, and its morphology in mammals varies with the type and quality of diet consumed. Interestingly, there was no pattern among the three dietary guilds considered here in terms of the relative length of the total GI tract or combined (small plus large) intestine length. This is consistent with results of Schieck and Millar (1985). However, when I considered individual GI sections for only those species with a cecum, a majority of omnivores and the one carnivore had relatively longer small intestines and shorter small intestines. Conversely, a majority of herbivores had relatively shorter small intestines but longer large intestines. This same pattern was present (albeit weaker) for the relative length of the cecum; over half of the herbivores had long ceca for their body size, while a majority of the omnivores and one carnivore had relatively short ceca for their size. These observations strongly suggest there is an energetic trade-off among dietary guilds with regards to which GI section is longest. Schieck and Millar (1985) found that the lower digestive tract (the cecum and large intestine) was a much better predictor of diet than the small intestine or the total GI tract. Since each GI section has somewhat specialized function, future work should examine not only total GI length in a community context, but also section-specific metrics and how they differ among guild members.

COMPARING THE EFFECTIVENESS OF GASTROINTESTINAL AND CRANIODENTAL TRAITS

In this study, I used a series of classification analyses to explore whether gastrointestinal or craniodental trait sets are better predictors of dietary guild. When considering craniodental proportions, an LDA of the 31 species for which I obtained measurements was 70.97% accurate at predicting whether a species was a carnivore, omnivore, or herbivore, indicating that these measurements are reasonably effective continuous functional traits, a finding which is consistent with studies by Samuels (2009) and Kohli and Rowe (2019). Indeed, I used the same eight craniodental measurements as Kohli and Rowe (2019), and my LDA was only slightly less accurate than theirs, although most species differed between their study (based in the Great Basin of western U.S.) and mine. Considering GI traits, the LDA of the 24 species I obtained GI tracts from was similarly accurate (70.83%) at predicting dietary guild. Conversely, a taxonomically-reduced craniodental LDA including just the same 24 species in the GI analysis was notably poorer (66.67% accuracy), which indicates that GI measurements could be better at predicting dietary guild, despite the fact that not all GI sections (specifically, the cecum) were included.

The cecum is a unique structure and especially important for herbivorous species, given its role in processing poor quality diets characterized by high plant content. In order to expand the number of GI traits included in the classification analysis, I excluded the carnivores (and one omnivorous mole) and performed an ecologically-reduced LDA of the remaining 16 species but with all 12 GI traits (lengths, wet masses, and dry masses of 4 sections). This LDA was 87.5% accurate at predicting whether a species was an omnivore or an herbivore, and it performed better than an ecologically-reduced LDA of the craniodental traits on these same 16 species (81.25%), although in this case more GI than craniodental traits were used. Thus, although a trait-for-trait comparison of these trait sets is still difficult using all species and dietary guilds encountered in the Appalachians, GI traits used here appear to be effective continuous functional traits and comparable, or even more effective, in their dietary signal than craniodental traits when all GI sections including the cecum are considered.

APPALACHIANS SMALL MAMMAL COMMUNITY COMPOSITION

The site-level small mammal studies I compiled for this study were highly dispersed spatially (latitudinal range of 9.09 degrees), but there were nevertheless some similarities in species composition. Northern short-tailed shrews (*Blarina bravicauda*) were present at every site, and Eastern chipmunks (*Tamias striatus*) were present in every community but two. In addition, each community contained either *P. maniculatus* or *P. leucopus*, consistent with the abundance of these species across eastern North America. There was no major separation of latitudinally-binned communities in NMDS space; however, it was clear that northern sites were less variable than the mid-latitude or southern sites, indicating there is a core mammal fauna endemic to the northern sites that is also constituent, along with additional species, of southern sites. This lower relative endemicity at southern sites appears to reflect a mix of species typical of high- and low-latitudes, but exact low-latitude species varied between sites. One low latitude site had cotton mice (*Peromyscus gossypinus*), which were not found at any other site, while another low latitude site had marsh rice rats (*Oryzomys palustris*) present, a species that was also not found at any other site. The incomplete separation of latitudinally-binned sites indicates some nestedness in this fauna, and suggests that future trait-based studies should try and focus over even larger spatial and ecological gradients than the one considered here.

ENVIRONMENTAL REGRESSIONS OF GASTROINTESTINAL TRAITS

At higher latitudes, the growing season is shorter (Linderholm 2006) and annual productivity is lower, resulting in fewer absolute quantities of resources being available in a shorter temporal window. My hypothesis was that small mammal communities at higher latitudes should have a higher proportion of species with relatively longer GI tracts (possibly driven by relatively longer large intestines or ceca), which may help them to cope with this lower availability of resources. Indeed, regressions of community mean GI tract lengths against latitude were positive and statistically significant, indicating that communities at higher latitudes have longer relative GI tract lengths than those at lower latitudes. A regression of GI tract length against annual mean temperature (MAT), which should be inversely correlated with latitude, was negative and weakly significant. MAT is a more direct measure of climate and environmental conditions than latitude and the trend is in the direction I hypothesized. In addition, the regression of community mean GI length against precipitation seasonality (PS) was negative and weakly significant, with GI tract lengths being longer in communities with lower levels of precipitation seasonality.

Unlike regressions based on community mean GI tract length, a regression of the community weighted mean for latitude was not significant. In fact, none of the regressions of GI tract length against climate variables were statistically significant. However, although weighted means are preferable when abundances can be accurately measured, it is likely that at least some of my abundance data are biased by used of single trap types; specifically, Sherman live traps or similar which are not well-suited for targeting shrews, moles, and even arboreal squirrels. In these cases, sites with thousands of trap nights of effort may provide reliable species lists but unreliable abundance data. I have reported community weighted mean values in this study for comparison, but do not rely on these to make inferences about community assembly processes because of the above issues and the fact that many sites were dropped from these regressions. Future studies like mine would benefit from more comprehensive within-site sampling that utilizes multiple trap types.

CHOOSING FUNCTIONAL DIETARY TRAITS FOR FUTURE RESEARCH

Unlike for GI traits, there were no patterns in the regressions of the craniodental traits, including for latitude, MAT, and PS, which were the variables most predictive of community mean GI tract length. My craniodental metrics were unique in that I used scores from an LDA and not single 2D measurements, given that the whole set of measurements is required to capture the complex proportions of skulls. Still, the accuracy with which craniodental traits predicted dietary guild suggests that turnover in dietary guilds due to climate would be detectable in these regressions.

Small mammals can be difficult to monitor in terms of dietary ecology, and there is a lack of continuous functional trait proxies available to researchers. Even if there were patterns in the craniodental traits along the environmental gradients studied here, however, I suggest that GI traits are potentially preferred as a continuous functional dietary trait. First, it is unlikely that the skulls of small mammals respond to short term environmental shifts at the population level in ways that are easy to interpret as being indicative of dietary response. In contrast, the GI tract is highly plastic and has been shown to respond to changes in season, reproductive activity, and dietary quality within individuals and populations (Schieck and Millar 1985; Derting and Bogue 1993; Derting and Noakes 1995; Derting and Hornung 2003; Naya 2008). However, more work is required to collect GI traits from freshly-euthanized specimens and to identify which traits (e.g., based on total GI tract or specific sections) are most illuminating. For this goal, it is important that ecologists and researchers continue to work with museums, NEON, and other researchers to continue to expand the database of GI traits available. In addition, while this study used species means for GI morphology, future work should examine the interspecific variation as well as the intraspecific variation of GI morphology in a site-wise manner, if possible. Finally, a critical need exists to understand exactly how GI morphology relates to individual health , so future work should focus on linking GI morphology to fitness via gut microbiome composition, resistance to toxins, and other health-related outcomes.

CONCLUSION

In this chapter, I showed that GI morphology can indeed be used as an effective continuous trait capable of reflecting dietary ecology of Appalachian small mammal species. I evaluated this often-overlooked soft tissue trait and show that it is an effective continuous functional trait that is predictive of the dietary guild of a small mammal species. I also examined whether the trait was related to small mammal community assembly by regressing community mean GI metrics (total GI tract length) against latitude and climate in eastern North American small mammal communities. I found positive support for the hypothesized relationship with latitude, and a similar but weak relationship with both mean annual temperature and precipitation seasonality. No relationships were seen between craniodental proportions and latitude or climate variables. My work has generated substantial new natural history and trait data linked to small mammal specimens, enabling future and even more integrative work into how environmental change may impact mammal communities in eastern North America.

REFERENCES

CHAPTER II REFERENCES

Ayres, M. P. (1993). Global change, plant defense, and herbivory. In *Biotic interactions and global change* (pp. 75–94). Sinauer Associates. http://www.dartmouth.edu/~mpayres/pubs/Ayres_1993.pdf

Barnett, S. A. (1965). Adaptation of Mice to Cold. *Biological Reviews*, *40*(1), 5–51. https://doi.org/10.1111/j.1469-185X.1965.tb00794.x

Bozinovic, F., Rojas, J. M., Maldonado, K., Sabat, P., & Naya, D. E. (2010). Between-population differences in digestive flexibility in the olivaceous field mouse. *Zoology*, *113*(6), 373–377. https://doi.org/10.1016/j.zool.2010.08.002

Cameron, G. N., & Spencer, S. R. (1983). Field Growth Rates and Dynamics of Body Mass for Rodents on the Texas Coastal Prairie. *Journal of Mammalogy*, *64*(4), 656–665. https://doi.org/10.2307/1380522

Chivers, D. J., & Hladik, C. M. (1980). Morphology of the gastrointestinal tract in primates: Comparisons with other mammals in relation to diet. *Journal of Morphology*, *166*(3), 337–386. https://doi.org/10.1002/jmor.1051660306

Cripps, A. W., & Williams, V. J. (1975). The effect of pregnancy and lactation on food intake, gastrointestinal anatomy and the absorptive capacity of the small intestine in the albino rat. *British Journal of Nutrition*, *33*(1), 17–32. https://doi.org/10.1079/BJN19750005

Dehority, B. A. (2002). Gastrointestinal Tracts of Herbivores, Particularly the Ruminant: Anatomy, Physiology and Microbial Digestion of Plants. *Journal of Applied Animal Research*, *21*(2), 145–160. https://doi.org/10.1080/09712119.2002.9706367

Derting, T. L., & Austin, M. W. (1998). Changes in Gut Capacity with Lactation and Cold Exposure in a Species with Low Rates of Energy Use, the Pine Vole (*Microtus pinetorum*). *Physiological Zoology*, *71*(6), 611–623. https://doi.org/10.1086/515981

Derting, T. L., & Bogue, B. A. (1993). Responses of the Gut to Moderate Energy Demands in a Small Herbivore (Microtus pennsylvanicus). *Journal of Mammalogy*, *74*(1), 59–68. https://doi.org/10.2307/1381905

Derting, T. L., & Hornung, C. A. (2003). Energy demand, diet quality, and central processing organs in wild white-footed mice (Peromyscus leucopus). *Journal of Mammalogy*, *84*(4), 1381–1398. https://doi.org/10.1644/BEH-002

Derting, T. L., & Noakes III, E. B. (1995). Seasonal changes in gut capacity in the white-footed mouse (*Peromyscus leucopus*) and meadow vole (*Microtus pennsylvanicus*). *Canadian Journal of Zoology*, *73*(2), 243–252. https://doi.org/10.1139/z95-028

Doherty, M. M., & Charman, W. N. (2002). The Mucosa of the Small Intestine. *Clin Pharmacokinet*, *41*(4), 235–253.

Gallagher, R. V., Falster, D. S., Maitner, B. S., Salguero-Gómez, R., Vandvik, V., Pearse, W. D., Schneider, F. D., Kattge, J., Poelen, J. H., Madin, J. S., Ankenbrand, M. J., Penone, C., Feng, X., Adams, V. M., Alroy, J., Andrew, S. C., Balk, M. A., Bland, L. M., Boyle, B. L., … Enquist, B. J. (2020). Open Science principles for accelerating trait-based science across the Tree of Life. *Nature Ecology & Evolution*, *4*(3), 294–303. https://doi.org/10.1038/s41559-020-1109-6

Greiman, S. E., Cook, J. A., Tkach, V. V., Hoberg, E. P., Menning, D. M., Hope, A. G., Sonsthagen, S. A., & Talbot, S. L. (2018). Museum metabarcoding: A novel method revealing gut helminth communities of small mammals across space and time. *International Journal for Parasitology*, *48*(13), 1061–1070. https://doi.org/10.1016/j.ijpara.2018.08.001

Gross, J. E., Wang, Z., & Wunder, B. A. (1985). Effects of Food Quality and Energy Needs: Changes in Gut Morphology and Capacity of Microtus ochrogaster. *Journal of Mammalogy*, *66*(4), 661–667. https://doi.org/10.2307/1380792

Hammond, K. A. (1997). Adaptation of the Maternal Intestine During Lactation. *Journal of Mammary Gland Biology and Neoplasia*, *2*(3), 10.

Hammond, K. A., Roth, J., Janes, D. N., & Dohm, M. R. (1999). Morphological and Physiological Responses to Altitude in Deer Mice *Peromyscus maniculatus*. *Physiological and Biochemical Zoology*, *72*(5), 613–622. https://doi.org/10.1086/316697

Hammond, K. A., Szewczak, J., & KrÓl, E. (2001). Altitude and temperature effects on phenotypic plasticity. *The Journal of Experimental Biology*, *204*, 1991–2000. https://doi.org/10.1242/jeb.204.11.1991

Hammond, K. A., & Wunder, B. A. (1995). Effect of Cold Temperatures on the Morphology of Gastrointestinal Tracts of Two Microtine Rodents. *Journal of Mammalogy*, *76*(1), 232–239. https://doi.org/10.2307/1382331

Iverson, S. L., & Turner, B. N. (1974). Winter Weight Dynamics in Microtus Pennsylvanicus. *Ecology*, *55*(5), 1030–1041. https://doi.org/10.2307/1940353

Jankowski, J. A., Goodlad, R. A., & Wright, N. A. (1994). Maintenance of normal intestinal mucosa: Function, structure, and adaptation. *Gut*, *35*(1 Suppl), S1–S4. https://doi.org/10.1136/gut.35.1_Suppl.S1

Kingston, A. K. (2018). Longitudinal study of rat volar fat pad fixation and ethanol storage: Implications for the use of fluid-preserved specimens in morphological studies. *Journal of Anatomy*, *233*(5), 607–617. https://doi.org/10.1111/joa.12875

Kissling, W. D., Ahumada, J. A., Bowser, A., Fernandez, M., Fernández, N., García, E. A., Guralnick, R. P., Isaac, N. J. B., Kelling, S., Los, W., McRae, L., Mihoub, J., Obst, M., Santamaria, M., Skidmore, A. K., Williams, K. J., Agosti, D., Amariles, D., Arvanitidis, C., … Hardisty, A. R. (2018). Building essential biodiversity variables (EBV s) of species distribution and abundance at a global scale. *Biological Reviews*, *93*(1), 600–625. https://doi.org/10.1111/brv.12359

Kohli, B. A., & Rowe, R. J. (2019). Beyond guilds: The promise of continuous traits for mammalian functional diversity. *Journal of Mammalogy*, *100*(2), 285–298. https://doi.org/10.1093/jmammal/gyz054

Koteja, P. (1996). Limits to the Energy Budget in a Rodent, *Peromyscus maniculatus:* Does Gut Capacity Set the Limit? *Physiological Zoology*, *69*(5), 994–1020. https://doi.org/10.1086/physzool.69.5.30164243

Kristan, D. M., & Hammond, K. A. (2003). Physiological and morphological responses to simultaneous cold exposure and parasite infection by wild-derived house mice: *Intestinal* *parasites and cold exposure*. *Functional Ecology*, *17*(4), 464–471. https://doi.org/10.1046/j.1365-2435.2003.00751.x

Kurta, A. (1995). Rats, Mice, Lemmings and Voles. In *Mammals of the Great Lakes Region* (p. 155). The University of Michigan Press.

Laureto, L. M. O., Cianciaruso, M. V., & Samia, D. S. M. (2015). Functional diversity: An overview of its history and applicability. *Natureza & Conservação*, *13*(2), 112–116. https://doi.org/10.1016/j.ncon.2015.11.001

Lima, M., Bozinovic, F., & Jaksic, F. M. (1997). Body mass dynamics and growth patterns of leaf-eared mice Phyllotis darwini in a semi-arid region of the Neotropics. *Acta Theriologica*, *42*, 15–24. https://doi.org/10.4098/AT.arch.97-3

Mayor, S. J., Guralnick, R. P., Tingley, M. W., Otegui, J., Withey, J. C., Elmendorf, S. C., Andrew, M. E., Leyk, S., Pearse, I. S., & Schneider, D. C. (2017). Increasing phenological asynchrony between spring green-up and arrival of migratory birds. *Scientific Reports*, *7*(1). https://doi.org/10.1038/s41598-017-02045-z

McLean, B. S., Barve, N., Flenniken, J., & Guralnick, R. P. (2019). Evolution of litter size in North America's most common small mammal: An informatics-based approach. *Journal of Mammalogy*, *100*(2), 365–381. https://doi.org/10.1093/jmammal/gyz057

McLean, B. S., & Guralnick, R. P. (2021). Digital biodiversity data sets reveal breeding phenology and its drivers in a widespread North American mammal. *Ecology*, *102*(3). https://doi.org/10.1002/ecy.3258

McLean, B. S., Helgen, K. M., Goodwin, H. T., & Cook, J. A. (2018). Trait-specific processes of convergence and conservatism shape ecomorphological evolution in ground-dwelling squirrels. *Evolution*, *72*(3), 473–489. https://doi.org/10.1111/evo.13422

Millar, J. S., Xia, X., & Norrie, M. B. (1991). Relationships among reproductive status, nutritional status, and food characteristics in a natural population of *Peromyscus maniculatus*. *Canadian Journal of Zoology*, *69*(3), 555–559. https://doi.org/10.1139/z91-083

Molina-Montenegro, M. A., & Naya, D. E. (2012). Latitudinal Patterns in Phenotypic Plasticity and Fitness-Related Traits: Assessing the Climatic Variability Hypothesis (CVH) with an Invasive Plant Species. *PLoS ONE*, *7*(10), e47620. https://doi.org/10.1371/journal.pone.0047620

Munn, A. J., Snelling, E. P., Taggart, D. A., & Seymour, R. S. (2021). Ontogenetic scaling of the gastrointestinal tract of a marsupial foregut fermenter, the western grey kangaroo Macropus fuliginosus melanops. *Journal of Comparative Physiology B*, *191*(2), 371–383. https://doi.org/10.1007/s00360-020-01333-x

Myers, P., & Master, L. L. (1983). Reproduction by Peromyscus maniculatus: Size and Compromise. *Journal of Mammalogy*, *64*(1), 1–18. https://doi.org/10.2307/1380746

Naya, D. E. (2008). Gut size flexibility in rodents: What we know, and don't know, after a century of research. *Revista Chilena de Historia Natural*, *81*(4), 599–612. https://doi.org/10.4067/S0716-078X2008000400012

Naya, D. E., Bozinovic, F., & Karasov, W. H. (2008). Latitudinal Trends in Digestive Flexibility: Testing the Climatic Variability Hypothesis with Data on the Intestinal Length of Rodents. *The American Naturalist*, *172*(4), E122–E134. https://doi.org/10.1086/590957

Naya, D. E., Ebensperger, L. A., Sabat, P., & Bozinovic, F. (2008). Digestive and Metabolic Flexibility Allows Female Degus to Cope with Lactation Costs. *Physiological and Biochemical Zoology*, *81*(2), 186–194. https://doi.org/10.1086/527453

Naya, D. E., Karasov, W. H., & Bozinovic, F. (2007). Phenotypic plasticity in laboratory mice and rats: A meta-analysis of current ideas on gut size flexibility. *Evolutionary Ecology Research*, *9*, 1363–1374.

O'Connor, T. M. (1966). Cell dynamics in the intestine of the mouse from late fetal life to maturity. *American Journal of Anatomy*, *118*(2), 525–536. https://doi.org/10.1002/aja.1001180212

Parins-Fukuchi, C. (2018). Use of Continuous Traits Can Improve Morphological Phylogenetics. *Systematic Biology*, *67*(2), 328–339. https://doi.org/10.1093/sysbio/syx072

Post, E., & Forchhammer, M. C. (2008). Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1501), 2367–2373. https://doi.org/10.1098/rstb.2007.2207

Quay, W. B. (1974). Bird and Mammal Specimens in Fluid-Objectives and Methods. *Curator: The Museum Journal*, *17*(2), 91–104. https://doi.org/10.1111/j.2151-6952.1974.tb01228.x

Schieck, J. O., & Millar, J. S. (1985). Alimentary tract measurements as indicators of diets of small mammals. *Mammalia*, *49*(1), 93–104. https://doi.org/10.1515/mamm.1985.49.1.93

Schradin, C., & Pillay, N. (2006). Female striped mice (Rhabdomys pumilio) change their home ranges in response to seasonal variation in food availability. *Behavioral Ecology*, *17*(3), 452–458. https://doi.org/10.1093/beheco/arj047

Soares, J. C., Santos, C. S., Carvalho, S. M. P., Pintado, M. M., & Vasconcelos, M. W. (2019). Preserving the nutritional quality of crop plants under a changing climate: Importance and strategies. *Plant and Soil*, *443*(1–2), 1–26. https://doi.org/10.1007/s11104-019-04229-0

Speakman, J. R. (2008). The physiological costs of reproduction in small mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1490), 375–398. https://doi.org/10.1098/rstb.2007.2145

Verde Arregoitia, L. D., & D’Elía, G. (2021). Classifying rodent diets for comparative research. *Mammal Review*, *51*(1), 51–65. https://doi.org/10.1111/mam.12214

CHAPTER III REFERENCES

Blois, J. L., McGuire, J. L., & Hadly, E. A. (2010). Small mammal diversity loss in response to late-Pleistocene climatic change. *Nature*, *465*(7299), 771–774. https://doi.org/10.1038/nature09077

Bodmer, R. E. (1991). Influence of digestive morphology on resource partitioning in Amazonian ungulates. *Oecologia*, *85*(3), 361–365. https://doi.org/10.1007/BF00320611

Brown, J. H. (1973). Species Diversity of Seed-Eating Desert Rodents in Sand Dune Habitats. *Ecology*, *54*(4), 775–787. https://doi.org/10.2307/1935672

Brown, J. H., & Lieberman, G. A. (1973). Resource Utilization and Coexistence of Seed-Eating Desert Rodents in Sand Dune Habitats. *Ecology*, *54*(4), 788–797. https://doi.org/10.2307/1935673

Brown, J. H., Reichman, O. J., & Davidson, D. W. (1979). Granivory in Desert Ecosystems. *Annual Review of Ecology and Systematics*, *10*(1), 201–227. https://doi.org/10.1146/annurev.es.10.110179.001221

Codron, D., Brink, J. S., Rossouw, L., Clauss, M., Codron, J., Lee-Thorp, J. A., & Sponheimer, M. (2008). Functional differentiation of African grazing ruminants: An example of specialized adaptations to very small changes in diet: DIFFERENTIATION OF AFRICAN GRAZERS. *Biological Journal of the Linnean Society*, *94*(4), 755–764. https://doi.org/10.1111/j.1095-8312.2008.01028.x

Coweeta LTER. 2016. Mammal Species Commonly Present at Coweeta LTER ver 5. Environmental Data Initiative. https://doi.org/10.6073/pasta/2ec6e2ed77ddf3a5a3d06f5a288ef98a (Accessed 2022-02-19).

Crooks, K. R., Burdett, C. L., Theobald, D. M., King, S. R. B., Di Marco, M., Rondinini, C., & Boitani, L. (2017). Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. *Proceedings of the National Academy of Sciences*, *114*(29), 7635–7640. https://doi.org/10.1073/pnas.1705769114

Demers, C. 2018. Small mammals surveys, 1981 - 1996, Adirondack Long-Term Ecological Monitoring Program Project No. 10 by Adirondack Ecological Center of the State University of New York College of Environmental Science and Forestry, Newcomb, New York. Environmental Data Initiative ver 2. Environmental Data Initiative. https://doi.org/10.6073/pasta/5fbb6e06b7a5a059446c749a289a7030 (Accessed 2022-02-19).

Derting, T. L., & Bogue, B. A. (1993). Responses of the Gut to Moderate Energy Demands in a Small Herbivore (Microtus pennsylvanicus). *Journal of Mammalogy*, *74*(1), 59–68. https://doi.org/10.2307/1381905

Derting, T. L., & Hornung, C. A. (2003). Energy demand, diet quality, and central processing organs in wild white-footed mice (Peromyscus leucopus). *Journal of Mammalogy*, *84*(4), 1381–1398. https://doi.org/10.1644/BEH-002

Derting, T. L., & Noakes III, E. B. (1995). Seasonal changes in gut capacity in the white-footed mouse (*Peromyscus leucopus*) and meadow vole (*Microtus pennsylvanicus*). *Canadian Journal of Zoology*, *73*(2), 243–252. https://doi.org/10.1139/z95-028

Fick, S.E. and R.J. Hijmans, 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37 (12): 4302-4315.

Ford, W. M. (2000). *Woodland Salamander and Small Mammal Responses to Alternative Silvicultural Practices in the Southern Appalachians of North Carolina*. *54*, 241–250.

Ford, W. M., Menzel, M. A., McGill, D. W., Laerm, J., & McCay, T. S. (1999). Effects of a community restoration fire on small mammals and herpetofauna in the southern Appalachians. *Forest Ecology and Management*, 11.

Francl, K. E., Castleberry, S. B., & Mark Ford, W. (2004). Small Mammal Communities of High Elevation Central Appalachian Wetlands. *The American Midland Naturalist*, *151*(2), 388–398. https://doi.org/10.1674/0003-0031(2004)151[0388:SMCOHE]2.0.CO;2

Francl, K. E., & Small, C. J. (2013). Temporal Changes and Prescribed-Fire Effects on Vegetation and Small-Mammal Communities in Central Appalachian Forest, Creek, and Field Habitats. *Southeastern Naturalist*, *12*(1), 11–26. https://doi.org/10.1656/058.012.0102

Garcia-Solache, M. A., & Casadevall, A. (2010). Global Warming Will Bring New Fungal Diseases for Mammals. *MBio*, *1*(1). https://doi.org/10.1128/mBio.00061-10

Greiman, S. E., Cook, J. A., Tkach, V. V., Hoberg, E. P., Menning, D. M., Hope, A. G., Sonsthagen, S. A., & Talbot, S. L. (2018). Museum metabarcoding: A novel method revealing gut helminth communities of small mammals across space and time. *International Journal for Parasitology*, *48*(13), 1061–1070. https://doi.org/10.1016/j.ijpara.2018.08.001

Guo, Q., Hu, Z., Li, S., Li, X., Sun, X., & Yu, G. (2012). Spatial variations in aboveground net primary productivity along a climate gradient in Eurasian temperate grassland: Effects of mean annual precipitation and its seasonal distribution. *Global Change Biology*, *18*(12), 3624–3631. https://doi.org/10.1111/gcb.12010

Heske, E. J., Brown, J. H., & Mistry, S. (1994). Long-Term Experimental Study of a Chihuahuan Desert Rodent Community: 13 Years of Competition. *Ecology*, *75*(2), 438–445. https://doi.org/10.2307/1939547

Ho, C., Pennings, S. C., & Carefoot, T. H. (2010). Is Diet Quality an Overlooked Mechanism for Bergmann's Rule? *The American Naturalist*, *175*(2), 269–276. https://doi.org/10.1086/649583

IPCC, 2021: *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* [Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.)]. Cambridge University Press. In Press.

Hoffmann, A. A., & Sgrò, C. M. (2011). Climate change and evolutionary adaptation. *Nature*, *470*(7335), 479–485. https://doi.org/10.1038/nature09670

Jezkova, T., Olah-Hemmings, V., & Riddle, B. R. (2011). Niche shifting in response to warming climate after the last glacial maximum: Inference from genetic data and niche assessments in the chisel-toothed kangaroo rat (Dipodomys microps). *Global Change Biology*, *17*(11), 3486–3502. https://doi.org/10.1111/j.1365-2486.2011.02508.x

Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., Safi, K., Sechrest, W., Boakes, E. H., Carbone, C., Connolly, C., Cutts, M. J., Foster, J. K., Grenyer, R., Habib, M., Plaster, C. A., Price, S. A., Rigby, E. A., Rist, J., … Purvis, A. (2009). PanTHERIA: A species-level database of life history, ecology, and geography of extant and recently extinct mammals: *Ecological Archives* E090-184. *Ecology*, *90*(9), 2648–2648. https://doi.org/10.1890/08-1494.1

Kaminski, J. A., Davis, M. L., Kelly, M., & Keyser, P. D. (2007). Disturbance Effects on Small Mammal Species in a Managed Appalachian Forest. *The American Midland Naturalist*, *157*(2), 385–397. https://doi.org/10.1674/0003-0031(2007)157[385:DEOSMS]2.0.CO;2

Kellner, K. F., Urban, N. A., & Swihart, R. K. (2013). Short-term responses of small mammals to timber harvest in the United States Central Hardwood Forest Region: Small Mammal Responses to Timber Harvest. *The Journal of Wildlife Management*, *77*(8), 1650–1663. https://doi.org/10.1002/jwmg.613

Kelt, D. A., Brown, J. H., Heske, E. J., Marquet, P. A., Morton, S. R., Reid, J. R. W., Rogovin, K. A., & Shenbrot, G. (1996). Community Structure of Desert Small Mammals: Comparisons Across Four Continents. *Ecology*, *77*(3), 746–761. https://doi.org/10.2307/2265499

Kingston, A. K. (2018). Longitudinal study of rat volar fat pad fixation and ethanol storage: Implications for the use of fluid-preserved specimens in morphological studies. *Journal of Anatomy*, *233*(5), 607–617. https://doi.org/10.1111/joa.12875

Kissling, W. D., Dalby, L., Fløjgaard, C., Lenoir, J., Sandel, B., Sandom, C., Trøjelsgaard, K., & Svenning, J. (2014). Establishing macroecological trait datasets: Digitalization, extrapolation, and validation of diet preferences in terrestrial mammals worldwide. *Ecology and Evolution*, *4*(14), 2913–2930. https://doi.org/10.1002/ece3.1136

Kohli, B. A., & Rowe, R. J. (2019). Beyond guilds: The promise of continuous traits for mammalian functional diversity. *Journal of Mammalogy*, *100*(2), 285–298. https://doi.org/10.1093/jmammal/gyz054

Linderholm, H. W. (2006). Growing season changes in the last century. *Agricultural and Forest Meteorology*, *137*(1–2), 1–14. https://doi.org/10.1016/j.agrformet.2006.03.006

Li, Q., Sun, R., Huang, C., Wang, Z., Liu, X., Hou, J., Liu, J., Cai, L., Li, N., Zhang, S., & Wang, Y. (2001). Cold adaptive thermogenesis in small mammals from different geographical zones of China. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *129*(4), 949–961. https://doi.org/10.1016/S1095-6433(01)00357-9

Martin, S. A., Alhajeri, B. H., & Steppan, S. J. (2016). Dietary adaptations in the teeth of murine rodents (Muridae): A test of biomechanical predictions. *Biological Journal of the Linnean Society*, *119*(4), 766–784. https://doi.org/10.1111/bij.12822

Meiri, S., Dayan, T., & Simberloff, D. (2005). Variability and correlations in carnivore crania and dentition. *Functional Ecology*, *19*(2), 337–343. https://doi.org/10.1111/j.1365-2435.2005.00964.x

Merritt, J. 2019. Long Term Mammal Data from Powdermill Biological Station 1979-1999 (Reformatted to ecocomDP Design Pattern) ver 1. Environmental Data Initiative. https://doi.org/10.6073/pasta/4b33f15a95b323bf80fd0584a615dffa (Accessed 2022-02-19).

Mills, C. H., Gordon, C. E., & Letnic, M. (2018). Rewilded mammal assemblages reveal the missing ecological functions of granivores. *Functional Ecology*, *32*(2), 475–485. https://doi.org/10.1111/1365-2435.12950

Mitchell, J. C., Rinehart, S. C., Pagels, J. F., Buhlmann, K. A., & Pague, C. A. (1997). Factors influencing amphibian and small mammal assemblages in central Appalachian forests. *Forest Ecology and Management*, *96*(1–2), 65–76. https://doi.org/10.1016/S0378-1127(97)00043-1

Molina-Montenegro, M. A., & Naya, D. E. (2012). Latitudinal Patterns in Phenotypic Plasticity and Fitness-Related Traits: Assessing the Climatic Variability Hypothesis (CVH) with an Invasive Plant Species. *PLoS ONE*, *7*(10), e47620. https://doi.org/10.1371/journal.pone.0047620

Moritz, C., Patton, J. L., Conroy, C. J., Parra, J. L., White, G. C., & Beissinger, S. R. (2008). Impact of a Century of Climate Change on Small-Mammal Communities in Yosemite National Park, USA. *Science*, *322*(5899), 261–264. https://doi.org/10.1126/science.1163428

Morton, S. R. (1979). Diversity of Desert-Dwelling Mammals: A Comparison of Australia and North America. *Journal of Mammalogy*, *60*(2), 253–264. https://doi.org/10.2307/1379797

Naya, D. E. (2008). Gut size flexibility in rodents: What we know, and don't know, after a century of research. *Revista Chilena de Historia Natural*, *81*(4), 599–612. https://doi.org/10.4067/S0716-078X2008000400012

Naya, D. E., Bozinovic, F., & Karasov, W. H. (2008). Latitudinal Trends in Digestive Flexibility: Testing the Climatic Variability Hypothesis with Data on the Intestinal

Length of Rodents. *The American Naturalist*, *172*(4), E122–E134. https://doi.org/10.1086/590957

Nelson, D. L., Kellner, K. F., & Swihart, R. K. (2019). Rodent population density and survival respond to disturbance induced by timber harvest. *Journal of Mammalogy*, *100*(4), 1253–1262. https://doi.org/10.1093/jmammal/gyz094

NEON (National Ecological Observatory Network). Small mammal box trapping (DP1.10072.001). https://data.neonscience.org (accessed February 15, 2022)

NEON (National Ecological Observatory Network). Small mammal box trapping, RELEASE-2022 (DP1.10072.001). https://doi.org/10.48443/h3dk-3a71. Dataset accessed from https://data.neonscience.org on February 15, 2022

North Carolina Museum of Natural Sciences. NCSM Mammals Collection. http://ipt.vertnet.org:8080/ipt/resource.do?r=ncsm_mammals [Accessed 19, 3 2021].

Ozgul, A., Childs, D. Z., Oli, M. K., Armitage, K. B., Blumstein, D. T., Olson, L. E., Tuljapurkar, S., & Coulson, T. (2010). Coupled dynamics of body mass and population growth in response to environmental change. *Nature*, *466*(7305), 482–485. https://doi.org/10.1038/nature09210

Quay, W. B. (1974). Bird and Mammal Specimens in Fluid-Objectives and Methods. *Curator: The Museum Journal*, *17*(2), 91–104. https://doi.org/10.1111/j.2151-6952.1974.tb01228.x

Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., & Pounds, J. A. (2003). Fingerprints of global warming on wild animals and plants. *Nature*, *421*(6918), 57–60. https://doi.org/10.1038/nature01333

Samuels, J. X. (2009). Cranial morphology and dietary habits of rodents. *Zoological Journal of the Linnean Society*, *156*(4), 864–888. https://doi.org/10.1111/j.1096-3642.2009.00502.x

Scherbarth, F., & Steinlechner, S. (2010). Endocrine mechanisms of seasonal adaptation in small mammals: From early results to present understanding. *Journal of Comparative Physiology B*, *180*(7), 935–952. https://doi.org/10.1007/s00360-010-0498-2

Schieck, J. O., & Millar, J. S. (1985). Alimentary tract measurements as indicators of diets of small mammals. *Mammalia*, *49*(1). https://doi.org/10.1515/mamm.1985.49.1.93

Steven B. Castleberry, Michael T. Mengak, W. Mark Ford, Neotoma magister, *Mammalian Species*, Issue 789, 24 May 2006, Pages 1–5, https://doi.org/10.1644/789.

Stewart Jr., R. L., Kindlin, C. M., & Delis, P. R. (2008). An inventory of the small mammals of Letterkenny Army Depot, Franklin County, Pennsylvania. *Penn State University Press*, *81*(2/3), 59–65.

Ungar, P. S. (2015). Mammalian dental function and wear: A review. *Biosurface and Biotribology*, *1*(1), 25–41. https://doi.org/10.1016/j.bsbt.2014.12.001

University of Michigan Museum of Zoology. UMMZ Mammal Collection. https://ipt.lsa.umich.edu/resource.do?r=ummz_mammals [Accessed 19, 3 2021].

Upham, N. S., Esselstyn, J. A., & Jetz, W. (2019). Inferring the mammal tree: Species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLOS Biology*, *17*(12), e3000494. https://doi.org/10.1371/journal.pbio.3000494

Urban, N. A., & Swihart, R. K. (2011). Small mammal responses to forest management for oak regeneration in southern Indiana. *Forest Ecology and Management*, *261*(3), 353–361. https://doi.org/10.1016/j.foreco.2010.10.015

Verde Arregoitia, L. D., & D’Elía, G. (2021). Classifying rodent diets for comparative research. *Mammal Review*, *51*(1), 51–65. https://doi.org/10.1111/mam.12214

Wang, D.-H., Pei, Y.-X., Yang, J.-C., & Wang, Z.-W. (2002). *Digestive tract morphology and food habits in six species of rodents*. *52*(1), 51–55.

Wood, C. M., Witham, J. W., & Hunter, M. L. (2016). Climate-driven range shifts are stochastic processes at a local level: Two flying squirrel species in Maine. *Ecosphere*, *7*(2). https://doi.org/10.1002/ecs2.1240

APPENDIX A: SUPPLEMENTAL INFORMATION FOR CHAPTER II

Table A.1. Comparison of Regressions for Gastrointestinal Length and Wet Mass (Four Individual Sections and Total) Versus Time (Julian Day). For Each Section and the Total, 2nd, 3rd, and 4th-Order Polynomial Regressions Were Compared Using AIC, ΔAIC, and AIC Weights

Model	AIC	ΔAIC	AIC Weights
Stomach length			
2nd order	-236.57	0.00	0.97
3rd order	-229.62	6.95	0.03
4th order	-216.91	19.66	0.00
Cecum length			
2nd order	-175.97	0.00	0.96
3rd order	-169.31	6.67	0.03
4th order	-161.40	14.57	0.00
Small intestine length			
2nd order	99.88	0.00	0.90
3rd order	109.37	9.49	0.01
4th order	116.04	16.15	0.00
Large intestine length			
2nd order	-35.89	0.00	0.99
3rd order	-25.97	9.92	0.01
4th order	-19.81	16.08	0.00
Total length			
2nd order	142.98	0.00	0.99
3rd order	152.58	9.59	0.01
4th order	157.32	14.33	0.00
Stomach wet mass			
2nd order	-934.38	0.00	1.00
3rd order	-923.61	10.77	0.00
4th order	-917.44	16.93	0.00
Cecum mass			
2nd order	-918.00	0.00	0.98
3rd order	-909.91	8.08	0.02
4th order	-900.20	17.80	0.00
Small intestine wet mass			
2nd order	-851.07	0.00	0.99

3rd order	-840.90	10.16	0.01
4th order	-834.01	17.06	0.00
Large intestine wet mass			
2nd order	-931.17	0.00	0.99
3rd order	-921.23	9.94	0.01
4th order	-911.76	19.40	0.00
Total wet mass			
2nd order	-854.81	0.00	1.00
3rd order	-844.15	10.66	0.00
4th order	-837.15	17.66	0.00

Figure A.1. Boxplots Depicting Monthly Differences in Scaled Gastrointestinal Tract Wet Masses, Calculated as the Cubic Root of the Total Wet Mass Divided by Individual Head-Body Length

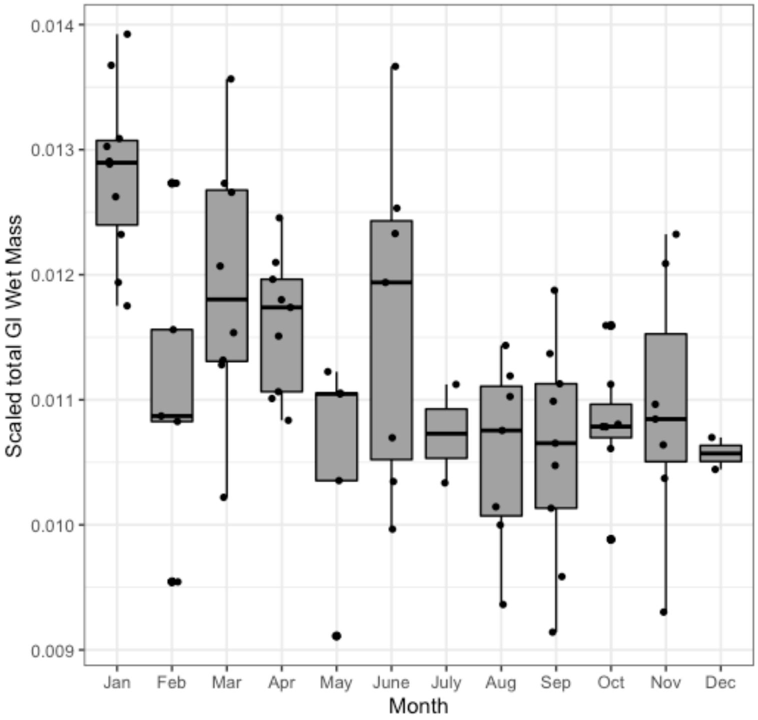
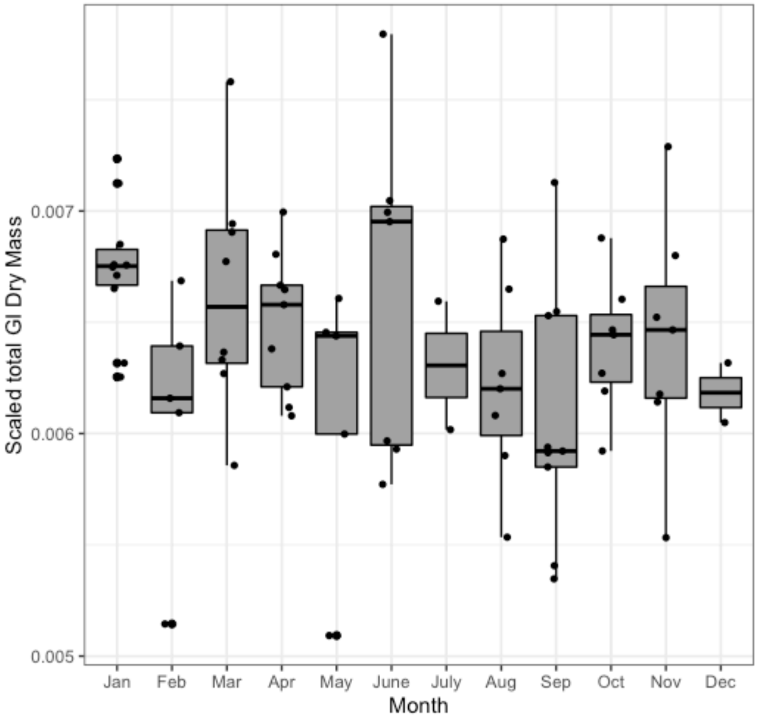


Figure A.2. Boxplots Depicting Monthly Differences in Scaled Gastrointestinal Tract Wet Masses, Calculated as the Cubic Root of the Total Wet Mass Divided by Individual Head-Body Length



APPENDIX B: SUPPLEMENTAL INFORMATION FOR CHAPTER III

Table B.1. Summary of Separate Linear Regressions Relating Community Measures of Craniodental Measurements to Environmental Variables and Latitude

Regression	Slope estimate	R^2	P-value
Community mean LDA 1			
Latitude	0.04	0.00	0.32
Temperature seasonality	0.00	-0.04	0.68
Annual mean temperature	-0.03	-0.02	0.44
Precipitation seasonality	-0.04	0.05	0.16
Annual mean precipitation	0.00	0.02	0.24
Community mean LDA 2			
Latitude	0.01	-0.03	0.54
Temperature seasonality	0.00	-0.05	0.91
Annual mean temperature	-0.02	-0.02	0.42
Precipitation seasonality	-0.01	-0.01	0.41
Annual mean precipitation	0.00	-0.05	0.94
Community-weighted mean LDA 1			
Latitude	-0.02	-0.08	0.79
Temperature seasonality	0.00	-0.08	0.90
Annual mean temperature	0.05	-0.04	0.51
Precipitation seasonality	-0.02	-0.08	0.99
Annual mean precipitation	0.00	-0.01	0.36
Community-weighted mean LDA 2			
Latitude	0.04	-0.02	0.39
Temperature seasonality	0.00	0.01	0.30
Annual mean temperature	-0.04	-0.03	0.44
Precipitation seasonality	0.00	-0.08	0.99
Annual mean precipitation	0.00	0.12	0.13

Figure B.1. Regressions of Community Mean (Top) and Community-Weighted Mean (Bottom) Scaled Total Gastrointestinal Tract Length Versus Temperature Seasonality, and Annual Mean Temperature

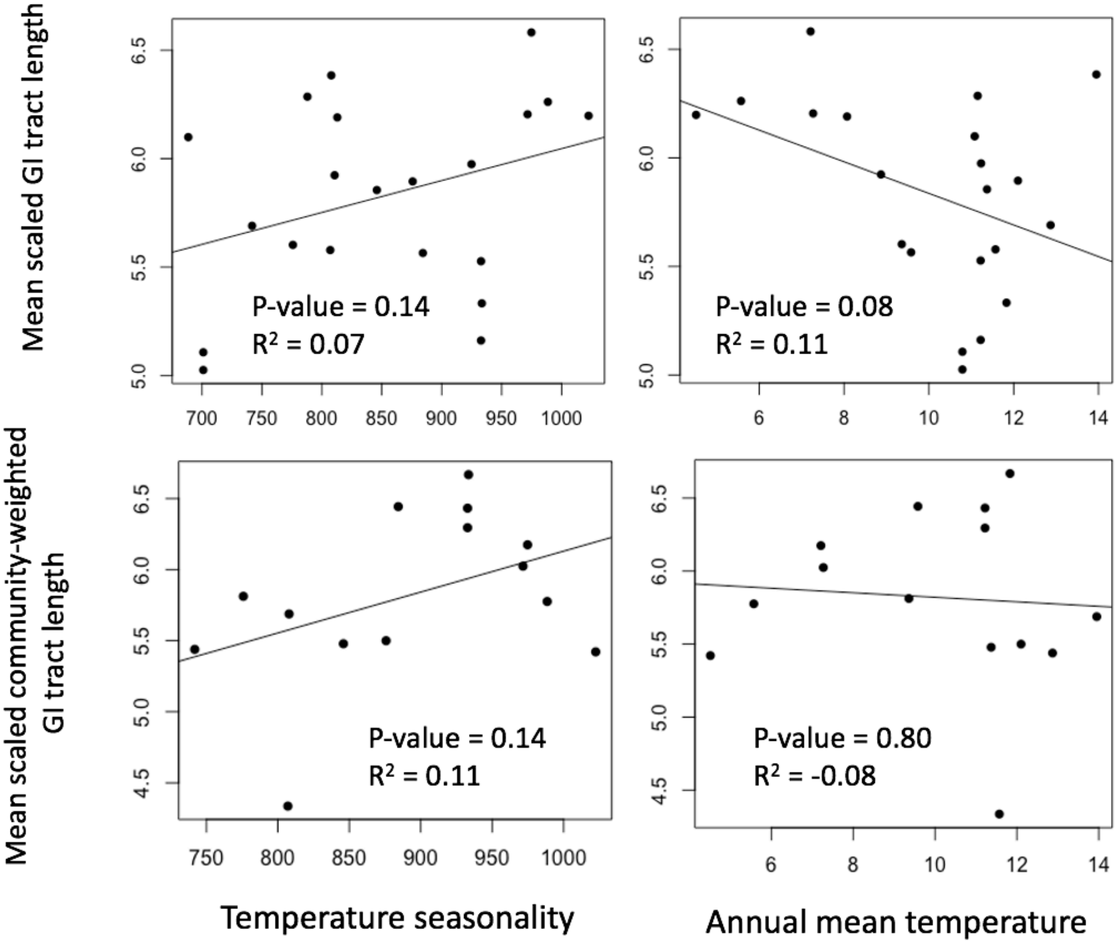


Figure B.2. Regressions of Community Mean (Top) and Community-Weighted Mean (Bottom) Scaled Total Gastrointestinal Tract Length Versus Precipitation Seasonality, and Precipitation