

ECOLOGICAL RELEASE AND ALLOMETRY EXPLAIN INSULAR  
GIGANTISM AND SHAPE VARIATION IN A WIDESPREAD NORTH  
AMERICAN RODENT

By

Mariah C. Schlis-Elias

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Thesis Committee:

Dr. Mollie Cashner, Committee Chair

Dr. Jason Malaney

Dr. Chris Gienger

First Name: <u>Mariah</u>	Last Name: <u>Schlis-Elias</u>
A#:	APSU Email:
Graduate Program: <u>Biology</u>	Concentration:
Type of Document ( <u>Thesis</u> ) Dissertation/Research Paper/Literacy Paper/Field Study):	

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Graduate Committee		
Major Professor	Name <u>Mollie F. Cashner</u> Signature <u>Mollie F. Cashner</u>	Date <u>3 December 2019</u>
Second Professor	Name <u>CM Gionn</u> Signature <u>CM Gionn</u>	Date <u>03 Dec 2019</u>
Third Professor	Name <u>DON C. DAILEY FOR JASON MALANEY</u> Signature <u>Don C. Dailey</u>	Date <u>3 Dec 2019</u>

<b>Received for the Graduate Academic Council by the Dean of the College of Graduate Studies</b>	
Name	
Signature	Date

## ABSTRACT

Island Rule is defined as a trend of gigantism in small-bodied species and dwarfism in large-bodied species inhabiting islands and island-like systems. Several hypotheses attempt to explain gigantism in small-bodied species including immigrant selection, thermoregulation and endurance, resource subsidy, and ecological release, but these are often incompletely tested and infrequently compared directly. In this study, we used geometric morphometrics to obtain indices of size and shape variation across 17 island populations of meadow voles (*Microtus pennsylvanicus*). We first test whether gigantism occurs in two geographically separated island systems inhabited by *M. pennsylvanicus* and then evaluate which of the above hypotheses best explains observed variation. Finally, we assess whether shape varies in accordance with size, geography, or other island-specific factors. Resource subsidy and immigrant selection are inapplicable to this system, so we focused on the two remaining hypotheses (thermoregulation and endurance, and ecological release) to evaluate significant signals of gigantism detected among Atlantic island populations. Despite linear models revealing that *M. pennsylvanicus* cranium size follows a weak pattern with temperature seasonality, results are inverse of Bergmannian expectations, contradicting the Thermoregulation and Endurance Hypothesis. In contrast, regression-based path analyses permitted us to detect significant associations between skull size and island-specific factors, including area and number of predators, each consistent with the Ecological Release Hypothesis. For this species, the primary source of shape variation in island populations is its variation with size due to static allometry. Random, residual (size and allometry-controlled) patterns of shape are likely explained by population-level differences that resulted from founder effects, genetic drift, or natural

selection and thus are unlikely a product of Island Rule. Taken together, our findings indicate that Island Rule is a latent evolutionary process that depends on biogeographic context. Further, allometry may manifest in important functional consequences as size varies according to expectations of Island Rule, but without corresponding independent selection on cranium shape. Unfortunately, these important evolutionary perspectives and insular variants are threatened by the introduction of non-native predators and projected sea level rise.

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## INTRODUCTION

Biogeographers have been fascinated by peculiar features and traits of insular organisms for over a century (Wallace 1860; Lomolino *et al.* 2006a). For example, Charles Darwin was among the first to document the remarkable diversity of island-dwelling organisms, famously revealing beak size and function in the Galápagos finches (Darwin 1859). Since then, biogeographers have continued to evaluate hypotheses related to form and function associated with island-dwelling species. In 1964, J. Bristol Foster highlighted gigantism in insular populations of rodents, while co-occurring large-bodied artiodactyls, carnivorans, and lagomorphs tended toward dwarfism. The increased interest in body size trends of island fauna that followed these initial observations led van Valen (1973) to pen the pattern as “the Island Rule”.

A renewed focus on island systems is emerging especially for unraveling the mechanisms responsible for evolutionary trends in insular organisms but also, unfortunately, because of warming climates and rising sea levels (Lomolino *et al.* 2006, Millien & Damuth 2004, Lokatis & Jeschke 2018). Insular systems yield opportunities to identify areas with high evolutionary potential critical to species resilience and longevity, which are important for conservation (Moritz 1999, Russell & Kueffer 2019). Moreover, evidence suggests that patterns like Island Rule act upon vertebrate populations isolated in habitat fragments (Gaines *et al.* 1997, Schmidt & Jensen 2003, 2005; Fietz & Weis-Dootz 2012), implying that evolutionary trends in body size are not restricted to island systems, but rather, apply to environments with characteristics analogous to insularity (Itescu 2019).

Both genetic and environmental factors influence physical features of populations and species, and consequently, numerous hypotheses attempt to explain observed, insular patterns of body size variation. Island-centric hypotheses for small-bodied organisms include thermoregulation and endurance (*i.e.*, Bergmann's Rule; Bergmann 1847), immigrant selection, resource subsidy, and ecological release (Millien & Damuth 2004, Lomolino *et al.* 2012, McClain *et al.* 2013, Durst & Roth 2015). Each of these hypotheses proposes differential responses of body size that may operate independently or in conjunction to produce observed trends.

If gigantism is occurring in island-dwelling populations and thermoregulation and endurance drives this trend, larger rodents are expected at higher latitudes, in colder or more seasonal climates, with expectant patterns mirrored in mainland populations. Functionally, thermoregulation drives size patterns because larger-bodied organisms express a larger volume to surface ratio which enables them to more efficiently conserve heat (Salewski & Watt 2017). This relationship between body volume and surface area often presents larger individuals with a selective advantage in colder, more variable conditions (Meiri 2010).

Immigrant selection and resource subsidy are additional hypotheses that may apply to small-bodied organisms. When immigrant selection is operating, larger-bodied organisms are frequently found on islands more isolated from the mainland because smaller-bodied organisms often fail to reach distant islands (Millien & Damuth 2004). Immigrant selection is primarily applicable to populations established after island formation. For example, Lomolino (1984) found that both rodents and shrews were

influenced by immigrant selection since larger-bodied individuals more frequently survived over-ice dispersal events, resulting in a bias toward larger individuals on more isolated riverine islands. Conversely, the resource subsidy hypothesis specifically pertains to predators, in that small-bodied species are expected to evolve larger body sizes on islands if they consume aquatic prey (Lomolino *et al.* 2012). This is because aquatic prey are frequently more abundant in island systems due to the constant proximity to shorelines. Gigantism in some island-dwelling bear populations may be attributed to this hypothesis (Hilderbrand *et al.* 1999).

Lastly, if ecological release is responsible for size variation, then the largest organisms are expected on the smallest, furthest from the mainland, and/or predator-depauperate islands. This far-small island effect is the product of the species-area relationship, which is often magnified in higher trophic organisms such as predators (Holt *et al.* 1999). Consequently, for island-dwelling prey such as rodents whose predator avoidance strategies rely on being small to avoid detection, lack of island predators releases them from this body size constraint (McClain *et al.* 2013).

In spite of the variety of organisms that seemingly respond to insularity through changes in body size, there remains contention about pattern generality (Meiri *et al.* 2006). For example, Meiri *et al.* (2004) questioned if the pattern exists at all, suggesting Island Rule is, instead, a product of sampling bias. Despite these critiques, most Orders of mammals reflect patterns consistent with Island Rule hypotheses (Lomolino *et al.* 2013, Faurby & Svenning 2016), but the trend is less consistent across other vertebrates including birds (Clegg & Owens 2002, Mathys & Lockwood 2009), reptiles (Boback & Guyer 2003,



Meiri 2007, Jaffe *et al.* 2011, Itescu *et al.* 2014, Runemark *et al.* 2015), and amphibians (Montesinos *et al.* 2011, Mageski *et al.* 2015, Rebouças *et al.* 2018). Similarly, invertebrates are enigmatic (Palmer 2002, Welch 2010) although empirical evidence suggests factors associated with insularity may reshape variation in plants (Biddick *et al.* 2019). Island Rule has been consistently scrutinized, especially considering author-driven biases and HARKing (Hypothesizing After Results are Known), so direct tests of this phenomenon are imperative (Lokatis & Jeschke 2018) to better link pattern with process.

In this project, we use the broad geographic distribution of meadow voles (*Microtus pennsylvanicus*) to assess if and how cranial size and shape variation are attributable to alternative causal hypotheses of Island Rule. Specifically, we compare cranial size and shape patterns of voles within and among two independent sets of island populations including the Outer Lands of New England (Atlantic) and the Alexander Archipelago (Pacific). We paired island populations with populations from the neighboring mainland and applied geometric morphometric methods and associated analyses to evaluate alternative hypotheses. For example, we used centroid size, a geometric morphometric index that is commonly applied as a proxy for body size (Barčiová & Macholán 2006; Cardini *et al.* 2007; Souto-Lima & Millien 2014), to assess size variation in island and mainland populations. Next, we used Procrustes shape coordinates for analyzing hypotheses of shape variation among island and mainland populations of voles.

First, we test the prediction that island-dwelling voles are larger than mainland voles using Kruskal-Wallis tests and pairwise Wilcoxon Rank Sum tests with a Bonferroni correction in each region. Second, we evaluate each of the four causal hypotheses. Given

that the resource subsidy hypothesis is specific to predators, we conclude that it is not applicable to this system of rodents that consume terrestrial vegetation (Reich 1981). Likewise, the continental nature of all islands included in this project suggest that immigrant selection is not relevant to this system since geologic evidence implies that terrestrial organisms would have been able to freely migrate across exposed continental shelf to areas that now make up these islands (Weddle & Choate 1983, Darvill *et al.* 2018), so we do not directly assess these two hypotheses. We do test predictions of the Thermoregulation and Endurance, and Ecological Release Hypotheses.

To determine the amount of size variation accounted for by thermoregulation and endurance versus ecological release, we use a pair of competing linear models with population mean centroid size as the response variable. For the Thermoregulation and Endurance Hypothesis (TEH), we use regressions to evaluate three alternative predictions, including whether larger voles occur at higher latitudes, in colder, or more seasonal climates. Similarly, for the Ecological Release Hypothesis (ERH), we use regression-based analyses of variance (ANOVAs) to evaluate three alternative predictions, including whether larger voles occur on smaller, more distant (from mainland), or predator-depauperate islands. Additionally, we apply information theoretic approaches to select the optimal model for each hypothesis (TEH and ERH), then directly compare the support of the optimal TEH and ERH models in reference to the null model since the response variable is treated equally across analyses.

Because linear modeling fails to account for directionality of responses and indirect effects, we also conduct a series of path analyses to determine if mean centroid size is

optimally predicted by a combination of ecological release variables. Since mammalian and reptilian predation pressures can have differential impacts on mammalian prey (Madison 1978), we carefully compared and evaluated alternative characterizations of island predators in different path analyses to test competing predictions about how mean centroid size may respond to different predators and predation pressure. Alternative path models included the predictions that larger voles occur on 1) islands lacking predators altogether (presence/absence), 2) islands with a smaller number of predator species, 3) islands lacking specific predator types (presence/absence of mammalian and reptilian predators), or 4) islands with fewer species of each predator type. Because evaluating model fit is non-trivial and there remains no consensus of the ideal approach to determining optimal models, we used a suite of path model fit indices (*i.e.*,  $\chi^2$ , CFI, RMSEA, and  $R^2$ ) to select the optimal model from this series of competing path models.

Because shape variation may provide insight into how morphological diversity may manifest from alternative evolutionary processes (*i.e.*, drift and natural selection) and because size and shape may both covary (allometry) and vary independently (non-allometric variation; Marcy *et al.* 2016), we pivot to shape variation. We treat dorsal and ventral shape coordinates separately because both have specific functional roles in the skull (food acquisition and processing – ventral; protection of brain and sensory organs – dorsal; Figueirido *et al.* 2011). To test predictions that dorsal and ventral shape varies among populations in each region, we carry out Principal Components Analyses (PCA) on Procrustes shape coordinates colored by population to visualize variation, then test for significant differences in shape along the first two component scores (PC1 and PC2) using ANOVA. Then, we apply multivariate analyses of covariance (MANCOVAs), static

allometry plots, and pairwise slope tests to compare and evaluate predictions that dorsal and ventral shape covary with size and population in each region. Finally, we extract residual shape coordinates from MANCOVAs to assess if size and static allometry-corrected shape (*i.e.*, “pure” shape) is associated with island characteristics (area, distance from the mainland, presence of mammalian and reptilian predators). To do so, we used a second set of PCAs on residual shape colored by each variable, followed by ANOVAs on PC1 and PC2 scores to test if residual shape differs among levels of these variables on each face of the cranium in each region.

### *Study System*

We selected *M. pennsylvanicus* as the focal taxon for this project for three primary reasons. One advantage is that the range of meadow voles is distributed across the entire east-west spread of North America including islands along each coast. This presents a great opportunity to study insular body size evolution since we can test hypotheses relating to both size and shape within and among populations of two disparate geographic regions (hereafter referred to as the Atlantic and Pacific regions, respectively) within a single species.

Another advantage of using meadow voles as our focal taxon is that there is evidence of island-dwelling populations displaying unique cranial characteristics and increased body size, at least along the Atlantic coast (Miller 1896, Chamberlain 1954, Wheeler 1956). These changes are so pronounced that three of the Atlantic island populations are designated as morphologically distinct subspecies or species; the Block Island meadow vole (*Microtus provectus*, now a subspecies of *M. pennsylvanicus*), the Gull

Island meadow vole (*Microtus nesophilus*, extinct), and the Muskeget Island meadow vole (*Microtus breweri*, retains specific designation; Reich 1981). Despite these size-related taxonomic descriptions, no formalized studies of body size or shape variation in insular populations of meadow voles have been conducted to date, for either the Atlantic or Pacific coastal populations.

Lastly, we selected *M. pennsylvanicus* as the focus of this study since evidence suggests microtine rodents have an unusually rapid capacity for evolution, especially when subjected to island environments (Guthrie 1965, 1971; Cucchi *et al.* 2014). Collectively, these studies indicate that significant craniodental change can be achieved in this clade over time scales as short as a few decades (Lomolino 1984, Cucchi *et al.* 2014), making them an ideal study system for macroevolutionary processes like Island Rule within a relatively young set of islands (Weddle & Choate 1983, Darvill *et al.* 2018).

## MATERIALS AND METHODS

### *Specimen Sampling*

We located and selected skull specimens for each population by querying (May 2017) VertNet (vertnet.org) and Arctos (arctos.org) databases. In total, we examined 839 cranial morphologies of *Microtus pennsylvanicus* (see Appendix) that represent eighteen pairwise island and mainland populations. In the Atlantic region, we compared eleven island populations with mainland individuals ranging 8 degrees of latitude (38.09 – 46.09°N) from Maine, south to New Jersey, with the westernmost individuals sampled from Pennsylvania (Fig. 1A). In the Pacific region, we compared voles from seven islands in the Alexander Archipelago ranging 8.5 degrees of latitude (56.36 – 64.86°N) with

mainland populations sampled from Alaska, British Columbia, and Yukon Territory (Fig. 1B). The populations sampled within these two regions fit within the Eastern and Northwestern mitochondrial clades of *M. pennsylvanicus* that Jackson and Cook (in press) detected, respectively. It is important to note that while we include the Muskeget Island (Massachusetts) population of *Microtus breweri* in this study, Jackson and Cook (in press) demonstrated that *M. breweri* is nested within the Eastern clade of *M. pennsylvanicus*. Moreover, the recent (< 3,000 years ago) separation of Muskeget Island from Nantucket imply that *M. breweri* diverged from *M. pennsylvanicus* within the last 3,000 years (Tamarin & Kunz 1974). Therefore, we treated all *M. breweri* samples as descendent of mainland *M. pennsylvanicus* (Adler & Wilson 1985).

To avoid error associated with inaccurate or obscured landmarks, we excluded any severely damaged skulls (over a quarter of the cranium broken) or those with flesh attached. We photographed skulls on both dorsal and ventral surfaces using Canon EOS Rebel T-series DSLR cameras, eliminating parallax error (Busch 2012). To keep the skulls both balanced and oriented during photographing, we made a clay mold that we placed each specimen on. A metric ruler was placed parallel to the skull in each image for scale standardization and the lens surface was positioned 11 cm above each specimen during photographing.

#### *Landmarking and Error Assessment*

We used twenty-three and twenty-seven landmarks (Supplementary Tables S1-S2) to capture both dorsal and ventral variation of skulls, respectively (Fig. 2A). We selected landmarks based on previous evidence of geographic variation in meadow vole skulls (Miller 1896; Chamberlain 1954; Wheeler 1956) and that are important for capturing size

and shape variation in rodents (Zelditch *et al.* 2004, Barčiová & Macholán 2006, Marcy *et al.* 2016). Despite bilateral symmetry, we placed landmarks on both sides of the skull because previous geometric morphometric analyses suggest single-sided landmarks are subject to mathematical error that can negatively impact the reliability of shape estimates (Cardini 2016). Because *M. pennsylvanicus* experiences indeterminate growth (Campbell & Dobson 1992) we assigned each vole an age score based on the rubric defined by Snyder (1954) to eliminate ontogenetic influence on the data and analyses. According to this rubric, age scores 4-5 indicate juveniles, a 6 indicates subadults, and scores 7-12 indicate adults. Following scoring, we excluded juveniles, subadults, and senescent adults (score 12; see below) from further consideration.

Following age determination, we used tpsDig 2.32 (Rohlf 2018) to digitize landmarks on each specimen and set a scaling factor to 1 cm. We assessed digitization and orientation error within the dataset using a complementary pair of techniques from the protocol of Adriaens (2007). Briefly, digitization error is a measure of the repeatability of landmark placement, quantified by landmarking multiple copies of the same photo. Orientation error is a measure of the repeatability of specimen placement during photographing, assessed by taking multiple photos of the same specimen after positioning it on the specimen mold as consistently as possible. Because geographic variation can influence error estimates, we assessed both digitization and orientation error for a subset of subspecies in our dataset. Taken together, we evaluated five samples using five replicate photos for each represented population, and determined that digitization and orientation error each accounted for < 1% of observed variation in the dataset so no additional corrective actions were applied (Adriaens 2007).

### *Data Preparation*

Independent evolutionary history and phylogeographic variation across populations can introduce bias in morphometric tests (Meiri *et al.* 2008), so for all analyses we treated Atlantic and Pacific populations separately due to their phylogenetic distinctness (Jackson & Cook, in press) and geographic separation. Moreover, two island systems enabled us to simultaneously evaluate whether signals of Island Rule were congruent between regions. Despite techniques that allow analysis of dorsal and ventral landmarks jointly (Davis *et al.* 2016), we opted to evaluate hypotheses of Island Rule for both dorsal and ventral perspectives separately because we are interested in assessing functional variation (*e.g.*, mastication – ventral vs. protection – dorsal) related to allometry. Additionally, more samples had to be excluded in the ventral data than the dorsal data due to a greater tendency for the delicate ventral structures to be broken.

The research questions of this project require indices of size and shape variation across several populations of island-dwelling voles. Consequently, we first estimated the coordinates of missing landmarks using the multivariate regression method available in the *geomorph* 3.1.2 package in R v.3.6.0 and then applied a Generalized Procrustes Analysis (GPA). GPA is a statistical method that uses raw landmark coordinates and superimposes the landmark configuration of each specimen in order to separate variation in size from shape, while simultaneously removing uninformative variation due to rotation and translation (Zelditch *et al.* 2004). From the results of GPA, we extracted the centroid size of each specimen, a factor frequently applied as a proxy for body size (Barčiová & Macholán 2006; Cardini *et al.* 2007; Souto-Lima & Millien 2014).



Next, using the Procrustes coordinates obtained from the GPA we conducted a Principal Components Analysis (PCA) to simultaneously decompose sampled variation into fewer components that maximizes captured variation, generate a model suitable for evaluating shape variation, and visualize any outliers in the data. From PCA, we found that specimens with more than 2 missing landmarks resulted in extreme outliers, likely due to the additive effects of multiple estimated landmark positions, so we excluded any specimens with  $> 2$  missing landmarks.

We then generated box plots of dorsal centroid size from each adequately sampled population (minimum of 10 samples per island – see sensitivity analyses below). We examined outliers detected in these plots for any additional potential problems, such as senescent individuals (age group 12) or if individual samples were assigned an inaccurate scaling factor during digitization. We excluded from analyses any excessively large, senescent individuals in order to conservatively treat the data for potential bias toward larger sizes due to the indeterminate growth in voles (Campbell & Dobson 1992).

Because of conflicting evidence of sexual dimorphism in *M. pennsylvanicus* (Boonstra *et al.* 1993, Ostfeld & Heske 1993) which can bias size-related analyses, we evaluated sexual dimorphism by applying a two-sample t-test comparing male and female centroid sizes for each population that conform to normality assumptions ( $n = 10$ ). For populations that violated the assumption of normality ( $n = 1$ ), we used a Wilcoxon Rank Sum test. Collectively, we detected no significant dimorphic differences for any population, so we pooled sexes in all subsequent analyses.

### *Sensitivity Analyses*

Insufficient sampling can negatively influence analyses of geographic variation, especially when estimating parameters likely responsible for Island Rule (Gienger *et al.* 2018). Therefore, we conducted analyses to evaluate the sensitivity of centroid size mean and variance to sample size by calculating these parameters from progressively smaller subsamples of populations. We applied randomized selection experiments on the two sets of populations with the largest sample size in each region following the procedure of Cardini *et al.* (2015) which is tailored to geometric morphometric data. With this approach, the mean and variance are considered robust for any subsample that fails to differ from the whole population sample by  $> 5\%$ . In all analyses, mean centroid size of the smallest subsamples (the smallest of which represented five individuals) differed from the total population value by a maximum of 2.8%. Conversely, centroid size variance was only robust until sample size reached  $\sim 40$  individuals. Because we are most interested in evaluating Island Rule based on mean centroid size, rather than variance, we excluded any island populations from analysis with fewer than 10 samples (Supplementary Figure S1). This reduced the number of islands tested to eight in the Atlantic region and three in the Pacific region.

### *Thermoregulation and Endurance vs. Ecological Release*

We compared the ability of competing hypotheses to account for size variation across populations of voles using regression-based tests. To determine if island-dwelling voles are larger than mainland voles, we first conducted Kruskal-Wallis tests on the dorsal centroid size of the Atlantic and Pacific populations. Following a significant test, we used pairwise Wilcoxon Rank Sum tests, applying a Bonferroni correction, to determine which

pairs of populations were significantly different. Special attention was placed on mainland-island differences in size rather than island-to-island size differences since we are primarily interested in evaluating if Island Rule influences size variation across island populations of voles.

To assess the TEH, we evaluated how latitude and climatic conditions may explain observed variation in size using regressions. First, we obtained 2.5-minute raster data (~4 km resolution) of bioclimatic variables from the WorldClim dataset and then extracted temperature seasonality (bio4) and minimum temperature of the coldest month (bio6) for each georeferenced sampling point. We tested the relationship between these variables and the population means of Atlantic dorsal centroid size by carrying out a series of regressions on every combination of the variables. We chose linear regressions because preliminary tests indicated that our data optimally fit a linear model (linear relationships, normality, and homoscedasticity of residuals). We applied information theoretic techniques, specifically Akaike Information Criterion corrected for small sample size (AICc) and AICc weights, to infer the most appropriate model(s) following the rules of Burnham and Anderson (2004).

An alternative to Bergmann's Rule for explaining size variation is the Ecological Release Hypothesis. We evaluated ERH in a similar manner to Bergmann's Rule by carrying out a series of analyses of variance (ANOVA) on all combinations of the variables; island area, distance to the mainland, presence of mammalian or reptilian predators on mean dorsal centroid size of each Atlantic population. In these models, island area and distance to the mainland were formatted as binary factors. We classified islands as "large" if they have an area  $\geq 500 \text{ km}^2$  and "small" if their area is  $< 500 \text{ km}^2$ . We

classified distance from the mainland as “far” for islands with an uninterrupted distance of  $\geq 10$  km from the mainland coast and “near” for those with an uninterrupted distance of  $< 10$  km, assuming no island-to-island migration. We selected these thresholds based on the known immigration capacity of *M. pennsylvanicus* (Lomolino 1984, 1989) and the species-area relationship (Whitehead & Jones 1969, Santos *et al.* 2016). We designated mammalian and reptilian predator variables as “present” or “absent” for an island depending on if stable populations of at least one species of each predator type were documented in the literature and/or museum collections (Supplementary Tables S3-S5). “Mainland” was included as a level of each variable to include the mainland population in these models. Table 3 summarizes the raw characteristics of each island analyzed. As with the Bergmann’s Rule regressions, we utilized AICc and AICc weights to select the best models from this series of ANOVAs. Finally, we compared the best Bergmann’s Rule and Ecological Release models using  $R^2_{\text{adj}}$  and AICc weights to determine which competing hypothesis optimally explains observed centroid size variation.

### *Path Analysis*

Next, we pivoted to path modeling to examine the explanatory power of, and the relationships among ecological release variables in more detail. To accomplish this, we carried out a series of path analyses using the R package *lavaan 0.6-5* (Rosseel 2012). Path analysis is a powerful statistical technique nested within the broader framework of structural equation modeling (SEM, Grace *et al.* 2010). SEM enables the testing of multivariate, causal relationships among variables through the specification of pathways connecting them. This technique is an alternative to classic linear models that enables

evaluation of causal relationships by formally assessing the directionality of effects, both direct and indirect, among variables (Fan *et al.* 2016).

Because preliminary tests identified factors associated with ecological release as potentially influencing observed geographic size variation, we included variables hypothesized to drive ecological release, including island area, distance from the mainland, and presence of predators in a series of path models. We structured the models to determine if the relationship between island area, distance to the mainland, and presence or amount of predators individually predicted centroid size, or if a combined set of interactions among variables better account for an effect of island area and distance to the mainland on predators. Moreover, path analyses allowed us to 1) statistically evaluate the correspondence between hypothesized multivariate path models and data, 2) estimate the strength of both direct and indirect pathways between variables, and 3) directly evaluate the reliability of predictors (McCune & Grace 2002, Fan *et al.* 2016).

We calculated the area of each island using the polygon tool in Google Earth Pro to trace the shoreline. To account for the large areal differences across sampled islands, we log-transformed island area for path analyses. We calculated the distance of each island to the nearest mainland using the path tool in Google Earth Pro. We measured this value by determining the minimum, uninterrupted distance between the part of an island that was closest to the mainland and the mainland shoreline. We determined the number and type of predators on each sampled island based on documented island occurrences derived from museum collections, as well as through literature references.

In these path models, treatment of the variable predation differed to address several questions relating to how centroid size responds to predator type and differential predation

pressure in this system. First, to determine if the simple presence of predators impacts size variation in voles, we formatted the predator predictor as a binary presence/absence variable. Second, since predation intensity differs by type of predator (Madison 1978), we applied the binary predator variable split into presence/absence of mammalian predators or reptilian predators, respectively. To evaluate if the number of predator species (as an estimate of predation pressure) is more important to predicting vole size (Pearson 1971), we ran two path analyses formatting the predator variable as a total count of all predator species, and lastly, as a count of the mammalian and reptilian predator species separately.

To estimate variable importance, we employed the normal theory maximum likelihood method in these path models. To select the optimal path model from this series, we considered the outcome of several fit indices ( $X^2$ , CFI, and SRMR), and the amount of variation in each response variable accounted for by explanatory variables ( $R^2$ ). The  $X^2$  test compares the fit of the path model to the data compared to a null model (non-significant  $P$ -values and low  $X^2$  statistic desired), the Comparative Fit Index (CFI) compares how well the path model fits the data compared to a model assuming independence among variables (values closer to 1 are desired), and the Standardized Root Mean Residual (SRMR) is an absolute fit index that provides a measure of model error. For SRMR, values  $< 0.06$  are desired indicating lower error and thus better model fit. We could not assess the fit of the two path models that combined predator types since no degrees of freedom remained.

### *Raw Shape Variation*

Because our questions relate to both size and shape variation, we revisit the Procrustes shape coordinates. After excluding excessive missing landmark and age outliers, we conducted a series of PCAs on these coordinates of superimposed landmarks.

We colored resulting PCAs by population and overlaid 95% confidence ellipses of each population to visualize variation among groups. To test for significant overall shape differences among islands and between islands and the mainland, we extracted the scores of the first and second PCs and carried out an ANOVA on each of these components for both regions and both faces of the skull (eight tests total). We followed up significant ANOVAs with pairwise Tukey Honestly Significant Difference (HSD) tests to determine which populations differed. These tests provide a broad perspective of shape variation in this system, which is further dissected into components including allometric and residual, or non-allometric, population-level variation.

### *Allometry*

Allometry, the covariation between size and shape, is known to influence the form of organisms at multiple functional levels (Klingenberg 2016). In this system, we made ontogenetic allometry irrelevant by eliminating juvenile and subadult specimens and we further excluded influences of evolutionary allometry by working at a narrow taxonomic and phylogenetic scale within each focal region (Outomuro & Johansson 2017). We are, however, interested in addressing static allometry which is size-associated change in shape within an age group (Klingenberg 2016). To accomplish this, we carried out a multivariate analysis of covariance (MANCOVA) on the Procrustes coordinates of each specimen and log-transformed centroid size among populations and included the interaction term between centroid size and population. We carried out MANCOVAs using a residual randomization permutation procedure (rrpp) set at 1,000 iterations and we repeated the analysis for both dorsal and ventral datasets in both regions. For datasets with a significant interaction between population and size, we ran pairwise comparison tests of the slopes to

determine which population, or set of populations, had differing allometric trajectories. We applied *rrpp* to pairwise slope tests as well. Together, these analyses enabled us to decouple shape variation due to allometry and shape variation associated with specific populations.

### *Residual Shape Variation*

Since shape in voles may be evolving independent of the influences of size and geography, we used a series of analyses to evaluate residual, or pure (*i.e.*, non-allometric), shape variation. After assessing the influence of static allometry and population on shape variation, we extracted shape residuals from the allometry model of each dataset in order to analyze pure (*i.e.*, allometry-corrected) shape variation. We conducted a PCA on shape residuals to visualize the remaining shape variation. We extracted the first and second PC scores from this analysis and conducted ANOVAs on both components across island variables. If pure shape is responding evolutionarily to Island Rule factors, we expect to detect significant differences in PC scores. Like size analyses, we included island area, distance from the mainland, presence of mammalian predators, and presence of reptilian predators in ANOVAs. We applied the same area, isolation, and predator thresholds as described in the Ecological Release Hypothesis assessment of centroid size (see above).

## **RESULTS**

### *Centroid Size by Population*

We found broad support for the hypothesis that island-dwelling voles are larger than mainland voles. For example, the Kruskal-Wallis test on centroid size by population in the Atlantic region is significant ( $X^2_8 = 120.85$ ,  $P < 0.0001$ ) indicating that at least one pair of populations differ in centroid size. When comparing islands to the mainland,



pairwise Wilcoxon Rank Sum tests indicate that five of the eight island populations (62.5%) have significantly larger skulls than mainland populations (Fig. 3, Table 1). When comparing islands to islands, seven island pairs have significantly different centroid sizes (Table 1). In the Pacific region, the Kruskal-Wallis test on centroid size by population is significant ( $X^2_3 = 11.39$ ,  $P = 0.0098$ ), again indicating at least one significant pairwise difference in centroid size. However, we failed to detect a significant difference in centroid size among any island-mainland pair (0.0%), although the Admiralty Island population approaches significantly larger skulls compared to mainland populations (Fig. 3,  $P = 0.1050$ ). The only significant difference in centroid size for the Pacific region is Admiralty Island compared to Kadin Island ( $P = 0.0220$ ), with larger voles occurring on Admiralty Island (Table 2).

#### *Thermoregulation and Endurance vs. Ecological Release*

For analyses of thermoregulation and endurance, we initially ran regressions on all combinations of the variables latitude (L), temperature seasonality (S), and minimum temperature of the coldest month (T). However, we detected a suppression effect caused by latitude based on the negative common effect values obtained through commonality analysis (Nathans *et al.* 2012). Because of this, we excluded models with interactions of S or T with L from the model selection process. Both AICc and AICc weights indicate that the best TEH model is the one that includes seasonality ( $w_i = 0.61$ , Table 4). According to Burnham and Anderson's (2004) model selection rules, the null and minimum temperature models have moderately strong support given that both models have  $\Delta AICc$  less than 4.00. In contrast, the L and S\*T models have considerably less support since their  $\Delta AICc$  are between 4.00 and 7.00.

In general, we found weak and inconsistent support for size-related variation due to the TEH. In the Atlantic region, the best-supported TEH model (seasonality, see above) accounted for 22% of observed size variation, but inverse to the expectations of Bergmann's Rule (Fig. 4C). Plots of the relationships between centroid size and the other two variables demonstrate that there is no signal of size responding to latitude (Fig. 4A) and a non-significant, positive signal of size responding to minimum temperature of the coldest month (Fig. 4B). The trend of centroid size with temperature is actually opposite of expectations according to the TEH.

The series of ANOVAs on ecological release variables demonstrate that island area coupled with the presence of predators influence centroid size. This is illustrated by the substantial to moderate AICc support of models including combinations of the three variables (Table 5). The best-supported model ( $w_i = 0.39$ ) includes both area and reptilian predators. Of note, the smallest  $R^2_{\text{adj}}$  value out of the best-supported models is 0.48 while the largest is 0.65, almost triple the size variation accounted by the optimal TEH model. In direct comparison of the optimal models from each alternative hypothesis and the null, we find that ecological release is a more appropriate framework for evaluating gigantism in this system ( $w_i = 0.99$ , Table 6).

### *Path Analysis*

Results of the four path analyses we carried out are summarized in Table 7. We could not assess model fit for either of the models that combined the mammalian and reptilian predator variables since the number of estimated parameters equals the sample size ( $df = 0$ ). Despite this obstacle, path modeling consistently indicates that island area and predators are influential factors on centroid size. Based on fit indices and the  $R^2$  for

each response variable, we favor the model that treats mammalian and reptilian predators separately and formats them as counts (Fig. 5). This is because this path model accounts for over 60% of size variation and over 50% of variation in predator variables, which distinguishes this model from the two that combine predator types. Additionally, in comparison to the model treating mammalian and reptilian predators as presence/absence, the model formatting these predator types as counts has a better fit to the data. Both CFI and SRMR favor the path model with mammalian and reptilian predators as counts since these values are within the excellent range ( $CFI > .95$ ,  $SRMR < .06$ ), while the path model with mammalian and reptilian predators formatted as presence/absence performs poorly according to CFI ( $< .90$ ) and falls within the acceptable range of SRMR ( $< .10$ ).

In the optimal path model based on model selection criteria, all factors are partial regressions and so the relationships are the product of co-varying effects. For example, island area had a significant direct relationship on both the number of mammalian and reptilian predators ( $P = 0.014$  and  $0.004$ , respectively), but a non-significant direct relationship on mean centroid size. In fact, each unit increase in island area results in an expected increase of 1.2 mammalian and 0.8 reptilian predator species. Based on our data, Long Island had nine mammalian predators and four reptilian predators, whereas Muskeget Island had no mammalian or reptilian predators (see supplemental material). This is notable since the Atlantic island population most similar in size to the mainland was sampled from Long Island, while the largest voles were detected on Muskeget Island.

Indirectly, area through each type of predator had a significant negative relationship with mean centroid size but manifest with differential effects. An addition of one mammalian predator is predicted to alter unit centroid size by  $-0.022$ , while the addition of

a reptilian predator is predicted to alter unit centroid size by -0.001. Combined, the direct and indirect effects of area and predators on centroid size explained 60.4% of skull size variation across Atlantic island populations. Using the unstandardized coefficients, the total effect of island area on skull size is -0.044 (direct = -0.021, indirect reptile = -0.001, indirect mammal = -0.022) indicating that a change of 100 km<sup>2</sup> in area corresponds to a 4.4% change in skull size. From the standardized coefficients, of all the direct effects on centroid size estimated, the number of mammalian predators has the strongest influence on centroid size ( $\beta = -0.56$ ,  $P = 0.108$ ), followed by island area ( $\beta = -0.54$ ,  $P = 0.426$ ), isolation ( $\beta = -0.45$ ,  $P = 0.332$ ), and number of reptilian predators ( $\beta = -0.02$ ,  $P = 0.961$ ).

Taken together, our results suggest that number of mammalian predators, which is significantly influenced by area, is driving size change in meadow voles. Moreover, these results suggest a limited role of reptilian predators because we detect an exceptionally weak effect of the number of reptile predators on centroid size in the path model (Fig. 5). We also detect a correlation with mammalian and reptilian predators on islands (Table 8). This suggests that the significant impact of reptile predators detected in the best-supported ecological release ANOVA was likely due to the indirect effect of island area on reptile predators.

### *Shape Analyses*

PCA on Procrustes shape coordinates indicate that the first two principal components (PC) capture roughly 40% of dorsal and ventral cranium shape variation in each region (Fig. 6). All subsequent PC axes each accounted for < 10% of the remaining shape variation. PCAs on dorsal and ventral cranium shape in the Atlantic region show broad overlap across all populations. Despite this, differences in the shape and orientation

of 95% confidence ellipses, in addition to the spread of ellipse centers indicate at least some shape differences among populations on both PC1 and PC2 (Fig. 6A & 6C). In contrast, dorsal and ventral shape PCAs in the Pacific region show a greater separation between the island populations sampled compared to the mainland indicating significant shape differences. PC2 of dorsal cranium shape and PC1 of ventral cranium shape are where this island-mainland separation is most distinct (Fig. 6B & 6D).

Along dorsal PC1 in the Atlantic region, there appears to be a tendency for island populations to have relatively narrower braincases compared to the mainland. Along PC2, the primary shape change is associated with an increased length of the interparietal bone in the antero-posterior direction (Fig. 6A). Ventral shape along PC1 in the Atlantic region indicates a posterior shifting of the maxillary-jugal suture of the zygomatic arch. Ventral PC2 shows a more subtle change in shape through variation in the position of the occipital condyles relative to the paroccipital processes (Fig. 6C).

Dorsal PC1 in the Pacific region describes a similar change in shape to that of the Atlantic populations. We detect a shift from a relatively narrower braincase with a shorter and narrower interparietal bone (characteristic of individuals from Admiralty and Mitkof Islands) to a broader braincase with a wider and longer interparietal bone (Kadin Island and the Mainland). PC2 describes a change in the size of the frontal bones with island populations tending to have smaller, more anteriorly-positioned frontals while the mainland has larger, more posteriorly-positioned frontals (Fig. 6B). For ventral shape, PC1 describes an increasing breadth between the auditory bullae relative to the zygomatic arches and a decrease in the length of the rostrum relative to the braincase. Island

populations in this region have a clear tendency toward a narrower space between bullae and longer rostrum, while the mainland populations are characterized by more space between bullae and a shorter rostrum. PC2 of ventral shape describes a change in the position of the occipital condyles relative to the paroccipital processes, similar to trends observed in the Atlantic populations, but there is no clear distinction between Pacific populations along this axis (Fig. 6D).

All ANOVAs carried out on PC1 and PC2 scores of these PCAs were significant, except for PC2 in Pacific ventral cranium shape ( $P < 0.001$  in each case, Pacific ventral PC2  $P = 0.184$ ). Pairwise Tukey HSD tests reveal that six of eight island populations are significantly different in dorsal shape on PC1 compared to the mainland (Table 9). Long Island differed significantly from the same six island populations along this axis. Along dorsal PC2, only three islands differed from the mainland. However, there is a greater number of island-island differences along this axis. Atlantic ventral ANOVAs demonstrate that six islands differ from the mainland in shape along PC1, and these same islands differed from Long Island (Table 10). Along ventral PC2, four islands differed from the mainland, with a greater number of island-island differences.

PC1 on Pacific dorsal shape indicates that Admiralty and Mitkof islands differ in shape from the mainland. Along PC2, all three islands differ from the mainland (Table 11). Lastly, Pacific ventral shape demonstrates a significant difference in shape along PC1 among all island-mainland pairs (Table 12).

### *Allometry*

In all four MANCOVAs, we detected a significant association between skull size and shape ( $P = 0.001$  in each case). Static allometry accounted for 16.2% and 10.4% of dorsal cranium shape variation in the Atlantic and Pacific regions, respectively. In contrast, allometry accounted for only 4.5% and 6.5% of ventral cranium shape variation in each region (Table 13). We also detected a significant association between population and shape in every MANCOVA ( $P = 0.001$  in each case). For dorsal cranium shape, population accounted for 13.4% and 10.2% of variation in the Atlantic and Pacific regions. For ventral shape, population accounted for 17.4% and 20.2% of the variation (Table 13).

In the two dorsal shape MANCOVAs, a significant interaction between skull size and population was observed ( $P_{\text{Atlantic}} = 0.004$ ,  $P_{\text{Pacific}} = 0.017$ ). This significant interaction implies that the allometric slope differs by population (Fig. 7A-B). The pairwise slope tests that followed indicate that eight population pairs have different slopes in the Atlantic dorsal data (Table 14), while only the slopes of Admiralty Island and the Mainland differed in the Pacific dorsal data (Tables 15). No significant interaction between skull size and population was observed in the ventral cranium data of either region (Fig. 7C-D).

In general, allometry of the dorsal cranium of *M. pennsylvanicus* is characterized by an increased prominence of the processes at the posterior of the braincase (including the mastoid-exoccipital and lambdoidal crests). Dorsal allometry in this taxon is also characterized by a narrowing of the braincase relative to zygomatic breadth (Fig. 7A-B). Conversely, shape changes associated with ventral allometry in *M. pennsylvanicus* differ by region. In the Atlantic populations, ventral allometry is associated with a relative broadening of the space between the occipital condyles and a relative shift in the antero-

posterior position of the maxillary-jugal suture on the zygomatic arch (Fig. 7C). Ventral allometry in the Pacific populations differs in that the most prominent change is a lengthening of the rostrum relative to the braincase and a narrowing of the space between auditory bullae (Fig. 7D).

### *Residual Shape*

After controlling for shape variation due to allometry and population differences, PCAs on residual shape variation failed to detect any discernable patterns in shape associated with island characteristics including island area, distance from the mainland, or the presence of mammalian and reptilian predators (Fig. 8). All ANOVAs on PC1 and PC2 scores factored by these variables failed to reject the null hypothesis of no difference in shape among the different levels of the variables.

## **DISCUSSION**

Our results provide evidence that signals of Island Rule can be detected at finer taxonomic levels than was previously thought (Itescu 2019) and we detect three important patterns concerning size and shape variation. Within *Microtus pennsylvanicus*, insular gigantism evolved on islands with features consistent with expectations of the Ecological Release Hypothesis, with the lack of mammalian predators emerging as the most significant factor. However, mammalian predators are significantly, indirectly influenced by island area as well. Conversely, our analyses of shape variation indicate that, at least for this species on these islands, cranium shape does not appear to respond to insularity in concordance with body size. While the results of our allometric analyses suggest there is active shape divergence occurring across populations, at least two scenarios may account



for this observed variation including insufficient time for significant shape evolution to occur and founder effects. Each of these broad patterns has important implications for understanding the impacts of insularity and warrants further discussion, but also raises concerns with emerging effects of climate change.

*Insular gigantism evolves in accordance with the Ecological Release Hypothesis*

We considered and evaluated the four causal hypotheses proposed to account for insular gigantism in small-bodied mammals (Lomolino *et al.* 2012) including thermoregulation and endurance (Bergmann's Rule), immigrant selection, resource subsidy, and ecological release. In the Atlantic region, we detected significantly larger voles on five of the eight islands tested (Fig. 3). The results of our causal hypothesis tests suggest that this trend is not attributable to Bergmann's Rule (Fig. 4). In fact, across islands in both regions, we find evidence of an unexpected inverse Bergmannian pattern where Pacific region voles show an overall tendency to be smaller in size compared to the lower latitude Atlantic region populations (Fig. 3). This seemingly paradoxical result has at least two caveats, however. First, it is possible that the tests we conducted were at too narrow a latitudinal range, and thus did not have enough power to detect a trend if it does exist (Meiri *et al.* 2007). However, if these data do represent a true absence of association between size and latitude/bioclimate variables, then this finding adds to the list of potential exceptions to Bergmann's Rule (Sargis *et al.* 2018). Second, Jackson and Cook (in press) suggest that Atlantic and Pacific island voles perhaps belong to different species, but certainly belong to evolutionarily divergent lineages. Consequently, the differences detected between regions could be the product of evolutionary history and not ecogeographic variation.

Similarly, in terms of Island Rule, we fail to detect the larger magnitude of body size change expected in higher latitude islands (Fig. 4). Since these trends are inconsistent with Bergmann's Rule and Lomolino's TEH, we conclude that this causal hypothesis is a poor fit for this system.

While immigrant selection often enables larger animals to occupy islands, we outright rejected this hypothesis because geological evidence suggests that the islands tested in the Atlantic region were connected to the mainland during the glacial periods and perhaps as recently as 3,000 years ago (Weddle & Choate 1983). Subsequently, as ice sheets retreated, newly un-glaciated land became exposed enabling organisms to colonize and perhaps freely migrate, including voles. Consequently, populations of *M. pennsylvanicus* likely were isolated on the islands as sea levels rose while most of the continental shelf was submerged leaving present-day islands (Weddle & Choate 1983).

Similarly, parts of the Alexander Archipelago were glaciated by the Cordilleran ice sheet at the Last Glacial Maximum (LGM, Darvill *et al.* 2018). With the retreat of ice sheets, organisms would have been able to access all parts of the archipelago and only later become isolated on the islands as sea levels rose (Darvill *et al.* 2018). Across both regions, glacial retreat and colonization events likely occurred between 17 and 6 thousand years ago (Weddle & Choate 1983, Darvill *et al.* 2018). Furthermore, while some Alexander Archipelago mammals show signals of an island refugium hypothesis (Dawson *et al.* 2014, Sawyer & Cook 2016, Sawyer *et al.* 2017), island populations of *M. pennsylvanicus* fail to reflect an analogous signal, instead suggesting recent, post-Pleistocene colonization with subsequent isolation (Jackson & Cook, in press). Because all island populations were likely

isolated in relative temporal proximity to each other, this suggests that the Immigrant Selection Hypothesis is an inappropriate model for this system and thus likely invalid. This conclusion is further supported by non-significant associations between isolation and centroid size (Table 5, Fig. 5). Because the Resource Subsidy Hypothesis concerns increased body size in predators that consume aquatic prey, it is likely an irrelevant hypothesis for this herbivorous species too.

Results of path modeling suggest that the mean centroid size of an island population in the Atlantic region has the strongest direct relationship with mammalian predators, which is in turn influenced by island area. Although the *P*-values for all direct effects on mean centroid size were marginally or not significant, this is likely due to a limitation in statistical power that results from the limited number of island populations available. When combined, the total effect of 100 km<sup>2</sup> change in area results in a 4.4% expected change in skull size. Because this study is focused on voles that inhabit a limited number of islands, the sampled populations are likely representative of the observed effects across all populations.

In the favored path model, each island variable had a direct, inverse relationship with mean centroid size (*e.g.*, larger skulls on smaller islands, distant islands, or islands without predators). This inverse pattern is precisely as predicted by the Ecological Release Hypothesis. Additionally, path modeling revealed indirect influences on centroid size via a positive direct relationship between island area and both types of predators. Therefore, while area biogeographically influences reptilian predators, reptilian predators fail to manifest in significant size differences and fail to have a relative influence on mean

centroid size of voles. Consequently, if we had relied on ANOVA alone, we may have been misled, thus highlighting the merits of path modeling approaches to decoupling the joint effects of alternative predictor variables on the response variable. This finding of a lack of mammalian predators driving gigantism while reptilian predators display a weaker effect is consistent with previous research that detected gigantism in insular *Peromyscus* despite a presence of reptilian predators on the island (Kuhn *et al.* 2016). Taken together, both direct and indirect relationships were expected given island biogeographic predictions and their differential effects across trophic levels (Holt *et al.* 1999).

The optimal model detected a non-significant positive relationship between island isolation and number of predators, which is opposite of expectations of the ERH. Three scenarios may account for this discrepancy. First, anthropogenic introductions are globally common and introductions of non-native predators (*e.g.*, domestic cats) and limited evidence of either re-introductions of extirpated native predators or introductions of congeners from neighboring islands within the Atlantic region (Miller 1896, Blackburn *et al.* 2004, van der Geer 2018) could explain this unexpected result through artificial immigration. Second, a more complex biogeographic process such as island-to-island, or stepping-stone, colonization may account for excessive predators on distant islands (Gilpin 1980). Finally, like voles, predators are expected to have been isolated on distant islands during glacial retreat, leaving remnant populations. While phylogeographic data are lacking for predators from this region, if predators were isolated during glacial retreat then immigration processes are likely inapplicable for predators as well, perhaps providing the most likely explanation for this unanticipated pattern.

Despite failing to detect larger-skulled voles within the Pacific region, this does not necessarily fail to follow expectations of the Ecological Release Hypothesis. The Alexander Archipelago islands are large (4362 km<sup>2</sup> and 544 km<sup>2</sup> for Admiralty and Mitkof Islands, respectively), and they are closer in proximity to one another and the mainland when compared to the Atlantic islands. With the exception of Kadin Island which is relatively small (6.68 km<sup>2</sup>), the large sizes and proximity of islands to the mainland are expected to inhibit the evolution of larger body sizes in small organisms like *M. pennsylvanicus*. One variable that all the Pacific islands we tested share, however, is a presence of several mammalian predators which directly prevent ecological release. Given that lack of predators seems to be the driving force of gigantism in the Atlantic region, it is thus unsurprising that we fail to observe gigantism in the Pacific, predator-laden region.

*Shape variation is explained by population-level differences in static allometry*

Based on previous morphological studies of *M. pennsylvanicus* in the Atlantic region (Miller 1896, Chamberlain 1954, Wheeler 1956), it was unsurprising that PCAs on raw shape coordinates demonstrated variation among populations. Similarly, we were not surprised to detect differences in static allometry among populations since dramatic intraspecific differences in allometric trajectories are known to occur in other rodents (Marcy *et al.* 2016). What was interesting from our results of the initial PCAs on shape coordinates and the allometry MANCOVAs that followed was that the composite shape variable represented by PC1 closely resembles the predicted shape changes associated with static allometric growth (Figs. 6 – 7). While the initial PCAs only incorporated shape coordinates, the allometric function used size as a covariate to predict the shape of

individuals. Since the deformation grids of these two differing analyses resemble one another so closely, it illustrates that the greatest source of shape variation in these populations is their variation in size.

Upon further analysis of each population's allometries, we determined that there are significant differences in the allometric slope of populations in both regions' dorsal data, but not ventral data. While these slope differences could be a consequence of differing sample sizes per population, this scenario is unlikely since a similar trend is not observed in the ventral data whose sample sizes are slightly lower. An increased allometric slope indicates a greater degree of shape change for every unit of size change. This leads to more exaggerated allometric change in populations with steeper slopes. The degree of allometry expressed by a population is one way that different functional morphologies can arise (Marcy *et al.* 2016). Therefore, it is possible that these differences in slope evolved in some populations as an adaptive response to some aspect of insularity or they could be an artefact of a process like founder effects.

While significant differences in slope preclude a test for differences in y-intercepts, some patterns still emerge. In every allometry plot, the mainland population is positioned at the lowest predicted shape with all islands shifted to higher predicted shape values. This indicates that for any given size, island populations express a greater predicted shape value when compared to mainland populations. Similar to differences in slope, a trend like this could be a result of founder effects or, in this case, the accelerated rate of evolution observed in island systems (Millien 2006). The isolation of these populations as sea level rose and subsequent changes in the island environment likely presented meadow voles with

a new suite of environmental conditions and perhaps novel selective pressures that are driving skull shape in a different direction than the mainland populations. Founder effects combined with accelerated evolution in island systems could at least partially explain why we detect significant shape variation in the Pacific region, but not size differences as in the Atlantic region.

Another pattern apparent in the allometric plots is that the overall magnitude of shape variation differs between the dorsal and ventral cranium. The range of values plotted along the y-axis decreases from 0.10 to only 0.03 in the ventral plots. This indicates that the shape of the ventral cranium is not as variable as the dorsal cranium. This pattern is consistent with others reported in the literature which are often associated with higher evolutionary constraints placed on the ventral cranium due to its function in feeding behavior (Figueirido *et al.* 2011, Arbour *et al.* 2019).

After accounting for the dependence of shape on size, we failed to detect any signal of residual shape associated with island variables (Fig. 8). The pattern of points in each panel suggest that all the remaining shape variation is random, naturally occurring variation in these populations. Ultimately, cranium shape appears to be evolving due to alterations in allometric growth in this species rather than through non-allometric variation. Since allometric changes do not solely appear in islands where significant size increases were detected, this suggests that allometric trajectories are responding to additional variables independent of size. For example, Marcy *et al.* (2016) found that dramatic differences in allometric slopes and y-intercepts of populations of pocket gophers (Genus *Thomomys*) produced diverse cranial and humeral morphologies that facilitated adaptation to different

soil characteristics. Furthermore, Cardini and Polly (2013) assessed the role of allometry in the tendency for larger mammals to have longer faces and demonstrated that skull size can impact functional and adaptive aspects of morphology when it introduces constraints on form. While the larger size of voles in some Atlantic islands will inherently pull along, and even amplify, shape change due to the relationship between size and shape, shape is still responding to something else in order to produce the patterns observed in the Pacific region and in Atlantic islands where gigantism was not detected. Evaluating whether this pattern was generated by founder effects or as a response to insularity requires further study with additional sampling.

### *Conclusions*

We carried out geometric morphometric analyses on a widespread species of vole that inhabits multiple island systems across North America. Our results are among the first to indicate that Island Rule can be detected at the intraspecific level. In contrast to many Island Rule studies that evaluated body size evolution over geological time scales (Lomolino *et al.* 2013), this study provides new evidence that significant body size evolution can occur over relatively short timescales.

In meadow voles, we determined that insular gigantism is driven by ecological release, especially by release from predation when compared to alternative hypotheses (thermoregulation and endurance, immigrant selection, resource subsidy). Although gigantism was not observed in all islands sampled, the exceptions to Island Rule are readily explained by features of those islands which would preclude ecological release. We further suspect that if the nature of any of these Pacific islands were to change, such as through



the local extirpation of predators, the voles inhabiting them would follow a similar evolutionary trajectory to that of the Atlantic populations.

This project highlights the sensitivity of island endemics to introduced predators in regions where they have already begun adapting to an absence of predators. Of note, two populations of *M. pennsylvanicus* at its range margins have gone extinct (Allen 1942, List *et al.* 2010) and there is no reason to assume that other populations are less vulnerable to environmental disturbance.

Our analyses of shape variation revealed that, contrary to suggestions that an “island rule of shape” (Wright *et al.* 2016, Csiki-Sava *et al.* 2018) may occur, all detectable patterns of shape variation in this species were attributed to the association between cranium size and shape (static allometry). No associations between pure (size and allometry-corrected) shape and island characteristics were detected. This suggests that non-allometric cranium shape may not respond to insularity in the same manner as body size. It is, however, possible that specialized anatomical features like wings may indeed express a predictable response to insularity, as proposed by Wright *et al.* (2016).

We found that the ventral cranium of *M. pennsylvanicus* displays more subtle changes in shape, as compared to the dorsal cranium. This may indicate the presence of morphological constraints on ventral shape, possibly related to the preservation of functional traits related to feeding mechanisms (Figueirido *et al.* 2011, Cardini & Polly 2013, Arbour *et al.* 2019). Exploration of this hypothesis necessitates further study.

While this project was limited in scope to studying islands with pre-existing collections of *M. pennsylvanicus* skulls, the strength of conclusions drawn in this system would benefit from further collection of specimens from other islands that *M. pennsylvanicus* inhabits. This project would be augmented by the addition of a genetic component to explore the molecular or phenotypically plastic mechanisms driving observed morphological change. This study presents a new application of path analysis to explore causal hypotheses related to Island Rule and broadens the previously-accepted scope of this ecogeographic rule to include finer-scaled taxonomic levels. From this evidence, we conclude that Island Rule is a latent evolutionary process whose manifestation in an organism depends on environmental context and that allometry may result in important functional consequences of Island Rule on cranium shape.

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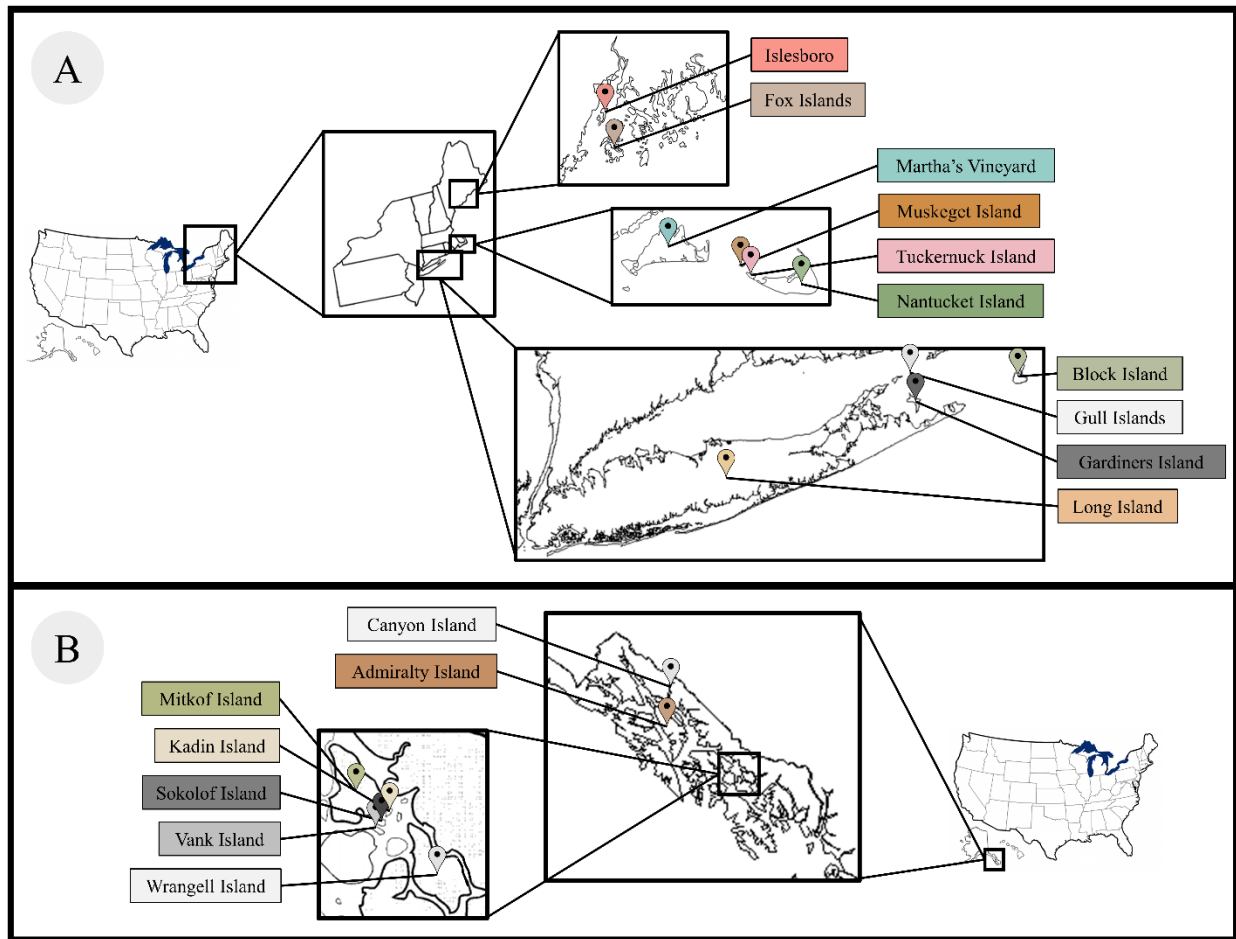
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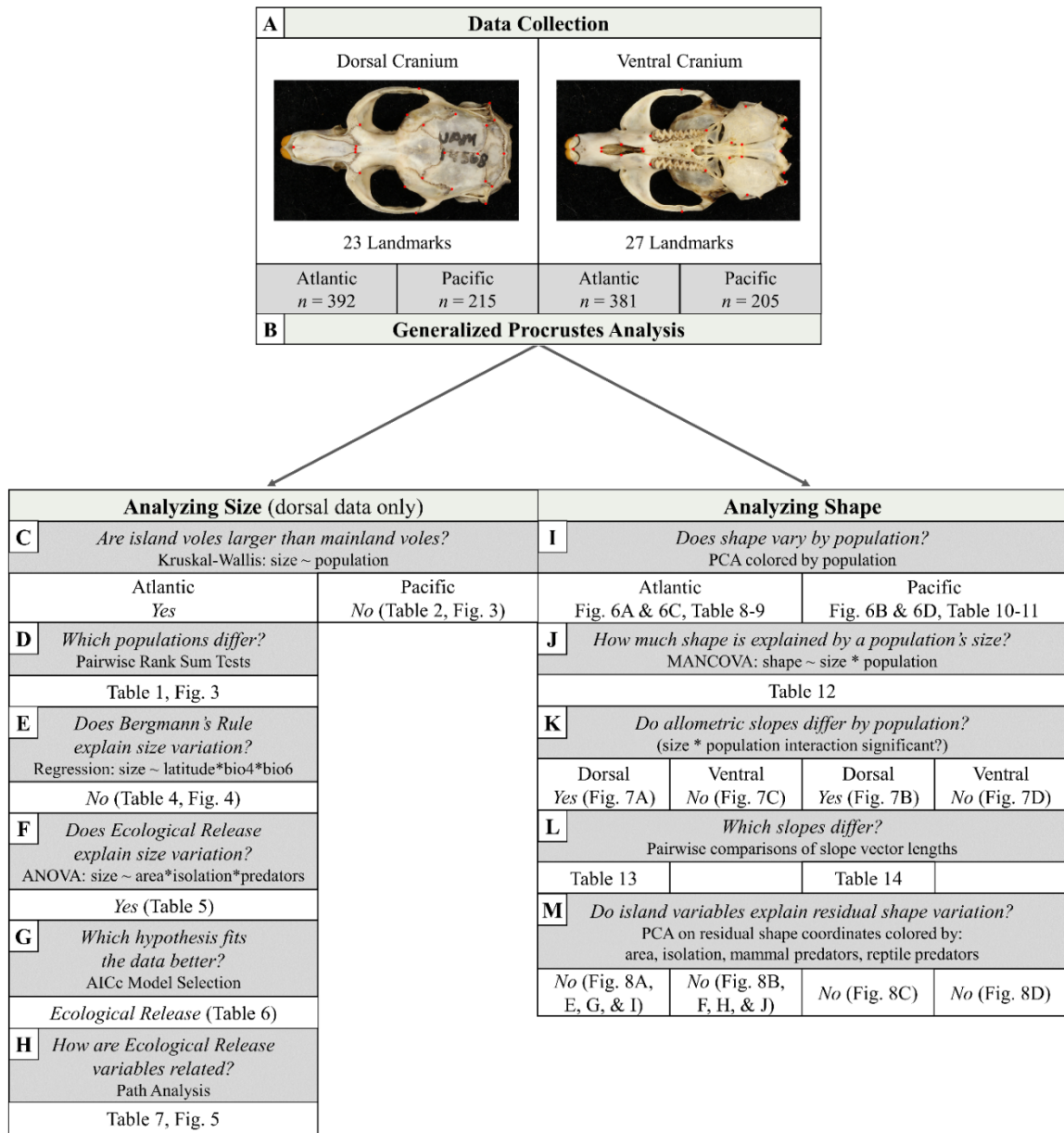


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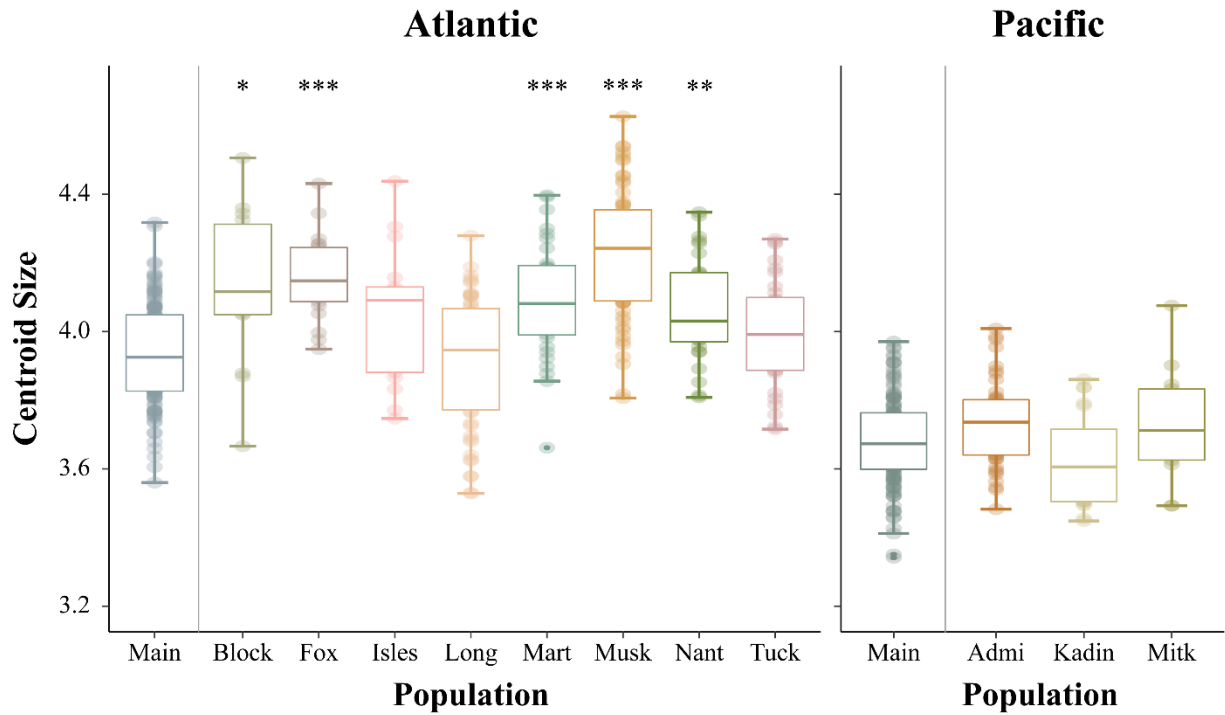
## FIGURES



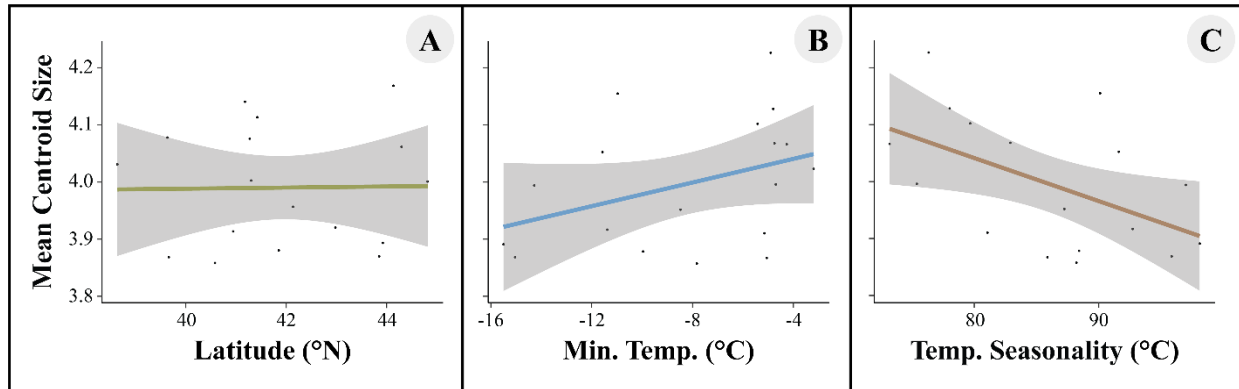
**Figure 1.** Maps indicating the locations of islands sampled in the Atlantic (A) and Pacific (B) regions to evaluate alternative causal hypotheses of Island Rule in meadow voles (*Microtus pennsylvanicus*). Islands colored in grayscale were not used in analyses due to limited availability of specimens.



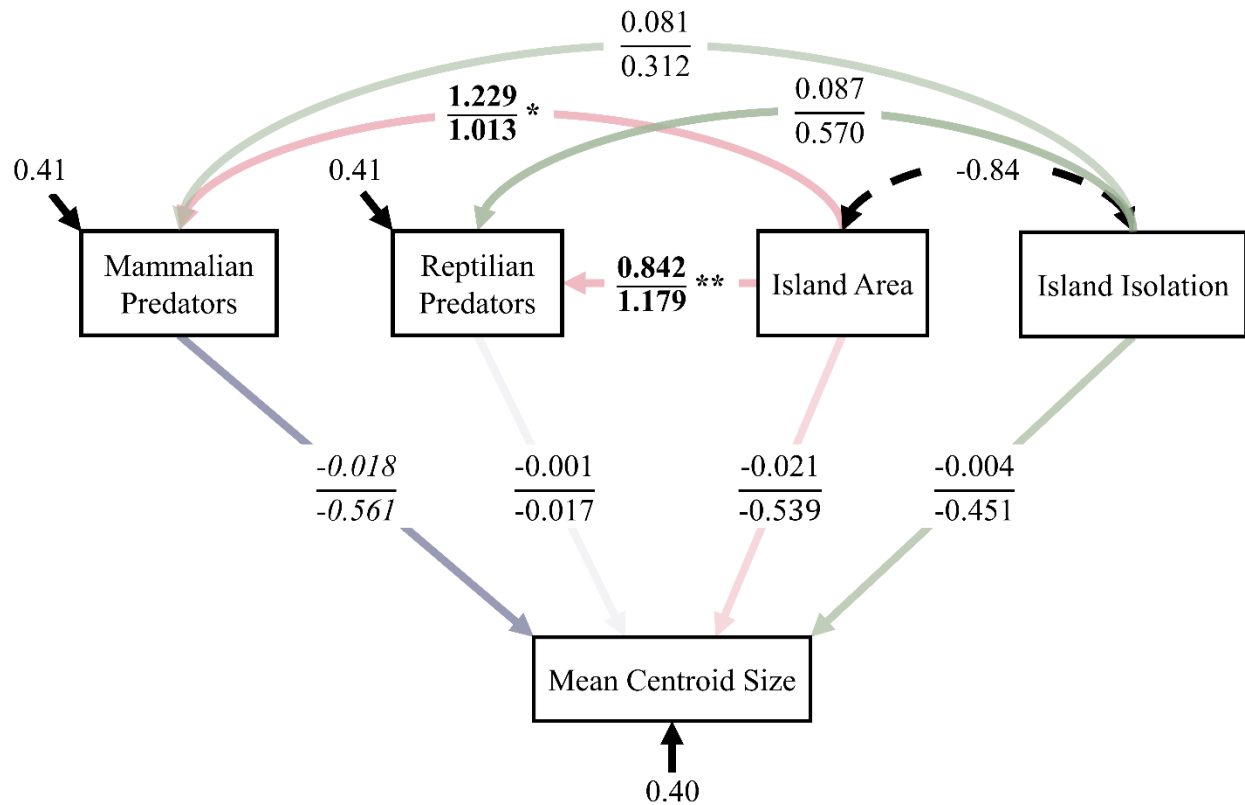
**Figure 2.** Research questions, methods, and analyses summary. White boxes below each question serve as directories to relevant results (tables and figures). **A.** 2D photographs were taken of each specimen on their dorsal and ventral faces. Landmarks were digitized using the tps suite of software (Rohlf 2018). **B – M.** We conducted all statistical analyses in R and used *geomorph* 3.0 (Adams 2019) for all geometric morphometric-specific techniques. **E – F.** We carried out a regression (E) and ANOVA (F) on all combinations of variables. **H.** We conducted a series of path analyses on the same dataset using different formats of the predator variables. See methods and associated Tables/Figures for more details. **J – L.** We applied residual randomization permutation procedures to assess significance of the tests associated with allometry.



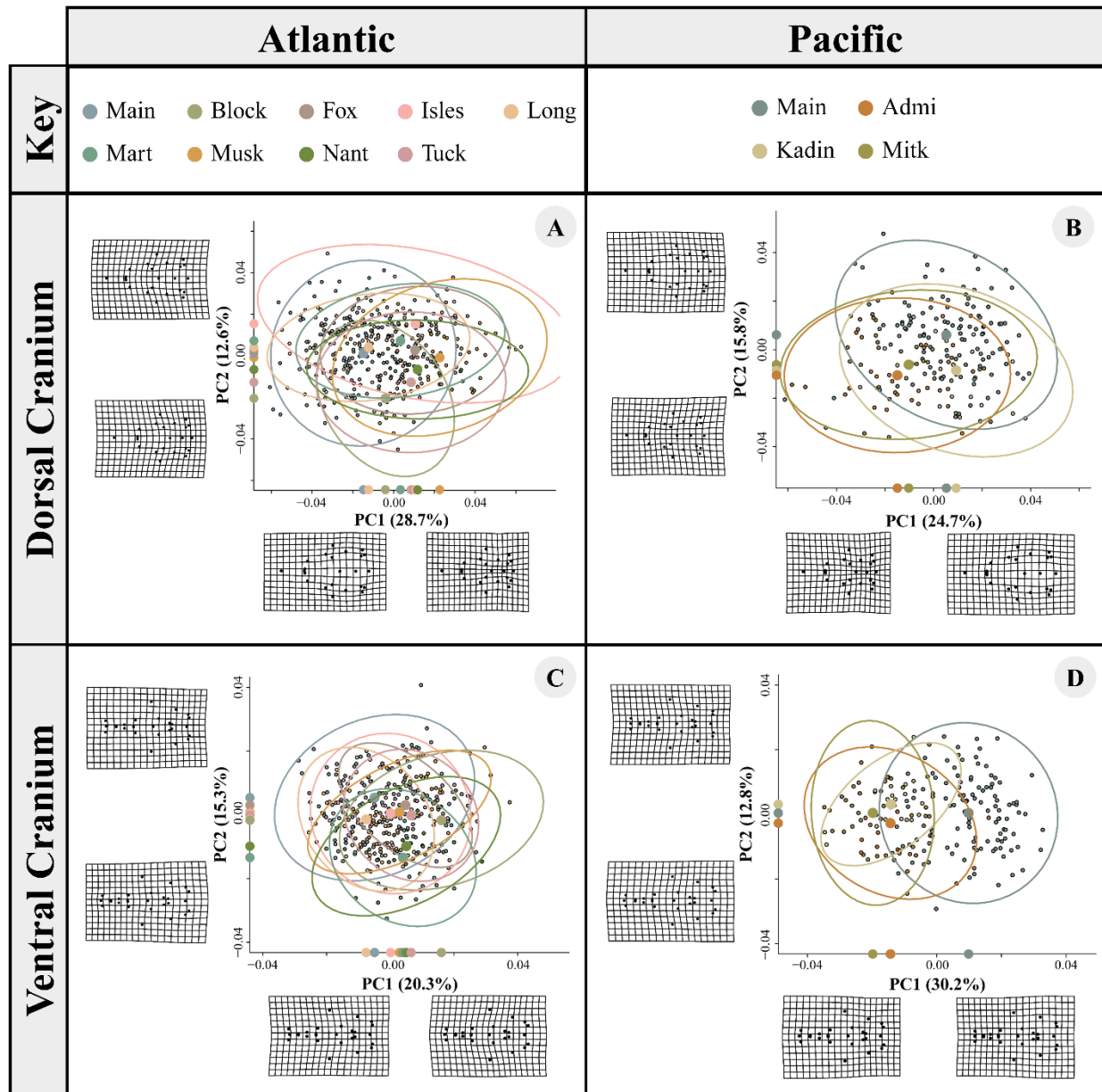
**Figure 3.** Box plots displaying variation in dorsal cranium centroid size in Atlantic and Pacific region populations. Population names are abbreviated. The mainland population of each region is located along the left axis of plots. Asterisks indicate the pairwise significance level of island centroid size relative to the mainland (\* =  $P < .05$ , \*\* =  $P < .01$ , \*\*\* =  $P < .001$ ). Boxes represent the interquartile range (IQR) with the line dividing the boxes representing the median. Whiskers extend to 1.5x the IQR.



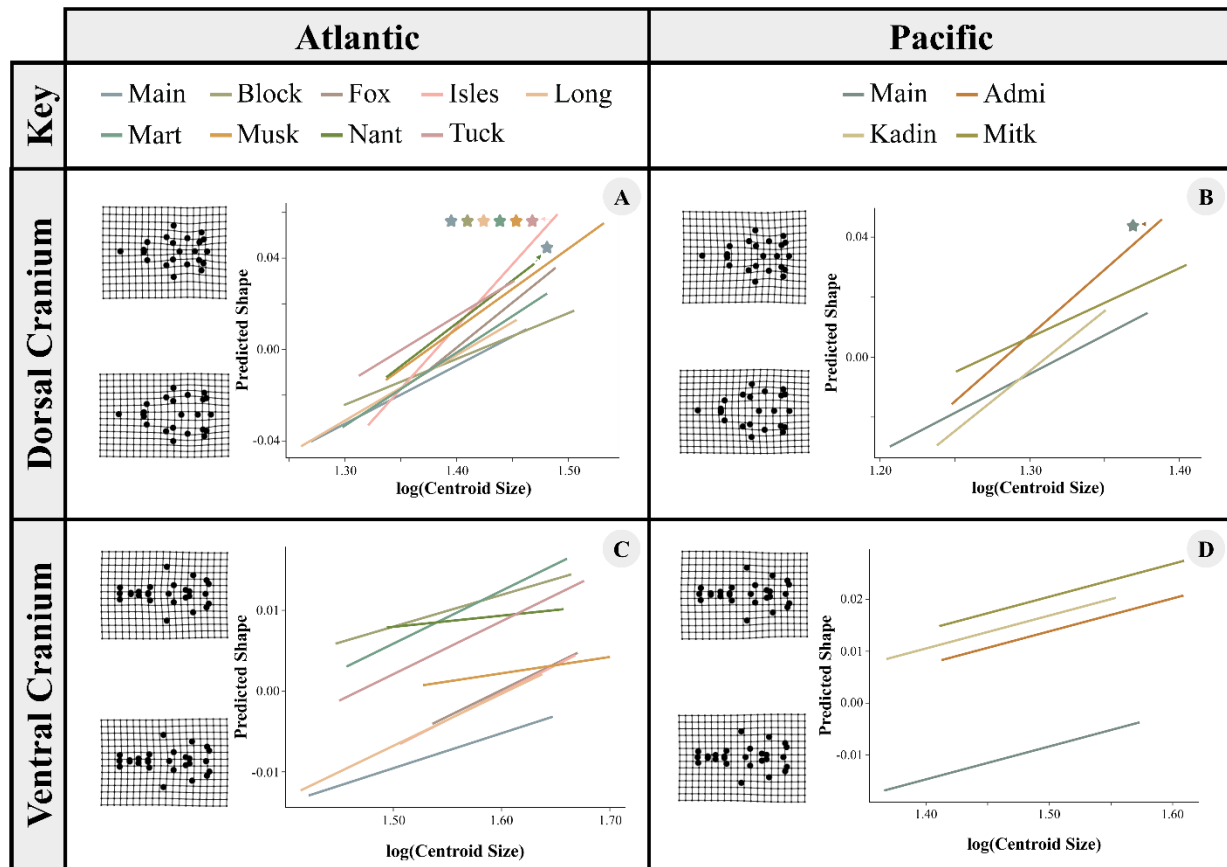
**Figure 4.** Linear regressions of thermoregulation and endurance-related variables on population mean centroid size for meadow voles (*Microtus pennsylvanicus*) including **A.** Latitude ( $F_{1,16} = 0.01$ ,  $P = 0.922$ ,  $R^2_{\text{adj}} = -0.06$ ), **B.** Minimum Temperature of the Coldest Month ( $F_{1,16} = 2.66$ ,  $P = 0.123$ ,  $R^2_{\text{adj}} = 0.09$ ), and **C.** Temperature Seasonality ( $F_{1,16} = 5.76$ ,  $P = 0.029$ ,  $R^2_{\text{adj}} = 0.22$ ). Latitude is in °N, Minimum Temperature of the Coldest Month (bioclimatic variable 4) is measured in °C, and Temperature Seasonality (bioclimatic variable 6) is calculated as the standard deviation of mean monthly temperatures in °C (O'Donnell & Ignizio 2012). The shaded area along each regression line indicates the 95% confidence interval of the regression line. Plot A demonstrates no association between latitude and size (traditional definition of Bergmann's Rule). Plots B and C demonstrate an inverse of Bergmann's Rule since size is expected to decrease with increasing temperature and increase with increasing seasonality.



**Figure 5.** Visual representation of the best-supported path model for predicting centroid size in meadow voles (*Microtus pennsylvanicus*) occupying the Atlantic islands. Solid lines indicate a causal relationship with the arrowhead directed at the responding variable. Dotted, double-headed arrows indicate a correlation between exogenous variables (the value within the dotted line is  $r$ ). Upper values reported within each causal pathway are the unstandardized partial regression coefficients and lower values report the standardized  $\beta$ -coefficients indicating the relative strength of associations. Bold indicates a significant  $P$ -value (\* =  $P < 0.05$ , \*\* =  $P < 0.01$ ) for that relationship and italics indicate marginal significance ( $0.10 > P > 0.05$ ). The opacity of solid arrows represents their  $P$ -value (more opaque = smaller  $P$ ). Short, black arrows directed at endogenous variables indicate their associated standard error term. Colors reflect the source of a relationship (pink = island area, green = island isolation, purple = predators).

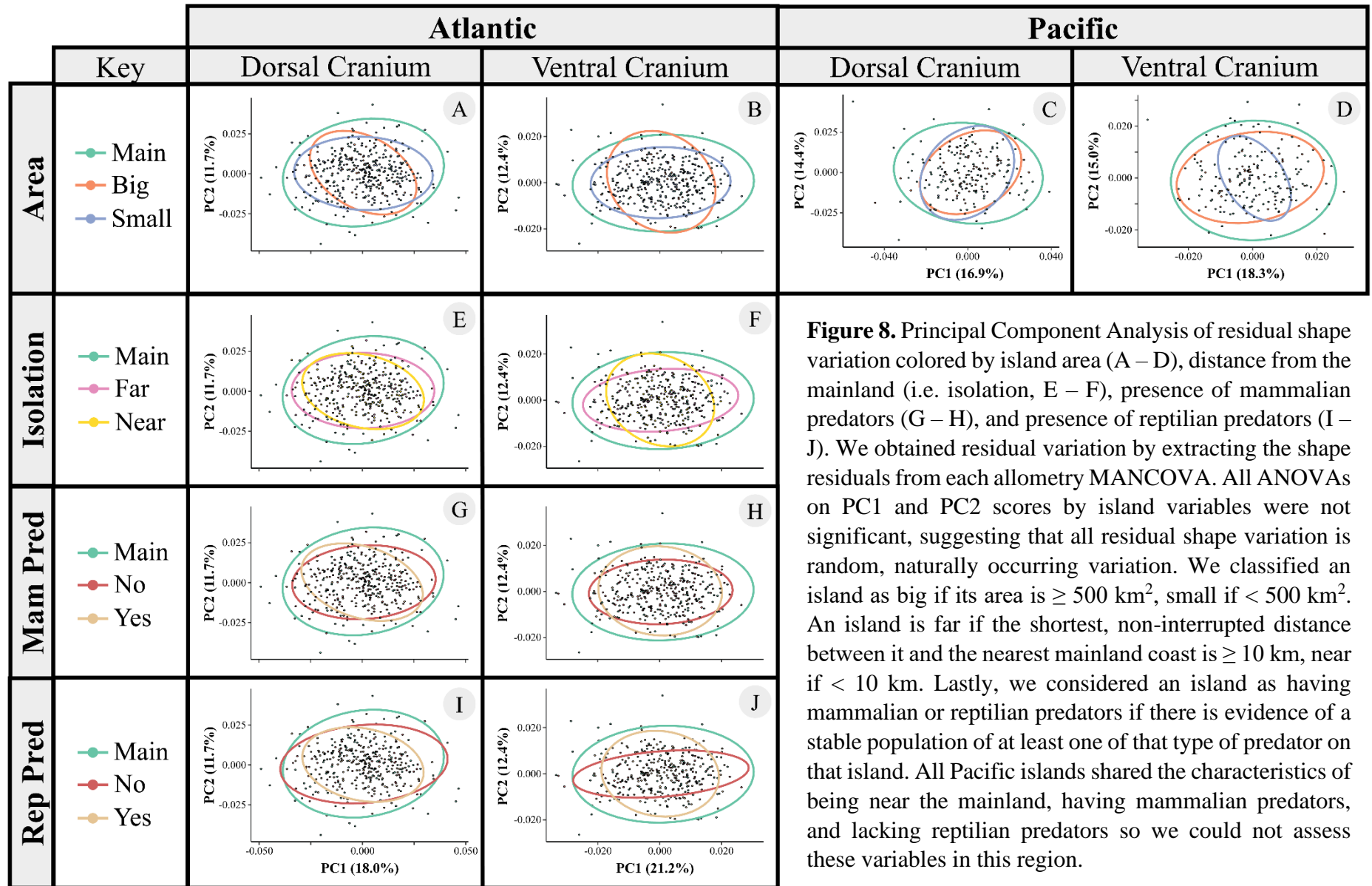


**Figure 6.** Principal Component Analysis of cranium shape. Points and 95% confidence ellipses are colored by population. Points positioned along each axis are the ellipse centers of each population, indicating the dispersion of populations across PC1 and PC2. Deformation grids along each axis indicate the shapes associated with maximum and minimum values. Dorsal cranium PC1 (A & B) describes the change in relative size of the frontal, parietal, and interparietal bones associated with allometry. Dorsal cranium PC2 captures a relative lengthening of the rostrum and frontal bones. Ventral cranium PC1 (C & D) describes increased zygomatic breadth relative to the rest of the skull associated with allometry. Ventral cranium PC2 captures the extension of the premaxilla anterior to the incisive alveoli.



**Figure 7.** Cranial shape related to allometry colored by population. Deformation grids reflect the shape change associated with increased centroid size. For dorsal cranium shape (A & B), allometry results in a relative constriction of braincase bones due to broadening of the braincase. In ventral cranium shape (C & D), allometry results in a relative broadening of the zygomatic arches and relative narrowing of the auditory bullae. Colored stars in dorsal cranium panels indicate pairwise differences in slope. In the Atlantic region (A), Islesboro has a significantly steeper slope than most other populations while Nantucket has a steeper slope only compared to the mainland. In the Pacific region (B), Admiralty Island has a significantly steeper slope than the mainland. We did not detect any significant differences in slope for either ventral cranium dataset.





**Figure 8.** Principal Component Analysis of residual shape variation colored by island area (A – D), distance from the mainland (i.e. isolation, E – F), presence of mammalian predators (G – H), and presence of reptilian predators (I – J). We obtained residual variation by extracting the shape residuals from each allometry MANCOVA. All ANOVAs on PC1 and PC2 scores by island variables were not significant, suggesting that all residual shape variation is random, naturally occurring variation. We classified an island as big if its area is  $\geq 500 \text{ km}^2$ , small if  $< 500 \text{ km}^2$ . An island is far if the shortest, non-interrupted distance between it and the nearest mainland coast is  $\geq 10 \text{ km}$ , near if  $< 10 \text{ km}$ . Lastly, we considered an island as having mammalian or reptilian predators if there is evidence of a stable population of at least one of that type of predator on that island. All Pacific islands shared the characteristics of being near the mainland, having mammalian predators, and lacking reptilian predators so we could not assess these variables in this region.

## TABLES

**Table 1.** Pairwise comparisons of centroid size in the Atlantic dorsal cranium dataset. Statistical significance was evaluated with pairwise Wilcoxon Rank Sum tests using the Bonferroni correction. Values reported are *P*-values with bold indicating  $P < .05$ . Italics indicate  $P < .10$ . Populations are abbreviated to 4-5 letters.

	Main	Block	Fox	Isles	Long	Mart	Musk	Nant	Tuck
Block	<b>0.035</b>	-							
Fox	<b>&lt; 0.001</b>	1.000	-						
Isles	0.475	1.000	1.000	-					
Long	1.000	<i>0.089</i>	<b>&lt; 0.001</b>	0.724	-				
Mart	<b>&lt; 0.001</b>	1.000	1.000	1.000	<b>0.001</b>	-			
Musk	<b>&lt; 0.001</b>	1.000	1.000	<i>0.098</i>	<b>&lt; 0.001</b>	<i>0.087</i>	-		
Nant	<b>0.009</b>	1.000	1.000	1.000	<b>0.035</b>	1.000	<b>0.007</b>	-	
Tuck	1.000	1.000	<b>0.016</b>	1.000	1.000	0.469	<b>&lt; 0.001</b>	1.000	-

**Table 2.** Pairwise comparisons of centroid size in the Pacific dorsal cranial dataset. Statistical significance was evaluated with pairwise Wilcoxon Rank Sum tests using the Bonferroni correction. Values reported are *P*-values with bold indicating  $P < .05$ . Populations are abbreviated to 4-5 letters.

	Main	Admi	Kadin	Mitk
Admi	0.105	-		
Kadin	0.340	<b>0.022</b>	-	
Mitk	1.000	1.000	0.521	-

**Table 3.** Characteristics and sample size of populations analyzed including area and distance from the mainland (for island populations), number of mammalian predators, and number of reptilian predators. Area and Isolation values were obtained using the polygon and path tools in Google Earth Pro, respectively. Number of each predator type was informed by museum specimen collections and the literature.

Population	<i>n</i>	Area (km <sup>2</sup> )	Isolation (km)	Mammalian Predators (# of species)	Reptilian Predators (# of species)
<i>Atlantic Region</i>					
Mainland	124	NA	NA	12	12
Block	14	25.20	14.76	0	3
Fox	21	90.90	8.37	0	0
Isles	17	12.60	2.85	1	1
Long	54	3630.00	0.40	9	4
Mart	32	265.00	5.68	1	4
Musk	64	1.02	28.30	0	0
Nant	28	120.80	16.75	1	4
Tuck	32	3.63	33.08	0	1
<i>Pacific Region</i>					
Mainland	123	NA	NA	9	NA
Admi	47	4362.10	3.32	4	NA
Kadin	20	6.68	4.86	2	NA
Mitk	13	544.00	5.73	4	NA

**Table 4.** Bergmann's Rule Hypothesis model comparisons. Regressions were used to assess the explanatory power of latitude (L), temperature seasonality (S), and minimum temperature of the coldest month (M) on dorsal cranium centroid size. A model was run on each variable individually and the combination of S and T. Latitude acted as a suppressor in combination with the bioclimatic variables, so we excluded those models from the final selection process. AICc and AICc weights were used to identify the best-supported model. Bold indicates the best-supported model ( $\Delta\text{AICc} < 5.00$ ).

Model Parameters	<i>K</i>	<i>P</i>	$R^2_{\text{adj}}$	AICc	$\Delta\text{AICc}$	$w_i$
Null	2	< 0.0001		-23.93	2.62	0.16
Latitude	3	0.9219	-0.06	-21.03	5.52	0.04
<b>Seasonality (S)</b>	<b>3</b>	<b>0.0289</b>	<b>0.22</b>	<b>-26.55</b>	<b>0.00</b>	<b>0.61</b>
Min. Temperature (T)	3	0.1226	0.09	-23.79	2.77	0.15
S*T	5	0.1338	0.17	-20.68	5.88	0.03

**Table 5.** Ecological Release Hypothesis model comparisons. ANOVA models were used to assess the explanatory power of island area (A), isolation (I), and presence of mammalian (M) and/or reptilian (R) predators on dorsal cranium centroid size. A model was run on all combinations of these variables. AICc and AICc weights were used to identify the best-supported models. Bold indicates the best-supported models ( $\Delta\text{AICc} < 5.00$ ).

Model Parameters	<i>K</i>	<i>P</i>	$R^2_{\text{adj}}$	AICc	$\Delta\text{AICc}$	$w_i$
Null	2	< 0.0001		-23.93	11.96	0.00
<b>Area (A)</b>	<b>2</b>	<b>0.0009</b>	<b>0.56</b>	<b>-34.55</b>	<b>1.34</b>	<b>0.20</b>
Isolation (I)	2	0.0076	0.41	-29.37	6.52	0.01
<b>Mammal Predators (M)</b>	<b>2</b>	<b>0.0031</b>	<b>0.48</b>	<b>-31.54</b>	<b>4.35</b>	<b>0.04</b>
<b>Reptile Predators (R)</b>	<b>2</b>	<b>0.0009</b>	<b>0.56</b>	<b>-34.60</b>	<b>1.29</b>	<b>0.20</b>
A*I	3	0.0036	0.53	-30.62	5.27	0.03
<b>A*M</b>	<b>3</b>	<b>0.0024</b>	<b>0.55</b>	<b>-31.69</b>	<b>4.21</b>	<b>0.05</b>
<b>A*R</b>	<b>3</b>	<b>0.0005</b>	<b>0.65</b>	<b>-35.89</b>	<b>0.00</b>	<b>0.39</b>
I*M	4	0.0256	0.41	-23.46	12.43	0.00
I*R	4	0.0074	0.52	-27.20	8.69	0.00
<b>M*R</b>	<b>3</b>	<b>0.0032</b>	<b>0.53</b>	<b>-30.93</b>	<b>4.96</b>	<b>0.03</b>
A*I*M	5	0.0193	0.49	-21.76	14.14	0.00
A*I*R	5	0.0046	0.61	-26.51	9.38	0.00
<b>A*R*M</b>	<b>4</b>	<b>0.0019</b>	<b>0.62</b>	<b>-31.30</b>	<b>4.59</b>	<b>0.04</b>
I*R*M	5	0.0200	0.48	-21.64	14.26	0.00
All (A*R*I*M)	6	0.0127	0.57	-19.72	16.17	0.00

**Table 6.** Direct comparison of best-supported Bergmann's Rule and Ecological Release linear models. We used AICc and AICc weights to select the best hypothesis. The best model is in bold.

Model Parameters	$K$	$P$	$R^2_{\text{adj}}$	AICc	$\Delta\text{AICc}$	$w_i$
Null	2	< 0.0001		-23.93	11.96	0.00
Seasonality	3	0.0289	0.22	-26.55	9.34	0.01
<b>Area*Reptile Predators</b>	<b>5</b>	<b>0.0005</b>	<b>0.65</b>	<b>-35.89</b>	<b>0.00</b>	<b>0.99</b>

**Table 7.** Summary of Ecological Release Hypothesis path models. Each model differs in how the predator variable is formatted. The first two models combine mammalian and reptilian predators into one variable, either as a binary presence/absence term or as a count of the number of all mammalian/reptilian predator species. The final two models treat mammalian and reptilian predators as two separate variables, again either in presence/absence form or a species count.  $R^2$  values indicate the amount of variation in each endogenous variable explained by the model. The model best fit to the data is in bold.

Model Parameters	$\chi^2 (P)$	CFI	SRMR	$R^2$	Significant Paths
Predators Combined					
Presence/Absence	- (NA)	-	-	0.678 (size) 0.191 (pred)	area → size pred → size
Total Count	- (NA)	-	-	0.569 (size) 0.766 (pred)	area → pred
Mammal/Reptile Separated					
Presence/Absence	2.476 (0.116)	0.850	0.095	0.681 (size) 0.503 (mam) 0.191 (rep)	area → size rep → size
<b>Total Count</b>	<b>0.313 (0.576)</b>	<b>1.000</b>	<b>0.024</b>	<b>0.604 (size)</b> <b>0.595 (mam)</b> <b>0.591 (rep)</b>	<b>area → mam</b> <b>area → rep</b>



**Table 8.** Correlation matrix of best-fit path model variables.

	log(area)	isolation	mammal predators	reptile predators	mean centroid size
log(area)	1.00				
isolation	-0.84	1.00			
mammal predators	0.75	-0.54	1.00		
reptile predators	0.70	-0.42	0.50	1.00	
mean centroid size	-0.60	0.31	-0.73	-0.49	1.00

**Table 9.** Atlantic region dorsal cranium PC1 and PC2 pairwise comparisons. The lower triangle results the pairwise  $P$ -values for PC1 and the upper triangle those for PC2. Bold indicates  $P < .05$ . Italics indicate  $P$ -values between .05 and .10. Populations are abbreviated to 4-5 letters.

	Main	Block	Fox	Isles	Long	Mart	Musk	Nant	Tuck
Main	-	< <b>0.0001</b>	0.9999	<b>0.0061</b>	0.9578	0.5037	0.9900	0.1955	< <b>0.0001</b>
Block	0.5767	-	<b>0.0002</b>	< <b>0.0001</b>	< <b>0.0001</b>	< <b>0.0001</b>	<b>0.0002</b>	<i>0.0860</i>	0.7654
Fox	< <b>0.0001</b>	0.4508	-	0.1582	0.9999	0.9734	0.9883	0.3983	<b>0.0056</b>
Isles	< <b>0.0001</b>	0.4930	1.0000	-	0.1193	0.6274	<b>0.0017</b>	< <b>0.0001</b>	< <b>0.0001</b>
Long	0.9971	0.8946	<b>0.0003</b>	<b>0.0011</b>	-	0.9892	0.6542	<b>0.0445</b>	< <b>0.0001</b>
Mart	<b>0.0001</b>	0.9625	0.9339	0.9457	<b>0.0119</b>	-	0.2079	<b>0.0084</b>	< <b>0.0001</b>
Musk	< <b>0.0001</b>	<b>0.0002</b>	0.2583	0.3955	< <b>0.0001</b>	<b>0.0003</b>	-	0.7180	<b>0.0056</b>
Nant	< <b>0.0001</b>	0.2597	0.9999	1.0000	< <b>0.0001</b>	0.7743	0.2687	-	0.7852
Tuck	< <b>0.0001</b>	0.5547	0.9999	0.9999	<b>0.0001</b>	0.9810	<b>0.0277</b>	0.9993	-

**Table 10.** Atlantic region ventral cranium PC1 and PC2 pairwise comparisons. The lower triangle results the pairwise P-values for PC1 and the upper triangle those for PC2. Bold indicates  $P < .05$ . Italics indicate P-values between .05 and .10. Populations are abbreviated to 4-5 letters.

	Main	Block	Fox	Isles	Long	Mart	Musk	Nant	Tuck
Main	-	0.1293	0.9747	0.4622	<b>0.0003</b>	< <b>0.0001</b>	<b>0.0382</b>	< <b>0.0001</b>	<i>0.0516</i>
Block	< <b>0.0001</b>	-	0.8487	0.9993	1.0000	<b>0.0024</b>	0.9890	0.1459	0.9998
Fox	<b>0.0057</b>	<i>0.0671</i>	-	0.9934	0.6140	< <b>0.0001</b>	0.9899	< <b>0.0001</b>	0.9411
Isles	0.6885	<b>0.0018</b>	0.9257	-	0.9985	< <b>0.0001</b>	1.0000	<b>0.0097</b>	0.9999
Long	0.8698	< <b>0.0001</b>	<b>0.0005</b>	0.2187	-	< <b>0.0001</b>	0.9141	<b>0.0039</b>	0.9995
Mart	<b>0.0019</b>	<b>0.0172</b>	0.9999	0.9605	<b>0.0001</b>	-	< <b>0.0001</b>	0.8675	< <b>0.0001</b>
Musk	<b>0.0002</b>	<b>0.0015</b>	0.9988	0.9907	< <b>0.0001</b>	0.9999	-	< <b>0.0001</b>	0.9998
Nant	<b>0.0009</b>	<i>0.0578</i>	1.0000	0.8760	< <b>0.0001</b>	0.9999	0.9951	-	<b>0.0018</b>
Tuck	< <b>0.0001</b>	0.1341	0.9997	0.5525	< <b>0.0001</b>	0.9898	0.8164	0.9998	-

**Table 11.** Pacific region dorsal cranium PC1 and PC2 pairwise comparisons. The lower triangle results the pairwise P-values for PC1 and the upper triangle those for PC2. Bold indicates  $P < .05$ . Italics indicate P-values between .05 and .10. Populations are abbreviated to 4-5 letters.

	Main	Admi	Kadin	Mitk
Main	-	< <b>0.0001</b>	<b>0.0003</b>	<b>0.0222</b>
Admi	< <b>0.0001</b>	-	0.9535	0.7743
Kadin	0.7998	< <b>0.0001</b>	-	0.9697
Mitk	<b>0.0226</b>	0.8520	<b>0.0172</b>	-

**Table 12.** Pacific region ventral cranium PC1 and PC2 pairwise comparisons. The lower triangle results the pairwise P-values for PC1 and the upper triangle those for PC2. Bold indicates  $P < .05$ . Italics indicate P-values between .05 and .10. Populations are abbreviated to 4-5 letters.

	Main	Admi	Kadin	Mitk
Main	-			
Admi	< <b>0.0001</b>	-		
Kadin	< <b>0.0001</b>	0.9999	-	
Mitk	< <b>0.0001</b>	0.3601	0.4350	-

**Table 13.** Assessing allometry: MANCOVA results of dorsal and ventral cranium shape by centroid size and population in both regions. Statistical significance was determined by randomized residual permutation with 1000 iterations.

	<i>df</i>	SS	MS	$R^2_{\text{adj}}$	<i>F</i>	<i>P</i>
<b><i>Atlantic Region</i></b>						
Dorsal Cranium Shape						
log(size)	1	0.1270	0.1270	0.1619	87.3708	0.001
population	8	0.1055	0.0132	0.1345	9.0734	0.001
log(size):population	8	0.0173	0.0022	0.0220	1.4845	0.004
residuals	368	0.5348	0.0015	0.6817		
total	385	0.7846				
Ventral Cranium Shape						
log(size)	1	0.0126	0.0126	0.0454	21.3106	0.001
population	8	0.0480	0.0060	0.1735	10.1721	0.001
log(size):population	8	0.0043	0.0005	0.0155	0.9059	0.737
residuals	359	0.2116	0.0006	0.7656		
total	376	0.2764				
<b><i>Pacific Region</i></b>						
Dorsal Cranium Shape						
log(size)	1	0.0358	0.0358	0.1042	26.2526	0.001
population	3	0.0349	0.0116	0.1017	8.5338	0.001
log(size):population	3	0.0068	0.0023	0.0199	1.6672	0.017
residuals	195	0.2659	0.0014	0.7743		
total	202	0.3434				
Ventral Cranium Shape						
log(size)	1	0.0108	0.0108	0.0651	16.7659	0.001
population	3	0.0337	0.0112	0.2022	17.3648	0.001
log(size):population	3	0.0018	0.0006	0.0110	0.9434	0.540
residuals	186	0.1203	0.0006	0.7218		
total	193	0.1666				

**Table 14.** Post-hoc pairwise comparisons of slopes (allometric trajectories) in the Atlantic dorsal cranium dataset. *P*-values of each test are reported in the upper triangle, while the absolute difference between pairs of slope vector lengths is reported in the lower triangle. Bold indicates *P*-values < .05. Italics indicate *P*-values between .05 and .10, indicating some signal of divergence in slope. Statistical significance was tested by randomized residual permutation with 1000 iterations. Populations are abbreviated to 4-5 letters.

	Main	Block	Fox	Isles	Long	Mart	Musk	Nant	Tuck
Main	-	0.794	0.126	<b>0.001</b>	0.218	0.137	<i>0.097</i>	<b>0.013</b>	0.419
Block	0.021	-	0.134	<b>0.006</b>	0.605	0.317	0.422	<i>0.057</i>	0.670
Fox	0.208	0.187	-	0.482	0.275	0.425	0.350	0.898	0.241
Isles	0.292	0.270	0.083	-	<b>0.008</b>	<b>0.038</b>	<b>0.012</b>	0.308	<b>0.008</b>
Long	0.063	0.041	0.146	0.229	-	0.532	0.724	0.109	0.972
Mart	0.104	0.083	0.104	0.187	0.042	-	0.763	0.317	0.562
Musk	0.083	0.062	0.125	0.208	0.021	0.021	-	0.186	0.734
Nant	0.194	0.173	0.014	0.098	0.131	0.090	0.110	-	0.133
Tuck	0.060	0.039	0.149	0.232	0.003	0.045	0.024	0.134	-

**Table 15.** Post-hoc pairwise comparisons of slopes (allometric trajectories) in the Pacific dorsal cranium dataset. *P*-values of each test are reported in the upper triangle, while the absolute difference between pairs of slope vector lengths is reported in the lower triangle. Bold indicates *P*-values < .05. Italics indicate *P*-values between .05 and .10, indicating some signal of divergence in slope. Statistical significance was tested by randomized residual permutation with 1000 iterations. Populations are abbreviated to 4-5 letters.

	Main	Admi	Kadin	Mitk
Main	-	<b>0.024</b>	0.142	0.491
Admi	0.164	-	0.847	0.388
Kadin	0.145	0.020	-	0.523
Mitk	0.074	0.090	0.070	-



## APPENDIX

Population	Catalog Number	Sex	Age Score	Scientific Name
Block Island, RI	CUMV 8277	Female	10	<i>M. provectus</i>
	CUMV 8278	Male	10	<i>M. provectus</i>
	CUMV 8279	Male	11	<i>M. provectus</i>
	CUMV 8280	Male	11	<i>M. provectus</i>
	CUMV 8281	Male	11	<i>M. provectus</i>
	CUMV 8282	Female	9	<i>M. provectus</i>
	MVZ 74628	Female	9	<i>M. pennsylvanicus provectus</i>
	MVZ 74629	Male	8	<i>M. pennsylvanicus provectus</i>
	MVZ 74630	Female	10	<i>M. pennsylvanicus provectus</i>
	USNM 242335	Female	8	<i>M. pennsylvanicus provectus</i>
	USNM 288822	Female	9	<i>M. pennsylvanicus provectus</i>
	USNM 288823	Male	10	<i>M. pennsylvanicus provectus</i>
	USNM 288825	Female	11	<i>M. pennsylvanicus provectus</i>
	USNM 288826	Female	9	<i>M. pennsylvanicus provectus</i>
Fox Islands, ME	UMMZ 107132	Male	8	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 107133	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	USNM 149206	Female	10	<i>M. pennsylvanicus shattucki</i>
	USNM 149207	Female	11	<i>M. pennsylvanicus shattucki</i>
	USNM 149208	Female	11	<i>M. pennsylvanicus shattucki</i>
	USNM 149300	Male	11	<i>M. pennsylvanicus shattucki</i>
	USNM 149301	Male	10	<i>M. pennsylvanicus shattucki</i>
	USNM 149302	Male	10	<i>M. pennsylvanicus shattucki</i>
	USNM 149303	Male	12	<i>M. pennsylvanicus shattucki</i>
	USNM 149305	Female	10	<i>M. pennsylvanicus shattucki</i>
	USNM 149307	Female	12	<i>M. pennsylvanicus shattucki</i>
	USNM 149308	Male	11	<i>M. pennsylvanicus shattucki</i>
	USNM 149309	Male	12	<i>M. pennsylvanicus shattucki</i>
	USNM 149400	Male	12	<i>M. pennsylvanicus shattucki</i>
	USNM 149401	Male	9	<i>M. pennsylvanicus shattucki</i>
	USNM 149402	Male	10	<i>M. pennsylvanicus shattucki</i>
	USNM 149403	Female	12	<i>M. pennsylvanicus shattucki</i>
	USNM 149404	Female	11	<i>M. pennsylvanicus shattucki</i>
	USNM 149405	Female	12	<i>M. pennsylvanicus shattucki</i>
	USNM 149406	Female	11	<i>M. pennsylvanicus shattucki</i>
Islesboro, ME	USNM 149407	Female	12	<i>M. pennsylvanicus shattucki</i>
	MCZ 53643	Male	9	<i>M. pennsylvanicus pennsylvanicus</i>
	MCZ 53644	Undetermined	9	<i>M. pennsylvanicus pennsylvanicus</i>
	MCZ 56101	Female	9	<i>M. pennsylvanicus pennsylvanicus</i>
	MCZ 56102	Female	9	<i>M. pennsylvanicus pennsylvanicus</i>
	MCZ 56103	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	MCZ 56105	Male	6	<i>M. pennsylvanicus pennsylvanicus</i>
	MCZ 56107	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	MCZ 56108	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	MCZ 56109	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	MCZ 56110	Male	7	<i>M. pennsylvanicus pennsylvanicus</i>
	MCZ 56111	Male	7	<i>M. pennsylvanicus pennsylvanicus</i>
	MCZ 56112	Female	7	<i>M. pennsylvanicus pennsylvanicus</i>
	USNM 150084	Female	12	<i>M. pennsylvanicus shattucki</i>
	USNM 150086	Female	11	<i>M. pennsylvanicus shattucki</i>
	USNM 150089	Female	12	<i>M. pennsylvanicus shattucki</i>
	USNM 150092	Male	12	<i>M. pennsylvanicus shattucki</i>
	USNM 150093	Male	12	<i>M. pennsylvanicus shattucki</i>

Population	Catalog Number	Sex	Age Score	Scientific Name
Long Island, NY	AMNH 187054	Female	11	<i>M. pennsylvanicus</i>
	AMNH 187055	Male	9	<i>M. pennsylvanicus</i>
	AMNH 187056	Male	8	<i>M. pennsylvanicus</i>
	AMNH 187057	Female	10	<i>M. pennsylvanicus</i>
	AMNH 187058	Male	8	<i>M. pennsylvanicus</i>
	AMNH 187059	Female	9	<i>M. pennsylvanicus</i>
	AMNH 187060	Male	7	<i>M. pennsylvanicus</i>
	AMNH 187061	Female	7	<i>M. pennsylvanicus</i>
	AMNH 187062	Female	9	<i>M. pennsylvanicus</i>
	AMNH 187063	Male	8	<i>M. pennsylvanicus</i>
	AMNH 238238	Male	9	<i>M. pennsylvanicus</i>
	AMNH 238239	Female	7	<i>M. pennsylvanicus</i>
	AMNH 238240	Male	7	<i>M. pennsylvanicus</i>
	AMNH 238241	Male	7	<i>M. pennsylvanicus</i>
	AMNH 238242	Female	7	<i>M. pennsylvanicus</i>
	AMNH 238243	Male	9	<i>M. pennsylvanicus</i>
	AMNH 238245	Female	8	<i>M. pennsylvanicus</i>
	AMNH 238249	Female	10	<i>M. pennsylvanicus</i>
	AMNH 238250	Male	9	<i>M. pennsylvanicus</i>
	KU 47673	Female	8	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 47675	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 47676	Female	9	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 47677	Male	6	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 47678	Male	7	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 47679	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	MSB 29750	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	MVZ 96833	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	MVZ 96877	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	MVZ 104258	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	MVZ 104259	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	MVZ 104260	Male	10	<i>M. pennsylvanicus pennsylvanicus</i>
	MVZ 104261	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	NYSM 1299	Female	11	<i>M. pennsylvanicus</i>
	NYSM 1302	Male	11	<i>M. pennsylvanicus</i>
	NYSM 1311	Male	11	<i>M. pennsylvanicus</i>
	NYSM 1315	Male	12	<i>M. pennsylvanicus</i>
	NYSM 1319	Male	11	<i>M. pennsylvanicus</i>
	NYSM 1323	Female	7	<i>M. pennsylvanicus</i>
	NYSM 1325	Female	11	<i>M. pennsylvanicus</i>
	NYSM 1328	Male	11	<i>M. pennsylvanicus</i>
	NYSM 1329	Male	7	<i>M. pennsylvanicus</i>
	NYSM 1331	Male	10	<i>M. pennsylvanicus</i>
	NYSM 1332	Male	9	<i>M. pennsylvanicus</i>
	NYSM 1334	Male	12	<i>M. pennsylvanicus</i>
	NYSM 1335	Female	8	<i>M. pennsylvanicus</i>
	NYSM 1337	Female	10	<i>M. pennsylvanicus</i>
	NYSM 1338	Female	11	<i>M. pennsylvanicus</i>
	NYSM 1377	Male	11	<i>M. pennsylvanicus</i>
	NYSM 7483	Female	10	<i>M. pennsylvanicus</i>
	NYSM 7484	Female	11	<i>M. pennsylvanicus</i>
	NYSM 7485	Female	12	<i>M. pennsylvanicus</i>
	NYSM 7490	Female	10	<i>M. pennsylvanicus</i>

Population	Catalog Number	Sex	Age Score	Scientific Name
Long Island, NY	NYSM 7512	Male	10	<i>M. pennsylvanicus</i>
	NYSM 7513	Male	12	<i>M. pennsylvanicus</i>
Martha's Vineyard, MA	UMMZ 100977	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 100981	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 100985	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 100987	Male	10	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102101	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102103	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102106	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102107	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102108	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102109	Female	12	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102111	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102112	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102113	Male	10	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102115	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102116	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102117	Female	7	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102119	Female	9	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102120	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102121	Male	10	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102122	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102124	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102126	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102127	Male	8	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102129	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102133	Female	8	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102136	Male	8	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102137	Male	9	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 107100	Female	12	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 107101	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 107102	Female	12	<i>M. pennsylvanicus pennsylvanicus</i>
	USNM 247046	Undetermined	10	<i>M. pennsylvanicus pennsylvanicus</i>
	USNM 261724	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
Muskeget Island, MA	CUMV 11869	Female	9	<i>M. breweri</i>
	CUMV 11870	Male	8	<i>M. breweri</i>
	CUMV 11873	Female	11	<i>M. breweri</i>
	CUMV 11874	Male	10	<i>M. breweri</i>
	CUMV 11875	Female	10	<i>M. breweri</i>
	CUMV 11877	Female	12	<i>M. breweri</i>
	CUMV 11882	Female	10	<i>M. breweri</i>
	CUMV 11883	Female	11	<i>M. breweri</i>
	KU 133610	Female	10	<i>M. breweri</i>
	KU 133611	Male	10	<i>M. breweri</i>
	KU 133612	Male	8	<i>M. breweri</i>
	KU 133613	Female	11	<i>M. breweri</i>
	KU 133616	Male	11	<i>M. breweri</i>
	KU 133617	Female	9	<i>M. breweri</i>
	KU 133618	Female	11	<i>M. breweri</i>
	KU 133619	Female	12	<i>M. breweri</i>
	KU 133620	Female	12	<i>M. breweri</i>
	KU 133621	Male	11	<i>M. breweri</i>

Population	Catalog Number	Sex	Age Score	Scientific Name
Muskeget Island, MA	KU 133622	Male	12	<i>M. breweri</i>
	KU 133627	Female	12	<i>M. breweri</i>
	KU 133629	Male	11	<i>M. breweri</i>
	KU 133630	Male	11	<i>M. breweri</i>
	KU 133631	Male	12	<i>M. breweri</i>
	KU 133632	Female	12	<i>M. breweri</i>
	KU 133633	Female	12	<i>M. breweri</i>
	KU 133634	Female	12	<i>M. breweri</i>
	KU 133637	Male	12	<i>M. breweri</i>
	KU 133639	Female	12	<i>M. breweri</i>
	KU 133640	Male	10	<i>M. breweri</i>
	KU 133641	Male	11	<i>M. breweri</i>
	KU 133826	Male	12	<i>M. breweri</i>
	KU 133827	Male	12	<i>M. breweri</i>
	KU 133828	Male	11	<i>M. breweri</i>
	KU 133839	Male	12	<i>M. breweri</i>
	KU 133844	Female	11	<i>M. breweri</i>
	KU 133854	Male	12	<i>M. breweri</i>
	KU 133856	Female	11	<i>M. breweri</i>
	KU 133857	Female	11	<i>M. breweri</i>
	KU 133858	Female	10	<i>M. breweri</i>
	KU 133860	Female	12	<i>M. breweri</i>
	KU 133863	Female	11	<i>M. breweri</i>
	KU 133865	Male	12	<i>M. breweri</i>
	MVZ 54409	Female	11	<i>M. pennsylvanicus breweri</i>
	UConn 8103	Male	11	<i>M. breweri</i>
	UConn 8104	Female	12	<i>M. breweri</i>
	UConn 8105	Female	12	<i>M. breweri</i>
	UConn 8106	Female	12	<i>M. breweri</i>
	UConn 8107	Male	12	<i>M. breweri</i>
	UConn 8108	Male	8	<i>M. breweri</i>
	UConn 8110	Female	11	<i>M. breweri</i>
	UConn 8111	Male	12	<i>M. breweri</i>
	UConn 8112	Female	12	<i>M. breweri</i>
	UConn 8114	Male	12	<i>M. breweri</i>
	UConn 8115	Female	12	<i>M. breweri</i>
	UConn 9629	Female	9	<i>M. breweri</i>
	UConn 9718	Male	7	<i>M. breweri</i>
	UConn 16090	Female	11	<i>M. breweri</i>
	UConn 16091	Male	12	<i>M. breweri</i>
	UConn 16092	Male	12	<i>M. breweri</i>
	UConn 16093	Female	12	<i>M. breweri</i>
	UConn 16094	Female	12	<i>M. breweri</i>
	UConn 16095	Male	11	<i>M. breweri</i>
	UConn 16096	Female	11	<i>M. breweri</i>
	UConn 16097	Female	12	<i>M. breweri</i>
Nantucket Island, MA	UConn 8081	Female	11	<i>M. breweri</i>
	UConn 8083	Male	11	<i>M. breweri</i>
	UConn 8085	Male	11	<i>M. breweri</i>
	UConn 8091	Male	12	<i>M. breweri</i>
	UConn 8092	Male	11	<i>M. breweri</i>
	UConn 8095	Female	11	<i>M. breweri</i>

Population	Catalog Number	Sex	Age Score	Scientific Name
<b>Nantucket Island, MA</b>	UCONN 8096	Female	11	<i>M. breweri</i>
	UCONN 8097	Female	11	<i>M. breweri</i>
	UCONN 8100	Female	11	<i>M. breweri</i>
	UCONN 8101	Female	10	<i>M. breweri</i>
	UCONN 8102	Female	12	<i>M. breweri</i>
	UCONN 9665	Male	12	<i>M. breweri</i>
	UMMZ 100991	Male	7	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 100992	Female	9	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 100996	Female	7	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 100997	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 100998	Male	9	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 101000	Male	8	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 101006	Female	9	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 101007	Male	10	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 101997	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 101998	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 101999	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102000	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102001	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102002	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102003	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102004	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
<b>Tuckernuck Island, MA</b>	UMMZ 102050	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102051	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102052	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102053	Female	8	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102054	Female	9	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102058	Male	9	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102059	Female	9	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102060	Female	9	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102061	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102065	Female	8	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102066	Male	9	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102070	Male	8	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102071	Female	7	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102075	Female	9	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102076	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102079	Female	7	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102081	Male	8	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102082	Male	10	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102083	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102084	Male	9	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102086	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102087	Male	10	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102089	Male	9	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102090	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102091	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102092	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102093	Female	12	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102094	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 102095	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 107038	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>

Population	Catalog Number	Sex	Age Score	Scientific Name
<b>Tuckernuck Island, MA</b>	UMMZ 107039	Female	12	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 107040	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
<b>Mainland Connecticut</b>	KU 8686	Female	8	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 8687	Female	8	<i>M. pennsylvanicus pennsylvanicus</i>
<b>Delaware</b>	KU 9755	Male	8	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 9756	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	MCZ B-160	Female	9	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 141276	Male	8	<i>M. pennsylvanicus nigrans</i>
	KU 141277	Male	10	<i>M. pennsylvanicus nigrans</i>
	KU 141278	Male	12	<i>M. pennsylvanicus nigrans</i>
	KU 141279	Undetermined	12	<i>M. pennsylvanicus nigrans</i>
	KU 141280	Male	10	<i>M. pennsylvanicus nigrans</i>
<b>Maine</b>	UMMZ 100971	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 100972	Male	9	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 100973	Male	9	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 100975	Female	7	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 107134	Female	7	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 107136	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 123765	Female	12	<i>M. pennsylvanicus pennsylvanicus</i>
	USNM 83770	Female	9	<i>M. pennsylvanicus pennsylvanicus</i>
	USNM 83776	Female	9	<i>M. pennsylvanicus pennsylvanicus</i>
	USNM 118035	Male	10	<i>M. pennsylvanicus pennsylvanicus</i>
	USNM 118037	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	USNM 149030	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	USNM 149032	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	USNM 570540	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	USNM 570545	Female	9	<i>M. pennsylvanicus pennsylvanicus</i>
	USNM 570546	Male	10	<i>M. pennsylvanicus pennsylvanicus</i>
	USNM 570549	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
<b>Maryland</b>	CUMV 2723	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 47684	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 47685	Male	9	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 47686	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 47687	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 47688	Female	8	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 47689	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 47690	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 47691	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 47692	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 47693	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 103108	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 143049	Male	7	<i>M. pennsylvanicus nigrans</i>
<b>Massachusetts</b>	MCZ 63644	Male	10	<i>M. pennsylvanicus pennsylvanicus</i>
	MCZ B-942	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	MCZ B-943	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	MCZ B-1032	Female	9	<i>M. pennsylvanicus pennsylvanicus</i>
	MCZ B-1033	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	MCZ B-1035	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	MCZ B-2381	Female	9	<i>M. pennsylvanicus pennsylvanicus</i>
	MCZ B-2423	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	MCZ B-5413	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>

Population	Catalog Number	Sex	Age Score	Scientific Name
<b>Mainland</b>				
Massachusetts	MCZ B-5414	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	MCZ B-5416	Female	9	<i>M. pennsylvanicus pennsylvanicus</i>
	MCZ B-5417	Female	9	<i>M. pennsylvanicus pennsylvanicus</i>
	MSB 43357	Male	9	<i>M. pennsylvanicus pennsylvanicus</i>
	MSB 43358	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	MSB 43360	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	MSB 43361	Female	12	<i>M. pennsylvanicus pennsylvanicus</i>
	MSB 43362	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	MSB 47913	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	MSB 47914	Male	10	<i>M. pennsylvanicus pennsylvanicus</i>
	MSB 98193	Male	12	<i>M. pennsylvanicus</i>
	MSB 98194	Female	11	<i>M. pennsylvanicus</i>
	MSB 98196	Female	11	<i>M. pennsylvanicus</i>
	MSB 98197	Female	11	<i>M. pennsylvanicus</i>
	MSB 98199	Male	12	<i>M. pennsylvanicus</i>
New Hampshire	KU 9504	Male	10	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 9507	Male	9	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 9510	Female	8	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 11202	Male	10	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 11203	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 11206	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 11298	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 11300	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 11301	Male	9	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 11307	Female	12	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 11308	Male	8	<i>M. pennsylvanicus pennsylvanicus</i>
	MSB 292710	Female	10	<i>M. pennsylvanicus</i>
	MSB 292869	Male	11	<i>M. pennsylvanicus</i>
	MSB 296385	Male	10	<i>M. pennsylvanicus</i>
	MSB 296395	Male	10	<i>M. pennsylvanicus</i>
New Jersey	UMMZ 75070	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 107156	Male	10	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 107157	Female	12	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 107158	Female	12	<i>M. pennsylvanicus pennsylvanicus</i>
New York	CUMV 1317	Female	7	<i>M. pennsylvanicus pennsylvanicus</i>
	CUMV 1812	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	CUMV 1813	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	CUMV 2322	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	CUMV 3835	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	CUMV 3926	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	CUMV 4138	Male	9	<i>M. pennsylvanicus pennsylvanicus</i>
	CUMV 4277	Female	12	<i>M. pennsylvanicus pennsylvanicus</i>
	CUMV 5246	Male	9	<i>M. pennsylvanicus pennsylvanicus</i>
	CUMV 5257	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	CUMV 8291	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	CUMV 14036	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	CUMV 14037	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	CUMV 14039	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	CUMV 14042	Female	12	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 18526	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 143173	Male	10	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 143175	Male	10	<i>M. pennsylvanicus pennsylvanicus</i>

Population	Catalog Number	Sex	Age Score	Scientific Name
<b>Mainland</b>				
<i>New York</i>	KU 143177	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 143178	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 143179	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 143182	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 147580	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 107174	Male	10	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 107175	Female	10	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 107198	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 107199	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
<i>Pennsylvania</i>	CUMV 4133	Male	9	<i>M. pennsylvanicus pennsylvanicus</i>
	CUMV 4135	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 59443	Female	9	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 59444	Male	10	<i>M. pennsylvanicus pennsylvanicus</i>
	KU 141281	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	MSB 43312	Male	11	<i>M. pennsylvanicus pennsylvanicus</i>
	MSB 53394	Male	9	<i>M. pennsylvanicus pennsylvanicus</i>
	MSB 53396	Male	8	<i>M. pennsylvanicus pennsylvanicus</i>
	MSB 53397	Female	8	<i>M. pennsylvanicus pennsylvanicus</i>
	MSB 53402	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
<i>Vermont</i>	UMMZ 86945	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 88376	Male	12	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 88475	Female	11	<i>M. pennsylvanicus pennsylvanicus</i>
	UMMZ 100976	Female	12	<i>M. pennsylvanicus pennsylvanicus</i>



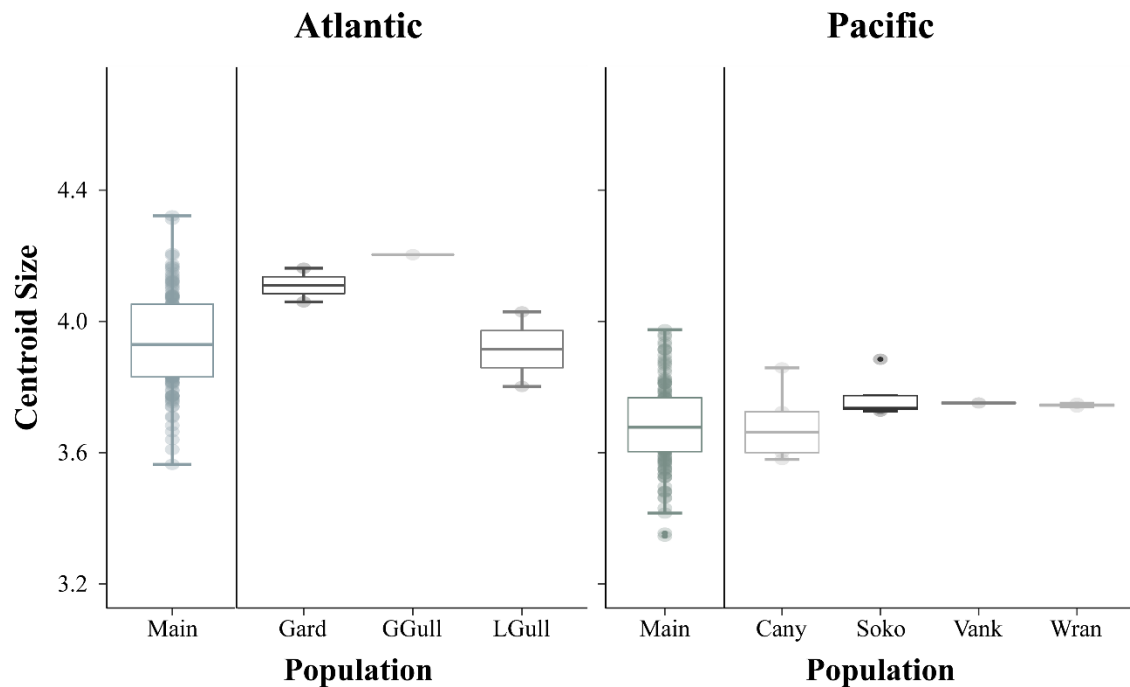
Population	Catalog Number	Sex	Age Score	Scientific Name
Admiralty Island, AK	MVZ_77	Male	9	<i>M. pennsylvanicus admiraltiae</i>
	MVZ_78	Male	8	<i>M. pennsylvanicus admiraltiae</i>
	MVZ_79	Male	10	<i>M. pennsylvanicus admiraltiae</i>
	MVZ_135	Female	9	<i>M. pennsylvanicus admiraltiae</i>
	MVZ_158	Female	10	<i>M. pennsylvanicus admiraltiae</i>
	MVZ_161	Female	9	<i>M. pennsylvanicus admiraltiae</i>
	MVZ_175	Female	12	<i>M. pennsylvanicus admiraltiae</i>
	MVZ_180	Male	11	<i>M. pennsylvanicus admiraltiae</i>
	MVZ_182	Male	12	<i>M. pennsylvanicus admiraltiae</i>
	MVZ_183	Male	11	<i>M. pennsylvanicus admiraltiae</i>
	MVZ_476	Male	12	<i>M. pennsylvanicus admiraltiae</i>
	MVZ_478	Male	12	<i>M. pennsylvanicus admiraltiae</i>
	UAM_14561	Male	11	<i>M. pennsylvanicus admiraltiae</i>
	UAM_14562	Female	12	<i>M. pennsylvanicus admiraltiae</i>
	UAM_14566	Male	11	<i>M. pennsylvanicus admiraltiae</i>
	UAM_14567	Male	10	<i>M. pennsylvanicus admiraltiae</i>
	UAM_14568	Male	12	<i>M. pennsylvanicus admiraltiae</i>
	UAM_14569	Female	12	<i>M. pennsylvanicus admiraltiae</i>
	UAM_14570	Male	12	<i>M. pennsylvanicus admiraltiae</i>
	UAM_14571	Female	12	<i>M. pennsylvanicus admiraltiae</i>
	UAM_14572	Male	12	<i>M. pennsylvanicus admiraltiae</i>
	UAM_14573	Male	12	<i>M. pennsylvanicus admiraltiae</i>
	UAM_14575	Male	12	<i>M. pennsylvanicus admiraltiae</i>
	UAM_14576	Male	11	<i>M. pennsylvanicus admiraltiae</i>
	UAM_14577	Female	11	<i>M. pennsylvanicus admiraltiae</i>
	UAM_14578	Male	12	<i>M. pennsylvanicus admiraltiae</i>
	UAM_14579	Male	12	<i>M. pennsylvanicus admiraltiae</i>
	UAM_14580	Female	11	<i>M. pennsylvanicus admiraltiae</i>
	UAM_14581	Female	12	<i>M. pennsylvanicus admiraltiae</i>
	UAM_14582	Female	12	<i>M. pennsylvanicus admiraltiae</i>
	UAM_47227	Male	10	<i>M. pennsylvanicus admiraltiae</i>
	UAM_47228	Female	7	<i>M. pennsylvanicus admiraltiae</i>
	UAM_47229	Male	11	<i>M. pennsylvanicus admiraltiae</i>
	UAM_47231	Male	7	<i>M. pennsylvanicus admiraltiae</i>
	UAM_47232	Female	10	<i>M. pennsylvanicus admiraltiae</i>
	UAM_47238	Female	11	<i>M. pennsylvanicus admiraltiae</i>
	UAM_48624	Male	11	<i>M. pennsylvanicus admiraltiae</i>
	UAM_50714	Female	12	<i>M. pennsylvanicus admiraltiae</i>
	UAM_51040	Female	10	<i>M. pennsylvanicus admiraltiae</i>
	UAM_51041	Female	12	<i>M. pennsylvanicus admiraltiae</i>
	UAM_51042	Male	11	<i>M. pennsylvanicus admiraltiae</i>
	UAM_51043	Female	11	<i>M. pennsylvanicus admiraltiae</i>
	UAM_51044	Female	10	<i>M. pennsylvanicus admiraltiae</i>
	UAM_52307	Female	12	<i>M. pennsylvanicus admiraltiae</i>
	UMMZ_107118	Male	9	<i>M. pennsylvanicus admiraltiae</i>
	USNM_130046	Male	10	<i>M. pennsylvanicus admiraltiae</i>
	USNM_130250	Female	11	<i>M. pennsylvanicus admiraltiae</i>
Kadin Island, AK	UAM_36586	Male	7	<i>M. pennsylvanicus</i>
	UAM_36587	Male	8	<i>M. pennsylvanicus</i>
	UAM_36588	Female	8	<i>M. pennsylvanicus</i>
	UAM_36589	Female	7	<i>M. pennsylvanicus</i>
	UAM_36593	Female	9	<i>M. pennsylvanicus</i>
	UAM_36595	Male	11	<i>M. pennsylvanicus</i>

Population	Catalog Number	Sex	Age Score	Scientific Name
<b>Kadin Island, AK</b>	UAM_41641	Female	7	<i>M. pennsylvanicus</i>
	UAM_41642	Female	9	<i>M. pennsylvanicus</i>
	UAM_44509	Female	7	<i>M. pennsylvanicus</i>
	UAM_74783	Female	9	<i>M. pennsylvanicus</i>
	UAM_74786	Male	7	<i>M. pennsylvanicus</i>
	UAM_74801	Female	9	<i>M. pennsylvanicus</i>
	UAM_74802	Female	7	<i>M. pennsylvanicus</i>
	UAM_74803	Male	8	<i>M. pennsylvanicus</i>
	UAM_74804	Male	7	<i>M. pennsylvanicus</i>
	UAM_74805	Female	7	<i>M. pennsylvanicus</i>
	UAM_74806	Female	10	<i>M. pennsylvanicus</i>
	UAM_74807	Female	7	<i>M. pennsylvanicus</i>
	UAM_74808	Female	6	<i>M. pennsylvanicus</i>
	UAM_74809	Female	9	<i>M. pennsylvanicus</i>
<b>Mitkof Island, AK</b>	UAM_14818	Female	10	<i>M. pennsylvanicus</i>
	UAM_14927	Male	11	<i>M. pennsylvanicus</i>
	UAM_22917	Male	11	<i>M. pennsylvanicus</i>
	UAM_22919	Female	7	<i>M. pennsylvanicus</i>
	UAM_23188	Male	10	<i>M. pennsylvanicus</i>
	UAM_23192	Male	8	<i>M. pennsylvanicus</i>
	UAM_31014	Female	10	<i>M. pennsylvanicus</i>
	UAM_31016	Male	7	<i>M. pennsylvanicus</i>
	UAM_31017	Female	7	<i>M. pennsylvanicus</i>
	UAM_31019	Male	8	<i>M. pennsylvanicus</i>
	UAM_31020	Female	10	<i>M. pennsylvanicus</i>
	UAM_31278	Male	12	<i>M. pennsylvanicus</i>
	UAM_31279	Female	10	<i>M. pennsylvanicus</i>
<b>Mainland Alaska</b>	MSB_136425	Male	9	<i>M. pennsylvanicus</i>
	MSB_136480	Undetermined	10	<i>M. pennsylvanicus</i>
	MSB_136489	Female	11	<i>M. pennsylvanicus</i>
	MSB_136608	Male	11	<i>M. pennsylvanicus</i>
	MSB_136609	Female	10	<i>M. pennsylvanicus</i>
	MSB_136610	Male	9	<i>M. pennsylvanicus</i>
	MSB_136673	Female	8	<i>M. pennsylvanicus</i>
	MSB_136676	Male	10	<i>M. pennsylvanicus</i>
	MSB_136677	Female	10	<i>M. pennsylvanicus</i>
	MSB_136678	Male	8	<i>M. pennsylvanicus</i>
	MSB_136679	Male	10	<i>M. pennsylvanicus</i>
	MSB_136680	Female	10	<i>M. pennsylvanicus</i>
	MSB_136681	Female	11	<i>M. pennsylvanicus</i>
	MSB_136769	Male	11	<i>M. pennsylvanicus</i>
	MSB_137102	Female	12	<i>M. pennsylvanicus</i>
	MSB_137173	Male	10	<i>M. pennsylvanicus</i>
	MSB_137656	Female	10	<i>M. pennsylvanicus</i>
	MSB_137657	Male	10	<i>M. pennsylvanicus</i>
	MSB_138000	Female	8	<i>M. pennsylvanicus</i>
	MSB_138152	Female	9	<i>M. pennsylvanicus</i>
	MSB_144037	Male	12	<i>M. pennsylvanicus</i>
	MSB_148898	Male	11	<i>M. pennsylvanicus</i>
	MSB_156786	Male	12	<i>M. pennsylvanicus</i>
	MSB_164892	Male	11	<i>M. pennsylvanicus tananaensis</i>
	MSB_164893	Female	10	<i>M. pennsylvanicus tananaensis</i>

Population	Catalog Number	Sex	Age Score	Scientific Name
<b>Mainland</b>				
Alaska	MSB_164894	Female	11	<i>M. pennsylvanicus tananaensis</i>
	MSB_164895	Female	12	<i>M. pennsylvanicus tananaensis</i>
	MSB_164896	Male	12	<i>M. pennsylvanicus tananaensis</i>
	MSB_164898	Male	11	<i>M. pennsylvanicus tananaensis</i>
	MSB_164899	Male	12	<i>M. pennsylvanicus tananaensis</i>
	MSB_164900	Female	12	<i>M. pennsylvanicus tananaensis</i>
	MSB_164904	Female	12	<i>M. pennsylvanicus tananaensis</i>
	MSB_164908	Male	11	<i>M. pennsylvanicus tananaensis</i>
	MSB_164921	Male	11	<i>M. pennsylvanicus tananaensis</i>
	MSB_164922	Female	11	<i>M. pennsylvanicus tananaensis</i>
	MSB_164937	Male	9	<i>M. pennsylvanicus alcorni</i>
	MSB_164938	Female	10	<i>M. pennsylvanicus alcorni</i>
	MSB_193343	Female	12	<i>M. pennsylvanicus</i>
	MSB_193480	Male	12	<i>M. pennsylvanicus</i>
	MSB_195107	Male	11	<i>M. pennsylvanicus</i>
	MSB_195119	Male	9	<i>M. pennsylvanicus</i>
	MSB_269529	Male	11	<i>M. pennsylvanicus drummondii</i>
	MSB_269530	Male	8	<i>M. pennsylvanicus drummondii</i>
	MSB_269534	Female	12	<i>M. pennsylvanicus</i>
	MSB_269615	Female	10	<i>M. pennsylvanicus</i>
	MSB_269616	Female	10	<i>M. pennsylvanicus</i>
	MSB_269617	Female	11	<i>M. pennsylvanicus</i>
	UAM_64680	Male	10	<i>M. pennsylvanicus</i>
	UAM_64683	Male	10	<i>M. pennsylvanicus</i>
	UAM_64684	Male	12	<i>M. pennsylvanicus</i>
	UAM_64685	Male	12	<i>M. pennsylvanicus</i>
	UAM_64699	Male	11	<i>M. pennsylvanicus</i>
	UAM_64700	Female	7	<i>M. pennsylvanicus</i>
	UAM_64702	Female	9	<i>M. pennsylvanicus</i>
	UMMZ_115870	Male	12	<i>M. pennsylvanicus drummondii</i>
	UMMZ_123795	Male	9	<i>M. pennsylvanicus tananaensis</i>
	USNM_98916	Male	12	<i>M. pennsylvanicus drummondii</i>
	USNM_98917	Male	10	<i>M. pennsylvanicus drummondii</i>
	USNM_98918	Male	12	<i>M. pennsylvanicus drummondii</i>
	USNM_98920	Female	12	<i>M. pennsylvanicus drummondii</i>
	USNM_98922	Female	12	<i>M. pennsylvanicus tananaensis</i>
British Columbia, CA	UAM_48541	Male	8	<i>M. pennsylvanicus</i>
	UAM_48617	Female	9	<i>M. pennsylvanicus</i>
	UAM_48619	Male	10	<i>M. pennsylvanicus</i>
	UAM_48620	Male	11	<i>M. pennsylvanicus</i>
	UAM_48621	Male	9	<i>M. pennsylvanicus</i>
	UAM_48622	Female	10	<i>M. pennsylvanicus</i>
	UAM_48623	Male	8	<i>M. pennsylvanicus</i>
	UAM_48625	Female	9	<i>M. pennsylvanicus</i>
	UAM_52277	Male	10	<i>M. pennsylvanicus</i>
	UAM_59826	Male	11	<i>M. pennsylvanicus</i>
	UAM_59827	Female	10	<i>M. pennsylvanicus</i>
	UAM_59832	Female	7	<i>M. pennsylvanicus</i>
	UAM_59833	Male	9	<i>M. pennsylvanicus</i>
	UAM_59835	Female	8	<i>M. pennsylvanicus</i>
	UAM_59836	Female	7	<i>M. pennsylvanicus</i>
	UAM_59837	Male	8	<i>M. pennsylvanicus</i>

Population	Catalog Number	Sex	Age Score	Scientific Name
<b>Mainland</b>				
<i>British Columbia, CA</i>	UAM_59851	Female	10	<i>M. pennsylvanicus</i>
	UAM_59852	Male	10	<i>M. pennsylvanicus</i>
	USNM_170781	Male	8	<i>M. pennsylvanicus rubidus</i>
	USNM_170783	Male	12	<i>M. pennsylvanicus rubidus</i>
	USNM_170784	Male	11	<i>M. pennsylvanicus rubidus</i>
	USNM_170785	Male	9	<i>M. pennsylvanicus rubidus</i>
	USNM_170786	Female	12	<i>M. pennsylvanicus rubidus</i>
	USNM_170788	Female	12	<i>M. pennsylvanicus drummondii</i>
	USNM_170789	Male	12	<i>M. pennsylvanicus drummondii</i>
	USNM_170790	Male	12	<i>M. pennsylvanicus drummondii</i>
	USNM_170792	Female	11	<i>M. pennsylvanicus drummondii</i>
	USNM_170793	Female	8	<i>M. pennsylvanicus drummondii</i>
	USNM_170803	Male	9	<i>M. pennsylvanicus drummondii</i>
	USNM_170804	Female	11	<i>M. pennsylvanicus drummondii</i>
	USNM_170806	Male	10	<i>M. pennsylvanicus drummondii</i>
	USNM_174433	Female	12	<i>M. pennsylvanicus drummondii</i>
	USNM_206114	Male	12	<i>M. pennsylvanicus rubidus</i>
	USNM_206115	Male	12	<i>M. pennsylvanicus rubidus</i>
	USNM_206116	Female	11	<i>M. pennsylvanicus rubidus</i>
	USNM_206117	Male	12	<i>M. pennsylvanicus rubidus</i>
	USNM_206118	Male	11	<i>M. pennsylvanicus rubidus</i>
<i>Yukon Territory, CA</i>	MSB_144084	Female	10	<i>Microtus pennsylvanicus</i>
	MSB_144161	Female	10	<i>Microtus pennsylvanicus</i>
	MSB_144168	Male	9	<i>Microtus pennsylvanicus</i>
	MSB_144179	Male	12	<i>Microtus pennsylvanicus</i>
	MSB_144426	Female	10	<i>Microtus pennsylvanicus</i>
	MSB_144447	Female	11	<i>Microtus pennsylvanicus</i>
	MSB_144466	Male	9	<i>Microtus pennsylvanicus</i>
	MSB_144479	Female	10	<i>Microtus pennsylvanicus</i>
	MSB_145310	Male	11	<i>Microtus pennsylvanicus</i>
	UAM_34176	Male	12	<i>Microtus pennsylvanicus</i>
	UAM_36585	Female	10	<i>Microtus pennsylvanicus</i>
	UAM_58898	Female	10	<i>Microtus pennsylvanicus</i>
	UAM_58900	Male	9	<i>Microtus pennsylvanicus</i>
	UAM_58901	Female	11	<i>Microtus pennsylvanicus</i>
	UAM_58902	Male	10	<i>Microtus pennsylvanicus</i>
	UAM_58903	Male	11	<i>Microtus pennsylvanicus</i>
	UAM_58909	Male	10	<i>Microtus pennsylvanicus</i>
	UAM_58910	Male	7	<i>Microtus pennsylvanicus</i>
	UAM_58912	Male	10	<i>Microtus pennsylvanicus</i>
	UAM_58913	Male	10	<i>Microtus pennsylvanicus</i>
	UAM_58915	Male	11	<i>Microtus pennsylvanicus</i>
	UAM_58925	Male	9	<i>Microtus pennsylvanicus</i>
	UAM_58926	Female	10	<i>Microtus pennsylvanicus</i>
	UAM_58927	Male	10	<i>Microtus pennsylvanicus</i>
	UAM_58928	Male	10	<i>Microtus pennsylvanicus</i>

## SUPPLEMENTARY MATERIAL



**Figure S1.** Box plots of dorsal centroid size from island populations excluded from analyses due to limited sample availability. Small sample size islands are positioned to the right of the mainland population from each region for comparison. Island abbreviations are as follows: Gard = Gardiners Island (NY), GGull = Great Gull Island (NY), LGull = Little Gull Island (NY), Cany = Canyon Island (AK), Soko = Sokolof Island (AK), Vank = Vank Island (AK), and Wran = Wrangell Island (AK).

**Table S1.** Anatomical description of dorsal cranium landmarks. (R) and (L) denote location of bilateral landmarks on the right and left side of the skull, respectively.

Number	Description
1	Anteriormost point of the nasal suture
2	Posteriormost point of the nasal suture
3	Lateral, posterior corner of the right nasal bone
4	Lateral, posterior corner of the left nasal bone
5	Frontal/Maxillary suture where it meets the orbit (R)
6	Frontal/Maxillary suture where it meets the orbit (L)
7	Vertex of the post-orbital crest (R)
8	Vertex of the post-orbital crest (L)
9	Lateralmost point of the jugal/squamosal suture (R)
10	Lateralmost point of the jugal/squamosal suture (L)
11	Junction of the frontal, parietal, and temporal sutures (R)
12	Junction of the frontal, parietal, and temporal sutures (L)
13	Junction of the frontal/parietal suture at the midline
14	Junction of the temporal ridge and parietal suture (R)
15	Junction of the temporal ridge and parietal suture (L)
16	Anteriormost point of the interparietal bone at the midline
17	Lateral, anterior corner of the interparietal bone (R)
18	Lateral, anterior corner of the interparietal bone (L)
19	Lateral, posterior corner of the interparietal bone (R)
20	Lateral, posterior corner of the interparietal bone (L)
21	Posteriormost point of the interparietal bone at the midline
22	Distal-most point of the mastoid/exoccipital crest (R)
23	Distal-most point of the mastoid/exoccipital crest (L)

**Table S2.** Anatomical description of ventral cranium landmarks. (R) and (L) denote the location of bilateral landmarks on the right and left side of the skull, respectively.

Number	Description
1	Anteriormost point of the premaxilla bone
2	Lateralmost point of the incisive alveolus (R)
3	Lateralmost point of the incisive alveolus (L)
4	Anteriormost point of the incisive foramen (R)
5	Anteriormost point of the incisive foramen (L)
6	Junction of the premaxilla/maxillary suture with the incisive foramen (R)
7	Junction of the premaxilla/maxillary suture with the incisive foramen (L)
8	Posteriormost point of the incisive foramen (R)
9	Posteriormost point of the incisive foramen (L)
10	Anteriormost point of the M1 alveolus (R)
11	Anteriormost point of the M1 alveolus (L)
12	Lateralmost point of the maxillary/jugal suture (R)
13	Lateralmost point of the maxillary/jugal suture (L)
14	Posteriormost point of the palatine bone at the midline
15	Posteriormost point of the M3 alveolus (R)
16	Posteriormost point of the M3 alveolus (L)
17	Posteriormost point of the pterygoid process (R)
18	Posteriormost point of the pterygoid process (L)
19	Junction of the basisphenoid/basioccipital suture with the auditory bulla (R)
20	Junction of the basisphenoid/basioccipital suture with the auditory bulla (L)
21	Ventral-most groove of the external auditory meatus (R)
22	Ventral-most groove of the external auditory meatus (L)
23	Ventral-most point of the foramen magnum at the midline
24	Ventral tip of the paroccipital process (R)
25	Ventral tip of the paroccipital process (L)
26	Lateralmost corner of the occipital condyle (R)
27	Lateralmost corner of the occipital condyle (L)

**Table S3.** Atlantic island mammalian predator checklist. Predator presence was determined by querying VertNet (vertnet.org) and Arctos (arctos.org) museum databases, in addition to the literature including primarily those cited on Animal Diversity Web (University of Michigan 2014). Scientific names are listed in alphabetical order. Four to five letter abbreviations are used for each island.

Scientific Name	Block	Fox	Isles	Long	Mart	Musk	Nant	Tuck
<i>Blarina brevicauda</i>			x	x	x		x	
<i>Canis latrans</i>				x				
<i>Mephitis mephitis</i>				x				
<i>Mustela frenata</i>				x				
<i>Neovison vison</i>				x				
<i>Urocyon cinereoargenteus</i>				x				
<i>Vulpes vulpes</i>				x				



**Table S4.** Pacific island mammalian predator checklist. Predator presence was determined by querying VertNet (vertnet.org) and Arctos (arctos.org) museum databases, in addition to the literature including primarily those cited on Animal Diversity Web (animaldiversity.org). Scientific names are listed in alphabetical order. Four to five letter abbreviations are used for each island.

Scientific Name	Admi	Kadin	Mitk
<i>Canis latrans</i>			x
<i>Canis lupus</i>			x
<i>Martes americana</i>	x		x
<i>Martes caurina</i>	x		x
<i>Mustela erminea</i>	x	x	x
<i>Neovison vison</i>	x	x	x
<i>Ursus arctos</i>	x		

**Table S5.** Atlantic island reptilian predator checklist. Predator presence was determined by querying VertNet (vertnet.org) and Arctos (arctos.org) museum databases, in addition to the literature including primarily those cited on Animal Diversity Web (animaldiversity.org). Scientific names are listed in alphabetical order. Four to five letter abbreviations are used for each island.

Scientific Name	Block	Fox	Isles	Long	Mart	Musk	Nant	Tuck
<i>Chelydra serpentina</i>	x			x	x		x	
<i>Coluber constrictor</i>					x			
<i>Lampropeltis triangulum</i>				x	x		x	
<i>Nerodia sipedon</i>	x			x			x	
<i>Thamnophis sirtalis</i>	x		x	x	x		x	x