Effect of weather during development on cranial morphometrics of American marten (*Martes americana*)

by

Josh G. Pigeon

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Department of Biological Sciences
University of Alberta

Abstract

Globally, climate change is affecting species in a myriad of ways. Rapid morphological change has been proposed to be a consequence of climate change, but evidence is minimal. Furthermore, any such rapid morphological change is expected to be a phenotypic response rather than evolutionary. Adaptive, neutral, and non-adaptive phenotypic plasticity in the form of reaction norms and developmental noise such as fluctuating asymmetry can provide insights into a population's ability to adapt to increased variability and extremes in weather, which are more common due to climate change. Using geometric morphometrics, I explored patterns of covariation between morphological variation in a population of American marten (*Martes americana*) near Nordegg, Alberta, and variation in weather metrics during periods when young are growing during prenatal (February–April) and postnatal (May–July) development. Analysis of variation in cranial morphology revealed significant covariation between the symmetric component of morphological variation and weather metrics during early postnatal development. I did not find significant covariation between the asymmetric component of morphological variation (fluctuating asymmetry) and weather during development. My findings are congruent with other studies, and point to both direct and indirect effects of "climate-induced" weather variation, including the potential of a feeding ecology mechanism as an explanation for the covariation.

Preface

This thesis is original work by Josh Pigeon. To date, this work has not been submitted for publication. A version of this thesis will be submitted for publication in *Global Change Biology*.

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"Homogeneity is a death sentence"

- Lulu Miller, *Why Fish Don't Exist*

Introduction

The current climate change crisis has led to populations facing environmental changes such as increased variability and extremes of weather (Hoffmann et al., 2010; IPCC, 2022) with effects on individual fitness and population stability (Sergio et al., 2018). Adaptive norms of reaction often are observed in response to fluctuating environments (Lalejini et al., 2021). Migration, phenological, genomic and morphological changes due to climate change have all been documented across disparate taxa, including flora and fauna (Chen et al., 2011; IPCC, 2022; Parmesan et al., 2003). However, evidence of rapid changes in morphological shape in response to climate are relatively sparse (Boutin & Lane, 2014). Despite many hypothesizing the potential for rapid morphological response to changing climate (Ryding et al., 2021; Tabh & Nord, 2023), most studies evaluating the impact of variation in weather variables have observed phenological variation, and few have observed morphological variation (Boutin & Lane, 2014; Parmesan, 2006; Radchuk et al., 2019). Those studies that have documented rapid responses in morphology were primarily studying variation in body size (Gardner et al., 2011; Hantak et al., 2021; Sheridan & Bickford, 2011; Yom-Tov et al., 2008). Most studies of shape variation generally explored variation among species, or on larger temporal or spatial scales (Colella et al., 2018; Giannico & Nagorsen, 1989; Law, 2019; McGuire, 2010).

Alongside selection, variation is one of the foundational pillars of Darwin's theory of evolution (Darwin, 1859). Without variation, selection forces would have nothing to act upon. We have understood for over a hundred years that a genotype can produce more than one phenotype, because forces other than genetics can influence the expressed phenotype (Johannsen, 1911). Despite this, an idea has prevailed that if we map a genome in its entirety, and build strong enough computers, we could compute the organism that nature would produce

(Brenner, 2010). Many, however, push back on this idea with the claim that this drastically underestimates the external forces that influence phenotypic variation (Lewontin, 2000).

Phenotypic variation is the result of one of three forces: genetic, environment, and stochastic forces (Hirsh, 1963). The environmental forces on phenotypic variation occur through phenotypic plasticity, defined as the production of different phenotypes from a given genotype in response to environmental conditions (Pigliucci, 2001). Phenotypic plasticity is closely related to, but distinct from the concept of norms of reaction. A reaction norm is a function that describes the shape (or pattern) of variation in phenotypes by a single genotype when exposed to a range of environments (Pigliucci, 2001; Schlichting & Pigliucci, 1998; Schmalhausen, 1949). Phenotypic plasticity is a property of a reaction norm that informs the degree (or amount) and pattern of variation in phenotypes produced by a genotype across different environments (Pigliucci, 2001). Although reaction norms and phenotypic plasticity are often confounded, they are distinct aspects of a larger picture. Whether plastic or not, a genotype will produce a reaction norm; the difference is that a non-plastic trait will produce a flat reaction norm (Figure 1 A, E). It is noteworthy that in addition to variation occurring at scales such as intra-species and intra-population, intra-individual variation also occurs (Pigliucci et al., 2006). Developmental variation in skull morphology, however, when compared to other types of variation such as behavioural, physiological, and biochemical, is an example of variability that would require substantial time to reverse, if reversable at all (Pigliucci et al., 2006). Thus, reaction norms in form of skull shape variation in response to whether that occurred during development should remain to be seen long after development. A growing body of literature argues reaction norms play more of a role in evolution, adaptation, and speciation than has been previously understood (Chevin et al., 2010; Ghalambor et al., 2007; Pfennig et al., 2010). Reaction norms are therefore gaining more attention in the context of climate change and predicting whether species will be able to survive their rapidly changing environments via phenotypic plasticity.

Variation in shape morphology can be caused by developmental noise, which includes a number of processes that disrupt development at the molecular and biochemical level (Palmer, 1994). Fluctuating asymmetry (FA) has been promoted as a measurable phenotypic response to be used as evidence of developmental stress (Benítez et al., 2020; Palmer & Strobeck, 1986; Parsons, 1992). FA defines small, random deviations in bilateral symmetry (Ludwig, 1932), and is generally distributed normally around a mean of symmetry (Palmer, 1994). Whether FA is related to fitness remains controversial (Clarke, 1995a; Leung & Forbes, 1996; Palmer, 1999), however FA as a measure of developmental stress generally has been supported (Leung & Forbes, 1996; Møller & Swaddle, 1997). A gap exists in the literature between ecological studies of patterns between skeletal FA and weather and the lab experiments studying the underlying mechanisms of the relationship; ecological studies should regard developmentally relevant weather metrics, not annual values. Whereas most ecological experiments have studied the effect of weather using seasonal or annual temperature and precipitation values (Maestri et al., 2015; Willmore et al., 2005), exploration of the mechanisms of FA study variation in ambient temperature conditions during development (e.g. Benderlioglu & Dow, 2017; Eriksen et al., 2003; Gest et al., 1986; Gonzalez et al., 2014; Mooney et al., 1985). Ecological studies that compared developmental stages when exposed to increased weather variability and extremes found more FA during early, rapid developmental periods (Breno et al., 2011; Klingenberg, 2019; e.g. Romero et al., 2023; Zakharov et al., 2001).

In recent decades, the field of morphometrics has evolved dramatically (Adams et al., 2013). Traditional morphometrics, the multivariate study of morphometrics consisting primarily of linear distances, was the dominant research method in the past (Reyment, 1996), and is still a common approach for studying variation in shape (e.g. Faleh et al., 2013; Mori et al., 2019; Wereszczuk et al., 2023). Traditional morphometrics provide useful tools for answering questions of variation in size, allometry (a change in shape relative to size), or broad questions regarding the presence of variation in shape (Rohlf & Marcus, 1993). Rather than using traditional measurements (e.g. linear distances, angles, ratios), geometric morphometrics uses a set of landmarks in the form of Cartesian coordinates to represent a shape configuration (Corti, 1993). By capturing the geometry of a form through landmarks, the information present in morphological configurations increases exponentially as the number of landmarks increases without exponentially increasing the number of measurements required (Slice, 2007). Additionally, analysis of a configuration of landmarks retains the geometry of each point relative to all the other points, whereas with traditional morphometric analyses the relationships between measurements is lost, making it impossible to reconstruct the original form based on the results of analyses (Rohlf & Marcus, 1993). Analysis that retains the geometric information of the configuration as a whole allows for not only the determination of the presence of significant variation in shape, but also the determination of how structures within the configuration change relative to others, allowing an entire new set of research questions (Rohlf & Marcus, 1993). An additional benefit of an analyses that retain the full shape configuration is that shape differences can be visualized, which allows for communication of complex shape changes compared to a table of coefficients that would be produced using traditional morphometrics (Klingenberg, 2013). Retention of shape configuration might open avenues for new questions regarding the mechanisms underlying the morphometric variation.

American marten (*Martes americana*) are economically and ecologically important species, being trapped for the fur trade and acting as an indicator species for old-growth forest condition (Cheveau et al., 2013; Fryxell et al., 2004). As such, marten has been a focus for forest management planning (Thompson et al., 2012; Watt et al., 1996). Marten respond behaviorally to inclement weather, such as modifying activity patterns and prey selection. Marten can be active in both daylight and during the night, shifting seasonally and geographically (Zielinski, 2000), depending on many factors. Variable activity patterns could be due to changes in prey abundance (More, 1978), to avoid weather extremes (Strickland & Douglas, 1987), or to avoid predation (Drew, 1995). In addition to changes in activity timing (Zielinski et al., 1983), marten reduce activity during winter (Clark et al., 1987; Mustonen & Nieminen, 2012), and will fast during extremely cold temperatures (Strickland & Douglas, 1987) for up to 5 days (Mustonen & Nieminen, 2012; Thompson & Colgan, 1994). Fasting to avoid extreme cold is increasingly likely when snow depth decreases and marten are not able to use the subnivean environment, a common occurrence in areas like the eastern slopes of the Rocky Mountains where chinook winds occur (Burrows, 1903). While fasting, cortisol levels increase significantly (Nieminen et al., 2007), evidence of the stress such a behavioural decision imposes, and might result in FA during in-utero development. At a larger temporal scale, marten also respond to changes in climate. As with many other species, there is evidence of marten responding geographically to climate change (Baltensperger et al., 2017). Body size of marten increases in conjunction with a warmer climate, both temporally and geographically (Wereszczuk et al., 2021; Yom-Tov et al., 2008, but see Yom-Tov 2010 for opposite effect among pine martens (*M. martes*) in Europe).

In this study, I used a multivariate, geometric morphometric approach to explore patterns between variation in morphology and weather for a population of American marten in westcentral Alberta, Canada. I expected to see evidence of a reaction norm in morphometric shape in response to the weather during two focal developmental periods (in-utero and early postnatal development), as skull morphology responds to temperature (Souto-Lima & Millien, 2014) and precipitation (Tseng & Flynn, 2018). Also, I expected to see more FA during colder winters, because marten are likely fasting more during these winters (Thompson & Colgan, 1994), which should result in higher levels of cortisol (Nieminen et al., 2007). For FA, I expected to see stronger covariation when exploring temperature, precipitation, and snow depth during the period of in-utero development (Benderlioglu & Dow, 2017; Eriksen et al., 2003). I also expected skull size to increase in more temperate years, based on Yom-Tov et al. (2008) that reported this pattern.

Study area

Marten were trapped within 30 km of Nordegg in Clearwater County, Alberta, Canada (52.445933, -116.023204, Figure 2), and donated to the Royal Alberta Museum. The 100 km^2 area of foothills/subalpine ecoregion varies between 1,200–1,700 m above sea level. The area is characterized as boreal upland, and is predominantly made up of coniferous forest, with densely clustered streams, and patches of old growth forest (Rayner et al., 1984). Aspect and forest fires primarily determine the vegetation composition, with lodgepole pine (*Pinus contorta*) and grassy understory on the warmer, fire-prone southwest facing slopes, and older patches of white spruce (*Picea glauca*) on the northeast slopes. Recently disturbed south-facing slopes include trembling aspen (*Populus tremuloides*). Depressional areas with high moisture due to seepage accumulate organic matter and become bog and fen vegetation-rich areas with black spruce (*Picea mariana*), tamarack (*Larix laricina*), and dwarf birch (*Betula nana*). The higher altitude subalpine region of these fluvial areas have forests of white spruce, Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) most commonly occur. Fisher (*Martes pennanti*) are a competitor and occasional predator of the marten (Suffice et al., 2017), and increasingly present in the area, likely due in part to lower snow depth (Krohn et al., 2005).

Mean winter temperature of the area is -9°C, with minimum and maximum means ranging from -17°C to 0°C. The estimated spring mean is ~ 3°C, with minimum and maximum means 5°C to 9°C. Annual frost-free days range from 20 to 100. Total precipitation from spring and summer range from 190–400 mm, and autumn and winter totals range from 150–250 mm. Snow cover in this area is low, likely due to snow redistribution by wind and chinooks. Climate variability in the Nordegg region is high for two reasons: variation related to changes in aspect, and variation related to the movement of the Arctic front across the region. Southwest facing slopes get more sun, and are thus warmer, drying, and have less snow on the ground than northeast facing slopes. Secondly, the weather in the study area varies annually due to the effect of the northern Arctic oscillation on the location of the Arctic Front between the Boreal and Cordilleran climates (Ladd and Gajewski, 2010; Wu et al., 2006). If the front falls to the west of the study area, the Boreal climate will likely result in a cold dry winter. If the front falls to the east of the study area, Pacific air from the west results in a higher likelihood of more moderate temperatures and increased precipitation (Cordilleran climate). Nordegg resides in the north-western most corner of the Kiska/Willson Public Land Use Zone, and partially within the West Country Public Land-Use Zone.

Methods

Animal Data

A collection of 175 complete, identifiable marten skulls at The Royal Alberta Museum in Edmonton, Alberta, were used for the study, collected between 2004 and 2021 in the study area. Of those, 120 were identified as young-of-the-year based on the methods and thresholds outlined by Flynn and Schumacher (2016). Sex is required to age individuals using these methods. Of the young-of-the-year, 98.3% (118/120) of the skulls were sexed when collected. Remaining individuals were below the threshold of yearlings regardless of sex. For males, the length of coalesced temporal muscles (LTMC) must measure <28 mm to confidently be classified as juvenile (age <1 yr). For females, the width between the temporal muscles (WBTM, before coalescence) should be >1.0 mm to be classified as juvenile. Ideally, males with LTMC between 20–30 mm and females with WBTM between 0.1–2.5 mm should be verified using cementum aging analysis (Magoun et al., 1988 in Flynn & Schumacher, 2016). I did not use cementum age analysis to avoid damaging the museum specimens. However, 6.5% of females and only 5% of males were in these intermediary ranges. Additionally, these measurements would have ideally been taken before muscle becoming desiccated or removed, because the muscle and thus evidence of muscle attachment to the skull might have shrunk during desiccation.

The mean number of skulls per year was seven (range 2 to 12). While many of the sampled years have an insufficient number of skulls for annual analysis, statistical methods allow for the entire sample to be analyzed as one group of 121 individuals. Skulls offer a good sample for study; skeletal structures allow for greater precision (Lougheed et al., 1991), skull shape varies greatly and presents with both asymmetric as well as symmetric variation among groups and individuals, and skull size offers a good proxy for body size (Johnson, 1990).

Landmark Selection and measurement

Prudent landmark selection is important for geometric morphometrics, especially when the study focuses on subtle asymmetries (Palmer, 1994). Landmarks should be homologous, repeatable, and create a configuration that effectively represents the morphology of interest (Zelditch et al., 2012). Finding homologous landmarks across the individuals is relatively straightforward, because all individuals were the same species. Finding landmarks that are highly repeatable while adequately capturing the shape of the skull is more difficult. Much of the skull's shape is curved, which can produce more measurement error, because the apex of a long curve can be difficult to capture accurately. Such landmarks are suboptimal, but adequate for developmental studies (Zelditch et al., 2012), if not relied on excessively. Finding discrete structures means the number of usable landmarks is restricted to anatomy with clear endpoints of or joining points between structures. I focused on skull shape changes, so the landmarks must adequately capture the general shape of the skull to observe variation in shape. Another consideration when selecting landmarks is the measurement error during digitization. If the structure is too small or requires a high resolution to be observed, the process of digitization might render it unusable.

Landmarks were a subset from Collela et al. (2018; Figure 3). The subset was homologous across all specimens, measurable with a high degree of precision, and maintained throughout the scanning process. Landmarks on or related to teeth were retained for analysis that pertained to postnatal development, because teeth and skulls develop within the temporal span examined (Clark et al., 1987). Teeth were not included for analysis for in-utero development. Skulls were scanned and digitized using a NextEngine 3D laser scanner and Scan Studio software (NextEngine, United States). Three orientations were taken for each skull, because the scanner could not capture the top and bottom of the object for any given orientation. Each orientation included eight scans, rotating the skull 45 degrees between each scan. All orientations were then merged and fused into a single, complete 3D object. Landmarks were set digitally using Stratovan Checkpoint (Version 2018.08.07; Stratovan Corporation, 2018), and were recorded in three-dimensions. To reduce measurement error, landmarks were recorded by one observer, with two replicate landmark configurations produced for each skull three to six weeks apart (Palmer, 1994), and replicates were averaged for analysis to reduce the effect of remaining measurement error (Graham, 2021). Landmarks were placed using digital software as manual measurements are less repeatable (Muñoz-Muñoz & Perpiñán, 2010), which was supported in a preliminary analysis comparing manual and digital methods of landmarking.

Procrustes Fit and Geometric data cleaning

Before analysis, landmark data were subjected to a generalized least-squares Procrustes analysis (GPA). Data cleaning and analysis was performed using MorphoJ (Klingenberg, 2011) and the geomorph package in R (v4.0.6, Baken et al., 2021). The GPA calculates a centroid of each individual's landmark configuration by calculating "the square root of the sum of squared distances of all the landmarks to their center of gravity" (Klingenberg, 2015). Individuals were then superimposed about their centroids, isometrically scaled to a common centroid size (the sum of distances between and landmarks and the centroid), and rotated to the least sum of squared distances between homologous landmarks, so that any variation among individuals is purely shape variation (Rohlf & Slice, 1990). The symmetric and symmetric components of shape were then dissected using the following methods from Klingenberg et al. (2002). To dissect the components, first each landmark configuration is reflection about its median axis. After reflection, the original and reflected homologous landmarks are averaged. The averaged landmark configuration is used to analyze the symmetric component of shape, and the difference between the original and reflected homologous landmarks is used to analyze the asymmetric component of shape. Missing landmarks due to damage or lost resolution from the scanning process were estimated. The function to estimate missing landmarks aligns the individual's missing landmarks to a reference individual obtained from the complete individuals in the set and uses a thin-plate spline method to estimate the missing landmark on the target specimen (Gunz et al., 2009). Outliers were assessed and fixed by swapping mis-ordered landmarks.

Preliminary assessment of the relative magnitude of shape variation

After a GPA is performed, a Procrustes analysis of variance (Procrustes ANOVA) is an important next step in any geometric morphometrics study, because it is well suited for analysis of shape data that have been configured using a least-squares method and can determine if the biological shape variation is significant relative to the measurement error (Palmer, 1994; Palmer & Strobeck, 1986). Comparing variation from biological sources to that of measurement error is especially important because FA is often evident as small variation, and can be smaller than variations due to measurement error (Palmer, 1994). However, the Procrustes ANOVA has limitations because it uses a single value to represent 'shape' of each individual. Variation among individuals is quantified as the mean distance from the consensus shape at each landmark. Differences between sides (a signal of directional asymmetry) are calculated as the mean distance between the left and right landmarks. The individual x side interaction effect determines the influence of fluctuating asymmetry (and antisymmetry if present). Therefore, the Procrustes ANOVA cannot distinguish non-isotropic shape variation between landmarks, and effectively assumes isotropic variation among landmarks of a single configuration. The Procrustes ANOVA is therefore best suited for analysis of variation in size (represented using a single value, the centroid size) and to analyze the relative magnitude of each effect (year, sex, individual) relative to measurement error. A multivariate analysis of variance test (MANOVA) is better suited to assess the statistical significance of each effect (year, sex, individual, side, individual*side) on the variation in shape. The MANOVA test statistic, Pillai's trace, uses a sum of squares matrix to determine variation in shape (Klingenberg, 2015; Klingenberg et al., 2002), and can thus determine the significance of shape variation despite it being non-isotropic, which is common in biological shape variation.

Assessment of morphological variation

A principal component analysis (PCA) reduces dimensionality of large datasets without losing information within the dataset by creating uncorrelated variables (variates) that sequentially maximize variance, making the dataset easier to interpret. A PCA in traditional morphometrics (i.e., a set of length measurements of specific structures) generally uses a correlation matrix of measurements to compute the variance of each principal component (PC). However, a covariance matrix is better suited for a PCA of geometric morphometric data because the Procrustes coordinate data are already scaled among configurations (Klingenberg & Zaklan, 2000). Before to conducting a PCA, covariance matrices are generated for the symmetrical and asymmetrical components of shape. Using separate covariance matrices allows us to analyze symmetric and asymmetric shape changes independent of each other, which is important because these shape changes almost certainly have different causes. PCA in the context of geometric morphometrics not only reduces the number of axes of variation to a manageable number, but also allows us to clearly visualize where most of the variation is occurring within the configuration by creating a figure identifying the magnitude and direction of change for all landmarks associated with a PC (Klingenberg, 2013).

Weather Variables

Weather data were collected by the Nordegg Climate Station (Nordegg CS), operated by Environment and Climate Change Canada. Sampling locations were <15 km of Nordegg CS. Gaps in temperature variables were filled using the Adjusted Homogenized Canadian Climate Data from Rocky Mountain House (RMH), as they were highly correlated (minimum temperature $R^2 = 0.88$, $P < 0.001$; maximum temperature $R^2 = 0.92$, $P < 0.001$). RMH is a dataset consisting of weather station data, adjusted to account for known measurement error and differences in measurement methods over time (Mekis and Vincent, 2011). RMH data also might include data from nearby stations to extend the time span of the dataset. A linear regression of temporally overlapping Nordegg CS and RMH data was fit and used to supplement missing Nordegg CS data with adjusted RMH data using the slope and intercept. Precipitation values were obtained from the Alberta Climate Information Services (ACIS) Nordegg CS data set. The ACIS Nordegg CS dataset has been quality controlled and missing data replace by interpolation. This ACIS Nordegg CS dataset was more complete, with some degradation in accuracy via interpolation, but was still significantly correlated with the raw weather station data ($R^2 = 0.93$, $P < 0.001$). The ACIS dataset still had missing data, which I filled in where possible using the RMH, and the two datasets were significantly correlated ($R^2 = 0.57$, $P < 0.001$). Data were once again transformed by linear regression, however the intercept was forced to zero, because days with no precipitation should be 0 mm once adjusted. Despite interpolating precipitation from another dataset, there were still years with significant gaps, making those years unusable for some analyses. Snow depth was missing for a significant number of years, and no other snow depth source was found for interpolation of missing data. For this reason, snowfall and snow depth were estimated using the snow water equivalence methods of Dawe & Boutin (2012): daily snow depth estimates were calculated using mean temperature and precipitation values. If the mean temperature the following day was < 0°C, that day's estimated snowfall is added to the accumulated snowpack from the previous day. If the mean temperature was ≥ 0°C, the estimated melt parameter (also calculated using the mean temperature and precipitation) was subtracted from the accumulated snowmelt estimate. Compared to the limited snow depth data from Nordegg CS, the estimated accumulated snow depth was moderately correlated ($R^2 = 0.45$, $P < 0.001$). This correlation level was likely because the snow density estimate was based on the density of freshly fallen snow, and because the model failed to consider snow movement by wind.

The mean value of maximum and minimum daily temperature, total precipitation, and adjusted average snow depth were calculated for the in-utero and early development stages. The analysis of correspondence, two-block partial least squares (2B-PLS), requires covariates to be standardized.

Weather covariates

Many studies use mean temperature to study the effects of climate change (Thornton et al., 2014). When studying the influence of a complex, multivariate system like weather on a population or ecosystem, multiple, biologically relevant metrics should be considered. The two timespans investigated were the approximate in-utero development period (February–April) and the postnatal early development period (May–July) (Clark et al., 1987). Average minimum and maximum daily temperatures, standard deviation of minimum and maximum temperature values, total precipitation, average accumulated snow depth, and average Pacific Decadal Oscillation were considered. Number of days above or below biologically relevant thresholds of these weather metrics also were considered. For example, Thompson and Colgan (1994) noted a significant decrease in winter activity of marten at ambient temperatures below -15 °C, so the number of days where the mean temperature was below -15 °C was considered. A threshold for snow depth related to decreased activity or increased stress was not available, but Hiltner (2022) noted a steep increase in occupancy probability when snow depth was > 20 cm. Snow depth ≤ 20 cm would make it difficult for marten to use the subnivean space, so the number of days with snow depth > 20 cm also was considered. Snowfall events > 5 cm were considered because these larger snowfall events increased activity (Weir & Corbould, 2007), and make the terrain more difficult for fishers to traverse due to differences in foot loading between the two species (Buskirk & Powell, 1994; Krohn et al., 2005).

Analysis of covariation

Multiple regression was used to estimate the relationship between size and the weather covariates. This analysis uses a single value to represent ‘size’: centroid size. For this reason, it was tested separately from the analyses of shape. To test for covariation between variation in skull shape and variation in weather, I used a two-block partial least squares analysis (2B-PLS). This 2B-PLS method is useful for studies of covariation between shape variables and ecological variables (e.g. Corti et al., 1996; Noback et al., 2011; Russo et al., 2022). A 2B-PLS analysis compares two matrices (or blocks) of variables, in this case a matrix of Procrustes coordinates of shape variables and a matrix of weather covariates, to find relationships of covariation between the two sets of covariates, both within and among the two matrices. Similar to a PCA, this process produces new variables, PLS axes, but in this case these new variables account for as much covariance as possible between matrices rather than solely accounting for as much total variance as possible. Also, similarly to a PCA, each axis correlates only with the corresponding axis from the other block, and is uncorrelated with any other axes.

This analysis was chosen over a canonical correspondence analysis (CCA), a similar analysis, for the following reasons, highlighted by Rohlf and Corti (2000) and Zelditch (2004). First, a CCA acts like a multiple regression in that it considers the contribution of a single independent variable on the correlation coefficients when the effects of the others are held constant. The strongest variable in one block will be associated with as much covariance as possible, leaving the residual variance to be explained by the following variables. In contrast, the 2B-PLS treats all of the variables in each block symmetrically, and considers the correlation of each variable with a given axis that explains covariation with the other block. Second, 2B-PLS is not sensitive to the redundancy of the x, y, and z Procrustes coordinates in the shape matrix. Third, 2B-PLS analysis can directly visualize the shape variations of each axis using thin-plate splines. The weather covariate can be visualized as eigenvectors that show how correlated each weather covariate is with each axis. This test is conducted on the symmetric and asymmetric components of shape separately, allowing us to explore patterns of variation of each shape component separately. A permutation test was used to test the significance of correlation between the blocks. By running 1000 permutations of the test, randomly associating the variables between blocks, I can determine if the amount of covariance between blocks, as well as the covariance explained by each PLS axis is greater than expected by chance (Rohlf & Corti, 2000; Zelditch, 2004).

Results

Shape and size variation

The Procrustes ANOVA of the centroid size showed significant variation in size among individuals ($F_{101,120} = 1261.60$, $P > 0.0001$), sexes ($F_{2,120} = 110.28$, $P < 0.0001$), and years ($F_{16,120} = 3.17$, $P = 0.0002$; Table 1). The Procrustes ANOVA of shape serves to show that all shape variation (including symmetric, directional asymmetric, and fluctuating asymmetric) are significantly greater than measurement error (Table 2). Using the shape MANOVA test I found significant variation in symmetric shape among individuals (Pillai's trace = 49.88, $P < 0.0001$) and years (Pillai's tr. = 9.00, $P = 0.0002$), but not sex (Pillai's tr. = 1.17, $P = 0.38$; Table 3). The MANOVA test of asymmetric shape variation showed significant variation among years (Pillai's tr. = 9.35, $P < 0.0001$) but not sex (Pillai's tr. = 0.99, $P = 0.96$), and significant levels of variation between the left and right side (directional asymmetry) (Pillai's tr. = 0.97, $P > 0.0001$), as well as the interaction effect between individual and side (fluctuating asymmetry) (Pillai's tr. = 46.12, $P < 0.0001$; Table 3). There is a significant, but weak correlation between variations in symmetric shape and variations in size (percent of variation predicted = 5.06%, $P < 0.0001$) (Figure 4). Larger skulls tend to be narrower, and have a longer rostrum relative to the length of the cranium. There was no significant correlation between variations in asymmetric shape and variations in size ($P = 0.39$) (Figure 5). I also did not find a significant relationship between log centroid size and early development weather variables ($P = 0.63$).

The PCA results allow us to visualize the nature of the shape variation. PC1 of the symmetric component of shape variation consists of a longer rostrum relative to the length of the cranium, smaller zygomatic arches and a narrower skull (Figure 6; see figure 3 for landmark location). PC1 of the asymmetric component of shape variation consists of a misaligned rostrum and cranium, with a crook in the center of the skull, as well as asymmetry of the incisive foramen, tympano-occipital fissure, and pterygoid (Figure 7).

Shape and weather variation

The 2B-PLS analysis of the symmetric component of shape variation revealed significant covariance between the variation in shape and weather covariates during early, postnatal development (RV coefficient = 0.142, $P < 0.0001$). PLS axis 1 of Block 1 and 2 were significantly correlated, and represented the majority of covariance of the PLS analysis (% total covariance = 59.277, $R^2 = 0.634$, $P < 0.0001$) (Figure 8). Average daily maximum temperature, followed by precipitation and lag year precipitation were strongly associated with the shape changes of PLS 1 Block 1 (PLS coefficients = 0.530, 0.468, and 0.459, respectively). Greater precipitation and warmer daily temperatures covaried positively with shorter, narrowing of the zygomatic arches at each end, narrower mandibular fossae, longer and narrower rostrums and shorter cranium. Significant variation of the pterygoid process also was present. Covariance between symmetric shape variate and in-utero weather covariates was not significant ($P = 0.037$, PLS 1 $P = 0.15$). I found no significant covariance between the asymmetric component of shape and any weather covariates (in-utero $P = 0.88$, PLS 1 $P = 0.95$; early development $P = 0.023$, PLS 1 $P = 0.059$). Running the 2B-PLS with threshold values replacing the raw weather metrics yielded the same results, with slight variation in the percent of total covariance of each covariate.

Discussion

The greatest impacts of climate change have occurred during the past 20 years (IPCC, 2022). I studied marten skulls spanning those 20 years and have demonstrated that their morphology covaried annually with weather.

Skull shape covaried among years significantly with weather during May–July, the key period for development when young marten grow to full length (Clark et al., 1987). Morphological variation covaried most with increasing average maximum daily temperature, precipitation, and precipitation during the previous spring (lag year), suggesting both direct and indirect relationships between weather variation and shape morphology. Although global climate has changed most significantly in the last 20 years (IPCC, 2022), annual weather metrics in Nordegg show little trend during those years (Figure 10 A). However, during the early developmental periods for marten both temperature and precipitation varied widely (Figure 10 B & C).

The symmetric component of shape variation in the marten skulls covaried significantly with weather to which marten were exposed during early, postnatal development. Warmer, wetter springs are associated with longer, narrowed rostrum, shorter cranium, shortened zygomatic arches, and extended pterygoid processes. This is congruent with other studies of carnivores (Lynch, 2019; Tseng & Flynn, 2018). Specifically, covariation between precipitation and the same type and direction of skull shape variation has been documented (Tseng & Flynn, 2018). The early postnatal rapid growth stage appears to be sensitive to ambient temperature (Al-Hilli & Wright, 1983; Serrat, 2013; Zhou & Lui, 2021). Skull shortening might be a byproduct of the biochemical processes in bone development, and the decrease in the cell proliferation during bone growth in response to colder temperatures (Serrat et al., 2008). Based on my study alone it is difficult to determine whether this morphological response is adaptive, neutral or a maladaptive response to stress (Boutin & Lane, 2014; Eriksson et al., 2023; Merilä & Hendry, 2014). However, if the reaction norm was adaptive and in the direction of an optimal form for that year's environment, there are a few possible ecologically adaptive explanations for the variation in shape.

As the weather becomes more temperate and more closely resembles the weather in western B.C. and Alaska, one might expect the shape of the skull to more closely resemble that of the Pacific marten (*Martes caurina*) that have shorter, wider rostrums (Colella et al., 2018; Wright, 1953). Our results indicate, however, the shape change with more temperate weather accentuated the differences between American marten and Pacific marten. This might seem counterintuitive, but we should consider the effect of weather fluctuation on the marten to be through their feeding ecology, because marten physiology and behaviour shift seasonally in response to prey availability, including shifting primary prey (Ben-David et al., 1997; Buskirk & Macdonald, 1984; Raine, 1987), shifting periods of activity (More, 1978; Zielinski et al., 1983), and fasting (Nieminen et al., 2007). Evidence suggests the shorter rostrum is an adaptation to increase bite force, which a generalist with variable prey would require (Slater et al., 2009). The broader, shorter rostrum to increase bite force is associated with coastal environments, where a generalist predator like the pacific marten preys on crustaceans when small rodents are not readily available (Ben-David et al., 1997). The rostrum shape I found in conjunction with warmer, wetter springs and wetter previous springs might be a response to an abundance of prey, specifically small rodents. If small terrestrial prey are abundant, allowing American marten to specialize, a faster bite could provide a greater advantage than a strong bite. Shorter, wider rostrum (and by association mandible) allows for greater bite forces by increasing the leverage of the jaw musculature, whereas an elongate, narrower rostrum would prioritize bite speed by lengthening the jaw-out lever (Slater et al., 2009). A feeding ecology explanation also might explain the increased pterygoid process (located behind the palate, landmarks 10 & 11), because pterygoid muscles assist with chewing and biting (Osborn, 1995).

Due to the nature of geometric morphometrics (Parsons et al., 2003), I quantified both variation and the nature of that variation. I observed similar variation in symmetric shape from the PCA and 2B-PLS. The similarity between tests is relevant because it indicates the predominant variation in shape is essentially the same shape variation that covaries with weather covariates. Had the first one or two axes of the PCA and 2B-PLS results focused on entirely distinct shape variation, it would indicate that although there is significant covariation between shape and weather, the shape that covaries significantly with weather is a small portion of the shape variation I observed. The ability to visualize how the skull shape is varying also is valuable because it can inform future research into the potential mechanisms influencing the skull structures by highlighting which structures within a configuration have the highest variability.

Despite finding significant variation in size among years, I found no significant correspondence between size and weather covariates, although studies have shown a correlation between body size and climate (Wereszczuk et al., 2023; Yom-Tov et al., 2008). These studies might have captured a longer-term trend, rather than individual responses to environmental factors. Our analysis found a small but significant correlation between variation in asymmetric shape and size. This correlation might be associated with cranial evolutionary allometry, a pattern among disparate mammalian orders (Cardini et al., 2015) that describes among-individual as well as among-species variation wherein larger individuals and species have longer rostrums and relatively smaller brain cases, and smaller individuals and species have relatively shorter rostrums and larger braincases (Cardini & Polly, 2013).

I found significant among-year variation in fluctuating asymmetry (FA), but I was unable to detect significant covariation between morphometric asymmetry and weather. Developmental instability might be buffered by behavioural adaptation to weather fluctuations. For example, increased use of the subnivean environments by the marten during colder weather might buffer any effects of cold temperatures on FA. With sufficient snow, they might be able to avoid the stress of extreme cold, making the correspondence between weather and FA difficult to detect with this analysis. However, these subnivean behavioural adaptations to weather variation are possible only with adequate snow depth. If climate change decreases snow depth to the point that it is not usable for subnivean movement, we might see a large, abrupt change in marten adaptability. Detecting statistically significant levels of FA seems to be more common with the advent of more precise measurement and statistical methods, but we still do not have a clear understanding of its origins (Klingenberg, 2022). This lack of clarity despite significant FA might be why the disagreement regarding the validity of FA as a measure of developmental instability, let alone fitness, remains (Clarke, 1995b, 1998; Leung & Forbes, 1996; Palmer, 2000). Our results also reinforce the difficulty of avoiding false-positive results when studying FA (Palmer & Strobeck, 2003). The graphical output of the asymmetry component easily can be interpreted as clear patterns of FA covarying with weather covariates (Figure 9). However, with the permutation test, this interpretation was not supported and covariation was not statistically significant (J. Marugán-Lobón, personal communication, September 14, 2023). This highlights a criticism of studying FA within the context of developmental instability and fitness; without (and potentially even with) thoughtful and attentive methodology, seemingly significant results can be biologically meaningless (Palmer, 1996; Palmer & Strobeck, 2003).

As climate change continues to increase weather variability and extremes (IPCC, 2022), we will almost certainly continue to see changes in the morphology of organisms. Climate is a complex combination of variables, each with direct and indirect effects on ecology. Remarkably, however, by focusing on weather data for the spring developmental period for young marten I found a strong pattern of symmetric covariation between marten morphology and weather. Climate change is a relatively recent phenomenon, therefore in most cases we do not have data across a long enough timespan to understand the full extent of its influence. Thus, we should continue to monitor populations over a longer timespan. Additionally, based on this research I can not say whether these adaptations are adaptive, let alone how such adaptations would be advantageous. Therefore, we should explore the mechanisms of these morphological changes to understand if and how they might be adaptive, including research regarding biomechanics and predator-prey relationships in the context of climate change.

Tables

Table 1. Metadata for marten skull specimens, by year. Years with incomplete weather data were excluded from analysis pertaining to the developmental period with missing data.

Year	Males	Females	Sex unk	Feb–Apr	May–Jul
2004	7	3	2	✓	✓
2005	4	6	-	✓	✓
2006	2	1	-	✓	✓
2007	3	3	-	✓	✓
2008	4	4	-	INC	✓
2009	5	2	-	INC	✓
2010	2	-	-	✓	✓
2011	3	5	-	✓	✓
2012	2	6	-	✓	✓
2013	3	4	-	✓	✓
2014	4	1	-	✓	✓
2015	7	4	-	✓	✓
2016	9	2	-	✓	✓
2017	4	2	-	✓	✓
2018	3	3	-	✓	✓
2019	2	2	-	✓	✓
2021	2	4	-	✓	✓
Total	66	52	2	= 120	

Table 2. Procrustes ANOVA of centroid sizes of American marten skull landmark configurations. Marten were collected between 2004–2021 near Nordegg, Alberta, Canada.

Effect	SS	MS	df	F	P (param.)
Year	22.052478	1.378280	16	3.19	0.0002
Sex	95.015108	95.015108	1	220.16	<.0001
Individual	43.157886	0.431579	100	1272.83	<.0001
Error	0.041339	0.000344	120		

Table 3. Procrustes ANOVA of shape of American marten skull landmark configurations. The 'Side' effect represents variation in directional asymmetry, and the 'Ind * Side' interaction effect represents fluctuating asymmetry and antisymmetry.

Effect	SS	MS	df	F	P (param.)
Year	0.02646508	0.0000280350	944	1.66	<.0001
Sex	0.00868294	0.0000735842	118	4.36	<.0001
Individual	0.10068276	0.0000168959	5959	5.88	<.0001
Side	0.00296356	0.0000493927	60	17.19	<.0001
Ind * Side	0.02051156	0.0000028728	7140	2.83	<.0001
Error	0.01450457	0.0000010157	14280		

Table 4. Shape MANOVA test of shape variation of American marten skull landmark configurations. The 'Side' effect represents variation in directional asymmetry, and the 'Ind * Side' interaction effect represents fluctuating asymmetry and antisymmetry.

Symmetric component of shape variation			Asymmetric component of shape variation		
Effect	Pillai tr.	P (param.)	Effect	Pillai tr.	P (param.)
Year	9.00	0.0002	Year	9.35	<0.0001
Sex	1.17	0.3877	Sex	0.99	0.9591
Individual	49.88	<0.0001	Side	0.97	<0.0001
			Ind*Side	46.12	<0.0001

Figures

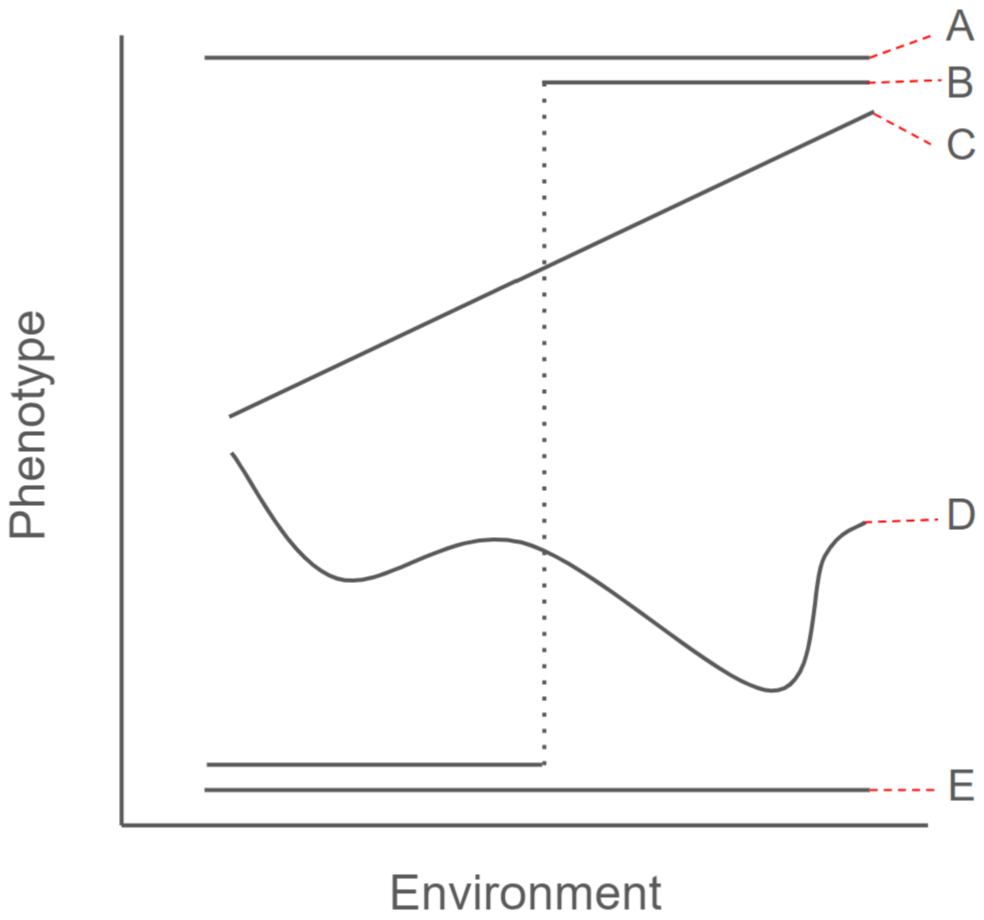


Figure 1. A theoretical representation of various reaction norms. A and E represent genotypes that produce phenotypes that differ from each other, but are non-plastic. B,C, and D represent traits that are all plastic, but illustrate various shapes a plastic reaction norm can take. Adapted from Fusco and Minelli (2010).

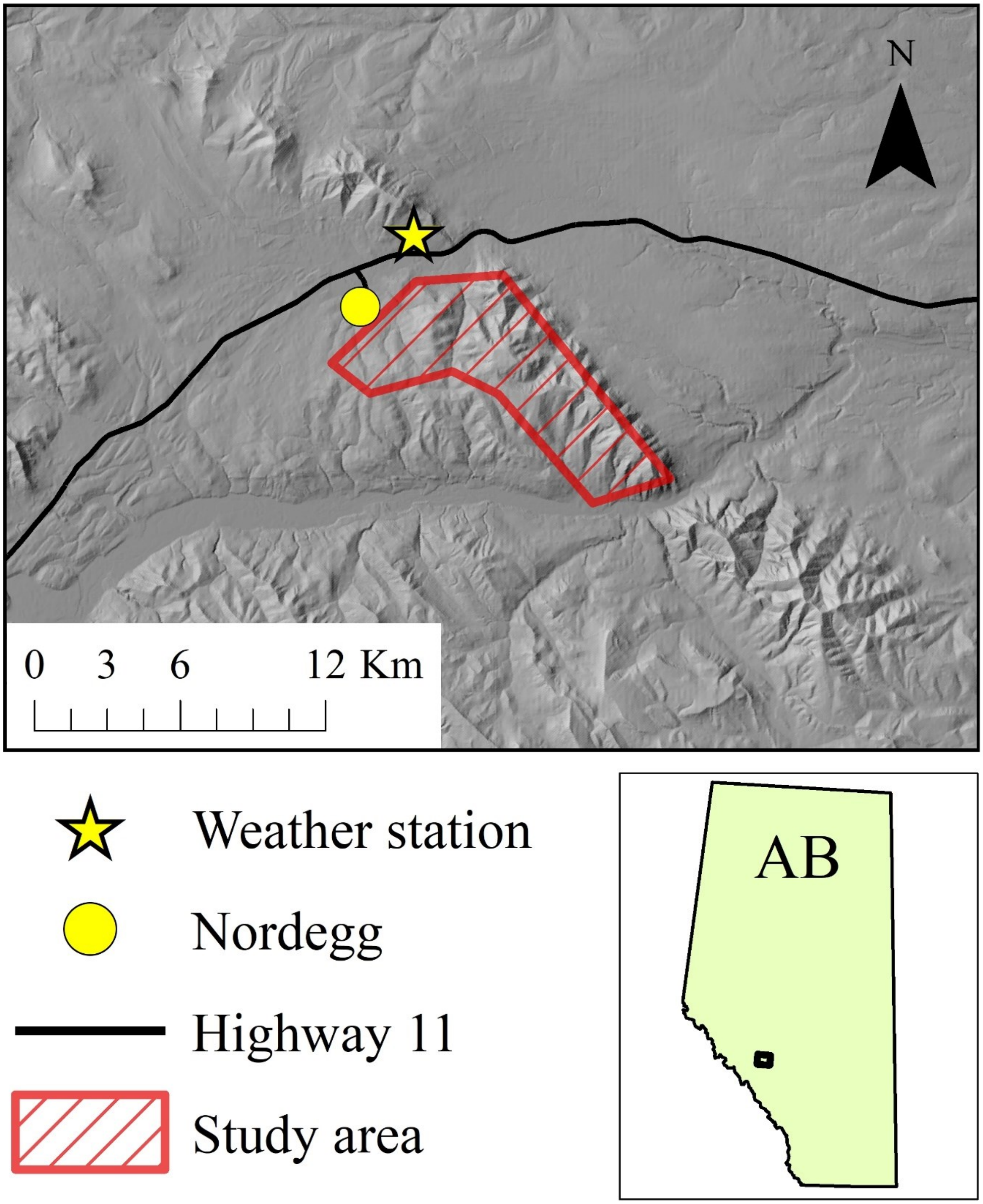


Figure 2. Map of study area, in Registered Fur Management Area 538 in Wildlife Management Unit 328. The area is near Nordegg, Alberta, and all specimens were trapped within the study area. The Nordegg Climate Station, used for analysis, is immediately north of the study area.

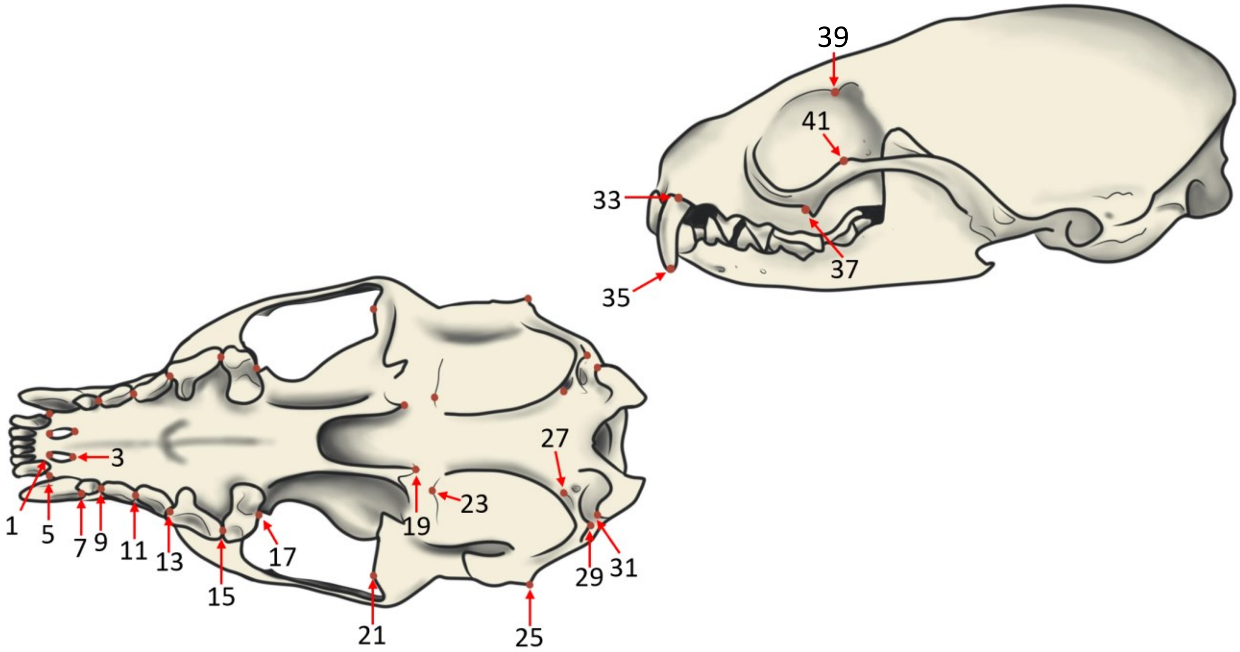


Figure 3. Location of cranial landmarks recorded on American marten skulls used in geometric morphometric analysis. Points indicate the landmark on one side, but landmarks were recorded on both sides and used in analyses. Drawing by Natika Pigeon.
1/2: The anterior-most point of the incisive foramen
3/4: The posterior-most point of the incisive foramen
5/6: Anterior point of base of canine
7/8: Posterior point of base of canine
9/10: Anterior point of base of second premolar
11/12: Anterior point of base of third premolar
13/14: Posterior point of base of third premolar
15/16: Anterior point of base of molar
17/18: Posterior crest of molar
19/20: Posterior-most point of pterygoid process
21/22: Anterior-most point of the retroarticular process
23/24: Anterior point of styliform process of the auditory bullae
25/26: Lateral end point of auditory meatus
27/28: Medial end point of tympano-occipital fissure
29/30: Posterior-most point of the jugular process
31/32: Anterior lateral tip of occipital condyle
33/34: Lateral point of base of canine
35/36: Apex of the canine
37/38: Infraorbital foramen
39/40: Zygomatic process of frontal bone
41/42: Frontal process of zygomatic bone

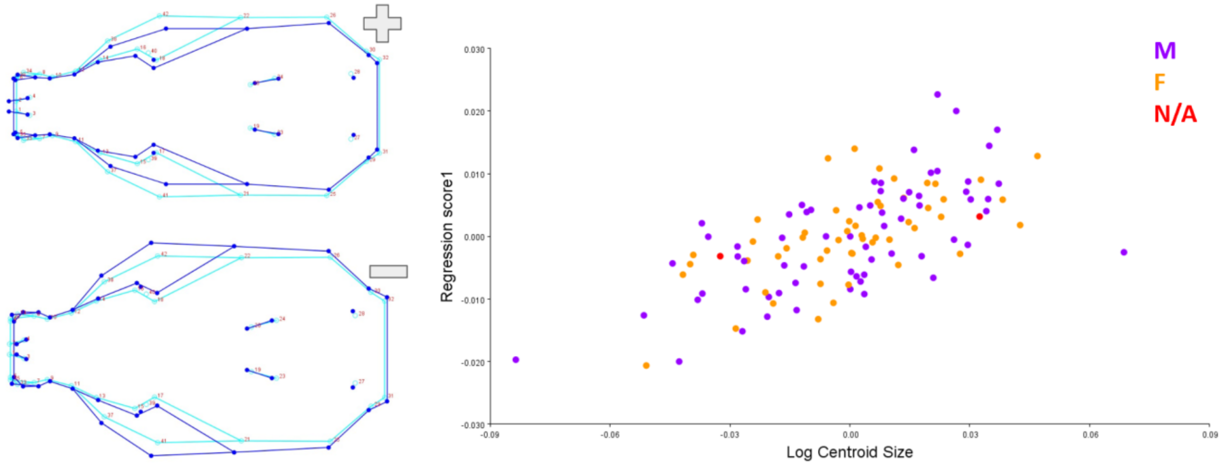


Figure 4. Linear regression of log centroid size as a factor of the symmetric shape component regression score of American marten skull landmark configurations, corrected for sex differences. American marten were collected near Nordegg, Alberta during 2004–2021. Green = females, blue = males, and red = individuals of unknown sex. % predicted = 5.1%. Significance for the permutation test against the null hypothesis of independence was evaluated at *P* <0.0001. The regression score represents variation of shape, as depicted in the wireframe drawings, that was most strongly associated with the log centroid size after Procrustes alignment (Drake and Klingenberg, 2008). The light blue wireframe is the average ‘consensus’ shape. The dark blue wireframes are the shape changes associated with positive (above) and negative (below) regression scores. The scale factor for the wireframes is 1.0, indicating an increase of the long centroid size by a unit of one.

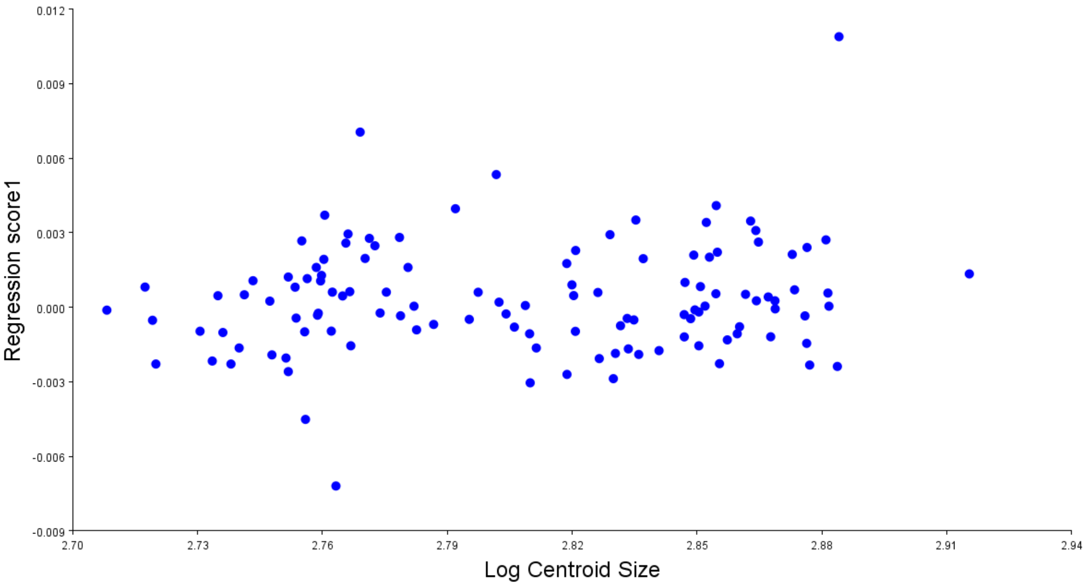


Figure 5. Linear regression of log centroid size as a factor of asymmetric shape component regression. score of American marten skull landmark configurations. Asymmetric shape scores are determined by comparing the differences in distance between left and right landmark pairs to the centroid. The regression score represents the variation of shape that is most strongly associated with log centroid size (Drake and Klingenberg, 2008). American marten were trapped near Nordegg, Alberta during 2004–2021. P-Value from permutation test against the null hypothesis of independence = 0.39.

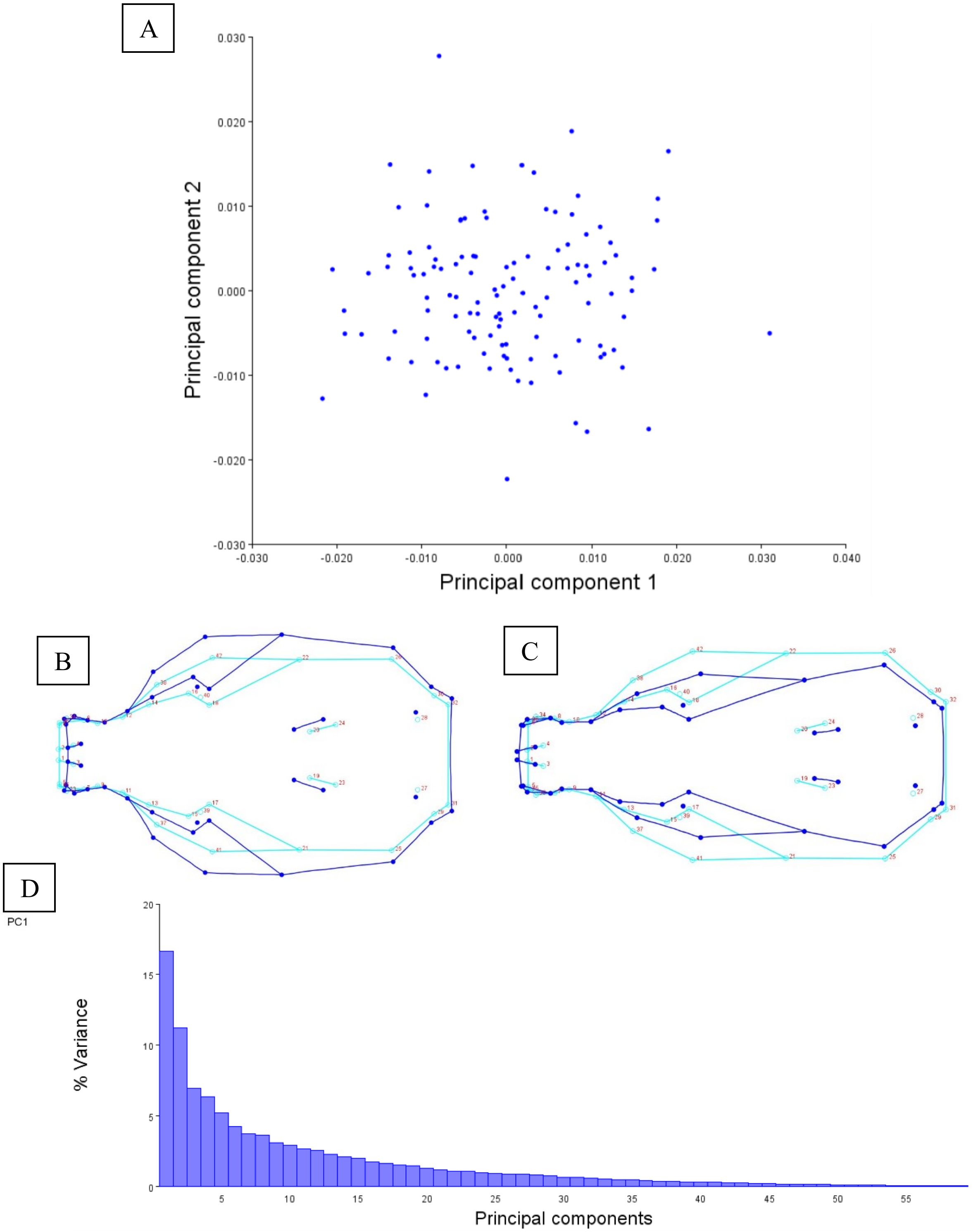


Figure 6. Covariation between two symmetric components of variation of American marten skull landmark configurations. Principal Component 1 (PC1) represents the shape changes that account for the greatest amount of variation among individuals (16.6%, D). The light blue wireframe is the average ‘consensus’ shape. The dark blue wireframes are the shape changes associated with the negative (B) and positive (C) PC values for PC1, with a scale factor of 0.1 Procrustes distance units. Panel D indicates the percent of total covariance attributed to each PC. American marten were collected near Nordegg, Alberta during 2004–2021.

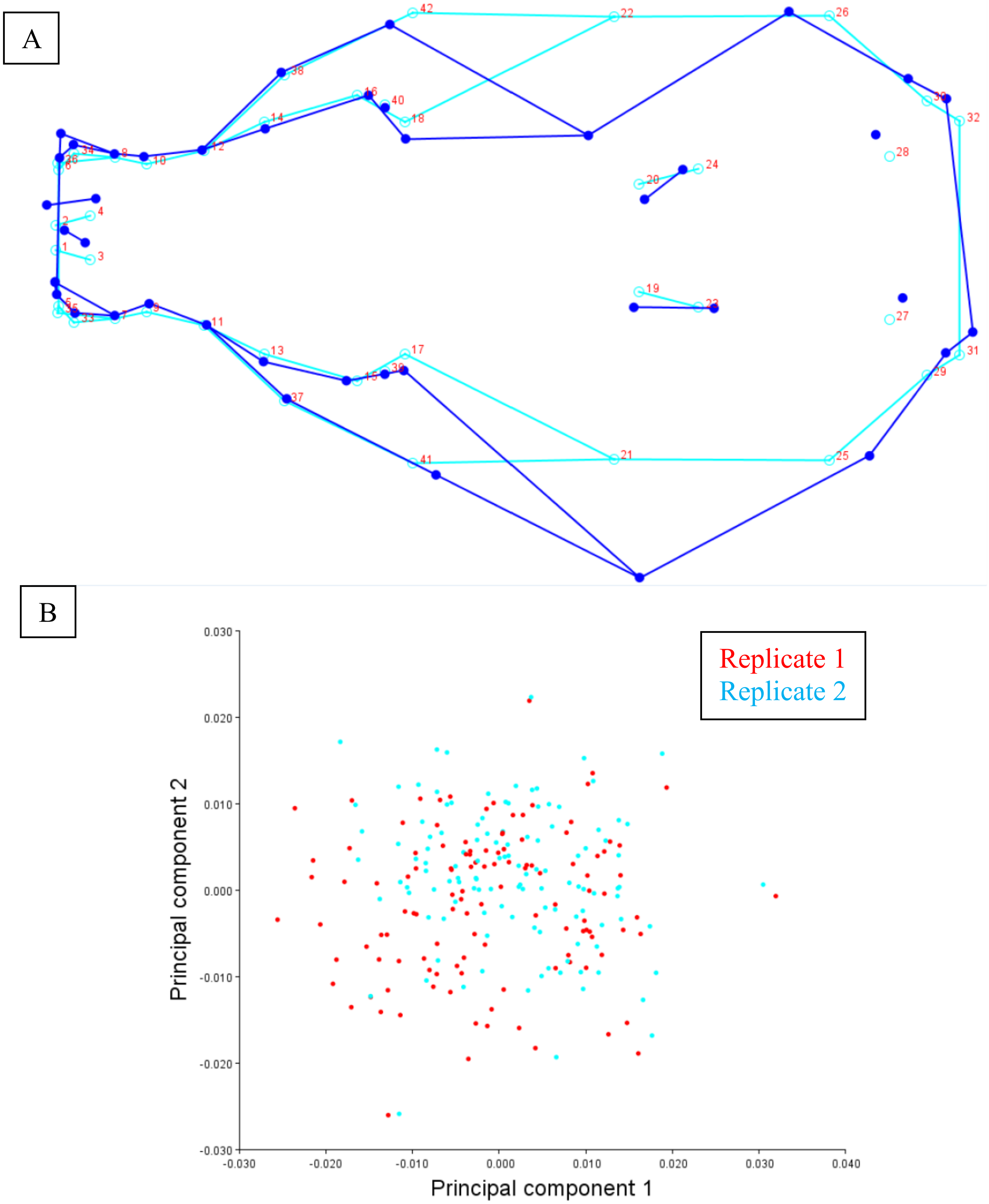


Figure 7. PC1 variation from the PCA of the asymmetric component of American marten skull landmark configurations (A). The light blue wireframe is the average ‘consensus’ shape. The dark blue wireframes are the shape changes associated with positive PC1 values, with a scale factor of 0.1 Procrustes distance units. Two replicates of each individual were included separately to assess the amount of variation in asymmetric shape due to measurement error. Panel B indicates the PC scores of each individual for PC1 and PC2, coloured by replicate. American marten were collected near Nordegg, Alberta during 2004–2021.

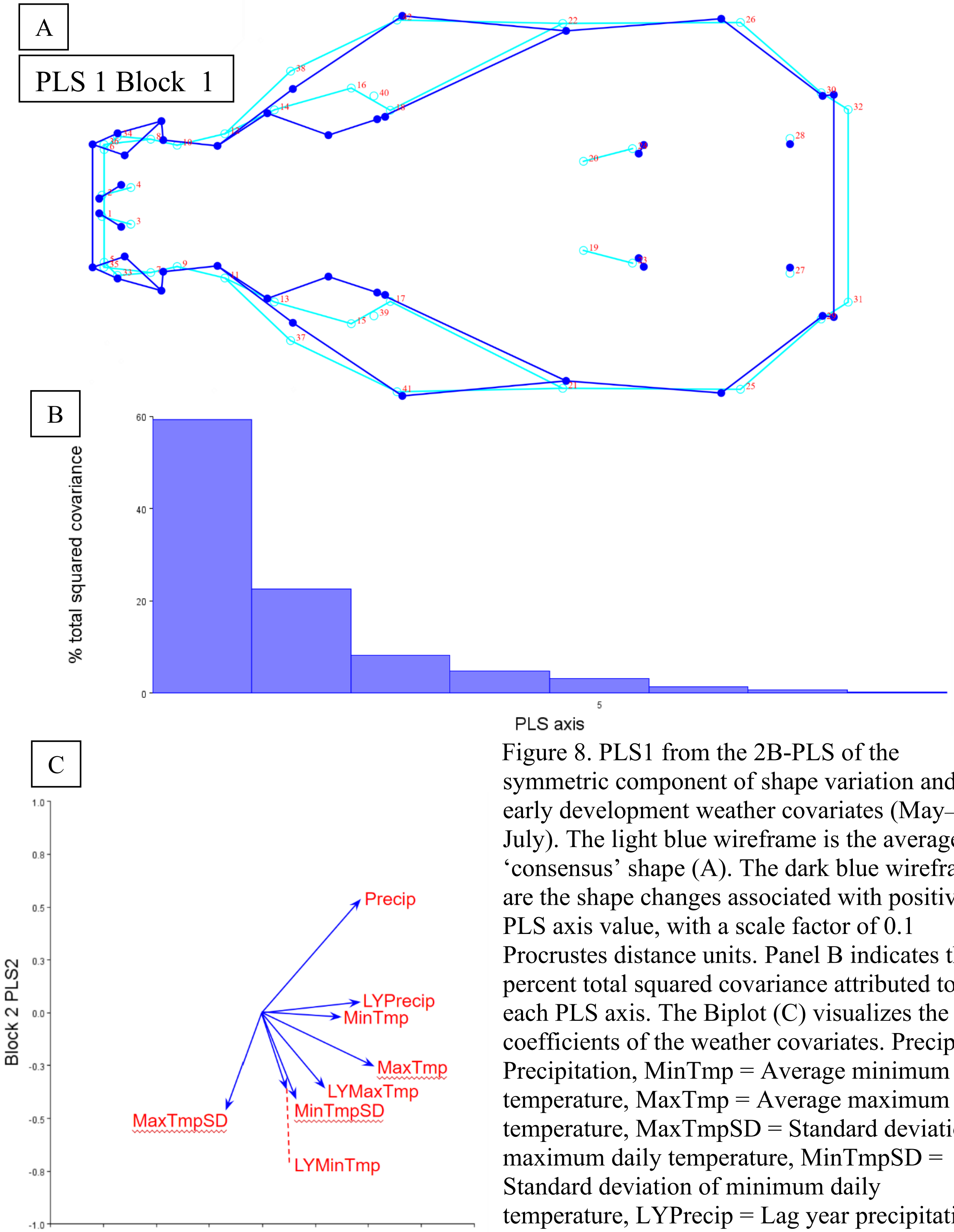
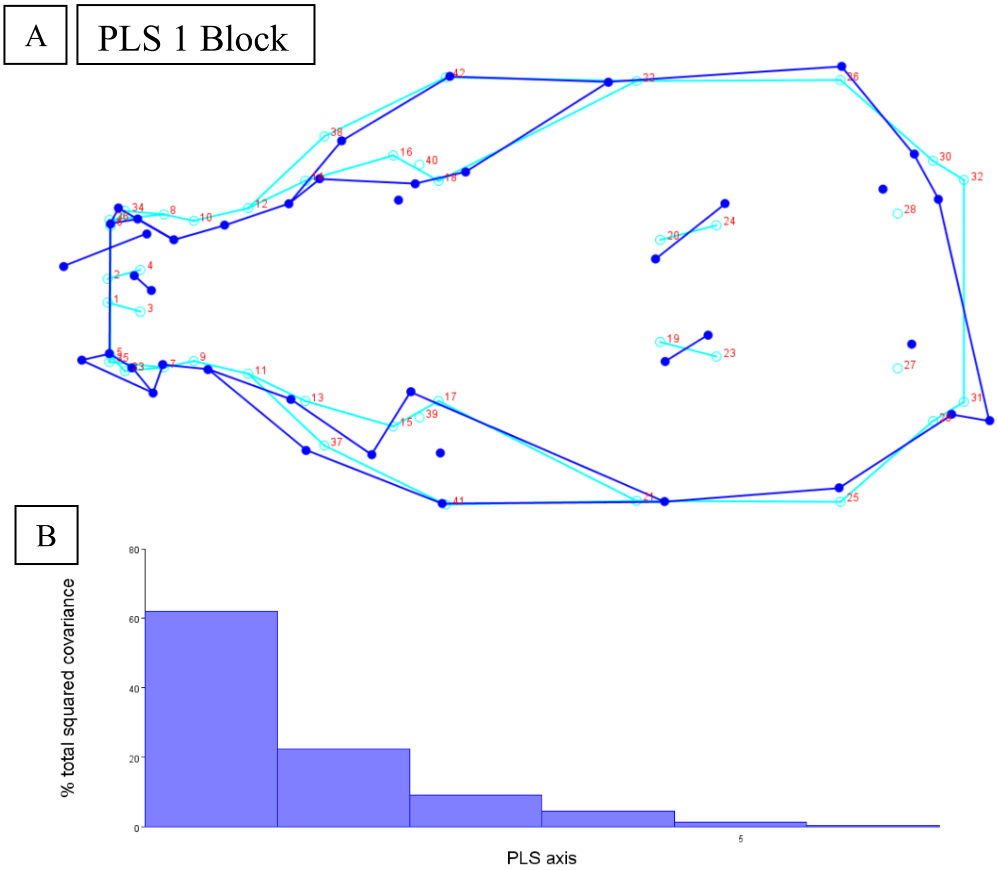


Figure 8. PLS1 from the 2B-PLS of the symmetric component of shape variation and early development weather covariates (May–July). The light blue wireframe is the average ‘consensus’ shape (A). The dark blue wireframes are the shape changes associated with positive PLS axis value, with a scale factor of 0.1 Procrustes distance units. Panel B indicates the percent total squared covariance attributed to each PLS axis. The Biplot (C) visualizes the PLS coefficients of the weather covariates. Precip = Precipitation, MinTmp = Average minimum daily temperature, MaxTmp = Average maximum daily temperature, MaxTmpSD = Standard deviation of maximum daily temperature, MinTmpSD = Standard deviation of minimum daily temperature, LYPrecip = Lag year precipitation, LYMaxTmp = Lag year average maximum daily temperature, LYMinTmp = Lag year average minimum daily temperature. American marten were collected near Nordegg, Alberta during 2004–2021.



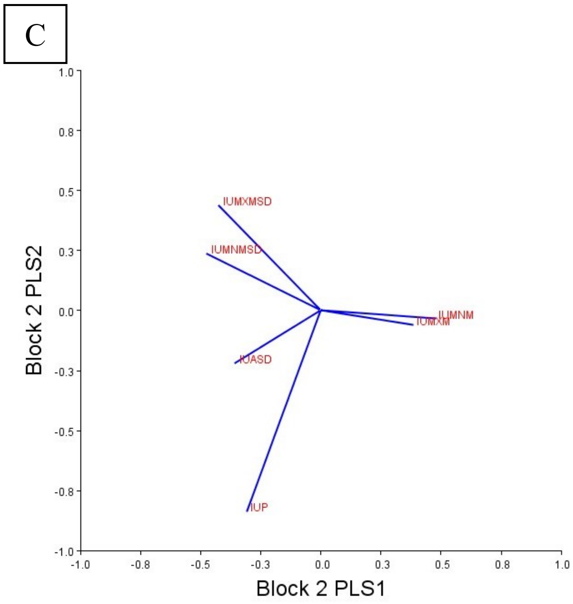


Figure 9. PLS 1 from the 2B-PLS of the asymmetric component of shape variation and in utero weather covariates (February–April). The light blue wireframe is the average ‘consensus’ shape (A). The dark blue wireframes are the shape changes associated with positive PLS axis value, with a scale factor of 0.1 Procrustes distance units. Panel B indicates the percent total squared covariance attributed to each PLS axis. The Biplot (C) visualizes the PLS coefficients of the weather covariates. IU indicates the in-utero period of development. P = Precipitation, MNM = Average minimum daily temperature, MXM = Average maximum daily temperature, ASD = average snow depth, MXMSD = Standard deviation of maximum daily temperature, MNMSD = Standard deviation of minimum daily temperature. American marten were collected near Nordegg, Alberta during 2004–2021.

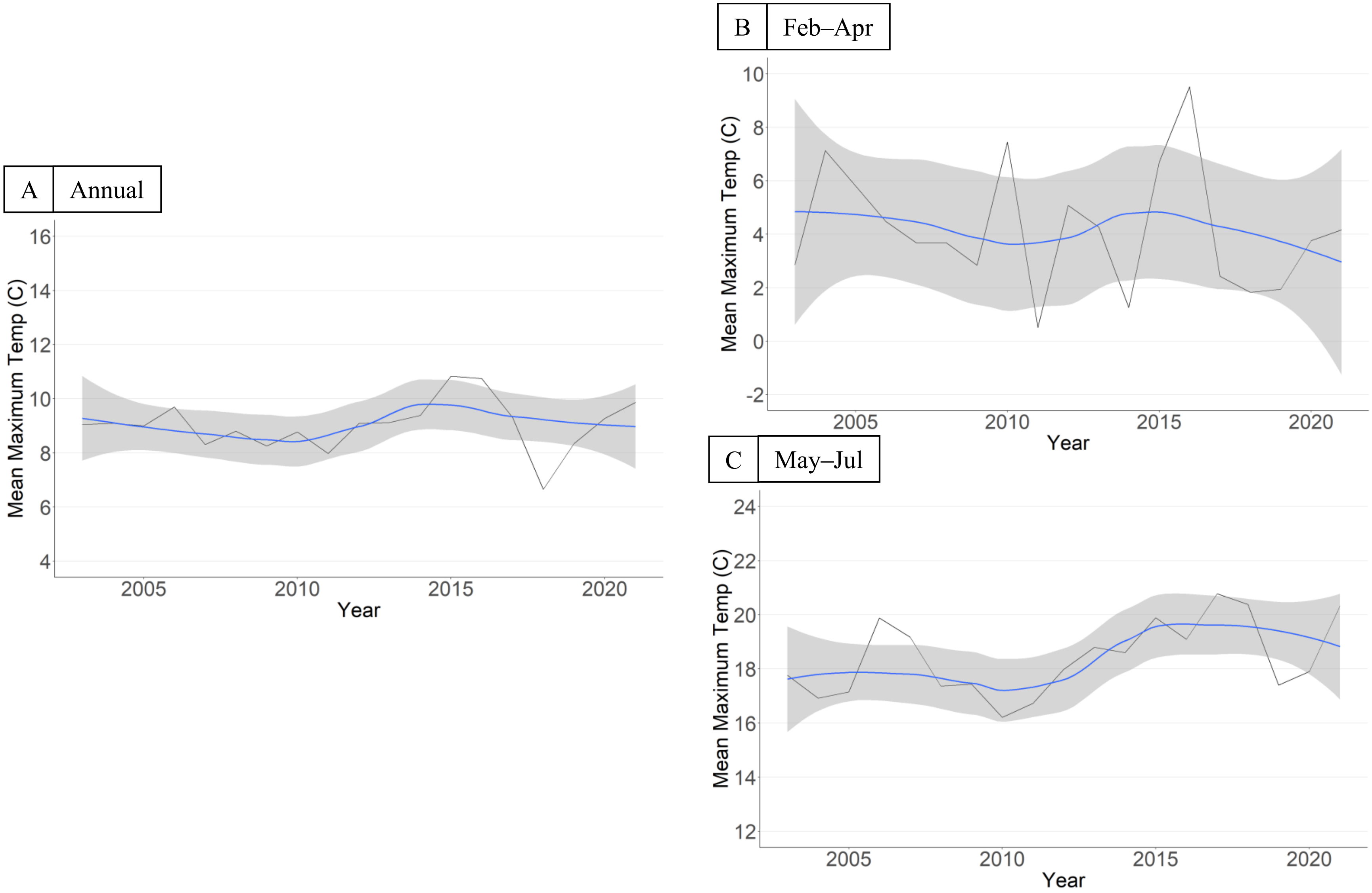


Figure 10. Average maximum temperature values in Nordegg, AB, from different timespans of the year. Panel A indicates the average daily maximum for the year, panel B is the average daily maximum during the in-utero developmental period (February–April), and panel C is the average daily maximum during the early postnatal developmental period (May–July). Figures were scaled to allow for visual comparison of the magnitude and pattern of variation among years.

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