Chipping in: variation in functional diversity of the North American beaver (*Castor canadensis*) during distribution range expansion.

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Table of Contents

Abstract:

In response to climate warming, many species are shifting their distributions poleward, leading to the introduction of new species in Northern ecosystems. In the subarctic, woody shrubs have become more abundant and robust, water bodies have shifted from bedfast ice to floating ice regimes during winter, and melting permafrost has changed the topography and hydrology, facilitating pond development. Consequently, North American beaver (*Castor canadensis)* populations have begun entering the "greened" tundra ecosystem across North America. As a specialized rodent that modifies ecosystems by foraging woody vegetation and damming riverine habitats, completely altering forest composition and hydrology, it is important to understand the drivers and predictors of low arctic beaver establishment to inform conservation and wildlife management practices.

In this thesis, I reviewed our existing understanding of which climatic, environmental, and vegetation factors influence beaver abundance, establishment, habitat selection, and foraging behaviour in the literature. This review highlighted that vegetation composition and traits, such as stem size and abundance, were considered as strong proxies for beaver forage and abundance, while climate, environment, and geomorphology increase the potential of habitat selection and establishment. Additionally, beavers' requirements change over time as the rodent completely alter their habitats and forest structure through ecosystem engineering. Therefore, it is crucial to distinguish between habitat characteristics before and after establishments to better understand the drivers of beaver colonization and abundance.

Secondly, I aimed to address how these environmental and vegetation factors affect the functional adaptation of beavers over their Canadian distribution. Using geometric morphometrics, I tested the hypothesis that beaver skulls are locally adapted to their environment by relating environmental factors to functional traits in beaver skulls across Canada. I found that beaver functional morphology is significantly associated with vegetation and climate variables. Specifically, functional changes in the masticatory regions of the skull are related with changes in forest composition, biomass, ecozone, and climate, suggesting that beavers are adapted to their habitat based on selective foraging. These findings provide insight into the adaptive potential of newly established beavers in the sub-arctic to better predict future range shifts and provide information for future management practices.

Résumé:

Suite au réchauffement climatique, de nombreuses espèces déplacent leur répartition vers les pôles, ce qui entraîne l'introduction de nouvelles espèces dans les écosystèmes nordiques. Dans la toundra, les arbustes ligneux sont devenus plus abondants et robustes, les plans d'eau sont passés d'un régime de glace fixe à un régime de glace flottante, et la fonte du pergélisol a modifié la topographie et l'hydrologie, facilitant le développement des étangs. Par conséquent, les populations de castor du Canada (*Castor canadensis*) ont commencé à s'établir dans l'écosystème de la toundra "verte". En tant que rongeur spécialisé qui modifie les écosystèmes en se nourrissant de végétation ligneuse et construisant des barrages, il est important de comprendre les prédicteurs d'établissement de populations arctiques de castors afin d'informer les pratiques de conservation et de gestion de la faune.

Dans cette thèse, j'ai revu l'état des connaissances actuelle sur les facteurs climatiques, environnementaux, et de végétation qui influencent l'abondance, l'établissement, la sélection de l'habitat, et le comportement de recherche de nourriture du castor dans la littérature. Cette revue a mis en évidence que la composition et les traits de la végétation, tels que la taille et l'abondance des tiges, sont considérés comme des variables indicatrices de l'abondance des castors, tandis que le climat, l'environnement et la géomorphologie sont liés au potentiel d'établissement dans un habitat. En outre, les besoins des castors évoluent au fil du temps, car les rongeurs modifient significativement leur habitat et la structure des forêts. Par conséquent, il est important de prendre en compte les qualités de l'habitat avant et après l'établissement d'une colonie pour mieux comprendre les facteurs de sélection de l'habitat et d'abondance du castor.

Ensuite, j'ai déterminé comment ces facteurs environnementaux affectent l'adaptation fonctionnelle des castors au Canada. En utilisant la méthode de morphométrie géométrique, j'ai testé l'hypothèse selon laquelle les crânes de castors sont adaptés localement à leur environnement en établissant un lien entre les facteurs environnementaux et les traits fonctionnels des crânes de castor. J'ai démontré que la morphologie fonctionnelle du castor est significativement associée aux variables de végétation et du climat. Plus précisément, les changements fonctionnels dans les régions masticatrice du crâne sont liés aux variations de la couverture forestière, de l'écozone et du climat, ce qui suggère que le castor est adapté localement à son habitat par le biais d'une recherche sélective de nourriture. Ces résultats permettent de mieux comprendre le potentiel d'adaptation des castors dans la toundra afin de

mieux prédire les futurs changements d'aire de répartition et de fournir des informations pour les futures pratiques de gestion de cette espèce.

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A big thank you to all the natural history museum staff who helped me find my way around the collections and supported me with data collection. To Burton Lim from the Royal Ontario Museum, and Kamal Khidas from the Canadian Museum of Nature, I thank you for allowing me into your collections and working with me during the trying time of the pandemic. To Anthony Howell from the Redpath Museum, thank you for accepting a plastic bag of frozen beaver heads with a big smile, and transforming them into beautiful museum specimens. This project could not have been possible without your collaboration and help.

I also thank Laura Pollock for being part of my supervisory committee and providing me with great advice, insights, and discussing really cool ideas with me that ultimately helped shape my thesis.

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Lastly, I need to thank Jillian Schneidman, my friends, my parents, and my sister Madison for their support, encouragement, and most importantly, for putting up with me talking about beavers at all hours of the day. Do not worry – that will not change!

Contribution of the authors:

This thesis consists of two chapters, including two manuscripts to be submitted to a peer-reviewed scientific journal. The candidate designed the studies, collected all relevant data, and conducted the analyses. Dr. Virginie Millien, the supervisor of this project, collaborated actively in all these steps. Contents of both chapters were written by Jonathan Diamond and were edited and received intellectual input from Dr. Virginie Millien, who is a co-author of the manuscripts.

The intention is for chapter one to be submitted to the Journal of Mammal Research, and for chapter 2 to be submitted to Frontiers in Mammal Science.

List of Figures and Tables:

Chapter 1

Chapter 2

List of Abbreviations:

Chapter 1:

CO_2 – Carbon Dioxide ……………………22

PRISMA – Preferred Reporting Items for Systematic Reviews and Meta-Analyses ……………………23

Chapter 2:

ANOVA – Analysis of Variance ……………………65

GPA – Generalized Procrustes Analysis ……………………65

MAT – Mean annual temperature ……………………66

MAP– Mean annual precipitation ……………………66

MODIS – Moderate Resolution Imaging Spectroradiometer ……………………66

PCA – Principal Components Analysis ……………………67

Introduction:

General Introduction:

Quantifying morphological variance, or morphometrics, is a well-defined and effective tool for ecologist and evolutionary biologists to better understand how evolutionary pressures interact with species and populations. Both theory and empirical evidence support the general consensus in the field that the morphology of phenotypic traits is related with the fitness of individuals and their survival, as most vital behaviors and biological functions are dependent on the design of their functional systems (Kingsolver and Huey, 2003). Functional morphology, a proxy for functional phenotypic expression (Richter and Wirkner, 2014), is the study of the function and performance of morphological traits (Ferry-Graham, 2002; Rybczynski, 2008), from major features such as the shape of the bill in birds, or small features such as variations in soft bone structures in small mammals.

Analysing differences in the shape of key functional traits has provided insights into fundamental evolutionary concepts. Adaptive radiations provide one of the best examples of the evolution of morphology in response to requirements defined by ecological conditions of a habitat (Foster et al., 2008; Tokita et al., 2017). For example, the beak and cranial morphology of Darwin’s finches (*Geospiza* sp.) in the Galapagos Islands rapidly adapted to their unique niches based on foraging specialization (Foster et al., 2008; Tokita et al., 2017). In fact, the association between morphology and the environment has long been used to inform the range of functions being performed across a taxonomic unit, such as individuals, populations, or species (Ferry-Graham, 2002; Martínez et al., 2014; Souto-Lima and Millien, 2014). For example, rodents’ diet is often strongly related to their bite force, which can be quantified and compared using cranial morphology, because skull shape constrains the arrangement of muscle masses and lever arms that drive bite force (Maestri et al., 2016b). Therefore, it is possible to infer the functional potential for feeding of a taxonomic group, based on its skull morphology (Cornette et al., 2015; Maestri et al., 2016b). As such, it is possible to uncover how specific environmental and ecological factors influence the morphology of functional traits, providing insight into how well adapted an individual is to their habitat (Stumpp et al., 2018). This can be particularly useful for comparing key morphological features in groups of widely distributed and highly specialized species that differ in habitat.

One particularly well-suited study system for evaluating the connection between functional traits and the environment are members of the family *Rodentia.* Rodents are the most diverse order of mammals with over 2000 recognized species occurring across a vast distribution (Samuels, 2009). Consequently, rodents inhabit many unique environments and often exhibit locally adapted phenotypes closely related to their habitat (Korth, 1994; Monteiro et al., 2003; Samuels, 2009; Kubiak et al., 2018; Baumgartner and Hoffman, 2019). Further, many rodent species and populations are undergoing rapid morphological change in response to climate change and habitat loss induced environmental pressures (Pergams and Lawler, 2009; Wolf et al., 2009; Fischer et al., 2011; Stumpp et al., 2018; Baumgartner and Hoffman, 2019). As such, rodents are often considered for evaluating the adaptive response to climate change (Millien et al., 2017; Baumgartner and Hoffman, 2019).

One rodent, however, that is far less frequently evaluated for its adaptive potential in a changing environment, is the North American beaver (*Castor canadensis*). In fact, the beaver is vastly distributed across North America (GBIF.org, 2022) and has well known foraging preferences that, despite some generalities, vary from habitat to habitat (Salandre et al., 2017; Mahoney and Stella, 2020). The semi-aquatic rodent is well-adapted for incisal biting, having significantly greater bite force than predicted based on their body mass (Cox and Baverstock, 2016). This is achieved through their optimized cranial morphology, allowing them to generate tremendous biting power along efficient moment arms (Cox and Baverstock, 2016). Despite this, their diet is variable and in some cases, such as in subarctic ponds, is made up mostly of soft-tissue vegetation (Milligan and Humphries, 2010).

Furthermore, over the last few decades, the beaver has undergone a range shift, with populations expanding into the tundra – a historically beaver free environment (Cox and Baverstock, 2016; Tape et al., 2018). This range shift is of utmost importance to monitor, as the beaver is an efficient ecosystem engineer, that across its North American wide distribution, alters environments via selective foraging, and dam and channel building (Mahoney and Stella, 2020). Remarkably, in their traditional ecosystems, beaver modifications improve biodiversity, increase wetland connectivity, and provide ecosystem services, such as improved water quality and wildfire reductions, by converting terrestrial ecosystems into wetlands (Hood and Larson, 2015; Fairfax and Whittle, 2020; Mahoney and Stella, 2020). However, in the subarctic, beaver impacts may be less positive. Beaver damming substantially increases water surface area of tundra water bodies, which is a catalyst for increased permafrost thawing (Tape et al., 2018). The thawing of the permafrost impacts the low arctic landscape, as well as releases greenhouse gasses into the atmosphere (Tape et al., 2018; Jones et al., 2020). Further, beaver damming is altering winter water temperature, potentially impacting the aquatic biome downstream of dams (Tape et al., 2018). Therefore, as a widely distributed and specialized rodent with potential impacts on northern ecosystems, it is important to better understand how and why these beavers are adapted to their environment.

Research Goals:

My thesis is divided into two chapters. In the first chapter, I systematically reviewed the literature on North American beaver abundance, establishment, habitat selection, and foraging across their distribution. The goal is to better understand which key environmental and vegetation factors influence beaver habitat and foraging in a time of rapidly changing climate and range shift.

The findings from this chapter informed my second chapter, in which I related functional adaptations of the beaver crania with environmental factors. Specifically, using a dataset of 117 beaver skulls accessioned in museum collections, I quantified beaver skull functional morphology across the northern part of its range and modelled the effect of environmental factors on cranial functional morphology. This chapter provides insight into the adaptive potential of newly established beavers in the sub-arctic for the purpose of better predicting future range shift and providing information for future management practices.

Altogether, my thesis presents critical information on how and why beavers establish and forage across habitats, and how those behaviours and choices are related to functional cranial morphology and local adaptation. This information will be useful for conservation biologists attempting to better understand the patterns of beaver range expansion into the sub-arctic. Further, by relating environmental conditions to functional adaptations, we gain key insight into the adaptive potential of the beaver in diverse environments. This will be useful to ecosystem managers throughout the entire beaver range, hoping to better predict the impact of beaver herbivory and engineering.

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Chapter 1

How ecosystem variability influences North American beaver abundance and colony establishments: a literature review.

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Abstract:

In response to climate warming, species are shifting their distributions poleward, leading to the introduction of new species in Northern ecosystems. Given subarctic warming, woody shrub abundance has increased, bedfast ice water bodies have shifted to floating ice regimes during winter, and rapidly melting permafrost has facilitated pond development. Consequently, North American beaver (*Castor canadensis*) populations have entered the North American tundra, with established colonies in Alaska, the Northwest Territories, and Northern Québec. The beaver is a specialized rodent that modifies ecosystems, completely altering forest composition and hydrology. Despite these affects, gaps remain in how ecological factors influence beaver establishments and foraging behaviours across their distribution. Here, we systematically reviewed the available and current literature on factors predicting beaver abundance, establishment, habitat selection, and foraging across their range. The search resulted in 31 relevant studies discussing both environmental and vegetation factors related to beaver abundance, establishment, habitat selection, and forage. We found that just over 25% of the articles assessed newly established beaver sites, while the remainder focused on already established colonies. Further, 19 articles discussed vegetation composition, 15 discussed geomorphology, 14 discussed vegetation quality, 13 discussed climate and environments, and 8 discussed other variables. Overall, vegetation composition and traits were considered as strong proxies for beaver forage and abundance, while climate and environment, and geomorphology provided strong insight into the potential of habitat selection and establishments. Lastly, as an extremely widely distributed semi-aquatic mammal, factors had variable impacts based on habitat differences, highlighting the importance of regional effects on beaver abundance, establishment, habitat selection, and forage.

Keywords: *Castor canadensis*, ecosystem engineer, selective foraging, habitat selection, range expansion

1.0 Introduction:

1.1 – A Changing Arctic

Global arctic and pan-arctic ecosystems are undergoing rapid biotic and abiotic changes at the hand of climate change (Walsh et al., 2011; Tape et al., 2018). Since the turn of the century, arctic surface air temperature has increased between 2-3 times faster than the global average (Bush and Lemmen, 2019). Accelerated warming has led to declines in arctic sea-ice cover, glacial mass, and snow cover, while increasing coastal erosion, storm surges, greenhouse gas release, and wildfires (Fraser et al., 2014; MacDonald and Birchall, 2020).

Annual temperature increase in the terrestrial tundra is also transforming the landscape geologically, hydrologically, and biotically. Particularly, increased permafrost melting and the shrubification, or extensive expansion and increase in abundance of tall deciduous shrubs such as *Salix* spp., *Alnus* spp., and *Betula* spp., is transforming the ecology of the tundra (Fraser et al., 2014; Jung et al., 2017; MaudePelletier et al., 2019). For instance, lichen populations are declining and being replaced by deciduous shrubs; local disturbances, such as wildfires or cryoturbation, are more frequent, providing vegetation better access to soil minerals and resulting in a greener tundra; thermokarsts and pond development have significantly accelerated, altering the topography and hydrology of the low arctic and further facilitating shrub expansion and growth (Schuur et al., 2007; Fraser et al., 2014; Mekonnen et al., 2021). Consequently, many tundra habitats, particularly those along riparian ecosystems or areas of permafrost thaw, have been "greened" with increased abundance of photosynthetic and deciduous vegetation, resulting in a transformed low arctic ecosystem (Tape et al., 2018).

One consequence of global warming is that many species are shifting their distributions poleward, leading to the introduction of new species into Northern ecosystems (Tape et al., 2018; Jones et al., 2020). For example, northern moose (*Alces alces gigas*) and the snowshoe hare

(*Lepus americanus*) have capitalized on the shrubification and warming of the low arctic, expanding their range from the boreal forest into tundra habitats that now provide them with adequate forage and cover from predators (Tape et al., 2016a; Tape et al., 2016b). The shrubified and warmer tundra has also welcomed another species of particular importance: the North American beaver (*Castor canadensis*) (Jung et al., 2017; Tape et al., 2018). In recent years, beaver populations have been reported in the tundra across the North American continent, with established colonies seen beyond the tree lines of Alaska, Yukon, and Northern Québec (Jarema, 2006; Jung et al., 2017; Tape et al., 2018).

1.2 – Beaver Ecology

The beaver is a classic example of a keystone species because it modifies entire ecosystems via felling woody plants; building burrows, canals, and dams; and through intensive herbivory to best meet its ecological requirements (Mahoney and Stella, 2020; Brazier et al., 2021). Consequently, its ecosystem engineering impounds large areas that increase wetland size and volume, reduces sediment movement speeds, changes water chemistry, and impacts vegetation and wildlife biodiversity (Smith et al., 1991; Margolis et al., 2001; Hood and Larson, 2015; Brazier et al., 2021). Beaver impounded wetlands also have increased habitat heterogeneity, increased aquatic biodiversity, and improved ecosystem resilience (Law et al., 2019). Additionally, beavers will excavate long canals that significantly increase wetland connectivity and perimeters that provide novel habitats supporting species that would otherwise not be present (Nummi et al., 2011; Hood and Larson, 2015; Willby et al., 2018; Brazier et al., 2021). Further, beavers forage and fell large woody vegetation, exposing the forest understory to more solar radiation, improving its success and diversity (Brazier et al., 2021). Beaver disturbances are also long lasting, with clear effects of beaver occupation remaining for years after sites have been abandoned (McMaster and McMaster, 2001). As such, beavers are highly disruptive to the habitat and influence both abiotic and biotic ecosystem components, altering wetland geomorphology, hydrology, and biodiversity.

1.3 – Beaver Range Expansion into the Sub-Arctic

While beaver disturbances are common throughout much of North America, beaver activity is considered a new and potentially detrimental phenomenon in the arctic (Tape et al., 2018; Jones et al., 2020). Impounding arctic riparian ecosystems promotes permafrost degradation and replaces tundra riparian ecosystems with wetlands. This consequently facilitates further shrubification in the tundra, altering the fragile ecological balance of the low arctic, and impacting critical ecosystem services for local wildlife, and communities (Tape et al., 2018; Jones et al., 2020). Further, as beaver herbivory is very intensive and drastically alters forest communities, northern wildlife may be negatively impacted. For example, Tape et al. (2019) showed that beaver herbivory in Alaska has reduced forage and habitat for moose and snowshoe hares, already impacting those populations with unknown lasting effects (Tape et al., 2018). Additionally, beaver damming has major effects on water surface area expansion, which further accelerates tundra permafrost degradation (Jones et al., 2020). Permafrost degradation plays a significant role in the global carbon cycle and climate because beyond the landscape-level disruption of degrading soil, thawed soil exposes microbial organic-matter that begins decomposing, releasing CO2 and other greenhouse gases (Walter Anthony et al., 2021). Therefore, as a prolific agent of change, it is critical to better understand the drivers of low arctic beaver establishment to inform conservation and wildlife management practices.

To do this, we must first consider what factors limit, or encourage, the establishment of beaver colonies across their entire distribution. While beaver habitat suitability has been evaluated before, these assessments have mostly focused on beaver foraging and are generally limited to one region (Jenkins, 1975; Allen, 1982; Stoffyn-EgliPatricia and Martin, 2011; Mahoney and Stella, 2020). Further, what is far less understood is the relationship between vegetation traits, such as wood density and vegetation quality, with beaver foraging activity across large spatial scales. Additionally, many environmental factors likely influence beaver establishments as well, such as stream gradient, percentage of forest cover, or topography (Touihri et al., 2018). Therefore, with the aim of better understanding which factors encourage, or limit, beaver establishment, or abundance, we conducted a systematic review of the literature and synthesize current knowledge on beaver habitat selection, abundance, establishment, and foraging behaviour across North America, with a focus on the influence of environmental and vegetation variables. We also investigated whether these studies evaluated the importance of environmental and vegetation variables differently in newly inhabited habitats compared to previously established ones.

2.0 Methods:

2.1 - Systematic Review

For this review, we conducted a systematic PRISMA search (Figure 1) in the Web of Science database (Moher et al., 2015) on April 5th, 2022, using the following search terms: TOPIC: (("Castor canadensis" OR "north american beaver") AND ("central place forag*" OR "forage* select*" OR diet* OR browse OR forage* OR harvest OR habitat* OR “environment* factor*”) AND (distribution OR range OR expansion OR establish*)). Only research articles published on or after January 1st, 2000, were considered to ensure that studies would be recent, and have methodologies, reporting, and statistical analyses that were similar enough to make strong and unbiased connections between them.

Next, each study had their field of research, title and key words, and abstracts scanned and read to determine relevance. We determined a study to be relevant for this analysis based on five selection criteria: (1) Studies had to be in a relevant or related field, such as but not limited to, ecology, biodiversity conservation, environmental sciences, and zoology. Papers listed under research areas such as engineering, life science, and cell biology were not included. (2) Studies had to specifically focus on the North American beaver. If a study compared the Eurasian beaver or any extinct beaver to the North American beaver, the study must have evaluated and reported results for the species C*astor canadensis*. (3) Studies must take place in North America. While certain European and South American countries are inhabited by the North American beaver, these beavers were recently reintroduced, and their establishment was largely driven by human decisions related to introduction programs (Anderson et al., 2009; Parker et al., 2012). (4) Studies must have addressed important factors or theories (such as central place foraging) associated to beaver success or establishment within a habitat. (5) Lastly, studies should not be experimental or theoretical, and must report empirical data.

After studies were filtered based on the above five criteria, articles were checked for any duplication or errors, and then verified to be peer-reviewed. The remaining studies were then extracted as a library into Endnote for review (The EndNote Team, 2013). Next, papers were read and assessed, where information, themes, and factors pertaining to beaver establishments, abundance, and foraging success across North America was extracted.

Papers were also categorized as either “newly established” or “previously established” based on how long the beaver colonies being evaluated have been present at a site. If a paper evaluated or compared these types of establishments, they would be considered in both groups. Then, due to small sample size, factors in each degree of establishment were pooled into environmental (includes the total frequencies for geomorphology, environment, and climate) and vegetation (includes the total frequencies for composition and quality) factors. Using a Chi Square test on the pooled factors, we evaluated which factors, environmental or vegetation, were most frequently important across differing degrees of establishment.

3.0 Results

3.1 Systematic Review

Initial search results produced *n* =162 studies. Over the 22 years included in the search, at least one article matching the search criteria was published each year, with an average of 7.36 articles per year, and a maximum of 14 in 2021. Overall, the number of publications generally increased over time, with 55% of the articles being published between 2014 and 2022 (Figure 2). Once filtered by appropriate field, *n*=130 articles remained. Articles could be described by more than one field; therefore, articles included were classified as ecology (n=90), conservation biology (n=40), zoology (n=36), environmental sciences (n=29), and six other biological domains (n=26) (Figure 3). After titles and abstracts screening, 99 articles were excluded, resulting in 31 papers to be analysed in depth (Fig. 3, Table 1). Of those 31 papers, 23 described key environmental variables, while 24 focused on vegetation variables. Due to the interconnectedness of these variables, some articles included critical information for both, and were included in each category. Further, 8 (25.8%) articles considered dispersal sites and/or new beaver establishments, compared to the 23 (74.2%) that focused on currently occupied beaver sites or indicators.

In total, 19 (61.2%) papers addressed the impacts of vegetation composition on beaver forage, abundance, and establishments (Figure 3, Table 1). This category includes the discourse surrounding the importance of the composition of preferred or non-preferred species of woody trees and shrubs, as well as aquatic vegetation. Similarly, 14 (45.1%) articles considered the effects of vegetation qualities on beaver forage, abundance, and establishments (Figure 3, Table 1). Here, vegetation quality encompasses many vegetation traits, such as stem size and abundance. Further, the distance between vegetation and beaver impoundments was included in this category due to its known influence on beaver foraging (Gallant et al., 2016). Additionally, 15 (48.4%) studies considered the implications of geomorphology on beaver abundance, and establishments (Figure 3, Table 1). For the purpose of this review, we considered variables concerning hydrology, such as stream gradients, widths, and open water areas as geomorphic due to the tight connection between landforms and hydrology when considering their influence on the beaver. Next, 12 (38.7%) papers discussed the influence of climate and environmental variability (Figure 3, Table 1). While this category remains broad, key variables considered were temperature and precipitation, seasonality, spatial variance, disturbances (i.e., wildfires), and environmental variability. Lastly, 8 (25.8%) articles consider "other" factors that we grouped together due to low inclusion rates across the total review (Figure 3, Table 1). Despite low numbers, they remain important. Examples of these factors are human-beaver interactions, predation, and beaver demographics.

Lastly, when considering variation across degree of beaver establishment, we found that geomorphology (86%) was the most assessed factor for new establishments, while vegetation quality (54%) and composition (63%) were most frequent for previously established sites (Figure 4). Further, the Chi Square test on the pooled factors of environment and vegetation factors revealed that the relative difference between factors assessed was significantly different ($X^2 = 4.80$, $p < 0.03$). Papers evaluating newly established beaver sites reported the importance of environmental factors most frequently (~71%), whereas papers considering previously established sites reported factors more evenly but focused more on the effect of vegetation at those sites (environment ~43%, vegetation ~57%).

4.0 Discussion

When considering beaver habitat selection, abundance, establishment and foraging, the literature revealed that these processes are multi-faceted, with the relative importance of different factors varying from region to region. Nonetheless, four major groups of factors are important to consider for beaver habitat selection and foraging: 1) vegetation composition, 2) vegetation quality, 3) geomorphology, and 4) environmental and climate variables. In general, these factors have varying impacts on the beaver depending on general habitat qualities and characteristics. Indeed, the beaver is likely influenced by these factors in a hierarchical fashion that varies across regions. Further, as ecosystem engineers that optimize their habitats, it is crucial to consider habitat qualities before and after establishments to better understand the drivers of beaver habitat selection and abundance. Generally, vegetation composition and traits (were considered as good proxies for beaver foraging choice and abundance, while climate, environment, and geomorphology provided insight into the potential for habitat selection and establishment success.

This difference is likely related to the significant ecosystem modifications beavers make on a habitat. This finding highlights the importance of considering beaver abundance, habitat, and success beyond evidence suggested from a single snapshot of environmental and vegetation factors at a given time. Nonetheless, each factor provides insight into different characteristics of beaver abundance, habitat selection, forage, and success that provide information usable to develop models and management strategies.

4.1 – Influence of Vegetation on Beaver Establishment and Foraging

Vegetation Composition and the Choosy Generalist

Unsurprisingly, the most common factor influencing beaver abundance was vegetation composition. The beaver is a well-known choosy generalist that has foraging preferences, such as willow species, and has species they avoid, such as most conifers (Brenner, 1962; Jenkins, 1975; Donkor and Fryxell, 1999; Gallant et al., 2004; Mahoney and Stella, 2020). As such, woody and herbaceous species composition have been included in beaver habitat suitability models since the 1980s, where an abundance of generally preferred species would often be considered as a proxy of potential for beaver establishments (Allen, 1982). Based on this concept, a habitat with an abundance of the more well-documented preferred beaver prey, such as poplar (*Populus spp*.), willow (*Salix spp.),* alder (*Alnus spp.)*, and/or birch (*Betula spp*.), would be considered as a suitable habitat for the beaver (Allen, 1982). The reason for why, when all else is equal, a specific species is chosen over another is not entirely clear, but it is likely related to seasonal and annual variation in its nutritional quality, abundance, and ease of forage (Jenkins, 1979). Nonetheless, beaver habitat selection has been reported to be positively correlated to higher amounts of preferred species across their distribution (Wang et al., 2019; Ritter et al., 2020). However, beaver preference for a plant species can depend on a myriad of factors, leading to variance in selection rates across different habitats.

First, the selection of a species may be related to the function the vegetation will serve. The brown rodent is a unique herbivore as it forages specific vegetation for distinct purposes. In addition to being heavily driven by nutrition, beavers forage for building materials. In fact, beavers are known to occasionally select generally avoided species, such as conifers, for the construction of dams and rafts designed for food cache transportation and storage (Slough, 1978; Milligan and Humphries, 2010). These findings are consistent with others that have observed conifers being felled for building, despite normally otherwise being avoided (Jarema, 2006; Mahoney and Stella, 2020). Therefore, over time as beaver dams and lodges become more established, the foraging preferences of a colony may evolve from a larger proportion of construction materials in hardwoods to a greater proportion of nutritious herbaceous plants and softer shrubs that require far less effort and risk of predation to collect (Bergman and Bump, 2018).

Additionally, variation in foraging selection may be the result of over-consumption of terrestrial woody vegetation in previous seasons, leading to a shifted forest community with less preferred plants - especially in boreal habitats with limited soil nutrients and slower regeneration times (Bergman and Bump, 2018). When this happens, beavers may adapt their diet, and be less selective in their consumption, foraging lower quality terrestrial plants (Gallant et al., 2004). However, this may be tolerable because beaver impoundments improve the habitat quality for many herbaceous plants, inflating soft-tissue plant abundance compared to that of a linearly flowing body of water, providing more opportunity for the beaver to prey on soft-tissue vegetation instead (Tape et al., 2018). Consequently, the beaver may be able to supplement their diet with soft tissue vegetation when nutritious woody plants are scarce.

Lastly, the dietary proportion of hardwoods to herbaceous plants varies with seasonality, where summer is used for preparing the food cache, and the spring for dam maintenance due to increased water-flow from snowmelt (Gallant et al., 2016). For example, in subarctic environments, ice and snow cover may prevent beavers from safely preying on terrestrial plants, thus encouraging the consumption of aquatic plants during the winter months (Milligan and Humphries, 2010). In fact, stable isotopes analyses have revealed that ~60-80% of subarctic beavers' fall and winter diets are composed of aquatic vegetation, compared to ~50% in the summer months (Milligan and Humphries, 2010). Farther south, beavers in Ohio, USA, have been reported to have similar consumptions with soft-tissue vegetation making up significant portions of their summer diet (Svendsen, 1980). Therefore, aquatic vegetation is clearly important across habitats, despite not being evaluated frequently (Milligan and Humphries, 2010). As such, beaver foraging and abundance is related to the availability of preferred plants, both woody and soft tissue. However, this relationship is not clear cut, as beavers' dependence of preferred species may change depending on their habitat, and stage of colonization.

Vegetation Quality and the Choosy Generalist

Another recuring factor influencing beaver establishment and foraging was vegetation quality and traits. As an herbivore, a beaver's success in an environment is related to their ability to safely forage. Where high abundance of easily accessible stems exists, a beaver will likely have high success of establishing (Francis et al., 2017; Mumma et al., 2018). Similarly, in habitats with high vegetation abundance near water, beavers have greater foraging success and establish more readily (Mumma et al., 2018; Mahoney and Stella, 2020). Additionally, the frequency of medium diameter stems also likely encourages beaver success in a habitat due to improved foraging opportunity (Mahoney and Stella, 2020). Therefore, there may be a strong connection between beaver establishment, forage success, and vegetation traits. However, as ecosystem engineers all the above traits may be influenced by beaver presence, making it hard to discern what encourages beaver success or what is a product of it. Nonetheless, it is likely that beaver selective foraging is also related to vegetation traits in addition to, or perhaps more so than species (Mahoney and Stella, 2020).

The amount of effort a beaver must use will factor into what stems are being selected. Often, beaver foraging is described by the central place foraging theory, which predicts that beaver selectivity for preferred species will increase with the distance they must travel out of the water (Donkor and Fryxell, 1999; Raffel et al., 2009; Gerwing et al., 2013a). This is because as distance increases, so does the risk of predation. In central British Columbia, Gerwing et. al (2013) found that the majority of beaver foraging occurred close to the water, with few stems foraged beyond 25m from the water (Gerwing et al., 2013a). The authors noted, however, that species selectivity was not affected by distance, while stem size selection was, suggesting that species selectivity may be less important than other factors (Gerwing et al., 2013a). Accordingly, Mahoney and Stella (2020) showed that selective preference is indeed related to the size, or diameter, of stems in addition to the distance from their occupied body of water (Mahoney and Stella, 2020). These findings are consistent with Raffel et. al (2009), who drew the same conclusion in Ohio, USA (Raffel et al., 2009). This implies that beaver selectivity is not limited to species. Instead, it is multi-tiered, with different factors influencing their foraging choices. A glaring example of this is that in the Adirondacks, located in New York state, USA, beavers have been observed to preferentially select for American beech, despite this being an avoided species elsewhere (Mahoney and Stella, 2020). Therefore, beaver foraging selection is likely a function of the size distribution of abundant stems rather than only species specific (Mahoney and Stella, 2020).

In addition to foraging, stem abundance will have impacts on home range size. Beavers have a home range where resources are spatially and temporally heterogenous, with their core areas consisting of a lodge, escape cover, and preferred foraging material (Havens et al., 2013). As choosy generalists that aim to center their colonies around preferred prey, beavers have been seen to enlarge their home ranges to improve access to woody plants when necessary (McClintic et al., 2014). In habitats with historically adequate woody plant abundance, this may be related to woody plants taking longer than 1 year to regenerate, so beavers must expand their range to avoid a temporal depletion of their preferred woody forage (McClintic et al., 2014). Alternatively, Labrecque-Foy et al. (2020) found that beavers may alternate lodges to avoid species depletion in smaller home ranges (Labrecque-Foy et al., 2020). On the other hand, habitats composed of less preferred vegetation will see beavers with larger home ranges to meet their energy requirements (Havens et al., 2013). Therefore, the beaver has many strategies for dealing with different vegetation regimes in their home range, often findings ways to gain increased access to preferred forage.

More generally, beaver abundance is likely related to the availability of deciduous vegetation. Mumma et al. (2018) reported that in boreal northeast British Columbia, Canada, beaver occurrence is driven by vegetation cover, with upland forests having less beavers than deciduous swamps (Mumma et al., 2018). They reason that this may be related to upland habitats being less suited for damming (Mumma et al., 2018). Wang et al. (2019) argue that the beavers' habitat selection is hierarchal, and forest cover is a second- and third-order factor (Wang et al., 2019). In fact, they found that second-order habitat selection was more associated to land-cover (i.e. herbaceous wetland, shrubs, hardwood forest, etc.) than water bodies, and herbaceous wetlands being the most important third-order association (Wang et al., 2019). Similarly, Gerwing et al (2013) demonstrated that in central British Columbia, Canada, beaver foraging choice was also hierarchal, starting with large scale factors such as site selection, medium scale factors such as distance from water, and ending with fine scale factors such as forest compositions (Gerwing et al., 2013a). Further, St. Pierre et al. (2017) found that hardwood cover was a driver of beaver abundance at the landscape-scale in Québec, Canada (St-Pierre et al., 2017). Specifically, they found that beaver dam density per kilometer of stream increased with hardwood cover in particular ecoregions, such as Abitibi and James Bay Lowlands, the Central Laurentians, and Anticosti Island, while the lack of forest cover was associated to the lowest beaver abundance across all ecoregions (St-Pierre et al., 2017). Despite these studies exemplifying the importance of vegetation cover for beaver abundance, St. Pierre et al (2017) highlight that this relationship is highly variable across ecoregions (St-Pierre et al., 2017). In areas where resources and hardwood cover are more limited, such as northern ecoregions or the boreal forest (characterized by coniferous cover), forage availability becomes more important (St-Pierre et al., 2017). This seen with beaver abundance increasing in Alaska alongside shrubs exhibiting range expansion into the tundra (Tape et al., 2018).

Ecosystem engineers

Often, beaver abundance and occurrence studies consider beaver habitats once the beaver has already been established. As effective ecosystem engineers, it is important to consider that established beaver habitats will be better suited for beaver survival with the associated increase in herbaceous plants and edge habitat woody shrubs (Ritter et al., 2020). In fact, established beaver sites have been documented to be of better quality than that of dispersal sites (DeStefano et al., 2006). Generally, dispersal sites have lower abundance of preferred woody prey than that of the beaver’s natal colony (DeStefano et al., 2006). However, this may depend on beaver densities. A beaver colony nearing carrying capacity will be forced to establish in sub-optimal conditions and rely on their engineering to improve the habitat (Scrafford et al., 2018). For example, despite having sub-optimal willow condition, reintroduced beavers in Yellowstone still reached carrying capacity, and simultaneously improved willow condition over time (Scrafford et al., 2018). Given their ability to improve vegetation as they establish, Wang et al.'s (2020) and Gerwing et al.'s (2013) concept of hierarchal habitat selection is likely at play. As such, it is critical to consider what other factors may influence beaver habitat selection and abundance, either independently or in association with vegetation composition and traits.

4.2 – Influence of Environment and Climate on Beaver Establishment and Forage

Geomorphology

As with vegetation factors and properties, beaver establishment is limited by landscape level factors. In fact, geomorphic factors impact beaver forage, abundance, and establishment. Some key geomorphic factors identified in the literature as significant influences on beaver presence include river flow speed, river width, stream slope or gradient, elevation, type of water body, water depth and bank substrate (Stevens et al., 2007; Gerwing et al., 2013a).

Geomorphology is strongly associated with the biotic components of an ecosystem, as erosion and bedrock composition can be an important source of nutrients for vegetation (Hahm et al., 2014). As herbivores relying on substantial amounts of forage, geomorphic composition and resistivity may indirectly limit or encourage beaver establishments. For instance, Mortenson et al.'s (2008) study on beavers in the Grand Canyon found that beaver presence over a 5-year span was dependent on geomorphic river reach and was associated with low to medium rock formation resistivity (Mortenson et al., 2008). This is not surprising, because high resistivity reaches limited vegetation due to less bedrock erosion and poor substrate. Conversely, low, and moderate geomorphic reaches tended to have extensive space for vegetation to establish, in addition to greater channel width and increased meandering, which were both positively associated to native shrub and marsh development (Mortenson et al., 2008). As such, beaver habitat quality in the Grand Canyon was tightly associated to geomorphic rock reach.

Along with bedrock composition, physical characteristics of streams may limit beaver success. Stream width plays a role in how much risk of injury a beaver may face (Crawford et al., 2015). Beavers occupying rivers and open water areas of greater width have been observed to have four times the number of injuries compared to those harbouring small and easy to defend tributaries (Crawford et al., 2015). For instance, wider streams incur a greater likelihood of conspecific aggression, potentially limiting how many beavers can establish (Crawford et al., 2015). One could then suggest that very narrow streams would be ideal as a beaver habitat due to the associated safety. Jakes et al. (2007) also found that stream size, and all of its associated correlates, such as stream width, depth, annual water flux, and cross-sectional area most greatly influenced beaver impoundments (Jakes et al., 2007). They suggest, however, that preferred wetlands are ~ 2500 Ha across, and wetlands outside of the 500 – 5000Ha range would be avoided (Jakes et al., 2007). Therefore, streams that are too narrow would likely not be considered as a viable habitat for a beaver, despite lower risk of predation. As such it is evident that stream width has multiple influences of varying degrees on beaver establishments. This is likely related to differences among sites – as made evident by the higher importance of stream width along the Savannah River Site in South Carolina compared to many Québec ecoregions, such as Abitibi and the James Bay Lowlands (Jakes et al., 2007; St-Pierre et al., 2017). This is unsurprising, as different ecoregions may have vastly different vegetation regimes and landscapes influencing the importance of stream width compared to other factors.

Stream gradient has also been considered as a limiting factor for beaver establishment. Many studies across different habitats demonstrate that topography and mean stream gradient are among the top variables impacting beaver presence and dam abundance (Anderson and Bonner, 2014; St-Pierre et al., 2017). Specifically, in areas of high topographic relief (i.e. greater than 3% slopes) stream gradient is increasingly important for beaver habitat selection (Jakes et al., 2007; St-Pierre et al., 2017). Logically, it would be more likely for beavers to reside along gently flowing streams of low gradients, compared to rapids, steep slopes, and high stream gradients because of the associated increase in energetic costs for daily movements (Barela et al., 2021). Further, flow rates that are too strong make dam building very difficult, if not impossible, limiting dam abundance along steep stream gradients (Macfarlane et al., 2017). As such, low gradient streams are often considered as an indicator for suitable beaver habitat, if other variables such as forage quality and availability are met (Anderson and Bonner, 2014; Macfarlane et al., 2017). Yet, Macfarlane et al. (2017) observed that while generally beavers would not build dams on steep gradients, dams did sparsely occur at high gradients between 17-23% - which exceeds previous estimates for beaver damming limitations (Macfarlane et al., 2017). Simultaneously, Macfarlane et al. (2017) showed that very low gradients may reduce dam building, because less dams would be required to reduce stream flow when it is already very weak (Macfarlane et al., 2017). Hence, even when dams are infrequent or absent, low gradient habitats may remain suitable for beaver presence and establishment, making it critical to distinguish that the absence of beaver dams does not always mean the absence of beavers (Allen, 1982; Macfarlane et al., 2017).

In fact, beavers will readily accept riverine and postglacial lakes where damming is not always necessary (Smith and Peterson, 1991; Bergman and Bump, 2018; Bashinskiy, 2020). Over time, beavers may persist in lakes better than streams depending on the site (Smith and Peterson, 1991; Bergman and Bump, 2018; Bashinskiy, 2020). Bergman and Bump (2018) evaluated beaver density and persistence in Michigan lakes, and found that both total aquatic macrophyte cover and lake perimeter were highly associated with beaver occupancy in lakes (Bergman and Bump, 2018). Macrophyte cover may be more important in lakes because building materials are less required when aquatic vegetation can make up a significant proportion of a beaver's diet (Milligan and Humphries, 2010; Bergman and Bump, 2018). Lakes may also provide access to large shorelines for safe foraging over time, allowing for continual regeneration of their preferred terrestrial vegetation (Slough and Sadleir, 1977; McClintic et al., 2014). Additionally, lakes are good habitats for beavers when they have stable water supply, depth, and low average water level fluctuation (Slough and Sadleir, 1977; Macfarlane et al., 2017). Additionally, these criteria are often also valuable in stream habitats that have been or will be dammed, since dams can manage wetland depth and fluctuation levels if needed (Allen, 1982; Smith and Peterson, 1991).

Climate and Environment

Beyond geomorphology, climate has been proven to impact beaver survival, distribution, and establishment (Jarema et al., 2009; Campbell et al., 2012). Jarema et al. (2009) showed while several non-climate variables were strong predictors of variation in beaver abundance across Québec, 97% of that variation could be accounted for by climate variables (Jarema et al., 2009). The top climate predictor variables found in that study were growing days, potential evapotranspiration, and temperature variables, while non climate variables were related to predation, and forest cover (Jarema et al., 2009). Campbell et al. (2012) found similar results with respect to the Eurasian beaver, highlighting that climate variability may be more important than climate means for predicting the abundance of both species (Campbell et al., 2012).

Therefore, as the climate warms up, beaver abundance has and will continue responding. For instance, while most beaver density changes are projected to occur away from their range-edge, the semi-aquatic generalist will still expand its range into newly suitable habitats like the subarctic (Jarema et al., 2009).

With climate warming, there also comes increased risk of natural disturbances like wildfires that may impact the beaver (Fairfax and Whittle, 2020). In Elk Island National Park, Alberta, where both prescribed fires and beavers are abundant, Hood et al. (2007) found that repeated fires and even single burns decreased beaver abundance (Hood et al., 2007). During droughts, fires may reach wetland edges and damage lodges and dams, leading to beaver dispersal with potentially reduced survivability due to decreased cover from predation (Hood et al., 2007). Alternatively, if a beaver chooses to remain in a burned area, they may need to increase foraging distances to find unburned vegetation, incurring greater predation risk (Hood et al., 2007).

Conversely, beaver damming may be considered a tool for climate and wildfire resiliency (Fairfax and Whittle, 2020). In Western United States, Fairfax and Whittle (2020) found that beaver corridors are minimally affected by wildfires compared to undammed ones (Fairfax and Whittle, 2020). Therefore, while frequent fires may discourage beaver abundance, further research is warranted due to the promising potential for wildfire resilience beavers invoke.

Anthropogenic Influence

In addition to natural disturbances, anthropogenic factors impact beaver abundance. Historically this is clear as humans trapped beavers to near extirpation until the 20th century (Mahoney and Stella, 2020). Presently, this interaction is more related to habitat loss and human-beaver conflicts (Havens et al., 2013; Charnley et al., 2020). Scamardo et al. (2022) estimated that, due to increases in agriculture, urbanization, and vegetation loss, Colorado state can only support approximately 1.36 million dams, compared to 2.39 million historically (Scamardo et al., 2022).

Further, human infrastructure, such as roads, have often been considered as a restrictive factor for beaver dam abundance (Jakes et al., 2007). However, Jakes et al. (2007) found that road crossings did not reduce dam abundance in South Carolina (Jakes et al., 2007). Conversely, many studies, including Jakes et al (2007), found that beavers will often select road crossings or culverts for establishment because these areas have slower water flow, reducing the energy required for damming (Jakes et al., 2007; Touihri et al., 2018). Although, this is not always the case and other studies have found that road crossings have no impact on dam abundance (St-Pierre et al., 2017). Nonetheless, beavers become nuisances when they interact with roads or other infrastructure, therefore, proximity to humans may increase mortality, and subsequently decrease their abundance depending on the jurisdiction (Havens et al., 2013). As such, anthropogenic impacts are profound on beaver abundance, with some potential positive relationships along roadsides, and major declines invoked due to habitat loss.

5.0 – Conclusion

The North American beaver is a key component of many biomes, has great potential for climate resilience, and is also expanding its range. As such, continuous modeling and understanding of what limits or encourages their habitat selection, establishments and abundance is important in this time of global change.

Beaver abundance, habitat selection, and establishment is multi-tiered, relying on a magnitude of factors that vary in nature and relative importance across their distribution. Both abiotic and biotic variables may be important factors useful for modelling beaver distribution in North America. Vegetation composition, vegetation quality, geomorphology, and climate and environment stand out as key variables for future modelling and are likely hierarchical in terms of importance for beaver habitat selection and abundance. Additionally, discerning the relative importance of factors across their range proves difficult, with variables' importance varying across regions. As such, we suggest future works consider both large scale environmental and vegetation factors as well as regional ecological variables when considering beaver habitat selection and abundance. Lastly, as ecosystem engineers it is critical to also consider the temporal scale of beaver establishments, where beavers improve their habitat over time. Therefore, habitat variables prior to beaver establishment will be vastly different compared to post colonization. As such, we must be cautious when developing occurrence models relying on environmental conditions of already successful beaver habitats.

Figures

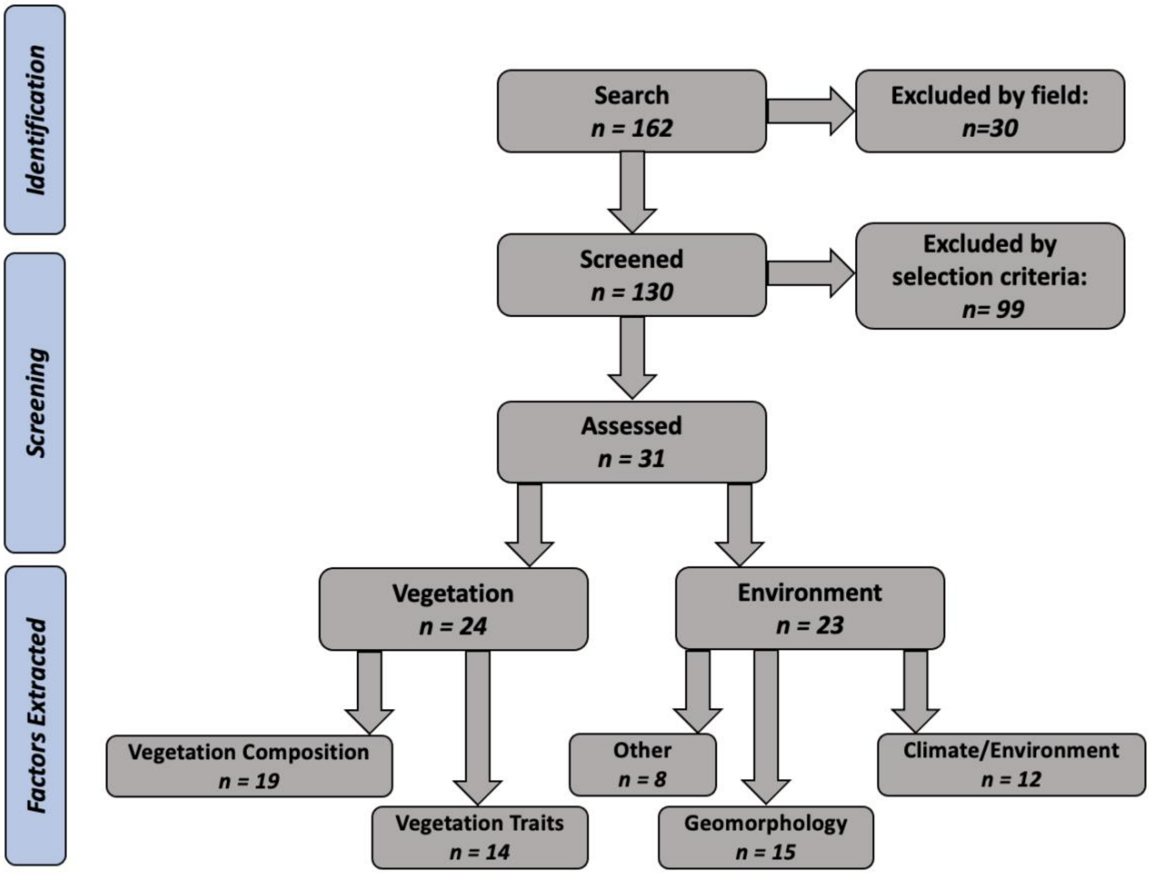


Figure 1: PRISMA flow diagram of systematic review of the literature from the Web of Science database. The initial search resulted in 162 papers, and after screening, 31 papers were fully assessed. The number of articles analyzing each factor of interest is listed.

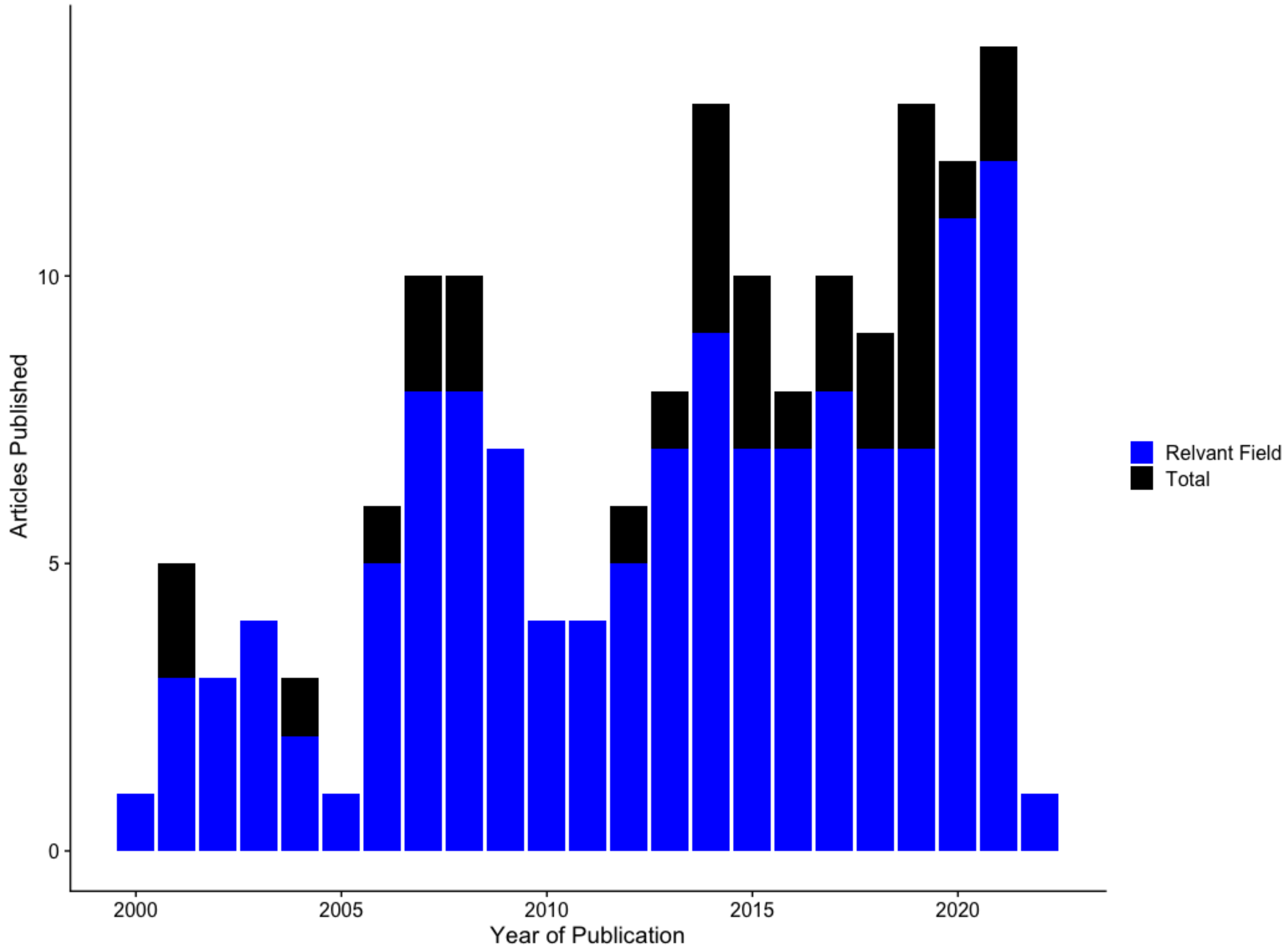


Figure 2: Number of articles per year based on my web of science search results. Papers ranged from 1 per year to 14, with an average of 7.36 articles in a given year. Bars in blue represent papers categorized as being from a relevant field (n=130), while black is the grand total (n=162).

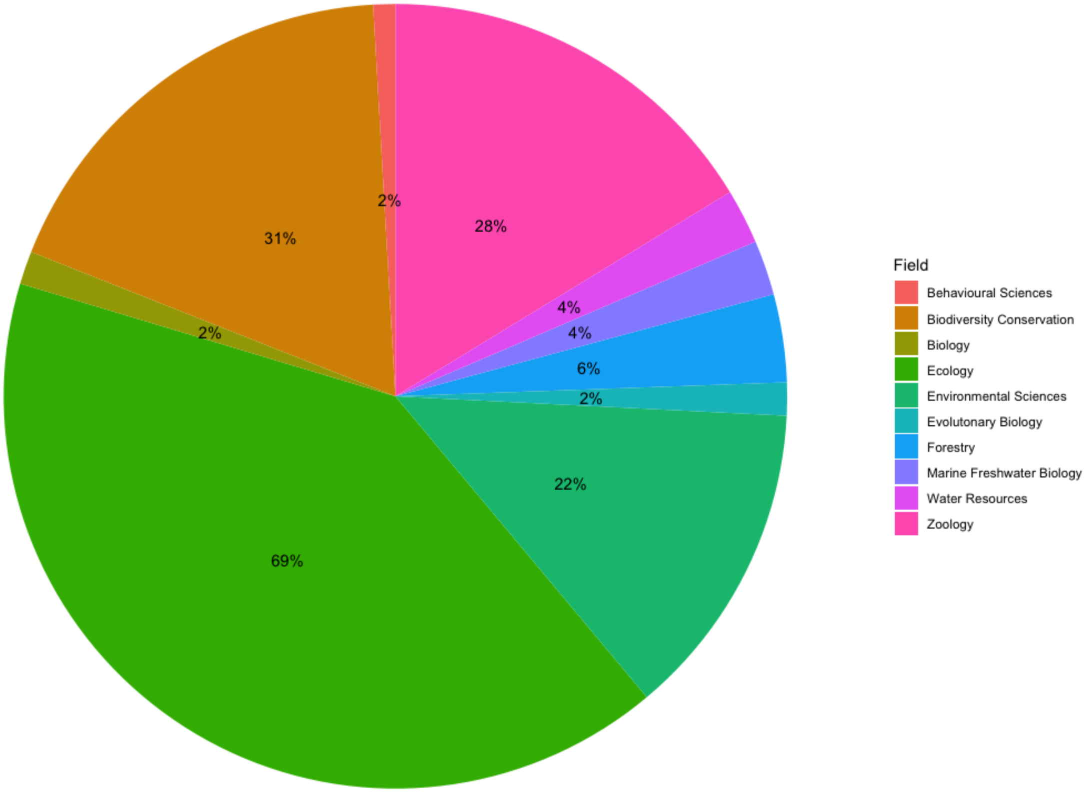
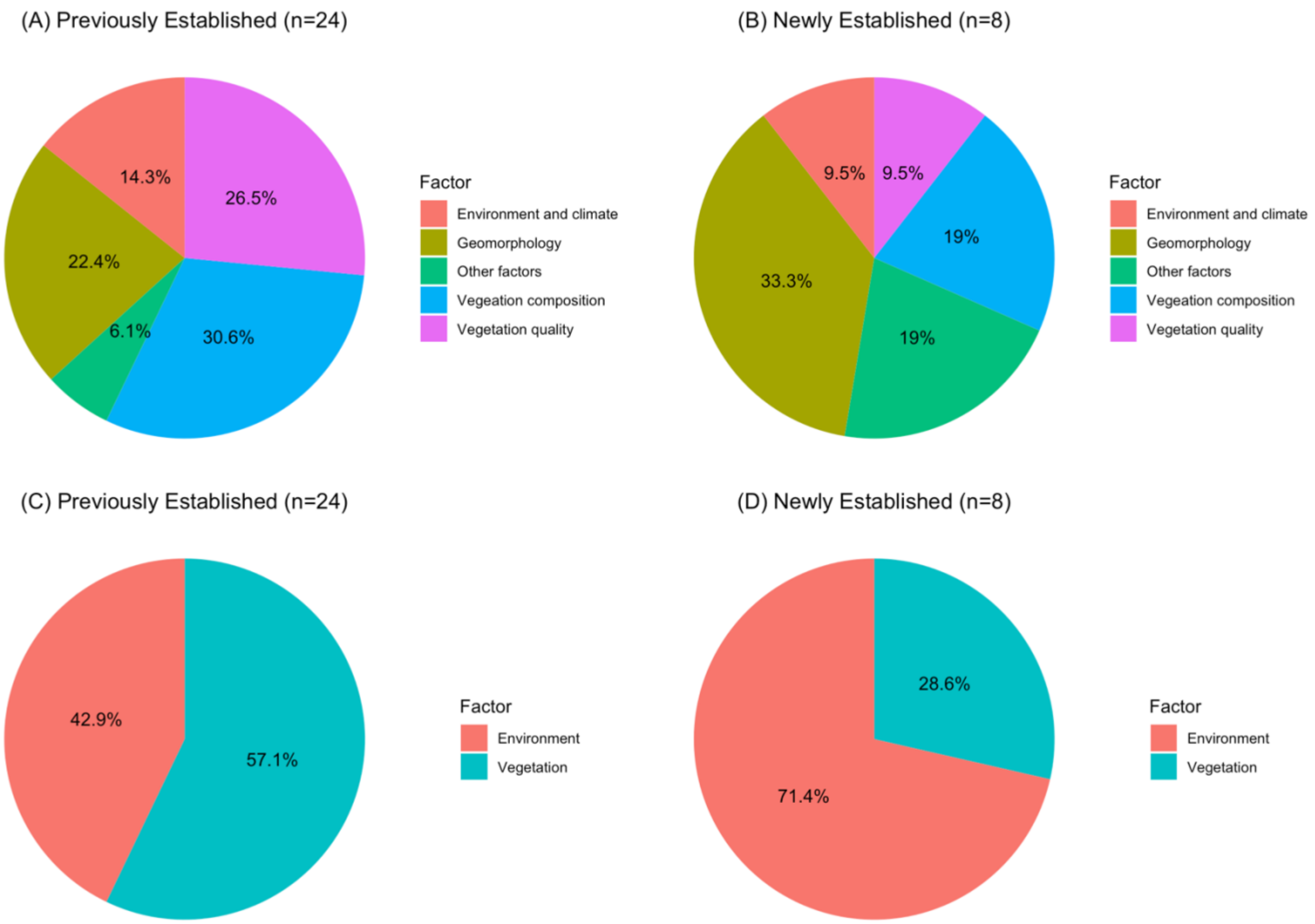


Figure 3: Proportion of scientific disciplines of the (*n=130*) articles after being filtered by field. Percentages surpass 100% as some articles are described by multiple categories. Ecology describes 69%, biodiversity conservation describes 31%, and zoology describes 28% of articles included.


(A) Previously Established (n=24)

(B) Newly Established (n=8)

(C) Previously Established (n=24)

(D) Newly Established (n=8)

Figure 4: Frequencies of factors considered in studies included in this review. (A) and (B) show the proportions of occurrence of the raw factors considered across all studies, whereas (C) and (D) represent the pooled environmental and vegetation groups of factors.

Tables

Authors	Title	Year	Themes	Standardized factors	Degree of Establishment
Barela, IA; Burger, LM; Wang, GM; Evans, KO; Meng, QM; Taylor, JD	Spatial transferability of expert opinion models for American beaver habitat	2021	Establishment success and relocation	Vegetation Composition, Geomorphology, Predation	Long Established
Mahoney, MJ; Stella, JC	Stem size selectivity is stronger than species preferences for beaver, a central place forager	2020	Beaver selective foraging	Vegetation Composition, Vegetation Traits, Distance from pond	Long Established
Charnley, S; Gosnell, H; Davee, R; Abrams, J	Ranchers and Beavers: Understanding The Human Dimensions of Beaver-Related Stream Restoration on Western Rangelands	2020	Beaver restoration	Anthropogenic Factors	Long Established
Barela, I; Burger, LM; Taylor, J; Evans, KO; Ogawa, R; McClintic, L; Wang, GM	Relationships between survival and habitat suitability of semi-aquatic mammals	2020	Habitat suitability and survival	Vegetation Abundance, Climate, NDVI	Long Established
Labrecque-Foy, JP; Morin, H; Girona, MM	Dynamics of Territorial Occupation by North American Beavers in Canadian Boreal Forests: A Novel Dendroecological Approach	2020	Home ranges, forage depletion, alternating lodges, water levels	Vegetation Abundance, Vegetation Composition, Geomorphology	Long Established
Ritter, TD; Gower, CN; McNew, LB	Habitat conditions at beaver settlement sites: implications for beaver restoration projects	2020	Ecosystem engineering - improving their own habitat quality. Stream selection	Vegetation Composition, Geomorphology	New Establishments
Wang, GM; McClintic, LF; Taylor, JD	Habitat selection by American beaver at multiple spatial scales	2019	Hierarchical habitat selection by beavers as related to spatial distributions of food	Vegetation Composition, Open Water	Long Established
Tape, KD; Jones, BM; Arp, CD; Nitze, I; Grosse, G	Tundra be dammed: Beaver colonization of the Arctic	2018	Beavers in Subarctic. Effects on tundra habitat. Insights into what enabled them to enter the area.	Vegetation Abundance, Climate, Ice Regimes, Geomorphology	New Establishments
Mumma, MA; Gillingham, MP; Johnson, CJ; Parker, KL	Where beavers (*Castor canadensis*) build: testing the influence of habitat quality, predation risk, and anthropogenic disturbance on colony occurrence	2018	Beaver occurrence drivers, habitat quality.	Vegetation Abundance, Open Water, Vegetation Composition	Long Established

Scrafford, MA; Tyers, DB; Patten, DT; Sowell, BF	Beaver Habitat Selection for 24 Yr Since Reintroduction North of Yellowstone National Park	2018	Beaver willow dynamics	Geomorphology, Vegetation Composition	New Establishments
Francis, RA; Taylor, JD; Dibble, E; Strickland, B; Petro, VM; Easterwood, C; Wang, GM	Restricted cross-scale habitat selection by American beavers	2017	Beaver habitat selection	Vegetation Abundance	Long Established
St-Pierre, ML; Labbe, J; Darveau, M; Imbeau, L; Mazerolle, MJ	Factors Affecting Abundance of Beaver Dams in Forested Landscapes	2017	Spatial distribution of beaver dams	Spatial, Geomorphology, Vegetation Composition	Long Established
Gallant, D; Leger, L; Tremblay, E; Berteaux, D; Lecomte, N; Vasseur, L	Linking time budgets to habitat quality suggests that beavers (Castor canadensis) are energy maximizers	2016	Time budgets and habitat quality as energy maximizers	Vegetation Composition, Vegetation Abundance	Long Established
Johnston, CA; Windels, SK	Using Beaver Works to Estimate Colony Activity in Boreal Landscapes	2015	Beaver pond identification	Vegetation Composition, Open Water	Long Established
Morrison, A; Westbrook, CJ; Bedard-Haughn, A	Distribution of Canadian Rocky Mountain Wetlands Impacted by Beaver	2015	beaver and wetland distribution	Geomorphology	Long Established
Crawford, JC; Bluett, RD; Schauber, EM	Conspecific Aggression by Beavers (*Castor canadensis*) in the Sangamon River Basin in Central Illinois: Correlates with Habitat, Age, Sex and Season	2015	Conspecific aggression in beavers (behaviour)	Geomorphology	Long Established
Rossell, CR; Arico, S; Clarke, HD; Horton, JL; Ward, JR; Patch, SC	Forage Selection of Native and Nonnative Woody Plants by Beaver in a Rare-Shrub Community in the Appalachian Mountains of North Carolina	2014	Foraging of woody plants (native and invasive)	Vegetation Composition	Long Established
McClintic, LF; Taylor, JD; Jones, JC; Singleton, RD; Wang, G	Effects of spatiotemporal resource heterogeneity on home range size of American beaver	2014	Home ranges spatiotemporal dynamics (NDVI and woody plant cover increased home range)	Vegetation Composition, NDVI	Long Established
Severud, WJ; Windels, SK; Belant, JL; Bruggink, JG	The role of forage availability on diet choice and body condition in American beavers (*Castor canadensis*)	2013	Body condition and aquatic and woody vegetation availability	Vegetation Composition, Aquatic Vegetation	Long Established
Havens, RP; Crawford, JC; Nelson, TA	Survival, Home Range, and Colony Reproduction of Beavers in East-Central Illinois, an Agricultural Landscape	2013	Home range determinants	Anthropogenic Factors, Vegetation Traits, Climate	Long Established
Gerwing, TG; Johnson, CJ; Alstrom-Rapaport, C	Factors influencing forage selection by the North American beaver (*Castor canadensis*)	2013	Foraging behaviour	Spatial, Distance from Pond, Vegetation Composition, Hierarchical factors	Long Established

Bloomquist, CK; Nielsen, CK	Demography of Unexploited Beavers in Southern Illinois	2010	Survival rates, recruitment, and dispersal	Environmental Variation, Demographics	Long Established
Raffel, TR; Smith, N; Cortright, C; Gatz, AJ	Central Place Foraging by Beavers (*Castor canadensis*) in a Complex Lake Habitat	2009	Beaver selective foraging, central place foraging	Vegetation Composition, Vegetation Traits, Distance from pond	Long Established
Demmer, R; Beschta, RL	Recent History (1988-2004) of Beaver Dams along Bridge Creek in Central Oregon	2008	Beaver dam abundance and dimensions	Vegetation Composition, Geomorphology	New/Long Established
Mortenson, SG; Weisberg, PJ; Ralston, BE	Do beavers promote the invasion of non-native *Tamarix* in the Grand Canyon riparian zone?	2008	Beaver relation to *Salix* and *Tamarix*	Vegetation Composition, Geomorphology	Long Established
Hood, GA; Bayley, SE	Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada	2008	Beaver impact compared to env/clim variables on open water.	Open Water	Long Established
Hood, GA; Bayley, SE; Olson, W	Effects of prescribed fire on habitat of beaver (*Castor canadensis*) in Elk Island National Park, Canada	2007	Effect of fire (disturbance) on beaver	Disturbances	New/long Establishments
DeStefano, S; Koenen, KKG; Henner, CM; Strules, J	Transition to independence by subadult beavers (*Castor canadensis*) in an unexploited, exponentially growing population	2006	Survival rates and dispersal, habitat quality	Anthropogenic Factors, Vegetation Traits, Geomorphology	New Establishments
Cunningham, JM; Calhoun, AJK; Glanz, WE	Patterns of beaver colonization and wetland change in Acadia National Park	2006	Wetland and beaver surveys	Vegetation Composition, Geomorphology	New Establishments
Breck, SW; Wilson, KR; Andersen, DC	Beaver herbivory of willow under two flow regimes: A comparative study on the green and Yampa Rivers	2003	Beaver herbivory, seasonality and species abundance	Vegetation Composition	Long Established
McKinstry, MC; Anderson, SH	Survival, fates, and success of transplanted beavers, *Castor canadensis*, in Wyoming	2002	Relocation, survival	Spatial, Geomorphology, Predation	New Establishments

Table 1: List of the 31 research articles with their extracted themes and factors. Themes and factors extracted were those relevant to this review; when known, the relative stage of establishment of the beaver colony was noted.

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Connecting Statement

In chapter one I reviewed the relationship between environmental factors and beaver abundance, establishment, habitat selection, and foraging. I found that climate and geomorphology influenced beaver habitat selection, while vegetation composition and traits were related to beaver foraging and abundance. Further, I present the idea that as an extremely widely distributed species, environmental factors had variable relative impacts based on habitat differences, highlighting the importance of context when considering beaver establishment, abundance, and foraging.

As a morphologically specialized rodent occurring in varied environmental conditions, and with variable foraging behaviour, and habitats, the beaver presents a strong case for evaluating the effects of changing environmental conditions on functional adaptations across a species' distribution range. By modeling the effects of their environment on beaver functional morphology, it then becomes possible to evaluate if the beaver is locally adapted to their environment, and how their functional morphology enables them to establish and/or alter their ecosystem.

Despite being an ecologically impactful rodent expanding its range, there exits little research investigating the relation between beaver cranial morphological, climate, and environmental conditions across its distribution range. Therefore, the following chapter attempts to address this gap, by relating key environmental and vegetation variables to beaver functional morphology. The findings in this chapter will then inform future conservation and management strategies for the beaver by incorporating their local adaptations when predicting their future range expansion and abundance.

CHAPTER 2

Chipping in: functional morphology of the North American beaver in a changing environment.

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Abstract:

Climate warming and immense anthropogenic activity is changing environments and ecosystems across the globe forcing species and populations to respond, either via dispersal, adaptation, or both. In fact, the arctic biota is shifting substantially faster than the global average, allowing many new species to expand their range poleward. One such species, is the North American Beaver (Castor Canadensis), a highly morphologically specialized rodent capable of greatly modifying ecosystems by altering forest composition through selective foraging and by flooding the landscape through dam and channel building. Knowing that rodent cranial morphology is highly related to functional requirements for foraging, the beaver makes an ideal system for evaluating their local potential across environmental change. As such, we test the hypothesis that beaver skull morphology is optimized for their local environmental and habitat conditions across Canadian ecosystems. We found that temperature, above ground biomass, and ecozones significantly affect the morphology of key masticatory functional traits. Our results suggest that the beaver is locally adapted to environmental conditions related to their selective foraging behaviour. This work provides insight into the adaptive potential of newly established beavers in the sub-arctic to better predict future range shifts and provide information for future management practices.

Keywords: Local Adaptation, Range Expansion, Functional Morphology, Cranial Morphology, Environmental Condition

1 Introduction:

The Earth is currently warming at unprecedented rates (Bush and Lemmen, 2019), and as a response, many species are shifting their range poleward (Tape et al., 2016b; Tape et al., 2018; Bateman et al., 2020). In fact, the arctic and sub-arctic are amongst the most rapidly changing environments on the planet, warming 2-3 times faster than the global average (Bush and Lemmen, 2019). Due to rapidly melting permafrost, longer summers, and more frequent disturbances onset by climate change, increasingly tall deciduous shrubs have expanded into the sub-arctic (Mekonnen et al., 2021). Consequently, herbivores across North America have followed suit, expanding their own range into this newly suitable environment (Tape et al., 2016b; Tape et al., 2018).

Multiple mechanisms exist for populations to track their desired environments in times of rapid ecological change (Chevin et al., 2010). Populations may disperse, tracking their preferred habitat via range shift, as seen in the tundra, undergo rapid genetic evolution via selection, or rely on phenotypic plasticity to improve their fitness in their environment (Chevin et al., 2010; Baumgartner and Hoffman, 2019). The latter two will often result in populations being locally adapted in their functional traits, being well suited for their new niche requirements (Baumgartner and Hoffman, 2019). This is because a population facing adverse ecological pressures, whether it be habitat loss, drought, or increased competition, must respond with physiological and/or morphological adaptations to persist (Fischer et al., 2011; Bocedi et al., 2013). However, populations may also disperse while becoming locally adapted to a new habitat, gaining a net increase in fitness through both processes (Baumgartner and Hoffman, 2019). As such, in times of rapid climate and environmental change, it is important to consider if and how populations evolve in their phenotype while also shifting distribution.

Rodentia make a strong study system for evaluating such a conundrum, as they are widely distributed and display a large array of phenotypic adaptations (Korth, 1994; Samuels, 2009). Rodents are the more diverse clade of mammals and exhibit locally adapted phenotypes closely related to their habitat (Monteiro et al., 2003; Samuels, 2009; Kubiak et al., 2018; Baumgartner and Hoffman, 2019). As such, many rodent species and populations are undergoing rapid morphological change in response to climate change and habitat loss induced environmental pressures (Pergams and Lawler, 2009; Wolf et al., 2009; Fischer et al., 2011; Stumpp et al., 2018; Baumgartner and Hoffman, 2019). One particularly well-suited, yet understudied, species for evaluating phenotypic responses to environmental pressures during range shift is the North American beaver (*Castor canadensis*), a widely distributed and morphologically specialized species recently expanding its range into the subarctic (Tape et al., 2018).

Over the last few decades, beaver abundance has drastically increased in sub-arctic ecosystems in Alaska, Northwest Territories, and Northern Quebec (Jarema et al., 2009; Tape et al., 2018). Beaver ponds have doubled in number across most Alaskan habitats between 2003-2017 (Tape et al., 2022). This expansion is attributed to the increased availability of woody shrubs and open water during winters, and to longer growing seasons experienced in the tundra over the last 20 years (Tape et al., 2018; Tape et al., 2022).

Beaver range expansion may have drastic consequences on the sub-arctic ecosystem. Beavers radically impact ecosystems' abiotic and biotic features by building dams and networks of channels, consequently altering flow regimes, stream connectivity, and biodiversity (Johnston and Naiman, 1990; Nummi and Holopainen, 2014; Hood and Larson, 2015; Tape et al., 2022). Beavers are also selective herbivores that greatly decrease forest biomass of preferred species, changing the forest composition (Johnston and Naiman, 1990; Mahoney and Stella, 2020). In the sub-arctic, these impacts may be more pronounced. Water surface area increases caused by beaver activities is known to exacerbate permafrost thaw, increasing tundra soil degradation and the release of greenhouse gases (Tape et al., 2022). Additionally, beaver dams create warm water refugia for aquatic species historically limited by temperature or nutrient availability, enabling range shifts in other taxa (Tape et al., 2022). Lastly, beaver disturbances are not short lived, with beavers remaining at a site for many years and their constructions continuing to alter ecosystems even after abandoned, emphasizing the long-term implications of increased beaver abundance in the tundra (McMaster and McMaster, 2001; Tape et al., 2022).

Notably, the beaver is a prolific agent of ecological change without the need for tools, relying solely on their highly specialized functional traits, such as their skull, to enact change. First, beavers possess hypsodont cheek teeth adapted for woody and aquatic plant diet (Stefen, 2009). Next, their ever-growing incisors, specialized for gnawing and anchoring, are used for foraging food and building material (Cox and Baverstock, 2016). Further, the beaver’s skull configuration has been optimized for effective mastication, bite force, and overall gnawing functions (Cox and Baverstock, 2016). Specifically, the morphology of their skull enables such optimized gnawing that their bite force (550-740N) is greater than expected based on body mass and incisor dimensions (Cox and Baverstock, 2016). This is attributed to the mechanical efficiency of their masticatory system, generating tremendous muscular force enabled by skull morphology (Cox and Baverstock, 2016). Beavers are also amongst the largest rodents and have a dorsoventrally deep rostrum and broad zygomatic arch which support important musculature for mastication, such as the superficial masseter and temporalis muscles (Korth, 1994; Samuels, 2009; Cox and Baverstock, 2016). Larger superficial masseter and temporalis muscles are associated with increased mechanical advantage of incisor biting, and are especially important for cutting hard materials such as wood (Samuels, 2009). Therefore, quantifying beaver skull morphology can provide direct insight into their mastication, diet, and foraging functions (Samuels, 2009).

The present distribution of the North American beaver ranges from ~25° latitude in the South, up to ~69° latitude in the North (GBIF.org, 2022). If the beaver skull morphology is optimized for wood foraging [19], and given the variety of forest compositions, environments, and habitats in which beavers occur, we expect key functional differences across beaver populations. Yet, little research has investigated the relation between morphological variation in the beaver skull and climate and environmental variation across its distribution range. Here, we aim to address this gap by quantifying beaver skull functional morphology across the northern part of its range and model the effect of environmental factors on skull morphology. We test the hypothesis that beaver skull morphology is optimized for their local environmental and habitat conditions. This work provides insight into the adaptive potential of newly established beavers in the sub-arctic to better predict future range shifts and provide information for future management practices.

2 Materials and Methods:

2.1 Specimens

We included in the dataset a total of 117 beaver skulls, collected in Canada, spanning 15.363° latitude, ranging from 42.601° to 57.964°, and spanning 62.110° longitude, ranging from -119.733° to -57.623°, from a total of 62 distinct sites (Figure 1). As such, our sample spans a significant portion of the north eastern and some western portion of the beaver's distribution (GBIF.org, 2022). Skulls included were collected between 1885 – 2021, with 7 skulls having unknown collection dates (Table 1A). All skull specimens are accessioned in natural history museums, including 17 skulls from the Redpath Museum, McGill University, 44 from the Royal Ontario Museum and 55 from the Canadian Museum of Nature (Table 1A).

2.2 Age categories

We considered only adult specimens for this study. As individual age of each specimen was almost never available, we developed a custom key designed to age skulls from the ventral view of a standard photograph (Figure 1A.). The key was based on previous aging methods for both extinct and extant C*astor* species but avoids the need for destructive or microscopic methods (Mayhew, 1978; Bejenaru et al., 2015; Yang et al., 2021). While this key makes the aging process more accessible, the key was not designed to age skulls precisely to the year. Rather, the key was well suited for distinguishing adult specimens from juveniles and categorizing skulls into 5 general age stages (i.e., 1-juvenile, 2-sub adult, 3-young adult, 4-mid-life adult, and 5-old adult) based on wear patterns of the molars, and developmental features of the skull. To limit the effects of ontogeny and because beaver skulls exhibit minimal cranial growth in adulthood, only juvenile specimens were excluded from the dataset. Skulls of both sexes were included in this analysis and are presented together because beavers exhibit no sexual dimorphism in their cranial morphology (Bond, 1956).

2.3 Morphometrics data

First, photographs of the ventral view of beaver skulls were taken using a Nikon D3100 camera with a Micro NIKKOR 85mm lens by the same investigator (JD). Next, we quantified 2D cranial shape with geometric morphometrics, an objective coordinate-based approach for shape analysis (Zelditch et al., 2012). We placed a total of 24 homologous landmarks on the ventral view of beaver skulls that outlined one half of the skull-(Figure 2). Landmarks were digitized in R (R Core Team, 2020) using the *Stereomorph* package (Olsen and Westneat, 2015), and were treated as a series of Cartesian Coordinates with each specimen having their own unique configuration. Shape analysis was conducted using the configuration of the half skull to minimize variance caused by asymmetry of the skulls (Mutumi et al., 2021).

2.4 Preliminary Analysis

2.4.1 Measurement error

We estimated measurement and digitization error in our sample following the methodologies in Claude (2008) (Claude, 2008). We randomly selected and landmarked three skulls from each of the three museums, generating a sample of 9 skulls with 3 repeats. We ran a Procrustes ANOVA (iterations set to n=999) using the *procD.lm* function in *geomorph* (Adams and Otárola-Castillo, 2013) to determine the significance of variance among repeats compared to among specimens, where we observed no significant effect of the repeats ($p > 0.05$).

2.4.2 The Effect of Age and Size on Cranial Morphology

We performed a Generalized Procrustes Analysis (GPA) with the *geomorph* package in R (Adams and Otárola-Castillo, 2013) to superimpose and align the landmark data in a manner that reduces the effects related to position, orientation, and scale (Mitteroecker and Gunz, 2009; Zelditch et al., 2012) and visually inspect skull shape variation across our sample. We also used GPA to estimate centroid size, a proxy of skull size, for each skull.

We then used the *procD.lm* function in *geomorph* (iterations set to n = 999) to run a Procrustes ANOVA, and test for the effects of size and age on skull shape (Adams and Otárola-Castillo, 2013). The relationship between shape and size was significant in our sample of adult beaver skulls ($p < 0.001$, effect size (z) = 5.71) (Figure 3), while age (categories 2-5) was not ($p > 0.05$). Therefore, we used the residuals of a linear model with skull shape as a response variable and centroid size as an independent variable in all subsequent analyses.

2.5 Climatic and Environmental Data

Mean annual temperature (MAT) and mean annual precipitation (MAP) data at 1.0 km^2 resolution was obtained from AdaptWest, with both climate variables selected due to their known association with beaver abundance (Jarema et al., 2009; Project, 2015). A 1.0 km^2 resolution was ideal for our analysis because beaver home ranges are generally 0.7 – 1.2 km long. As such, 1.0 km^2 resolution climate data serves as a good indicator of the average climate experienced by a given individual (Havens et al., 2013).

Additionally, we retrieved forest attribute variables from Canada's National Forest Inventory (NFI) (Beaudoin et al., 2017). We considered three forest attributes at 250m^2 resolution along the MODIS (Coops et al., 2009) grid, in our analysis: 1) tree land cover, as the percent of vegetated treed polygons, 2) non-tree vegetation landcover, as the percent of vegetated non-treed polygons, 3) percent needleleaf, as the percent composition of all needleleaf species of treed polygons, and 4) total above ground biomass, as the mean total live above-ground dry biomass of polygons (includes all trees >1.3). To match our desired resolution, the rasters were aggregated by a factor of 4 using the *raster* package in R, converting them to a ~1.0 km^2 resolution (Hijmans et al., 2015).

Lastly, we collected an ecological classification raster at 1.0 km^2 resolution, also derived from MODIS remote sensing data (Coops et al., 2009). This raster was composed of statistical ecosystem regionalization's, which represent environmentally unique ecozones that were then subject to a 14-class stratification. These 14 terrestrial ecozones are considered as strong proxies for Canadian ecological regions based on topography, productivity, and land cover (Coops et al., 2009) (for full descriptions see Coop et al. (2009)). Details on how to access the raster files can be found in the appendix (Table 1A).

2.6 Statistical Analysis

2.6.1 Principal Component Analyses

All statistical analyses were conducted in R version 4.1.2 (R Core Team, 2022). We conducted a principal components analysis (PCA) on the residuals of the shape ~ size model (Mitteroecker and Gunz, 2009). We then extracted the first 7 PC scores that cumulatively explained over 67% of the variance (Table 1).

Next, we generated deformation grids illustrating the projected configurations of landmarks at the maximum and minimum of the first 7 PC axes, visualizing skull shape variation along each PC. All visualizations were generated using the *geomorph* package in R (Adams and Otárola-Castillo, 2013).

2.6.2 Spatial and temporal variation

We assessed the effect of time (collection year) and space (latitude) on beaver cranial morphology using linear models. As such, we fit seven linear models between the PC scores of the first 7 PC axes, and the latitude and year of collection of the specimen using the *stats* package in R (R Core Team, 2020). We also included an interaction term between the latitude and year to evaluate if the pattern of spatial variation in skull morphology had changed over time.

2.6.3 Drivers of variation: climate and environmental factors

Individual skull size and shape data were aggregated by site in all subsequent analyses. We first tested for the presence of spatial and temporal autocorrelation in our size and shape variables using a Moran's I statistics in the *spdep* (Bivand et al., 2015). When significant, we included an autocorrelation structure term in the models (~ latitude + longitude for spatial, and ~ 1|year for temporal) using the *corSpatial* function in the *nlme* package (Janis and Robeson, 2004; Pinheiro et al., 2017). Next, we performed a series of generalized least squares models (restricted log-likelihood) with the size (centroid size, derived from the GPA) and shape variables (allometry adjusted PC2 – PC7) as the response variables using the *nlme* package (Pinheiro et al., 2017). Additionally, we performed a linear mixed effect model with PC1 as the response variable and year of collection as a random factor to account for temporal variation observed in this shape variable. In each model we included the following uncorrelated (R <0.6) explanatory factors: MAT, MAP, ecozone, percent treed landcover, percent non-treed vegetated landcover, percent needleleaf, stand density, and total above ground biomass. Model convergences were then checked by visual inspection and revealed that a Gaussian error distribution was appropriate for all response variables.

3 Results:

3.1 Quantifying Shape Variance via Principal Components Analysis

The first 7 axes of the PCA performed on the residuals (allometry-free shape variables) explained over 67.71% of the total variance and were considered in subsequent shape analyses. Deformation grids of the maximum and minimum PC scores along with the loadings (Table 2A) highlighted that variance along PC1 (21.17%) mostly reveals a narrowing of the skull and an anterior movement of the tooth row in the positive direction (Figure 4). The zygomatic arch, and the rostrum also exhibit shape change with a stretched rostrum and shorter zygomatic arch being positively associated with PC1 (Figure 4). Similarly, PC 2 (12.18%) is positively associated with a wider zygomatic breadth, and a funnel shaped rostrum towards the incisors (Figure 4). PC3 (11.49%) is associated with changes in rostrum length, posterior skull length, and in the positioning of the maximum reach of the zygomatic arches (Figure 4). Along PC4 (7.46%), the shape of the zygomatic arch, both in breadth and attachment to the skull are most notable (Figure 4). PC5 (5.46%) has similar shape variance across all landmarks and represents more subtle shape variation. PC6 (4.90%) is associated with changes in the rostrum width as well as the rostrum attachment point to the maxilla (Figure 4). Lastly, PC7 (4.42%) shows a widening and narrowing of the skull with a pulling and stretching of the posterior end of the zygomatic arch (Figure 4).

3.2 The Effect of Latitude and Time on Cranial Morphology

We fitted linear models to predict the effect of latitude and year of collection on centroid size and PC1 to PC7. For PC1, the model explains a statistically significant and moderate proportion of variance (adj. $r^2 = 0.22$, $p < 0.001$). Specifically, the effect of latitude was statistically significant and positive ($F = 19.73$, $p < 0.001$), the effect of year was statistically significant and positive ($F = 2.047$, $p < 0.001$), and the interaction term between year and latitude was statistically significant and negative ($F = 11.70$, $p < 0.001$) (Table 2, Figure 5). There was no significant effect of latitude and year on centroid size and the other shape variables (all $p > 0.05$).

3.3 Spatial Autocorrelation

Spatial autocorrelation was present for centroid size (Moran's I = 0.176, $p < 0.002$) and for PC1 (Moran's I = 0.116, $p < 0.022$). The remaining PC axes evaluated showed no significant spatial autocorrelation.

Temporal autocorrelation was present for PC2 (Moran's I = 0.099, $p < 0.001$) and for PC3 (Moran's I = 0.041, $p < 0.002$). The remaining PC axes and Centroid size showed no significant temporal autocorrelation.

As such, the best correlation structure was a spatial correlation structure with either spatial or temporal components matching the model's autocorrelation. Once the correlation term was included in the model, the ACF and variogram plots reveal that autocorrelations were minimized within a 95% confidence interval.

3.4 Environmental and Climate Drivers of Morphological Variance

Overall, percent treed cover and total above ground biomass increased in warmer and wetter regions, while non-treed cover was more associated with colder dry regions (Figure 6). Additionally, percent needleleaf composition was associated to colder regions with lower biomass (Figure 6). Lastly, ecozone values increased in colder and drier regions and varied with forest composition (Figure 6).

Next, none of the climate and environment factors had a significant effect on centroid size, PC1, PC2, PC3, PC5, and PC6 (Table 3). Ecozone had a significant negative effect on PC4 and PC7, and PC7 decreased with mean annual temperature (Table 3, Figure 7).

4 Discussion:

In this study, we used geometric morphometrics to quantify beaver skull morphology across Canadian ecosystems. As such, we tested the hypothesis that beaver skull morphology is optimized for their local environmental and habitat conditions. Firstly, we found that beaver skull morphology varied significantly on both temporal and spatial scales. We also found that beaver skull craniology significantly varied across Canadian habitats and was related to specific environmental and climate factors, such as ecozones, temperature, and total above ground biomass. The most significant variation in skull shape occurred along key functional traits such as the rostrum, tooth row, and zygomatic arch, suggesting a connection between functional adaptations and environmental conditions. As such we present evidence supporting the hypothesis that beaver skull morphology is locally adapted to environmental conditions.

4.1 Temporal and Spatial Variation in Beaver Cranial Morphology

We found significant temporal and spatial variation in the beaver cranial morphology along PC1. Specifically, the width of the rostrum at the contact point of the superficial masseter and temporalis decreased along a latitudinal gradient (Figure 5). Functionally, the rostrum width and associated masticatory musculature are directly related to feeding strategy and biting efficiency (Cox and Baverstock, 2016). Further, the contact point of the zygomatic arch and the skull is shifted anteriorly at high latitudes, changing the loading angle of the masseter muscles. Therefore, beavers with a wider rostrum support larger muscles and improved moment arm angles when biting (Samuels, 2009; Cox and Baverstock, 2016). As such, our findings suggest that at lower latitudes, beavers likely have greater access to optimal forage, such as preferred species, thin stems, and proximity to riparian vegetation, requiring less optimized mastication apparatuses (Cox and Baverstock, 2016). Conversely, beaver craniology at high latitude environments is more adapted for larger bite force, together with further specialization of their masticatory apparatus.

Interestingly, we found no effect of latitude or of temperature on size, contradicting the predictions of Bergmann's rule (Bergmann, 1847). Previous works have also found Bergmann's rule to not apply to some mammals, particularly in rodents (Souto-Lima and Millien, 2014; Alhajeri and Steppan, 2016b). In northern climates, the beaver's size exhibits drastic seasonal changes related to dietary shifts during the winter, when food is limited to their cache (Smith and Jenkins, 1997). This seasonal variance has been reported to be more significant during longer winters, therefore, beavers at higher latitudes likely experience the greatest shifts. As such, beaver size is strongly associated with their local diets, forage cache quality, and seasonality.

Lastly, our sample was composed of a large temporal range and exhibited morphological variance over time. This is unsurprising because rodents have frequently been reported to have rapidly changed morphologies over the last 100 years (Pergams and Lawler, 2009). For instance, Millien et al. (2017) found that significant cranial morphological variation in two mice species occurred over only 50 years (Millien et al., 2017). Furthermore, the major bottleneck experienced by the beaver in the early 20th century (Muller-Schwarze, 2011) may have facilitated such rapid morphological change. However, given that most of our recently collected specimens are also occurring at the highest latitudes in our data, the temporal trend we report here may also be partly due to sampling bias.

4.2 The Effects of Vegetation Cover on Beaver Cranial Morphology

It is axiomatic that environmental pressures have an influence on the evolutionary adaptation of species. Indeed, speciation is often driven by the influence of ecological and environmental variation across populations that become reproductively isolated (Schluter and

Conte, 2009). In parallel, intra-specific adaptive variation exists when widely distributed species are exposed to divergent pressures, and dispersal is limited (Herrel et al., 2008; Shuai et al., 2018). As such, when different populations of the same species are exposed to differing environmental conditions, localized adaptations often arise both due to genetic variance or phenotypic plasticity (Herrel et al., 2008; Shuai et al., 2018).

Within-species functional diversity is common in mammals, especially in rodents (Monteiro et al., 2003; Martínez et al., 2014; Souto-Lima and Millien, 2014; Maestri et al., 2016a; Kubiak et al., 2018). For example, Kubiak et al. (2018) found that populations of the subterranean rodent *C. minutus* in different habitats were functionally and morphologically divergent based on soil hardness and vegetation cover. Similarly, Monteiro et al. (2003) described intraspecific variation in the cranial morphology of *T. apereoides* as a product of environmental gradients and forage type, where masticatory traits responded to pressures related to diet (Monteiro et al., 2003).

In line with previous works, we found significant intraspecific morphological variation across beaver functional features related to mastication. Specifically, most of the observed cranial shape variation was related to narrowing, broadening, and lengthening along the rostrum and masticatory apparatus, and to the placement of the molar tooth row. As a selective herbivore, that has context dependant foraging preferences, such variability in the masticatory apparatus is not surprising (Mahoney and Stella, 2020).

Further, skull shape was significantly associated with total above ground biomass. In areas of greater biomass, associated with lower needleleaf percentage but higher broadleaf percentage, beaver skulls increased in surface area and shifted their zygomatic arch anteriorly. This optimized configuration could support larger masseter and temporalis muscles, while also improving biting angles and moment arms, leading to increased bite force (Maestri et al., 2016b). This is likely associated to an increased foraging of hard woody trees, which are typically broadleaved and of greater biomass. Given that rodent bite force is influenced by diet, and not the other way around (Maestri et al., 2016b), our results suggest that beavers will exhibit local adaptations to increase their bite force when food sources are physically harder.

On the other hand, areas with lower biomass will likely have longer travel time for foraging, and lower abundance of preferred species. Hence, the beaver may forage woody trees less frequently to avoid risk of predation or over expenditure of energy and consume softer tissued plants instead (Milligan and Humphries, 2010; Salandre et al., 2017). Our results suggest this to be the case, where the beaver exhibits less specialized morphology for high bite force in areas of low biomass (Cox et al., 2012; Maestri et al., 2016b). In fact, trends of cranial morphology in areas of lower biomass, which are associated with lower broadleaf tree cover (Figure 6) support this hypothesis. In such areas, beaver skulls had longer rostrums and larger check teeth, typical of chewing herbivores and generalists (Samuels, 2009; Maestri et al., 2016b). Despite their selective nature, beavers have been found to forage on most plants – including species they typically avoid (Slough, 1978; Mahoney and Stella, 2020). In fact, beaver habitat selection is hierarchical with foraging choice being a lower order priority, implying that in habitats with high amounts of quality nutrition, the beaver may not optimize their feeding apparatuses if all other important conditions are met (Gerwing et al., 2013b). For example, lotic environments do not require dam building, and are associated with a higher degree of macrophyte consumption (Milligan and Humphries, 2010; Bashinskiy, 2020). In subarctic and temperate lotic ponds, beaver diets can be greater than ~50% aquatic vegetation (Jenkins, 1975;

Milligan and Humphries, 2010). As such, beaver cranial morphology may adapt to have more generalizations when woody plants are consumed less frequently.

It has been previously reported that temperature and precipitation may impact rodent size (Souto-Lima and Millien, 2014), however, we found no such association with the beaver. In fact, we found no association with beaver skull size across our explanatory variables. These findings are surprising, as previous works done on herbivorous rodents, found that increased food availability was correlated with larger body size (Alhajeri and Steppan, 2016a). While this size increase may be associated with improved mastication in regions with increased vegetation (Maestri et al., 2016b), larger cranial size may also be a signal of improved fitness as a product of increased forage availability (Alhajeri and Steppan, 2016a; Stumpp et al., 2018). Despite this, however, we found no such association. It may be possible that an expected increase in skull size and muscle mass may be offset by improved masticatory efficiency through a narrower skull, leading to size not being associated directly to diet or climate (Maestri et al., 2016b).

Moreover, ecoregions significantly affected shape along PC4 and PC7. In ecoregion clusters representing boreal forests, the beaver skull had a slightly narrower zygomatic breadth, larger base of the zygomatic arch, and slightly wider rostrum than in more southern temperate regions. The cranium in the boreal regions also had less area for large muscle attachments, likely attributed to lower bite force (Maestri et al., 2016b). Given the avoidance of conifers, beavers in the boreal forest are likely less optimized for tree cutting, and are well suited with a more generalist phenotype having a varied diet (Maestri et al., 2016b). Conversely, in high ecoregion clusters, representing taiga shield, taiga plain, and the Hudson plain, cranial morphology becomes wider. This suggests that beavers in subarctic ecozones require efficient biting of high force. This is surprising, as these regions are characterized by deciduous shrubs of intermediate stems and not large trees. However, with a high percentage of preferred shrub cover in these regions (Tape et al., 2018), it is likely that woody vegetation comprises a significant component of their forage. However, being at higher latitudes, general wood density, and subsequently nutritional value, decreases in woody vegetation (Rossi et al., 2015), as such, beavers in the higher ecozones likely need to forage more frequently than their southern counterparts. This, however, requires more research.

While Milligan and Humphries (2010) found that subarctic beaver diets are largely composed of aquatic vegetation, the proportion was dependant on whether a beaver was inhabiting a pond compared to a stream, where the latter consumed more woody shrubs (Milligan and Humphries, 2010). Here, most specimens from the tundra inhabited a riverine system, and likely foraged woody vegetation. Therefore, skull cranial adaptations for tundra specimen inhabiting lentic systems are adapted for higher efficiency biting of woody shrubs (Cox and Baverstock, 2016; Maestri et al., 2016b). This key distinction highlights the importance of considering the regional-level habitat effects on beaver functional morphology.

4.3 The Effects of Climate on Beaver Cranial Morphology

Climate variables have significant predictive power for North American beaver abundance, and have been shown to be very effective (Jarema et al., 2009). Additionally, climate variables have been reported to be good predictors of rodent morphology. McGuire (2010) found that climate clines were a good predictor for *M. californicus* molar shape, while Kang et al. (2020) found that increases in mean annual temperature and precipitation led to variance in *E. baileyi* skull morphology (McGuire, 2010; Kang et al., 2020).

Here, climate variables significantly influenced beaver cranial morphology. For instance, colder temperature was associated with an elongation of the rostrum. Rodent thermoregulation is partly through their nasal turbinates, therefore, increased surface area of the rostrum improves that process in very cold habitats (Costa et al., 2013; Stumpp et al., 2018). Similarly, increased humidity associated with high precipitation hinders rodent thermoregulation, therefore, we would expect skulls to respond with elongated rostrums in humid habitats (Costa et al., 2013; Stumpp et al., 2018). However, we did not find such a relation between annual precipitation and beaver skull shape. This is likely because beavers are already well-adapted to humidity as semi-aquatic mammals. Overall, our results confirm that mean annual temperature is directly related to changes in functional traits associated with thermoregulation, where colder environments select for wider rostrums.

Temperature may also have indirect effects on beaver skull functional morphology. For example, colder regions likely have shorter and sparce vegetation, longer winters, and less productivity (Rossi et al., 2015; Mekonnen et al., 2021). Therefore, climate variables serve as a good proxy for environmental variables influencing beaver functional morphology that may not be directly captured with spatial data (Jarema et al., 2009; McGuire, 2010; Terray et al., 2022). This is consistent with our results, where rostrums exposed to high MAT are more morphologically adapted for higher bite force.

Others have suggested a similar relationship between climate variables and morphology (Millien et al., 2006; Wolf et al., 2009). For example, Millien et al. (2006), argued that climate variables covaried significantly with vegetation making it difficult to discern their effects on rodent morphology directly (Millien et al., 2006). As members of the family *Rodentia*, this is likely also the case for beavers. As such, we found that while climate variables may provide insight into functional morphology with respect to thermoregulation, it is essential to also consider environmental variables to better interpret the impacts of the climate and environmental effects separately.

4.4 Locally Adapted Beavers

One aim of this study was to assess the local adaptative potential of beavers to their environment. If beavers were locally adapted, we would expect to see a strong association between local climate and environmental factors with skull functional morphology (Maestri et al., 2016a). Our results suggest that beavers are in fact locally adapted, having clear morphological variance being well predicted by environment and climate factors. Interestingly, our findings are consistent with previous work on the European beaver, highlighting morphological variation across populations (Teleky et al., 2018).

Most notably, we found significant variation in functional traits associated with diet that are closely related to biomass, and forest composition. For a rodent with such well documented foraging preferences, our findings may shed some light onto how adaptations may relate to local diet (Mahoney and Stella, 2020). This is especially relevant in areas where beavers are foraging typically-avoided species, such as the Adirondacks in New York (Mahoney and Stella, 2020).

Further, we found cranial adaptations in beavers at their northern range edge in the tundra ecozone. The adaptations are, as with the other ecoregions, heavily influenced by foraging and diet composition. The tundra is composed of deciduous shrubs of preferred stem size, and due to longer winters, can be consumed for longer periods in their food cache compared to other habitats (Milligan and Humphries, 2010; Tape et al., 2018). Similarly, tundra aquatic vegetation has a shorter growing period, making woody shrubs more important year-round. Evidently, this is dependent on the type of water body a colony is established in, where lotic environments encourage a higher macrophyte diet (Milligan and Humphries, 2010). Given the morphological significance of diet across their range, we propose that beaver local adaptations will vary across lotic and lentic tundra ecosystems. Because our sample was bias towards lentic subarctic environments, we suggest investigating morphological variance of low arctic beavers across lotic and lentic systems

Based on our findings, beavers in the sub-arctic appear to be functionally adapted to these environments, with cranial masticatory optimizations. However, regional considerations still need to be considered to gain a fuller picture, where lotic and lentic populations are compared. Nonetheless, it is important that northern conservation managers consider the beaver as a species that is not merely passing by, but rather as a functionally well-adapted agent of change in this dynamic and rapidly evolving ecosystem.

Figures

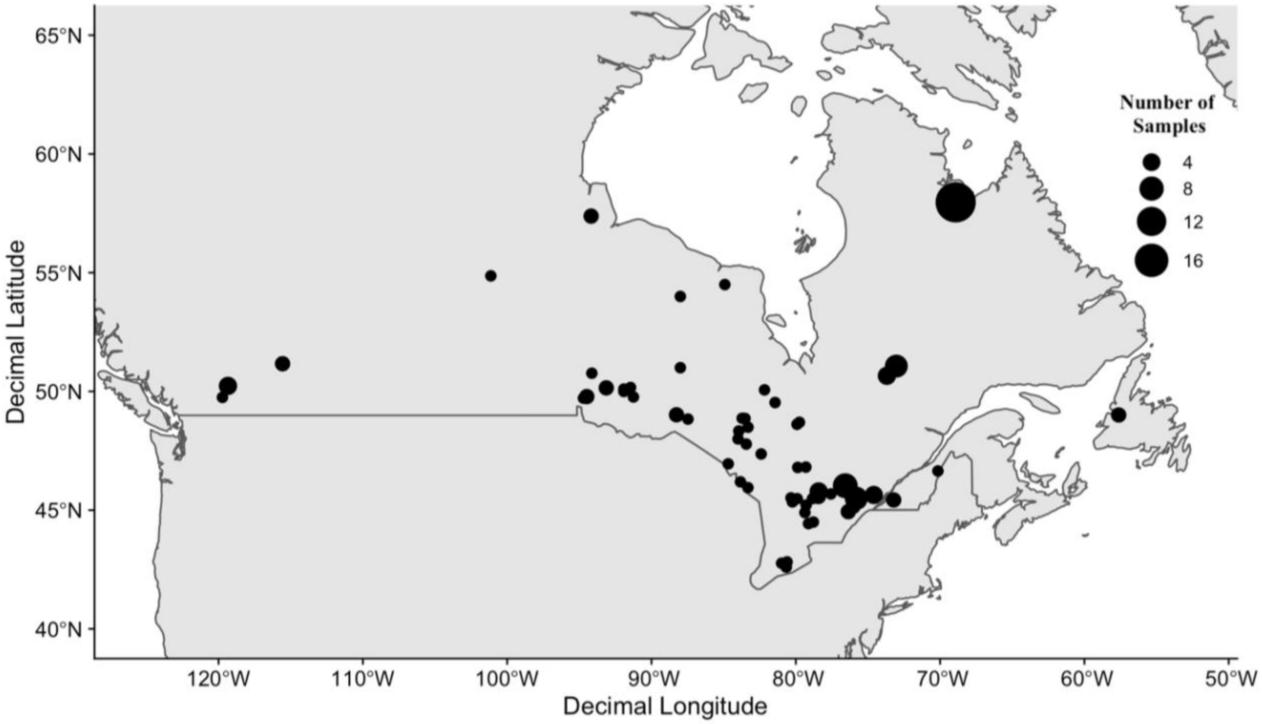


Figure 1: Sample sizes and localities of the study specimens of *Castor canadensis*. The size of the circle symbol illustrates sample size at each location. Skull counts per location ranged from 1 skull to 17, and a total of 117 skulls were included in this study.

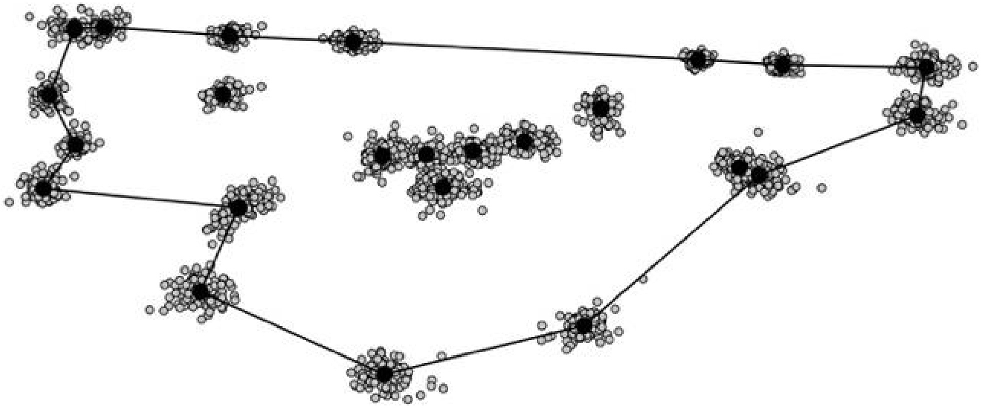


Figure 2: Landmark configuration of 117 adult beaver skulls in ventral view. A detailed description of the landmarks is provided in Appendix (Figure 2A). Black points represent the consensus (average) configuration, and each gray point represents the landmark position of a single specimen. The consensus configuration is outlined by a wireframe to aid in the interpretation of the visualization.

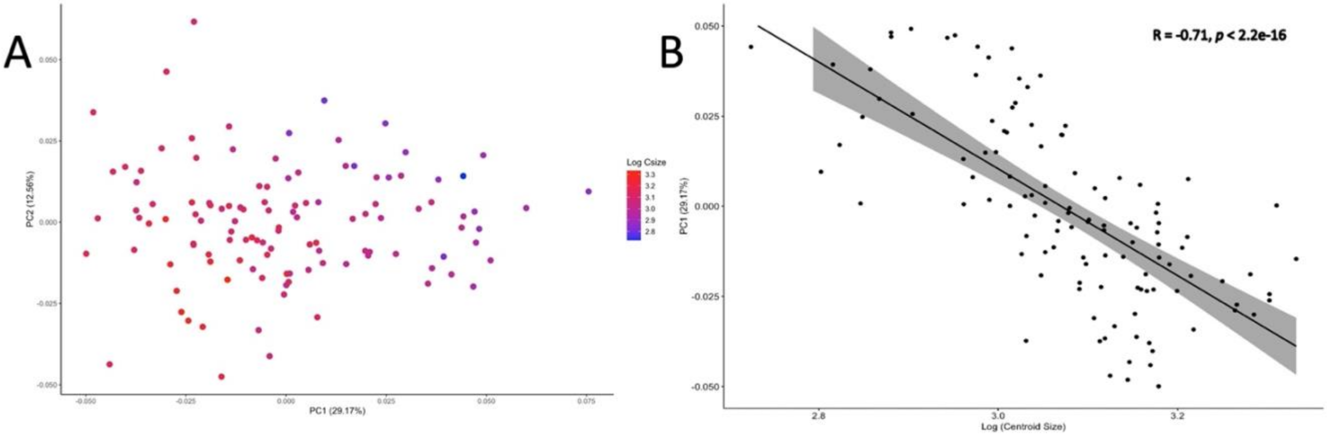


Figure 3: The relationship between skull shape and size, or allometry, in adult beaver skulls for the 117 individuals included in this study. (A) overall shape variation along the raw PC1 and PC2 axes; symbol colors illustrate centroid size, from large (red) to small (blue). Overall, a larger size is associated with a lower loading along PC1. (B) the negative relation between raw PC1 and size (Pearson's R = -0.71, p <2.2e-16) with 95% confidence interval of the linear model in gray shading.

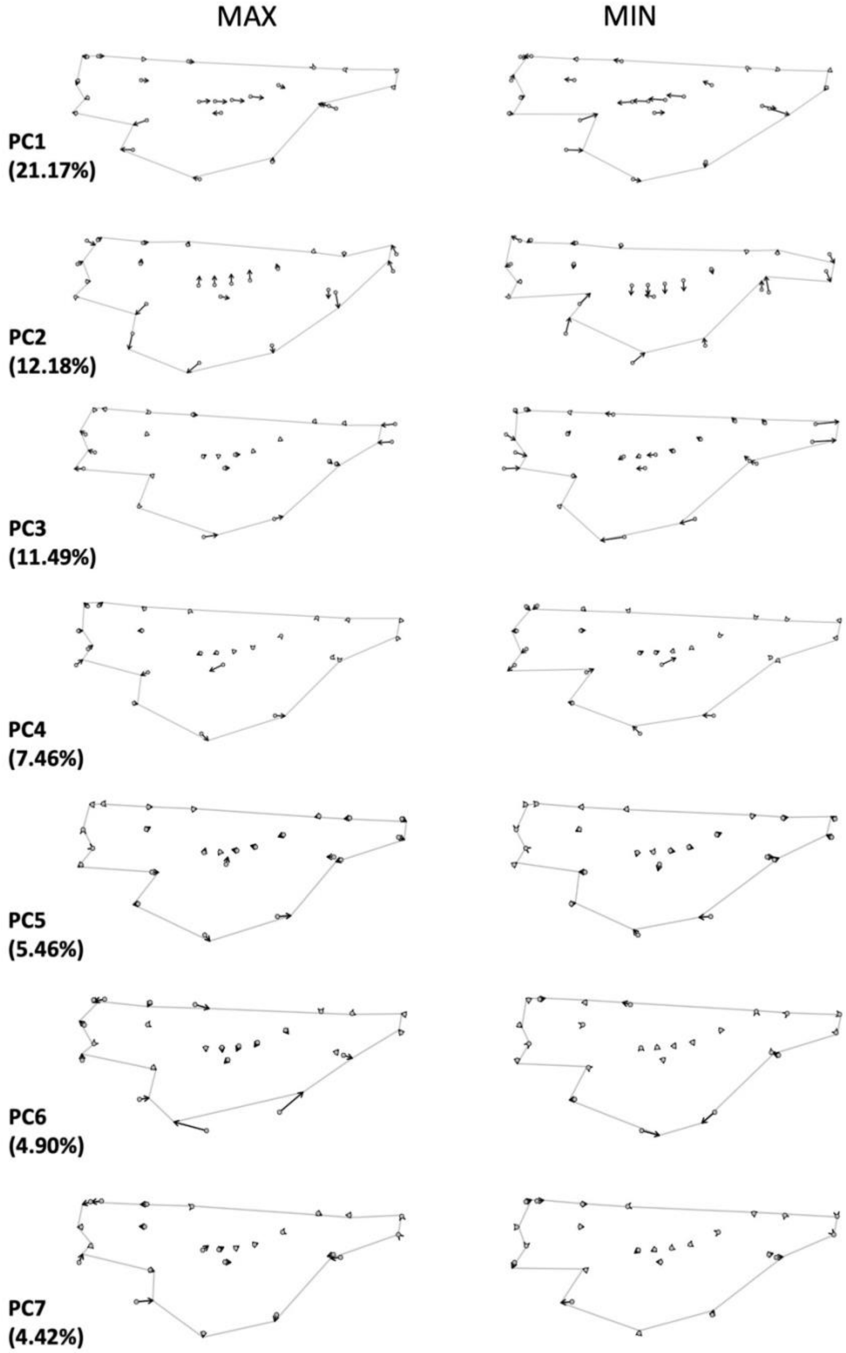


Figure 4: Shape variation along the 7 first PC axes explaining over 67% of the overall skull shape variance. Gray points represent the mean landmark configuration of the full sample, and the black arrows are vectors illustrating the direction and amount of change in skull shape between the two most extreme configuration along each PC axis.

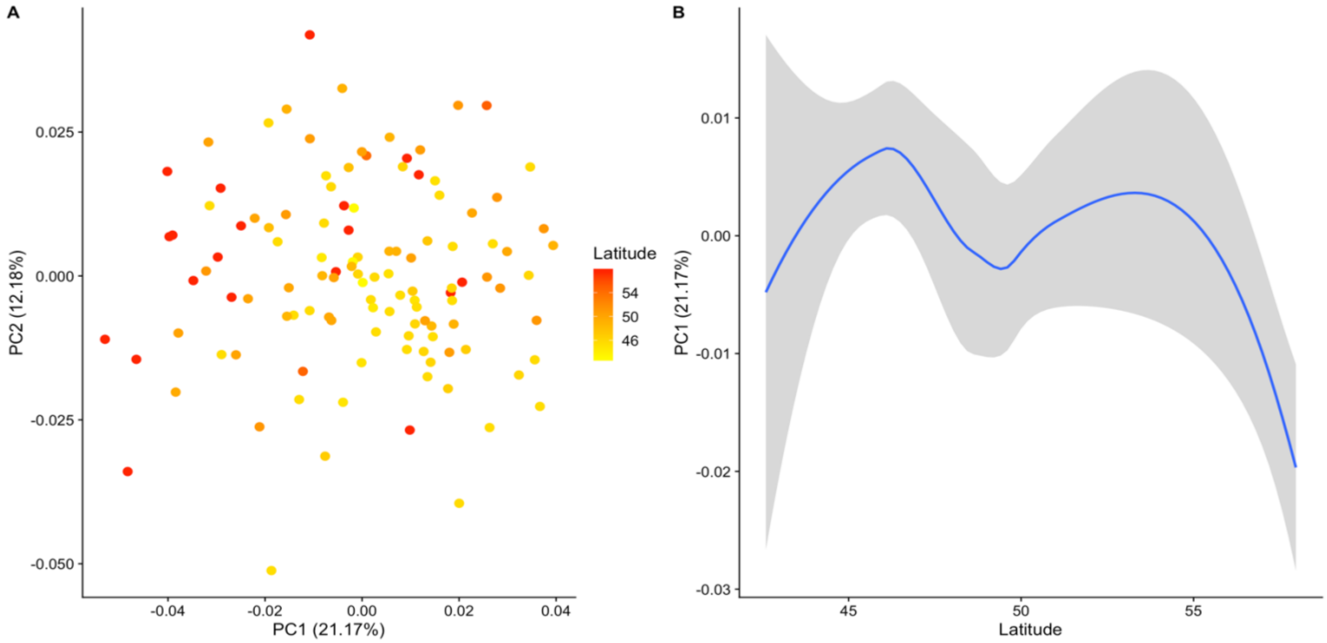


Figure 5: (A) PC scores of PC1 and PC2 (corrected for size) illustrating intra-specific overall skull shape variation across latitude. Red colors indicate higher latitude and yellow colors indicate lower latitudes. (B) The negative relation between PC1 and latitude (F=19.73, p<0.01), illustrated here with a smoothed curve and 95% confidence intervals.

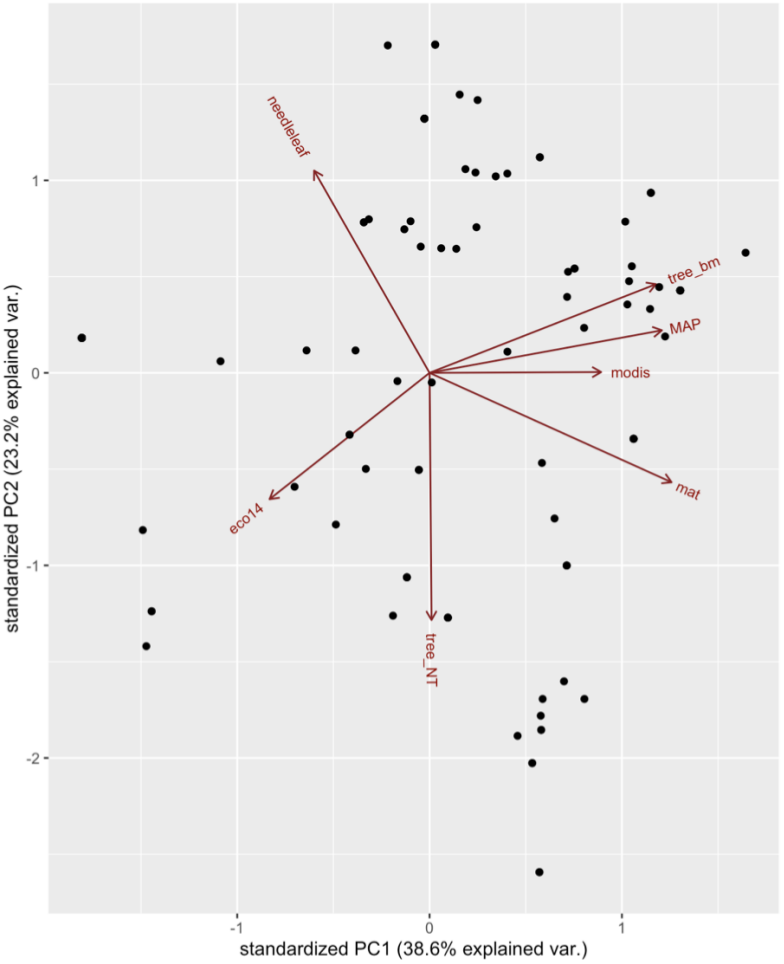


Figure 6: PCA biplot illustrating the relation between the environmental and vegetation factors included in the analyses. Tree_bm refers to total above ground biomass, tree_NT refers to percent non-treed vegetation cover, modis refers to percent treed vegetation cover, and eco14 refers to the ecozones.

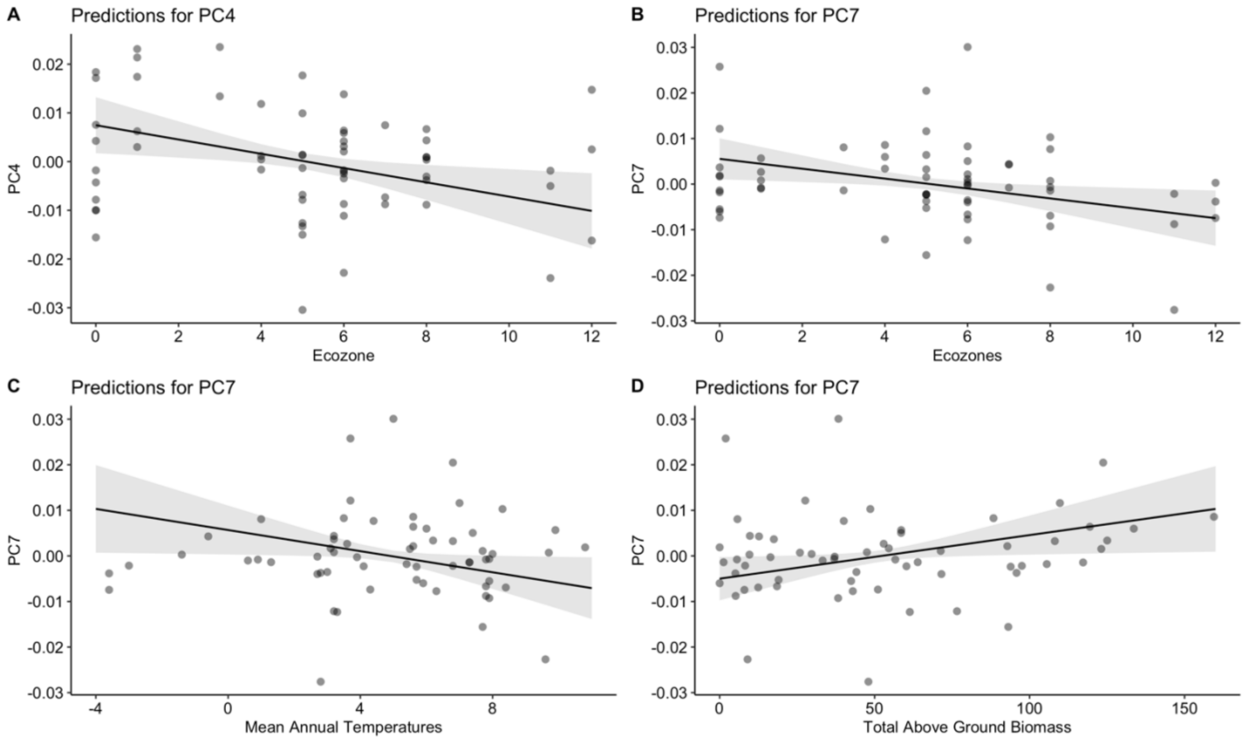


Figure 7: Predicted values (estimates) for generalized least squares models of A) PC4, and B-E) PC7 with only significant fixed effects displayed. Raw data are shown as gray points, while the predicted model is shown in black with the confidence interval in gray shading. See Coops et al. (2009) for details on ecozone clusters.

Tables

PC AXIS	EIGENVALUE	VARIANCE EXPLAINED (%)	CUMULATIVE VARIANCE EXPLAINED (%)
PC 1	0.00044815	21.823957	21.82396
PC 2	0.00025003	12.175662	33.99962
PC 3	0.00023604	11.494712	45.49433
PC 4	0.00015251	7.426954	52.92129
PC 5	0.00011220	5.463667	58.38495
PC6	0.00001007	4.903649	63.28860
PC7	0.00009077	4.420339	67.70894

Table 1: Eigenvalues and variance explained for the 7 first PC axes explaining over 67% of the total variance.

	PC 1		
Predictors	*Estimates*	*CI*	*p*
Intercept	-4.85377	-7.82865 – -1.87889	**0.002**
Latitude	0.09669	0.03985 – 0.15352	**0.001**
Year of Collection	0.00249	0.00098 – 0.00399	**0.001**
Latitude X Year of Collection	-0.00005	-0.00008 – -0.00002	**0.001**
Observations	110		
R^2 / R^2 adjusted	0.240 / 0.218		

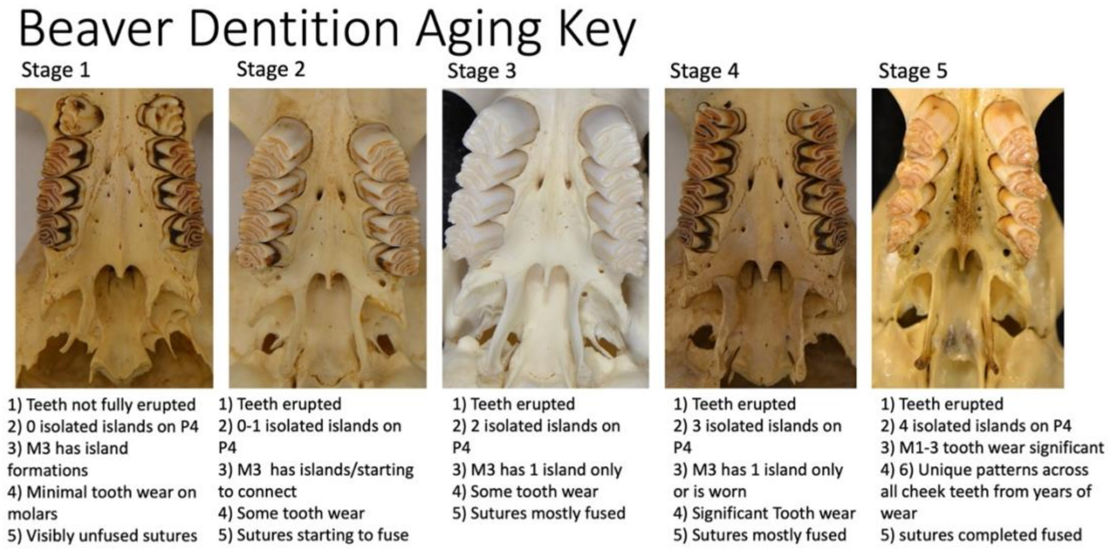
Table 2: Latitudinal and temporal variation in skull shape (PC1). Latitude and Year of collection had a significant effect on PC1, alone and in interaction.

		Centroid Size			PC1			PC2			PC3	
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Intercept	20.96971	16.68937 – 25.25004	**<0.001**	-0.01540	-0.04620 – 0.01541	0.3159	0.01350	-0.00897 – 0.03597	0.2335	0.00920	-0.01041 – 0.02880	0.3511
Mean Annual Temperature	-0.05962	-0.40775 – 0.28852	0.7327	0.00065	-0.00166 – 0.00296	0.5649	0.00025	-0.00156 – 0.00205	0.7852	0.00081	-0.00076 – 0.00238	0.3071
Percent Vegetation Tree Cover	-0.00638	-0.05346 – 0.04070	0.7869	0.00011	-0.00018 – 0.00040	0.4428	0.00018	-0.00006 – 0.00043	0.1377	0.00010	-0.00012 – 0.00031	0.3709
Ecozone	0.01132	-0.26015 – 0.28280	0.9337	0.00031	-0.00153 – 0.00215	0.7294	0.00018	-0.00125 – 0.00161	0.8047	-0.00039	-0.00164 – 0.00086	0.5325
Mean Annual Precipitation	0.00048	-0.00429 – 0.00526	0.8399	0.00000	-0.00003 – 0.00004	0.8820	-0.00002	-0.00005 – 0.00000	0.0554	-0.00002	-0.00004 – 0.00000	0.1070
Total Above Ground Biomass	0.00967	-0.01724 – 0.03658	0.4745	-0.00001	-0.00019 – 0.00016	0.8734	-0.00008	-0.00023 – 0.00006	0.2680	-0.00002	-0.00015 – 0.00010	0.7069
Percent Needleleaf Cover	-0.00638	-0.04525 – 0.03248	0.7432	0.00004	-0.00022 – 0.00030	0.7530	0.00000	-0.00021 – 0.00021	0.9931	-0.00004	-0.00022 – 0.00015	0.6975
Percent Vegetation Non-Tree Cover	0.02550	-0.02023 – 0.07123	0.2685	0.00002	-0.00028 – 0.00032	0.8988	-0.00020	-0.00045 – 0.00004	0.1029	-0.00001	-0.00022 – 0.00021	0.9561
N				32_{year}								
Observations	62			62			62			62		

		PC4			PC5			PC6			PC7	
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Intercept	0.00352	-0.01400 – 0.02104	0.6887	0.00166	-0.01346 – 0.01678	0.8266	0.00403	-0.00958 – 0.01765	0.5550	0.01386	0.00012 – 0.02760	**0.0481**
Mean Annual Temperature	-0.00048	-0.00188 – 0.00093	0.5003	-0.00048	-0.00169 – 0.00073	0.4323	0.00105	-0.00004 – 0.00215	0.0587	-0.00116	-0.00226 – -0.00006	**0.0398**
Percent Vegetation Tree Cover	-0.00001	-0.00020 – 0.00019	0.9551	-0.00010	-0.00026 – 0.00007	0.2408	0.00003	-0.00012 – 0.00018	0.6792	-0.00007	-0.00022 – 0.00008	0.3774
Ecozone	-0.00147	-0.00258 – -0.00035	**0.0109**	0.00020	-0.00076 – 0.00117	0.6717	-0.00029	-0.00115 – 0.00058	0.5106	-0.00108	-0.00196 – -0.00021	**0.0160**
Mean Annual Precipitation	0.00000	-0.00002 – 0.00002	0.9792	0.00001	-0.00001 – 0.00002	0.5343	-0.00001	-0.00002 – 0.00001	0.2198	0.00000	-0.00002 – 0.00002	0.9873
Total Above Ground Biomass	0.00002	-0.00009 – 0.00013	0.7206	0.00007	-0.00003 – 0.00017	0.1473	-0.00005	-0.00014 – 0.00004	0.2734	0.00010	0.00001 – 0.00018	**0.0351**
Percent Needleleaf Cover	0.00004	-0.00012 – 0.00020	0.6094	-0.00006	-0.00020 – 0.00008	0.3748	0.00008	-0.00004 – 0.00021	0.1892	-0.00012	-0.00025 – 0.00000	0.0588
Percent Vegetation Non-Tree Cover	0.00016	-0.00003 – 0.00035	0.1036	0.00004	-0.00012 – 0.00021	0.6084	-0.00009	-0.00024 – 0.00006	0.2356	0.00009	-0.00006 – 0.00024	0.2156
Observations	62			62			62			62		

Table 3: The effect of environmental and vegetation factors on beaver skull size and shape Generalized least squares models on centroid size, and shape variables (PC2 to 7), and linear mixed effect model on PC 1, with year of collection included as a random effect.

Appendix



Beaver Dentition Aging Key

Stage 1

1) Teeth not fully erupted
2) 0 isolated islands on P4
3) M3 has island formations
4) Minimal tooth wear on molars
5) Visibly unfused sutures

Stage 2

1) Teeth erupted
2) 0-1 isolated islands on P4
3) M3 has islands/starting to connect
4) Some tooth wear
5) Sutures starting to fuse

Stage 3

1) Teeth erupted
2) 2 isolated islands on P4
3) M3 has 1 island only
4) Some tooth wear
5) Sutures mostly fused

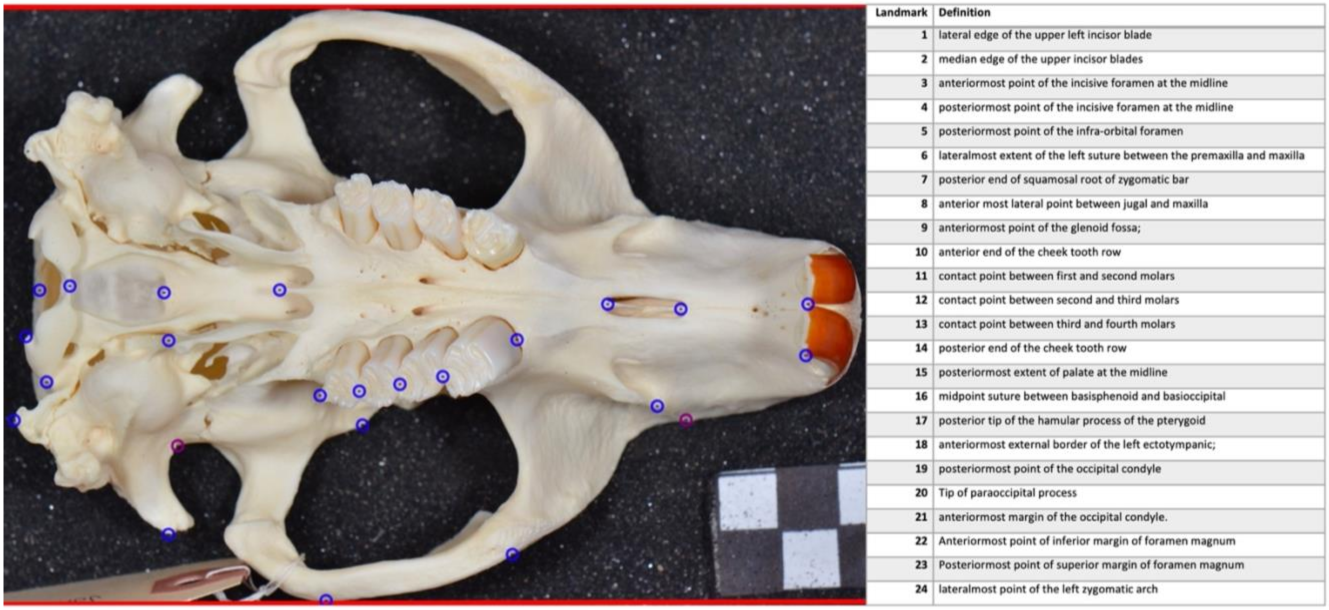
Stage 4

1) Teeth erupted
2) 3 isolated islands on P4
3) M3 has 1 island only or is worn
4) Significant Tooth wear
5) Sutures mostly fused

Stage 5

1) Teeth erupted
2) 4 isolated islands on P4
3) M1-3 tooth wear significant
4) 6) Unique patterns across all cheek teeth from years of wear
5) sutures completed fused

Figure 1A: Beaver Aging Key developed to distinguish adults from juveniles, and to categorize relative life stage using the ventral views of the beaver skull.



Landmark	Definition
1	lateral edge of the upper left incisor blade
2	median edge of the upper incisor blades
3	anteriormost point of the incisive foramen at the midline
4	posteriormost point of the incisive foramen at the midline
5	posteriormost point of the infra-orbital foramen
6	lateralmost extent of the left suture between the premaxilla and maxilla
7	posterior end of squamosal root of zygomatic bar
8	anterior most lateral point between jugal and maxilla
9	anteriormost point of the glenoid fossa;
10	anterior end of the cheek tooth row
11	contact point between first and second molars
12	contact point between second and third molars
13	contact point between third and fourth molars
14	posterior end of the cheek tooth row
15	posteriormost extent of palate at the midline
16	midpoint suture between basisphenoid and basioccipital
17	posterior tip of the hamular process of the pterygoid
18	anteriormost external border of the left ectotympanic;
19	posteriormost point of the occipital condyle
20	Tip of paraoccipital process
21	anteriormost margin of the occipital condyle.
22	Anteriormost point of inferior margin of foramen magnum
23	Posteriormost point of superior margin of foramen magnum
24	lateralmost point of the left zygomatic arch

Figure 2A: Positions of the 24 landmarks digitized on the ventral view of the skull and their anatomical definition.

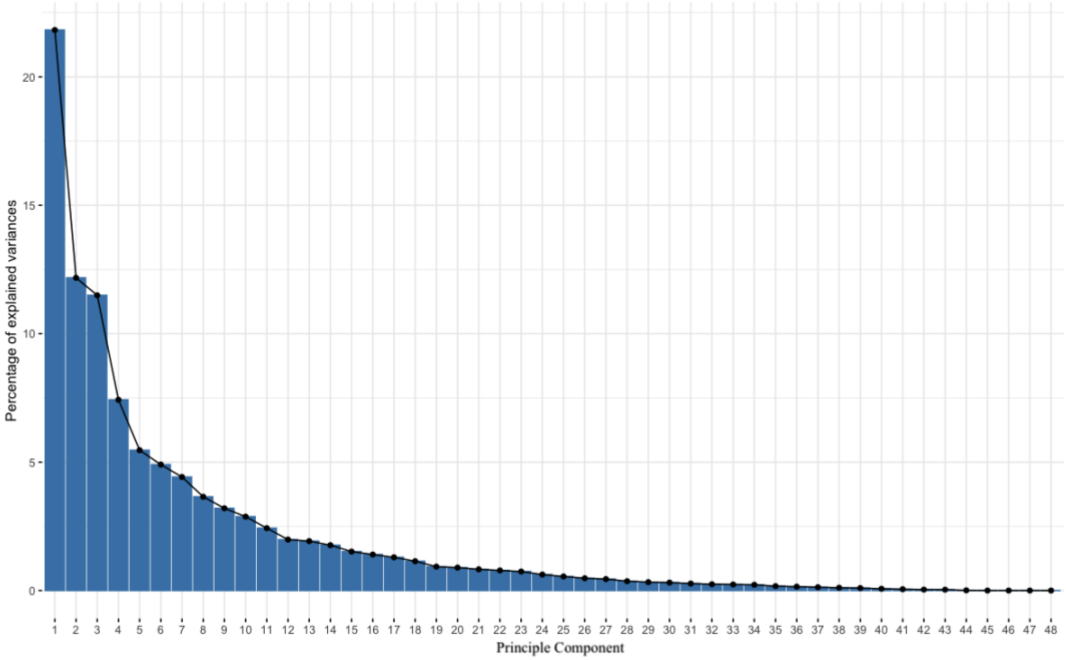


Figure 3A: Scree plot of the percent variance explained by each principal component (PC) of the allometry corrected overall shape. The first axis explains 21.82% of variance, and the first seven axes cumulatively explain 67.71% of the overall shape variance. Only the first five PC axes explain over 5% of variance.

CATALOGUE NUMBER	AGE STAGE	LATITUDE (DEG. N)	LONGITUDE (DEG. W)	YEAR
CMN_11004	4	50.659231	-73.687067	1921
CMN_11005	3	50.659231	-73.687067	1921
CMN_11179	2	48.493554	-83.313468	1930
CMN_13208	2	46.95	-84.683333	1935
CMN_14839	3	57.370088	-94.172534	1936
CMN_14840	3	57.383333	-94.183333	1936
CMN_14841	2	57.383333	-94.183333	1936
CMN_19801	4	49.008959	-57.623026	1949
CMN_19802	4	49.008959	-57.623026	1949
CMN_25381	4	45.506769	-75.813245	1982
CMN_26456	2	46.65	-70.15	1957
CMN_28659	2	45.15743	-76.034778	1961
CMN_28668	2	44.937139	-76.361319	1961
CMN_28669	2	44.937139	-76.361319	1961
CMN_28672	2	45.430066	-73.216675	1961
CMN_28673	4	45.15743	-76.034778	1961
CMN_28674	3	45.430066	-73.216675	1961
CMN_37355	2	45.447183	-75.70679	1969
CMN_41089	3	45.416667	-75.7	1975
CMN_45479	2	45.60201	-76.112971	1981
CMN_45621	2	45.395833	-75.990278	1980
CMN_47898	4	51.066667	-73.033333	1980
CMN_47899	2	51.066667	-73.033333	1980
CMN_47900	2	51.066667	-73.033333	1980
CMN_47901	2	51.066667	-73.033333	1980
CMN_47903	2	51.066667	-73.033333	1980
CMN_4847	4	45.966667	-76.483333	1920
CMN_59473	2	45.639594	-74.59224	1984
CMN_75025	2	45.474815	-76.024696	1976
CMN_75096	4	45.506769	-75.813245	1976
CMN_75126	2	45.506769	-75.813245	1977
CMN_75233	2	45.506769	-75.813245	1977
CMN_75368	2	45.416667	-75.7	1981
CMN_75384	2	45.506769	-75.813245	1981
CMN_75458	3	45.639594	-74.59224	1984
CMN_76570	3	45.639594	-74.59224	1985
CMN_8722	3	46.02987	-76.570989	1927
CMN_8723	2	46.02987	-76.570989	1927
CMN_8727	2	46.02987	-76.570989	1927
CMN_8728	2	46.02987	-76.570989	1927
CMN_8729	2	46.02987	-76.570989	1927
CMN_8730	2	46.02987	-76.570989	1927

CMN_M57	3	50.659231	-73.687067	1885
CMN_Z-117	2	45.416667	-75.7	1976
RMMA2021.09.01	2	57.9641109	-68.921483	2020
RMMA2021.09.02	2	57.9641109	-68.921483	2020
RMMA2021.09.03	4	57.9641109	-68.921483	2021
RMMA2021.09.04	2	57.9641109	-68.921483	2021
RMMA2021.09.05	2	57.9641109	-68.921483	2021
RMMA2021.09.06	3	57.9641109	-68.921483	2021
RMMA2021.09.07	3	57.9641109	-68.921483	2021
RMMA2021.09.08	4	57.9641109	-68.921483	2021
RMMA2021.09.09	3	57.9641109	-68.921483	2021
RMMA2021.09.10	4	57.9641109	-68.921483	2021
RMMA2021.09.11	4	57.9641109	-68.921483	2021
RMMA2021.09.12	4	57.9641109	-68.921483	2021
RMMA2021.09.13	2	57.9641109	-68.921483	2021
RMMA2021.09.14	2	57.9641109	-68.921483	2021
RMMA2021.09.15	4	57.9641109	-68.921483	2021
RMMA2021.09.16	3	57.9641109	-68.921483	2021
RMMA2021.09.17	2	57.9641109	-68.921483	2021
ROM_111458	4	42.82186	-80.605617	1986
ROM_111459	3	42.60101	-80.659669	unknown
ROM_11693	4	50.7666667	-94.133333	unknown
ROM_16653	3	45.59643	-78.44821	1946
ROM_16746	4	42.7666667	-80.983333	1946
ROM_16835	2	47.3666667	-82.4	1946
ROM_16986	3	48.86231	-83.5188	1946
ROM_18079	2	49.5333333	-81.433333	unknown
ROM_18342	3	45.57605	-78.43473	1947
ROM_18409	4	48.83545	-87.47451	1947
ROM_18521	2	46.19207	-83.83329	1947
ROM_18548	5	45.4833333	-79.9	1947
ROM_18551	2	45.6833333	-77.566667	1947
ROM_18583	5	49.0166667	-88.266667	1948
ROM_18584	3	49.0166667	-88.266667	1948
ROM_18752	4	45.78852	-78.41596	1948
ROM_18753	4	46.79971	-79.86751	1948
ROM_18780	3	45.5166667	-80.333333	1948
ROM_18840	3	45.78852	-78.41596	1948
ROM_18901	2	45.57605	-78.43473	1948
ROM_19565	2	48.86769	-83.71669	1948
ROM_19593	3	49.7833333	-94.483333	1949
ROM_19625	2	48.3333333	-83.95	1949
ROM_19686	2	49.7833333	-94.483333	1949
ROM_19689	4	48	-84	1949

ROM_19985	4	44.5	-78.783333	1949
ROM_21797	4	45.95	-83.316667	unknown
ROM_2302050001	3	49.7166667	-94.716667	1920
ROM_23133	4	51.1666667	-115.56667	unknown
ROM_23134	3	51.1666667	-115.56667	unknown
ROM_2510160399	3	48.7	-79.75	1925
ROM_2510160400	4	48.6166667	-79.916667	1925
ROM_25535	3	50.1	-91.916667	1905
ROM_25540	4	50.1666667	-91.45	1952
ROM_25545	2	51	-88	1952
ROM_25559	4	50	-91.916667	1952
ROM_25568	2	50.15	-93.133333	1952
ROM_25569	2	50.15	-93.133333	1952
ROM_25582	2	49.7666667	-91.25	1953
ROM_25592	3	54	-88	1953
ROM_27164	3	54.8666667	-101.13333	1955
ROM_27979	2	44.4333333	-79.120102	1957
ROM_2806130002	2	45.2166667	-79.283333	1928
ROM_30437	2	49.75	-119.73333	1955
ROM_30438	2	50.2333333	-119.35	1955
ROM_30439	2	50.2333333	-119.35	1955
ROM_30440	2	50.2333333	-119.35	1955
ROM_3104270014	3	44.9	-79.366667	unknown
ROM_31245	2	45.48684	-78.84203	1947
ROM_32220	4	47.7833333	-83.433333	1957
ROM_3308010002	3	50.0666667	-82.166667	1933
ROM_3405260003	4	45.78852	-78.41596	1934
ROM_42773	2	46.81371	-79.30275	1967
ROM_86531	3	54.5	-84.916667	1981
ROM_91278	2	45.5786	-78.48025	1946
ROM_91444	3	45.35	-80.233333	1985

Table 1A: Specimens included in this study. Geographic coordinates are in decimal degrees. ROM: Royal Ontario Museum, CMN: Canadian Museum of Nature, RMMA: Redpath Museum McGill University.

	Percent Variance	Cumulative Percent		Percent Variance	Cumulative Percent		Percent Variance	Cumulative Percent
PC 1	21.82	21.82	**PC 17**	1.29	89.76	**PC 33**	0.24	98.92
PC 2	12.18	34.00	**PC 18**	1.14	90.90	**PC 34**	0.22	99.14
PC 3	11.49	45.49	**PC 19**	0.93	91.83	**PC 35**	0.17	99.31
PC 4	7.43	52.92	**PC 20**	0.89	92.72	**PC 36**	0.15	99.47
PC 5	5.46	58.38	**PC 21**	0.83	93.55	**PC 37**	0.13	99.59
PC 6	4.90	63.29	**PC 22**	0.78	94.33	**PC 38**	0.11	99.70
PC 7	4.42	67.71	**PC 23**	0.74	95.07	**PC 39**	0.10	99.80
PC 8	3.65	71.36	**PC 24**	0.62	95.69	**PC 40**	0.07	99.87
PC 9	3.20	74.56	**PC 25**	0.55	96.24	**PC 41**	0.05	99.92
PC 10	2.88	77.44	**PC 26**	0.48	96.72	**PC 42**	0.04	99.96
PC 11	2.43	79.87	**PC 27**	0.45	97.16	**PC 43**	0.03	99.99
PC 12	1.98	81.85	**PC 28**	0.36	97.53	**PC 44**	0.01	100
PC 13	1.92	83.78	**PC 29**	0.33	97.86	**PC 45**	0	100
PC 14	1.77	85.54	**PC 30**	0.31	98.17	**PC 46**	0	100
PC 15	1.52	87.06	**PC 31**	0.27	98.44	**PC 47**	0	100
PC 16	1.40	88.46	**PC 32**	0.25	98.68	**PC 48**	0	100

Table 2A: Percent of overall shape variance explained by each principal component (PC). The first seven PCs explain 67.71% of the variance.

LANDMARK	PC1	PC2	PC3	PC4	PC5	PC6	PC7
1.X	0.1537	-0.0873	0.0352	-0.0212	0.1877	-0.05831	0.048405
1.Y	-0.0664	0.1013	0.0405	-0.0477	0.0372	-0.08441	0.017424
2.X	-0.0181	-0.2487	0.2535	-0.3261	-0.1939	0.616937	0.138482
2.Y	0.1011	-0.1740	-0.0594	0.0270	0.1633	0.292537	0.223824
3.X	-0.2852	-0.0187	-0.1091	-0.0851	0.2425	0.117692	-0.51518
3.Y	0.0132	-0.2252	-0.2598	0.0786	0.0266	0.011561	-0.06957
4.X	-0.0342	0.1627	-0.0517	-0.2005	-0.0480	-0.08042	0.069673
4.Y	-0.1209	-0.0148	0.1159	0.0007	-0.0103	0.045983	0.018532
5.X	0.1304	0.0750	-0.0025	-0.1911	-0.0047	-0.22219	0.261704
5.Y	-0.0097	-0.0100	0.0632	-0.1363	-0.0107	-0.04407	0.049196
6.X	-0.2050	0.1655	0.2134	0.5159	-0.0816	-0.05006	-0.01548
6.Y	-0.0065	0.0008	-0.0247	0.2301	-0.2158	0.113813	0.033011
7.X	-0.0321	-0.0420	0.0346	-0.0121	0.1527	-0.10723	-0.10506
7.Y	0.0114	-0.0138	-0.0898	-0.0459	-0.0036	-0.05242	0.052961
8.X	0.3138	-0.0684	0.0676	0.0200	0.1186	-0.13448	-0.10222
8.Y	-0.0244	0.2061	0.1335	0.0501	-0.0723	-0.01934	-0.03891
9.X	0.2943	-0.0980	0.1186	0.0614	0.1329	-0.12942	-0.09757
9.Y	-0.0168	0.1857	0.1449	0.0917	-0.0618	-0.0225	-0.09488
10.X	0.2842	-0.0347	0.0546	0.1155	0.0277	-0.00902	-0.09567
10.Y	-0.0028	0.1634	0.1502	0.0636	-0.0906	0.010785	-0.12638
11.X	0.0728	0.2175	-0.3852	-0.0127	-0.2334	0.072217	0.035007
11.Y	0.0468	0.1499	0.1352	-0.1215	0.0868	-0.0143	0.032798
12.X	-0.3692	-0.0184	0.0789	-0.0327	0.3004	0.029004	0.251475
12.Y	0.1244	-0.2227	-0.2512	0.0758	0.0313	-0.08638	-0.000034
13.X	-0.2089	-0.5083	0.1820	-0.0894	-0.4824	-0.42369	-0.07425
13.Y	0.0446	-0.1588	-0.1396	0.2668	0.2918	0.017628	0.119548
14.X	0.0691	0.2046	-0.3856	-0.0158	-0.2025	0.027335	0.034325
14.Y	0.0158	0.1542	0.0976	-0.1203	0.0720	-0.05589	-0.01183
15.X	0.0516	0.0616	0.0994	0.0571	-0.1058	0.019148	0.225068
15.Y	-0.0076	-0.0139	0.0098	-0.0899	-0.0386	-0.06628	0.018684
16.X	-0.3080	-0.0813	-0.2237	0.2463	-0.1651	0.2013	-0.06394
16.Y	-0.1158	-0.1659	-0.1521	0.1335	-0.0035	-0.03054	0.030711
17.X	0.2647	-0.0310	0.1019	0.1500	-0.0440	0.039354	-0.13831
17.Y	0.0359	0.1620	0.1688	0.0833	-0.1160	0.090157	-0.22751
18.X	0.1725	0.0389	-0.0124	0.1076	-0.1322	0.033647	0.201771
18.Y	-0.0198	0.0986	0.0383	-0.0126	-0.0781	0.029173	0.013444
19.X	0.1451	-0.0467	0.1157	0.0584	0.0473	0.314871	-0.16721
19.Y	-0.0272	0.0471	0.0396	-0.0704	-0.0455	-0.05129	0.009316
20.X	-0.1178	0.1623	0.0778	0.0560	0.0989	-0.04724	0.33968
20.Y	0.0069	-0.1373	-0.0061	-0.1107	-0.0293	-0.0479	0.063195
21.X	0.0012	-0.0741	0.0226	-0.0013	0.1241	-0.05424	-0.1105

21.Y	-0.0022	0.0248	-0.0505	-0.0461	-0.0037	-0.06118	0.041476
22.X	-0.2587	-0.0263	0.0395	0.0507	0.2669	-0.10003	0.114123
22.Y	0.0543	-0.0947	-0.1798	0.0060	-0.0005	0.010354	0.086413
23.X	-0.0563	0.1563	-0.1067	-0.1981	-0.0468	-0.00756	-0.04892
23.Y	-0.0456	-0.0566	0.0582	-0.1161	-0.0212	-0.0313	-0.05474
24.X	-0.0600	0.1394	-0.2185	-0.2530	0.0407	-0.04762	-0.18541
24.Y	0.0115	-0.0061	0.0175	-0.1894	0.0927	0.045807	-0.18667

Table 3A: Loadings on the first seven PC axes of the 2D coordinates of each 24 landmarks used in this study.

Source file name	Attribute Title	Resolution	Link	Description
ensemble_ssp126_2011_MAT.tif	Mean Annual Temperature	1000m	https://adaptwest.databasin.org/pages/adaptwest-climatena/	Mean annual temperature (°C)
ensemble_ssp126_2011_MAP.tif	Mean Annual Precipitation	1000m	https://adaptwest.databasin.org/pages/adaptwest-climatena/	Mean annual precipitation (mm)
CA_EcoDom_14Class.tif	Ecozones (14 class)	1000m	https://open.canada.ca/data/en/dataset/41d008f7-f083-4801-b7c0-c2bf5a83a757	14 class stratification of regionalized spatial cluster data *.
NFI_MODIS250m_2011_kNN_LandCover_Veg_v1.tif	Treed Vegetated Land Cover	250m	https://open.canada.ca/data/en/dataset/ec9e2659-1c29-4ddb-87a2-6aced147a990	Percent of vegetated treed polygons. At least 10% of the polygon area, by crown cover, consists of tree species of any size
NFI_MODIS250m_kNN_LandCover_VegNonTreed_v0.tif	Non-Treed Vegetated Landcover	250m	https://open.canada.ca/data/en/dataset/ec9e2659-1c29-4ddb-87a2-6aced147a990	Percent of vegetated non-treed polygons
NFI_MODIS250m_kNN_Structure_Biomass_TotalLiveAboveGround_v0.tif	Total live above ground biomass	250m	https://open.canada.ca/data/en/dataset/ec9e2659-1c29-4ddb-87a2-6aced147a990	Mean total live above-ground dry biomass of polygons. Includes all trees > 1.3m with bark, main stem, stump and top. Derived from models.
NFI_MODIS250m_kNN_SpeciesGroups_NeedleLeaf_Spp_v0.tif	Percent Needleleaf	250m	https://open.canada.ca/data/en/dataset/ec9e2659-1c29-4ddb-87a2-6aced147a990	Percent composition of all needle-leaf species

Table 4A: Variable attributes included in this analysis; data were retrieved from AdaptWest and Open-Government Canada, two spatial data repositories for North America and Canada, available at (https://adaptwest.databasin.org, https://open.canada.ca). * cluster 1: Evergreen Needleleaf, cluster 2: Evergreen Needleleaf, cluster 3: Evergreen Needleleaf, cluster 4: Evergreen Needleleaf, cluster 5: Evergreen Needleleaf, cluster 6: Mixed Forest, cluster 7: Deciduous Needleleaf , cluster 8: Cropland, cluster 9: Baren/Sparse Vegetation, cluster 10: Grasslands, cluster 11: Woody Savanna, cluster 12: Open Shrub land, cluster 13: Open Shrub land, cluster 14: Open Shrub land (see Coops et al., 2009 for more details).

Works Cited

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General Conclusion:

In this thesis, I investigated the factors impacting beaver abundance, habitat selection, and forage, and how environmental variables related to beaver functional morphology. My aim was to quantify beaver skull functional morphology across the Canadian portion of its range and to model the effect of key environmental factors on beaver cranial morphology. I analyzed the relation between beaver skull shape and size with environmental and vegetation conditions using a set of spatial variables and museum specimen. Specifically, I quantified beaver cranial shape using geometric morphometrics (Zelditch et al., 2012), and related the primary axes of shape variance to forest cover and composition, total above ground biomass, ecozones, temperature, and precipitation to gain insight into adaptive potential of the beaver in a time of range expansion. Quantifying morphological variance of functional traits across environments has been recognized as an effective means for detecting local adaptations in rodents (Souto-Lima and Millien, 2014).

I found that environment and geomorphology were key considerations for beaver establishment, while vegetation composition and traits were important for beaver foraging and abundance. Additionally, I found that beaver cranial morphology was significantly affected by environmental factors, such as forest composition, ecozone, above ground biomass, and temperature. This suggests that the beaver may be locally adapted to its environment across its range, with a shift towards enhanced masticatory apparatuses in areas of increased foraging of woody vegetation. As a selective herbivore, that has context dependant foraging preferences, having a diverse masticatory apparatus is not surprising (Mahoney and Stella, 2020). This finding is consistent with the literature on *Rodentia,* where environmental condition, habitat, and vegetation have been associated with local adaptations (Martínez et al., 2014; Kubiak et al., 2018). Furthermore, we found there to be an effect of ecozone on beaver functional morphology, with beavers in the tundra being functionally well adapted to their habitat. In fact, despite a high dietary intake of soft-tissue vegetation in the subarctic summers, beavers in the far north are optimized for high bite force and efficiency with a short rostrum and wide skull (Cox and Baverstock, 2016; Maestri et al., 2016b). This suggest that in addition to soft tissue vegetation, beavers are consuming and foraging a considerable amount of woody vegetation in this environment. Furthermore, as explained in the literature, beaver foraging varies between lentic and lotic environments. Therefore, it is likely that subarctic beavers in lakes may have different local adaptions than those established in streams.

As such, these findings are very insightful into the functional potential of the North American beaver across its Canadian range. These results also highlight the importance of considering local adaptations of functional traits in future models considering beaver foraging, behaviour, and establishments. This may be especially useful in areas where beavers forage outside of the expected and in areas where beavers are expanding their range.

Future work should consider the genetic variability of the beaver to discern if beaver local adaptations are phenotypic plasticity or genetic variance. Further, future studies should consider both if the habitat lotic or lentic, and the degree of beaver establishment, as these considerations greatly influence beaver behaviours and foraging, likely influencing their local morphological potential.

Lastly, the many communities residing in Northern Canada are facing higher than average climate pressures and the beaver may add another layer of change to the low-arctic ecosystem. Therefore, in a time of beaver range expansion into the tundra (Tape et al., 2018), it is timely to better understand the local functional optimizations of the beaver across their range to inform management strategies.

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