Factors Influencing Beaver (*Castor canadensis*) Population Fluctuations, and Their Ecological Relationship with Salmonids

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Dedication

I dedicate this thesis to my biggest fans, my parents David Bice and Kathleen Johnson, who have always stood by side while I pursued my personal, professional, and above all, scientific endeavors.

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CHAPTER ONE

A Review of Beaver–Salmonid Relationships and History of Management Actions in the Western Great Lakes (USA) Region

SUMMARY

Within the western Great Lakes (WGL) U.S. region (Michigan, Minnesota, Wisconsin), the ecological impacts that North American beavers (*Castor canadensis*) have on cold-water streams are generally considered to negatively affect salmonid populations where the two taxa interact. Here, we review the history of beaver-salmonid interactions within the WGL region, describe how this relationship and management actions have evolved over the past century, and review all published studies from the region that have evaluated beaver-salmonid interactions.

Our review suggests the impact beavers have varies spatially and temporally, depending on a variety of local ecological characteristics. We found beaver activity is often deleterious to salmonids in low-gradient stream basins, but generally beneficial in high-gradient basins; and ample groundwater inputs can offset the potential negative effects of beavers by stabilizing the hydrologic and thermal regimes within streams. However, there was an obvious lack of empirical data and/or experimental controls within the reviewed studies, which we suggest emphasizes the need for more data-driven beaver-salmonid research in the WGL region. Resource managers are routinely faced with an ecological dilemma between maintaining natural environmental processes within cold-water ecosystems and conducting beaver control for the benefit of salmonids, and this dilemma is further complicated when the salmonids in question are a non-native species. We anticipate future beaver-salmonid research will lead to a greater understanding of this ecologically-complex relationship that may better inform managers when and where beaver control is necessary to achieve the desired management objectives.

INTRODUCTION

North American beaver (*Castor canadensis*) activities affect many fish and wildlife species (Rosell et al. 2005, Windels 2017), but of particular interest to resource managers in the western Great Lakes (WGL) region is the effect that beaver activity has on salmonids (family Salmonidae) in tributaries and inland streams within the region. As ecosystem engineers, beavers disproportionately alter their environment through their dam-building and selective foraging habits (Rosell et al. 2005). Beaver dams impact streams by impounding the flow of running water, thereby reducing stream discharge and velocity (Naiman et al. 1988). Conditions upstream of the dam change from lotic to lentic, causing sediment, organic material, and water to accumulate (Naiman et al. 1986, Gurnell 1998). Over time, this leads to further alterations to stream hydrology, channel geomorphology, and riparian biogeochemical pathways (Naiman et al. 1988, 1994). These stream modifications can have cascading effects on salmonids, depending on local ecosystem characteristics. Most salmonid species spawn in stream sections with a slope between 0.5% and 3% (Beechie et al. 2008), coinciding with slopes preferred by beaver (Allen 1983); as such, interactions between the two taxa have important implications for the long-term growth, sustainability, and size and age structure of local salmonid populations.

Brook trout (*Salvelinus fontinalis*) is the only native salmonid species that regularly uses WGL streams, though several non-native Pacific salmonid species have been introduced since the late 19th century (Crawford 2001) and use WGL tributaries for spawning and rearing habitat (e.g., rainbow trout [*Oncorhynchus mykiss*]; Biette et al. 1981), Chinook salmon [*O. tshawytscha*], and Coho salmon [*O. kisutch*]; Carl 1982). Most salmonid introductions and subsequent stocking programs were in response to declining commercial fisheries, stream habitat degradation, and to enhance recreational angling opportunities within Great Lakes streams (Mills et al. 1993). In the early 20th century, beaver populations in the region began to recover from two centuries of overharvest (Knudsen 1963, Longley and Moyle 1963) at the same time that resource managers were focused on increasing salmonid populations, leading sportsmen and resource managers to begin evaluating the impact that growing beaver populations had on cold-water stream ecosystems (Knudsen 1962).

Each management agency within the WGL region currently uses some form of control measures (e.g., trapping, beaver removal, and dam removal) on cold-water salmonid streams where beaver populations exist, though no synthesis on beaver-salmonid studies or previous management programs within the region has been conducted to date. For the purpose of this review, we consider the WGL region to be coincident with the Laurentian Mixed Forest Province (unit code 212; Cleland et al. 2007) (geographic extent is similar to the Northern Lakes and Forest Ecoregion; Omernik and Gallant 1988), where all published studies to date have been conducted (Figure 1.1). We present an overview of beaver-salmonid relationships within the WGL region, with a focus on how management practices have evolved over the past century. Our intent was not to duplicate the content of two other comprehensive global reviews of beaver-fish interactions (Collen and Gibson 2001, Kemp et al. 2012), but to provide a refined review of beaver-salmonid interactions that will be useful for biologists, natural resource managers, and other interested parties, particularly in the WGL region.

The first section details the early history of beavers, native and non-native salmonids, and the efforts by resource managers within the WGL region to increase population sizes of both taxa. We then review the main effects that beaver activities have on salmonid populations and habitat characteristics, summarize results from all published studies conducted within the WGL region, and identify information gaps where additional research can improve our understanding of the beaver-salmonid relationship. This last section is most pertinent to beaver's effects on brook, brown (*Salmo trutta*), and to a lesser degree rainbow trouts, as these species interact with beavers more often than other salmonid species within WGL stream systems. Finally, we review the history of beaver management actions on cold-water streams in the WGL region, and present recommendations for resource managers to use when designing management strategies aimed at addressing current and future beaver-salmonid conflicts.

HISTORY OF SALMONIDS AND BEAVER IN THE WESTERN GREAT LAKES REGION

Salmonid history

Agricultural and logging practices in the late 19th and early 20th centuries had a substantial impact on stream habitats in the WGL region. Vast tracts of old growth forest within the WGL region were clear-cut during this period, causing hydrologic and geomorphologic changes to streams (Fitzpatrick and Knox 2000, Whelan 2004) resulting from increased sediment loading, and stream flow and discharge rates (Verry et al. 1983, Verry 1986). The kinetic energy from log transportation down streams, coupled with large scale de-snagging and blasting operations, also had an enormous impact on streams (Whelan 2004, Zorn et al. 2018), while land conversions during the homesteading era permanently altered the hydrologic and sediment dynamics of nearby stream systems (Fitzpatrick and Knox 2000, Anderson et al. 2006b). Both short- and long-term modifications to the lands surrounding WGL streams likely had a negative impact on historic native salmonid populations and habitats (DuBois and Pratt 1994). Indeed, logging, habitat degradation, and overexploitation are believed to have caused the extirpation of the Arctic grayling (*Thymallus arcticus*) from Michigan streams (Vincent 1962, Westerman 1974).

The first hatchery and stocking programs in the WGL region began in response to the declining native salmonid populations during the end of the 19th century. Atlantic salmon (*Salmo salar*), Chinook salmon, rainbow trout, brown trout, and cutthroat trout (*O. clarki*) were stocked in the WGL region by 1900 (Emery 1985, Whelan 2004). Most of these early introductions failed to produce self-sustaining populations (Emery 1985, Crawford 2001, Whelan 2004); however, successful introductions of brook, brown, and rainbow trouts did occur in portions of the WGL region. The first steelhead (potamodromous rainbow trout) populations were established in areas separate from where they were originally introduced (Westerman 1974), and in the late 19th century brook trout were stocked along Minnesota's Lake Superior coastline, expanding their range into thousands of miles of suitable habitat (Smith and Moyle 1944, Waters 1999). Brown trout have been stocked in Michigan since 1884, where they have since become an important component of inland fisheries due to their ability to survive in warmer and more degraded streams than brook trout (Westerman 1974, Unfer and Pinter 2017).

The decline of lake trout (*Salvelinus namaycush*) fisheries in lakes Michigan and Superior during the mid-20th century led to a second era of salmonid stocking throughout the WGL region. The unintentional introduction of the invasive Sea Lamprey (*Petromyzon marinus*) after construction of the Welland Canal (Smith and Tibbles 1980), coupled with overexploitation of lake trout, led to the collapse of lake trout fisheries by the 1950s (Smith 1968, Lawrie and Rahrer 1973, Wells and McLain 1973). Following the establishment of alewives (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*), resource managers returned to stocking non-native salmonids to restore and diversify commercial fisheries, and control the non-native Alewives and rainbow smelt (Smith 1968, Crawford 2001, Whelan 2004). Chinook salmon, Coho salmon, and rainbow trout were introduced into the WGL region during this era, establishing successful and important sport and commercial fisheries (see: Parsons 1973, Emery 1985, Crawford 2001 for extensive summaries of salmonid introductions into the Great Lakes).

Today, many non-native salmonids continue to be stocked in the WGL region. The Michigan Department of Natural Resources (MDNR) currently stocks Chinook salmon, Coho salmon, and brown trout into Lake Michigan; splake (male brook trout × female lake trout) into lakes Huron and Superior; rainbow trout into lakes Huron, Michigan, and Superior; and brown and rainbow trouts into inland streams (MDNR 2018). Minnesota currently stocks steelhead into Lake Superior, and brown and rainbow trouts into inland streams (Great Lakes Fishery Commission 2018). Finally, the Wisconsin Department of Natural Resources (WDNR) stocks brown trout, rainbow trout, and splake into lakes Michigan and Superior; Chinook and Coho salmons into Lake Michigan; and brown and rainbow trouts into inland streams (J. Mosher 2017, WDNR, personal communication). With the exception of the Lake Superior North shore steelhead population (MNDNR 2016), the effects of beaver activity on non-native adfluvial salmonids remains largely unknown. Most of these species use WGL tributaries for spawning and rearing habitat, and are likely affected by beavers in some capacity.

Managers within the WGL region are particularly concerned about interactions between beavers and native brook trout. There are 2 variations of brook trout (tributary and coaster) that are distinguished by different morphological and life history traits (Burnham-Curtis 2000, D'Amelio 2002, Wilson et al. 2008). Tributary, or ‘resident’, brook trout reside entirely within riverine ecosystems and are generally smaller in size, while coasters are an adfluvial form of brook trout that are larger and mature at a later age than residents (Ridgway 2008, Wilson et al. 2008). Historically abundant throughout Lake Superior and select Lake Huron tributaries, coasters were highly prized among anglers and provided a productive fishery until the population crashed by the early 1900s due to overexploitation and habitat degradation (Huckins et al. 2008, Schreiner et al. 2008). Today, coasters exist in isolated remnant populations along the Lake Superior coastline (Wilson et al. 2008). The Great Lakes Fishery Commission developed a coaster brook trout rehabilitation plan in 2003 designed to aid brook trout proliferation throughout the Lake Superior basin (Newman et al. 2003, Schreiner 2008). The main objective of the plan is to establish wide-spread populations of brook trout that can successfully co-exist with naturalized, non-native salmonids (Newman et al. 2003). In addition to stocking programs and managing human exploitation, the plan also identifies controlling beaver activity as a potential method for improving and maintaining spawning and rearing habitat (Newman et al. 2003). Following release of the rehabilitation plan and a related conference synthesizing coaster brook trout research in 2003 (Coaster Brook Trout Initiative), research on Lake Superior brook trout populations has increased substantially (e.g., Ridgway 2008, Huckins et al. 2008, Wilson et al. 2008, Dumke et al. 2010).

Brown and resident brook trouts are the most common salmonids within WGL streams, and inland management of these salmonid species has largely focused on improving stream habitat and riparian land-use practices following the logging era. Stream improvement methods included using riprap for erosion control, wood and rock deflectors, log dams, tree plantings, stream bank debrushing, and waterfall modifications (Hunt 1988, Avery 2004, Goldsworthy et al. 2016). Inland management programs have generally been conducted at the local or watershed scale, though Michigan (Zorn et al. 2018) and Wisconsin are currently developing state-wide inland salmonid management plans to guide salmonid management over the coming years. Though beaver management has often been a peripheral part of management plans aimed at improving stream habitats and increasing salmonid populations, some resource managers in the WGL region beaver management is believed to be the most cost-effective salmonid habitat improvement method (Avery 2004, Willging 2017).

Beaver history

Before the fur trade reached the WGL region (approx. 1650), Native Americans harvested beavers as a secondary source of food and clothing (Schorger 1965). Following European contact, beaver pelts quickly became the most important trade good for Native Americans in the region, particularly as beaver numbers declined in the eastern U.S. The fur trade began in the WGL region towards the end of the 17th century and continued through the middle of the 19th century until beaver numbers diminished as a result of extensive exploitation (see: Ross 1938, Longley and Moyle 1963, Schorger 1965 for summaries of the fur trade within the WGL region).

Harvest by Native Americans during the pre-settlement era was likely far less than harvests during the fur trade era, when the Hudson Bay Company sold nearly 500,000 pelts annually in Europe (Obbard et al. 1987, Müller-Schwarze 2011). Many of these pelts came from Canada, but the WGL region quickly earned a reputation for producing some of the highest quality pelts available (Schorger 1965). Native Americans conducted most of the beaver trapping in the region, trading pelts with English and French colonists. Accurate estimates of pre-settlement beaver abundance are lacking (one estimate that includes Ontario puts the population at 2 million beaver; Alcoze 1981), but pelt records from the WGL region indicate that beaver populations were robust.

As the fur trade declined, settlers in the WGL region continued unregulated trapping of beavers, further reducing beaver abundance in the region (Knudsen 1963) and subsequently leading to periods of closed or partially closed trapping seasons. Wisconsin was the first state to enact partially closed trapping seasons from 1865–1879, beaver trapping was allowed only from November 1–May 1. Several full-season closures followed over the next several decades: 1893–1898, 1903–1916, and 1924–1933 (Knudsen 1963). Beaver management in Minnesota followed a similar trajectory, with the first law restricting harvest occurring in 1875 (Longley and Moyle 1963). However, unrestricted harvest limits during the open season led to further population declines, until the state completely prohibited the take of beavers at any time of year in 1909 (Longley and Moyle 1963). Beavers were not harvested again until 1919 when trappers were issued a license to remove nuisance beavers (Longley and Moyle 1963). Michigan did not have its first closed beaver season until 1920, and it remained closed until the beaver population had increased dramatically during the 1920s (Bradt 1935b).

During this period of closed harvest seasons, wildlife managers across the WGL region also conducted a number of relocation and reintroduction efforts to assist beaver propagation. It was common for landowners to request the release of beavers on their property, which were often nuisance animals that needed to be removed from other locations (Bradt 1935b). One noteworthy reintroduction effort occurred in Itasca State Park, MN in 1901 when 3 beavers arrived in Minnesota from Canada and were subsequently released into the park (Longley and Moyle 1963). Over the next two decades local managers monitored the beavers' progress, and by 1921 it was estimated that nearly 1000 beavers resided in the park (Longley and Moyle 1963). This event has reached folklore status in Minnesota, in part, because it demonstrates the rapidity at which beavers can reproduce and colonize new areas. As a result of the restricted trapping seasons and conservation efforts from game managers, beaver populations began to irrupt throughout the WGL region.

The rapid colonization and growth of beavers in the WGL region was likely further influenced by ecological factors that promoted beaver expansion. The timber harvest practices that severely degraded streams in the WGL region also altered forest composition across the region, including general shifts in forest structure from communities dominated by conifers to communities dominated by deciduous trees (White and Mladenoff 1994, Schulte et al. 2007). In Michigan and Wisconsin, selective logging of white pine (*Pinus strobus*), hemlock (*Tsuga canadensis*), and old growth hardwoods, followed by periods of intense slash fires, converted large tracts of forest to sugar maple (*Acer saccharum*), aspen (*Populus grandidentata* and *P. tremuloides*), and oak (*Quercas* spp.) (Whitney 1987, White and Mladenoff 1994). As a result of logging and fire suppression management practices, Minnesota forests that had been adapted to periodic fire regimes underwent composition changes that resulted in forests dominated by aspen, spruce (*Picea* spp.), and balsam fir (*Abies balsamea*) (Friedman and Reich 2005). Aspen in particular has repeatedly been shown to be a preferred food item for beavers (e.g., Aldous 1938, Stegeman 1954, Hall 1960), and the dramatic increase in the distribution and abundance of aspen is thought to have played a substantial role in the rapid beaver population recovery (Knudsen 1963, Longley and Moyle 1963, WDNR 2015).

The reduction of natural predators in the WGL region also likely contributed to beaver population recovery. In the early 20th century, state and federal bounties for wolves (*Canis lupus*) led to significant wolf population declines across the region (Boitani 2003). Considering beavers have been shown to be an important food source for wolves (Mech 1970, Gable et al. 2016, 2018), even accounting for up to 50% of seasonal wolf diets (Voigt et al. 1976, Gable et al. 2017), suppressed wolf populations could have allowed for beaver population expansion at an even faster rate (Hartman 1994). Black bears (*Ursus americanus*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), Canada lynx (*L. canadensis*), and mountain lions (*Felis concolor*) also occasionally prey on beavers (Baker and Hill 2003), and reduced populations of these other predators through the 1970s may also have contributed to the rapid beaver expansion.

REVIEW OF BEAVER INFLUENCE ON STREAMS AND SALMONIDS IN THE WESTERN GREAT LAKES REGION

Methods

We reviewed the effects of beaver activity on salmonid population ecology, growth rates, and habitat quality in the WGL region. We performed literature searches using ‘Google Scholar’ and ‘Web of Science’; keyword searches included ‘beaver and trout’, ‘beaver and salmonids’, ‘Michigan beaver and trout’, ‘Minnesota beaver and trout’, ‘Wisconsin beaver and trout'. Additional relevant articles were obtained from bibliographies of acquired articles with emphasis on study site location, fish species, and beaver activity. Our review was limited to studies that have been published in peer-reviewed journals, theses and dissertations, and reports from state agencies that have been published or made publicly available. We acknowledge that state, federal, and tribal agencies from the WGL region likely have unpublished data pertaining to beaver-salmonid interactions. However, we have based this review only on data and reports that are readily available to the public.

We reviewed 21 studies evaluating beaver-salmonid interactions in Michigan, Minnesota, and Wisconsin (Table 1.1), which spanned 1935–2012, the most recent year that a beaver-salmonid study has been published. Some published reports from the WGL region contain duplicate data (e.g., Avery 1992 and Avery 2002; and Hale and Jarvenpa 1950 and Hale 1966), so we selected only one of these reports for representation in Table 1.1. Each study was evaluated to determine if the conclusions were based on empirical data or were anecdotal in nature. From each article, statements pertaining to the effect of beaver on salmonids were evaluated as positive, negative, or no effect. Since relatively little research has been conducted in the WGL region, in each section we first present the main effects that beaver activity has on salmonid populations and habitat characteristics from studies across the taxa's ranges. We then review the main results from studies conducted within the WGL region, and identify information gaps where future research could be conducted.

Stream hydrology and geomorphology

Beaver dams generally create lower but more consistent flows in stream systems (Cook 1940, Bruner 1989, Hägglund and Sjöberg 1999), increasing the water-holding capacity of a watershed, elevating the water table, and suppressing peak discharges (Finnegan and Marshall 1997, Bouwes et al. 2016). Beaver dams reduce stream energy and increase retention time by dissipating energy through the dam materials and riparian vegetation (Woo and Waddington 1990, Dunaway et al. 1994), and creating more complex flow pathways (Majerova et al. 2015). Generally, stream velocity is greater and substratum is coarser below beaver dams compared to above dams, potentially benefitting fish that depend on those habitat characteristics (Smith and Mather 2013). Salmonids living in areas with low stream flow or drought can also benefit from beaver dam presence (Cook 1940, Knudsen 1962, Bruner 1989, Hägglund and Sjöberg 1999), as streams with beaver impoundments can retain water longer during dry periods than streams without beaver dams (Parker 1986, Gurnell 1998). Beaver dams can augment low stream flows by recharging alluvial aquifers, and while the amount of water storage behind dams is relatively minor in comparison to the recharged aquifers (Dunne 1978, Lowry 1993), beaver ponds can nonetheless provide refuge for salmonids during low flow periods (provided water temperatures remain within thermal limits).

Most research evaluating how beaver dams influence hydrologic pathways has been conducted in mountainous areas, so the effects of beaver dams on stream hydrology in the WGL region are likely different. In contrast to mountainous areas where salmonid streams are often sourced by snowmelt, WGL salmonid streams are sourced by precipitation and groundwater inputs. Consequently, the distribution and abundance of salmonids in the WGL region are generally determined by reach and watershed characteristics that influence the hydrologic and thermal regimes of stream systems (Lyons 1996, Wehrly et al. 2003). In particular, reach geomorphology, catchment area, and bedrock and quaternary (surficial) geologies can reasonably predict the spatial assemblage of salmonid populations (Wiley et al. 1997, Wang et al. 2003), due to their influence on groundwater flow patterns. Salmonid presence is correlated with hydrologically stable stream systems (Zorn et al. 2002) that are generally comprised of surficial materials with greater hydraulic connectivity, such as glacial outwashes and coarse-textured glacial till landforms (Wiley et al. 1997). However, within the WGL region there is substantial variation in bedrock and surficial geologies (Soller et al. 2009). Glacial erosion and deposition resulted in diverse landforms throughout the WGL region that differ in their ability to hold and transport water (Neff et al. 2005), and this heterogenous composition makes extrapolating results of beaver-salmonid studies from one area to another difficult. How beaver dams may influence lateral and longitudinal flow pathways will likely differ between surficial materials, though this topic remains largely unexplored within the region. Though no discernible patterns of surficial geology were found in the reviewed studies (Table 1.1), it’s likely that patterns may emerge if surficial geology is evaluated alongside local watershed, topographic, and thermal characteristics. Our sample size is not large enough to draw such conclusions, but future research may be able to reexamine this issue.

Beaver ponds increase the spatial heterogeneity and longitudinal complexity between stream reaches by altering the geomorphology of stream systems (Naiman et al. 1988). Salmonid populations are dependent on habitat heterogeneity, with different life stages requiring unique habitat characteristics and a degree of connectivity to fulfill their distinctive life history (Bjornn and Reiser 1991, Schlosser 1991). As such, increased habitat complexity from beaver activity may positively influence salmonid populations by providing a greater selection of places to forage, rest, and avoid high flow events (Bouwes et al. 2016). Since beaver ponds are ephemeral in nature, they may also benefit fish by offering a unique heterogenous habitat component that functions on a spatiotemporal scale (Fausch et al. 2002).

Cold-water streams in the WGL region have been observed to become wider and shallower following repetitive dam construction (Salyer 1935). Following beaver trapping and dam removal in a Pine County, Minnesota stream, the stream channels became deeper and narrower, and the pool-riffle ratio improved (Haugstad 1970). Other observations included the narrowing of stream channels, and an increase in average stream flow velocity and coarse gravel substrate following woody debris and beaver dam removal on Lake Superior tributaries (DuBois and Schram 1993, Dumke et al. 2010). We note that in some systems the narrowing of channels may cause streams to become incised and/or entrenched, and particularly in Western U.S. stream systems beavers are commonly used as a biological restoration tool to reduce channel incision (Burchsted et al. 2010, Pollock et al. 2014). In the Peshtigo River watershed, Wisconsin, an increase in beaver colonies reduced water flow rates in feeder streams (Patterson 1951), while in central Wisconsin, beaver activity may have positively influenced salmonid populations by retaining water within ponds while other stream sections dried up (Knudsen 1962).

Water quality characteristics

Water chemistry —. The effects of beaver activity on water chemistry vary regionally and are dependent upon original conditions (Collen and Gibson 2001), and the impact of beavers on dissolved oxygen (DO) levels is particularly important to salmonids. Beaver activities may decrease DO levels in a stream by increasing water temperatures and reducing stream flow, the latter of which also decreases stream aeration. Although Smith et al. (1991) suggested the influence of beaver dams on DO levels is localized to within impoundments as stream water quickly achieves complete reoxygenation just downstream of the dam. As beaver ponds age and expand, increases in microbial respiration within flooded soils and allochthonous inputs of organic matter also occur (Pollock et al. 1995, Songster-Alpin and Klotz 1995, Bertolo et al. 2008). Some of the organic matter gets deposited as sedimental layers within the impoundments (Johnston and Naiman 1987), further reducing DO levels (commonly referred to as sediment oxygen demand).

Observations from the WGL region have generally found beaver activity negatively affects DO levels (Table 1.1). Prior to beaver dam removal, DO levels were recorded as low as 0.1 mg/L within beaver ponds in one Wisconsin watershed (Avery 2002). However, a reinvestigation of this study concluded there was only a 2 mg/L improvement in DO after beaver dam removal, even with beaver ponds creating localized areas of oxygen depletion (Popelars 2008). In Pine County, Minnesota, Klein and Newman (1992) recorded the lowest DO levels in dammed stream sections, but found DO levels increased into suitable salmonid thresholds after dam removal. Salyer (1935) stated that the organic matter present in beaver ponds throughout Michigan streams reduced DO levels, but that reduction varied from minute to extreme depending on the system.

Beaver impoundments also affect other water chemistry characteristics including pH and dissolved nutrient levels (Smith et al. 1991). Beaver activity alters the distribution and loading of nutrients within riparian ecosystems, where impoundments act as nutrient sinks with greater concentrations of dissolved organic material relative to other stream sections (Naiman et al. 1986, Johnston and Naiman 1987, Naiman et al. 1994). In particular, beaver impoundments sequester large amounts of dissolved carbon, phosphorous, and nitrogen (Dillon et al. 1991, Naiman et al. 1994, Johnston 2012, 2014), which may benefit salmonids in nutrient-poor ecosystems. However, a recent meta-analysis suggests that phosphorous retention generally occurs only in older ponds (Ecke et al. 2017). An early study from the Michigan Upper Peninsula (UP) found beaver ponds to be more acidic than other stream reaches (Salyer 1935), yet recent research indicates that beaver wetlands actually increase the acid-neutralizing capacity of streams by retaining acidic inputs within sediment layers (Smith et al. 1991, Cirmo and Driscoll 1993, Margolis et al. 2001, Błędzki et al. 2010). This may benefit salmonids in stream systems with high acid deposition, but this has not yet been examined.

Water temperature —. Stream temperature is often the most important limiting factor for suitable salmonid habitat in the WGL region, and beaver activity can influence stream temperatures in several different ways. Beaver activities can indirectly increase water temperatures by impounding streams and reducing canopy cover, leading to increased rates of solar radiation (Evans 1948, Patterson 1951, Christenson et al. 1961, Hale 1966). Beaver ponds can maintain water temperatures independent of air temperature changes (Weber et al. 2017), as impoundments can force water around and beneath beaver dams, cooling it as it seeps through the ground and back into the stream (White 1990, Westbrook et al. 2006, Müller-Schwarze 2011). Temperature stratification can also occur in deep ponds, potentially providing salmonid species with thermal refugia during warmer months (Gard 1961, Benson 2002, Bouwes et al. 2016). The effects of beaver dams on water temperature may differ with beaver pond age and size (Cook 1940, Call 1970), as newer ponds generally have greater percolation through the dam relative to older ponds, reducing water retention time (Call 1970).

Observations on stream temperature were the most commonly cited effects from within the WGL region, with most studies reporting negative effects from beaver activity (Table 1.1). Stream temperatures in the Peshtigo River watershed in Wisconsin were elevated due to reduced streamside cover from beaver activity (Patterson 1951), and similar observations were made in the Knife River, Minnesota (Smith and Moyle 1944). In the same study, summer water temperatures were significantly cooler following beaver dam removal (Smith and Moyle 1944), and more recently, water temperatures below beaver dam outlets in the Knife River watershed were within the stressful and/or lethal threshold limits of brook trout more than 50% of the time (Peterson 2012). Water temperatures in the Pemonee River watershed, Wisconsin were cooler following beaver dam removal, and remained cooler even 18 years after the initial dam removal efforts (Avery 2002). However, beaver activity had no significant influence on stream temperatures within several study systems in the WGL region (Adams 1949, 1954, Shetter and Whalls 1955, Hale 1966, Klein and Newman 1992, DuBois and Schram 1993, Dumke et al. 2010). Additionally, Hale (1966) believed salmonids used beaver ponds as thermal refuge in a Lake Superior tributary in Minnesota, while McRae and Edwards (1994) found beaver dams reduced the magnitude of thermal diel fluctuations within their study area. McRae and Edwards (1994) also examined the influence of beaver dam density and beaver pond size on stream temperatures, concluding that temperature was not influenced by either factor. We note their study area (Peshtigo River watershed) has ample groundwater inputs throughout the stream system, which may partially explain the observed stable thermal regimes.

The effects of beaver activity on water temperature have received more attention and research in the WGL region than other aspects of the beaver-salmonid relationship. However, we believe some of the recorded effects on water temperature may be misleading as they were often recorded at locations where water temperatures are likely higher than the average stream temperature (e.g., surface water temperatures, or at the immediate outlet of beaver dams). Recording temperatures at the bottom of beaver ponds and/or from a moderate distance (>50 m) downstream of dams could obtain a more accurate representation of how beavers influence thermal regimes.

The spatial assemblage of salmonids within the WGL region are closely tied to the thermal regimes of stream systems (Lyons 1996, Wehrly et al. 2003). As cold-water species, salmonids' persistence within streams is reliant on just that—*cold water*. That beaver dam presence increases stream temperatures within the WGL region appears conclusive (Table 1.1); yet, whether this increase in temperature has a deleterious impact on salmonids is dependent on whether the resultant water temperature exceeds salmonid temperature limits, or if thermal refugia are not readily accessible. If the resultant water temperature remains within salmonid thermal tolerance limits, then beaver dam presence should not be considered to negatively affect stream temperatures. There is a tendency to conclude that any increase in temperature is a negative attribute; however, this is only true when the increased temperature has a negative effect on salmonid fitness. Many streams within the WGL region that contain salmonids have natural temperature regimes that approach salmonid thermal limits, and beaver presence within these stream systems is more likely to raise stream temperatures above salmonid thermal limits. Understanding the natural thermal regimes of streams is important to recognize whether beaver dam presence will ultimately stress and/or lead to salmonid mortality, and whether these patterns will change under varying environmental conditions.

Influence on spawning attributes

Spawning habitat—. Salmonid reproductive success and population persistence is dependent on the ability of individuals to reach spawning grounds and dig redds in habitat suitable for egg survival (Beechie et al. 2008). Habitat variables that affect site selection by salmonids include gravel size, water velocity, depth, and temperature (Essington et al. 1998, Armstrong et al. 2003, Beechie et al. 2008). Salmonid eggs require free-flowing cold water in order to provide enough oxygen to the developing embryos (Chapman 1988), and many salmonid species (e.g., brook trout and Chinook salmon) exhibit a preference for spawning sites within the hyporheic zone where groundwater upwellings and surface water flow pathways interact (Curry and Noakes 1995, Geist and Dauble 1998). Salmonids generally dig redds in reaches with coarse-textured gravel substrates, and the distribution of suitable habitat may limit salmonid populations within stream systems (Kondolf and Wolman 1993). Limited spawning habitat availability may lead to redd superimposition (Curry and Noakes 1995), although some salmonid species (e.g., brown trout) also display a behavioral preference to spawn on existing redd sites even in low redd densities (Essington et al. 1998). Redds that are dug too deep into substrates can reduce egg hatching success due to the effects on temperature and diminished access to free-flowing water (Crisp 1996, Sternecker et al. 2012). Additionally, the deposition of fine sediments may reduce egg survival and emergence (Chapman 1988), but this may be offset if stream flows are high enough to prevent sediment buildup (Payne and Lapointe 1997, Armstrong et al. 2003).

Beaver activities can affect salmonid spawning habitats by altering sediment dynamics within stream systems. Organic materials are deposited as layers of fine sediment within beaver impoundments (Johnston and Naiman 1987), which can ultimately affect salmonid populations when the fine sediments bury gravel substrates (Alexander and

Hansen 1986, Waters 1995, Lisle 2010). Based on a sample of 353 active beaver ponds located throughout Wisconsin, layers of mineral and organic matter were present in 100% of bottom sediments, with all samples revealing silt layers ranging from approximately 1 to 5 cm in depth (Christenson et al. 1961, Knudsen 1962). Patterson (1951) suggested that brook trout were unable to spawn due to siltation and blocked migration caused by beaver dams in Wisconsin streams, and Salyer (1935) observed that silt was deposited over salmonid eggs in Michigan streams. Scarcity of age-0 brook trout upstream of dams and decreased viability of eggs located directly downstream were observed in a Minnesota stream (Hale 1966). Beaver dam removal was also observed to reduce sand bed loading and expose gravel substrates, improving access to salmonid spawning sites (Haugstad 1970, DuBois and Schram 1993, Dumke et al. 2010). Contrarily, the retention of siltation behind an impoundment may lead to a greater prevalence of gravel substrate downstream (Levine and Meyer 2014), potentially improving salmonid spawning habitat (Grasse 1951).

Movement barrier—. Beaver dams can limit salmonids' access to suitable spawning habitat by impeding movements within stream reaches. Limitation of these movements may lead to a decline or extirpation of salmonid populations in streams or stream segments (Bylak et al. 2014), and the degree to which beaver dams impede salmonid movement can often be influenced by stream flow conditions (Schlosser 1995a, Snodgrass and Meffe 1998). Salmonids that spawn during higher stream flows in spring (e.g., rainbow trout) may find dams passable, while other species that spawn during lower average stream flows (e.g., brook trout) may be unable to bypass dams and potentially force them to spawn in less suitable habitat (Grasse and Putnam 1955). Shallow plunge pools can hinder brook trout's ability to jump (Kondratieff and Myrick 2006), which may further restrict the fish's ability to pass beaver dams during low flow conditions. Brook trout passed dams more frequently than brown trout in Utah during periods of high stream flow by taking advantage of side channels and increased stream flow over and through dams (Lokteff et al. 2013).

Beaver dams were frequently reported to impede salmonid migration in published studies within the WGL region (Table 1.1). However, only two of the studies used tagged fish to evaluate how beaver dams affected salmonid movements. Salyer (1935) found salmonids could readily pass dams downstream, but not upstream, where better spawning habitats were generally located; and Avery (2002) noted an increase in the spatial distribution of brook trout following beaver dam removal, suggesting that the dams impeded movement into some reaches. Other studies from the WGL region speculated or used anecdotal evidence to conclude beaver dams impede salmonid migration (Table 1.1). Because most of the published research from the WGL region on this topic is speculative, it is possible salmonids are actually able to bypass some beaver dams. Logically the presence of dams hinders salmonid movements greater than if the dams were not present; but that does not necessarily mean fish are *unable* to bypass the dams and thereby limit up/downstream migration. Ultimately, more research is needed to determine which salmonid species are better able to navigate dams; the characteristics of dams (e.g., height, permeability) that are more likely to restrict salmonid movements; the stream flow conditions that often restrict salmonid movements; and finally, whether restricted movements will have an appreciable impact on salmonid populations. From a population perspective, if beaver dams restrict passage under certain scenarios the detrimental effects may be exacerbated if the dams limit access to the often-limited spawning habitat sites during the spawning season(s). Using telemetry studies to monitor fine-scale salmonid movements could provide a greater understanding into the ability salmonids have to bypass beaver dams (e.g., Lokteff et al. 2013).

Individual growth rates

Beaver dam presence tends to positively affect salmonid growth rates (Cook 1940, Patterson 1951, Shetter and Whalls 1955, Rosell and Parker 1996, McCaffery 2009). During low-flow summer months, juvenile brook trout adopt a habitat-use strategy that reduces energetic demands by seeking out deep, low-velocity pools (Sotiropoulos et al. 2006), which likely includes utilizing beaver impoundments. Beaver activity can also lead to increased invertebrate productivity. Aquatic invertebrates are a primary food source for several age classes of stream-dwelling salmonids, and invertebrate populations readily respond to changes in stream systems induced by beaver activities (McDowell and Naiman 1986). As a section of stream changes from lotic to lentic, invertebrate composition generally shifts from filter-feeding insects to collector-gatherers (Sprules 1941, McDowell and Naiman 1986). Beaver ponds may have a lower species diversity of invertebrates, but generally have a higher total biomass and density of aquatic organisms relative to other stream reaches (Rupp 1955, Gard 1961, McDowell and Naiman 1986). However, stream sedimentation can decrease the abundance of invertebrate orders

Ephemeroptera, Plecoptera, and Trichoptera which are important food sources for all salmonid life stages, potentially limiting growth rates (Hale 1966, McMahon 1983, Waters 1995). Increased sedimentation may also cause an increase in burrowing invertebrates, thereby reducing the amount of vulnerable prey available to salmonids and impairing growth (Suttle et al. 2004). The interplay of sedimentation, invertebrate community shifts, and salmonid growth rates is complex and warrants additional research, as most of the information regarding how beavers influence these dynamics remains speculative.

Salmonids tend to be larger within beaver impoundments relative to other stream sections (Hägglund and Sjöberg 1999, Bylak et al. 2014), and results from published studies in the WGL region generally support this conclusion (Table 1.1). In a Lake Superior tributary in Minnesota, the largest brook trout were found within beaver ponds, with growth attributed to higher populations of minnows (Hale 1966). Higher water temperatures associated with beaver ponds may also contribute to increased salmonid growth (Rosell and Parker 1996), though considering many salmonid streams within the WGL region are already near the upper thermal limits of salmonids during summer months (see *Water quality* section), this increase in temperature may be deleterious. Avery (2002) found the average size of age-1 brook trout to be larger after removing beaver dams from a watershed in northeastern Wisconsin, attributing the increase in growth rate to decreased water temperatures, increased gravel exposure, and increased aquatic invertebrate biomass. The summer after a beaver dam collapsed in a Lake Superior tributary in Minnesota, Hale (1966) observed invertebrate species composition more closely resembled communities found in streams rather than beaver ponds. These results suggest invertebrate composition can respond quickly to changes in stream habitat, and corroborates the findings from Avery's (2002) study.

The observation of larger fish within beaver ponds does not necessarily reflect a faster growth rate, but is perhaps a function of how beaver dams influence the distribution of different salmonid age classes. Indeed, beaver dams have been shown to influence the spatial distribution of fish (see next section), so creel data alone cannot definitively indicate that beaver ponds positively influence salmonid growth rates. Future research from the WGL region could use a paired study design to compare salmonid growth rates in streams with and without beaver ponds to determine the influence that beaver ponds exert on growth rates.

Population dynamics

In general, beaver ponds influence the spatial and temporal distribution of fish species and age classes within stream systems by increasing the heterogeneity of habitat features (Schlosser 1995a, Snodgrass and Meffe 1998, Schlosser 1998, Snodgrass and Meffe 1999, Schlosser and Kallemeyn 2000, Mitchell and Cunjak 2007). Research from Minnesota has shown that beaver ponds can influence the spatial assemblage of fish, where fish abundance was higher in upland ponds and species richness was greater in streams and collapsed ponds (i.e., ponds with degraded dams that are not actively retaining water) (Schlosser and Kallemeyn 2000). Further, species richness and species composition can vary within and among beaver ponds over time (Snodgrass and Meffe

1998), but currently no study that has evaluated fish assemblages within beaver ponds has included a salmonid component. In addition to providing refuge for salmonids during summer months and periods of low flow, salmonids may benefit from overwintering habitat provided by large pools above beaver dams (Cunjak 1996, Virbickas et al. 2015). Many streams within the WGL region freeze during winter so beaver ponds may provide invaluable refuge for salmonids, but this has not been empirically tested to date. Conversely, extended ice cover on beaver ponds could also contribute to winter fish kills if conditions within the ponds become hypoxic (Keast and Fox 1990, Fox and Keast 1990).

Beaver ponds can also affect fish population dynamics by creating population source-sink relationships within stream systems (Schlosser 1995a, 1995b). Beaver ponds can offer greater rearing habitat availability within streams (Leidholt-Bruner et al. 1992), and the lateral habitats along the shallow, littoral edges of beaver ponds may be critical for the survival of juvenile fish (Moore and Gregory 1988, Schlosser 1991, 1995b). Beaver ponds can thereby act as key source areas for fish species (Fausch et al. 2002), depending on the spatial variation of pond morphology and the permeability of pond boundaries within stream systems (Schlosser 1995a, 1998). For brook trout, beaver ponds serve as potential source areas due to abundant benthic fauna that can be exploited (Gard 1961). Johnson et al. (1992) found beaver ponds with habitat factors that promote high brook trout densities actually led to localized populations of small, stunted brook trout, suggesting brook trout growth rates are density dependent. Source-sink dynamics of fish populations are complex, and all studies that have found source-sink population dynamics within beaver ponds did not include salmonids in their evaluation. Yet, given that beaver dams increase the complexity and heterogeneity of stream systems, it seems probable that source-sink dynamics of salmonid populations could develop within beaver pond complexes where fish could have access to a variety of habitats across suitable spatial and temporal scales.

Beaver activities can alter biotic interactions between salmonids and other species that may affect predation risk. Beaver ponds provide habitat for a variety of bird and mammal predators, including great blue herons (*Ardea herodias*), osprey (*Pandion haliaetus*), mergansers (*Mergus* spp.), northern river otters (*Lontra canadensis*), American mink (*Neovison vison*), and northern raccoons (*Procyon lotor*) (Windels 2017). Because salmonids can become concentrated in beaver ponds, they may face increased predation pressure as a result (Salyer 1935, Needham 1938), though this has not been tested to date. In Wisconsin, reduced salmonid catch rates were noted following an increase in piscivorous fish populations, including Northern Pike (*Esox lucius*), likely due to the shallow, grassy habitat and higher water temperatures within beaver ponds (Knudsen 1962). Conversely, the increased habitat heterogeneity from dam creation may provide refuge from predators for various life stages (Snodgrass and Meffe 1998).

Beaver activity has also been suggested to increase the prevalence of disease and parasites in salmonids (Knudsen 1962). Greater siltation and water temperatures can induce stress in salmonids, thereby increasing their susceptibility to disease (Grasse 1951, Wood and Armitage 1997, Gordon et al. 2004). Observations in Michigan streams showed increased prevalence of trematodes associated with black spot disease (Miller 1940), and parasitic nematodes in salmonids inhabiting beaver ponds (Salyer 1935). The prevalence of gill lice (*Salmincola edwardsii*), a parasite that is often found in beaver impoundments, has reportedly increased recently in several Wisconsin streams (WDNR 2015). More research is needed to understand whether beaver ponds are responsible for facilitating parasite proliferation within these stream systems.

Salmonid population densities in the WGL region have been shown to increase following beaver dam construction (Salyer 1935, Bradt 1935b, Hale and Jarvenpa 1950, Patterson 1951, Knudsen 1962). Similar to growth rates, angler catch rates from within beaver ponds tend to be greater than other stream sections (Table 1.1), which could lead to misconceptions of larger salmonid population sizes than are actually present within the streams. In several Lake Superior tributaries in Minnesota, greater brook trout densities were actually found in streams with less beaver activity (Hale 1966), and in Pine County, Minnesota streams, the removal of beaver dams resulted in improvements in brook trout catch rates (Haugstad 1970). In a long-term Wisconsin study, the distribution and abundance of brook trout was substantially improved 4 and 18 years after beaver dam removal (Avery 2002); however, another Wisconsin study found that beaver dam removal had little impact on brook trout population density, while the density of younger brown and steelhead trouts increased (DuBois and Schram 1993). Patterson (1951) found decreases in populations of brook and brown trouts several years after beaver occupation of stream reaches, but the declines were likely influenced by intense angling pressure that occurred following the aggregation of fish within the ponds.

While beaver dam removal projects can provide insight into salmonid population responses, few studies have used a paired study design to objectively compare population responses. Moreover, because population responses may take several years to emerge (e.g., Avery 2002), accurate evaluations of how beavers influence salmonid populations likely requires a long-term monitoring plan that is often logistically challenging to implement. Future evaluations of how beaver dams influence salmonid population dynamics should include both a paired study design and a long-term monitoring plan in order to adequately evaluate population responses that may have a temporal delay.

Conclusions from beaver-salmonid review

Our review found surprisingly little empirical data evaluating beaver-salmonid interactions in the WGL region, limiting what conclusions we can draw from existing information on the subject. The majority of the studies occurred before 1970, and many studies relied heavily on anecdotal observations for their conclusions (Table 1.1). Few studies employed any statistical analysis, and only four studies were published in peer-reviewed journals. Species descriptions were often left as "trout" which further obscures the generalizability of results. Nonetheless, the studies we reviewed are often used as justification for implementing beaver management programs (e.g., WDNR 2015) despite an absence of experimental controls or systematic sampling methodologies. Additionally, the majority of the WGL region studies reviewed were conducted in clustered locations within the WGL region (Figure 1.1). To date, no beaver-salmonid studies from Michigan, Minnesota, or Wisconsin have occurred outside of the Laurentian Mixed Forest Province, though we believe that most state agencies have a large amount of unpublished data pertaining to beaver-salmonid interactions. Considering the sparse information that is currently available to the public, we believe the dissemination of this data could provide valuable insight into how beavers affect salmonids within the region. However, state agencies are often limited in their capacity to conduct and/or publish studies as a result of funding and staff shortages, likely contributing to the lack of publicly available data from the WGL region.

Despite the variability of results found within the WGL region, some patterns did emerge from the studies evaluated. Beaver activity tended to benefit salmonids during the first 2–4 years following dam construction. Salmonids likely take advantage of the pools and increased habitat heterogeneity that newly created impoundments offer them by using these features for refugia and food sources. Yet over time, the accumulation of sediment and alterations to water quality characteristics and discharge regimes often has a deleterious effect on local salmonid populations. Additionally, beaver activity was more often deleterious in low-gradient stream systems (i.e., slopes < 2%; Rosgen 1994). The few studies evaluating the impact of beaver in relatively high-gradient systems (Salyer 1935, Evans 1948, Hale and Jarvenpa 1950, Hale 1966) reported positive effects more often than other studies. Beaver dams fail more frequently in high-gradient stream reaches (Gurnell 1998), and thus ponds upstream of dams tend to be younger on average than those in low-gradient reaches. Ponds in high-gradient systems may fail before they are able to degrade and become unsuitable habitat for trout. Nonetheless, this general pattern has inconsistencies, as Hale (1966) reported that beaver dams often persisted beyond 4 years in his study area with high-gradient streams, and resulted in ponds that were poor brook trout habitat.

REVIEW OF BEAVER MANAGEMENT ON SALMONID STREAMS IN THE WESTERN GREAT LAKES REGION

Rise of beaver-salmonid conflicts

Despite extensive poaching that occurred during closed trapping seasons in the 1920s, by 1930 beavers had expanded their range to every major salmonid stream in Michigan (Bradt 1935a, Salyer 1935). In response, the Michigan state legislature ordered the first beaver-salmonid study in 1933 (Bradt 1935a). This first report (Salyer 1935) was an extensive combination of field-based observations and experimental manipulations, and relied heavily on input from local fish and game chapters that were noticeably divided about the “beaver problem”. Though results from experimental stream sections indicated that beaver activity tended to be deleterious for salmonid populations (Table 1.1), Salyer (1935) acknowledged that beaver could become an aid for salmonid streams if managed correctly, particularly in the high-gradient tributaries of Lake Superior. Salyer also suggested that a balance between the three desirable natural resources (beaver, salmonids, forest) was needed (Figure 1.2); however, he does not elaborate on this point, and concluded his report by noting that beavers should not occupy cold-water streams without active control.

In response to Salyer's (1935) report, the Civilian Conservation Corps removed more than 5,000 beaver dams from Michigan cold-water streams over a 2-year period (Bradt 1947). This action was coupled with extensive trapping efforts and resulted in a precipitous decline in the Michigan beaver population. It should be noted that following the extensive dam removal project, Michigan anglers noticed fishing success actually declined in UP salmonid streams (Carbine 1944), suggesting the project overshot its management goals. Indeed, though Carbine (1944) advocated for beaver control in the UP and believed Salyer (1935) incorrectly asserted that beaver presence was good for salmonids in Lake Superior tributaries, he wrote: "There is no denying that it was a sad day when that program was started (p. 29)." Wildlife management was still in its infancy in the 1930s, and though Salyer's recommendations were aggressive and ultimately resulted in poorer fishing conditions, they were also emblematic of the growing emphasis placed on scientific research and experimental manipulation that characterized his era of resource managers. Salyer recognized that effectively managing for beaver, salmonids, and timber resources was a complex and polarizing issue that required extensive research into understanding the intricacies of the beaver-salmonid relationship. His investigation laid the foundation for WGL region beaver-salmonid research, prompting managers in Minnesota and Wisconsin to begin similar investigations into beaver-salmonid interactions in their states.

Controversy regarding beaver-salmonid management reached Wisconsin by the mid-1930s and was the catalyst for the first beaver dam removal efforts in Wisconsin (Hunt 1988), when 740 beaver dams were removed from northern streams (Christenson et al.

1961). Despite harvesting nearly 50,000 beavers from 1934–1944, the beaver population continued to increase in the late 1940s (Christenson et al. 1961, Knudsen 1963). In 1949, the Wisconsin Conservation Department issued an official statement acknowledging the increasing problem that beavers posed to fish and timber management (Christenson et al. 1961), prompting a decade-long investigation to determine the best possible multiple-use management plan for beaver, salmonid, and forest resources (Knudsen 1962). Wisconsin Conservation Department trappers also live-trapped and relocated 2,200 nuisance beavers from 1951–1957 as part of the state-wide beaver management plan (Knudsen and Hale 1965). Knudsen (1962) concluded that while beavers provide greater value to Wisconsin communities than previously assumed, salmonid and timber resources must be prioritized over beaver in some areas, particularly on slow-moving, low-gradient streams where beaver activity was detrimental to salmonid habitat. Management recommendations included adopting specialized harvest sites to reduce beaver impacts on salmonid streams and timber resources, but beaver populations should otherwise be maximized due to the economic and aesthetic values associated with beaver presence (Knudsen 1962). The management recommendations are emblematic of an increased focus on using adaptive management strategies that were more responsive to competing beaver, salmonid, and forest resources occupying the same area (Figure 1.2).

In Minnesota, three studies (Smith and Moyle 1944, Hale 1950, 1966) were conducted along the north shore of Lake Superior to evaluate what impact beaver impoundments were having on salmonid streams. While most of Minnesota had open trapping seasons starting in 1939, the north shore had closed or partially closed trapping seasons nearly every year into the 1960s (Hale 1966). Due to increased beaver activities in the region, higher stream temperatures were attributed to a lack of shade produced by beaver meadows (Smith and Moyle 1944). This led to a proposed management program for the Knife River in the 1940s, which included beaver and dam removal, and stream habitat improvement projects (Smith and Moyle 1944). Most of the north shore streams are relatively high-gradient, and results from Hale's (1950, 1966) studies found beaver presence to have some benefits for brook trout. Hale (1966) concluded that a low beaver population was preferable for the north shore watershed, but did not recommend any particular management objectives.

Progression of adaptive management strategies

As beaver management progressed throughout the WGL region, resource managers began to use adaptive management recommendations that came out of early investigations. In the early years of beaver management, it was clear that some strategies had detrimental effects on beaver, salmonids, or both. Long-term studies like Knudsen (1962) led to a new era of resource management that used an adaptive approach towards evaluating beaver-salmonid-forest relationships (Figure 1.2).

Salmonid streams in east-central Minnesota tend to be low-gradient, and by the 1960s the beaver population continued to grow (MNDNR, unpublished data; Figure 1.2) and anglers reported poor fishing conditions in reaches occupied by beaver. Following the results from a study which substantiated beaver presence to negatively impact salmonid populations (Haugstad 1970), a habitat improvement project began that centered on beaver dam removal and eradication from the streams. Over a 2-year period, 617 beavers and 482 beaver dams were removed from streams, resulting in 120 km of "fair" to "good" quality salmonid habitat and noticeably larger salmonid populations (Haugstad 1970). In addition to the regular open trapping season, professional and permit trappers assisted in the beaver eradication efforts. Despite some landowners' resistance to the eradication efforts, Haugstad (1970) concluded that a liberal beaver-trapping season should be used throughout counties with prime salmonid streams. Results from a later study within the same basin suggested that beaver activity negatively affected salmonids (Klein and Newman 1992), but the authors' management recommendations reflected a shift towards using a more nuanced approach to beaver-salmonid interactions. Klein and Newman (1992) recommended managers should consider site-specific plans that balance the economic costs and ecological benefits incurred by conducting beaver management.

By the 1970s in Wisconsin, three main beaver control methods were utilized: (1) removal of beavers and structures by Wisconsin Department of Natural Resources (WDNR) personnel; (2) removal of beavers and structures by permitted private citizens; and (3) extension of beaver seasons and regular bag limits on waters with recurring problems (Payne and Peterson 1986). Beaver and human populations continued to rise across the state at this time, along with the number of beaver complaints. An analysis of beaver complaint trends in two northern Wisconsin counties found most complaints involved timber resources and roads, while fish habitat comprised only 4-5% of all complaints (Payne and Peterson 1986). These results were similar to those reported across the state from 1950–59, when fish complaints accounted for 5% of all complaints (Knudsen 1962). It should be noted that beaver removal from salmonid streams was not limited to those originating from complaints filed with the state, as extensive beaver dam removal projects by WDNR personnel were also occurring across Wisconsin.

Hunt (1988) suggested beaver and dam removal was a widespread habitat management strategy used across Wisconsin from 1953–1985, though little data is available until the 1980s. An extensive dam removal effort occurred in Wisconsin's Penomee River watershed, where 546 beaver dams were removed from 1982–1986 (Avery, 1992). In the late 1980s, the WDNR began a partnership with the U.S. Department of Agriculture Animal and Plant Health Inspection Service Animal Damage Control program (APHIS-ADC) to conduct dam removal in salmonid streams (Dickerson 1989), in addition to supplemental trapping of beavers from individual streams (Willging 2017, Ribic et al. 2017). One such beaver management program has occurred in the Chequamegon-Nicolet National Forest (CNNF) since 1988 (Willging 2017). The program targeted the most heavily impacted streams first, and in 1988 alone, 480 beaver and 668 dams were removed from streams in the CNNF (Dickerson 1989). Since then, aerial and ground surveys have been conducted annually to identify beaver presence and inform beaver management priorities to maintain stream systems in free-flowing conditions (Willging 2017). Ribic et al. (2017) recently conducted an analysis on the long-term effects the CNNF beaver program had on beaver colony density through 2013, and results found the control program was successful in reducing beaver colony densities along targeted streams. The success of this management strategy is not entirely surprising, as history has repeatedly shown intense trapping efforts can successfully reduce or eradicate local beaver populations from an area. Nonetheless, the CNNF management program demonstrates the effectiveness of using a targeted approach towards resolving a beaver-salmonid conflict, and is an example of a program that successfully used wildlife management to achieve its habitat restoration goals (Willging 2017).

The Wisconsin beaver and dam removal programs began at a time when the beaver population was approaching its maximum level (Figure 1.2). Low fur prices likely discouraged recreational trapping efforts, causing the beaver population to spike and a resultant increase in the number of beaver complaints to over 2,000 annually (WDNR 1990). At this time, the WDNR also experimented with a trapper subsidy program to assist with population reduction efforts (WDNR 1990). A team was assembled in 1990 to overhaul beaver management strategies, and culminated in the development of the 1990 Wisconsin beaver Management Plan (WDNR 1990). One of the key management objectives to come out of the 1990 Wisconsin beaver Management Plan was the development of 4 distinct beaver management zones, each with slightly different regulations (WDNR 1990). The zones were primarily based on regional beaver densities, frequency and category of beaver complaints, and incorporation of regional waterfowl data, with the intent of designing a program that used a greater adaptive management approach. Regarding salmonid streams, the zones also differed in quantity and quality of streams as determined by the 1980 statewide stream classification project (WDNR, 1980). Large, heavily impacted cold-water streams in the northern management zones were made a management priority, using a combination of APHIS-ADC personnel, WDNR trappers, and locally contracted trappers to conduct targeted beaver and dam removals similar to the CNNF program (WDNR 1990).

Current beaver management on salmonid streams

In 2001, Michigan established their current beaver adaptive management program based on two primary principles: (1) beaver, salmonids, and their habitats are managed for human needs and wants; and (2) the less common natural resource (i.e., cold-water streams) must be provided for, while still providing opportunities for beavers to exist (MDNR 2005). High-quality salmonid streams were identified by state fisheries divisions and approved by designated eco-region teams. Local managers are responsible for responding to and determining nuisance beaver presence on salmonid streams. The management plan also states that a zone of intact vegetation is required around the stream in order to protect water quality, and this zone is managed by local forestry divisions to discourage beaver use. Nuisance control is carried out by a combination of Wildlife, Law Enforcement, Forest Management, and Parks and Recreation Management personnel, depending on the region and type of land (public or private) on which the nuisance beavers are located.

Since the 1970s, the Minnesota DNR (MNDNR) has used beaver management on salmonid streams to maintain connectivity and modify habitat conditions in selected streams (D. Paron 2017, MNDNR, personal communication). For example, the MNDNR has conducted beaver and beaver dam removal in the Knife River watershed since 1994.

The watershed contains approximately half of all accessible adfluvial salmonid spawning and rearing habitat along the north shore of Lake Superior, making it a management priority in the region (MNDNR 2016). Relative to other north shore watersheds, the Knife River is comparatively low-gradient and is one of the only areas where wild steelhead spawn. Beaver control is carried out by contract trappers and MNDNR personnel, and is funded by revenue generated from fishing licenses and trout stamps (MNDNR 2016).

In 2015, the WDNR created a “Beaver Task Force” to develop a new beaver Management Plan to be used through 2025 that is considerably more extensive than other management plans in the WGL region. The northern Wisconsin beaver population has been on a steady decline for the last 2 decades (Figure 1.2), prompting the WDNR to increase research efforts across the state (WDNR 2015). In particular, WDNR managers have adopted an interdisciplinary approach to better inform management practices by understanding the positive and negative effects that beavers have on their ecosystems. The WDNR received input from stakeholders across the state that included trappers, tribal communities, public and private land managers, biologists, and citizens, in order to create a plan that effectively addresses the multiple-use beaver-salmonid-forest management strategy that has existed in the state since the 1960s (WDNR 2015). WDNR personnel plan to increase research throughout multiple ecoregions in the state, including using paired experimental design studies that incorporate reference streams to compare with stream manipulations. At present, APHIS-ADC continues to conduct beaver control on 200 salmonid streams totaling approximately 2400–2700 km (WDNR 2015, Willging 2017).

MANAGEMENT IMPLICATIONS

Salmonid research and management has shifted towards using a landscape ecology perspective to understand how large-scale ecological processes influence the spatiotemporal dynamics of fish populations. The physical and hydrologic properties of landscapes can be applied with reasonable accuracy to describe the nature and quality of riverscapes (see earlier sections), and this perspective has led to significant advances in fish biology and management (Fausch et al. 2002). One of the difficulties with managing beaver-salmonid interactions is that beaver activity can affect salmonid habitat characteristics differently at the stream or even reach scale, and resource managers are faced with reconciling these disparate perspectives of scale when managing beaver-salmonid conflicts. Early beaver management on salmonid streams was often conducted under the assumption that the effects beavers have on salmonids in one area are transferrable to other areas in the region. However, managers have become increasingly cognizant of the spatial variability of the beaver-salmonid relationship, and there has been a greater focus on using small-scale, adaptive management strategies to resolve beaver-salmonid conflicts. Finely calibrated beaver and dam removal efforts may be just as effective as large-scale removal programs (McRae and Edwards 1994, Ribic et al. 2017), and this approach has the added benefit of minimizing the impact on local beaver populations.

There is also a temporal component of the beaver-salmonid relationship that could be taken into account when designing management plans. In our review, we commonly found beaver dams may benefit salmonids in the first 2–4 years following dam creation before negative effects arise. We suggest that in some areas where beaver management occurs on an annual basis, an alternative management strategy could be conducting beaver management more sporadically (e.g., every 3–5 years). This strategy may mitigate the long-term negative effects of beaver activity on salmonid populations while still preserving the short-term benefits, and would also reduce the costs of labor and resources associated with conducting annual beaver management. Because dams generally persist on the landscape much longer in low-gradient streams, this management strategy is probably more applicable to those stream systems. Intensive beaver control may nonetheless be needed in areas where other habitat restoration efforts occur simultaneously, as beaver presence for even a short period of time may nullify the resources invested in restoring stream habitats.

Numerous stakeholders are influenced by beaver-salmonid interactions, and striking a balance between the often-conflicting groups is no easy task (Willging 2017). Within the WGL region, non-profit organizations such as trout Unlimited and local steelhead organizations are heavily involved with salmonid habitat management projects. Trout Unlimited has established successful partnerships with state and federal agencies to assist with salmonid management goals throughout the WGL region, and recently the Lake Superior Steelhead Association was awarded multiple grants to conduct beaver dam removal and habitat rehabilitation within the Knife River watershed along Lake Superior (ML 2014, Ch. 256, Art. 1, Sec. 2, Subd.5(h)). Though non-profit organizations advocating for beaver conservation are relatively uncommon throughout the region, many conservationists are opposed to beaver management programs on salmonid streams.

Indeed, controversy over management strategies has existed in the WGL region since the first beaver-salmonid studies, and continues to this day (WDNR 2015). Considering management decisions influence anglers, trappers, waterfowl hunters, foresters, and conservationists alike, resource managers must often make decisions that are unpopular with one or more of these groups. Where possible, the justification for making unpopular management decisions should be informed by empirically collected data that accurately characterizes the nature of the beaver-salmonid relationship of the stream region(s) in question.

Many salmonid populations in the WGL region are non-native species, which further complicates management priority decisions. The ecological impacts introduced salmonids have on stream ecosystems has not been comprehensively evaluated across the WGL region, but their introduction likely has a significant effect on resource competition with native salmonids (Krueger and May 1991). Brown trout have been shown to exclude brook trout from resting positions in streams and prey on juvenile brook trout in a Michigan stream (Fausch and White 1981), and brown trout replaced brook trout when habitat disturbances occurred in Valley Creek, Minnesota (Waters 1983). Yet, many anglers prefer to fish for non-native salmonids, influencing management decisions in the WGL region. In streams along the north shore of Lake Superior, for example, anglers prefer to fish for non-native steelhead and Kamloops rainbow trouts over native brook trout (Gartner et al. 2002, Schroeder 2013). Per survey results, individual anglers in the north shore report fishing for steelhead for more than 11 years on average (Gartner et al. 2002), indicating that steelhead presence in cold-water streams has a long-term influence on anglers' decision to fish in the watersheds; whether this preference continues in the event that coaster brook trout populations recover remains to be seen. In its current state, angling culture in the WGL region often favors the preservation and even proliferation of non-native salmonid populations despite the potential ecological consequences.

The effects of climate change may also have a substantial impact on salmonids. Many cold-water streams within the WGL region already approach the thermal tolerance for salmonids (Wehrly et al. 2003), and predicted increases in summer air temperatures could raise stream temperatures even further. Salmonids are expected to endure substantial habitat loss in the WGL region under projected climate change models (Sinokrot et al. 1995, Lyons et al. 2010, Herb et al. 2016), and beaver activity may exacerbate this problem in some areas. Contrarily, beaver ponds may offer valuable refugia for salmonids within streams during periods of drought by retaining water longer; and for many wildlife species, beaver wetlands provide essential open water habitat that actually mitigate the negative effects of drought (Hood and Bayley 2008). Beaver populations may also be negatively impacted by a changing climate, which further complicates this relationship. Though little research has been conducted evaluating the impact of climate on beavers, preliminary research from Wisconsin indicates that both wetter years and years with moderate droughts are associated with lower beaver colony densities (Ribic et al. 2017). Similarly, studies on the closely related Eurasian beaver *Castor fiber* suggest that increases in climatic variability and precipitation may negatively affect beaver reproduction and resource availability (Campbell et al. 2012, 2013, 2017). Understanding the complex beaver-salmonid relationship and implementing appropriate management plans may become even more challenging for researchers and managers in a changing climate, and future research should examine how this relationship could evolve.

CONCLUSIONS

Throughout the past century there has been a dramatic shift in beaver management practices that have occurred throughout the WGL region. Following the near extirpation of beavers due to overharvesting and habitat loss, early management was focused on promoting population growth through reintroductions and closed trapping seasons. Beaver populations rebounded within a few decades, and new management goals aimed at population control were established throughout the region. The first beaver control measures on salmonid streams, and in the region in general, tended to overshoot their targets and often led to significant declines in local beaver populations. By incorporating scientific-based research into game and fish management, over time resource managers increasingly used localized, adaptive management strategies to mediate beaver-salmonid interactions.

The Great Lakes region once supported abundant populations of native salmonids, attracting anglers from afar and providing an economic resource to local communities. Due to overexploitation, habitat degradation, and competition with non-native species, native salmonid populations crashed, prompting rehabilitation efforts throughout the WGL region. Despite the varying success of historical salmonid stocking programs, their impact on modern day fisheries and fishery management practices cannot be understated.

Today, habitat degradation and climate change are considered some of the most serious management issues concerning salmonid populations within the WGL region, and many agencies are involved in the continuous monitoring of stream systems and local salmonid populations. The degree to which beaver management is prioritized as a habitat restoration tool varies greatly within the WGL region, ranging from a peripheral component of many management plans to an integral component of others. Nonetheless the beaver-salmonid relationship has received considerable interest from public and scientific communities alike, and has remained a contentious issue within the WGL region since it first arose nearly a century ago. Agencies are currently addressing beaver-salmonid interactions through an ongoing effort to co-manage each species at sustainable population levels, while recognizing the recreational and ecological impact that each species provides.

While most research conducted in the WGL region has shown that beaver activity has a deleterious effect on salmonid populations, we found several examples where beaver activity was found to benefit salmonids (Table 1.1). We have highlighted numerous information gaps throughout this review that could enhance our understanding of the beaver-salmonid relationship, and identified scenarios when salmonids may benefit from beaver presence. All three states in the WGL region have prioritized the habitat requirements of salmonids over the presence of beavers in portions of the state, primarily because cold-water streams are a scarcer resource and angling is a popular source of recreation for citizens. As ecosystem engineers and a keystone species, beavers provide valuable ecological services to forest ecosystems in the WGL region (Johnston 2017), and removing beavers from stream reaches where their presence may actually benefit salmonids results in a lose-lose situation for forest ecosystems and natural resource management goals. We suggest the decision to remove beavers from cold-water streams should consider secondary ecosystem consequences associated with decreased beaver presence before implementing management plans.

Prior to European colonization, beavers and salmonids (native brook trout) were presumably able to coexist on the landscape without human intervention, and interactions between the two taxa were therefore the result of natural ecological processes within WGL stream ecosystems. What is different now from historical conditions? Why do many areas within the WGL region now require beaver control in order to maintain healthy, sustainable salmonid populations? Many resource managers believe that beaver populations are larger now than they have historically been due to the increase in young forest, though this hypothesis has yet to be rigorously tested. It is possible that beaver activities have always had a predominantly negative impact on salmonids (brook trout) in the WGL region, and the natural ecological processes are very similar to what is found in the region today. Anglers may therefore expect larger salmonid populations in WGL streams than are supportable based on natural processes. Identifying the historical conditions that existed prior to European colonization may provide insight into how beaver-salmonid dynamics have deviated over the past three centuries (beyond the introduction of non-native salmonids to WGL streams), and that information could be used to guide current and future resource management plans in cold-water streams. But even with historical context, resource managers will still often be confronted with the ecological and ethical dilemma that many currently face: should WGL cold-water streams be managed for the benefit of maintaining robust, well-dispersed salmonid populations; or be managed to replicate ‘natural’ ecological processes, even to the potential detriment of salmonids? The answer to this question will undoubtedly vary throughout the WGL region, depending on local ecological conditions, and cultural and resource management priorities. We hope our synthesis is a catalyst for further beaver-salmonid research from the WGL region, and encourages scientifically based management plans that identify when and where beaver control is necessary to achieve the desired resource management objectives.

Table 1.1. Summary of the main effects found from 21 beaver-salmonid studies conducted within the WGL region. Average stream gradient was inferred from author's comments, or obtained from stream assessments. Surficial geology was obtained from (Soller et al. 2009). Textured grain size is further identified as coarse (C), fine (F) or medium (M), and 'patchy' indicates that bedrock is exposed. Analysis type was considered "empirical" if quantitative results were presented; "anecdotal" if no quantitative results were presented; or "mixed" if quantitative results were presented for only some of the study's variables. Results from each study were evaluated to determine if beaver activity had a beneficial (↑), no effect (⇆), or deleterious (↓) effect on salmonids. Studies with multiple arrow types in a cell indicate that multiple effects were found in different portions of the study area.

Reference	State	Avg. gradient	Surficial geology	Data type	Stream temp.	Siltation	Migration barrier	Spawning habitat	Stream flow	Water chem. (DO, pH)	Population size	Avg. catch rate	Avg. catch size
DuBois and Schram (1993)	WI	Low	Glacial outwash (C)	Mixed	⇆[a]	↓[a]		↓			↑ / ↓[a]		
Haugstad (1970)	MN	Low	Glacial outwash (C) / glacial till (C)	Anecdotal	↓	↓		↓	↓		↓		
Klein and Newman (1992)	MN	Low	Glacial outwash (C) / glacial till (C)	Empirical	⇆ / ↓	⇆ /↓		↓	↓	↓	↑ /↓		
McRae and Edwards (1994)	WI	Low	Glacial outwash (C) / glacial till (C)	Empirical	↑ / ⇆ /↓								
Patterson (1951)	WI	Low	Glacial outwash (C) / glacial till (C)	Mixed	↓[a]	↓[a]	↓	↓			↑ / ↓[b]		↑ / ↓
Adams (1949)	MI	High	Glacial till (C)	Empirical	⇆ / ↓					⇆ / ↓		↑	
Adams (1954)	MI	High	Glacial till (C)	Empirical	⇆ / ↓		⇆			⇆ / ↓		↑ / ⇆	
Avery (2002)	WI	Low	Glacial till (M)	Empirical	↓			↓	↑ / ↓		↓	↓	↓
Christenson *et al.* (1961)[C]	WI	Mixed	Glacial till (M)	Mixed	⇆[a]	↓[a]	↓	↓	↓	↓	↑[b]		↑[b]

Table 1.1 (continued).

Reference	State	Avg. gradient	Surficial geology	Data type	Stream temp.	Siltation	Migration barrier	Spawning habitat	Stream flow	Water chem. (DO, pH)	Population size	Avg. catch rate	Avg. catch size
Shetter and Whalls (1955)[C]	MI	High	Glacial till (M)	Empirical	⇆				⇆			⇆	
Dumke *et al.* (2010)	WI	Low	Glacial till (F)	Empirical	⇆	↓		↓	↓				
Evans (1948)	MN	High	Glacial till (M), patchy	Mixed	⇆ / ↓[a]		⇆						
Hale (1950)	MN	High	Glacial till (M), patchy	Empirical								↑	↑
Hale (1966)[C]	MN	High	Glacial till (M), patchy	Mixed	⇆		↓				↑[a]	↓[a]	↑[a]
Peterson (2012)	MN	Low	Glacial till (M), patchy	Empirical	↓								
Smith and Moyle (1944)	MN	Low	Glacial till (M), patchy	Empirical	↓								
Bradt (1935b)	MI	Mixed	Mixed	Anecdotal								↓	↓
Carbine (1944)	MI	High	Mixed	Anecdotal	↓		↓					↑	↑
Knudsen (1962)	WI	Mixed	Mixed	Anecdotal	↓	↓	⇆		↑		↑ [b]		↑ [b]
Salyer (1935)	MI	Mixed	Mixed	Mixed	⇆[a]	↓	↓[a]	↓		↓[a]	↑ / ↓[b]	↑ /↓[b]	
Twork (1936)[C]	MI	Unk.	Unk.	Mixed	⇆[a]	↑	↓		⇆		↑		

[a] Denotes quantitative variables from studies that use mixed analyses.

[b] Beneficial effects on salmonids found only in first 2–4 years after dam establishment.

[c] Christenson et al. (1961), Hale (1966), and Shetter and Whalls (1955) found increased water temperatures downstream of dams, and Twork (1936) stated a decrease in temperature after dam removal; however, stream temperatures did not exceed the thermal limits for Brook Trout (20–24 °C).

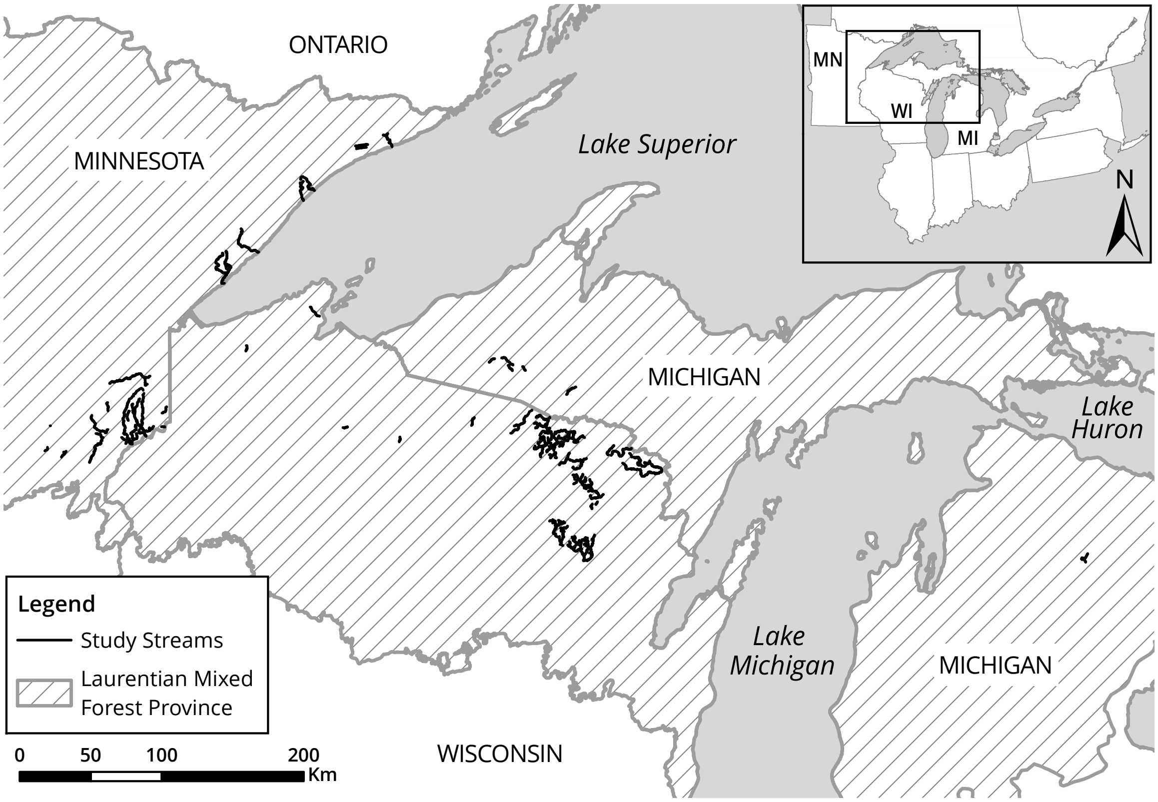

Figure 1.1. Map showing where beaver–salmonid studies have been conducted in the western Great Lakes region. Most of the studies are clustered regionally in northeast Wisconsin, east-central Minnesota, the north shore of Lake Superior, and the Upper Peninsula of Michigan. Several studies (Bradt 1935b, Salyer 1935, Twork 1936, Carbine 1944) did not include spatial information and are not pictured here.

	Logging and Settlement Era *1870–1930*	*Early Management Era* *1930–1960*	*Late Management Era* *1960–1990*	*Current Management Era* *1990–present*
Native salmonids	Land-use practices degrade streams, native salmonid populations decline. First Brook Trout hatchery programs begin.	Stream, riparian habitat improvement methods developed. First beaver-salmonid studies initiated in WGL.	Technical advancements and increased revenue expand stream habitat improvement projects.	Establish diffuse populations of native salmonids that can reproduce naturally and coexist with non-native salmonids.
Non-native salmonids	Early stocking era begins, to supplement native salmonid populations decimated by human development, overexploitation.	Second stocking era begins after Lake Trout populations crash due to Sea Lamprey invasion and overharvest.	Hatchery programs continue in effort to diversify fisheries and control invasive forage species.	Meet commercial and recreational fishery demands without impairing genetic diversity of native salmonids.
Beaver	Beavers nearly extirpated. Relocation and reintroduction efforts occur to promote colonization and propagation.	Beaver populations irrupt. First management plans implemented, goal of balancing beaver-salmonid needs.	Increased use of localized, adaptive management strategies to control beaver populations.	Interdisciplinary approach to manage beaver-salmonid resources, and maintain ecological integrity of forests.

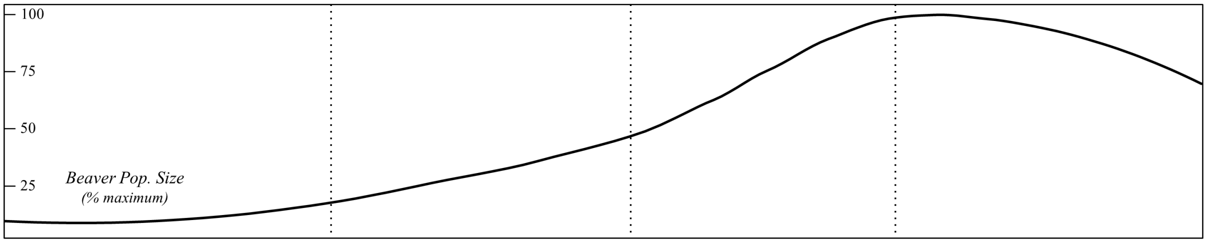

Figure 1.2. Timeline of major events from different management eras and a graph of the approximate beaver population trend from the western Great Lakes (WGL) region (1870–present). The beaver population trendline was estimated from a combination of historical pelt records (Obbard et al. 1987), unpublished beaver colony count data from the Minnesota Department of Natural Resources, and population data from the Wisconsin Department of Natural Resources (WDNR 2015). Percent maximum refers to the percentage of the maximum beaver population size after European settlement. Presettlement beaver abundance is unknown but was likely 50–100% of the 1990 peak.

CHAPTER TWO

Factors Influencing Annual Rates of Change in the Number of Beaver Colonies

SUMMARY

Understanding how wildlife populations respond to density-dependent (DD) and density-independent (DI) factors is critically important for wildlife management and research, as this knowledge can allow us to predict population responses to forcing mechanisms such as climate, predation, and exploitation. Recent advancements in statistical methods have allowed researchers to disentangle the relative influence each factor has on wildlife population dynamics, but this work is ongoing. Using a long-term dataset collected from 1975 to 2002, we sought to evaluate the relative influence DD and a suite of covariates (weather, harvest, habitat quality, and wolf [*Canis lupus*] predation) had on annual rates of change in the number of beaver (*Castor canadensis*) colonies among 15 populations in northern Minnesota, USA.

We modeled changes in beaver colony densities using a discrete-time Gompertz model within a Bayesian inference framework, and compared model performance among three global models using Deviance Information Criterion (DIC) widely available information criterion (WAIC): a DI model without covariates; a DD model without covariates; and a DD model with covariates. Our results provide strong evidence for compensatory (negative) DD within beaver colony dynamics. We found no evidence that covariates related to harvest, wolf predation, or habitat quality significantly influenced beaver colony growth rates, but cold winters (lag-0), spring drought (lag-0), and fall drought conditions (lag-2) were correlated with greater colony growth rates. Despite strong evidence of the effect of environmental covariates on beaver colony dynamics, prediction of colony dynamics using these covariates showed only minimal improvements. We

suggest the lack of improvement in prediction was the result of model over-fitting, indicating our significant covariate effects may not be biologically relevant.

Our analysis demonstrates how reliance on information criterion values may lead to erroneous conclusions in time-series analyses, and using a hindcasting approach like the one we present here may help determine whether model results are biologically relevant or merely statistically significant. Our results highlight the importance of long-term monitoring programs for evaluating the efficacy of predictive ecological models. That beaver populations are primarily intrinsically regulated has important management implications depending on whether the objectives concern eradicating beavers from unwanted regions, mitigating conflicts, or facilitating rewilding or colonization efforts.

INTRODUCTION

Wildlife population dynamics are influenced by density-dependent and density-independent mechanisms, yet detecting and quantifying the relative importance each factor has on fluctuating populations remains challenging (Koons et al. 2015). Density-independent factors (e.g., weather variables) can limit population size by influencing the long-term behavior of the population, whereas density-dependent factors, such as territoriality, competition, and disease, influence a population’s tendency to approach equilibrium (i.e., regulation; Sinclair 1989, Turchin 1995, Sinclair and Pech 1996). These mechanisms influence wildlife population vital rates, and in conjunction with immigration and emigration, they cause population fluctuations through time (Royama 1992, Boyce et al. 2006). Recent statistical advances have spurred new efforts to disentangle the relative influence of density-dependent and density-independent mechanisms in wildlife population dynamics (e.g., Wang et al. 2009, Rotella et al. 2009, Creel and Creel 2009, Pasinelli et al. 2011, Koons et al. 2015, Ferguson et al. 2017). While these approaches are commonly used to forecast wildlife dynamics, validation of these forecasts remains a relatively unexplored frontier in ecology.

Ecological forecasting has emerged as a robust conceptual framework that evaluates models based on their ability to make verifiable predictions about future ecological dynamics based on current data. The science of ecological forecasting has rapidly advanced over the past few years, and there is a growing need to empirically assess how well current theory and inferential methods make ecological predictions (Dietze et al. 2018). While new techniques have been developed to describe how to partition uncertainty in predictions (Petchey et al. 2015, Dietze 2017, Pennekamp et al. 2019), we still do not have a good understanding of how to determine which models lead to reliable predictions. Direct calculations of the predictive error may yield reliable measures of a model's forecasting ability, and provide an interpretable measure of a model's predictive power. A simple way to determine the forecasting ability of models is to withhold a portion of data from the fitting process (unseen data), then use the model to predict the withheld data and compare the predictions with the observed data (a process termed *hindcasting*). In many ecological studies there is simply not enough data to perform hindcasting, especially when considering the dynamics of large animal populations often occur on decadal time scales. Thus, long-term ecological studies can provide opportunities to assess the predictive ability of current model selection approaches. Assessing the reliability of model predictions will likely advance the study and management of wildlife populations by providing a tool to quantitatively test how factors influence future population dynamics, and may be a technique that is particularly important for species that are of special concern due to their rarity, presence in non-native environments (i.e., invasive species), or important ecological role within ecosystems.

Beavers (*Castor canadensis* and *C. fiber*) are ecosystem engineers whose abundance and distribution are increasing in North America, Europe, and Asia, and the reintroduction and conservation of beavers is becoming an increasingly valuable tool to restore ecosystem functions (Burchsted et al. 2010, Pollock et al. 2014, Law et al. 2017, Willby et al. 2018). Beaver alterations to stream and riparian ecosystems have many positive effects for native ecosystems (Naiman et al. 1986, Johnston 2017), such as mitigating the impact of climate for fish and wildlife species (Hood and Bayley 2008), and increasing habitat heterogeneity, species diversity, and species richness within beaver-modified environments (Naiman et al. 1988, Wright et al. 2002, Rosell et al. 2005, Windels 2017, Willby et al. 2018). On the other hand, beaver dam-building and foraging habits can be destructive to anthropogenic and natural resources (Bhat et al. 1993, Jensen et al. 2001). Further, deliberate introductions of *C. canadensis* outside of their natural range have resulted in substantial damage to South American ecosystems (Anderson et al. 2006a, Anderson and Rosemond 2007, Westbrook et al. 2017) and created interspecific competition with the native *C. fiber* in parts of Eurasia (Parker et al. 2013). Beavers are accordingly managed as a nuisance and/or exotic species throughout much of their geographic extent, in addition to being managed for their ecosystem engineering.

Relative to the extensive history of beaver management and exploitation in North America, surprisingly little is known about the population dynamics of this iconic species, particularly at the landscape or regional scale. But previous research suggests beaver population dynamics may be influenced by several factors, including population density, habitat quality, human exploitation, predation, and weather. Reduced fecundity (Payne 1984*a*) and delayed dispersal (Mayer et al. 2017a) have been observed in high density beaver populations, and the interaction of habitat quality, territoriality, and intraspecific competition is thought to regulate beaver colony densities (Bergerud and Miller 1977, Boyce 1981*a*, Novak 1987, Baker and Hill 2003). Beaver densities are robust under low to moderate harvest pressure (Müller-Schwarze and Schulte 1999) and may even exhibit compensation (Boyce 1981*b*); however, once mortality rates exceed

25–33% (typically 1.0–1.5 beaver/colony/year; Baker and Hill 2003), beaver populations tend to decline (Payne 1984*b*, 1989, Potvin et al. 1992). Predation was thought to cause population declines in two studies (Potvin et al. 1992, Romanski 2010), but recent research suggests there is little evidence that demonstrates predation can suppress beaver population sizes (Theberge and Theberge 2004, Gable and Windels 2018, Gable et al. 2018). Finally, several different weather variables have been found to affect beavers, including average spring (Campbell et al. 2013, Ribic et al. 2017) and winter temperatures (Smith and Jenkins 1997, Campbell et al. 2013), seasonal precipitation (Campbell et al. 2012, 2013), and drought regimes (Ribic et al. 2017). Understanding how beaver populations respond to intrinsic, anthropogenic, and environmental factors will not only increase our understanding of beaver population ecology in general, but by extension will also help elucidate how beaver-engineered environments may change in tandem with beaver population dynamics.

Here, we use a long-term dataset collected by the Minnesota (USA) Department of Natural Resources (MNDNR) to evaluate how density-dependent and density-independent covariates affect the annual rates of change in the number of beaver colonies (hereafter referred to as 'colony growth rates'). Our specific objectives with the present study were to (1) estimate the strength of density dependence among our beaver populations; (2) determine the relative influence that other covariates (weather, harvest, wolf [*Canis lupus*] predation, and habitat quality) had on annual colony growth rates; and (3) test the predictive value of our model assessments using an ecological forecasting approach. Due to the territorial nature of beavers and the previous observation of reduced fecundity in high density populations (Payne 1984*a*), we hypothesized density-dependent mechanisms significantly influenced beaver colony growth rates. We expected habitat quality would positively influence colony growth rates, as previous research has demonstrated reductions in habitat quality can affect colony persistence (Busher and Lyons 1999, Fryxell 2001). Although beaver reproduction may be compensatory in exploited populations (Payne 1984b, 1989, Boyce et al. 1999), we hypothesized harvest rates were high enough to negatively affect colony growth rates, as our study's time frame encompassed the "fur boom" of the 1980s when as many as 170,000 beavers were harvested annually in Minnesota. We expected weather variables to have a lesser impact, as beavers have the ability to partially de-couple their habitats from environmental conditions through their creation and maintenance of ponds. Consistent with recent research by Gable and Windels (2018), we hypothesized wolf predation did not impact colony growth rates.

METHODS

Study Area

Our study area encompassed approximately the northern half of Minnesota (Figure 2.1) within the Laurentian Mixed Forest Province that covers more than 9.3 million ha in the northeastern portion of Minnesota (Cleland et al. 2007). The study area lies in the transition zone between temperate deciduous and boreal (subarctic) forest ecoregions, and the vegetative composition varies considerably within the study area (MNDNR 2017). Fire-dependent oak (*Quercus* spp.) and jack pine (*Pinus banksiana*) forests are prevalent in the southern and western portions of the study area, while large swaths of black spruce (*Picea mariana*) bogs and tamarack (*Larix laricina*) swamps comprise portions of the western and northern sections. Mesic hardwood forests are common throughout the central and eastern sections of the study area, while coniferous forest communities are prevalent in the northeastern section. Human density varies widely throughout the study area, but most survey routes were conducted throughout sparsely populated areas.

Relevant temperature and precipitation averages for our study were obtained from the PRISM Climate Working Group. Average annual precipitation across our study's time frame (1972–2002, including time lag of 3 yr) ranged from 616.2 ± 95.8 mm to 773.0 ± 141.4 mm at each route, with an average of 66% of total precipitation falling during the growing season (May–Sep) (PRISM Climate Group 2014). Average winter temperatures (Dec–Mar) were similar across all routes, ranging from –11.2 ± 2.3 °C to –8.4 ± 2.2 °C. Average maximum May temperatures (spring green-up season) ranged from 18.3 ± 2.6 °C to 20.0 ± 2.5 °C.

Within our study area wolves are the main predator of beavers, which are an important food source for wolves during the ice-free season (Voigt et al. 1976, Gable et al. 2017). Minnesota's wolf population was expanding during our study's time frame after being listed on the Endangered Species Act in 1974 (MNDNR 2001). The wolf population grew from an estimated low of 750 individuals at the time of listing to approximately 2,450 by 1997-98, extending their range by nearly 30,000 km^2 (MNDNR 2001) that included colonizing four survey routes during our study's time frame (Figure 2.1). Although black bears (*Ursus americanus*) and coyotes (*C. latrans*) are also present within our study area (Hazard 1982), because there is no evidence to suggest predation rates from these species can influence beaver populations (except in unusual circumstances such as in isolated island populations; Smith et al. 1994) these species were not included in our assessment.

Annual Beaver Colony Surveys

The MNDNR conducted annual population surveys by identifying and counting active beaver colonies from a fixed-wing aircraft along 25 pre-determined routes from 1975 to 2002, a survey method that resource managers have used for many decades to estimate beaver populations (Johnston and Windels 2015). Observers distinguished active colonies by identifying the presence of a visible food cache, which is the colony's winter food source that consists of piles of semi-submerged logs and twigs and can be seen in the fall just prior to freeze-up (Payne 1981, Brown and Parsons 1982, Johnston and Windels 2015). Supplementary observations such as fresh mud on dams and/or lodges were also used to determine whether colonies were active in a given year. Surveys were conducted between 0900–1600 hours in assorted 2- and 4-person fixed-wing aircraft after leaf-off, but before ice formed on water features (mid-September–early November).

We digitized and calculated the length of each survey route in ArcGIS 10.5 (Environmental Systems Research Institute, Inc., Redlands, CA) using hand-drawn maps used by MNDNR personnel as reference. Route lengths (range: 94–336 km) and types were variable; three routes were flown in a series of linear transects, while seven routes followed waterways exclusively (e.g., lake shores, rivers, streams), and the remaining five routes used a combination of transect and waterway segments (Figure 2.1). We digitized each route by inferring the aircraft's flight path based on the reference maps (Figure 2.2), which resulted in density estimates of the number of active colonies/km surveyed by the aircraft.

Aerial cache surveys can be susceptible to observer bias (Novak 1987, Romanski 2010), so we limited our data selection to routes with the greatest consistency of survey conditions. We selected routes that had a maximum of three different primary observers throughout the entire survey period of each route. We then excluded individual surveys that were conducted at a mean flight altitude <60 m or >300 m, as we assumed detection probability decreased at those altitudes (Romanski 2010). Finally, we eliminated all routes where surveys were not conducted (or eliminated based on flight altitude) >20% of the survey time period (e.g., surveys conducted over a 15-yr period from the first to last observation could have no more than three missing years of survey data). Following this data selection process, we retained data from 15 of 25 routes with an average time series length of 22.3 yr (Table 2.1).

Variable Selection

Based on previous studies evaluating the impact of weather on beavers (Campbell et al. 2012, 2013, Ribic et al. 2017, Campbell et al. 2017), we selected four weather variables for our analysis: (1) mean maximum temperature during the spring green-up season (May); (2) growing season (May–September) drought index; (3) fall (August–October) drought index; and (4) winter severity (December–March temperature). We also selected spring (April–June) drought index, as we thought juvenile dispersal might have decreased during dry years when a lack of water on the landscape could have restricted connectivity between aquatic habitats. Temperature values were obtained from PRISM (NASCE 2017) using the R package *prism* (Hart and Bell 2015). We used monthly raster files at a 4 km scale of resolution, averaged values across the entire route using the 'Zonal Statistics as Table' tool in ArcGIS (exploratory analysis showed average temperature values did not differ significantly within routes), and used a Python script to summarize multiple monthly PRISM raster files at once within ArcGIS. We used Palmer Drought Severity Index (PDSI) values to evaluate drought conditions, obtained from the US drought portal (National Integrated Drought Information System 2018). PDSI values provide a standardized index (range: –7 to 7) for estimating the amount of water that is available for plants (Ribic et al. 2017); values <0 indicate drought conditions. Our study area encompassed three different PDSI climate divisions: North Central (2102), Northeast (2103), and East Central (2106). Routes that crossed multiple divisions were assigned PDSI values corresponding to the division containing the longest portion. All temperature and drought values were averaged (mean) across their timeframe of interest (e.g., the fall drought value was the mean average across August, September, and October monthly drought values).

We assessed habitat quality by developing an index of high-quality forage availability for each route. We first applied a 1 km "habitat buffer" around each route, which corresponds to the 800 m observer sight distance plus an additional 25% buffer to account for habitat characteristics of ponds that may have straddled the sight distance boundary (Figure 2.2). Beavers generally restrict their foraging to within 30–50 m of the riparian zone (Johnston and Naiman 1987, Donkor and Fryxell 1999, Martell et al. 2006), so we applied a second 50 m "forage buffer" around all water features within the habitat buffer to isolate only habitat characteristics that were available for beaver foraging (Figure 2.2). We extracted all stream features from the MNDNR hydrography dataset (MNDNR 2014) and all lake/wetland features from the Minnesota National Wetland Inventory (NWI) (MNDNR 2009); we selected only NWI features that consisted of 'unconsolidated bottom' (i.e., open water) classes within 'lacustrine' and 'palustrine' systems. We used the 1992 National Land Cover Database (NLCD; Vogelmann et al. 2001) as our habitat layer input, which corresponds to characteristics that were present in the middle of our timeframe. High-quality beaver habitat generally consists of deciduous and early successional forest communities (Novak 1987); therefore, we defined high-quality forage as "Deciduous" and "Mixed" forest classes. We took the total area of deciduous and mixed classes within the forage buffer divided by the total area within the habitat buffer, to obtain a final index that approximately equates to the relative abundance of high-quality forage within each route.

We also sought to evaluate whether the previous year's harvest season(s) had a significant impact on beaver populations. To estimate annual harvests, the MNDNR conducted annual mail surveys and multiplied the mean number of beavers harvested per respondent by the total number of licenses sold. Spring and fall harvests are approximately equal in Minnesota (J. Erb, unpublished data), so we summed the seasonal harvest estimates to obtain a single annual value. No spatially explicit harvest data exists for our timeframe, only statewide estimates. There was a limit of 10 pelts per license in 1975 and the harvest season was closed in 1976, but there was no harvest limit for beavers from 1977 to 2002. All routes were available to trappers excluding Kabetogama, where trapping ceased in 1975 when Voyageurs National Park was established.

To evaluate the influence of predation on beaver population growth rates, we used wolf density estimates as a proxy for predation pressure. Because wolf densities increase linearly with available ungulate prey biomass (Fuller 1989, Fuller et al. 2003), we estimated annual wolf densities for each route by calculating ungulate biomass index (BMI) values (Kuzyk and Hatter 2014, Mech and Barber-Meyer 2015). We used the following regression equation presented in Mech and Barber-Meyer (2015) to estimate annual wolf densities:

$$Wolves\ per\ 1000\ km^{-2} = 2.0622 + 3.5254 \times BMI \qquad \text{Equation 2.1}$$

where BMI was calculated by adding the density of white-tailed deer (*Odocoileus virginianus*)/km^2, plus 6 times the density of moose (*Alces alces*)/km^2 (the number of white-tailed deer “relative biomass equivalents” presented in Fuller et al. (2003). We obtained deer densities from MNDNR pellet survey estimates (Norton 2018, and MNDNR unpublished data), and moose densities from MNDNR aerial survey estimates (Karns 1982, Lenarz 1998, 2006, Murray et al. 2006).

For the four routes that experienced wolf range expansion (Cass, Cass-Crow, Itasca, Southern Pine; Figure 2.1), we estimated wolf densities as a proportion of the ungulate BMI-derived density for each year wolves were actively re-colonizing the area. We used wolf population recovery data presented by Hayes and Harestad (2000) to estimate how wolf densities within each route reached their predicted densities within six years of establishment. We then used the population estimates from Hayes and Harestad (2000) to estimate ungulate BMI-derived density proportions for each year of the re-colonization as follows: 0.12, year 1; 0.28, year 2; 0.52, year 3; 0.76, year 4; 0.84, year 5; and 1.00, year 6. We determined the first year of wolf re-colonization using a combination of annual scent-post surveys (Sargeant et al. 2003, and MNDNR unpublished data) and extensive wolf population surveys from 1978-89, 1988-89, and 1997-98, using the first year of wolf detection within 50 km of each route as the first year of re-colonization. We acknowledge the first wolf detection near a route may have been a dispersing individual rather than an established pack, but because we know wolves became established within each of these four routes during our study time period, we believe this method is adequate for estimating the approximate year of re-colonization.

Data Analysis[1]

To evaluate whether observer bias could have significantly impacted survey counts, we conducted an exploratory analysis to estimate observation error within our dataset by fitting our data to a discrete-time Gompertz state-space model with measurement error (Dennis et al. 2006). State-space models are frequently used in time-series analyses to decouple observation and process error from sampling variation, allowing researchers to estimate the relative contributions density-dependent and density-independent factors

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[1] Data analysis was performed by Jake M. Ferguson.

have on population dynamics (de Valpine and Hastings 2002, Clark and Bjørnstad 2004, Dennis et al. 2006, Koons et al. 2015). Not accounting for the influence of observation error can lead to erroneous conclusions about the relative strength of density dependence within wildlife populations (Turchin 1995, Freckleton et al. 2006). Results from our exploratory analysis suggested observation error did not have a significant effect on sampling variation within our dataset, and thus did not affect our estimates of the strength of density dependence.

Juvenile dispersal is thought to be the primary mechanism of population expansion (Baker and Hill 2003), so we selected our extrinsic variables and incorporated time lags into our analysis based on how we predicted each variable might affect juvenile dispersal, recruitment, and survival. Although population density and harvest can alter the timing of dispersal (Boyce 1981b, Mayer et al. 2017a), beavers typically disperse from their natal colony by age 2 or 3 (van Deelen and Pletscher 1996, Sun et al. 2000, McNew and Woolf 2005); thus, we incorporated time lags ranging from 0 to 3 years into our statistical model.

We modeled beaver colony dynamics using a model of contest competition, which describes the increasing utilization of available resources with increasing density (Hassell 1975). Our models described changes in the log density, $X_{i,j} = \ln\left(\frac{N_{i,j}}{A_i}\right)$, where $N_{i,j}$ is the abundance of population i in year j and A_i is the area surveyed for population i. We applied the Gompertz model (Dennis and Taper 1994) which includes the growth rate, a, and a strength of density dependence, b, along with a random effect to account for variation between subpopulations in the density-independent reproductive rate (u_i), that is not accounted for by covariates. We included the effects of environmental covariates ($\boldsymbol{Z_{i,j}}$) on the density-independent growth rate. The final quantity in the model is a variance term, $\varepsilon_{i,j}$, that accounts for unexplained inter-annual variation in the density of population *i* in year *j*.

$$X_{i,j} = a + u_i + (1 - b)X_{i,j-1} + \beta \boldsymbol{Z_{i,j}} + \varepsilon_{i,j}$$

$$u_i \sim \mathrm{Norm}(0, \sigma_a)$$

$$\varepsilon_{i,j} \sim \mathrm{Norm}(0, \sigma_i)$$

The environmental covariates used in this analysis ($\boldsymbol{Z_{i,j}}$) are described in the previous section. Briefly, they are the number of beaver harvested at the state-level in the previous year adjusted for route length, the estimated route-level wolf density in the current year, the route-level PDSI during the spring in the current year, the route-level PDSI during the growing season lagged two and three years, the route-level PDSI during the fall lagged two and three years, the route-level winter temperatures for the current year and lagged two years, and the route-level average maximum temperature in May lagged two and three years.

We used the deviance information criterion (DIC) and widely available information criterion (WAIC) (Watanabe 2010) to test (1) the full model described above (*DD_{cov} model*) against (2) the density-dependent model without covariates (*DD model*), and (3) a density-independent model without covariates (*DI model*). Both of these criteria were developed to approximate the out-of-sample prediction error (Gelman et al. 2014). Models were fit using MCMC implemented by Just Another Gibbs Sampler (JAGS) (Plummer 2003) by making 10^6 draws from the posterior. We thinned our resulting chain by every 10^2 draw due to strong autocorrelation in some parameters.

In addition to fitting the full dataset using the procedures described above, we tested the performance of model predictions by holding out the final 1/3 of observations for each population, fitting the models to this reduced dataset, then hindcasting the held-out data. We assessed predictive performance using the average root mean squared prediction error (MSPE) of the predicted density and the observed density. The MSPE for site k is given by $\text{MSPE}_k = \sqrt{\sum_{\{i=1\}}^{n} \left(D_i - \widehat{D}_i\right)^2}$. We then averaged the MSPE's across sites to get the overall MSPE. In order to determine whether model inferences were consistent between the full dataset and withheld dataset, we compared parameter estimates from each dataset using Deming regression implemented in the R package *deming* (Therneau 2018), which allows for errors in both dependent and independent variables.

RESULTS

The observed mean density of beaver colonies in our study sites was 0.59 (SD = 0.33) colonies/km. The average site densities ranged from a minimum of 0.28 colonies/km in Kanabec to 1.60 colonies/km in Kabetogama (Figure 2.3).

Our model selection procedure indicated that the DD_{cov} model performed best in terms of DIC, WAIC, and predictive performance (Table 2.2). However, improvement in the predicted density was small relative to the DD model. The average improvement in predictability was only 3% (minimum –52%, maximum 42%), less than we expected given the high ΔDIC (12.31) and ΔWAIC (14.14) values indicated strong evidence for the DD_{cov} model. We found no systematic differences between the covariates estimated from the full dataset and the covariates estimated from the holdout dataset, with all posterior estimates within 1 standard deviation of the one-to-one line that indicates equal estimates (Figure 2.4). Our estimate of the slope of the line that best explains the relationship between these points was 1.24 (SE = 0.19).

The average strength of density dependence across all populations was $\hat{b} = -0.64$ (SD = 0.07, Bayesian credible interval based on 95% of the highest posterior density [BCI] = −0.77 to −0.50; Table 2.3). We found the average log-intrinsic growth rate across all routes (density-independent growth) was $\hat{a} = -0.47$ (SD = 0.09, BCI = –0.66 to –0.29), with an average variation in the population-level growth rates of $\hat{\sigma}_a = 0.28$ (SD = 0.07, BCI = 0.17 to 0.46) (Table 2.3).

Of the 12 covariates we evaluated in the DD_{cov} model, three had a statistically significant influence on beaver colony growth rates. Average winter temperature during the same year was negatively correlated with growth rates ($\beta_4 = -0.04$, SD = 0.02, BCI = –0.09 to –0.01), indicating growth rates were higher in years with colder winters. Spring PDSI values during the same year ($\beta_8 = -0.05$, SD = 0.02, BCI = –0.09 to –0.02) and fall PDSI values lag-2 (β_{11} = –0.07, SD = 0.03, BCI = –0.13, –0.01) were both negatively correlated with colony growth rates, indicating a positive relationship between drought conditions and annual growth rates (PDSI values <0 indicate drought). Of the remaining nine covariates evaluated we found a weak, but statistically insignificant (i.e, SD posterior estimates did not overlap zero, but BCI estimates did) positive correlation between colony growth rates and habitat quality (β_2 = 0.15, SD = 0.08, BCI = 0.00 to 0.31). All other covariates did not have a significant influence on colony growth rates (Table 2.3).

DISCUSSION

Our results indicate inter-annual fluctuations in beaver colony densities are driven primarily by density-dependent mechanisms and perhaps, to a lesser extent, by weather variables (winter temperature, spring drought, fall drought [lag-2]; Table 2.3). Our estimate for the average strength of density dependence across all populations ($\hat{b}$ = −0.64) provides strong evidence that beaver populations in our study exhibited compensatory (negative) density dependence (Herrando-Pérez et al. 2012). Several density-dependent mechanisms have been previously identified that likely influence density-dependent colony growth rates. As a territorial species, beavers regulate colony density through scent-marking behavior (Aleksiuk 1968, Müller-Schwarze and Heckman 1980, Rosell and Nolet 1997) and intraspecific aggression (Bergerud and Miller 1977), but previous research has also shown density can affect the fecundity (Payne 1984*a*) and timing of natal dispersal in beavers (Mayer et al. 2017a) (and by extension, the age at first breeding; Mayer et al. 2017b). The absence of demographic data precludes us from determining which density-dependent mechanisms exerted the greatest influence on colony density fluctuations.

Despite the DD_{cov} model performing significantly better than the DD model, the DD_{cov} model's ability to predict future observations of colony densities was only slightly better (Table 2.2). We suggest the modest improvement in prediction ability is likely due to the DD_{cov} model over-fitting our data, which thus draws into question whether our significant covariate effects are biologically relevant. This is further supported by the perplexing direction of all statistically significant weather effects, which suggest positive correlations between beaver colony growth rates and drought conditions, and between colony growth rates and colder winters — results that contradict previous studies (Smith and Jenkins 1997, Campbell et al. 2012, 2013, Ribic et al. 2017, Brommer et al. 2017). However, we selected most of our weather variables based on two previous studies (Campbell et al. 2012, Ribic et al. 2017) that used multimodel inferential methods that may have also resulted in over-fit models. As a general rule, it is recommended to restrict model degrees of freedom to 5 to 10% of the effective sample size (Burnham and Anderson 2002, Giudice et al. 2012) and limit the number of models tested to avoid over-fitting data (Fieberg and Johnson 2015). Campbell et al. (2012) evaluated beaver survival and recruitment rates using numerous global models (63 and 32, respectively) for 242 individuals, while Ribic et al. (2017) had low statistical power to effectively evaluate colony density dynamics (5 parameters, n = 34; 10–12 parameters, n = 55); both of these statistical methods did not adhere to multimodel inference recommendations. Thus, given the potential problems with over-fit models in our analysis and previous studies, considerable uncertainty remains surrounding how weather variables affect beavers. Future studies may help interpret whether a previously unknown aspect of beaver ecology (e.g., early juvenile dispersal during drought conditions) is responsible for the significant and contradictory effects of weather in our data set, or if our results are statistically significant, but not biologically relevant due to our model over-fitting.

Both human harvest and wolf densities were not significantly correlated with beaver colony growth rates (Table 2.3). Harvest data was only available at the statewide scale, which probably limited our evaluation. However, in a broader sense, we wanted to determine whether coarse patterns of trapping intensity would have an overall effect on beaver populations. Our results suggest that was not the case and indicate that, on average, harvest intensity levels were moderate during our study. With regards to wolf predation, our results are consistent with recent research from northern Minnesota that demonstrated beaver populations can be resilient to intense predation pressure (Gable and Windels 2018); beaver colony density increased even after wolves were estimated to have removed more than 40% of beavers within their territory during the previous year, indicating mortality from wolf predation may be compensatory (Gable and Windels 2018) as has been suggested in harvested populations (Payne 1984b, 1989, Boyce et al. 1999). Although it could be argued that wolf predation rates on beavers may change in response to ungulate densities, implying our method to estimate wolf densities may not accurately assess predation pressure, there is currently no evidence to suggest this is true. More research is needed to understand the functional and numerical relationships between wolves, ungulates, and beavers (Gable et al. 2018), but our results support the notion that wolf predation rates on beavers are not high enough to suppress beaver colony densities in multiple-prey systems.

Our metric for habitat quality had a positive, but statistically insignificant effect on inter-annual beaver colony growth rates (Table 2.3). We elected to use NLCD habitat data from a single time period to evaluate whether broad forest type characteristics could influence beaver colony dynamics, but we did not find support for this hypothesis. Given previous studies have shown habitat quality can affect colony densities (Novak 1987, Busher and Lyons 1999), finer-scale habitat data may have produced a different result. Accounting for forest age in addition to forest type may have resulted in a better index of beaver habitat quality. However, the more likely scenario is that habitat quality probably affects long-term colony density trends rather than the inter-annual changes we evaluated in this study. Indeed, the degradation of habitat quality over time was suggested to have been responsible for long-term population trends within two study areas (Busher 1987, Busher and Lyons 1999).

The biggest limitation of using only aerial fall cache surveys to assess beaver population size is the absence of individual-based data, which likely limits what conclusions can be made about how various factors influence beaver population dynamics. Fall cache survey methods produce only a count of the number of active colonies along the survey route, which inherently assumes average colony size is universal across space and time (McTaggart and Nelson 2003). Yet, average beaver colony size can fluctuate spatially and temporally (Novak 1987, Baker and Hill 2003) and may even be higher in unexploited populations (Payne 1989, Müller-Schwarze and Schulte 1999) — characteristics that are not accounted for by this survey methodology. We suspect the absence of individual-based data may have limited our own conclusions about how various factors influenced beaver populations.

Beavers are a unique study species to research mammalian population dynamics at multiple temporal and spatial scales with relative ease. Beaver works such as dams and lodges are conspicuous on the landscape and therefore easy to count (Johnston and Windels 2015); a recent study from Finland has even demonstrated the efficacy of using citizen science to obtain colony estimates (Brommer et al. 2017). Likewise, numerous methods are available to researchers for collecting demographic data on beavers including lethal trapping (Payne 1982, 1984b, 1984a, Peterson and Payne 1986), live capture and telemetry (Smith et al. 2016), and non-invasive genetic sampling (Herr and Schley 2009, Schwartz et al. 2017) and remote camera (Bloomquist and Nielsen 2009) techniques. Possessing both individual-based and population-level data would reveal a greater understanding of how density-dependent and density-independent factors influence individuals, colonies, and populations differently, and will hopefully elucidate the mechanisms by which these disparate scales interact.

MANAGEMENT IMPLICATIONS

Our finding that beaver populations (when not exposed to excessive trapping — an important prerequisite given the extensive history of beaver overexploitation) are generally regulated by intrinsic density-dependent mechanisms and are resilient to external forcing factors has several important management implications depending on local objectives. Results from our analysis suggest trappers were unable to significantly influence regional beaver colony growth rates over the course of our study period. Given the recent decline in trapper participation and average pelt price, we thus expect beaver populations may increase in areas where public harvests have historically limited beaver populations and generate more conflicts with anthropogenic (e.g., roads, culverts, railroads) and natural resources (e.g., salmonid streams; Cutting et al. 2018, Johnson-Bice et al. 2018). But for areas where populations are largely saturated, like Minnesota, expending resources on lethal beaver control may be inefficient; however, this does not imply lethal control is not a viable option to solve beaver conflicts in the short-term. Our results are probably encouraging for areas where management objectives are focused on promoting beaver population increases. This includes riparian habitats within arid regions of the western USA, where beavers are increasingly being used as a natural habitat restoration tool (Burchsted et al. 2010, Pollock et al. 2014), and parts of Europe and Asia where rewilding beavers has generated extensive scientific and public support (Stringer and Gaywood 2016, Law et al. 2017, Gaywood 2018, Willby et al. 2018). Yet, there remain many regions where beaver engineering presents a serious threat to local environments, including South America (Anderson et al. 2006a, Anderson and Rosemond 2007) and, more recently, in tundra environments where beavers have expanded their range and engineered wetlands that are poised to disrupt permafrost regimes (Tape et al. 2018). For these areas where the objective is eradication, intensive management efforts will almost certainly be required in order to prevent further ecosystem degradation.

Table 2.1. Summary of the 15 survey routes from northern Minnesota. The number next to each route corresponds to its location in Figure 2.1.

Route name	Survey period	Years surveyed	Missing years
1. Red Lake	1975–1992	15	3
2. Hay-Kelliher	1975–2001	23	4
3. Northome	1975–1992	17	1
4. Koochiching N.	1987–2002	16	0
5. Kabetogama	1975–2002	27	1
6. Blackduck	1975–1992	15	3
7. West Vermillion	1975–1992	16	2
8. Ely-Finger Lakes	1975–2002	15	3
9. Kawishiwi	1977–1992	14	2
10. Central St. Louis	1975–2002	23	5
11. Itasca	1975–1992	16	2
12. Cass-Crow Wing	1975–2002	27	1
13. Cass County	1975–2002	27	1
14. Kanabec	1975–1992	16	2
15. Southern Pine	1975–2001	24	4

Table 2.2. Comparison of our three global models evaluated. Deviance Information Criterion (DIC), widely applicable information criterion (WAIC), and average root mean squared prediction error (MSPE) values are shown for each model. Results indicate the DD_{cov} model explains the greatest amount of variation and has the lowest prediction error for the beaver colony data.

Model	ΔDIC	ΔWAIC	MSPE
Density-dependent with covariates (DD_{cov})	–	–	0.10
Density-dependent without covariates (DD)	12.31	14.14	0.12
Density-independent without covariates (DI)	76.50	93.62	0.44

Table 2.3. Parameter estimates from the DD_{cov} model. Asterisks indicate effects where the 95% Bayesian credible interval (BCI) did not overlap 0. Negative Palmer Drought Severity Index (PDSI) parameter estimates indicate beaver population growth rates were positively correlated with drier seasons (PDSI values <0 represent drought conditions). The significant negative winter temperature parameter estimate indicates lower winter temperatures were positively correlated with larger growth rates.

Parameter	Interpretation	Mean	SD	BCI
a	Density-independent growth	–0.47*	0.09	(–0.66, –0.29)
b	Density dependence	–0.64*	0.07	(–0.77, –0.50)
σ_a	Variance in population-level density-independent growth	0.28	0.07	(0.17, 0.46)
β_1	Beaver harvest (lag 1)	0.02	0.02	(–0.01, 0.05)
β_2	Habitat quality	0.15	0.08	(0.00, 0.31)
β_3	Estimated wolf density (lag 0)	0.00	0.01	(–0.01, 0.01)
β_4	Avg. winter temperature (lag 0)	–0.04*	0.02	(–0.09, –0.01)
β_5	Avg. winter temperature (lag 2)	0.02	0.02	(–0.01, 0.05)
β_6	Max. May temperature (lag 2)	0.01	0.02	(–0.04, 0.05)
β_7	Max. May temperature (lag 3)	0.02	0.02	(–0.02, 0.05)
β_8	Spring PDSI (lag 0)	–0.05*	0.02	(–0.09, –0.02)
β_9	Growing season PDSI (lag 2)	0.01	0.03	(–0.05, 0.07)
β_{10}	Growing season PDSI (lag 3)	–0.01	0.03	(–0.07, 0.05)
β_{11}	Fall PDSI (lag 2)	–0.07*	0.03	(–0.13, –0.01)
β_{12}	Fall PDSI (lag 3)	–0.04	0.03	(-0.10, 0.02)

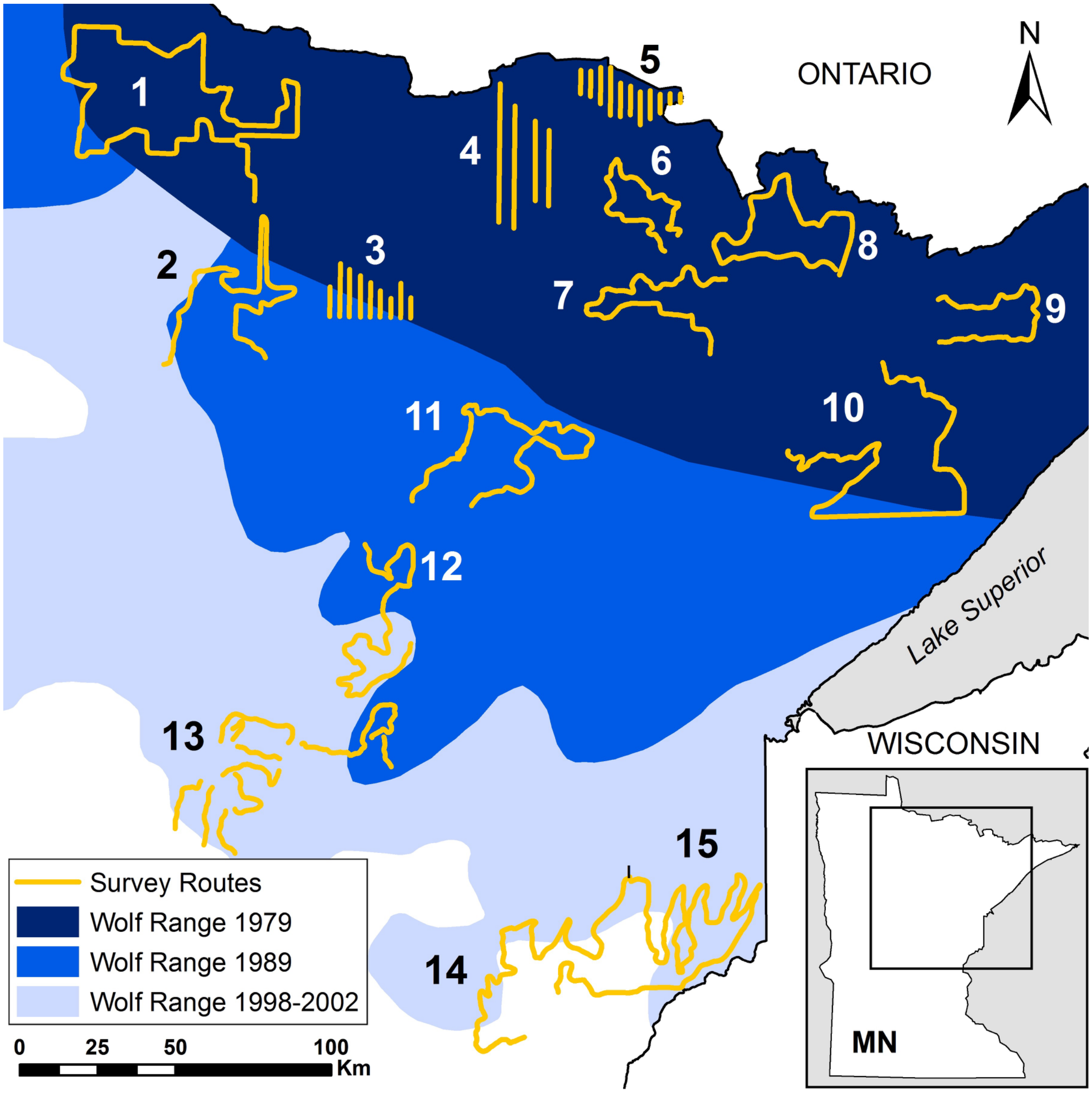

Figure 2.1. Map of the study area and location of each survey route. The Minnesota wolf population's range was expanding throughout the study's time frame, as indicated by the range maps created from wolf surveys conducted in 1978-79, 1988-89, 1997-98, and 2003 (no range expansion was found from 1998 to 2003). Results from the 1978-79 survey indicated route 2 (Hay-Kelliher) had established wolf packs and route 11 (Itasca) was undergoing re-colonization, but these packs were not included in the official range maps. Wolves were not present for route 14 (Kanabec) surveys, which ceased in 1992.

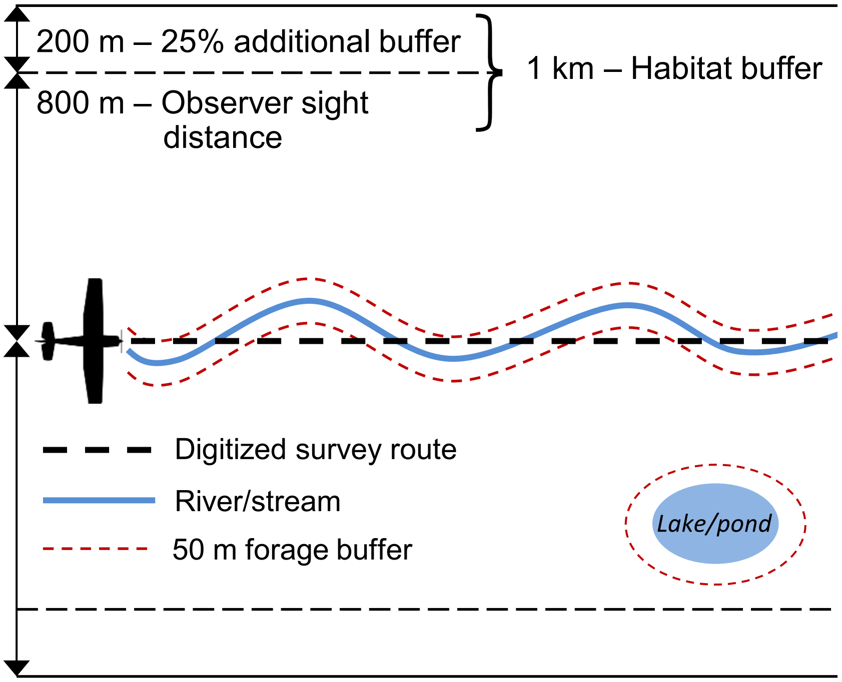

Figure 2.2. Graphic depicting how we digitized survey routes by delineating the aircraft's trajectory based on hand-drawn reference maps. Observers were instructed to count all colonies within 800 m of either side of the plane (observer sight distance). We then added an additional 25% buffer to account for any water features that may have straddled the observer sight distance. Within the 1 km habitat buffer, we applied a 50 m forage buffer around all water features and used the area within the forage buffer to assess habitat quality for each route.

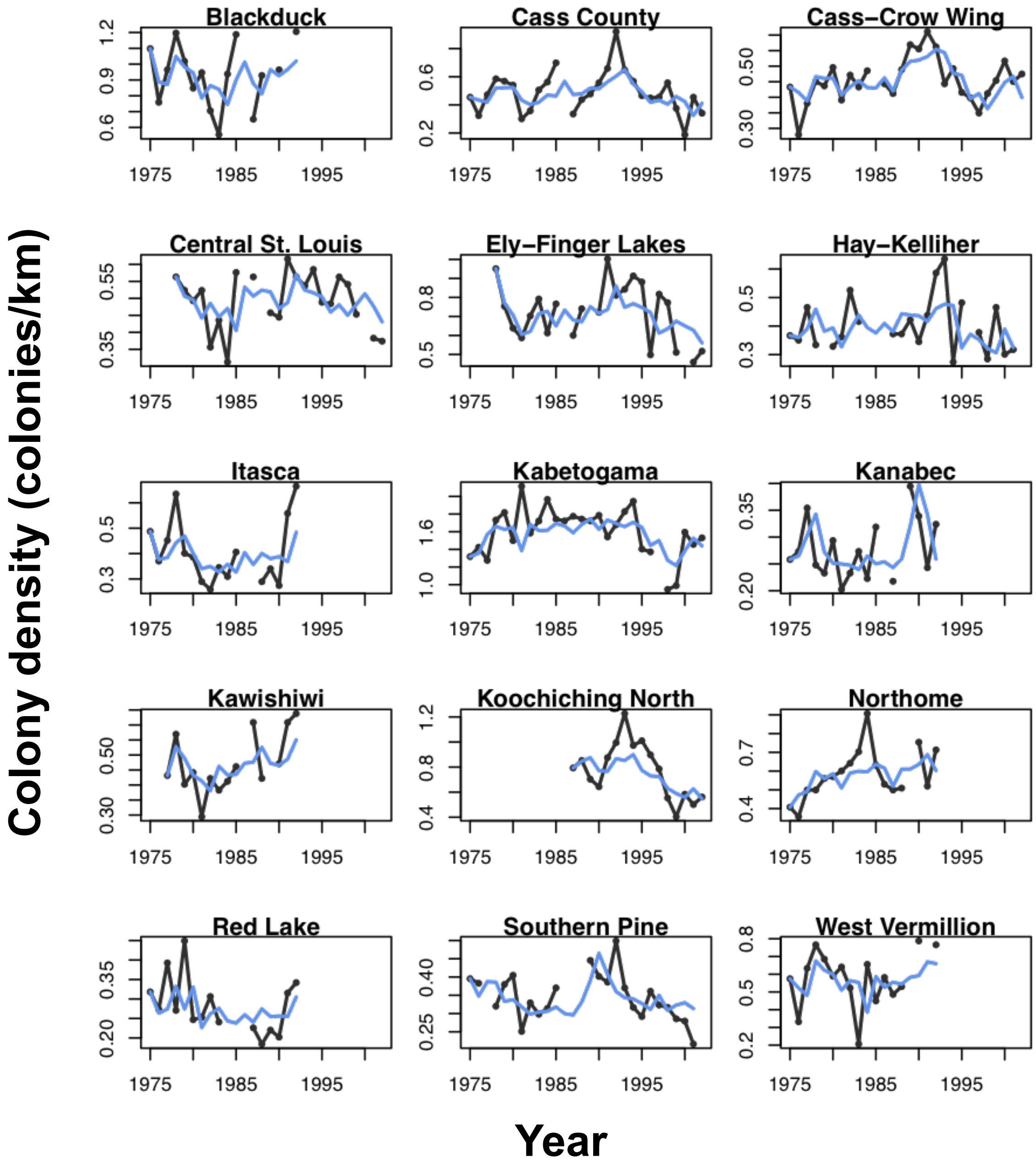

Figure 2.3. Composite image of raw (observed) data (black lines) and model fits (blue lines) for each route. Note that the y-axis limits are different for each route to highlight the trends within each route.

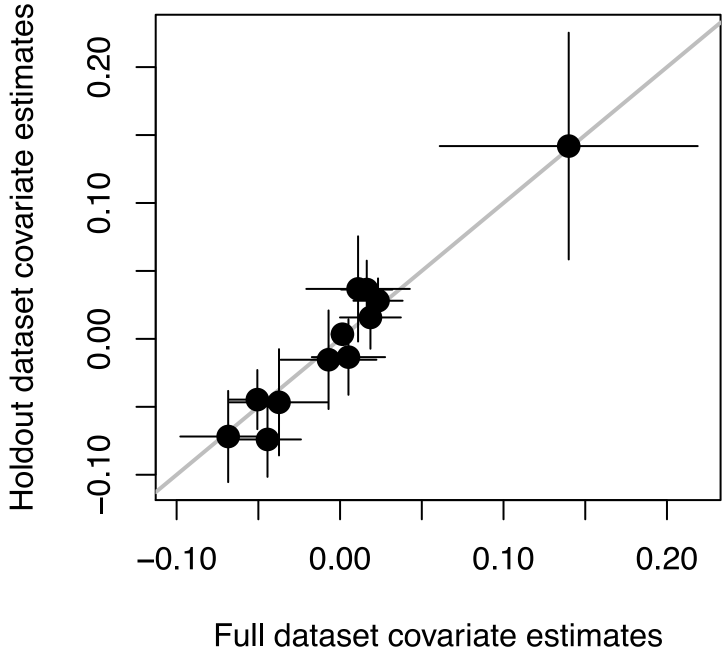

Figure 2.4. Plot of the beta coefficients for the estimates from the full dataset compared to the estimates from the dataset with 1/3 of observations held out. Estimates that are exactly equal will fall on the one-to-one line. No systematic differences between the full dataset and holdout dataset were found, as all posterior estimates were within one standard deviation of the one-to-one line.

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