ECOSYSTEM PIONEERS: BEAVER DISPERSAL AND SETTLEMENT SITE SELECTION IN THE CONTEXT OF HABITAT RESTORATION

by

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DEDICATION

This project is dedicated to my Mom and Dad. I learned a lot in graduate school, but it pales in comparison to what I learned about the natural world from my parents. You taught me how to observe and appreciate nature, and also how to not die when I am out in the wilds. This project is also dedicated to the beavers that were captured as part of my research efforts.

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ABSTRACT

The activities of beavers (*Castor canadensis*) provide a variety of benefits to stream systems by capturing and storing water and sediment, expanding riparian areas, and increasing habitat heterogeneity. Understandably, land and wildlife managers are interested in using beavers as a habitat restoration tool. However, streams targeted for restoration are often degraded and lack recent beaver activity, and therefore represent suboptimal habitat. The habitat selection process for beavers in suboptimal and unmodified habitats provides a natural analogue to beaver restoration, but the process is not well-understood. I radio-marked juvenile beavers and conducted beaver-use surveys in tributary streams of the Gallatin and Madison River drainages in southwest Montana to investigate dispersal, survival, and settlement site selection by beavers colonizing novel areas. My objective was to study beaver ecology in the context of beaver restoration to improve identification of suitable project locations. Beaver colony densities in the study area were low or average, though colony densities in suitable habitat were generally high. There was evidence of delayed dispersal, and as the density of active beaver colonies increased the probability of dispersal decreased. Radio-marked beavers that dispersed settled quickly and dispersal distances were highly variable. Most beavers settled in active colonies or other beaver-modified habitats, and colonization of unmodified stream segments was rare. My top habitat selection models indicated new settlement sites were located in stream segments characterized by low gradients, dense woody riparian vegetation close to the stream, and relatively narrow stream channels. Stream channels at new settlement sites were more variable both in cross-sectional and longitudinal depth and were more heavily influenced by secondary channels than unsettled sites. My results suggest beavers select for pre-engineered habitat over unoccupied stream segments, and in novel areas habitat conditions that facilitate stable dam construction appear most important. When choosing project locations, restoration practitioners should consider local beaver colony locations and densities to assess the potential for dispersers to reach the restoration site. Stream segments that provide dam resiliency and hiding cover should be targeted for initial restoration efforts, and pre-engineering of habitat prior to beaver occupancy may increase the probability of successful colony establishment.

CHAPTER ONE

LITERATURE REVIEW

Influence of Beaver Activity on Riparian and Wetland Ecosystems

Beavers (*Castor* spp.) exert profound influence on the wetland and riparian habitats they occupy through the construction of dams and lodges, digging of tunnels and channels, and removal and redistribution of woody vegetation. While the effects of beavers occupying an area can vary, in smaller headwater stream systems beaver activities expand and maintain healthy and productive riparian and wetland habitats (Naiman et al. 1988, Collen and Gibson 2001, Wright et al. 2002, Pollock et al. 2017). Beavers are considered a keystone species and an ecosystem engineer because they drastically modify the habitats they occupy, creating conditions that allow certain plant and animals species to inhabit an area where they may not otherwise occur (Jones et al. 1994, Power et al. 1996, Jones et al. 1997). Beaver colonies within a drainage exist as a "shifting mosaic of environmental conditions, dependent upon pond age and size, successional status, substrate, hydrologic characteristics, and resource inputs" (Naiman et al. 1988), providing a wide variety of habitat types in both the aquatic and terrestrial realms. It has been postulated that ecosystem engineers such as beavers contribute significantly to landscape habitat heterogeneity and can therefore increase species richness at the landscape scale (Naiman et al. 1988, Jones et al. 1997, Wright et al. 2002). Ultimately, the combination of the effects of beaver dams and beaver foraging habits associated with colonies influences plant and animal community composition, richness, and diversity in riparian areas (Naiman et al. 1988, Russell et al. 1999, Wright et al. 2002, Cooke and Zack 2008, Bartel et al. 2010).

Beavers alter their environment in many ways but their most influential effect comes from the impoundment of water through dam building (Macfarlane et al. 2015). Beaver dams exert a multitude of effects on the streams they impound, most importantly: 1) decreasing current velocity and stabilizing annual stream discharge by buffering runoff events which protects the stream system from excessive flood damage (Meentemeyer and Butler 1999, Pollock et al. 2003, Green and Westbrook 2009, Nyssen et al. 2011), 2) capturing and storing precipitation providing a surplus of water to augment low flows in the summer and fall (Naiman et al. 1986, Naiman et al. 1988, Westbrook et al. 2006, Jin et al. 2009, Nyssen et al. 2011, Majerova et al. 2015), 3) expanding the wetted area of streams by raising the water table which can promote the establishment of both woody riparian and aquatic vegetation (Naiman et al. 1988, Rosell et al. 2005, Green and Westbrook 2009, Westbrook et al. 2010), 4) increasing stream channel complexity by reconnecting stream channels to the floodplain and forcing overbank flow (Westbrook et al. 2006, Polvi and Wohl 2012, Polvi and Wohl 2013, Pollock et al. 2014, Majerova et al. 2015), and 5) increasing the retention of sediments and organic matter which can expand the width of the riparian zone and have substantial effects on nutrient cycling and invertebrate communities within dam-created ponds (McDowell and Naiman 1986, Naiman et al. 1986, Naiman et al. 1994, Gurnell 1998, Meentemeyer and Butler 1999, Butler and Malanson 2005, Pollock et al. 2007). As a colony ages, beavers will often expand their territory either by making existing dams larger, or by creating dams up- or downstream to flood new areas. Although stored sediment loss can be severe when dams are breached (Green and Westbrook 2009, Levine and Meyer 2014), drainages with healthy beaver populations can eventually be filled with dams of various successional states and can trap enough sediment over time to rebuild floodplains (Pollock et al. 2007).

The water and sediment retention capabilities of beaver-mediated habitats are even more critical in the face of increasing global temperatures. Over the next century, the changing climate is projected to cause widespread drought and water shortages especially in the arid and semi-arid regions of the western United States (Barnett et al. 2008, Hood and Bayley 2008, Baldwin 2015). Most of the precipitation in this region comes in the form of snowpack and climate models predict lower snowpack and earlier spring runoff, leaving inadequate water resources in the summer and fall seasons (Stewart et al. 2005, Hamlet 2006, Hidalgo et al. 2009, Baldwin 2015). Additionally, water resources are already spread thin due to increasing demand from expanding urban populations, industry, and agriculture. Retention of water in the higher elevation headwaters of major river systems will be critical to maintaining water resources and wildlife habitat in the future. The influence of strong beaver populations damming and restructuring streams across a landscape could significantly help offset the effects of climate change by sequestering carbon, increasing water storage, and contributing to increased ecosystem resilience (Naiman et al. 1988, Hood and Bayley 2008, Baldwin 2015).

History and Status of Beavers in North America

Populations of the North American Beaver (*Castor canadensis*) were once estimated at 60−400 million individuals before European settlement (Muller-Schwarze 2011). Starting in the mid-17th century beaver numbers began to decline in the eastern United States as they were heavily trapped to support a demand for beaver felt hats in Europe. As numbers diminished in the east, trapping expeditions began expanding into the relatively unexplored western part of the country to find new areas to trap beavers. The trapping of beavers continued unregulated through the early 1900s until beavers were almost extinct in North America. Once the demand for fur hats decreased, beavers were able to start their recovery and now, due in large part to changes in land management and stricter controls on trapping, beaver populations are recovering (Muller-Schwarze 2011).

Currently, there are thought to be 6−12 million beavers in North America, and although they have reoccupied most of their former range, their numbers still represent a fraction of the historic population. Considering the magnitude of influence beavers have on streams and rivers, the loss of water storage, sediment retention, and riparian habitat following their removal is substantial. Undoubtedly, beavers are an integral part of the ecosystems in which they are found, and current research widely supports their presence in stream systems as a substantial benefit to ecosystems and associated riparian and wetland habitats (Collen and Gibson 2001, Wright et al. 2002, Pollock et al. 2017).

Since the near-eradication of beavers in the United States, increased rates of stream incision and loss of in-channel sediment storage has led to widespread deterioration of streams and riparian areas (Armour et al. 1991, Marston 1994, Bernhardt

2005, Pollock et al. 2007). The severe declines in beaver populations coincided with overexploitation and subsequent degradation of western North American rangelands due to overgrazing (Russell 1905, Buckley 1993, Kauffman et al. 1997). Overgrazing, combined with other anthropogenic disturbances such as agriculture, logging, fire suppression, mining, and water development have taken a heavy toll on riparian areas and stream systems of the western United States (Armour et al. 1991, Dahl 1997, Goodwin et al. 1997, Dahl 2011). Consequently, many streams across the western United States are subject to erosional down-cutting as degraded uplands and lack of streamside vegetation allows erosion to proceed unabated which straightens stream channels, simplifies floodplains, and allows flood waters to gain high velocities (Marston 1994, Peacock 1994, Pollock et al. 2007, Burchsted et al. 2010). Under such conditions, streams experience severe narrowing of riparian zones as water tables drop and formerly wetted soils thick with riparian vegetation shift to drier upland habitat types (Dahl 2011, Pollock et al. 2014). Freshwater riparian and wetland habitat loss has been severe and widespread and currently the contiguous United States has less than 50% of its original wetlands (Dahl 2011).

Fortunately, due mostly to agriculture-based conservation programs and other incentives, the trend of riparian and wetland loss has been reversed and the United States is now experiencing a net gain in wetlands annually (Dahl 2011). Although many streams and rivers along with their associated upland habitats have been recovering since the era of overexploitation, much of the riparian areas are still in a state of degradation and in need of restoration (Bernhardt 2005, Dahl 2011). It is especially pertinent to rehabilitate historical riparian areas as they make up less than 2% of the western landscape yet provide resources for a disproportionately large number of species, including humans (Knopf et al. 1988). However, habitat restoration can be costly and labor intensive and consequently is often only applied to relatively small area (Bernhardt 2005). Therefore, passive, low cost, and low maintenance stream restoration options that can provide benefits at a large spatial scale are highly desirable.

Beavers as a Tool for Riparian and Wetland Habitat Restoration

Lake et al. (2007) argue that stream restoration projects commonly ignore major ecological principles that influence the ability of a stream system to recover to a more desirable state, a notion that is well-supported in the field (Jungwirth et al. 2002, Bernhardt 2005, Palmer 2008). Authors contend stream restoration practices too often emphasize form over function, opting for expensive and intrusive forms of restoration that quickly try to improve degraded streams to comply with a set standard (Palmer 2008). Short-term goals that improve a relatively small area are frequently the focus over long-term monitoring and large-scale application (Lake et al. 2007), and the high failure rate of such projects is well-documented (Bernhardt 2005, Palmer 2008). Recently, researchers have emphasized a need for ecology-based solutions that work to correct functional aspects of the biotic and abiotic factors that regulate stream systems while embracing the inherent instability that characterizes such systems (Palmer 2008). Rather than trying to force a system to react a certain way through intensive management, an ideal restoration practice adjusts or redirects components of the system that lead it to unravel towards gradually allowing it to improve. An ideal stream restoration strategy should also be as low impact and inexpensive as possible, use passive management techniques, and allow for spatial and temporal variation of stream channel and floodplain conditions over time (Jungwirth et al. 2002, Lake et al. 2007, Palmer 2008).

Beaver activity in streams can address many of the issues that hinder riparian restoration efforts, and encouraging beavers to colonize an area can be accomplished with relatively small budgets. As a result, beaver restoration projects are increasing in popularity and scope (Pilliod et al. 2017). Beaver restoration projects are especially common in the western United States where wetland and riparian areas are relatively scarce yet vitally important to ecosystem health, connectivity, and resiliency (Pilliod et al. 2017, Pollock et al. 2017). A robust body of scientific literature on the benefits of beavers, combined with greater public outreach in the form of nature documentaries and grassroots organizations, has led to increased recognition among human populations of the potential ecologic and economic benefits of healthy and well-managed beaver populations (McKinstry and Andersen 1999, Pollock et al. 2017). A wide range of studies have linked riparian habitat improvements to the presence of beaver colonies (see reviews by: Naiman et al. 1988, Collen and Gibson 2001, Pollock et al. 2017). In conjunction with these studies, researchers have attempted to understand habitat use and selection by beavers in order to identify key environmental conditions necessary for beavers to occupy an area (Howard and Larson 1985, Beier and Barrett 1987, Easter-Pilcher 1987, Dieter and McCabe 1989, Harris 1991, Barnes and Mallik 1997, Suzuki and McComb 1998, Scrafford et al. 2018). This body of habitat suitability research has been widely used to guide most beaver-mediated stream and habitat restoration projects implemented in the last 20 years (Pollock et al. 2017).

Beaver-mediated habitat restoration (hereafter, "beaver restoration") projects can vary widely in their goals, strategies, monitoring efforts, and budgets. Direct reintroductions of beavers to stream systems have been used in many instances (Albert and Trimble 2000, McKinstry and Anderson 2002, Babik and Meyer 2015, Woodruff 2015, Pilliod et al. 2017). Others have worked to improve riparian conditions to support a struggling beaver population or facilitate natural occupancy by beavers expanding from nearby source populations (Pollock et al. 2011, Bouwes et al. 2016, Pollock et al. 2017). Many projects use Beaver Dam Analogues (BDAs), or similar instream structures to accomplish initial stream restoration goals, and find their efforts become self-regulating when beavers take advantage of improved habitat conditions to occupy the site naturally (Pollock et al. 2011, Bouwes et al. 2016, Pollock et al. 2017). BDA-supported colonies can often provide a stepping stone for natural beaver occupation of other sites within a stream or drainage (Bouwes et al. 2016). Reinforcing existing beaver dams in danger of blowing out due to unstable stream conditions is another strategy for facilitating long-term beaver occupation in an area (Apple 1985, Pollock et al. 2011).

Beaver translocations are a popular way to deal with nuisance beavers and improve stream health (Pilliod et al. 2017). While beavers are naturally expanding into areas of their historic range, some stream systems may be isolated from source populations of beavers. Isolation may be due to poor stream conditions that act as barriers to dispersal movements, or lack of landowner tolerance between the source population and the isolated stream. Reintroductions of beavers into isolated streams may be a necessary step towards improving stream conditions. However, the process of capturing and moving beavers can be costly and controversial. If conditions at the release site are not appropriate, released beavers may suffer high mortality rates or immediately leave the area (McKinstry and Anderson 2002, Petro et al. 2015). Transient beavers that have left the restoration site may attempt to establish on adjacent lands where they can cause property damage and need to be trapped out (McKinstry and Anderson 2002, Pollock et al. 2017). If the potential for beavers to immediately leave a reintroduction site is high, wildlife managers may oppose any action they see as a misuse of time and money and that may strain relationships between agencies and private landowners.

Unfortunately, almost every project using beaver reintroductions has had a poor to modest success rate in getting released beavers to colonize the site targeted for restoration (McKinstry and Anderson 2002, Petro et al. 2015, Babik and Meyer 2015, Pollock et al. 2017). The tendency of released beavers to leave reintroduction sites may be due to the process of being trapped and transported, or may reflect inappropriate conditions at the release location. Several studies have noted transplanted beavers moving significant distances after reintroduction (Hibbard 1958, Knudsen and Hale 1965, McKinstry and Anderson 2002, Petro et al. 2015), and in some instances authors hypothesize beavers left reintroduction sites due to lack of suitable habitat (Albert and Trimble 2000, Pollock et al. 2017). It should be noted there are many beaver reintroduction efforts that go underreported (Pilliod et al. 2017), and success rates under varying environmental, sociological, and logistical constraints are unknown.

One of the first steps in any beaver restoration project is deciding whether to translocate beavers, support existing colonies, pre-engineer structures to encourage natural settlement, or construct beaver mimicry structures to improve stream conditions without an explicit goal of beaver occupation. Many factors can influence this decision including agency and landowner support, budgetary requirements, availability and efficacy of transporting beavers, local water rights regulations, impacts to fisheries and other wildlife, and potential for property damage (McKinstry and Andersen 1999, Collen and Gibson 2001, McKinstry and Anderson 2002, Pollock et al. 2017). While Pollock et al. (2017) and other documents provide guidance on strategy selection, the guidance is mostly based on expert knowledge or habitat suitability studies that have not accounted for suboptimal habitat quality that characterizes most restoration sites. Much time and money can be wasted if the appropriate strategy is not employed. For example, a restoration site where managers' plan on building beaver mimicry structures to encourage natural settlement may never be settled if the location is too isolated from a source colony. Similarly, a group may spend many thousands of dollars to capture, house, disease-test, transport, and release beavers to an area that may have been colonized naturally if dispersing beavers from local colonies were given a head start with some relatively inexpensive BDAs.

Many beaver restoration projects have been successful on fairly modest budgets, and this has spurred interest in using beavers as a standard tool for stream restoration. However, not all projects accomplish their goals. While it is often difficult to determine the exact reason beavers do not occupy a site targeted for restoration, it is reasonable to assume a major component of project failure is the selection of sites that do not have the appropriate stream morphology, vegetative characteristics, and hydrology to support beaver colonies. Each beaver restoration project has a unique set of conditions and challenges, and learning how to improve restoration efforts from past successes is hindered by major differences in stream and riparian conditions among restoration sites. Additionally, there is a lack of empirical data concerning pre-release habitat conditions to make inference on why particular restoration sites are more successful than others. While the literature is extensive on appropriate habitat conditions for beavers to colonize an area with good habitat, relatively little is known about how beavers select settlement sites when habitat is marginal in quality or limited in extent, as is the situation with most beaver restoration projects.

In order for land and wildlife managers to support beaver restoration projects, it is important to understand baseline habitat conditions where beavers have adequate resources to start a new colony. It is also important to understand how local environmental conditions and the distribution and density of beaver colonies influence the initial discovery and acceptance of a settlement site by beavers. The natural colonization process of dispersing juvenile beavers can provide important information on the dispersal and habitat selection process in similar environments as those frequently targeted for beaver restoration efforts.

Habitat Selection

Habitat selection by beavers has been well-studied both for the North America Beaver and the European Beaver (*Castor fiber*). Researchers usually deconstruct habitat selection into major components which influence the ability of beavers to establish, maintain, and expand a colony. Variables related to habitat are commonly divided into two groups: 1) stream geomorphology of both lotic and lentic systems beavers occupy, and 2) vegetation which is the primary food resource for beavers and is used to construct dams and lodges. My research focuses on stream systems so for the remainder of this thesis I will only be referring to habitat selection by beavers in lotic environments.

Stream geomorphology features reflect the form and function of the water, stream channel, substrate, and floodplain of lotic systems as well as the interaction of these features with one another and the uplands of the watershed (Sear et al. 2010). Stream geomorphology features impact beaver habitat selection by governing the location and durability of lodges and dams, while also affecting the growth form of vegetation and the ease with which beavers can access that vegetation. Dam and lodge sites need to have stable banks, be on low energy stream sections, and have adequate construction materials in order to maintain deep waters and expand access to other areas of the floodplain (Allen 1982, Muller-Schwarze 2011). Beavers must also be able to access woody vegetation while remaining fairly close to water which acts as their primary escape route from predators (Muller-Schwarze 2011). The procurement of food requires energy and as central-place foragers, beavers must balance distance to vegetation from their lodges and from the water with the size and nutritional value of the vegetation to avoid predation and fulfill their energy requirements (Jenkins 1975,1980; McGinley and Whitham 1985; Gallant et al. 2004).

There are a wide variety of habitat variables influencing the ability of beavers to occupy an area, and the complexity with which these variables interact is difficult to predict. Stream systems are inherently dynamic (Jungwirth et al. 2002), even more so in the western United States. For most systems in the West the snowmelt-dominated water regime results in large floods on an annual basis that scour banks, reshape stream channels, and shift the pathways along which water moves through the system. The constant change would be difficult for any stream-dwelling animal to cope with, but beavers are occupying streams and trying to establish a stable, well-defended territory into which much time and energy is expended constructing dams, digging channels, and building lodges. The power of the stream, the availability of forage and construction materials, and the medium on which dams and lodges must be built all affect the size of a colony and the length of time it remains active (Slough and Sadlier 1977, Howard and Larson 1985, Scrafford et al. 2018). Despite these complexities, researchers have suggested a set of components that seem to best describe beaver habitat selection and are somewhat consistent across study areas (Allen 1982, Muller-Schwarze 2011, Pollock et al. 2017). I will focus on many of these well-known beaver habitat variables to make my study comparable to others and more applicable in other locations. I will also investigate variables that may be unique to my particular system to better assess habitat selection at a local level.

Influence of Stream Geomorphology

Stream gradient has been measured in almost every study of beaver habitat selection and all studies have observed increasing beaver colony occupancy, density, and longevity with decreasing stream gradient (Slough 1976, Howard and Larson 1985, Beier and Barrett 1987, Easter-Pilcher 1987, Suzuki and McComb 1998, Curtis et al. 2004, DeStefano et al. 2006, Cox and Nelson 2008, František et al. 2010). Low gradient streams generally offer slower flows, wider floodplains, more preferred plant species, and greater assurance that dams and lodges will not be destroyed by high-energy flood waters (Allen 1982, Suzuki and McComb 1998). Additionally, damming activities in lower gradient streams with wider valley bottoms allows larger water impoundments with less dam construction and maintenance, increasing the amount of accessible resources and escape cover (Slough 1976, Johnston and Naiman 1990).

Stream width was found to be an important predictor of beaver colony presence, density, and persistence in many studies (Slough 1976, Howard and Larson 1985, Beier and Barrett 1987, Easter-Pilcher 1987, Barnes and Mallik 1997, Suzuki and McComb 1998, Curtis et al. 2004), though this metric is likely correlated with stream gradient in most areas. Some researchers found increasing stream width to be correlated with increasing probability of beaver occupancy (Beier and Barrett 1987, Easter-Pilcher 1987), and increasing colony longevity and density (Howard and Larson 1985). However, these studies were mostly on larger streams or rivers where dam building is not necessary for beavers to maintain a colony. In smaller streams most authors have found increasing stream width correlated with decreasing probability of beaver occupancy (Curtis et al.

2004), as well as decreasing dam density (Suzuki and McComb 1998) and overall colony density (Slough 1976). Conversely, in mountain streams of Montana Scrafford et al. (2018) observed no influence of stream width on colony presence or longevity. Stream width likely affects the ability of beavers to build dams in that wider streams may be harder to dam (Suzuki and McComb 1998), and also are associated with larger streams with greater potential for destructive high water events. At some point, streams get wide and deep enough that dam-building becomes unnecessary or impossible for beavers, and habitat preferences may shift to factors not associated with dam construction and maintenance. For these reasons, it is likely stream width by itself does not influence beaver activity in an area. Instead, stream width likely interacts with variables such as bank height, stream depth, and gravel bar size, all of which may influence the need for, and strength of, dams and lodges.

Stream depth has an effect on multiple aspects of beaver activities. Deeper streams generally have a more stable water supply throughout the year. Deeper streams may also require smaller dams as the primary purpose of beaver dams is to create adequate water depth for overwinter survival and predator avoidance. Many studies have linked increasing stream depth to increasing probability of occupancy (Easter-Pilcher 1987, Dieter and McCabe 1989, Suzuki and McComb 1998, Scrafford 2011) as well as increasing density (Beier and Barrett 1987), and persistence (Scrafford 2011) of beaver colonies. Contrarily, Barnes and Mallik (1997) suggest shallower streams may be easier to dam. There is likely a threshold for beavers where a deeper stream adequately covers lodge entrances and allows access to winter food caches without the need to construct dams, but when dam building is required it is easier for beavers to dam a shallower stream. Overall, the influence of stream depth and stream width will depend on the stability of the water supply, flow rate, and height of the stream banks, all of which are influential in determining what strategy beavers will employ to successfully colonize an area (i.e., dam building or bank dwelling).

Stream flow rate may be influential in settlement site selection by beavers because areas with higher flow rates may be more difficult to dam or may be more unstable. There is some evidence beavers prefer slower waters (Easter-Pilcher 1987, Harris 1991), but overall this factor is not well-understood. Few studies specifically measured flow rate in relation to beaver habitat suitability, likely because this metric is drastically altered by beavers once they occupy an area. Researchers mostly assume stream gradient is a good enough metric for evaluating flow rate in relation to beaver habitat selection (i.e., streams with higher gradient will have higher flow rate). However, flow rate is also influenced by the width and depth of the stream, suggesting discharge may be a better metric overall.

Several studies have evaluated stream sinuosity in relation to beaver colonization (František et al. 2010), colony presence (Easter-Pilcher 1987), and colony persistence (Scrafford et al. 2018). Stream sinuosity is related to many other hydrologic and geomorphologic variables in that it determines the capacity for dams to withstand high waters. Streams with greater sinuosity experience slower flow rates as the meandering of the stream dissipates energy. More sinuous streams also provide greater access to resources for beavers as they can cut across oxbows or forage on peninsulas that provide access to escape cover (Boyce 1974). Scrafford et al. (2018) posits streams with high sinuosity provide deep waters along the outside of bends which can be used by beavers in conjunction with or, in place of, constructing a dam (Boyce 1974, Hartman 1994). Personal observations in southwest Montana confirm that many of the lodges and bank dens used by beavers occur in deep holes on the outside bend of stream meanders.

Only Suzuki and McComb (1998) have explicitly attempted to relate floodplain width (sometimes referred to as “valley width”) to beaver use of an area, though other authors have commented on this variable in relation to beaver habitat suitability (Allen 1982, Vore 1993, Pollock et al. 2017). Researchers mostly agree that beavers prefer wider floodplains which are usually lower in gradient, have more sinuous stream channels, and allow for greater expansion of colonies as a result of dam building. The reason floodplain width has been absent from most beaver habitat selection studies may be the complexity with which other factors interact with floodplain width, rendering inference on the mechanisms underlying this variable difficult. Additionally, floodplains are categorized based on the level of flood event that is capable of inundating them with water (e.g., 100-year floodplain), so establishing which floodplain is most influential on beaver activity would likely be inconsistent across study areas. Logically, the most important floodplain width for beavers would be the immediate floodplain around the stream channel that would be flooded by damming activity (hydrologic floodplain). The width of the hydrologic floodplain would directly affect the expansion of stream waters behind a dam, influencing the ability of beavers to increase their foraging area. Hydrologic floodplain width would also impact the resiliency of dams which are more likely to withstand high flows if stream power is dissipated by being pushed out into the floodplain rather than pushing directly onto the face of the dam (Pollock et al. 2007).

Howard and Larson (1985) and Barnes and Mallik (1997) both found upstream watershed size to be an important factor influencing beaver colony density and the location of beaver dams, respectively. Furthermore, František et al. (2010) observed that watershed size became important to settlement by reintroduced European beavers only late in the colonization of a large river basin, when beavers were approaching the carrying capacity for the area. Upstream watershed size is likely related to the amount of water available for beavers to dam a stream and create a colony. Smaller watersheds may not be capable of supplying year-round water or may not contain large enough floodplains for beaver damming activities. Alternatively, a large watershed may cause severe water fluctuations leading to dam and lodge instability during high water events.

Scrafford et al. (2018) measured the distance from the colony center to the nearest secondary channel and found increasing longevity of beaver colonies with decreasing distance to secondary channels. He defined secondary channels as any channel around a beaver colony other than the main stem of the stream or river such as side channels, tributary confluences, or seeps and springs that parallel the main stem (Scrafford 2011). Overall, beaver colonies that took advantage of secondary channels were occupied more often than colonies located only on the main stem of a stream. The author hypothesized beavers select for these locations because the secondary channels provide a larger area for safe foraging and dam building (Scrafford et al. 2018). Secondary channels also act refugia from damaging high water events, which can be important for colony longevity and success especially in areas that experience damaging floods (Scrafford et al. 2018).

Gravel bar size is the distance between the vegetated bank of a stream and the water's edge (Scrafford et al. 2018). For beavers, the size of the gravel bars along a stream may influence the construction of dams and avoidance of predators. Generally, a relatively steep, stable bank is needed to anchor lodges and dams (Collins 1976, Scrafford 2011), and a larger distance between the water and streamside vegetation exposes beavers to predators and increases the amount of energy expended while foraging (Jenkins 1980, McGinley and Whitham 1985, Basey et al. 1990, Scrafford 2011). In mountain streams of Montana, Scrafford et al. (2018) found increasing gravel bar size resulted in decreased colony persistence and lower odds of historic beaver use on a given stream section. In Wyoming, Collins (1976) noted large sections of streams were unsuitable for beavers due to large gravel bars, which he hypothesized prevented beavers from establishing structures and was a key factor attributed to relatively low colony densities in some areas.

Beavers must dig channels and tunnels as well as excavate lodges or bank dens, so researchers hypothesize beavers prefer streams and stream sections with finer substrates. Studies of beavers in multiple areas confirm this assertion (Howard and Larson 1985, Easter-Pilcher 1987, Harris 1991, Pinto et al. 2009). Finer substrates facilitate easier digging of tunnels and channels and are more useful for construction as mud and silt are frequently used to seal lodges and dams. Conversely, beavers also use large rocks to their advantage as anchoring points for dams and as final building blocks to weigh down completed dams. Substrate is fundamentally linked to other important beaver habitat suitability metrics (e.g., sinuosity, gradient, plant growth), so it may be difficult to disentangle the interactions among these variables when making inference regarding the effect of substrate on beaver colonization.

Influence of Vegetation

The vegetative resource is probably the most studied aspect of beaver habitat suitability and selection. Researchers have used a variety of variables to compare the amount and character of vegetation in and around active beaver colonies to unused or abandoned sites. The presence of woody vegetation is essential for beaver occupancy and persistence in an area (Allen 1982, Muller-Schwarze 2011). Generally, beavers will use any species of woody material for construction activity, but are more selective in their choice of food species (Jenkins 1975, Muller-Schwarze 2011). Woody plant species make up the entirety of winter food caches for beaver colonies in freezing climates and are therefore a limiting resource that allows for overwinter survival (Allen 1982). While the availability of a stable food and construction resource is necessary for beavers to occupy an area, many studies have found vegetative variables to be poor predictors of beaver colony presence, density, and success, relative to the importance of stream geomorphology variables (Jenkins 1980, Howard and Larson 1985, Beier and Barrett 1987, Barnes and Mallik 1997, Scrafford et al. 2018). However, the presence of woody vegetation is absolutely essential for beavers to occupy a stream section, and therefore must be considered in any study of beaver habitat selection. Allen (1982) asserts the value of the vegetation for beavers is dependent on the density, size class, and species composition of woody vegetation, and most habitat suitability studies seek to quantify these aspects of streamside vegetation. Overall, researchers have found areas used by beavers have more woody riparian vegetation than areas with no beaver use (Curtis et al. 2004, Breck et al. 2012). A larger initial resource of woody plants may be necessary for construction of strong, stable dams at a new colony and thereafter a minimal amount of vegetation can provide necessary food resources to sustain a colony (Howard and Larson 1985). Woody vegetation can also change drastically with beaver occupancy, so it is difficult to discern cause and effect in terms of the state of riparian vegetation in and around beaver colonies.

Canopy cover can be a good indicator of the density of food and construction material available along a stream and can be measured in the field or using remote-sensing data and a GIS. Canopy cover of woody vegetation can be changed by beaver occupancy, causing some association of lower canopy cover with higher beaver densities (Suzuki and McComb 1998). Therefore, canopy cover is a useful metric for evaluating vegetation density preferences before major changes take place. A high canopy cover can help conceal lodges and heavily used pathways (Dieter and McCabe 1989), while also indicating a robust and potentially sustainable forage resource (Allen 1982).

The stem size of woody vegetation can influence the ability of beavers to balance energy requirements and predation risk associated with gathering of food and construction materials (Jenkins 1980, Gallant et al. 2004). Stem size also dictates the type and size of dams beavers can build, and some stem sizes may be inadequate for the stream channel that needs to be dammed. Researchers have found ~ 90% of beaver foraging occurs within 30 m of the water (Hall 1960, Jenkins 1980, Belovsky 1984, Gallant et al. 2004), and studies suggest that as beavers forage further from shore they select for smaller stem sizes of forage species. As a result, beavers may select against areas with larger trees because large trees take more energy to cut down and transport. The presence of large trees may also tamper the growth of smaller understory shrubs which are preferred by beavers for food (Cox and Nelson 2008). The overall preference for smaller stems and trunks of preferred forage species by beavers is well-documented (Shadle et al. 1943, Collins 1976, Allen 1982, Easter-Pilcher 1987, Barnes and Mallik 1997, Cox and Nelson 2008). However, these studies were mostly in areas where beavers harvest large trees for food and construction materials, and stem size preferences in willow-dominated systems are not well-understood. The trade-offs for beavers in terms of energy input into foraging may be greatly reduced or non-existent for willow-dominated streams because of the low-growing, relatively small, and more uniform stem sizes that characterize willow species.

The width of the woody riparian vegetation zone has been found to increase beaver presence and density (Beier and Barrett 1987, Cox and Nelson 2008). When considered alongside a metric of woody vegetation density, the width of the woody riparian vegetation zone gives a general sense of the food and construction material resource available. Riparian width also influences how isolated beavers are from human activities and other dangers. Edge habitat along the boundaries of riparian zones where willows thin out before transition to uplands are frequently patrolled by predators so a wider woody riparian vegetation zone may better protect beavers from predation.

Habitat Selection in Relation to Beaver Restoration

While the studies described above provide valuable information on habitat selection by beavers, it is difficult to interpret their results in the context of beaver restoration projects. Habitat suitability studies for beavers generally compare areas where beavers have established dams and lodges to either random locations (Easter-Pilcher 1987, Dieter and McCabe 1989, Harris 1991), or unoccupied and abandoned stream sections (Beier and Barrett 1987, Barnes and Mallik 1997, Suzuki and McComb 1998, Cox and Nelson 2008). With the results of these studies, researchers have pursued modeling potential beaver activity at landscape scales to better understand and map potential beaver habitat (Howard and Larson 1985, Macdonald et al. 2000, Carpenedo 2011, Macfarlane et al. 2015). However, beavers drastically modify their surroundings and in doing so fundamentally alter potentially important information about habitat conditions that promoted colonization at a specific location. As a result, many metrics used to assess suitable habitat may be altered by the time researchers collect data, and therefore may not accurately portray the state of the habitat when the colony was originally established.

The consequence of beaver-induced habitat manipulations to our understanding of habitat selection by beavers has not gone unnoticed by researchers. Many researchers designed data collection protocols to measure pre-colonization conditions even though the measurements occurred at established colonies (Howard and Larson 1985, Barnes and Mallik 1997, Suzuki and McComb 1998). Attempting to measure pre-colony conditions *post hoc* certainly provides better information about initial habitat conditions, but it is often difficult to detect what has and has not been modified by beavers as changes in water table elevation and stream channel morphology manifest in ways that cannot be reconstructed and measured. Several authors designed their research projects with the specific goal of evaluating habitat at sites newly settled by beavers (Harris 1991, Smith 1997, DeStefano et al. 2006). However, it appears abandoned colonies are preferred by dispersing beavers, and settlement in habitat minimally altered by beaver activity was rare in all studies. Therefore, a better understanding of pre-colonization habitat conditions in areas that have not been drastically modified by beaver activity is necessary to better understand colony site selection in the context of beaver restoration.

Beaver Dispersal

In the spring each year, young beavers disperse from their natal colonies and attempt to establish territories of their own. Dispersal usually occurs at around 1−3 years of age (Bradt 1938, Sun et al. 2000, McNew and Woolf 2005). There are several possible outcomes for a dispersing beaver depending on habitat quality and the density of beavers in the area:

1) The disperser may move into an active colony as a new breeder when a member of the original breeding pair dies or is expelled by the disperser (Brooks et al. 1980, Sun et al. 2000, Mayer et al. 2017b).

2) The disperser may occupy a recently abandoned colony with dams and lodges in place (Smith 1997, Sun et al. 2000).

3) The disperser may rebuild dams and lodges in a historically occupied segment, but where beavers have not been present long enough for the stream channel to return to a fairly pre-colony state.

4) The disperser may construct new dams and lodges in a previously unoccupied stream section.

5) The disperser may remain transient for a long time period while it looks for a mate and a suitable settlement site (Aleksiuk 1968, Collins 1976, Sun et al. 2000).

6) The disperser may return to its natal colony and either disperse again in the future or take over as a member of the breeding pair (Mayer et al. 2017b).

Key factors influencing the outcome of a dispersal and subsequent settlement site selection by beavers are local colony densities and the availability of territories. In areas with low beaver densities dispersal tends to increase and dispersers in high quality habitat will often find a suitable settlement site near their natal colony, while those in low quality habitat may have to travel long distances before settling (Howard and Larson 1985, Smith 1997, Cunningham et al. 2006). In areas with high beaver densities, dispersal from the natal colony is often delayed until suitable habitat becomes available or juveniles are expelled by the breeding adults (Smith 1997, Sun et al. 2000, Mayer et al. 2017b). The mechanisms behind delayed dispersal are complex, but researchers believe a combination of the availability and quality of unoccupied territories within dispersal range of the natal colony, as well as habitat quality at the natal colony, contribute to delayed dispersal (Stacey and Ligon 1991, Koenig et al. 1992, Smith 1997, Mayer et al. 2017a). Beavers that delay dispersal may increase lifetime inclusive fitness by acquiring experience and body mass before dispersal, cooperating in territory defense and predator avoidance, helping to build and repair structures, and participating in the raising of siblings (Stacey and Ligon 1991, Koenig et al. 1992, Mayer et al. 2017a). Beavers that do disperse in high quality habitat with high beaver densities may have to travel great distances, be more susceptible to predation, and endure attacks by territorial beavers as they try to find a suitable place to settle. If high quality habitat does not become available, or if the disperser cannot find high quality habitat anywhere along their dispersal route, they are often forced to settle in marginal and suboptimal habitats (Howard and Larson 1985, Harris 1991, Smith 1997, Cunningham et al. 2006, DeStefano et al. 2006, František et al. 2010, Scrafford 2011).

Suboptimal beaver habitats have lower quality or quantities of resources necessary for colony establishment and success (Smith 1997, Cunningham et al. 2006). Several studies have investigated settlement patterns of beavers colonizing new areas and found high quality habitat is usually settled first followed by settlement of marginal habitats as the population approaches carrying capacity (Howard and Larson 1985, Cunningham et al. 2006, DeStefano et al. 2006, František et al. 2010). In Montana, Scrafford et al. (2018) observed colonies settled first by a population of reintroduced beavers were occupied more often and for longer periods than colonies settled in later years indicating the colonies settled later were likely in poorer habitat. Howard and Larson (1985) also observed colony sites selected first had greater longevity and hypothesized habitat characteristics selected for during the settlement process may play a role in the length of time the site will be occupied by beavers.

In areas where most of the high quality habitat is occupied, dispersing beavers must attempt to establish colonies in novel locations with little to no previous beaver use and marginal habitat. These unmodified and suboptimal habitats are similar to the types of streams where most beaver restoration projects occur (Apple 1985, Albert and Trimble 2000, McKinstry and Anderson 2002, Bouwes et al. 2016, Pollock et al. 2017). The marginal habitats dispersing beavers are encountering therefore provide a natural analog to the types of stream sections where beaver colonization would be desirable as part of a restoration project. Logically, a stream system or riparian area targeted for restoration will be characterized by some combination of a narrow riparian zone, encroachment of upland vegetation types, lack of slow-moving pools and deep waters, and an incised stream channel, and many beaver restoration projects are explicit attempts to restore these types of degraded streams (Apple 1985, Albert and Trimble 2000, Pollock et al. 2011, Pollock et al. 2014, Bouwes et al. 2016). Studying the natural colonization process of beavers in suboptimal habitats that have been relatively unmodified by beaver activity will help identify key habitat conditions that should characterize restoration sites to encourage beaver colonization, as well as components of the stream system that may be manipulated through management actions to allow beaver colony creation and expansion.

CHAPTER TWO

HABITAT CONDITIONS ASSOCIATED WITH NEW SETTLEMENT SITES OF BEAVERS IN SOUTHWEST MONTANA

Introduction

An extensive body of scientific literature recognizes the habitat-modifying activities of beavers (*Castor* spp.) as instrumental in the creation, expansion, and maintenance of healthy and productive stream systems and associated riparian and wetland habitats (Naiman et al. 1988, Naiman et al. 1994, Jones et al. 1997, Gurnell 1998, Collen and Gibson 2001, Wright et al. 2002, Rosell et al. 2005, Pollock et al. 2007, Cooke and Zack 2008, Green and Westbrook 2009, Burchsted et al. 2010, Westbrook et al. 2010, Polvi and Wohl 2013, Majerova et al. 2015, Pollock et al. 2017). As a result, over the last half-century land and wildlife managers have recognized the potential benefits of beaver-mediated habitat restoration (hereafter “beaver restoration”; Heter 1950, Apple 1985, McKinstry and Andersen 1999, Macfarlane et al. 2014). Encouraging beavers to inhabit a stream system can be a passive and cost-effective management strategy for improving critical riparian habitats (Pollock et al. 2014, Pollock et al. 2017), which has led to a proliferation of beaver restoration projects in many areas throughout the United States (Heter 1950, Apple 1985, McKinstry and Anderson 2002, Babik and Meyer 2015, Woodruff 2015, Bouwes et al. 2016, Pilliod et al. 2017, Pollock et al. 2017). Beaver restoration projects are particularly common in the arid western part of the country where riparian and wetland habitats make up a small portion of the landscape but are critically important to ecosystems and regional economies (Knopf et al. 1988, Mitsch and Gosselink 2000).

Beaver restoration projects follow three basic strategies: 1) beaver translocation where beavers are captured and moved to a restoration site to start a new colony or reoccupy an abandoned colony (McKinstry and Anderson 2002, Babik and Meyer 2015, Woodruff 2015), 2) habitat improvements to promote natural colonization by beavers (Bouwes et al. 2016), or 3) construction of artificial structures meant to mimic beaver activity including Beaver Dam Analogues (BDAs; Pollock et al. 2011, DeVries et al. 2012, Bouwes et al. 2016). There can be much overlap among strategies, and often multiple approaches are used to achieve project goals (Pollock et al. 2017). For example, BDAs constructed to trap sediment and reconnect the stream channel to the floodplain may also provide starter dams that allow dispersing beavers to occupy the restoration site (Bouwes et al. 2016). Though strategies and techniques may differ, the overall objective with most beaver restoration projects is to promote a functioning, self-sustaining beaver colony or series of colonies to improve stream conditions over time.

The beaver habitat selection literature generally agrees that stream sections with good beaver habitat are characterized by low gradients, high sinuosity values, deep waters, narrow channels (when dam building is required), fine substrates, a supply of woody riparian vegetation near the stream, and sufficient upstream watershed size to supply water year-round (Howard and Larson 1985, Vore 1993, Barnes and Mallik 1997, Suzuki and McComb 1998, Cox and Nelson 2008, Pinto et al. 2009, František et al. 2010, Muller-Schwarze 2011). Most of these habitat metrics are included in formal evaluations of potential beaver restoration sites (Allen 1982, Vore 1993, Carpenedo 2011, Pollock et al. 2017). However, published habitat suitability studies which have provided the foundation for the selection of restoration sites have almost universally compared habitat conditions at established colonies to random locations (Easter-Pilcher 1987, Dieter and McCabe 1989, Harris 1991) or unoccupied stream sections (Beier and Barrett 1987, Barnes and Mallik 1997, Suzuki and McComb 1998, Cox and Nelson 2008). Other studies have focused on modeling the potential for beaver occupancy or damming activity at landscape scales based on important variables proposed in the habitat suitability literature (Howard and Larson 1985, Macdonald et al. 2000, South et al. 2000, 2001, Macfarlane et al. 2015) with little emphasis on specific, individual site conditions. All of these studies confound our understanding of habitat selection by beavers in relation to restoration scenarios because habitat conditions at established colonies may not accurately represent suitable habitat for beavers starting new colonies in novel areas.

Beaver restoration sites are commonly in areas beavers have not occupied for time frames ranging from several years to over a century, and are usually degraded or at-risk stream systems (Apple 1985, McKinstry and Anderson 2002, Woodruff 2015, Pollock et al. 2017). Therefore, to select appropriate restoration sites it is important to understand habitat conditions that allow for colony establishment in areas that are relatively unmodified by beavers. However, the habitat-modifying abilities of beavers makes it difficult for researchers to discern pre-colony habitat conditions at established colonies. Often within a few years of settlement beavers drastically change the vegetation, channel form, and substrate of the stream section containing their colony, leaving little evidence of the original habitat conditions that encouraged settlement (Naiman et al. 1988, Pollock et al. 2007, Hyvonen and Nummi 2008). As a result, it may not be possible to determine to what degree habitat conditions observed at established colonies are a reflection of settlement site selection patterns, or a reflection of beaver-induced habitat manipulations.

Because beavers cause such dramatic changes to streams and riparian areas, understanding initial settlement site selection may be the only way to understand habitat selection patterns in the context of beaver restoration. Previously, researchers have evaluated habitat in areas newly settled by dispersing beavers (Smith 1997, DeStefano et al. 2006), but in these studies most of the beavers settled in abandoned colonies where dams and lodges were already in place. As with active colonies, in abandoned colonies habitat conditions that would reflect pre-colonization selection patterns have usually been altered by recent beaver occupancy. The few studies that have evaluated pre-colony habitat conditions had low sample size (Harris 1991) or attempted to measure pre-colony conditions at established colonies (Howard and Larson 1985, Barnes and Mallik 1997, Suzuki and McComb 1998, Scrafford 2011). While the latter studies offer valuable clues about the settlement site selection process, researchers are likely missing important habitat components that could not be evaluated *post hoc*. In order to properly evaluate pre-colony habitat selection, researchers need to measure habitat conditions at settlement sites before those habitat conditions are changed by beavers.

Beavers generally disperse from their natal colonies between the ages of one and three years to establish a territory of their own (Sun et al. 2000, McNew and Woolf 2005). In order to establish a territory, dispersing beavers are faced with three general options: 1) find an active colony where a member of the breeding pair has died and move in as a new breeder (Brooks et al. 1980, Sun et al. 2000, Mayer et al. 2017b), 2) occupy an abandoned colony that already has dams and lodges in place (Smith 1997, Sun et al. 2000), or 3) start a new colony in unmodified and presumably suboptimal habitat (hereafter referred to as a "new settlement site"). The new settlement site option is likely more common if higher quality beaver habitat in the area is occupied and dispersers are forced to inhabit poorer quality territories (Harris 1991, Nolet and Rosell 1994, Smith 1997, Cunningham et al. 2006, DeStefano et al. 2006, František et al. 2010, Scrafford 2018). Similar to new settlement sites, beaver restoration projects often focus on encouraging beavers to establish in areas characterized by suboptimal habitat and lack of current or recent beaver activity (Bouwes et al. 2016, Pollock et al. 2017). Therefore, suboptimal habitats encountered by dispersing beavers provide a natural analog to the types of habitats beavers would be encouraged to colonize as part of a restoration project.

In order to better understand the selection of new settlement sites by beavers, I conducted beaver-use surveys along streams and rivers in the upper Gallatin and Madison River drainages in southwest Montana during fall 2015−fall 2017. Beaver-use surveys allowed me to map current and past beaver activity, search for new settlement sites, and better understand habitat conditions that may influence settlement dynamics across two major river drainages. I sought to compare habitat at newly settled stream segments to unsettled stream segments to better understand baseline conditions beavers may prefer when selecting settlement sites in unmodified and suboptimal habitats. My primary research objectives were to: 1) map stream sections that were relatively unmodified by beavers, 2) identify new settlement sites in unmodified habitats, 3) compare habitat at new settlement sites with unsettled sites to identify habitat conditions associated with colonization of novel areas, and 4) provide baseline information for landscape-level evaluations of beaver habitat suitability by providing empirical data for identifying reintroduction and restoration sites with the highest probability of success.

Methods

Study Area

I conducted beaver-use surveys along streams and rivers in the headwaters of the Missouri River system within the Custer-Gallatin National Forest in southwest Montana during July–November, 2015–2017. The Custer-Gallatin National Forest covers approximately 1.8 million acres and encompasses the upper Madison River drainage and the upper Gallatin River drainage (hereafter, "Madison drainage" and "Gallatin drainage"; Figures 1 and 2). Both rivers and many of their tributaries flow out of high-elevation mountain ranges in the Madison Range, Gallatin Range, and Yellowstone National Park.

The Madison drainage is composed of a mix of freestone, high-energy streams with rocky substrates and slower, spring-fed streams with sandy substrates. All of the streams in the Madison drainage except Beaver Creek flow into the 325,000 acre-ft Hebgen Reservoir. Streams are generally surrounded by extensive meadows or willow-dominated riparian areas while uplands are a mix of lodgepole pine (*Pinus contorta*) and mountain big sagebrush (*Artemisia tridentata vasevana*) grasslands. The dominant forage for beavers is willow (*Salix* spp.) that line stream corridors in the drainage, although aspen (*Populus tremuloides*) and cottonwood (*Populus trichocarpa*) are available in limited locations. Recreational trapping of beavers in the Madison drainage is highly regulated by the Montana Department of Fish, Wildlife and Parks (MFWP). In 1980, MFWP established the Upper Madison Beaver Management Area (UMBMA) in response to a severely declining beaver population due to overharvest (De Caussin 2013). The UMBMA is divided into seven management units each with a main stream or river. Trapping pressure over the past 10 years has been low, with 5−10 beavers in 1−2 management units harvested annually. Most of the management units have been closed to beaver trapping since the UMBMA was established. In the first year of my study, a trapper removed approximately eight beavers from a single colony on the South Fork of the Madison River, but otherwise no recreational trapping occurred during the study. MFWP issued permits in 2016 and 2017 for one management unit but the trappers did not harvest any beavers in those years. Beaver colony densities were high and estimated at 0.42 colonies/km of stream with ~ 49% of surveyed stream length in the drainage occupied by beavers.

The Gallatin drainage contains higher energy streams than the Madison drainage with narrower riparian zones, steeper gradients, and more limited beaver habitat (Table A2). Willow-dominated stream corridors flow through a mix of sagebrush grasslands and mixed-conifer forests. In the upper portions of the drainage the dominant forage for beavers is willow and in the lower portions beavers use a mixture of willow, alder (*Alnus incana*), aspen, and cottonwood. Recreational trapping has been prohibited in the drainage to protect populations of river otters (Julie Cunningham, MFWP, personal communication). Live-trapping efforts in the drainage indicated many extra non-breeding adults in the well-established colonies, suggesting delayed dispersal. Delayed dispersal is often associated with high densities and low availability of good quality territories (Stacey and Ligon 1991, Koenig et al. 1992, Smith 1997). I feel confident that although overall densities of beavers were low in the Gallatin drainage (0.25 colonies/km, 20% of surveyed stream length occupied), most sections of streams suitable for beaver habitation contained high densities of beavers. The Gallatin drainage also included three streams on a privately owned bison ranch, where beavers have recently been expanding and colonizing new habitats.

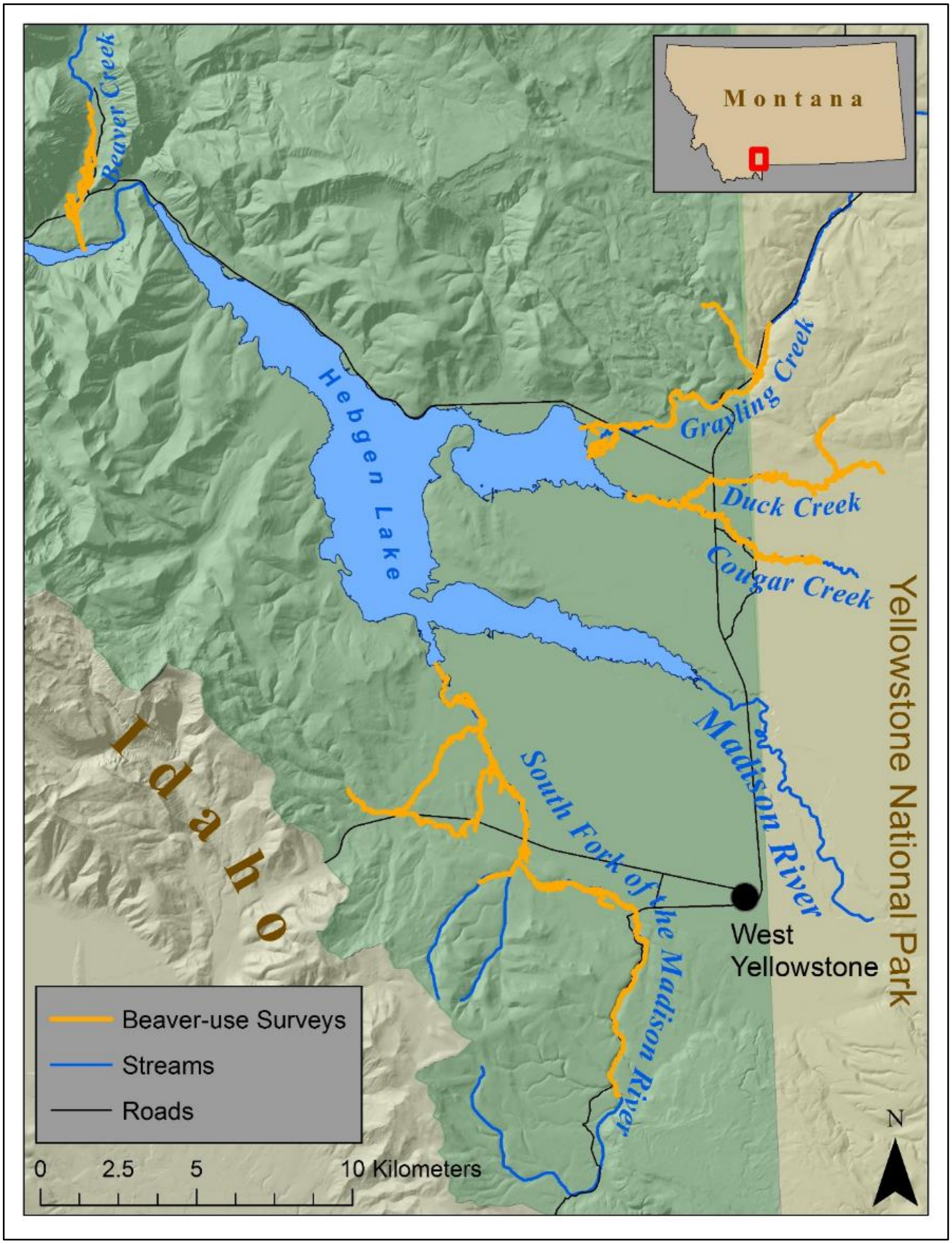

Figure 1. Extent of beaver-use surveys on beaver-occupied streams in the upper Madison River drainage in southwest Montana, USA.

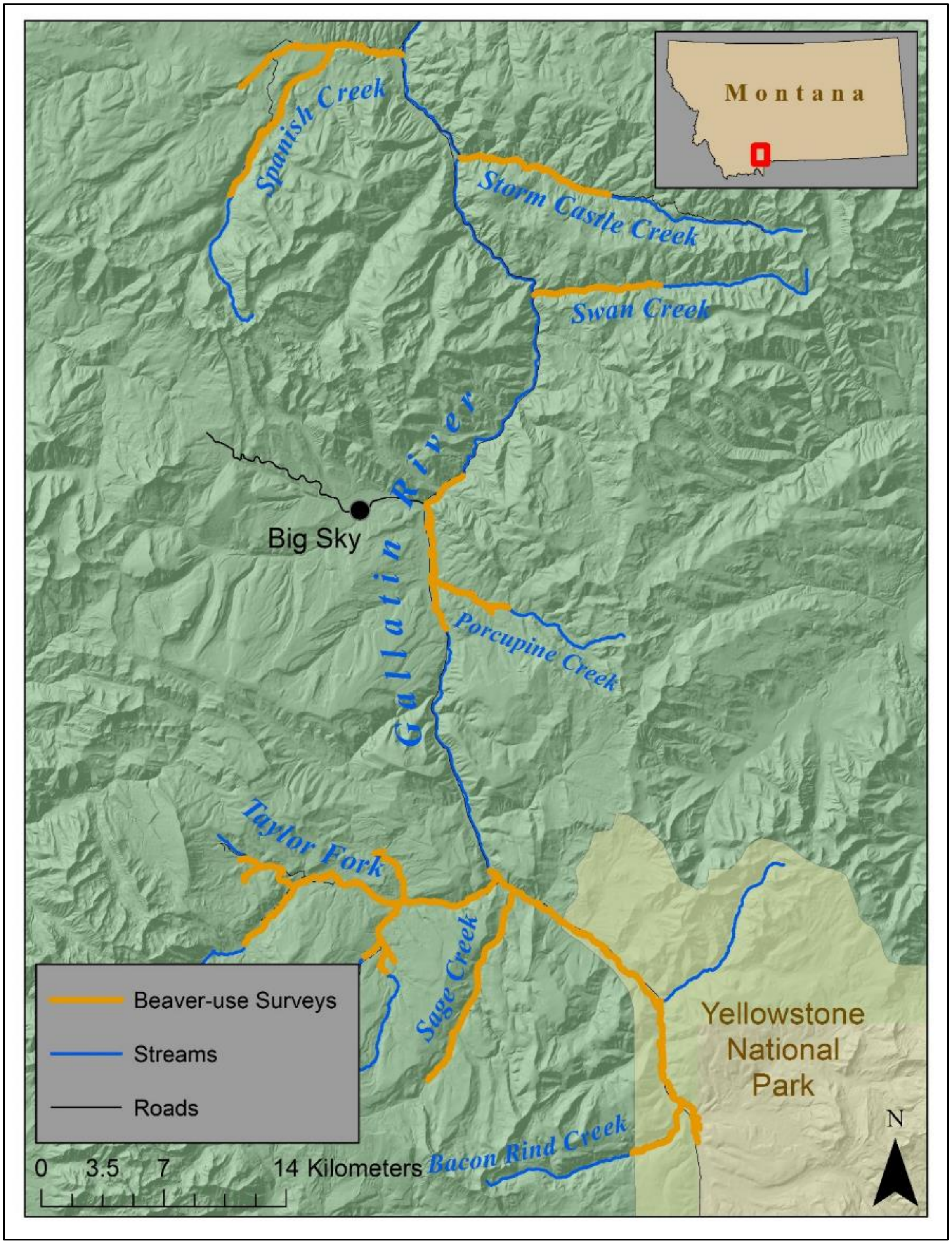

Figure 2. Extent of beaver-use surveys on beaver-occupied streams in the upper Gallatin River drainage in southwest Montana, USA.

Beaver-use Surveys

Prior to conducting field work, I consulted area biologists and used historical aerial imagery in the program Google Earth to evaluate streams in the study area for potential beaver occupancy. Suitable beaver habitat was defined as stream sections ≥ 400 m in length with gradients < 10% and a woody riparian vegetation zone that was wider than a single band of vegetation immediately adjacent to the stream channel (Allen 1982, Suzuki and McComb 1998, Muller-Schwarze 2011). I included all suitable stream lengths in the study area except for some streams and stream sections within Yellowstone National Park where regulations limited access. All of the surveyed streams had sign of at least one beaver colony present within the past 10 years.

I conducted beaver-use surveys during July−November, 2015−2017. Beaver-use surveys involved walking along each stream and marking all active and inactive beaver sign with a handheld GPS unit. Beaver sign included lodges, bank dens, dams, caches, clippings, and castor mounds, as well as beaver tracks and scat. For each marked sign I recorded whether it was active or inactive, its relative age for inactive sign, and for dams and lodges the size and impact of the structure (e.g., whether or not a dam was still holding water). A variety of evidence allowed me to discern active from inactive beaver sign as well as the relative age of the sign. Beaver-use surveys supported my objectives in three ways:

1. Search for and identify areas newly settled by beavers.
2. Delineate stream segments available for new settlement sites.

3. Estimate densities and locations of active beaver colonies that could impact the dispersal and settlement process.

I walked upstream during beaver-use surveys and ended when I had covered at least 1 km of stream beyond the last sign of past or present beaver activity. I investigated the remaining upper portions of streams using aerial imagery to confirm no more suitable habitat existed upstream of the survey end points. If no suitable habitat or sign of beaver activity was found upstream of the end point, I excluded the remaining stream length from the study. I followed this protocol to avoid including large sections of stream that were entirely unsuitable for beavers and did not represent the types of locations where beaver restoration projects would normally be implemented (Pollock et al. 2017). I did not survey the entirety of four streams due to time limitations, high beaver densities leaving little room for new settlements, or restricted access.

I waited to conduct beaver-use surveys until I observed dam and lodge construction throughout the study area in late summer. Late summer coincided with the end of the dispersal season when most dispersing beavers had likely chosen a settlement site for the year (Jackson 1990, Van Deelen 1991). I surveyed some stream sections in the spring which required different interpretations of beaver sign than fall surveys because of overwinter structure damage and disrepair, as well as seasonal changes in habitat use and beaver behavior. Therefore, I carefully interpreted beaver sign encountered on spring surveys to accurately classify stream sections in terms of beaver activity the previous fall. I then assessed aerial imagery to confirm my observations. I was unable to systematically survey all streams in the study area in 2015 so I used a combination of field notes from my fall 2015–spring 2016 field work, interviews with biologists and managers, 2015 aerial imagery from the National Agriculture Imagery Program (NAIP; 1-m resolution; USDA-FSA-APFO Aerial Photography Field Office, Salt Lake City, UT, USA), and historical imagery in the software program Google Earth to identify stream segments used by beavers in 2015.

Stream Segment Classification

I digitized all streams in the study area using ArcMap 10.3.1 software (Environmental Systems Research Institute, Inc., Redlands, CA, USA) and 2015 NAIP aerial imagery. I included backwaters, side channels, sloughs, and tributaries when the extra water body was ≥ 200 m in length. I then divided all stream lines into segments 400 m in length to act as the experimental units (hereafter, "sampling segments"). The length of 400 m was chosen based on an evaluation of the extent of beaver activity beyond major dams and lodges of active colonies in the study area. For all active colonies, I measured the maximum stream distance from major dams and lodges where clippings, castor mounds, and bank dens occurred. I calculated the average of these distances which was then rounded to 200 m. The sampling segment size (400 m) was meant to reflect the minimum size of a beaver colony, which would consist of one dam, one lodge, and an additional 200 m up- and downstream of those structures.

I overlaid all point locations of beaver sign on the sampling segments and symbolized the points by type of sign and whether the sign was active or inactive. I then classified sampling segments based on the level of beaver activity. I used only lodges and dams to delineate the extent of beaver activity classifications because lodges and dams are large and conspicuous and detection was high relative to other beaver sign. I considered other types of beaver sign to help discern the activity level of dams or lodges, but they did not contribute towards sampling segment classification.

I classified sampling segments into four categories: active, abandoned, relic, or unoccupied. An active sampling segment was dominated by recent beaver sign including major dams or lodges. A major dam or lodge was an actively maintained and well-used structure within 200 m of the main cluster of dams and lodges in the core use area of the colony (i.e., where I observed overwinter lodges and caches and where foraging activity was heaviest). Sampling segments classified as active estimated the actively defended colony boundaries and not the entire area of use for a given colony. I classified abandoned sampling segments as those that contained ≥ 2 unused dams or lodges and where no fresh beaver sign was present, indicating the site was relatively recently abandoned. Additional criteria for classifying a segment as abandoned included: 1) dams were still holding water or directly affecting the stream course and could be easily repaired, 2) vegetation was still recovering from past beaver use, and 3) lodges were immediately inhabitable or easily inhabited with minor repairs. I classified a sampling segment as being relic when it contained ≥ 2 unused dams or lodges with no evidence of recent maintenance. Criteria for a relic sampling segment classification included: 1) hydrology and vegetation of the segment was no longer directly influenced by beaver activity, 2) dams did not directly impact the course of the water and would need major repairs or complete rebuilds to be effective, 3) lodges were collapsed or would need major repairs to be useable, and 4) vegetation had mostly recovered to its former vigor.

Beavers had a colony at some point but had been gone long enough for stream to return to a somewhat pre-colony state, though more subtle beaver-mediated habitat manipulations may have existed. Finally, I classified a sampling segment as unoccupied when it contained ≤ 2 relic structures, and there was no sign a beaver colony was ever well-established in the area or had been gone long enough only minimal sign remained. The stream segment could be considered relatively unmodified by beavers at the time of the survey.

The presence of old dams and lodges can be a major driving factor of settlement site selection for beavers. Dams and lodges that are fully functioning or easily repaired save colonizing beavers time and energy while also offering safety from predators during colony establishment. Therefore, it is likely beavers would occupy sites with old dams or lodges even if other aspects of the habitat were not optimal. Because my primary interest was habitat-based drivers of settlement site selection in relatively unmodified habitats, I defined a new settlement site as one or more beavers constructing a dam and lodge within a single sampling segment or set of adjacent sampling segments that were classified as relic or unoccupied the year prior to settlement. I followed this protocol to minimize the potential impact of previous beaver structures on habitat selection. I used careful site examination and interpretation of beaver sign as well as aerial imagery to accurately identify new settlement sites. New settlement sites were characterized by: 1) dams that did not have built-up silt behind them and were composed entirely of fresh woody vegetation, 2) clippings that were all recent and matched the stem diameter of any relic clippings at the site, and 3) lack of well-worn trails, channels, or tunnels. Because I did not have stream segment classification data prior to 2015, I identified new settlement sites established in 2015 based on the relative age and type of beaver sign at those locations.

I used the spatial clustering of active sampling segments to estimate the number and spatial extent of active beaver colonies in the study area. Colony densities in the literature are often reported as the number of colonies per linear distance of stream or the number of colonies in a given area (Table 1). While colonies/distance is sufficient for describing overall numbers of beaver colonies, it does not adequately describe the spatial extent of occupied habitat as colonies can vary greatly in size. For example, the largest colonies in my study area take up 1−3 km of stream while smaller colonies or new settlement sites may only take up 400 m of stream. As a result, a stream 10 km long that contains five colonies 400-m in length and a stream 10 km long with five colonies 1,200-m in length would have identical values for colonies/km, even though the actual availability of unsettled stream segments is much higher in the first stream. Therefore, I calculated colony density estimates both as the number of colonies per kilometer of stream and the proportion of active sampling segments within each beaver activity classification (Table 1). Reporting both statistics provides a more accurate sense of colony densities and the availability of unsettled stream segments.

Table 1. Beaver colony densities reported in the literature for North America, 1968−2017.

Author	Location	Colony Density
Aleksiuk 1968	Alaska	0.40 colonies/km^2
Larson and Gunson 1983	Alberta/Manitoba	1.07 colonies/km^2
Cox and Nelson 2009	Illinois	0.40 colonies/km
Nelson and Nielsen 2011	Illinois (Central)	0.40 colonies/km
Nelson and Nielsen 2011	Illinois (Southern)	3.3 colonies/km^2
Robel et al. 1993	Kansas	0.39 colonies/km
Destefano et al. 2006	Massachusetts	0.43 colonies/km^2
Destefano et al. 2006	Massachusetts	0.70 colonies/km^2
Destefano et al. 2006	Massachusetts	0.83 colonies/km^2
Howard and Larson 1985	Massachusetts	0.83 colonies/km
Broschart et al. 1989	Minnesota	1.02 colonies/km^2
Smith 1997	Minnesota	1.7 colonies/km^2
Scrafford et al. 2018	Montana	1.33 colonies/km
Ritter et al. 2012	Montana (Beaverhead)	0.49 colonies/km
Ritter et al. 2012	Montana (Ruby)	0.53 colonies/km
Ritter et al. 2012	Montana (Clark Fork)	0.78 colonies/km
Ritter et al. 2012	Montana (Big Hole)	1.14 colonies/km
Payne 1982	Newfoundland	0.34 colonies/km^2
Bergerud and Miller 1977	Newfoundland	0.51 colonies/km^2
Collins 1976	Wyoming	0.9 colonies/km
Muller-Schwarze 2003	North America	0.23−1.09 colonies/km
This Study 2015−2017	*Montana (Gallatin)*	*0.25 colonies/km*
This Study 2015−2017	*Montana (Madison)*	*0.42 colonies/km*

Habitat Data Collection

I collected habitat data using two techniques to best capture the range of habitat conditions that may influence beaver settlement site selection. First, I collected data remotely using aerial imagery and a GIS (hereafter, “GIS-based habitat sampling”). The goal of the GIS-based approach was to offer a framework for broad-scale analysis of potential new settlement sites in a given area that could be accomplished without on-the-ground habitat assessments. Second, I collected fine-scale habitat data in the field by measuring habitat conditions that could not be obtained from remotely sensed data (hereafter, "field-based habitat sampling"). The goal of the field-based approach was to provide habitat recommendations to complement the more broad-scale GIS-based analysis. Field-based habitat sampling would be a necessary second step in a restoration project after GIS-based analyses so project leaders could confirm observations from remotely sensed data and identify other habitat limitations or opportunities that may not be apparent from a GIS-based assessment.

GIS-based Habitat Sampling. I evaluated habitat conditions for each sampling segment using ArcMap 10.3.1 software, a 10-m USGS Digital Elevation Model (DEM), and NAIP aerial imagery. My data covered three major habitat components hypothesized to influence the selection of new settlement sites by beavers: stream geomorphology, vegetation, and wetland types (Table 2). Stream geomorphology variables represent stream channel and geologic conditions that influence dam-building, lodge construction, and access to vegetation. Vegetation variables represent the quantity and distribution of available forage and construction resources. Wetland type variables use the Montana Natural Heritage Program's Wetland and Riparian Framework (WRF) to estimate the amount of various wetland classifications (Cowardin et al. 2013), within 30-m and 100-m buffers around each sampling segment. I used 30-m buffers to represent the core area of use for beavers (Hall 1960, Jenkins 1980, Belovsky 1984), while 100-m buffers represented the full area of use (Jenkins 1980, personal observation) and accounted for future colony expansion.

Table 2. GIS-based habitat covariates used to investigate settlement site habitat selection by beavers in the upper Gallatin and Madison River drainages in southwest Montana, USA.

Variable	Unit	Method	Hypothesized effect on new settlement site selection	Description
Stream geomorphology				
Sinuosity	N/A	Stream distance of sampling segment divided by straight-line distance between endpoints.	Positive linear	Higher sinuosity = slower flows, deeper waters on outside bends, greater access to forage.
Stream gradient (gradient)	% rise	Difference in elevation between start and end points divided by stream distance of sampling segment.	Negative linear	Lower gradient = dams more efficient and more resilient to high flows.
Floodplain width (floodplain)	m	Measured at 7−10 random points per sampling segment using aerial imagery.	Positive linear or positive pseudo-threshold	Wider floodplain = larger area for dams to flood, dissipation of flood waters.
Watershed size (watershed)	km^2	USGS StreamStats Batch Processing Tool: size of watershed upstream of sampling segment.	Positive linear or negative quadratic	Larger watersheds = more stable water supply but too large and spring runoff destroys dams and lodges.
Secondary channels	Number of secondary channels	Channel included if contained within sampling segment or < 100 m from either end of segment.	Positive linear	More secondary channels = increased foraging area, more efficient dams, protection from high flows.

Table 2. Habitat covariates (continued)

Vegetation				
Width of woody riparian vegetation zone (riparian width)	m	Measured at 7−10 random points per sampling segment using aerial imagery.	Positive linear or positive pseudo-threshold	Wider riparian zone = protection from predators, more forage, flood resiliency, and high water table. Effect may diminish at widths beyond beaver foraging distance.
Woody riparian vegetation canopy cover index (canopy cover[a])	Categorical	Estimated at 7−10 random points per sampling segment using aerial imagery. Visual assessment and classification: score of 1 = < 1/3 of line drawn across riparian zone intersects woody vegetation, 2 = 1/3−2/3 intersects vegetation, 3 = > 2/3 intersects vegetation. Average of canopy cover scores for each sampling reach.	Positive linear	Higher canopy cover = protection from predators, more forage and construction resources.
Woody riparian vegetation height index (forage height)	Categorical	Visual assessment and classification using field notes and aerial imagery: score of 1 = woody vegetation < 80 cm in height, 2 = 80−190 cm, 3 = > 190 cm.	Positive linear	Taller willows = greater volume of forage and construction resources. Interaction with canopy cover index = protection from predators.
Forage biomass index	N/A	Riparian width × (Canopy cover + Forage height)	Positive linear or positive pseudo-threshold	Greater woody vegetation biomass = more forage and construction resources. Effect may diminish when forage is overabundant.

Table 2. Habitat covariates (continued)				
Wetland type - (Montana Natural Heritage Program's Wetland and Riparian Framework Attribute Codes)				
Sparse-willow (PEMA, PEMF, Rp1EM, PEMC)	Proportion	WRF polygons intersected with 30 and 100-m buffers on all sampling segments.	Negative linear	Sparse woody riparian vegetation = low amounts of forage.
Willow-dominate (PSSA, PSSC, PSSF, Rp1SS, Rp1FO, Rp2FO, PFOA)	Proportion	WRF polygons intersected with 30 and 100-m buffers on all sampling segments.	Positive linear	Willow-dominated wetlands = abundant forage, hiding cover, and flood resiliency.
Gravel bar (PUSA, PUSC, R2USA, R2USC, R3USA, R3USC, R4SBA)	Proportion	WRF polygons intersected with 30 and 100-m buffers on all sampling segments.	Negative linear	Gravel bars = lower water table, poor dam sites, limited safety cover, and low forage.
Waterbody (R2UBH, R3UBF, R3UBG, R3UBH, R4SBC, PABF, PABG, L1UBH, L2USA, R2UBF)	Proportion	WRF polygons intersected with 30 and 100-m buffers on all sampling segments.	Positive linear	Waterbodies = represent stream channels, ponds, and lakes. Essential habitat component.
Colony density				
Distance to nearest active beaver colony	m	Straight-line distance from edge of sampling segment to edge of nearest active beaver colony.	Negative linear or negative quadratic	Good habitats on outskirts of active colonies and increased availability of mates. Too close leads to territory disputes.

[a] Measurement method includes the stream channel as riparian vegetation and therefore allows narrow riparian zones to have high canopy cover index values.

Field-based Habitat Sampling. For field-based habitat sampling, I defined the extent of new settlement sites based solely on the distribution of active beaver sign rather than the extent of classified sampling segments. I defined the spatial extent of new settlement sites as the stream corridor between the uppermost and lowermost major dam or lodge of the new colony as well as 200 m up- and downstream of these structures. Minimum new colony size was fixed at 600 m to account for possible shifting of colony boundaries as new colonies became established. Some new settlement sites consisted of a single dam and lodge, while others were made up of multiple dams and lodges over a larger area. I included the entire area of dam and lodge construction because I was not able to revisit all sites later in the year to determine if a certain section of stream was more fully settled before freeze-up. Therefore, some areas of the settled stream section may have been abandoned by the time the beavers chose an overwinter site and completed the settlement process. For the rest of this thesis, I will refer to settled and unsettled stream sections where I measured field-based habitat conditions as "sampling reaches." Please note these are not the same experimental units as "sampling segments" referred to in GIS-based habitat sampling, which are constrained to a length of 400 m.

I randomly selected unsettled sampling reaches within the same stream to act as paired sites to each settled sampling reach. I constrained unsettled sampling reaches to be the same length as the settled reach to which they were paired. If the new settlement site was previously a relic colony, I chose a paired sampling reach that was also a relic colony to account for possible selection for habitat conditions that were altered by previous beaver occupancy. Within each sampling reach, I generated 10−20 random points depending on the length of the reach (10 points for a 600-m reach with increasing number of points proportional to reach length). Random points were at least 20 m apart to avoid spatial autocorrelation within individual sampling reaches. I recorded habitat measurements at each random point that covered aspects of stream geomorphology and vegetation hypothesized to be important to beaver settlement site selection (Table 3).

The influence of many habitat characteristics on settlement site selection changes depending on whether or not beavers need to build dams to survive. Dam-building requires additional time, energy, and forage resources as well as consideration of stream channel characteristics that facilitate dam construction. In order to simplify the field-based habitat selection analysis, I assumed all settlement sites and paired unsettled sites occurred in streams where beavers must construct dams for colony establishment. I also assumed these streams had consistent perennial water and therefore the availability of a year-round water supply would not influence settlement site selection. Unlike the GIS-based habitat analysis, all of my hypotheses about the influence of field-based habitat characteristics on settlement site selection are based on these assumptions.

Table 3. Field-based habitat covariates used to investigate settlement site habitat selection by beavers in the upper Gallatin and Madison River drainages in southwest Montana, USA.

Variable	Unit	Method	Hypothesized effect on new settlement site selection	Description
Stream Geomorphology				
Stream width	cm	Width of stream channel	Negative linear (interaction with flow rate)	Narrower streams are easier to dam and dams are more resilient. Effect is present as long as flow rate is low enough for dam construction.
Stream depth (average)	cm	Depth at 1/4 stream width from each bank, 1/2 across stream, and at deepest point.	Positive linear (interaction with flow rate)	Deeper waters overall provide cover and require less dam building. Effect is present as long as flow rate is low enough for dam construction.
Stream depth (deepest)	cm	Deepest measurement at each sampling point.	Positive linear	Need only localized deep spots for initial lodge/den construction.
Standard deviation (SD) of cross-section stream depth	cm	Standard deviation of depth measurements at each sampling point.	Positive linear	Prefer deep spots for lodges/escape and shallow spots for feeding.
Width:depth ratio	cm	Average width of stream / average depth of stream.	Negative linear or negative quadratic	Stream channels too wide and shallow or too narrow and deep are hard to dam. Measures width and depth in one variable. Comparable across all streams.
Discharge	m^3/s	Cross-sectional area derived from depth and width measurements × flow rate measured using float method.	Negative linear or negative pseudo-threshold	High discharge makes dam construction more difficult and causes damage to dams and lodges during high water events.

Table 3. Habitat covariates (continued)

	Bank height[a]	cm	Vertical distance from surface of water to point where water would spill onto floodplain if dammed.	Negative linear (interaction with stream depth)	Select high banks when waters are shallow so dam will make waters deep enough. Select low banks for easier access to forage when waters are already deep.
	Substrate size index	index	Visual assessment and scored as: 1 = mud/silt, 2 = sand, 3 = gravel, 4 = cobble, 5 = rocks, or 6 = boulders. Average of substrate size scores for each sampling reach.	Negative linear	Smaller substrates are easier to excavate and more useful for dam and lodge construction.
	Channel complexity	%	Percent of sampling points ≤ 100 m from secondary channel. Sampling point scored as a 1 if channel is accessible to beavers within 100 m of point, scored as a 0 if point located on single-thread channel.	Positive linear	Greater channel complexity provides better dam sites, greater foraging area, and protection from high water events.

Table 3. Habitat covariates (continued)

Access to vegetation				
Gravel bar length[a]	cm	Distance from water's edge to forage or hiding cover.	Negative linear	Longer gravel bars make poor anchor points for dams and expose beavers to predation when foraging.
Distance to nearest preferred forage (D2PF)[a]	cm	Distance from water's edge to nearest willow, alder, aspen, or cottonwood with > 10 stems.	Negative linear	Denser forage provides more food and construction resources and greater cover.
Stem volume[a]	cm^3	(Average diameter of 10–20 stems of same plant measured for plant height/2)$^2 \times \pi \times$ forage plant height	Positive linear	Greater stem volumes provide more food and construction resources.
SD of stem volume[a]	cm^3	Standard deviation of stem volume measurements.	Positive linear	Prefer larger stems for construction and smaller stems for forage.

[a] Measurement taken on both sides of the stream at each sampling point

Data Analysis

GIS-based Data Analysis. I followed the recommendations of Manly et al. (2002) to estimate a resource selection probability function (RSPF) relating habitat variables to the probability of settlement by beavers. An RSPF is any function where the response reflects the probability of selection of a resource unit (Manly et al. 2002). In my study, I followed a used/unused study design where the resource units (sampling segments) were classified as used (newly settled) or unused (unsettled) based on the presence and age of beaver sign in the segment (Manly et al. 2002). I am confident I accurately distinguished use vs. non-use because beavers show high site fidelity by late summer and fall and are conspicuous when occupying an area due to habitat manipulations Additionally, I monitored ~ 94% of the sampling segments for three consecutive years with 100% being monitored for at least two consecutive years. I further evaluated uncertainty in segment classification using aerial imagery and interviews with local landowners, biologists, and recreationalists. Because beaver activity tended to increase in the study area from late summer to freeze-up in November, I opportunistically checked streams later in the fall that were surveyed early in the survey period to confirm segment classification had not changed. Although I did not formally test for detection probability in the context of segment classification, my field observations led me to believe misclassification of sampling segments was rare.

I used Spearman-rank correlation coefficients (r) to test for multicollinearity among habitat variables. I did not include any pairs of habitat variables with $|r| \geq 0.60$ in the same models. I used mixed-effects logistic regression to fit a RSPF to examine the influence of habitat variables on the probability a sampling segment would be newly settled by beavers. The importance of habitat variables to settlement site selection by beavers likely varies depending on environmental conditions in an area (McLoughlin et al. 2010). For beavers, this includes variability in colony densities, sources of mortality, and habitat components that may limit settlement in some stream systems. Additionally, habitat conditions of sampling segments within the same stream are correlated due to being close in space. To account for issues with autocorrelation among experimental units and spatial clustering of habitat conditions I used a random intercept effect of individual stream ID in the models (lme4 package for R; R Version 3.3.2, www.r-project.org, accessed 28 Dec 2017; Boyce et al. 2002, Bolker et al. 2009, Bates et al. 2015). I defined a success (1) in the analysis as a sampling segment that was settled in a given year but was classified as relic or unoccupied the year before. I defined a failure (0) as a sampling segment that was classified as relic or unoccupied for at least one year of the study and was not occupied by beavers. I excluded reoccupations of abandoned colonies and expansions of existing colonies because I was only interested in new settlement sites where beavers had to construct dams and lodges without relying heavily on previous beaver modifications. In abandoned colonies, I hypothesized a habitat suitability trade-off for beavers seeking settlement sites between baseline habitat conditions (e.g., vegetation, pond depth), and the availability of previous modifications. My objective was to assess the selection of new settlement sites in terms of pre-colony habitat suitability so I decided including abandoned segments would have confounded interpretation of my results.

I developed sets of candidate models representing *a priori* hypotheses of the influence of habitat variables on new settlement site selection by beavers. Prior to the development of multivariate models, I tested hypothesized pseudo-threshold relationships (Franklin et al. 2000) between the probability of settlement and floodplain width, riparian width, and forage biomass index, as well as a hypothesized quadratic relationship between the probability of settlement and watershed size and distance to the nearest active colony. I used a tiered approach to model evaluation by grouping the habitat covariates into three broad categories which were analyzed separately (Table 2). I ranked candidate models using Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002). As a general guideline, I considered all models < 2 ΔAIC_c from the top model parsimonious, though I was careful in my interpretation of model selection results following the recommendations of Anderson and Burnham (2002) and Arnold (2010). I only used the top-ranked models when making inference and selecting covariates for final model development. I used all the variables included in each of the top models for each habitat category to build a full model representing settlement site selection by beavers. In order to avoid over-fitting the final model, I limited the number of terms to four or fewer using a backwards elimination procedure. While such stepwise selection is not recommended for ecology-based studies (Whittingham et al. 2006), I was confident the three candidate model sets represented adequate use of *a priori* expectations based on biologically plausible hypotheses (Burnham and Anderson 2002), and therefore stepwise elimination would not introduce unintended bias and produce spurious results. I used AIC_c to rank the top 4-term model, top 3-term model, global model, and null model to evaluate the optimal number of parameters to best predict the response. Additionally, I incorporated a model that included the variables from the top 3-term model and the variable eliminated in the step before the 4-term model to make sure the elimination of this variable was not erroneous. I also tested for the need to include a variable for the distance to the nearest active colony to examine the possible influence of territoriality and mate-seeking on settlement site selection (Table 2). When multiple models were supported, I used model-averaged estimates of beta-coefficients for covariates in the final models to predict the influence of habitat variables on the probability of settlement ("AICcmodavg" package for R; Mazzerolle 2017). I evaluated effect sizes using 85% confidence intervals as suggested by Arnold (2010), which assured the AIC_c model selection procedures and parameter evaluation methods were compatible.

Prior to fitting models, I evaluated the influence of the random intercept grouping on the results of the modeling effort using two methods. First, I fit a pair of univariate models, one that included the random intercept term and one without this term, and tested for the significance of the random effect using a likelihood ratio test following the recommendations of Pinheiro and Bates (2000). Next, I plotted predicted values of the top fixed effects separately for each level of the random effect to evaluate the distribution of the random intercept terms ("ggplot2" package for R; Wickham 2009). The distribution of random intercepts provided a visual interpretation of variation in the probability of settlement that may be attributed to fundamental geomorphic and habitat differences among individual streams that could not be directly modeled.

I evaluated goodness-of-fit for the top habitat selection model by calculating marginal R^2 ($R^2_{GLMM(m)}$) and conditional R^2 ($R^2_{GLMM(c)}$; Nakagawa et al. 2013). Marginal R^2 is the proportion of variance explained by only the fixed effects in the model, while Conditional R^2 is the proportion of variance explain by both fixed and random effects.

Field-based Data Analysis. I used Spearman-rank correlation coefficients (r) to test for multicollinearity among habitat variables. I did not include any pairs of habitat variables with $|r| \geq 0.60$ in the same models. I used logistic regression to develop models testing the influence of habitat characteristics on the probability of settlement. Due to limited sample size of paired sites (n =19 pairs), I limited the number of terms in the models to three. Although there was spatial clustering of new settlement sites in some streams as described for the GIS-based analysis, my limited sample size prevented the use of a random effect to account for heterogeneity in habitat conditions and colony densities within individual streams that could not be directly modeled. Furthermore, I was not able to evaluate interaction terms, which I hypothesized would be influential on settlement site selection for many of the habitat variables (Table 3).

I developed sets of candidate models representing *a priori* hypotheses of the influence of habitat variables on new settlement site selection by beavers. Prior to the development of two-term models, I tested hypothesized pseudo-threshold relationships (Franklin et al. 2000) between the probability of settlement and discharge as well as a hypothesized quadratic relationship between the probability of settlement and width:depth ratio. I grouped the habitat covariates into two broad categories representing stream geomorphology and vegetation (Table 3). I analyzed the two categories separately and then used the most supported variables from each category to develop a final habitat selection candidate model set. I ranked candidate models using Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002) using the same model selection and inference protocols as for the GIS-based analysis.

Logistic regression modeling with small sample sizes and un-modeled heterogeneity has the potential to produce spurious results (Bolker et al. 2009). As a comparison to my modeling efforts, I used Wilcoxan non-parametric tests to look for differences in median habitat conditions between paired settled and unsettled sites. I took two approaches to these tests. First, I incorporated stream-specific differences in habitat components by limiting paired comparisons to those within the same stream system, while allowing multiple comparisons between settled sites and unsettled sites nearby that theoretically could have been settled. By structuring the comparisons in this way, I incorporated yearly settlement dynamics. For example, a sampling reach that was not settled until 2017 was considered available to be settled by beavers that settled a sampling reach in 2015 in the same stream. Conversely, a sampling reach that was settled in 2015 and remained settled through 2017 was not considered available to beavers settling a sampling reach in 2017. The multiple-comparisons approach allowed me to maximize the settled-unsettled pairings while incorporating time-varying availability of sampling reaches. For the second approach, I established set paired sampling reaches within individual streams by selecting the closest unsettled sampling reach to the settled reach and conducting a Wilcoxan signed-rank test between all reaches sampled in the study area during 2015−2017. For this approach I investigated additional habitat characteristics including variation (standard deviation) in stream width, depth, and bank heights within sampling reaches. The goal of these secondary analyses was to evaluate whether habitat selection patterns observed in the logistic regression models approximately matched patterns observed through standard hypothesis testing procedures, while accounting for stream-level variation that could not be incorporated into the logistic regression analysis due to a limited sample size.

Results

I conducted beaver-use surveys on 244 km of 27 different streams in the study area during July–November, 2015–2017; I surveyed 103 km of streams in the Madison drainage (Figure 1) and 141 km in the Gallatin drainage (Figure 2). I excluded 29 km of streams from the analyses as habitat along these sections was deemed unsuitable for new settlement sites due to steep stream gradients and lack of adequate woody riparian vegetation resources.

Overall, average colony density across the three years of the study was higher in the Madison drainage (0.42 colonies/km) than the Gallatin drainage (0.25 colonies/km), which was reflected in overall lower numbers of relic and unoccupied sampling segments in the Madison drainage (Table 4). The Gallatin drainage had one of the lowest colony densities reported in the literature (Table 1), while the Madison was comparable to other locations in Montana and the western United States. Proportions of beaver activity classifications were fairly constant during the study period and so were averaged over the three years (Table 4).

Table 4. Average number of 400-m stream segments within beaver activity classifications in the upper Gallatin and Madison River drainages in southwest Montana, USA, 2015−2017. Percentages reflect the proportion of the total segments within the drainage.

Segment classification	Gallatin (n = 354)	Madison (n = 259)	Total (n = 613)
Active	68 (23%)	120 (46%)	188 (32%)
Abandoned	27 (8%)	60 (23%)	87 (15%)
Relic	49 (15%)	24 (9%)	73 (12%)
Unoccupied	197 (58%)	56 (22%)	253 (42%)

During beaver-use surveys I classified a total 613 sampling segments in the study area. Of these, 370 were classified as relic or unoccupied for at least one year of the study and were therefore available to be newly settled by beavers. I identified 27 new settlement sites during 2015−2017; sixteen in the Gallatin drainage and 11 in the Madison drainage (Figures 3 and 4). The 27 new settlement sites resulted in 48 relic or unoccupied sampling segments becoming occupied during the study period. Thirty (63%) of the newly settled sampling segments were relic segments and 18 (37%) were unoccupied segments. The 48 newly settled sampling segments accounted for 13% of the relic and unoccupied segments over the course of the study. It is important to note abandoned sampling segments were settled at a similar rate over the course of the study as relic segments, with 27% (31/116) of available abandoned segments being settled compared to 31% (30/97) of available relic segments. However, the rate of settlement of abandoned sampling segments is under-estimated because I was unable to identify re-settlements of abandoned colonies that occurred in 2015. Only 7% (18/273) of available unoccupied segments were newly settled. There were 127 (21%) sampling segments classified as active for at least two years of the study and these were associated with an average of 81 active colonies across the entire study area during 2015−2017.

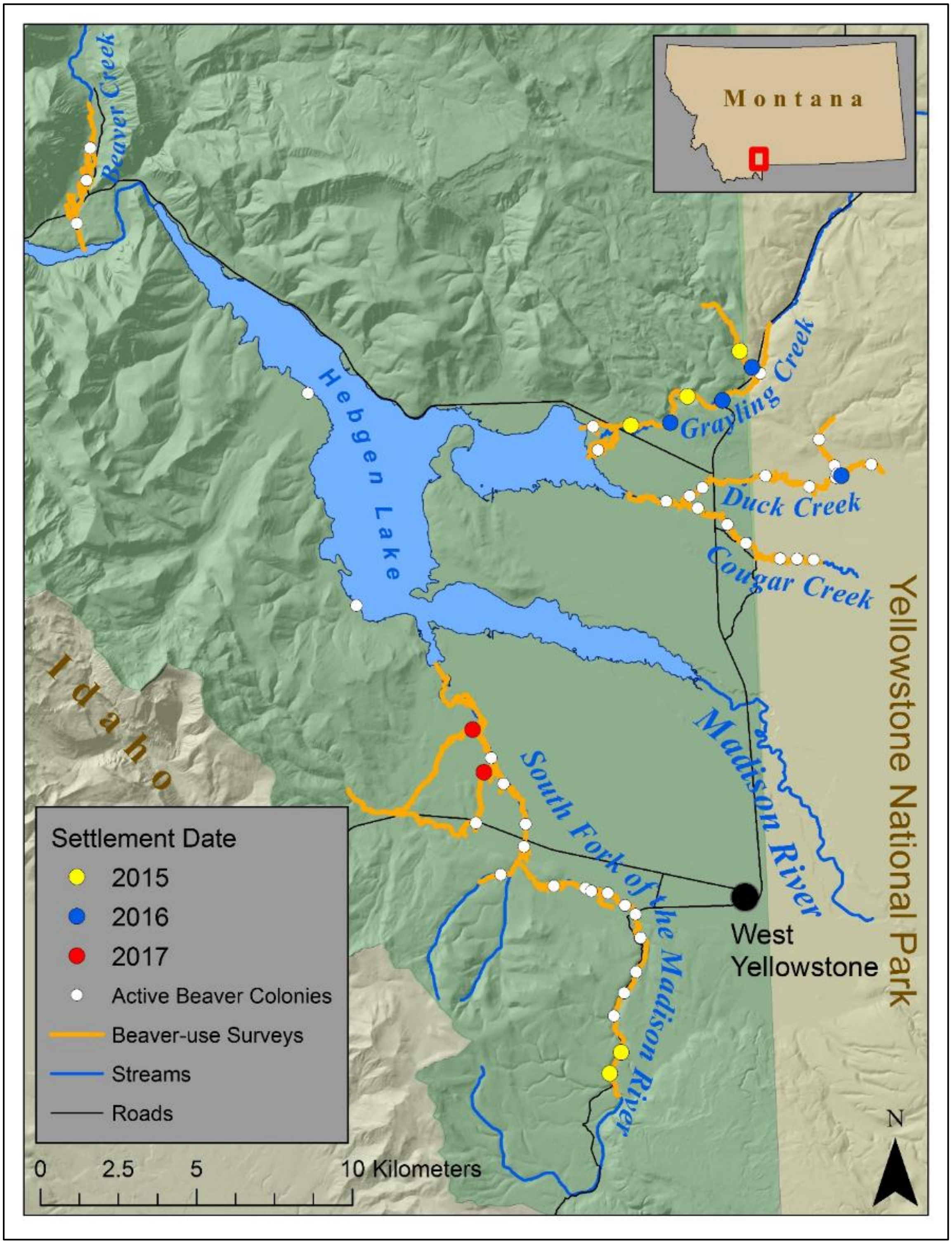

Figure 3. Locations of new settlement sites of beavers in the upper Madison River drainage in southwest Montana, USA. Active beaver colony locations reflect 2016 conditions.

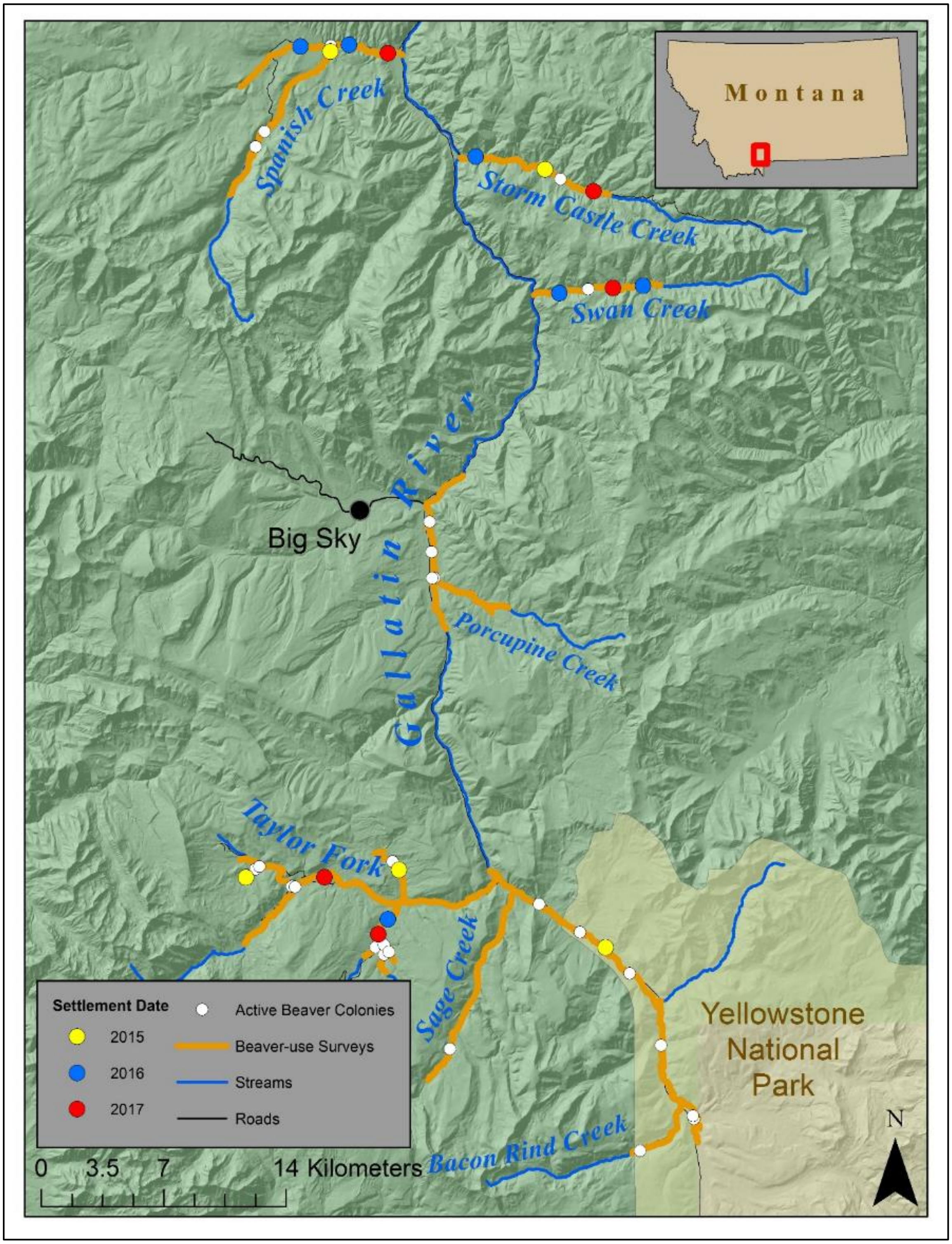

Figure 4. Locations of new settlement sites of beavers in the upper Gallatin River drainage in southwest Montana, USA. Active beaver colony locations reflect 2016 conditions.

I monitored 18 of the new settlement sites for at least one year post-settlement. In reference to the spatial extent these 18 colonies, five were active and expanding for at least one year after colonization while three stayed approximately the same size. The other 10 new settlement sites were abandoned the year following settlement and were not reoccupied before the end of the study period.

GIS-based Settlement Site Selection. The candidate model set representing habitat conditions related to stream geomorphology contained 31 models and seven models were considered parsimonious (Table 5a). The effects of stream gradient and sinuosity were well-supported, and models containing these terms received 75% and 46% of the relative support of the data, respectively. Variables for floodplain width (cumulative w_i = 0.22) and watershed size (cumulative w_i = 0.54) may be uninformative as 85% confidence intervals on the model-averaged coefficient estimates overlapped zero. I evaluated eight candidate models with variables related to vegetation. Canopy cover of woody riparian vegetation was the only variable that was well-supported (cumulative w_i = 0.92; Table 5b). The candidate set for the proportion of wetland types included 13 models, from which three were considered parsimonious (Table 5c). I evaluated the wetland type models for both 30-m and 100-m buffers around the sampling segments and found the 30-m scale explained more variation in the dataset so modeling results at the 100-m scale were not included in the final model development. The variables for waterbody wetland type (cumulative w_i = 0.81; Table 5c) and sparse-willow wetland type (cumulative w_i = 0.84; Table 5c) were well-supported by the data. The willow-dominate wetland type received less support (cumulative w_i = 0.67; Table 5c), but 85% confidence intervals did not overlap zero so this variable was included in final model development.

The final candidate model set combined habitat variables from the top models within each habitat category. Models included terms for stream gradient, sinuosity, and canopy cover of woody riparian vegetation as well as the proportion of sparse-willow, willow-dominate, and waterbody wetlands (Table 5d). The top settlement site selection model retained variables for stream gradient, canopy cover of woody riparian vegetation, and the proportion of sparse-willow and waterbody wetland types within 30 m of the stream. However, three models were supported by the data (Table 5d). Model-averaged coefficient estimates (SE) indicated a negative effect of the proportion of waterbody wetland type that was the strongest predictor of newly settled segments (β = -1.31 ± 0.46; Figure 5d). Stream gradient also had a negative effect (β = -0.72 ± 0.27; Figure 5a), while canopy cover index (β = 0.56 ± 0.21; Figure 5b) and the proportion of sparse-willow wetland type (β = 0.36 ± 0.24; Figure 5c) had positive effects on the probability of a sampling segment being settled (Figure 6). The terms for sinuosity and the proportion of willow-dominate wetland types were not well-supported and 85% confidence intervals on the model-averaged effect sizes overlapped zero (Table 5d; Figure 5). Distance to the nearest active colony contributed little explanatory power to the models.

Table 5. Model selection results testing the influence of habitat conditions on the probability of new settlement by beavers in the upper Gallatin and Madison River drainages in southwest Montana, USA, 2015−2017. Listed are all models considered parsimonious, the global model, and the null model.

Model	K	AIC_c	ΔAIC_c	w_i	Cum w_i
a. Stream geomorphology					
sinuosity + gradient + gradient × watershed	5	268.94	0.00	0.12	0.12
gradient + watershed size	4	269.14	0.20	0.10	0.22
sinuosity + gradient + watershed size	5	269.51	0.57	0.09	0.31
sinuosity + gradient	4	269.56	0.62	0.08	0.39
gradient	3	269.69	0.74	0.08	0.47
sinuosity + gradient + floodplain width	5	270.71	1.77	0.05	0.52
sinuosity	3	270.82	1.88	0.05	0.57
sinuosity + gradient + watershed + floodplain width + channel complexity[a]	7	273.12	4.18	0.01	---
1 (null model)	2	272.63	3.69	0.02	---
b. Vegetation					
canopy cover	3	267.40	0.00	0.47	0.47
riparian width + canopy cover + height[a]	5	271.46	4.06	0.06	---
1 (null model)	2	272.63	5.24	0.03	---
c. Wetland types					
waterbody + sparse-willow + willow	5	265.64	0.00	0.33	0.33
waterbody + sparse-willow	4	267.11	1.46	0.16	0.49
sparse-willow + willow + gravel + waterbody[a]	6	267.14	1.50	0.15	0.64
1 (null model)	2	272.63	7.19	0.01	---
d. Combined models					
gradient + canopy cover + sparse-willow + waterbody	6	254.17	0.00	0.39	0.39
gradient + canopy cover + waterbody	5	254.59	0.42	0.32	0.71
gradient + sinuosity + canopy cover + waterbody	6	256.00	1.83	0.16	0.87
gradient + sinuosity + canopy cover + sparse-willow + waterbody + willow + distance to active colony[a]	9	260.04	5.87	0.03	---
1 (null model)	2	272.63	18.46	0.00	---

[a] Global model

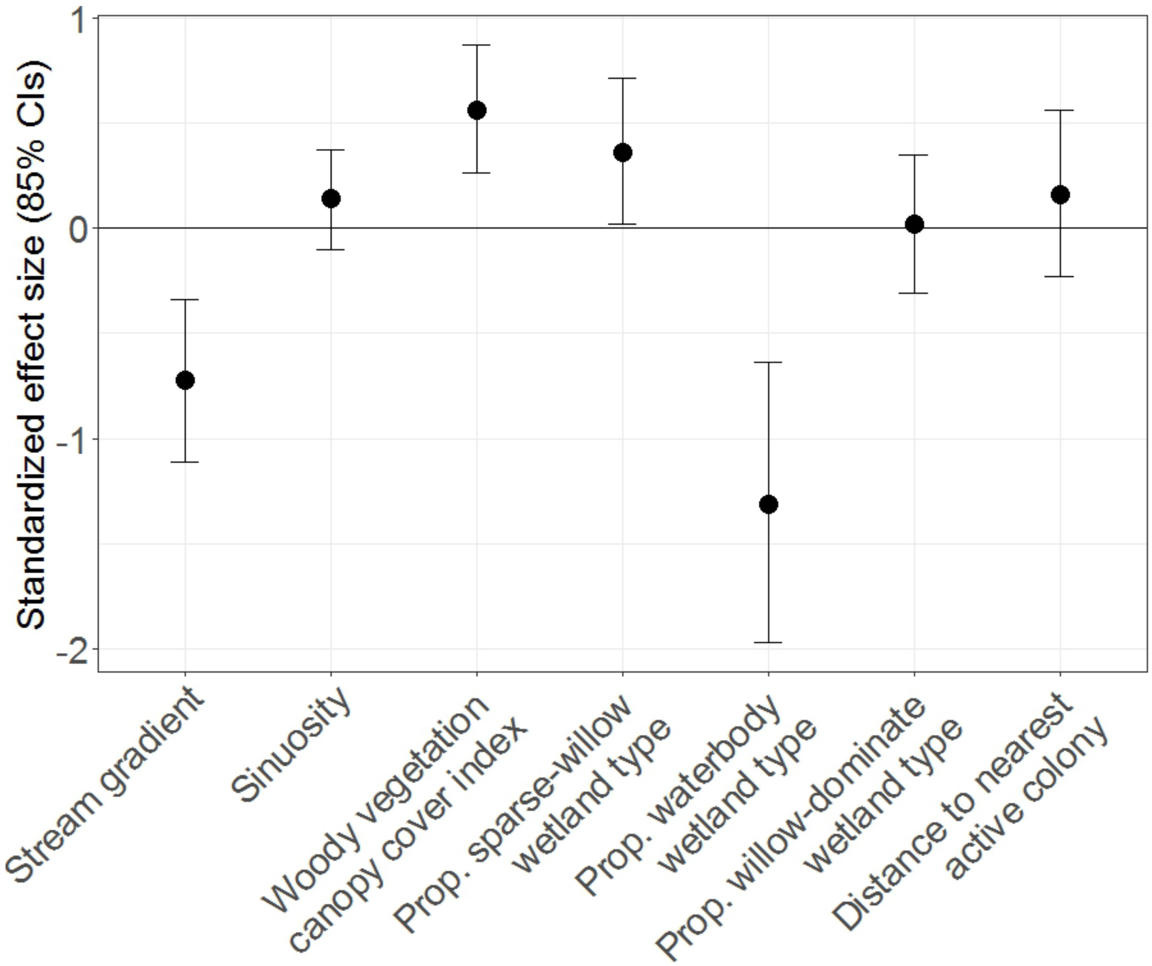

Figure 5. Model-averaged effects of GIS-based habitat variables on the probability that a stream segment will be newly settled by beavers in the upper Gallatin and Madison River drainages in southwest Montana, USA, during 2015−2017.

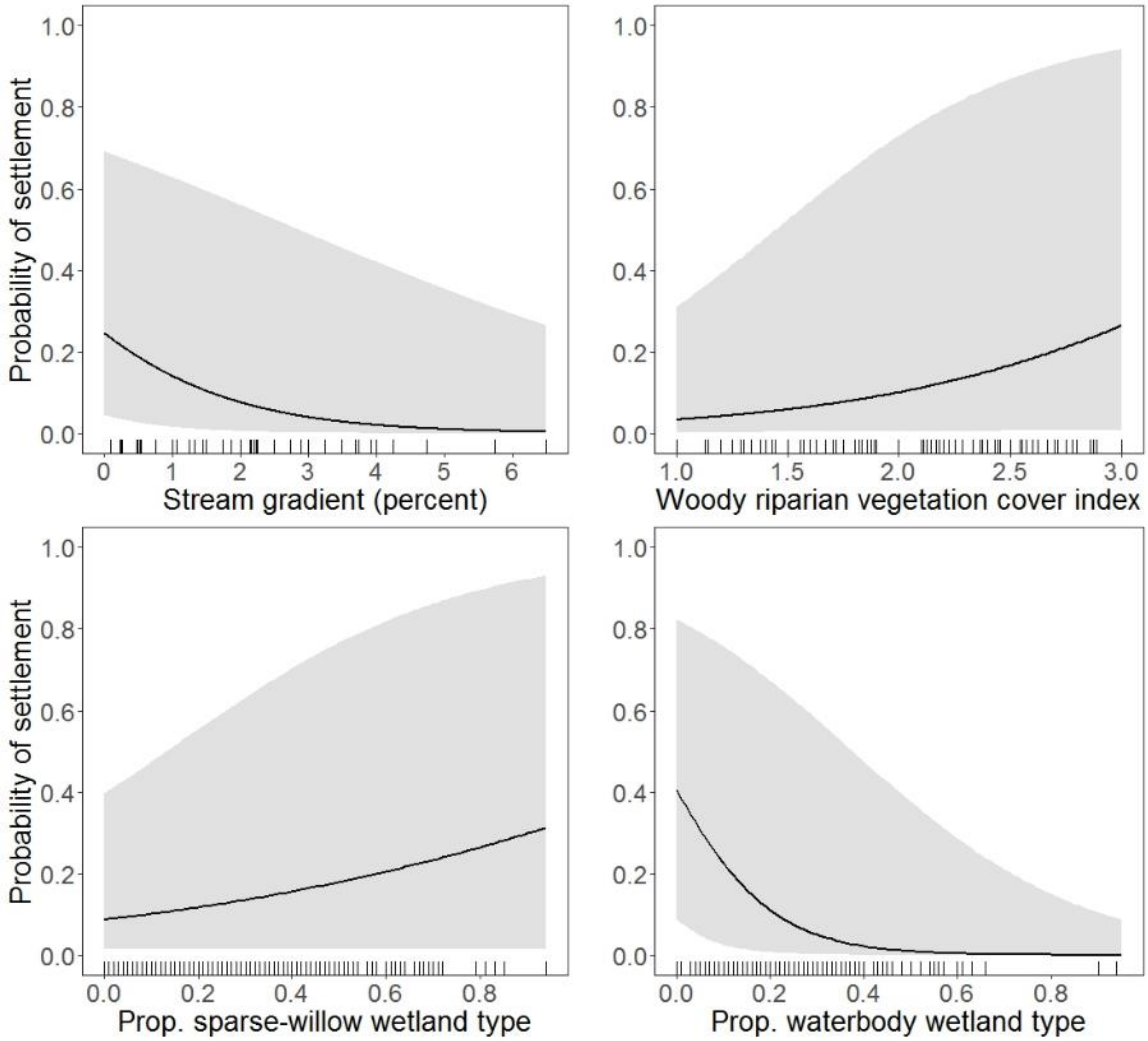

Figure 6. Effects plots of top habitat variables influencing the probability of new settlement by beavers in stream segments within the upper Gallatin and Madison River drainages in southwest Montana, USA. Shaded areas depict 85% confidence intervals.

Based on the results of a likelihood ratio test between a model that included the random intercept term and one that did not, I found strong support for a stream-level random effect ($P < 0.0001$). Some streams in the study area had higher baseline probabilities of settlement, and the spread of intercepts around the predicted fixed effect suggests wide variation in new settlement dynamics across streams (Figure 7). Marginal R^2 was low for the top habitat selection model ($R^2_{GLMM(m)} = 0.31$), indicating the fixed effects did not explain much variation in the dataset. The conditional R^2 improved model fit ($R^2_{GLMM(c)}$ = 0.52).

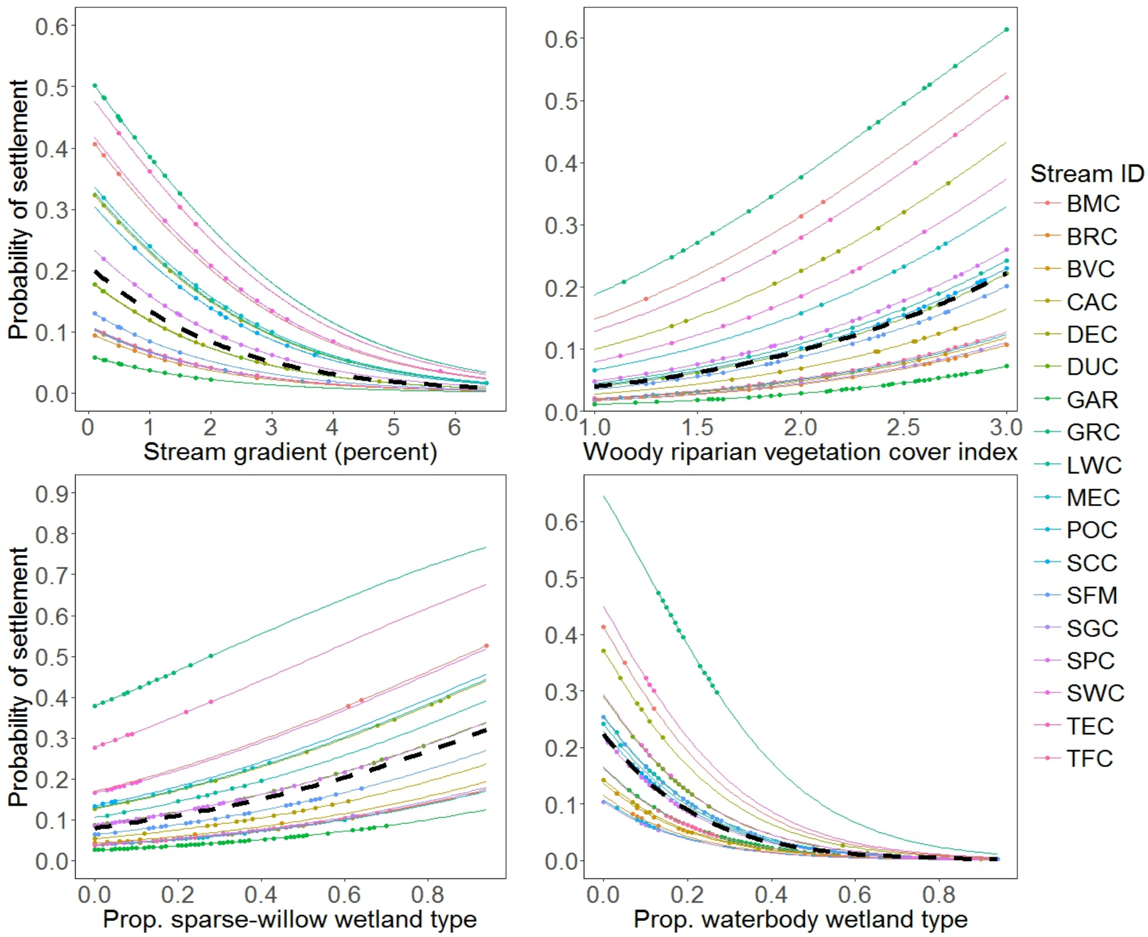

Figure 7. Random intercept effects plots for top habitat variables influencing the probability of new settlement by beavers in stream segments within the upper Gallatin and Madison River drainages in southwest Montana, USA. Black dashed lines depict average predicted fixed effects.

<u>Field-Based Settlement Site Selection</u>. Of the 27 new settlement sites identified in the study area during 2015−2017, I sampled 19 in the field along with 19 paired unsettled sites. The other eight new settlement sites could not be sampled in the field because beavers had already drastically manipulated fine-scale habitat conditions before the sites were discovered. Of the new settlement sites where habitat sampling took place, 11 were

previously relic colonies and eight were previously unoccupied. I sampled 12 new settlement sites in the Gallatin drainage and seven in the Madison drainage.

I considered 31 models in the candidate set of logistic regression models that included variables related to stream geomorphology. Three models were considered parsimonious and accounted for 39% of the model weight (Table 6a). The terms for channel complexity (cumulative w_i = 0.31; Table 6a), and width:depth ratio (cumulative w_i = 0.26; Table 6a) were the only terms included in the top models. However, the top models were close to two ΔAIC_c from the null model and confidence intervals on the model-averaged coefficients were large. I evaluated 28 models related to access to riparian vegetation. The top models contained terms for the average distance to preferred forage (cumulative w_i = 0.54; Table 6b), stem volume (cumulative w_i = 0.19; Table 6b), standard deviation of stem volume (cumulative w_i = 0.19; Table 6b), and the minimum gravel bar length (cumulative w_i = 0.07; Table 6b). The null model was considered parsimonious for the candidate set, so there is little evidence for an effect of vegetation variables on the probability of settlement. However, the 85% confidence interval on the term of average distance to preferred forage did not overlap zero, so I included it in final model development.

I included terms for channel complexity, width:depth ratio, and average distance to preferred forage in a combined candidate model set (Table 6c). I evaluated seven models that included all combinations of the three variables except interactions. Four models were considered parsimonious and accounted for 78% of the model weight. Model-averaged coefficients (SE) on the scaled habitat variables suggested increasing channel complexity had a positive effect on the probability of settlement (β = 0.76 ± 0.42; Figure 8). Increasing width:depth ratio had a negative effect on the probability of settlement (β = -0.59 ± 0.43; Figure 9), as did increasing average distance to preferred forage (β = -0.91 ± 0.72; Figure 9), but the 85% confidence intervals on the model-averaged effect sizes overlapped zero.

Table 6. Model selection results testing the influence of habitat conditions on the probability of new settlement by beavers in the upper Gallatin and Madison River drainages in southwest Montana, USA, 2015−2017. Listed are all models considered parsimonious and the null model.

Model	K	AIC_c	ΔAIC_c	w_i	Cum w_i
a. Stream geomorphology					
channel complexity + width:depth	3	53.97	0.00	0.18	0.18
channel complexity	2	54.71	0.75	0.13	0.31
width:depth	2	55.54	1.58	0.08	0.39
1 (null model)	1	56.15	2.18	0.06	0.45
b. Access to vegetation					
average distance to preferred forage	2	55.05	0.00	0.15	0.15
1 (null model)	1	56.15	1.10	0.09	0.24
average distance to preferred forage + SD of stem volume	3	56.57	1.52	0.07	0.31
SD of stem volume	2	56.64	1.59	0.07	0.38
minimum gravel bar length + average distance to preferred forage	3	56.69	1.64	0.07	0.45
stem volume	1	57.01	1.95	0.06	0.51
c. Combined models					
channel complexity + average distance to preferred forage	3	53.35	0.00	0.28	0.28
channel complexity + width:depth	3	53.97	0.61	0.20	0.48
channel complexity + width:depth + average distance to preferred forage	4	54.41	1.06	0.16	0.64
channel complexity	2	54.71	1.36	0.14	0.78
1 (null model)	1	56.15	2.80	0.07	---

[a] Global model

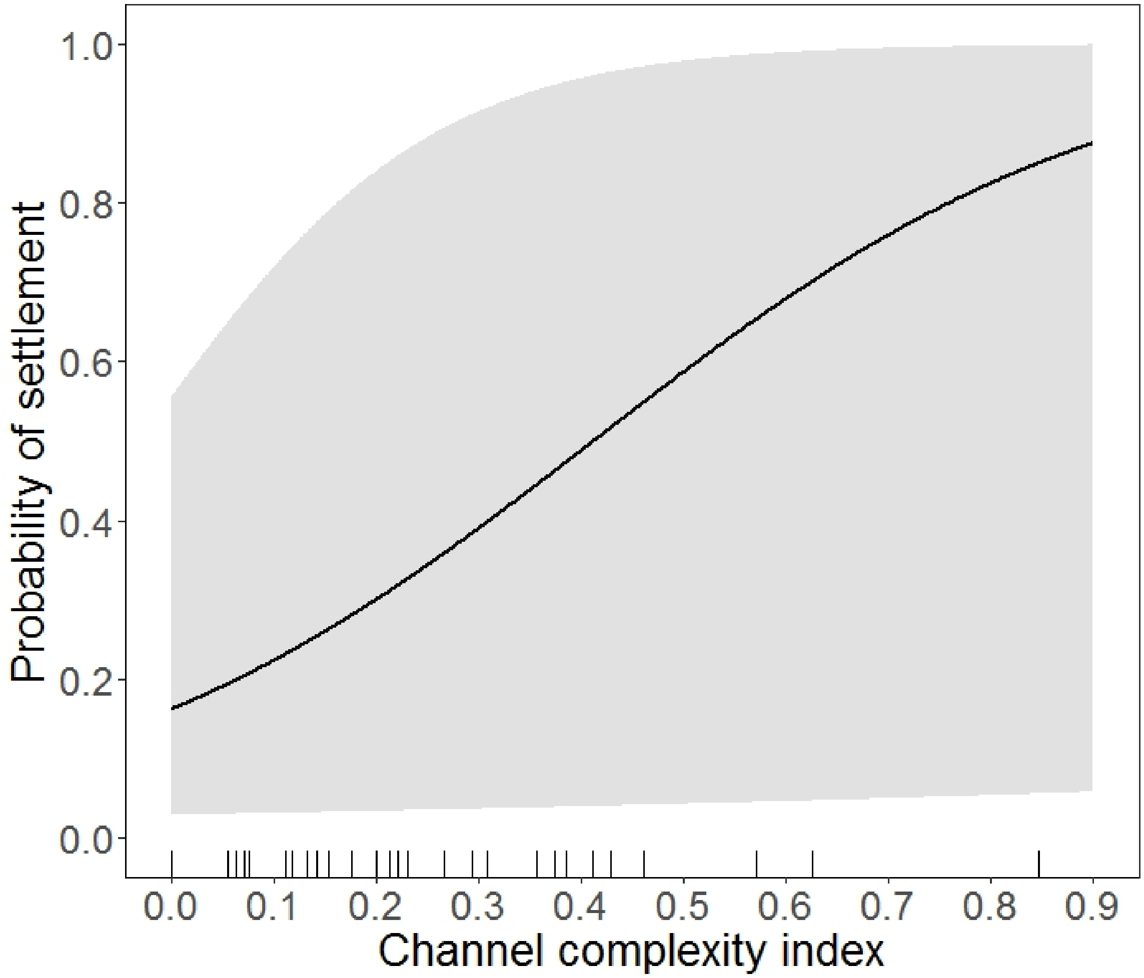

Figure 8. Effect plot of channel complexity index on the probability of new settlement by beavers in stream segments within the upper Gallatin and Madison River drainages in southwest Montana, USA. The shaded area depicts the 85% confidence interval.

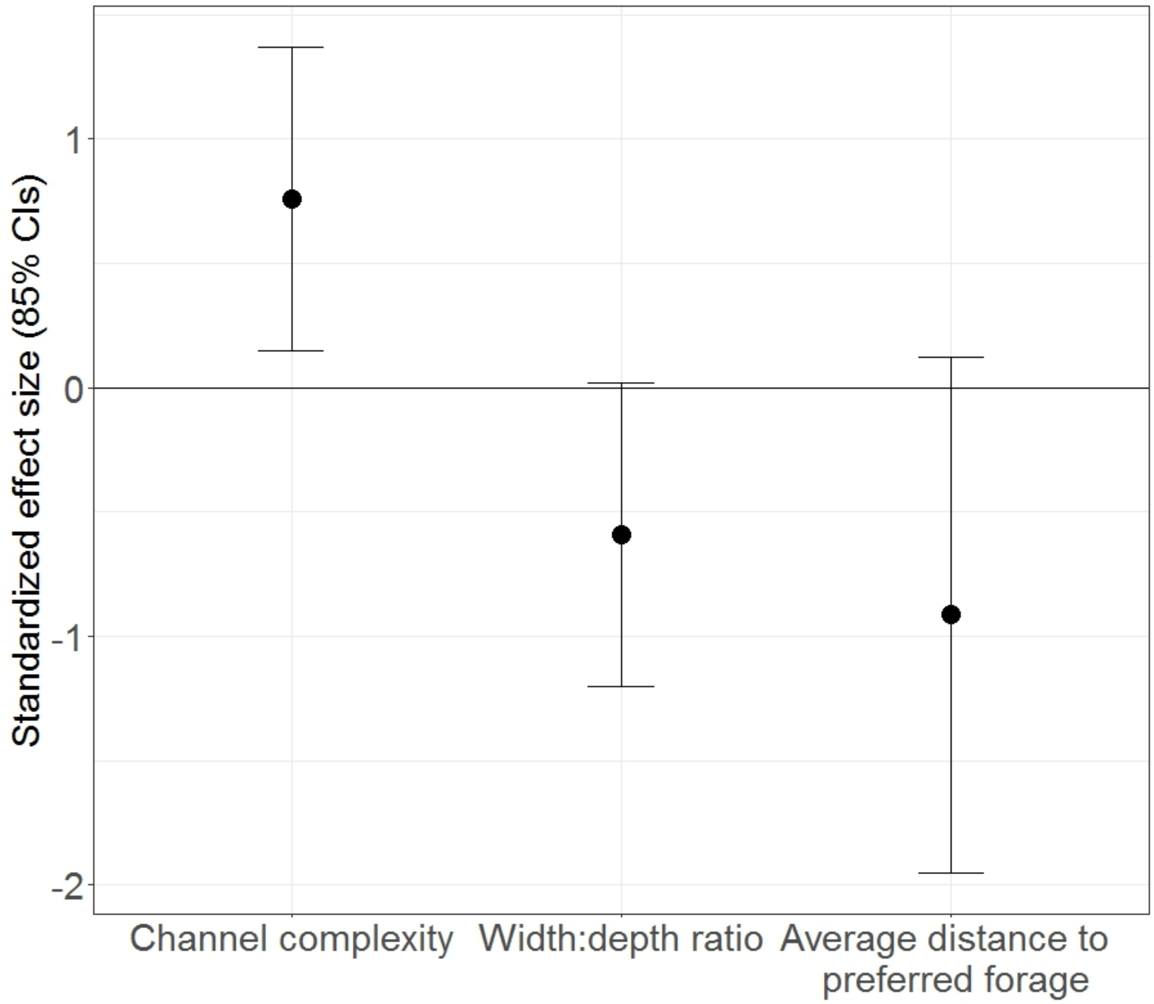

Figure 9. Model-averaged effects of habitat variables on the probability a stream segment will be newly settled by beavers in the upper Gallatin and Madison River drainages in southwest Montana, USA.

Paired Wilcoxan signed-rank test comparisons of habitat variables between settled and unsettled sampling reaches suggest settled sites had deeper waters overall, more variation in depth, smaller width:depth ratios, and more channel complexity (Table 7). The distance to preferred forage also appears to be lower overall at settled sites, though the pairing of settled and unsettled sites did not produce a significant difference.

Table 7. Mean (±SE) of habitat variables used to investigate settlement site selection by dispersing beavers in the upper Gallatin and Madison River drainages in southwest Montana, USA, 2015−2017 (SD = standard deviation).

Variable	Settled	Unsettled	P[a]
Stream width (m)	7.9 (2.3)	8.5 (2.4)	0.47
SD of stream width (m)	2.3 (2.8)	2.0 (2.1)	0.066
Stream depth (cm)	33.06 (1)	29.73 (0.78)	0.0082
SD of stream depth (cm)	12.27 (1.72)	9.69 (1.26)	0.0039
Deepest stream depth (cm)	44.04 (1.33)	39.89 (1.05)	0.018
SD of cross-section stream depth (cm)	11.4 (0.47)	10.22 (0.4)	0.020
Width:depth ratio (cm)	27.52 (1.01)	32.07 (1.18)	0.036
Discharge (m^3/s)	19.68 (0.91)	19.31 (0.89)	0.86
Gravel bar Length (cm)	138.42 (14.69)	142.6 (17.94)	0.98
Min. gravel bar length (cm)	24.25 (4.49)	40.94 (10.01)	0.74
Bank height (cm)	69.73 (3.16)	71.6 (2.73)	0.73
SD of bank height (cm)	69.50 (6.45)	71.77 (6.17)	0.86
Min. bank height (cm)	42.51 (2.47)	43.51 (1.47)	0.86
Distance to preferred forage (cm)	366.3 (35.38)	774.84 (143.01)	0.65
Min. distance to preferred forage (cm)	153.78 (22.78)	264.79 (44.2)	0.35
Channel complexity (index)	0.28 (0.03)	0.18 (0.02)	0.045
Substrate size (index)	3.59 (0.06)	3.66 (0.05)	0.48
Stem volume (cm^3)	844.9 (333.26)	897.6 (255.67)	0.42
SD of stem volume (cm^3)	1107.0 (388.24)	1468.1 (460.04)	0.31

[a] *P*-values based on Wilcoxan signed-rank test.

Using Wilcoxan rank-sum tests, I evaluated 83 total comparisons between settled and unsettled sampling reaches throughout the study area that were deemed biologically plausible (Table 8). When I limited comparisons to only those that occurred within the same stream, the sample size was 53. Overall, stream widths were narrower in settled sampling reaches, with 43% of all comparisons showing significantly narrower stream channels, as opposed to 25% that were significantly wider. When I considered same-stream comparisons, 42% of sampling reaches had narrower channels while only 13%

had wider stream channels. The deepest stream depth and overall stream depth were frequently significantly deeper at settled sampling reaches. As a result, width:depth ratios were smaller at settled sampling reaches, suggested settled sites had narrower and deeper streams. Significantly larger width:depth ratios at settlement sites were almost non-existent in same-stream comparisons. The average and minimum distance to preferred forage was generally smaller among all comparisons, and in same-stream comparisons this relationship occurred with greater frequency. A similar pattern was observed for stem volume and the standard deviation of stem volume with both metrics being significantly lower at settled sites for the majority of all comparisons and same-stream comparisons. Channel complexity index was higher at settled sites, with a vast majority of significant differences being sampling reaches with greater channel complexity. In all comparisons, 33% had significantly more complex channel structures and in same-stream comparisons nearly five times as many significant differences between settled and unsettled sampling reaches indicated settled reaches had greater channel complexity.

Table 8. Proportions of significant Wilcoxan rank-sum tests for habitat variables comparing stream reaches newly settled by beavers to unsettled stream reaches in the upper Gallatin and Madison River drainages in southwest Montana, USA, 2015−2017. “All comparisons” includes tests between reaches within different streams that were ≤ 6 km straight-line distance from the settled stream reach whereas “same-stream” only considers reaches within the same stream. Significance was set at $P < 0.10$, though the majority of the differences were more significant ($P < 0.05$; 411/490 significant differences and 166/218 significant differences for all comparisons and same-stream comparison, respectively).

Variable	All comparisons (n = 83)			Same-stream (n = 53)		
	Larger	Smaller	No Diff	Larger	Smaller	No Diff
Stream width (cm)	0.25	0.43	0.31	0.13	0.42	0.45
Deepest stream depth (cm)	0.34	0.17	0.49	0.25	0.038	0.72
Stream depth (cm)	0.30	0.12	0.58	0.21	0.00	0.79
SD of cross-section stream depth (cm)	0.20	0.096	0.70	0.076	0.00	0.92
Width:depth ratio (cm)	0.072	0.29	0.64	0.019	0.26	0.72
Flow Rate (m/s)	0.23	0.24	0.53	0.13	0.15	0.72
Discharge (m^3/s)	0.34	0.39	0.28	0.25	0.32	0.43
Gravel bar length (cm)	0.24	0.14	0.61	0.19	0.057	0.75
Min. gravel bar length (cm)	0.084	0.11	0.81	0.00	0.076	0.92
Bank height (cm)	0.16	0.27	0.58	0.11	0.26	0.62
Min. bank height (cm)	0.19	0.33	0.48	0.076	0.30	0.62
Distance to preferred forage (cm)	0.17	0.35	0.48	0.094	0.34	0.57
Min. distance to preferred forage (cm)	0.16	0.28	0.57	0.094	0.26	0.64
Channel complexity (index)	0.33	0.12	0.55	0.38	0.076	0.55
Substrate size (index)	0.12	0.084	0.80	0.057	0.038	0.91
Stem volume (cm^3)	0.13	0.38	0.49	0.088	0.40	0.51
SD of stem volume (cm^3)	0.098	0.40	0.50	0.053	0.40	0.54

Discussion

New settlement sites were uncommon in the study area, and only 13% of available relic and unoccupied sampling segments were colonized over a 3-year time period. Although my estimates of colony densities were average or low compared to other regions (Table 1), colony densities may be unreliable as authors' definitions of colony boundaries are highly variable. My results indicate most of the suitable beaver habitat in the study area was likely occupied. The majority of habitat metrics used to define high quality beaver habitat in previous studies are the same metrics characterizing sampling segments in the study area occupied by active colonies (Howard and Larson 1985, Scrafford et al. 2018; Table A3), suggesting the remaining habitat is of lower quality. As additional evidence, trapping efforts to support research of dispersal and survival of juvenile beavers indicated a high prevalence of adult beavers other than the breeding pair in colonies in the study area (Chapter 3), signifying delayed dispersal (Smith 1997, Sun et al. 2000, Mayer et al. 2017a;b). While the ecological drivers of delayed dispersal are complex, often high population densities and low quality habitat in unoccupied territories leads to delayed dispersal in territorial species (Stenseth and Lidicker 1992, Koenig et al. 1992).

The lower number of relic and unoccupied sampling segments available for new settlement sites in the Madison drainage was likely reflective of higher beaver activity in the Madison drainage. Beaver colony densities were higher in the Madison drainage which was probably due to better overall habitat quality (Table A2). High colony densities leads to frequent recolonization of abandoned territories so sampling segments in the Madison drainage were rarely allowed rest from beaver activity long enough to return to the relic or unoccupied state. As a result, 16 of the 27 new settlement sites were in the Gallatin drainage and six of the 10 remaining sites in the Madison drainage were located in one stream system. Many streams in the Madison drainage do not experience high-energy floods because of low stream gradients, spring-based water sources, and high stream sinuosity, which further reduced the number of relic and unoccupied stream segments in this drainage. My observations indicate the Gallatin drainage experiences higher-energy floods each spring which destroys dams and lodges and more rapidly converts active sampling segments to relic or unoccupied segments. This assertion highlights an important aspect of the segment classification protocols; differentiation between abandoned, relic, and unoccupied sampling segments is not a measure of time since occupation, but rather a measure of the state of beaver habitat manipulations. Because of this nuance, the prevalence of relic sampling segments in the Gallatin drainage and abandoned segments in the Madison drainage may be more reflective of differing stream flow dynamics between the two drainages than of overall beaver activity and historical occupation. The dramatic differences in stream conditions between these two drainages likely contributed to the individual stream variation in settlement probability I observed in the GIS-based habitat selection analysis (Figure 7).

Sampling segments classified as relic were settled at nearly twice the rate of unoccupied segments, suggesting preference for stream segments with previous beaver modifications in settlement site selection. Relic structures, especially lodges, were frequently used while colonizing beavers were constructing new dams and lodges in relic segments. It is unclear how the presence of such structures interacts with other habitat factors to influence the selection of a settlement site. Dispersing beavers may be more vulnerable to predation (McNew and Woolf 2005), so the existence of good hiding cover during colony establishment may be essential. The selection of previous beaver structures at a settlement site could therefore be strong enough to overshadow the influence of other habitat variables. Based on the results of this and other studies of beaver habitat selection (Chapter 1), there is evidence relic sampling segments were of higher quality compared to unoccupied segments (Table A4), which could be the result of habitat manipulations brought about by previous beaver occupancy. However, I cannot say with certainty that habitat at unoccupied sampling segments was not manipulated by previous beaver activity as well because the absence of old structures does not necessarily mean the segment was never occupied by beavers. Especially in highly dynamic stream systems, repeated flooding and shifting of the stream channel can eliminate any sign of past beaver use, even though plant growth and channel form may have been influenced by past beaver activity.

Consistent with expectations, beavers dispersing into novel areas in the upper Gallatin and Madison River drainages selected stream segments that provided woody riparian vegetation and geomorphological conditions that facilitated dam construction. New settlement sites were often located in higher energy streams and were therefore clustered in their distribution across the study area. My data indicate new settlement sites were established in poorer habitat compared to active and abandoned beaver colonies in the area, with narrower floodplains, steeper gradients, and lower amounts of preferred forage (Table A5). The suboptimal habitats where new settlement sites were established were mostly characterized by patchy forage resources and less sinuous streams where floodwaters breached dams and altered stream channels annually. Several authors have noted beaver colonies established in marginal habitats late in colonization phases are more dynamic as habitat is less stable and therefore difficult to occupy long-term (Nolet and Rosell 1994, František et al. 2010, Scrafford 2018). High densities of beavers in my study area relative to the amount of suitable habitat available suggests the best territories were generally occupied, which likely forced dispersing beavers into suboptimal habitats where long-term colony success was more difficult. As further evidence of this assertion, I observed a rapid rate of abandonment of new settlement sites within one year of establishment (56%). It is plausible new settlement sites in the study area were not chosen as locations where a colony could expand in the future, as most settlement sites were small and located in isolated patches of slightly higher quality habitat than other patches in the immediate area. Instead, dispersing beavers may use new settlement sites as temporary locations while they search for a better territory, and these new sites may not be meant to last more than a year or two. It is also possible that many of the new settlement sites I identified were not settled by dispersing beavers, but by resident beavers moving their colony to different locations in a stream over time to take advantage of shifting resource availability and cope with dam and lodge blow-outs.

GIS-based Settlement Site Selection. The probability of settlement was negatively associated with increasing stream gradient within sampling segments. My findings are consistent with habitat assessments at established colonies that universally show a negative relationship between stream gradient and colony occurrence, density, and longevity (Slough 1976, Howard and Larson 1985, Beier and Barrett 1987, Easter-Pilcher 1987, Barnes and Mallik 1997, Suzuki and McComb 1998, Curtis et al. 2004, Cox and Nelson 2008). My findings indicate stream gradient is also important for initial site selection. Low gradient stream segments allow beavers to flood a greater area through dam construction and increase the likelihood dams will withstand high water events as low gradient streams generally have lower stream power (McComb et al. 1990, Pollock et al. 2014). In streams characterized by mostly high gradients, segments with lower gradients offer rare areas of deposition, where stream flow is slowed and gravel and sandy substrates allow proliferation of forage species preferred by beavers (e.g., willow, cottonwood). Unlike other studies that commonly measured stream gradient over larger stream sections (≥ 1 km), I measured gradient individually for each sampling segment (400 m) providing some evidence low gradients may be selected at smaller spatial scales than previously assessed.

I found some support that stream sinuosity positively affected the probability of settlement by beavers. Sinuosity was an important predictor of beaver presence (Easter-Pilcher 1987), and success in other studies in Montana (number of years active : number of years since establishment; Scrafford et al. 2018). Stream sinuosity may be more important in higher gradient, snow-melt dominated stream systems of the western United States because more sinuous streams help dissipate flood waters, create deep holes on outside bends where beavers can find shelter even if a dam blow-out occurs, and increase the effective foraging area within a stream section (Scrafford et al. 2018). It is possible the true effect of sinuosity may function at a smaller spatial scale than my 400-m sampling segments (Hartman 1994, Scrafford 2011). Similar to Scrafford (2011), I noted frequent use of deep holes on outside bends along streams in the study area for lodge construction as well as for daytime resting locations of dispersing beavers prior to colony establishment (Chapter 3). In smaller streams and in suboptimal habitats within the study area these bends were the only locations where water was deep enough to cover the entrances of lodges and bank dens. Anecdotal observations indicated bank den entrances generally required 30–60 cm of depth while lodge entrances required depths > 60 cm. Beavers settling a stream segment may therefore only need a single prominent bend in the stream course and an undercut bank to supply ample water depth for initial lodge establishment suggesting sinuosity of the entire segment is not as important. Analysis of fine-scale habitat metrics at new settlement sites support this conclusion. Settled sampling reaches were more variable in depth than unsettled reaches nearby so pockets of deeper waters may have been responsible for much of the variation.

Canopy cover of woody riparian vegetation index was the only variable selected from the vegetation candidate set and one of the strongest predictors of settlement site selection. A wide variety of beaver habitat selection and suitability studies have noted increasing abundance of woody riparian vegetation associated with increasing occupancy, density, and longevity of beaver colonies (Howard and Larson 1985, Easter-Pilcher 1987, DeStefano et al. 2006, Cox and Nelson 2008). However, more often vegetation metrics are found to be of secondary importance to beaver habitat suitability compared to stream geomorphology variables (Howard and Larson 1985, Beier and Barrett 1987, Scrafford et al. 2018). Unlike these studies, I found canopy cover of woody riparian vegetation to be one of the best predictors of new settlement sites regardless of overall abundance of woody vegetation. Settlement sites frequently coincided with distinct patches of riparian vegetation along the stream where the canopy cover exceeded ~ 66%. Although the riparian width was small at many settlement sites compared to areas with abandoned and active colonies (Table A5), the vegetation was often dense and close to the stream (e.g., < 4 m). Many studies have noted a preference for vegetation close to the water and easily accessible to beavers (Easter-Pilcher 1987, Barnes and Mallik 1997, Scrafford 2011), and results from the field-based habitat analysis provide further evidence that riparian vegetation in close proximity to the stream channel was preferred at settlement sites. Dispersing beavers are thought to be at higher risk of mortality from predation as they are in unfamiliar environments and lack the protection of dams and lodges (McNew and Woolf 2005). Dense patches of riparian woody vegetation not only offer initial lodge and dam construction material, but also help in predator avoidance as beavers do not have to go far from their dam and lodge to forage and are better concealed.

The Montana Natural Heritage Program's Wetland and Riparian Framework provided a valuable source of geospatial data on the character and distribution of wetland types in the study area. I found the proportions of wetland types within 30-m buffers around the stream channel were better supported than from within a 100-m buffer. Many authors have reported that the majority of beaver activity occurs within 30 m of water (Hall 1960, Jenkins 1980, Belovsky 1984, Gallant et al. 2004). Also, most of the new settlement sites were located in areas with greatly reduced forage resources beyond

30−50 m from the stream channel, so it is unlikely beavers were assessing habitat beyond ~ 50 m when selecting settlement sites.

Two groupings of wetland types were good predictors of settlement site selection. I had hypothesized the sparse-willow wetland type would be negatively associated with the probability of settlement due to low amounts of forage, but I found evidence the relationship was actually positive. The sparse-willow wetland type represented areas directly adjacent to the stream that had short or patchy woody riparian vegetation. Many of these locations were old oxbows or sedge meadows that would be easily flooded by even a modest-size dam, while other areas were drier parts of the floodplain where water tables appeared to be lower. Therefore, it is unclear exactly what mechanism influenced the selection for the sparse-willow wetland grouping. Notably, five out of 27 new settlement sites I identified were located in a tributary drainage to the Gallatin River where the sparse-willow wetland type dominated the area, which may have biased the results. In this tributary drainage, the sparse-willow wetland type was associated with drier conditions whereas in all other areas this wetland type was mostly associated with low-lying, wetter areas. It is possible beavers seek locations with the sparse-willow wetland type because they will not be able to construct a large dam immediately at their new settlement site, so maximizing the efficiency of the infrastructure they are able to build is a priority. With low-lying areas close to the stream channel, a smaller dam may be sufficient to push water out onto the floodplain, increasing beavers' foraging area and relieving pressure on the dam during high water events (Pollock et al. 2011). Alternatively, selection for areas with the sparse-willow wetland type may be related to lower banks that allow beavers to access forage easily, minimizing the amount of time spent out of the water and vulnerable to predation.

Contrary to my hypothesis, I found the probability of beaver settlement decreased with increasing proportion of the waterbody wetland group within 30-m buffers around sampling segments. The waterbody wetland group represented all stream channels, ponds, and lakes in the study area, though the vast majority (~ 97%) of this wetland type was associated with stream channels. Most of the new settlement sites were located in narrower and higher elevation (1600–2309 m) sections of stream that corresponded to narrower channels and therefore a low proportion of the waterbody wetland type. Some researchers have hypothesized narrower stream channels may be easier to dam by beavers and dams in narrow streams are more likely to withstand high flows (Suzuki and McComb 1998, Pollock et al. 2014). However, the influence of stream width on dam construction and maintenance is almost certainly mediated by other factors including initial stream depth, discharge, and bank height (McComb et al. 1990, Pollock et al. 2014), and there was evidence from the field-based habitat analysis that stream depth and bank height were potentially important factors distinguishing settled and unsettled sites. Further research should address interactions among these habitat variables, and the complexity of interactions may explain why the influence of stream width on beaver habitat selection metrics has been inconsistent across study areas (Slough 1976, Howard and Larson 1985, Beier and Barrett 1987, Easter-Pilcher 1987, Barnes and Mallik 1997, Curtis et al. 2004, Pinto et al. 2009, František et al. 2010).

I hypothesized that for beavers seeking new settlement sites in suboptimal habitats, woody vegetation would be more important as it is often limited in these habitats and a greater amount of woody vegetation may be needed for initial dam and lodge construction (Howard and Larson 1985). My hypothesis was only partially supported, as most of the vegetation variables received virtually no support from the data (Tables 5 and 6). Other studies have also found stream geomorphological and hydrological conditions were better predictors of beaver occupancy and density than vegetation (Howard and Larson 1985, Beier and Barrett 1987, Scrafford et al. 2018). For new settlement sites, beavers may only perceive vegetation availability in the context of initial lodge and dam construction and immediate food needs, and resources needed for future colony expansion may not be considered at the time of initial settlement. Alternatively, beavers may be adaptable to low amounts of woody vegetation when constructing dams and lodges. I frequently observed beavers in new settlement sites using rocks, mud, conifers, and sagebrush for dam construction rather than willow or other woody vegetation. If alternative building materials are available beavers may be able to sustain smaller new settlement sites on just enough woody riparian vegetation for foraging and an overwinter food cache.

I further hypothesized beavers would be attracted to areas with more secondary channels as was observed in similar habitats in Montana (Scrafford et al. 2018). Secondary channels provide greater flood protection, increase the active foraging area, offer good dam establishment sites, and can be used to expand access to resources while remaining in a smaller overall area. Scrafford et al. (2018) noted beaver colonies in and around Yellowstone National Park were more successful when located near, or entirely within, secondary channels. It must be noted for their study the presence of secondary channels within beaver-occupied areas was a reflection of beavers selecting the best habitat available, and did not reflect habitat selection for beavers forced to settle in suboptimal habitats. While there was no evidence for an influence of the number of secondary channels on new settlement site selection in the GIS-based analysis, channel complexity was the most important variable distinguishing settled from unsettled sites in the field-based habitat analysis. For the GIS-based analysis, I only considered the number of side channels, backwaters, and tributaries that were semi-permanent (i.e., persisted for all three years of the study and were not caused by beaver damming activity). As a result, I did not account for smaller and more temporary secondary channels and in-stream structures in the GIS-based analysis. I followed this protocol to exclude temporary channels that may shift or disappear altogether during flood events over the 3-year timespan of the study. Conversely, since I measured field-based habitat conditions within one year of settlement, I included smaller and more temporary side channels and backwaters that could not be counted in the GIS-based analysis. Furthermore, the channel complexity index in the field-based habitat analysis measured the number of sampling points within a sampling reach that were ≤ 100 m from a secondary channel, whereas the number of secondary channels in the GIS-based analysis only represented the total number of secondary channels within 100 m of the sampling segment.

The reason for the differences between the two analyses in reference to secondary channels and channel complexity is likely two-fold. First, there was a lower availability of permanent secondary channels for new settlement sites because most of the well-established beaver colonies in the study area were located in areas with secondary channels. Analysis of occupied vs. unoccupied beaver habitat conditions in the study area indicated the presence of secondary channels was a strong predictor of sampling segments occupied by beavers, excluding new settlement sites (Ritter, unpublished data). Conversely, fine-scale channel complexity measured for the field-based habitat analysis was more readily available as a component of relic and unoccupied sites. Second, fine-scale channel complexity is likely more beneficial to beavers settling in unmodified habitats, as channel complexity at a finer scale is likely related to initial dam and lodge construction rather than long-term colony persistence and expansion, as would be the expected benefit of more permanent secondary channels.

Few of the habitat conditions I measured were good predictors of settlement site selection, and I found fairly weak effects from the top habitat variables on the probability of settlement overall. The uncertainty around my parameter estimates is at least partially due to a small sample size of new settlement sites. The marginal R^2 value for the top habitat selection model indicates only 31% of the variation in the data was explained by the top habitat variables. Because I conducted this study over a large geographic area, habitat information from a small number of new settlement sites was spread over many different streams and stream types with wide variation in stream geomorphology and other habitat components. Beavers in different streams are likely limited by different habitat factors. For example, a beaver settling in a low elevation, large stream may have more than enough riparian vegetation and will therefore be limited in terms of dam construction due to high stream power. Conversely, a beaver settling in a smaller headwater stream may be able to build dams quite easily to impound water, but be limited by low abundance of riparian vegetation. Inherent variation in environmental conditions among streams was apparent in initial tests for the significance of including a random effect in the models, and the improved fit indicated by the conditional R^2 value further supported considering individual stream differences as important sources of variation.

As an added complexity, beavers starting new colonies in suboptimal habitat in my study area were presumably choosing from the best of the worst in terms of habitat conditions. As a result, the habitat differences that promoted settlement in one site over another may have been more subtle. My study contrasts with other studies of beaver colonization where beavers were colonizing an area with good overall habitat quality, but where beavers had been extirpated in the past or their presence was previously not tolerated (František et al. 2010, Scrafford et al. 2018). Future studies should seek to examine new settlement site selection over longer time periods in smaller areas to establish greater sample size of newly settled sites while attempting to control for wide variation in stream types and riparian habitat conditions.

Field-Based Settlement Site Selection. The greatest differences in fine-scale habitat variables between settled and unsettled sites were related to the physical structure of stream channels as well as the character and distribution of forage resources. I found evidence settled sites had deeper waters, smaller width:depth ratios, greater channel complexity, and more variation in stream width. Additionally, settled sites were more variable in depth both latitudinal across the stream channel and longitudinal along the stream channel. Overall, these results suggest beavers selected areas with greater heterogeneity in stream channel form and deeper waters overall. Many studies have noted positive impacts of stream depth on beaver use metrics (Beier and Barrett 1987, Easter-Pilcher 1987, Dieter and McCabe 1989, Scrafford 2011). Specifically, Dieter and McCabe (1989) in North Dakota, Easter-Pilcher (1987) in Montana observed beavers preferred localized deeper spots and undercut banks along rivers for lodge sites as these spots facilitated excavation of a lodge entrance that was underwater even in the absence of a dam. In California, Beier and Barrett (1987) observed that streams with sign of beaver activity but where no colony was established were deeper than completely unoccupied areas, suggesting beavers had explored the area but not settled. The deeper waters may have allowed beavers to occupy areas temporarily during exploratory movements.

It is likely more heterogeneous stream channels provide beavers with wide range of micro-sites used to fulfill various aspects of colony establishment and survival. At almost every new settlement site beavers used a deep pool with an undercut bank as an initial lodge site, while the primary dam was built at the tail-out of the pool where the water became shallow and in-stream structures could be used to anchor the dam. In these instances, the beavers appeared to use the longitudinal variation in stream depth to their advantage; a smaller dam was needed to get adequate water depth, and the already deep pool offered shelter while the dam was under construction. My observations are similar to those of Scrafford (2011) in other mountainous streams in Montana who noted frequent use of outside bends on streams as lodge locations where beavers took advantage of pockets of deeper waters. Variation in stream depth perpendicular to the stream flow was also higher in settled reaches, and this may reflect selection for sites with deeper areas along the banks needed for lodges and bank dens as well as shallow spots to feed and groom adjacent to escape cover.

Beavers settled in stream segments with greater channel complexity, indicating new settlement sites were more heavily influenced by side channels, backwaters, and tributaries. Beavers likely select stream reaches with greater channel complexity because these areas dissipate flood waters which can destroy dams and lodges (Scrafford et al. 2018). Channel complexity also provides more flexibility in dam construction as beavers can manipulate water from several channels to achieve appropriate impoundment. Furthermore, channel complexity increases the density of feeding areas directly adjacent to water within a colony.

Settled sites generally had smaller stem volume of preferred forage, less variation in stem volume, and a shorter distance from the water to preferred forage. My results are consistent with other studies of beaver habitat suitability that have noted beavers selecting for smaller stems overall, and for areas where woody vegetation is close to the stream channel (Easter-Pilcher 1987, Barnes and Mallik 1997, Cox and Nelson 2009). However, other studies measured stem diameter only, without accounting for differences in plant height. My data indicate beavers select for areas with smaller stems, though this metric cannot be extrapolated to say overall biomass of stems was lower at settled sites. While many studies have found beavers prefer smaller stems, in most cases the selection of smaller stems was related to the energy required to harvest large trees vs. small trees in terms of how easily stems can be processed and transported back to water (Jenkins 1980, Gallant et al. 2004). In my study area, beavers fed almost exclusively on willows, and the largest of these willows were still small enough to be easily transported by beavers. It is therefore unlikely beavers were selecting for smaller stems in my study area to optimize foraging efficiency. It is possible my results are indicative of beavers selecting areas with more willows overall, and avoiding areas with alders, cottonwoods, and aspens, which generally have much larger stems and a greater diversity of stem sizes. Originally, I had hypothesized beavers would select for larger and more diverse sizes of stems to fulfill both construction and feeding requirements. The use of non-forage species (e.g., conifers, sagebrush, red-osier dogwood) to construct dams at new settlement sites may have alleviated the need for larger stems of preferred forage species. Therefore smaller stems, which are generally preferred for feeding, may have been selected purely on the basis of food quality.

It is important to note dispersing beavers are seeking not only an open territory to establish a colony, but also a mate, and mate-seeking may have confounded my habitat selection results. I was not able to account for mate-seeking in my study, though I did observe two radio-marked beavers from different colonies that appeared to be forming a pair-bond. One of the pair remained in a small area for most of the year following dispersal, while the other traveled widely around the basin. The traveling beaver was found in a consistent set of sites, but always returned to the location of the first beaver within a few days. The paired beavers attempted to establish a colony in a pond on a privately owned ranch in fall 2017, but after repeated destruction of their dams and lodges they abandoned the site. The two beavers dispersed again in different directions in the late fall and did not pair up again before the on-set of winter.

Management Implications

Beaver restoration projects are almost always implemented in areas that would be considered suboptimal beaver habitat. Therefore, it is important to understand subtle differences in suboptimal habitat that may promote settlement in one site over another. Beaver restoration projects are usually implemented within a single stream or a small drainage (Pollock et al. 2011, Babik and Meyer 2015, Woodruff 2015, Bouwes et al. 2016, Pollock et al. 2017), so evaluation of potential settlement sites within a project area is important to maximize management control over the project. For example, managers seeking to translocate beavers to an area may want to select release sites with the highest probability of providing adequate resources for released beavers to establish a colony. Alternatively, managers seeking to promote settlement in a specific degraded stream section would benefit from knowing if beavers are more likely to settle other areas nearby, necessitating the use of beaver mimicry structures or other techniques at the targeted restoration site to encourage colonization.

My research suggests beavers in mountainous streams dominated by willow seek settlement sites in areas with heterogeneous stream channels in terms of width, depth, and channel complexity. The results may indicate that stream channel heterogeneity, which is a major benefit of beaver-modified habitats to streams (Westbrook et al. 2006, Polvi and Wohl 2013, Majerova et al. 2015, Bouwes et al. 2016), is also selected for by beavers settling novel areas. New settlement sites were further characterized by narrow channels, low gradients, dense patches of preferred forage that are near the stream, and easily flooded areas around the stream channel. Selection for these characteristics suggests geomorphic conditions that facilitate dam resiliency are important for settlement sites. Many of the habitat components can be assessed using a GIS and aerial imagery, which provides a general overview of potential beaver settlement sites in a stream system. However, to be an effective baseline for beaver restoration efforts, potential sites will need additional evaluation with on-the-ground assessments to assess water depths, access to vegetation, and the potential for stable dam construction.

The selection of narrow, low-gradient stream segments with patches of riparian vegetation and complex channels provides evidence beavers in suboptimal habitat are drawn to areas with relatively large riparian footprints. Therefore, beavers may be best suited to enhancing areas where the riparian footprint is already somewhat developed, rather than growing a new footprint from scratch. If the riparian area is highly degraded beaver mimicry structures may be the best strategy to encourage sediment deposition and rebuild the riparian footprint with direct management actions. Beavers could potentially cause more damage to a stream if they are encouraged to settle in an area with a highly degraded riparian area, as clipping of scarce vegetation and frequent dam blow-outs could destabilize an already at-risk stream channel.

An important goal of most beaver restoration projects is to promote one or more successful colonies in an area and allow the beavers to expand outward from the initial colony or produce dispersers that settle more marginal habitats nearby. From the outset, project leaders should plan for beavers to move throughout a drainage over time, especially in areas with suboptimal habitats where long-term occupancy of one or two sites may be unwanted or unsuccessful given shifting resource quality and availability. New beaver settlements are likely even more dynamic in snowmelt-dominated stream systems of the western United States where dam blow-outs and channel-altering high water events are common (Collins 1976, Butler and Malanson 2005). Landowners suspected to be within dispersal range of the restoration site should be considered key stakeholders in any project as beavers seeking settlement sites may end up moving to private land and causing property damage issues if dams at the restoration site are repeatedly breached. Successful beaver restoration projects may exacerbate this issue when established colonies begin producing dispersing beavers that leave the natal colony to occupy new areas.

As with most wildlife species, my observations indicate selection of settlement sites by beavers functions at multiple spatial scales (Boyce 2006). Previous beaver habitat suitability and selection studies confirm this observation as researchers have found effects of habitat variables on habitat use and selection at scales ranging from 2.5 km stream segments (Cox and Nelson 2008) to the immediate area around dams (Suzuki and McComb 1998), and lodges (Easter-Pilcher 1987, Dieter and McCabe 1989, Harris 1991). My selection of a minimum sampling segment size of 400 m was based on the observed extent of beaver activity upstream and downstream of the main lodges and dams. However, for ~ 4 months of the year beavers in my study area are confined to one or two dams and lodges due to ice cover. The length and severity of winters in my study area means the specific location of the overwinter lodges and dams is of critical importance to survival. Future research should examine new settlement site selection at a finer scale to determine suitability of locations for dam and lodge construction. The selection of habitat features at smaller scales has been documented in other beaver site selection studies (Easter-Pilcher 1987, Dieter and McCabe 1989, Harris 1991, Hartman 1994), which suggests beavers look for a section of stream with adequate resources for a colony (2nd-order Selection; Johnson 1980), as well as specific areas within a stream section that are appropriate for dam and lodge construction (3rd-order selection). Therefore, managers seeking to implement beaver restoration projects should consider multiple spatial scales when selecting possible locations.

Ten of 18 new settlement sites I monitored for at least one year post-establishment were abandoned the year following settlement. Although many new settlement sites were quickly abandoned, in terms of stream restoration the sites were certainly not failures. I noted many of the abandoned sites were still providing benefits to the stream system even after beavers had left the area, consistent with other studies (Pollock et al. 2014). Drained ponds often exposed mineral-rich beds of sediment where new growth of riparian vegetation was already occurring. Not only were changes to the habitat around new settlement sites evident, but in most instances dams and lodges established the year before were still mostly intact, and this infrastructure would be useful for beavers reoccupying the area in the future. Indeed, many new settlement sites may seem unsuccessful at first, but they can set the seed for future colony establishment and propagation of beavers throughout the stream system over time.

CHAPTER THREE

DISPERSAL, SURVIVAL, AND SETTLEMENT SITE SELECTION OF JUVENILE BEAVERS IN SOUTHWEST MONTANA

Introduction

Beavers (*Castor spp.*) are recognized as primary examples of both ecosystem engineers and a keystone species (Jones et al. 1994, Power et al. 1996, Wright et al. 2002). When beavers occupy an area they manipulate the habitat to support their colony which causes significant changes to the stream channel and associated riparian habitats (Naiman et al. 1988, Collen and Gibson 2001, Rosell et al. 2005). Changes brought about by beaver activity can enhance stream systems through the capture and storage of water and sediment behind dams, reconnection of the stream to its floodplain, and redistribution of woody vegetation (Naiman et al. 1988, Pollock et al. 2003, Westbrook et al. 2006, Green and Westbrook 2009, Polvi and Wohl 2012, Majerova et al. 2015). Beaver activity introduces an important aspect of the disturbance regime to waterways, providing patches of unique habitats along streams and rivers that would otherwise not occur (McDowell and Naiman 1986, Naiman et al. 1986, Wright et al. 2004, Bartel et al. 2010). As beavers colonize a drainage, they increase habitat heterogeneity at a landscape scale and promote increased ecosystem resiliency, species richness and abundance, and landscape-level water storage capacity (Naiman et al. 1988, Russell et al. 1999, Wright et al. 2002, Cooke and Zack 2008). For these reasons and more, beavers are increasingly used as tools for passive, effective, and efficient stream and riparian habitat restoration (Albert and

Trimble 2000, Babik and Meyer 2015, Woodruff 2015, Bouwes et al. 2016, Pilliod et al. 2017, Pollock et al. 2017).

The inclusion of beavers in stream restoration strategies has increased dramatically in the last 50 years especially in smaller stream systems in the arid western part of North America (Pilliod et al. 2017, Pollock et al. 2017). It is in these types of waterways beavers can have their greatest impact, as dam-building raises water tables and promotes expansion of the riparian zone. Beaver-mediated habitat restoration (hereafter "beaver restoration") projects most often involve capturing and moving nuisance beavers to restoration sites in hopes of establishing a self-sustaining population that can improve the stream system over time (Pilliod et al. 2017). Other projects use artificial beaver dams or other habitat improvements to either encourage translocated beavers to colonize a particular location, support a struggling beaver population, or facilitate natural settlement by dispersing beavers from other colonies (Bouwes et al. 2016, Pollock et al. 2017). Regardless of the strategy employed, the vast majority of beaver restoration projects share a common goal of promoting beaver colonization of degraded or at-risk stream systems.

The appropriate strategy for implementing beaver restoration is critical to the success of any project. Project leaders must evaluate local environmental conditions and decide whether to capture and move beavers to a restoration site, improve habitat conditions to promote natural colonization, or mimic beaver structures without an explicit goal of beaver occupation (Pollock et al. 2017). The choice of strategy depends not only on the available habitat, but also the density and spatial distribution of active colonies in the area. If a well-established, active colony is within dispersal distance of a proposed restoration site, then dispersing beavers from that colony are likely encountering the site and choosing not to settle there. The lack of settlement at such sites provides evidence the habitat is not suitable for beaver occupancy. Of course, identifying sites within "dispersal distance" is key to understanding this aspect of restoration site selection. If natural colonization at a targeted beaver restoration site is unlikely due to geographic isolation or lack of nearby source colonies, project leaders must assess the habitat and determine if it is of sufficient quality for a beaver translocation effort. Regardless of the strategy involved, beaver restoration practitioners will benefit from better understanding beaver dispersal and settlement in systems similar to those being restored, and learning how to take advantage of this phase of beaver life history to better inform the development and implementation of restoration projects.

Dispersal is the primary method by which animals naturally occupy new habitats (Stenseth and Lidicker 1992). In this thesis, I define dispersal as the one-way movement of a beaver from its natal colony to a settlement site where breeding would presumably take place, often referred to as "natal dispersal" (Greenwood and Harvey 1982). In territorial mammals living in family units, population densities, availability of unoccupied territories, habitat quality of unoccupied territories, competitive ability of dispersers, and barriers to dispersal both in terms of movement and survival all impact the dispersal and settlement process (Koenig et al. 1992, Stenseth and Lidicker 1992). Complex interactions among these components make it difficult to test specific hypotheses about the motivating factors governing dispersal (Bowler and Benton 2005, Matthysen 2005). There is evidence that when population densities are high and the availability of good quality territories is low, animals will delay dispersal (Stacey and Ligon 1991, Koenig et al. 1992, Smith 1997). Delaying dispersal allows animals to gain experience and body mass to make them more competitive for the few territories that become available (Koenig et al. 1992, Smith 1997, Mayer et al. 2017a). Additionally, animals that delay dispersal can increase their lifetime inclusive fitness by helping defend the territory, gather resources, repair structures, and assist in the raising of young (Koenig et al. 1992, Mayer et al. 2017a). If population densities are low, dispersal may increase as juveniles are able to find open territories easily and are not subject to competition for resources (Aleksiuk 1968, Stenseth and Lidicker 1992, Smith 1997).

As a result of delayed dispersal, extended beaver families are common and if colony densities and habitat quality are high, colonies may consist of up to four generations of beavers (Nelson and Nielsen 2010, Muller-Schwarze 2011). However, high and low beaver densities are relative to habitat quality of both the natal colony and the available territories into which dispersers could move (Koenig et al. 1992). Delayed dispersal may therefore occur in two general situations:

1) Colony densities on a per stream length basis are low, but habitat quality is poor outside the occupied areas so dispersers are not able to find adequate resources for a successful colony (Stacey and Ligon 1991, Koenig et al. 1992).

2) Colony densities are high and habitat quality is good overall, but high population densities greatly reduce available habitat, known as the social fence hypothesis (Stenseth and Lidicker 1992, Hestbeck 1982). In such a situation,

territorial disputes with neighboring colonies may become more severe than inter-colony disputes due to over-crowding, resulting in delayed dispersal (Hestbeck 1982).

In both situations, delayed dispersal is dependent on habitat quality at the natal territory, and there is likely a threshold where delayed dispersers are no longer tolerated by the mating pair because there are not enough resources in the natal colony to sustain extra non-breeding adults (Stenseth and Lidicker 1992). In this situation, dispersal-age beavers may be forced to leave the natal colony even if good quality territories are not available nearby.

It has been theorized dispersing animals experience higher risk of mortality (Koenig et al. 1992, Stenseth and Lidicker 1992, Waser et al. 1994). Animals dispersing from family groups lose the increased vigilance associated with having family members around to detect predators and warn the group (Koenig et al. 1992). Dispersing beavers may be particularly vulnerable as their main protection from predators is deep water and strong lodges associated with established colonies (Bradt 1938). Territorial disputes are likely more common for dispersing beavers because they often must travel through the middle of active colonies along their dispersal route (Aleksiuk 1968, Boyce 1974). Territoriality may be another reason delayed dispersal is common in beavers in high density areas as dispersers must be in good physical condition to navigate through active colonies, avoid predators, and compete for settlement sites (Smith 1997, Mayer et al. 2017a).

Beavers that disperse are faced with many possible outcomes depending on local colony densities as well as the availability and quality of vacant territories. Dispersers may find an active colony where a member of the breeding pair has died and move in as a new breeder (Brooks et al. 1980, Sun et al. 2000), or they may force out a member of the breeding pair (Mayer et al. 2017a). Dispersers could also find an abandoned colony with lodges and dams in place and claim it as their own (Smith 1997, Sun et al. 2000, Mayer et al. 2017b). If dispersing beavers cannot move into pre-engineered habitats through one of these two options, they may either remain transient while waiting for a territory to open up, or start a new colony in relatively unmodified habitats (Aleksiuk 1968, Collins 1976, Van Deelen and Plestcher 1996, Sun et al. 2000, McNew and Woolf 2005). In the latter situation, unmodified habitats are often suboptimal in quality (Howard and Larson 1985, Cunningham et al. 2006, DeStefano et al. 2006, František et al. 2010). Studies of areas being newly colonized by beavers indicate good quality habitat is usually settled first and initial settlements are more successful in terms of size and longevity (Howard and Larson 1985, Scrafford et al. 2018). Later in the colonization phase as population densities increase, colonies are formed in suboptimal habitats and are increasingly dynamic as beavers abandon sites more often due to resource depletion or difficulty maintaining dams and lodges (Pinto et al. 2009, František et al. 2010, Scrafford 2011).

Clearly, managers hoping to implement beaver restoration strategies must have an adequate understanding of local habitat conditions as well as beaver colony locations and population dynamics in the restoration area. Simultaneously, managers must understand avenues through which beavers can occupy a restoration stream or stream section, as well as how the beavers will choose a colony location once they are there. In order to better inform the selection of beaver restoration strategies, I undertook a two-year project to identify drivers of dispersal, monitor dispersal movements, and estimate survival of juvenile beavers in stream systems in southwest Montana. The objectives of this study were to: 1) estimate distances and timing of dispersal and settlement for dispersal-age beavers, 2) examine dispersal and survival in the context of local colony densities and the availability of settlement sites, and 3) relate individual characteristics of dispersing beavers to the probability of dispersal, settlement, and survival. By studying this aspect of beaver life history in a natural environment, I can expand our understanding of the ecology of beavers traveling to and occupying new habitats, which can guide better assessments of beaver restoration sites and strategies.

Methods

Study Area

I captured and radio-marked beavers in high elevation, willow-dominated streams and rivers in the headwaters of the Missouri River system within the Custer-Gallatin National Forest in southwest Montana during September–November and March–April, 2015–2017 (Figures 10 and 11). Trapping occurred in the fall and early spring prior to the main dispersal season which takes place during spring−early summer. Capturing beavers before the main dispersal season minimized the probability of capturing beavers that were in the process of dispersing and whose natal colony would therefore be unknown. In order to increase the chances of capturing dispersal-age beavers I focused trapping efforts on larger colonies that were more likely to have multiple generations of beavers. Detailed environmental characteristics of the study area are described in Chapter 2 (pp. 34–38).

Capture and Radio-marking of Juvenile Beavers

I live-captured dispersal-age beavers in the study area during 5 Sept 2015–11 May 2016 and 2 Sept 2016–25 April 2017. I used cable snares set at dams, water channels, feeding paths, and other high-use areas in beaver colonies based on the methods of McKinstry and Anderson (1998), McNew et al. (2007), and Sullivan (2013). I set snares in the afternoon and evening and checked them starting at first light the following morning. All snares were checked before 9:00 each day. I measured the mass of captured beavers using a spring scale and assigned an age class based on mass. Age determination by mass in beavers can vary depending on location due to spatial and temporal differences in food availability and quality (Table B1). Additionally, it is difficult to separate live beavers into age classes based on mass after three years of age (Patric and Webb 1960, Collins 1976, Crawford et al. 2008). Research on the age-weight relationship in my study area further confirmed this assertion and provided project-specific calibrations of the age-mass relationship for captured beavers (Appendix B). As a result of age classification uncertainty, I felt confident in categorizing kits, yearlings, and two-year-old beavers based on mass, but I classified all other beavers as adults. I used drainage-specific predictions of growth rates for beavers in my study area to estimate age (Appendix B).

My primary interest was in yearling and two-year-old beavers because these age classes are the most likely to disperse the following spring (McNew and Woolf 2005, Muller-Schwarze 2011). However, beavers older than two years can make up a considerable portion of the dispersers in a beaver population each year (Smith 1997, Mayer et al. 2017a). Therefore, in order to maximize the number of dispersal-age beavers in the sample I included all captured beavers with masses ≤ 20 kg. I marked yearling, two-year-old, and smaller adult beavers, collectively classified as "juvenile" beavers, with uniquely numbered metal ear tags and tail-mounted radio transmitters equipped with mortality sensors (Rothmeyer et al. 2002, Smith et al. 2016), and released them at the capture location. Minimum battery life for the transmitters was 657 days (Series M3500, Advanced Telemetry Systems, Isanti, Minnesota, USA). Montana State University's Institutional Animal Care and Use Committee approved the capture and handling methods (Permit Number: 2015-20). All field personnel were trained in biosafety and animal handling prior to field work, and followed all IACUC and wildlife veterinarian-approved protocols.

Beaver Monitoring

I monitored beavers for dispersal movements and mortality using a handheld R-1000 telemetry receiver (Communications Specialists Inc., Orange, California, USA) and a 3-element yagi antenna two or more times per month from time of capture until ice-off in the spring. I increased relocations to ≥ 2 times per week as ice-off approached and beavers began to disperse. I homed in on daytime resting locations or used rough triangulation to discern if the radio-marked beavers had left their natal colony. When a radio-marked beaver left its natal colony I increased the frequency of relocations to monitor daily movements and the use of transient locations. I continued frequent monitoring of dispersing beavers until they exhibited signs of colonization (e.g., long-term site fidelity, lodge construction, dam building). I reduced monitoring of the radio-marked beavers to 1–2 times per month once streams and ponds in the study area froze over for winter. When I could not locate a beaver from the ground for > 7 consecutive days I searched the study area using fixed-wing aircraft with wing-mounted telemetry antennas. I monitored all beavers to the end of the study to identify any secondary movements away from settlement sites.

When I detected a mortality signal I homed in on the transmitter and evaluated the carcass and the immediate area to determine the cause of death. I classified mortalities as disease, human, predation, other, or unknown. I defined the mortality date as the date halfway between the last time the beaver was heard alive and the first time I heard the transmitter on mortality mode.

Beaver-use Surveys

In order to estimate densities and locations of active and inactive beaver colonies that could impact the dispersal and settlement process, I conducted beaver-use surveys on all beaver-inhabited streams in the study area except for some streams and stream sections within Yellowstone National Park where regulations limited access. I marked active and inactive beaver sign with a handheld GPS and used the spatial distribution of beaver sign to classify stream segments in the study area as: active, abandoned, relic, or unoccupied. I classified stream segments as active if beavers were maintaining dams and lodges, abandoned if dams and lodges were still in place but not maintained, relic if there was minimal sign of previous beaver colonization, and unoccupied if there was little to no beaver sign. Detailed protocols for beaver-use surveys and beaver activity classifications are described in Chapter 2 (pp. 39−45).

Data Analysis

I considered the colony from which a beaver was captured as its natal colony. I only trapped in large, well-established colonies so it unlikely captured beavers were in the process of dispersing when they were caught. I defined a dispersal event as any beaver traveling outside the estimated boundaries of the natal colony and not returning. I defined the dispersal date as the median date between the last time I recorded the beaver within its natal colony and the first time I recorded it away from the natal colony. I estimated the settlement date retroactively at the end of the year when I was sure all beavers had chosen overwinter sites. I defined the settlement date as the median date between the last day I detected the beaver as a disperser and the first day I detected it at its settlement site. For beavers that dispersed and settled immediately, I considered the settlement date to be halfway between the last relocation at the natal colony and the first relocation at the settlement site. I calculated the dispersal-settlement interval as the number of days between the estimated dispersal date and the estimated settlement date. I considered all sites where dispersing beavers remained for ≥ 30 days but did not overwinter as transient locations.

I calculated dispersal distance as the stream distance between the last location in the natal colony and the first location at the settlement site. However, stream distances may overestimate dispersal distances if beavers traveled over land, so I also calculated straight-line dispersal distances. Total dispersal distance was calculated as the sum of stream distances for all detected dispersal movements, which were any movements > 1 km undertaken by a radio-marked beaver conditional on the beaver not returning to its natal colony. I distinguished between dispersal movements and exploratory movements, the latter being a beaver traveling > 1 km from its natal colony then returning.

I used the multi-state model developed by Brownie et al. (1993), and further refined to include dead recoveries by Barker et al. (2005), to estimate state-specific survival and transition probabilities between dispersing and non-dispersing beavers. I designed and conducted analyses in the program MARK (Cooch and White 2016). I tracked beavers during monthly detection intervals and recorded them as being in one of two states for each month: non-dispersal or dispersal. Beavers in the non-dispersal state were located in the colony from which they were captured for every relocation during the detection interval, or had dispersed and settled in a new location and were considered no longer in the process of dispersing. Beavers in the dispersal state had left the boundaries of their natal colony during the detection interval and did not return, or had been in a dispersal state the previous interval but had not yet settled. Once a beaver left its natal colony, I assumed it stayed in the dispersal state for the entirety of at least one detection interval. Although some beavers dispersed and settled right away, I assumed these beavers did not fully settled at the site for at least one month and were therefore still in the dispersal state. I classified dispersing beavers this way to exclude exploratory movements by some beavers that would have otherwise been treated as dispersal and settlement events in the analysis.

I hypothesized beavers in the two states may experience different survival rates. Dispersers may experience greater mortality due to being in unfamiliar environments outside the safety of a well-established colony (Aleksiuk 1968, Stenseth and Lidicker 1992, McNew and Woolf 2005, Nelson and Nielsen 2010). Additionally, dispersing beavers are at greater risk of territorial disputes as they travel through active colonies in search of a settlement site (Bradt 1938). I hypothesized beavers in the non-dispersal state would have the highest survival rates because they have family members around to warn them of danger and access to familiar escape and hiding cover. I evaluated four state transition probabilities that were biologically feasible in the study area:

1) Non-dispersal → Non-dispersal = probability a beaver survives the interval and remains in the non-dispersal state (natal).

2) Non-dispersal → Dispersal = probability a beaver survives the interval and disperses (dispersal).

3) Dispersal → Non-dispersal = probability a beaver survives the interval and returns to the non-dispersal state (settlement). No beavers returned to their natal colonies after dispersing so return movements were not a factor in estimating this transition probability.

4) Dispersal → Dispersal = probability a beaver survives the interval and remains a disperser (transient).

Because I assumed beavers were radio-marked in their natal colonies and captured either before or after the dispersal season, all beavers started in the non-dispersal state. A beaver observed in the non-dispersal state at time *t* had four possible outcomes over a monthly time interval ($t + 1$): 1) survive and remain a non-disperser, 2) die a non-disperser, 3) survive and transition to a disperser, and 4) transition to a disperser and die. A beaver observed in the dispersal state at time t had four possible outcomes over a monthly time interval ($t + 1$): 1) survive and remain a disperser, 2) die as a disperser, 3) survive and transition back to a non-disperser (settlement), or 4) transition back to a non-disperser and die.

I started the multi-state analyses by modeling detection probability (p) and dead-recovery probability (r) as nuisance parameters. Once I had determined the best structure for these components, I developed two different candidate model sets. For the first set of models I grouped monthly detection intervals to test for the effects of year and season on apparent survival (S) and transition (ψ) probabilities. The time-varying analysis provided season-specific transition and survival rates while testing for effects of yearly variation on the parameters. The year in the analyses started in September to assure overwinter settlement of the dispersers. I delineated seasons to coincide with important environmental changes experienced by beavers in the study area:

1) Fall (Sept–Nov) = capture and radio-marking period, minor dispersal period.

2) Winter (Dec–Feb) = beavers bound to non-dispersal state due to ice and snow cover.

3) Spring (Mar–May) = primary dispersal period, important settlement period.

4) Summer (June–Aug) = important settlement period.

The winter time period coincided with beavers being highly restricted in their movements due to ice cover in the study area. Therefore, I did not consider dispersal to be possible during the winter season and I fixed the probability of transitioning to the dispersal state during the winter season to zero. While settlement should theoretically also not be possible during the winter time period, I observed one beaver that was able to move around enough in a spring-fed river to settle in December. However, this was also the only beaver I suspected may have been in the dispersal state when it was radio-marked.

I developed a second set of models to evaluate the effects of five individual-level covariates on the probability of dispersal and survival (Table 9). I did not have reason to hypothesize any of these same covariates would influence detection probability, so I kept detection probability as a state-varying parameter. I did not model survival as a function of local colony densities due to low variability in survival outcomes and heavy bias towards a single beaver colony where tularemia killed a disproportionately large number of radio-marked beavers. I did not model settlement probability as a function of any covariates due to low variation in dispersal outcomes. Only two of the radio-marked beavers that dispersed did not settle by the end of the study, one settled after the study had ended, and one died before it had occupied a new location long enough to be considered settled ($\geq$ 30 days). I hypothesized all individual-level covariates would influence dispersal probability (Table 9).

Table 9. Covariates used to investigate dispersal and survival probability for juvenile beavers in the upper Gallatin and Madison River drainages in southwest Montana, USA.

Variable	Method	Hypothesized effect on survival	Hypothesized effect on state transitions
Drainage	Madison drainage or Gallatin drainage	Different sources and levels of mortality between drainages.	Differences in colony density and territory availability between drainages may affect dispersal.
Mass (kg)	Mass at first capture. I adjusted the masses of beavers captured in the 2nd year downward to estimate their 1st-year mass based on local growth curves.	Heavier beavers more likely to survive territorial disputes and attacks by predators.	Heavier beavers more competitive and in better condition for travel and territory defense.
Colony size	Large or small. Large colonies had > 3 generations of beavers. Small colonies may have had three generations but were in small areas and were assumed to have few extra adults in the colony.	Beavers from large colonies may be in better condition and more likely to survive.	Large colonies are overcrowded and made up of delayed dispersers which are more likely to disperse as they are more competitive. Interaction with mass.
Active colony density (active density)[a]	Proportion of stream length classified as active for at least two years of the study. Does not include new settlement sites.	N/A	Interaction with mass and abandoned/relic segment density. Greater colony density delays dispersal if few open territories available.
Abandoned/relic segment density (abandoned density)[a]	Number of abandoned stream segments (400-m) per kilometer of stream.	N/A	Interaction with active colony density. When lots of open territories around, beavers of all ages and masses are more likely to disperse.

[a] Considered at regional scale (8 regions) and stream scale (12 streams). Regions were groupings of streams that were within dispersal distance of one another as determined by the longest dispersal distances observed in this study.

For each candidate set of models, I followed the recommendations of Cooch and White (2016) by: 1) developing a global model, 2) testing and accounting for over-dispersion using the median c-hat procedure, 3) fitting reduced models and selecting appropriate models for inference using $QAIC_c$, and 4) using model-averaging to evaluate strength of effects and parameter estimate uncertainty. Due to a limited sample size of radio-marked beavers (n = 55), I restricted the number of estimated parameters in each model to ≤ 11. Although I recorded monthly encounter histories for radio-marked beavers, I did not test for fully time-varying effects on the parameters of interest because such models would be over-parameterized. Instead, I considered models with seasonal effects on transition probabilities by pooling observational months. I ranked candidate models using Quasi-likelihood Akaike's Information Criterion adjusted for small sample sizes (QAICc; Burnham and Anderson 2002, Cooch and White 2016). As a general guideline, I considered all models < 2 $\Delta QAIC_c$ from the top model parsimonious and was conservative in my interpretation of model selection results following the recommendations of Anderson and Burnham (2002) and Arnold (2010).

Results

Beaver Trapping, Radio-marking, and Monitoring

I set cable snares in 32 beaver colonies in 18 different streams during fall 2015−spring 2017. My trapping efforts resulted in a total of 2,602 trap-nights (one snare set for one night). Overall capture success was low (5.5%), likely due to setting large numbers of snares to saturate travel pathways in the colonies. I classified snare trap sets into six categories (Table 10). I captured the greatest number of beavers at dam crossover sets (33.1%) and deep water channel sets (30.3%), but overall trap success (number of captures/number of attempts) was highest for shallow water channel sets (7.5%) and castor mound sets (7.2%).

Table 10. Trap type success using cable snares to live-capture beavers in the upper Gallatin and Madison River drainages in southwest Montana, USA, 2015−2017.

Set Type	Description	Number of attempts	Number of captures	% trap success (# captured / # nights) × 100	% of total captures (n = 142)
Dam crossover	Heavily used crossover point on dam.	817	47	5.8	33.1
Deep water channel	Travel channel deep enough that beaver would be swimming.	720	43	6.0	30.3
Shallow water channel	Travel channel with water but beaver would be walking or sliding.	306	23	7.5	16.2
Surface run	Beaver would be out of the water and on flat, dry land. Mostly feeding pathways.	401	9	2.2	6.3
Castor mound	Scent lure and fake mud mound to attract beavers.	180	13	7.2	9.2
Haul-out	Transition zone between water and land.	174	7	4.0	4.9

In total, I captured 142 beavers in 88 nights of trapping. At least 35 were recaptures of beavers caught previously, so I captured approximately 107 individual beavers over the course of the study. I did not mark kits and large adults so some beavers may have been captured more than once without my knowledge. I also trapped in the spring prior to the dispersal season to increase the sample size of dispersal-age beavers. I captured twenty beavers in the spring and radio-marked nine. I captured 38 beavers in the Gallatin drainage and 104 in the Madison drainage. I recorded 251 false triggers where the snare was closed and pulled tight (9.6% of trap-nights), and 167 where the snare had fallen over or was not pulled tight (6.4% of trap-nights). I set game cameras at several trap locations over the course of the study and found ducks, muskrats, and other wildlife recognized snares and passed through them without interfering with the snare, and therefore I assume false triggers were mostly caused by beavers. As a result, the naive estimate of the total number of snare encounters by beavers, including captures, was 393−560 (15.1−21.5% of trap-nights). I had one incidental capture of a young river otter which was released without incident.

The mass of captured beavers ranged from 5−29 kg. I caught 20 kits, 6 yearlings, 36 sub-adults, and 75 adults including recaptures. Of these, I fitted tail-mounted radio-transmitters on 6 yearlings, 23 sub-adults, and 26 adults; 20 were radio-marked in the Gallatin drainage and 35 in the Madison drainage (Figures 10 and 11). I considered beaver deaths within 14 days of capture to be trapping-related mortalities, and twelve radio-marked beavers died within this time frame. Eight of the beavers died the same night they were captured due to complications with snares. Most often, beavers wrapped themselves around enough vegetation to be strangled. Other beavers seemed to have been suffocated when one front leg and the neck were caught in the snare. The additional four beavers that died from 1−14 days after capture were all found to be infected with disease. Three of the four beavers were infected with tularemia (*Francisella tularensis*), a bacterial disease which is usually fatal and was responsible for seven other beaver deaths in the study. Therefore, the three beavers that died within 14 days of capture and had tularemia may not have been trapping-related mortalities. With this consideration, my trapping mortality rate was 6.3–9.2% and was comparable to other studies that used snares to live-capture beavers (McKinstry and Anderson 1998, McNew et al. 2007).

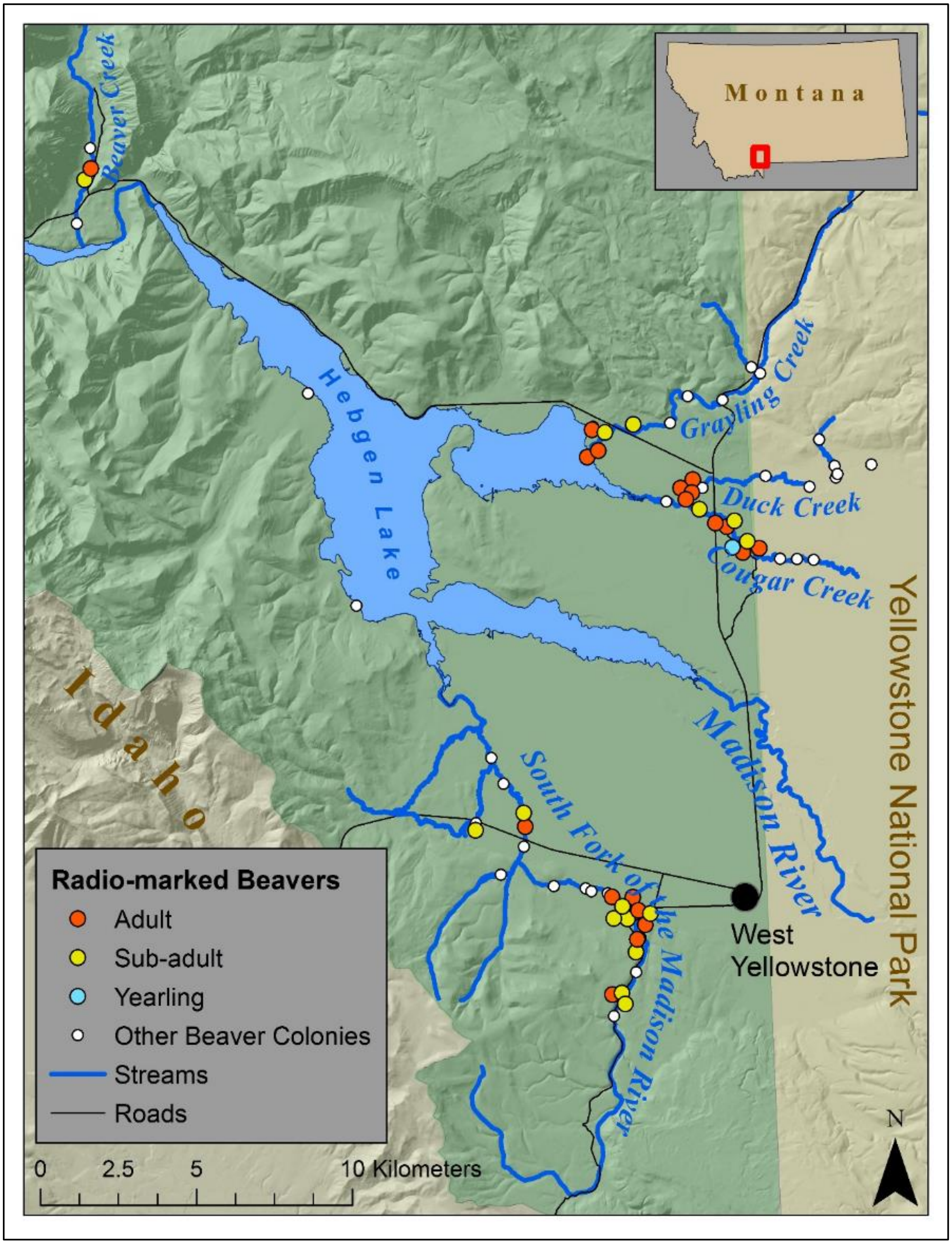

Figure 10. Capture locations of radio-marked juvenile beavers in the upper Madison River drainage in southwest Montana, USA.

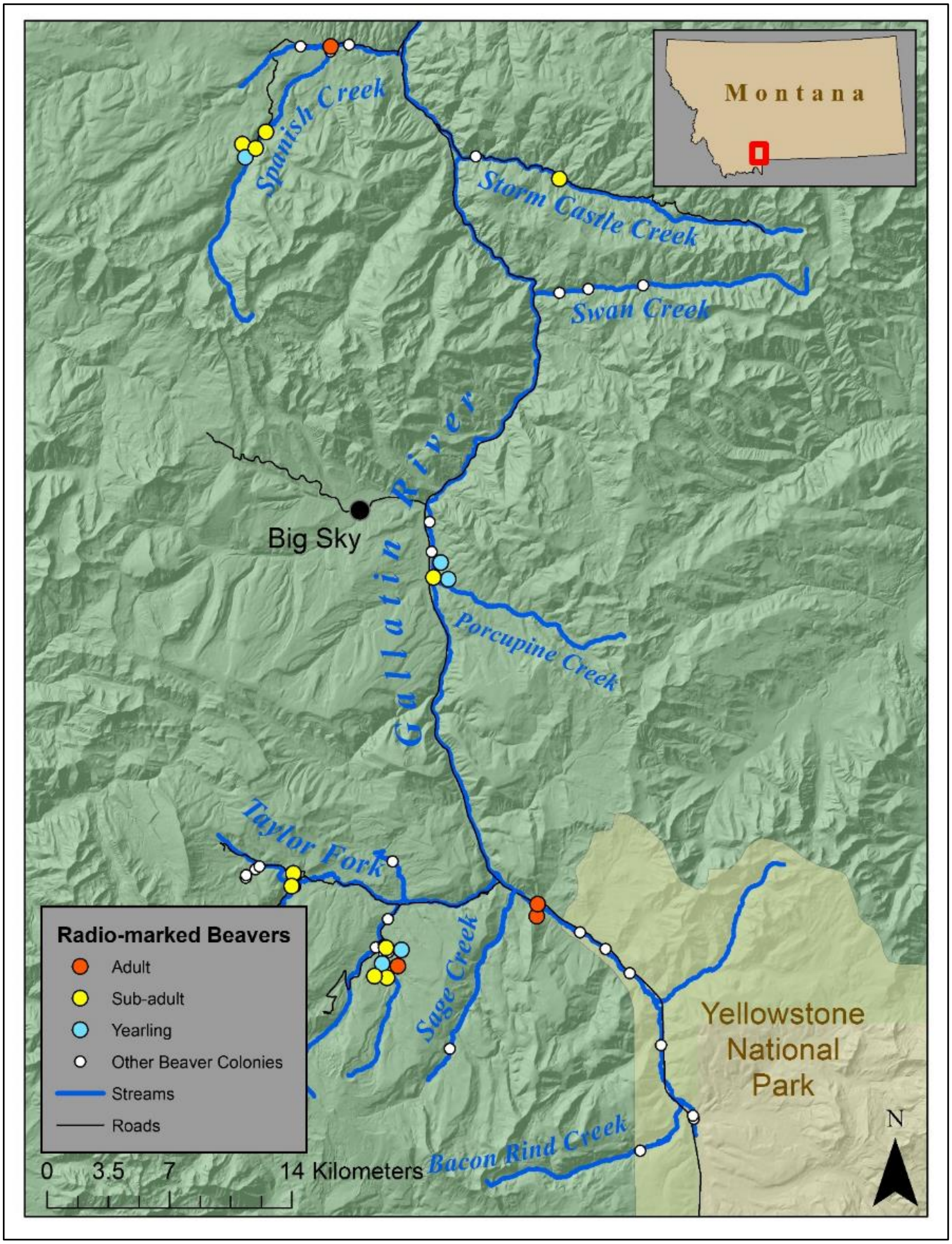

Figure 11. Capture locations of radio-marked juvenile beavers in the upper Gallatin River drainage in southwest Montana, USA.

Dispersal and Mortality Characteristics

Of 55 radio-marked beavers, 47 survived to ice-off the spring following their capture and were thus available to disperse. Seventeen beavers survived the first year of the study and were therefore potential dispersers again in spring 2017. Three of these seventeen dispersed in the first year and so were available to disperse again in 2017 as secondary dispersers. Therefore, I observed a total of 64 potential dispersal events over the course of the study. Sixteen individual beavers dispersed one time and two beavers dispersed in both years of the study bringing the total number of dispersal events to 18 (28% of potential dispersal events). Notably, I lost the signals for three beavers during the primary dispersal period (March−June) and I was unable to determine their fate.

The mean mass at the time of capture (±SE) for dispersing beavers was 15.8 kg (0.6; range = 12.2−19.5 kg; Figure 12). However, five beavers did not disperse until their second year in the study so this estimate was biased low. Based on my estimates of the age-mass relationship for beavers in southwest Montana (Appendix B), I was able to approximate the masses of beavers that dispersed in their second year. Therefore, regardless of the year in which beavers were captured, the age estimates were reflective of the year in which they dispersed. As a result, I classified seven dispersers as adults (32% of potential adult dispersers), ten as sub-adults (45% of potential sub-adult dispersers), and one as a yearling (25% of potential yearling dispersers). These totals include one beaver that dispersed as a sub-adult in 2016 and dispersed again in 2017 as an adult, and one beaver that dispersed as a sub-adult in both years.

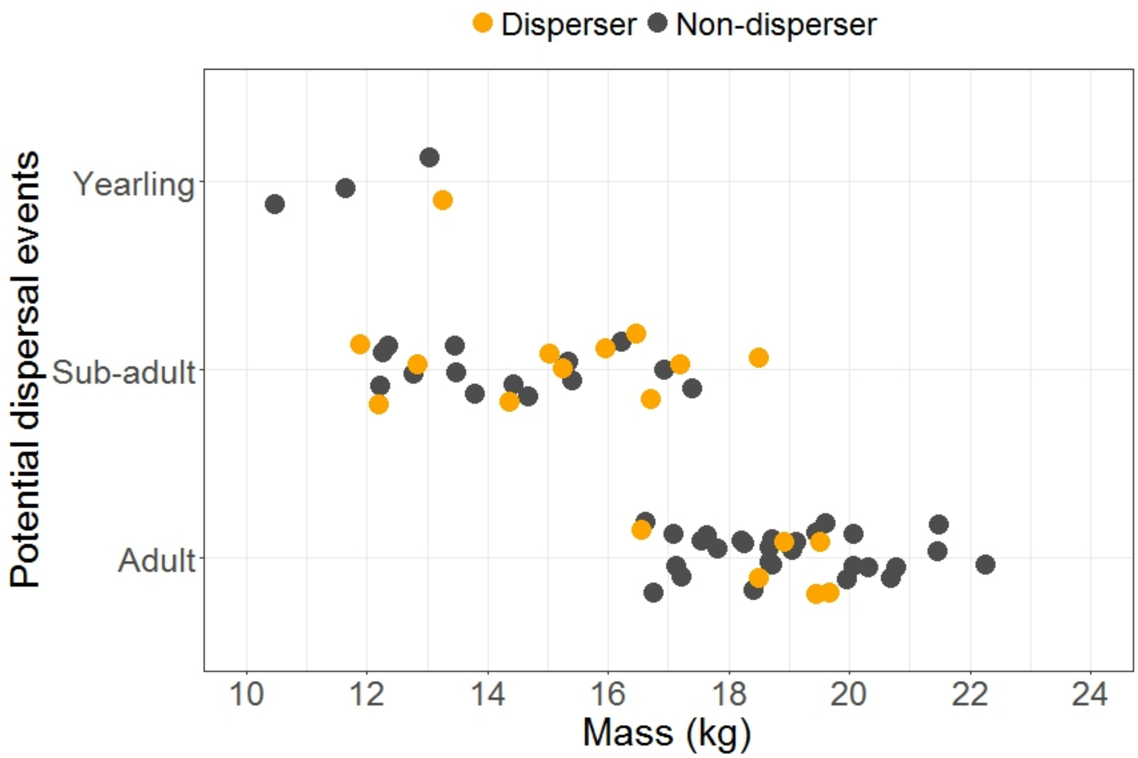

Figure 12. Masses of juvenile beavers radio-marked in the upper Gallatin and Madison River drainages in southwest Montana, USA, during fall and spring, 2015−2017. Each point represents the mass of a radio-marked beaver prior to the dispersal season and therefore radio-marked beavers that survived for both years of the study contribute two points. Age classifications overlap due to differing growth curves in the two river drainages.

Dispersal of the radio-marked beavers generally coincided with ice-off in the study area as waters began to rise due to snow melt (Figure 13). Dispersal-related movements peaked from late April through the middle of May when streams were approaching the apex of spring runoff which occurred around late May (Figure 13). The mean (±SE) dispersal date was 17 May (15 days; range = 7 March–25 November). Four beavers dispersed later in the season than the bulk of dispersers (i.e., after spring runoff), but I considered all of these to be abnormal dispersal situations. One of the late dispersers remained in a transient location just downstream of the eventual settlement site for 138 days before settling, so even though the beaver left the natal colony for the first time in early May, the final dispersal and settlement event occurred in September. The natal colony of one radio-marked beaver was destroyed due to road damage complaints, and the beaver remained around the natal colony location for most of the summer before dispersing and settling in a stream section 2.5 km upstream of the natal colony in October. One radio-marked beaver chose a settlement site but the initial dam and lodge were repeatedly destroyed to prevent property damage, and the beaver finally dispersed away from the settlement site to settle in an abandoned colony in a nearby stream. Finally, one beaver was captured in November and immediately traveled 6.3 km upstream to a small abandoned colony to overwinter. The next year, this beaver demonstrated an affinity for moving around the stream system on a nightly basis, so it is possible this beaver was on an exploratory movement when I caught it and the capture location was not actually its natal colony.

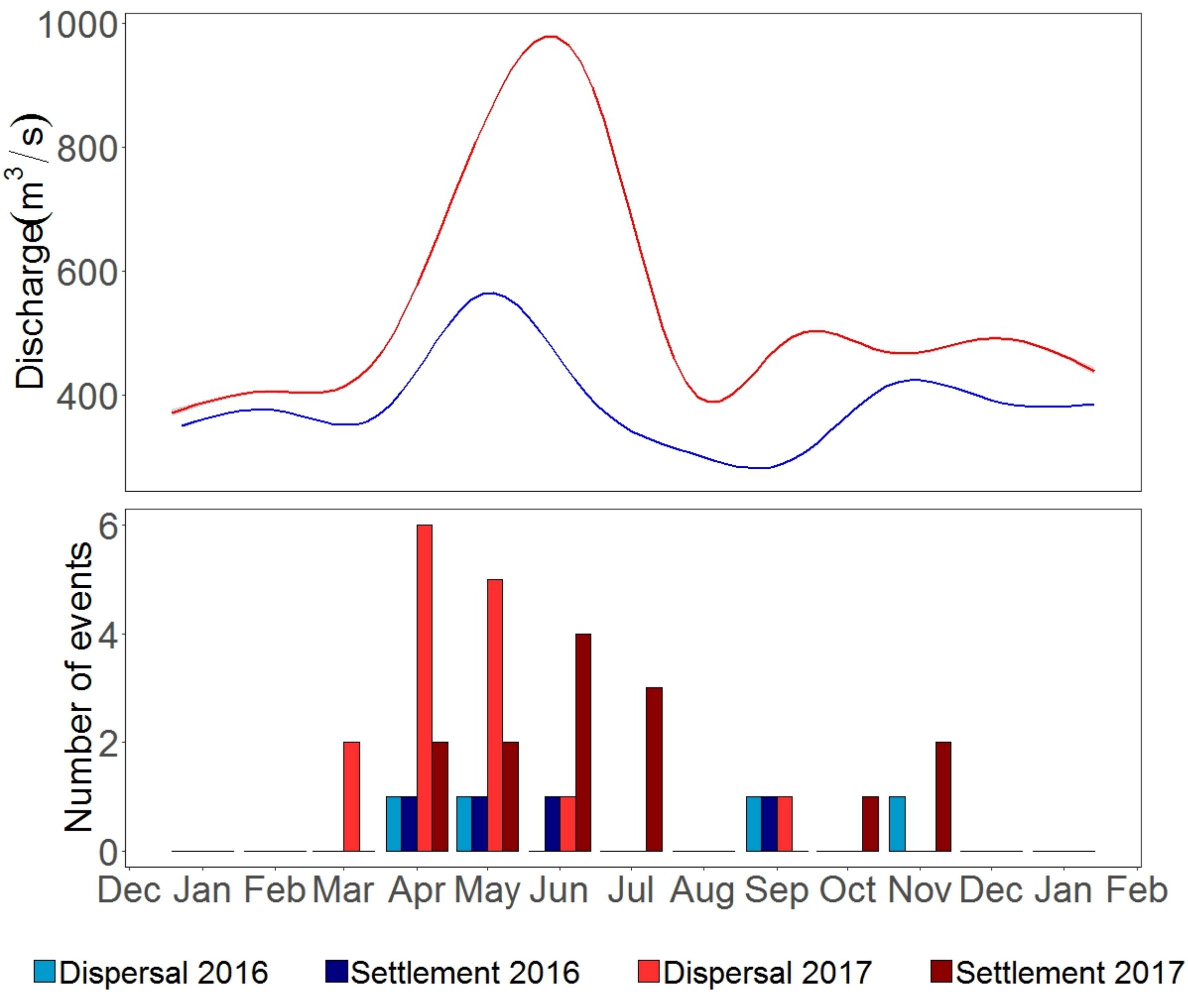

Figure 13. Dispersal and settlement events of beavers in the upper Gallatin and Madison River drainages in southwest Montana, USA, 2015−2017. Lines indicate discharge patterns for 2016 (blue) and 2017 (red) recorded at the U.S. Geological Survey streamflow station located on the Madison River near West Yellowstone, MT, USA. The number of dispersal movements among years should be interpreted with caution as there was a larger sample size of juvenile beavers that survived to the dispersal season in 2017 (n = 44) compared to 2016 (n =19). However, the monthly dispersal rate in 2017 (0.042) was still more than double the monthly dispersal rate in 2016 (0.017).

The mean dispersal-settlement interval was 40.9 days (range = 1–187 days), but the mean error around the true dispersal date was 10.5 days. I lost track of one beaver for 79 days, and this instance represented an outlier in the estimates of the error around the dispersal date. When I removed the 79-day outlier from the analysis, the mean dispersal date error was reduced to 6.4 days. I was unable to calculate the dispersal-settlement interval for two beavers because one did not settle before the end of the study and the other had a transmitter malfunction for most of the dispersal period. Six beavers dispersed and settled within 10 days. I suspected four additional radio-marked beavers also dispersed and settled within 10 days, but I lost track of these beavers temporarily and was therefore unable to calculate exact dispersal-settlement intervals. Settlement mostly coincided with waters receding from spring runoff (Figure 13). Four beavers remained transient for at least 41 days before selecting a settlement site prior to the onset of winter (Table C1), and transient intervals ranged from 74−138 days.

Dispersal distances between the natal colony and settlement site were highly variable with a mean (±SE) of 10.9 km (3.1; range = 0.7−42.3 km). I identified two outliers (41.3 and 42.3 km), so median dispersal distance (4.9 km) may give a better sense of the distribution of dispersal distances in the sample of dispersing beavers. Mean straight-line dispersal distance from the natal colony to the settlement site was 5.4 km (1.4; range = 0.7−18.4 km) and the median was 2.3 km. Some beavers settled in stream sections directly adjacent to their natal colonies while others crossed multiple stream drainages and passed through up to 12 active colonies along the dispersal route (Figures C3 and C5). I observed exploratory movements outside the boundaries of the natal colony by several beavers prior to dispersal. Two beavers traveled across significant portions of Hebgen Lake along their dispersal routes (Figure C5), and I saw evidence of overland travel by two dispersers. Dispersing beavers used old beaver lodges and bank burrows almost exclusively along their dispersal routes.

The mean settlement date was 30 June (range = 28 April–30 Nov). Of the 18 dispersal events recorded, 17 ended in settlement and one ended with the beaver dying before settlement. Seven dispersal events (38.9%) ended with beavers settling in colonies identified as active the year before, six (33.3%) settled in abandoned colonies, three (16.7%) settled in relic colonies, and one (5.6%) settled in a stream section that was previously unoccupied. The beaver that died before settlement site selection could be verified was occupying an abandoned colony.

A total of 10 radio-marked juvenile beavers died during the course of the study, and the survival rate was within the range of other studies of juvenile beavers. Six beavers from within the same drainage died due to the bacterial disease tularemia and five of those were from a single colony. One other death was attributed to infections of hepatitis and staphylococcus varieties. The three remaining deaths were due to predation by mountain lions (*Puma concolor*). All of the beavers killed by mountain lions were beavers who had dispersed during the study; two had settled in abandoned colonies and one had not yet settled before it was killed. I lost the signals for nine radio-marked beavers well before the predicted end of their battery life. The missing beavers may have dispersed outside the study area, died in such a way the transmitter was destroyed, or the transmitter malfunctioned. I was able to confirm malfunctioning transmitters on three of the missing beavers, indicating transmitter failure may have accounted for a substantial portion of the lost signals. I right-censored beavers with lost signals from the study.

Factors Affecting Dispersal Probability and Survival

The results of model selection based on information theory indicated a single top model of recapture probability and dead encounter probability (Table 11). The top model indicated the dead recovery rate was unrelated to dispersal state and I held the term constant in all subsequent models. Models in which detection probability varied by dispersal state had virtually all of the support from the data (Table 11). Thus, I retained state-specific detection probabilities in all subsequent models evaluating dispersal and survival probability.

Table 11. Nuisance parameter modeling results testing the influence of state (disperser, non-disperser) on detection probability (*p*) and dead recovery probability (*r*) for radio-marked juvenile beavers in the upper Gallatin and Madison River drainages in southwest Montana, USA, 2015−2017. Beavers were encountered during monthly detection intervals and assigned to either dispersal or non-dispersal state.

Model	K	AIC_c	ΔAIC_c	w_i	Cum w_i
ψ(c), p(state), S(c), r(c)	4	703.58	0.00	0.83	0.83
ψ(c), p(state), S(c), r(state)	6	706.70	3.11	0.17	1.00
ψ(c), p(c), S(c), r(c)	4	734.62	31.04	0.00	1.00
ψ(c), p(c), S(c), r(state)	4	736.79	33.21	0.00	1.00

I evaluated 11 models testing for time-varying effects on state transitions and survival rates (Table 12). There was a clear top model in this candidate set that allowed state transitions to vary by season and survival to vary by year. The annual survival rate was higher in 2016 (0.84, 95% CI = 0.76−0.93) compared to 2017 (0.67, 95% CI = 0.65−0.69). Monthly dispersal probability was highest during the spring season (0.095, 95% CI = 0.055−0.16), and lowest during summer (0.021, 95% CI = 0.0057−0.072). Monthly settlement probability was universally high as all but one dispersing beaver settled, and settlement was most common in the summer season. There was virtually no support for the null model which allowed transition probabilities for vary by state while holding all other terms constant.

Table 12. Model selection results testing the effects of time variation on state transition probabilities (ψ), detection probabilities (*p*), and state-specific survival probabilities (S) for radio-marked juvenile beavers in the upper Gallatin and Madison River drainages in southwest Montana, USA, 2015−2017. Beavers were encountered during monthly detection intervals and assigned to either dispersal or non-dispersal state.

Model	K	$QAIC_c$	$\Delta QAIC_c$	w_i	Cum w_i
ψ(state × season), p(state), S(year), r(c)	11	481.37	0.00	0.76	0.76
ψ(state × season), p(state), S(c), r(c)	10	483.91	2.55	0.21	0.97
ψ(state × season), p(state × year), S(c), r(c)	13	488.49	7.12	0.02	0.99
ψ(state × year), p(state), S(season), r(c)	9	494.21	12.84	0.00	1.00
ψ(state), p(state), S(year), r(state)	6	494.29	12.92	0.00	1.00
ψ(state), p(state), S(season), r(state)	8	494.36	13.00	0.00	1.00
ψ(state × year), p(state), S(year), r(c)	8	495.86	14.50	0.00	1.00
ψ(state × year), p(state), S(season), r(c)	10	496.26	14.89	0.00	1.00
ψ(state × year), p(state), S(c), r(c)	7	496.73	15.37	0.00	1.00
ψ(state × year), p(state × year), S(c), r(c)	9	498.82	17.45	0.00	1.00
ψ(state), p(c), S(c), r(c) [Null Model]	5	518.31	36.95	0.00	1.00

I evaluated 21 models testing the effects of individual covariates on state-specific survival and transition probabilities (Table 13). I started by modeling survival as a function of state, drainage, and beaver mass. The model that allowed survival to vary by drainage was better supported, so I allowed survival to vary by drainage in the rest of the candidate models. There was a clear top model in the candidate set that modeled dispersal probability as a linear function of active colony density and allowed survival to vary by drainage. The top model accounted for 84% of the total model weight and suggests that as active colony density within the natal stream of a beaver increased, the probability of dispersing from the natal colony decreased (Figure 14). The effect of active colony density was 6.1 times more supported than other covariate effects. The probability of settling (D-N) was near one for all models. Annual survival probability was higher in the Madison drainage (0.70, 95% CI = 0.67−0.73) than the Gallatin drainage (0.43, 95% CI = 0.42−0.44). Detection was close to one for beavers in the non-dispersal state in all models, so I fixed the value to one to provide more precise estimates of other parameters. The monthly probability of detecting a beaver in the dispersal state was lower than the non-dispersal state and was significantly less than one (0.65, 95% CI = 0.51−0.77), and dead recovery probability was low (0.32, 95% CI = 0.18−0.51). There was virtually no support for the null model which allowed transition probabilities to vary by state while holding all other terms constant.

Table 13. Model selection results testing the effects of state and individual covariates on state transition probabilities (ψ) and state-specific survival probabilities (S) for radio-marked juvenile beavers in the upper Gallatin and Madison River drainages in southwest Montana, USA, 2015−2017. Beavers were encountered during monthly detection intervals and assigned to either dispersal or non-dispersal state.

Model	K	$QAIC_c$	$\Delta QAIC_c$	w_i	Cum w_i
ψ(state × active density), p(state), S(drainage), r(c)	8	487.61	0.00	0.74	0.74
ψ(state + mass × active density), p(state), S(drainage), r(c)	9	491.48	3.87	0.11	0.85
ψ(state × colony size), p(state), S(drainage), r(c)	8	493.78	6.17	0.03	0.88
ψ(state × drainage), p(state), S(drainage), r(c)	8	493.98	6.36	0.03	0.91
ψ(state × mass), p(state), S(drainage), r(c)	8	494.99	7.38	0.02	0.93
ψ(state + mass × drainage), p(state), S(drainage), r(c)	9	495.29	7.68	0.02	0.95
ψ(state), p(state), S(drainage), r(c)	7	495.47	7.86	0.01	0.96
ψ(state + mass × colony size), p(state), S(drainage), r(c)	9	495.82	8.20	0.01	0.97
ψ(state + active density × abandoned density), p(state), S(drainage), r(c)	9	496.40	8.79	0.01	0.98
ψ(state + drainage), p(state), S(drainage), r(c)	9	496.72	9.11	0.01	0.99
ψ(state × abandoned density), p(state), S(drainage), r(c)	8	496.81	9.20	0.01	1.00
ψ(state + mass × abandoned density), p(state), S(drainage), r(c)	9	498.52	10.91	0.00	1.00
ψ(state), p(state), S(c), r(c)	6	498.59	10.97	0.00	1.00
ψ(state), p(state), S(mass × drainage), r(c)	8	499.08	11.47	0.00	1.00
ψ(state), p(state), S(state), r(c)	7	500.20	12.59	0.00	1.00
ψ(state), p(state), S(mass), r(c)	7	500.62	13.01	0.00	1.00
ψ(state + active density × abandoned density), p(state), S(drainage), r(c)	13	504.49	16.88	0.00	1.00
ψ(state × active density), p(c), S(drainage), r(c)	7	513.68	26.07	0.00	1.00
ψ(state × drainage), p(state), S(drainage), r(c)	9	517.05	29.44	0.00	1.00
ψ(state), p(c), S(c), r(c) [Null Model]	5	518.31	30.70	0.00	1.00
ψ(state), p(state), S(state), r(state)	8	530.47	42.86	0.00	1.00

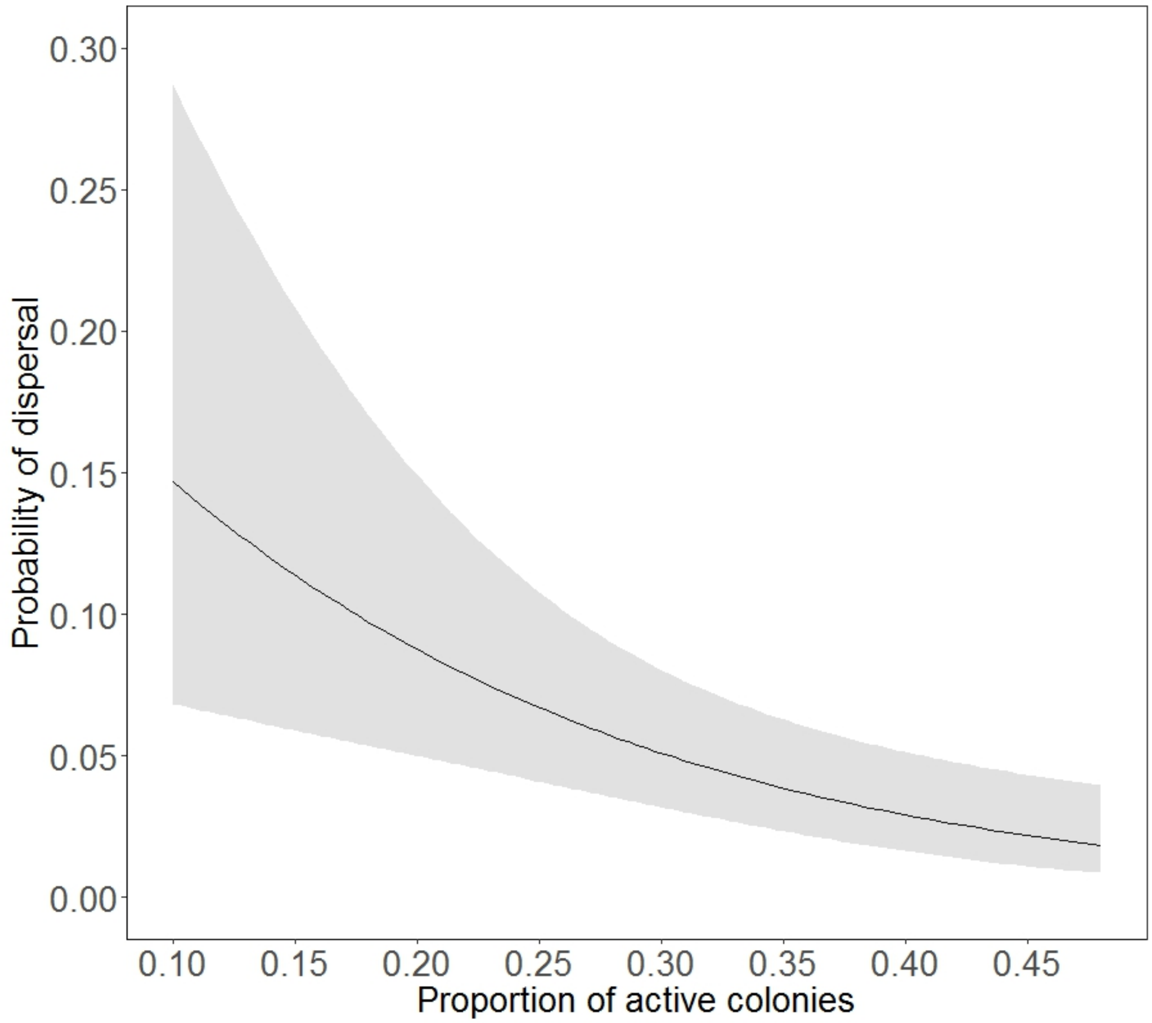

Figure 14. Effect of the proportion of active beaver colonies within the natal stream system on the monthly probability of dispersal for juvenile beavers in the upper Gallatin and Madison River drainages in southwest Montana, USA, 2015−2017. The shaded area depicts the 95% confidence interval.

The annual survival probability for all juvenile beavers in the study area was 0.62 (95% CI = 0.60−0.63). There was evidence for annual survival varying by dispersal state, with non-dispersers having a lower survival probability (0.61, 95% CI = 0.60−0.62) than dispersers (0.77, 95% CI = 0.64−0.91). Mass did not have an effect on survival (Table 13). The annual probability of dispersal was 0.26 (95% CI = 0.24−0.29). Monthly dispersal probability was not different between the Gallatin and Madison drainages, but was higher in 2017 (0.042, 95% CI = 0.025−0.069) compared to 2016 (0.017, 95% CI = 0.0047−0.060). The overall monthly probability that dispersing beavers settled during the study period averaged 0.42 (95% CI = 0.29−0.56).

Discussion

Beaver Trapping, Radio-marking, and Monitoring

Using snares to capture beavers was inexpensive and highly effective. I was able to set large numbers of snares in several colonies at once and check all traps within a 2−4 hour timespan each morning. As a comparison, clamshell-style traps or cage traps which are large and heavy would have restricted me to 5−10 traps per night in colonies much closer to roads. My trapping-related mortality rate was higher than studies that used non-snare traps (McNew et al. 2007). However, it was the lowest mortality rate of any snare-trapping study reported in the literature (McNew et al. 2007), which I attribute to incorporating knowledge gained from previous snaring efforts. The most successful snare sets were placed along heavily used travel pathways emanating from active lodges and crossing over major dams. I also noted success with snare sets baited with castor lure, though many of these sets were also travel pathways and may have been successful regardless of the use of castor lure.

During capture efforts I noted an abnormal lack of yearling beavers. Due to a high number of snares being triggered with no capture, I hypothesized yearling beavers may have been small enough to escape the snares. In an attempt to increase the sample size of yearling beavers, I moved the deer stop on the snares closer to the end of the snare to allow the loop to close tighter around smaller animals. The adjustment of the deer stop proved to be an error, and the mortality rate immediately increased with even a modest adjustment. Many more beavers were caught around the neck or around a single front leg and the neck, both scenarios that resulted in a disproportionately large number of capture-related deaths. Movement of the deer stop did not result in the capture of more yearling beavers. Therefore, I recommend researchers maintain a distance from the end of the snare to the deer stop of at least 34 cm to keep the mortality rate of captured beavers as low as possible (McNew et al. 2007).

Dispersal and Survival

The overall annual dispersal rate in my study area was the lowest reported in the literature, although there is wide variation in dispersal rates recorded across study areas (Table 14). Nelson and Nielsen (2010) observed a similarly low dispersal rate in Central Illinois, and assert that delayed dispersal in their study area may have contributed to the low dispersal rate. However, many other studies observed higher dispersal rates even in areas with high beaver densities so it is unclear why the dispersal rate in my study was low. In my study area I saw no evidence of overexploitation of resources at trapped colonies, and presumably habitat quality was high. High natal colony habitat quality may have allowed for higher rates of delayed dispersal than in other study areas and the presence of large numbers of individual beavers in many of the trapped colonies supports this notion. Additionally, in an effort to radio-mark as many dispersal-age beavers as possible I may have incidentally marked breeding adults in some colonies which would have an effect of lowering the dispersal rate.

Table 14. Dispersal rates for beavers reported in North America, 1968−2010. In all studies the authors targeted dispersal-age beavers for radio-marking.

Author	Location	Dispersal rate
This study	Montana	0.26
Leege 1968	Idaho	0.33
Van Deelen and Plestcher 1996	Montana	0.45
Smith 1997	Minnesota	0.42
Sun et al. 2000	New York	1.00
Destefano et al. 2006	Massachusetts	0.36
Nelson and Nielsen 2010	Illinois (Central)	0.29
Nelson and Nielsen 2010	Illinois (Southern)	0.47

I found support for seasonal changes in dispersal probability, and the mean dispersal date indicates the bulk of dispersal occurred as waters in the study area were rising towards peak runoff stage (Figure 13). Other studies have noted dispersal coinciding with spring runoff, though most were anecdotal observations (Bradt 1938, Townsend 1953, Van Deelen 1991, Smith 1997, Sun et al. 2000, DeStefano et al. 2006). It is unclear whether dispersal during runoff is in response to rising water levels or birth of kits in the spring, and the true driver of dispersal could be a combination of both factors. DeStefano et al. (2006) found beavers mostly dispersed in the spring even in systems with low levels of runoff, though McNew and Woolf (2005) found a more bimodal distribution of dispersal timings in stream and pond systems not dominated by runoff in Illinois. McNew and Woolf (2005) observed a pulse of dispersal in the fall when a large wetland area was flooded for waterfowl management purposes, and the authors suggest the increase in dispersal may have been a response to lodges and bank dens being flooded. My observations indicate radio-marked beavers in the study reduced the number of daytime resting locations used during high waters, possibly indicating lower availability of lodges and bank dens. The reduced availability of daytime resting locations, along with the presence of new kits in the colony, may exacerbate overcrowding in colonies with high densities of beavers and could promote dispersal of beavers that cannot find refuge in their natal colony. Over-crowding may explain why dispersal was more common in 2017, when spring runoff discharge levels were almost double those of 2016.

Juvenile beavers generally dispersed and settled quickly within the study area, and the use of transient locations was rare. Beavers that used transient locations stayed for long periods of time before moving to their eventual settlement site. In all cases, transient locations were abandoned or relic beaver colonies and were not heavily repaired during the transient interval. The lack of new construction suggests beavers were not settling at transient locations and then abandoning the sites but rather using them as temporary locations from which to launch exploratory movements, presumably to search for mates or better territories. Notably, two of the longer dispersal-settlement intervals were exhibited by beavers that had experienced some sort of disturbance to their chosen settlement site which prevented successful overwinter colonization, thus somewhat artificially inflating the dispersal-settlement interval for these individuals.

The mean dispersal distance between the natal colony and the settlement site in my study area was within the range of other studies of beaver dispersal (Table 15). Dispersing beavers have been observed traveling in excess of 40 km along their dispersal route (Beer 1955, Harris 1991), and other beavers have been documented traveling over 140 km (Libby 1957, Hibbard 1958, Nelson and Nielsen 2010). However, shorter dispersal distances of 4−18 km are more common (Table 15). The mean straight-line distance from the natal colony to the settlement site for the dispersing beavers was < 6 km, indicating that while many dispersing beavers traveled long stream distances to their settlement sites, most settled in stream sections close to their natal colony (Figures C1−C5).

Table 15. Dispersal distances (km) for beavers reported in North America, 1955−2010.

Authors	Location	Distance Type	Mean dispersal distance	Range
This study	Montana	Stream	10.9	2.0−42.3
Beer (1955)	Minnesota	Stream	22.7	0.5−82.1
Leege (1968)	Idaho	Straight-line	9.0	4.5−18.2
Van Deelen and Plestcher (1996)	Montana	Stream	8.4	2.9−22.2
McNew and Woolf (2005)	Illinois	Straight-line	5.9	1.0−20.9
DeStefano et al. (2006)	Massachusetts	Stream	4.6	0.4−11.4
Nelson and Nielsen (2010)	Illinois (Southern)	Straight-line	4.0	max 14
Nelson and Nielsen (2010)	Illinois (Northern)	Straight-line	14.0	max 247

Dispersing radio-marked beavers preferred to settle in habitats previously modified by beaver activity and 44% of dispersers settled in active colonies. Frequent settlement in active colonies was unexpected, as beavers are highly territorial and will act aggressively towards unrelated beavers entering their territories (Bradt 1938, Muller-Schwarze 2011, Crawford et al. 2015). Dispersing beavers may have moved into active colonies to take a position as a member of the breeding pair when one of the original members died or was forced out by the disperser (Brooks et al. 1980, Sun et al. 2000, Mayer et al. 2017b). It is also possible the resident beavers of the colony into which a disperser settled were killed or abandoned the site sometime between beaver-use surveys and the dispersal season.

All but one of the remaining dispersal events resulted in beavers settling in abandoned or relic colonies. Beavers took advantage of old beaver structures in these sites either by using a relic lodge as a daytime resting location during initial dam construction, or by repairing relatively intact dams and lodges at abandoned sites. The attraction to pre-engineered habitats was apparent, as some abandoned and relic sites were isolated amongst large sections of unoccupied habitat, yet were still selected by dispersers. Smith (1997) noted dispersing beavers preferred settlement sites with intact dams and lodges over sites where new structures would need to be built. Other studies have noted beavers colonizing sites near the natal colony (Sun et al. 2000, DeStefano et al. 2006), but the use of previous beaver infrastructure has rarely been reported, though it is likely common. Beaver restoration projects in the western United States have found greater success promoting beaver colonization when dams or rudimentary lodges were provided at the restoration site (Babik and Meyer 2015, Woodruff 2015, Bouwes et al. 2016, Pollock et al. 2017), effectively mimicking a relic or abandoned colony.

Many dispersers in my study area traveled through a variety of abandoned, relic, and unoccupied stream sections before finding a settlement site, providing evidence dispersing beavers do not settle at the nearest available territory. As with other studies, I observed many radio-marked beavers making long exploratory movements, often being gone for several nights before returning to the natal colony or transient location (McNew and Woolf 2005, Mayer et al. 2017b). Exploratory excursions likely allowed dispersers to assess local colony densities and the availability of mates while testing out several potential settlement sites (McNew and Woolf 2005). During beaver-use surveys I noted many partial dam-like structures in creek sections well-removed from active colonies. I interpreted these as possible trial sites used by dispersers to test if a dam could be built at the location. Alternatively, the partial dams may have been meant to slow the water enough cover the entrance of a bank den used by beavers traveling along the stream.

Based on my sample of radio-marked beavers there is little evidence dispersers will start new colonies in unoccupied habitat as long as there are relic or abandoned colonies available to occupy. The only beaver that settled in a previously unoccupied stream section had its natal colony destroyed due to road damage complaints. The beaver continued to occupy the destroyed colony for most of the year before dispersing and settling in unoccupied habitat 2.5 km upstream just before the onset of winter. While only one of the 18 dispersal events (6%) ended with a beaver occupying a previously unoccupied stream section, 10 out of 27 (37%) of new settlement sites discovered during beaver-use surveys were established in previously unoccupied habitat (Chapter 2). The discrepancy between the radio-marked beavers and the beaver-use surveys indicates settlement in unoccupied habitats, while still less common than settlement in beaver-modified habitats, is more common than my sample of radio-marked beavers would suggest. It is possible I did not get an adequate sample of some portion of the dispersal-age beaver population that was more likely to settle in unoccupied habitats. Based on the maturation hypothesis, when populations densities are high and the availability of good quality territories is low, dispersal will be low overall, but animals with greater competitive ability will be more likely to disperse and acquire good quality territories (Sun et al. 2000, Bowler and Benton 2005, Piper et al. 2015, Mayer et al. 2017b;a). Meanwhile, smaller animals will either not be able to disperse, or will be forced to settled in poor quality habitat due to being less competitive (Bowler and Benton 2005, Mayer et al. 2017a). In my study area, unoccupied stream segments had the poorest habitat conditions (Chapter 2). New settlement sites in unoccupied habitat may have been settled by yearlings that could not compete for good territories due to smaller body sizes, and the lack of yearlings in my sample of radio-marked beavers may have biased the results towards dispersal outcomes characterizing larger and more competitive beavers. The lower prevalence of yearlings in the trapped colonies may have been the result of larger delayed dispersers forcing yearlings out of the natal colony prior to my live-trapping efforts (Bowler and Benton 2005). In an attempt to capture as many dispersal-age beavers as possible I avoided trapping in smaller, more recently settled colonies so it is not clear if a particular age-class was more likely to be occupying these smaller and newer colonies.

Mayer et al. (2017b) posit five possible drivers of dispersal in beavers suggesting local population densities, overcrowding at the natal colony, presence of a new dominant adult, parental age, and competitive ability of dispersers (age and mass) all potentially influence dispersal timing and outcomes. I was able to test for an effect of local colony densities on dispersal using results of my beaver-use surveys. While I collected mass of dispersal-age beavers, I could not address the influence of parental age or the presence of a new dominant adult, and I could only make general observations about overcrowding based on live-capture efforts and observations of beaver sign at natal colonies.

In my study area, beaver colony densities in suitable habitat were high, though overall densities were average or below average (Chapter 2, Table 1). Active colony density was the strongest predictor of dispersal probability and the probability of dispersal decreased with increasing active colony density, suggesting negative density-dependent dispersal (Bowler and Benton 2005). It has been hypothesized negative density-dependent dispersal is more likely if animals are limited in their ability to move to an area with lower population densities (Mayer et al. 2017b). Dispersal was likely restricted in much of my study area. The Madison drainage is surrounded by mountain ranges and the only major avenues out of the basin for dispersers are hazardous sections of the Madison River, one leading into Madison Canyon in YNP and the other crossing a major dam and passing through a whitewater canyon. The Gallatin drainage is also mountainous and was characterized by long stretches of poor habitat and high beaver colony densities within isolated patches of suitable habitat.

I likely observed two different situations that led to delayed dispersal in my study area. In the Madison drainage, overall habitat suitability was high, and delayed dispersal was likely driven by high colony densities that limited the availability of territories (Koenig et al. 1992). Conversely, in the Gallatin drainage there was greater amounts of unoccupied habitat, but poor habitat quality may have limited the availability of territories. In either situation, the effect of active colony density on the probability of dispersal would be the same because colony density was relative to the overall availability of high quality habitat in the drainage.

When animals cannot find a suitable territory either due to habitat saturation or poor habitat quality, they may delay dispersal to gain experience and enhanced competitive ability. Delaying dispersal provides juvenile beavers better opportunity to compete for the few good quality territories that become available or take over their natal colony (Bowler and Benton 2005, Piper et al. 2015, Mayer et al. 2017a). While mass was not a significant predictor of dispersal probability in my analyses, half of all dispersal events were made by beavers ≥ 16.8 kg (Figure 12). The masses of these large dispersers indicates many of them were greater than two years of age, and some had similar masses as other radio-marked beavers later confirmed to actually be breeding adults. Therefore, a significant portion of the dispersing population was made up of large individuals, and body mass was likely overall greater for dispersers in my study area. Although an influence of mass on dispersal probability was not well-supported by my results, this could be due to the incidental marking of breeding adults in some colonies that may have skewed the non-disperser mass range towards larger animals. The shortage of yearling beavers in my sample, a potentially important segment of the dispersal population with smaller body sizes, may also have contributed to the lack of an effect of mass on dispersal.

It is also possible the mass of beavers interacts with other factors in more complex ways than I was able to model. Both smaller and larger beavers may be pushed out of their natal colonies due to over-crowding. Larger beavers may leave densely-populated colonies because they are forced out by the breeding pair who begin to perceive them as a threat. Larger beavers are also more competitive and may be more likely to disperse because they have a greater chance of acquiring a good territory. Conversely, smaller beavers may be more likely to be pushed out of a densely-populated colony because larger delayed dispersers out-compete the smaller animals for daytime resting locations and forage resources. In the trapped colonies in my study area, there was no evidence of resource limitation in terms of forage so I do not have reason to believe dispersal dynamics or body condition among beavers within the same colony was driven by competition for resources, though this may be a major factor in other areas. However, there was some evidence for limited availability of daytime resting locations during spring runoff. Additionally, the conspicuous lack of yearling beavers in my sample may have been due to smaller beavers leaving their natal colonies at a greater rate than larger dispersal-age beavers.

Similar to one of the study areas investigated by Nelson and Nielsen (2010), I observed lower survival rates for dispersers than non-dispersers due to a disease outbreak. However, in areas without disease outbreaks there is some evidence survival is similar between dispersers and non-dispersers (Van Deelen and Plestcher 1996, Destefano et al. 2006, Nelson and Nielsen 2010). A large number of radio-marked beavers in my study area died due to the bacterial disease tularemia, and most of these beavers died the fall or winter season after they were radio-marked. The timing of their deaths skewed my mortality observations towards beavers that died in the non-dispersal state and also explains why survival rates were much lower in the Gallatin drainage, as all of the tularemia deaths occurred in one stream system in this drainage. When disease outbreaks occur, dispersers may have greater survival rates because they are able to escape the colony before becoming infected. Notably, the only radio-marked beaver that did not die of tularemia in the colony where the outbreak occurred was a beaver that dispersed > 40 km away.

The higher survival rate of dispersers in my study area may also be because juvenile beavers often dispersed and settled quickly, so the opportunity for mortality to occur during the dispersal process was low. It should be noted the only deaths of radio-marked beavers not due to disease were three dispersers that had settled in recently abandoned colonies. All of these deaths were due to mountain lion predation. There were also five potential dispersal events that were of unknown fate due to transmitter failure or disappearance.

Unfortunately, I was not able to determine sex for the radio-marked beavers. I collected tissue samples from the tails of all captured beavers for use in DNA-based sex determination, but published primers did not work on my samples. The sex of dispersers in relation to distances and outcomes was of interest for this study, as other authors have reported sex-biased dispersal characteristics (Sun et al. 2000, McNew and Woolf 2005). However, observations have been inconsistent across study areas. In some instances, female beavers dispersed further than males (Sun et al. 2000), while in others overall dispersal distances were similar but males moved more often and for longer distances per move than females (Leege 1968, McNew and Woolf 2005). Other areas show no clear pattern in dispersal between sexes (Van Deelen 1991, Mayer et al. 2017b). Sun et al.

(2000) propose females may disperse further in high population densities due to selection pressures against inbreeding, but Smith (1997) observed males dispersing at higher rate in an area with high densities in Minnesota.

Management Implications

An explicit goal of beaver restoration projects is to promote beaver colonization of a stream or drainage either through translocation of beavers or by encouraging natural colonization through habitat improvements (Pilliod et al. 2017, Pollock et al. 2017). Beaver restoration practitioners should therefore be aware of local colony densities and the potential for natural dispersal to provide beavers at restoration sites. Allowing beavers to colonize a site naturally may be preferred in many instances because trapping, transporting, and monitoring translocated beavers is expensive, time-consuming, and unpopular with some wildlife management agencies. Furthermore, beaver translocation requires careful disease management to avoid spreading diseases that can wipe out other beaver populations, and disease-testing requires additional funding for lab equipment and quarantine facilities for captured beavers. For these reasons, it is important beaver restoration projects understand and account for the dispersal process to identify opportunities and limitations specific to each project area.

Beavers are willing to travel long distances to find appropriate habitat and can make such movements in relatively short periods of time. Dispersers will travel through multiple active colonies and extensive stretches of poor habitat. Understanding the dispersal characteristics of beavers provides an opportunity to classify potential project locations in terms of the restoration strategy to be implemented. If the restoration site is believed to be within dispersal range of an area with a healthy beaver population, beaver translocation can be considered a last resort as natural colonization should be possible with habitat improvements. An assessment of the proposed project area using aerial imagery should be sufficient to evaluate the location and distribution of active beaver colonies as well as potential dispersal routes. During an initial assessment of my study area, I noted several colonies in mountain meadows isolated by > 14 km of degraded or otherwise uninhabitable streams, providing evidence beavers were able to explore the furthest reaches of potential habitat.

For juvenile beavers in snowmelt-dominated stream systems there is evidence of a large pulse of dispersal during the rising phase of spring runoff, and settlement during the falling phase. Spring runoff therefore provides an opportunity to take advantage of the large number of beavers seeking settlement sites in an area. Even though spring floods may destroy pre-engineered structures in potential restoration sites, if the location is at least partially engineered prior to the onset of runoff there may be a greater chance of a dispersing beavers settling at the site. My data also indicate dispersal may increase substantially during years of high spring runoff, which presumably increases the opportunity for dispersers to encounter a restoration site.

Dispersing beavers prefer pre-engineered habitats. Stream sections containing abandoned and relic colonies were highly sought after by dispersing beavers in my study area, and old beaver structures were used almost exclusively along dispersal routes. Many new settlement sites were based around a set of abandoned dams and lodges or a single relic lodge. Of course, there may have been other long-term effects of previous beaver occupancy that were not so obvious. For example, a relic beaver colony may have caused localized sediment deposition in a stream section while the colony was active that promoted regeneration of woody plant species making the site more suitable for future settlement. Regardless of the ecological basis for the attraction of dispersing beavers to pre-engineered habitats, the selection for these sites is important in the context of beaver restoration. Restoration practitioners have provided substantial evidence of the benefits of pre-engineering habitats to promote beaver colonization. Many projects have used Beaver Dam Analogues (BDAs) and other mimicry structures to facilitate natural occupancy by beavers (Woodruff 2015, Bouwes et al. 2016, Pollock et al. 2017). Projects that used pre-engineered structures have generally been more successful at encouraging colonization and offer good evidence the selection for pre-engineered habitats is common in beavers. Clearly, beaver restoration projects should take advantage of the selection of pre-engineered habitats by beavers, either by constructing dams and lodges ahead of time, or selecting restoration sites with sign of previous beaver occupancy even if beavers have not been present for a long time. Beaver restoration practitioners should also be aware that beavers may not inhabit a targeted restoration site if other abandoned or relic colonies are nearby. In such a situation, the targeted restoration site will likely need to be engineered in such a way that it is more attractive to dispersers than the abandoned or relic colonies.

I found evidence of delayed dispersal in many areas that were surrounded by large amounts of unoccupied habitat. Furthermore, there was a low rate of colonization in unoccupied streams sections and colony persistence beyond two years after settlement in these types of habitats was rare. Beaver colony density may be relative to good quality habitat in that delayed dispersal can occur even if colony densities are overall low and large portions of streams are unoccupied. In the context of beaver restoration, my results suggest beavers will be reluctant to occupy unmodified habitat if any other options are available. Significant habitat improvements may be necessary to encourage beavers to occupy a degraded site targeted for restoration, and long-term colony success will require careful site selection, preparation, and monitoring.

The abandonment of beaver colonies due to disease outbreaks like the one observed in my study could cause major shifts in dispersal dynamics in a given area. The relatively sudden abandonment of many colonies on the landscape due to disease could cause dispersal to increase on the periphery of the outbreak area as juvenile beavers are able to find open territories (i.e., abandoned colonies) nearby. However, during recolonization of disease-affected areas, settlement in previously unoccupied habitats may decrease because dispersing beavers are not forced to settle in suboptimal habitats. Meanwhile, beaver densities on the periphery of the disease outbreak may be reduced by dispersal, which could further impact the probability of settlement in novel habitats outside of the diseased area.

Diseases such as tularemia have the potential to dramatically change beaver colony densities and distribution in a project area through widespread die-offs (Lawrence et al. 1956, Stenlund 1953). Disease management must be a primary consideration when beavers are to be translocated as part of a restoration project. Restoration practitioners must be careful to avoid spreading diseases to beaver populations in and around the project area which could potentially wipe out large numbers of beavers. Project leaders should also be aware that disease outbreaks may hamper their ability to take advantage of beaver dispersal, as the high availability of abandoned colonies may draw dispersers away from restoration sites.

CHAPTER FOUR

CONSIDERATION OF BEAVER DISPERSAL AND SETTLEMENT SITE SELECTION IN BEAVER RESTORATION

Introduction

Beavers (*Castor* spp.) are being increasingly used as wetland and riparian restoration tools by land and wildlife managers, especially in the western United States (Pilliod et al. 2017, Pollock et al. 2017) and Europe (Macdonald et al. 1995, Macdonald et al. 2000, South et al. 2000, South et al. 2001). When beavers dam streams, cut channels, and redistribute vegetation they create habitat patches with unique form and function relative to the rest of the stream (Naiman et al. 1988). The unique habitat patches beavers create can retain water and sediment, expand the riparian area around streams, enhance channel complexity and stream channel-floodplain connectivity, and facilitate greater patch-level and landscape-level habitat heterogeneity (Naiman et al. 1988, Collen and Gibson 2001, Wright et al. 2002, Rosell et al. 2005, Pollock et al. 2014, Bouwes et al. 2016). Beavers are often viewed as a relatively inexpensive, efficient, and self-sustaining strategy for habitat restoration that can be applied at large spatial scales. Beaver-mediated habitat restoration (hereafter, “beaver restoration”), represents a restoration approach that emphasizes restoring functional processes to degraded stream systems, a strategy widely viewed as more effective than more intrusive and short-term methods (Bernhardt 2005, Lake et al. 2007, Palmer 2008).

Beaver restoration can be summarized in two major components that are critical to project success:

1) Project leaders must select an appropriate location for restoration to take place. Restoration site decisions may be based on habitat availability, landowner interest/tolerance, agency stream monitoring and recovery requirements, or the availability of project locations in general. Project leaders must consider multiple scales of selection from the entire watershed down to specific sites within a stream segment where beaver dams or beaver mimicry structures could be built and beaver activity could be sustained. Unfortunately, due to the dynamic nature of streams and the complexity of beaver habitat selection, suitability of specific locations may change on an annual basis due to disturbance to vegetation, land management decisions, channel-altering high water events, and shifts in public perception.

2) Once a location has been identified, project leaders must decide on a strategy given the system under consideration. Three general strategies are most common: 1) translocating beavers from established colonies or property damage issue areas to restoration sites, 2) implementing construction of beaver mimicry structures such as Beaver Dam Analogues (BDAs) or other habitat improvements to improve the success of beaver translocation or promote natural colonization of a site by beavers, or 3) mimicking beaver activity in a stream without the explicit goal of beaver occupancy. The most successful projects often use a combination of these approaches. The choice of restoration strategy depends on a variety of factors including the spatial distribution of

active and inactive beaver colonies in the project area and potential routes of dispersal for beavers from active colonies to the restoration site.

The selection of restoration sites with the highest probability of success is critical to maintain funding and support for beaver restoration projects. Fortunately, a variety of beaver restoration projects have been implemented in the western United States in the past 50 years, and insights from these projects can help inform the selection of restoration sites in other areas. Additionally, there is a rich body of scientific literature on habitat selection by beavers as well as behavioral studies that can shed light on critical aspects of beaver ecology to inform restoration efforts (Table 16). The goal of this chapter is to summarize what I have learned about beaver dispersal and settlement site selection in the context of previous beaver habitat suitability research and beaver restoration efforts, and to offer recommendations for improving current strategies. I will present my recommendations in a way that mirrors the approach of many successful beaver restoration projects: 1) broad-scale analysis of suitable, marginal, and unsuitable beaver habitat, 2) selection of specific streams or stream segments in an area that are in need of, or could support, beaver restoration, and 3) selection of specific locations within a restoration site where actions will take place.

I provide recommendations for restoration site selection using a multi-tiered approach that reflects most agency-level decisions regarding beaver restoration (Macdonald et al. 2000, South et al. 2001, UDWR 2010, Carpenedo 2011). Step one is to estimate where beavers are or should be based on habitat and identify the “low-hanging fruit” in terms of restoration (i.e., good beaver habitat with no beavers). Initial broad-scale modeling allows project leaders to start by asking, “Why are there no beavers in these sites that seem like they should be occupied?” A landscape overview also starts to provide information on dispersal routes and possible landowner conflict issues. Second, when the low-hanging fruit has been identified, managers will want to switch their focus to suboptimal habitats as these areas have the greatest need for restoration. Managers may also start by targeting suboptimal habitats if they are constrained to a specific watershed or stream where good beaver habitat is rare or nonexistent. When good beaver habitat is limited, project leaders need to evaluate the best patches in otherwise suboptimal habitat. High quality habitat patches relative to the rest of the stream may be the areas with the highest probability of successful beaver occupancy and would therefore be the best location for encouraging settlement by beavers. Conversely, patches of good habitat may draw beavers away from a more targeted restoration site, requiring greater effort in site preparation and enhancement ahead of beaver occupancy. Finally, once the best patches of habitat have been identified, project leaders need to assess the potential sites in the field to look for issues or opportunities that could not be identified based on suitability modeling or aerial imagery. The final on-the-ground assessment is an opportunity to check for old beaver structures, evaluate stream depth and the availability of lodge locations, and identify other hazards that may prevent a project from being successful (e.g., adjacent landowners, easily blocked culverts, heavily used campsites nearby).

Broad-scale Beaver Habitat Suitability Analysis

Researchers have developed a suite of beaver habitat suitability indices and models for use in habitat mapping (Suzuki and McComb 1998, Carpenedo 2011), field assessments of potential restoration sites (Allen 1982, Vore 1993, Pollock et al. 2017), and estimating the number of colonies or dams a stream or watershed could support for beaver restoration/reintroduction planning (Macdonald et al. 2000, South et al. 2001, Macfarlane et al. 2014, 2015). Earlier models were descriptive in nature, and identified habitat based on classification of variables believed important to beaver habitat selection (Allen 1982, Vore 1993). More recent efforts have focused on the use of remote-sensing data and a GIS to develop suitability maps of streams and associated riparian areas that can be applied at large spatial scales (Macdonald et al. 2000, South et al. 2001, Carpenedo 2011, Macfarlane et al. 2015). Geospatial analysis and mapping has allowed for rapid examination of beaver habitat suitability at multiple spatial scales and has increased the efficiency of beaver restoration site selection. Fortunately, many of these models were developed in the western United States, and application of these models has resulted in a wealth of information about their utility and limitations.

One of the first comprehensive habitat suitability indices for beavers was a U.S. Fish and Wildlife Service Habitat Suitability Index developed by Allen (1982). The author emphasized basic beaver habitat requirements, but the conclusions were based on studies from a wide range of geographic locations. Vore (1993) reviewed the literature on habitat suitability and suggested habitat conditions and restoration approaches specific to Montana, and particularly sites where beavers may be reintroduced as part of a stream restoration effort. Vore’s assessment is similar to Allen (1982), but he interprets beaver habitat suitability in the context of beaver restoration and offers recommendations for increasing the success of beaver translocations. Suzuki and McComb (1998) studied beaver activity in Oregon and produced a habitat suitability model that incorporated both geospatial data (stream gradient, valley floor width) and field survey data (stream width) to classify streams based on their potential for supporting beaver damming activity. Carpenedo (2011) developed a habitat suitability model for the Big Hole Watershed in Montana. His model relied entirely on geospatial data and incorporated more fine-scale geospatial data than most GIS-based modeling efforts. The author also used local knowledge of habitat conditions to make the model highly specific to the watershed under evaluation. His model allows for greater flexibility, and has since been adjusted to evaluate other watersheds in Montana (personal communication).

More recently, Macfarlane et al. (2015) developed the Beaver Restoration Assessment Tool (BRAT), a geospatial modeling platform that outputs 250-m stream segments classified in terms of the number of beaver dams they could theoretically support. The BRAT provides recommendations for beaver restoration potential based both on the number of dams the site could support, and the potential for human conflict. The tool uses publicly available input datasets that cover: 1) a stable water source, 2) availability or streamside riparian vegetation, 3) ability of dams to persist through both low and high water events, and 4) stream gradients conducive to efficient dam construction in terms of providing enough ponded water for beavers. The BRAT has been widely used to evaluate potential beaver habitat for beaver restoration. The authors tested the BRAT in Utah and found the tool was good at predicting dam density against a test dataset, and since then several other states have begun using the tool to model potential beaver habitat (Macfarlane et al. 2014).

While there are a wide variety of studies focused on beaver habitat selection (Table 16), few studies were conducted on stream systems in the western United States where beavers must build dams. Therefore, the utility of these studies for informing habitat selection in the context of beaver restoration may be questionable, yet most of the habitat suitability modeling I outlined above relies on these foundational studies to map and predict beaver habitat. Besides the lack of region-specific information on beaver habitat selection, the majority studies also follow a general protocol of comparing habitat conditions between occupied sites and unoccupied or abandoned sites, or relating habitat conditions to beaver colony density and longevity (Table 16). Focusing on already-occupied beaver habitats is useful for producing models of good beaver habitat for predicting where beavers are or where they should be on a landscape. However, because beavers are ecosystem engineers, within a few years of occupation their activities begin to drastically change the habitats in and around their colony. Long-term occupancy can even modify valley bottoms and influence stream gradient over large areas (Westbrook et al. 2010, Polvi and Wohl 2012). The dramatic effects of beaver activities may cause researchers to overemphasize certain habitat conditions that are changed as a result of beaver activity as being important for beaver occupancy, even though original site conditions that promoted settlement are fundamentally altered. This issue is particularly relevant to beaver restoration because in a restoration scenario beavers are often being encouraged to settle in suboptimal and marginal habitats. Because habitat conditions are inherently worse at restoration sites, habitat selection patterns may be quite different from those suggested by comparing occupied and unoccupied habitats. Furthermore, beavers may experience more dramatic tradeoffs in marginal habitats, for example, forgoing easy access to forage for a location with greater potential for dam resiliency.

It is possible habitat conditions in active beaver colonies also reflect conditions selected for at initial settlement sites. However, few studies have adequately addressed initial site selection. Information is particularly lacking in ecosystems and environmental conditions similar to those that characterize beaver restoration sites in the western United States (Table 16). The ideal study to inform beaver restoration in this region would: 1) be conducted on streams small enough to be dammed by beavers since dams on smaller streams are the main agent of habitat restoration, 2) be conducted in the snowmelt-dominated stream systems in the western United States, and 3) establish or attempt to establish stream conditions prior to colonization by beavers. To date, no studies of beaver habitat selection have fulfilled all of these criteria (Table 16). The number of studies that fulfill the first two objectives are lacking as well, so even current models of optimal beaver habitat may not be adequately calibrated to stream systems in western North America.

Table 16. Summary of beaver habitat suitability literature in the context of providing information for beaver restoration in western North America, 1977−2018.

Authors	Occupied vs. Unoccupied or Density/ Longevity	Smaller streams?	Dams?	Western U.S.	Pre-colony Conditions (*post hoc*)
Slough and Sadlier 1977	X	X	X		
Howard and Larson 1985	X	X	X		X
Beier and Barrett 1987	X	X	X	X	
Dieter and McCabe 1989	X	X		X	
Hartman 1996	X				
Barnes and Mallik 1997	X	X	X		X
Smith 1997			X		X
Suzuki and McComb 1998	X			X	X
Curtis et al. 2004	X	X	X		
Destefano et al. 2006			X		X
Cox and Nelson 2009	X	X			
Pinto et al. 2009	X	X			
Frantisek et al. 2010	X				
Scrafford et al. 2018	X	X	X	X	X

Beaver Habitat Selection in Suboptimal and Unmodified Habitats

Habitat suitability models highlight basic resources necessary for persistence of beaver colonies, and are effective for predicting fundamental components of beaver habitat over large areas. Highly suitable beaver habitat is important to identify as it may represent the low-hanging fruit in terms of restoration. Once highly suitable beaver habitat has been identified and prioritized in a project area, the next step is to identify areas beavers may not be able to establish easily on their own. These habitats have usually been degraded in some way, for example, through channel incision or loss of riparian vegetation. Encouraging beavers to establish colonies in suboptimal and marginal habitats is particularly challenging, and may require significant site preparation and pre-engineering for success. Additionally, habitat selection patterns may shift in such environments as beavers likely experience tradeoffs due to potential limitations to food and construction material as well as more challenging geomorphic conditions for dam and lodge construction.

Few studies have evaluated habitat selection by beavers starting new colonies in novel areas (Table 16), yet this situation is the best natural analogue to beaver restoration scenarios. In Chapter 2, I presented the results of a two-year study on the selection of settlement sites by dispersing beavers in stream segments relatively unmodified by beaver activity and generally suboptimal in habitat quality. The results of my research suggest beavers seeking settlement sites in novel areas prefer stream segments with habitat characteristics such as:

1) Relatively low gradients that reduce stream power acting on dams and facilitate localized areas of sediment deposition conducive to flow dissipation and woody riparian plant growth.

2) Narrower stream channels that may be easier to dam and provide deeper waters.

3) Patches of dense woody riparian vegetation close to the water with stems that are of appropriate size and density for dam and lodge construction at the location.

4) A diversity of water depths that offer pools of deeper water for lodge and bank den construction and excavation as well as shallower areas where dam building is easier and more efficient.

5) Low-lying floodplains next to the stream that dissipate flood waters and make expansion of the ponded area behind dams easier.

6) Channel complexity in the form of small side channels, backwaters, and tributaries that allow for lateral expansion of colony boundaries, provide anchor points for dams, and offer diverse options for stream channel manipulations.

While there was some evidence for selection of these habitat components at new settlement sites, effect sizes were small, and the importance of certain variables varied based on conditions specific to each stream. One possible reason for the small effect sizes was the wide variety of stream types and associated riparian conditions in my study area, from small rivers meandering through sandy floodplains, to high-gradient mountain streams flowing through rocky, conifer-forested canyons. Stream-to-stream variation causes certain habitat components to be more or less important for beavers starting a new colony given the particular set of environmental conditions they face in a stream. For example, a dispersing beaver seeking a new settlement site in a small stream with limited forage availability may be more tolerant of high stream gradient because the stream is unlikely to gain enough power to blow out dams so settling near the best forage is most important. Alternatively, a beaver settling in a large stream with abundant woody riparian vegetation may seek lower gradient stream segments as dam resiliency will be the limiting factor in such a location.

Beaver restoration practitioners should carefully consider habitat factors that will limit beaver occupancy in a project location, and assess possible tradeoffs between access to forage and dam resiliency for their particular stream. The tradeoffs beavers face when settling in novel areas should also influence decisions regarding pre-restoration site preparations. Project leaders should assess which components of the habitat are of sufficient quality, and implement manipulations to improve those that are not. Habitat manipulations may include constructing dams and lodges to improve the odds of beaver occupancy, or bringing in additional woody vegetation at the restoration site to provide necessary resources to newly colonizing beavers while riparian vegetation at the location improves (Apple 1985).

In Chapter 3, I presented results from radio-marking 55 dispersal-age beavers in the upper Gallatin and Madison River drainages. Insights from this aspect of the project are also useful in the context of identifying potential settlement sites in novel areas. The spatial distribution of active colonies and potential dispersal routes all may influence whether beavers will encounter a restoration site naturally, or whether beaver translocation may be necessary to promote colonization. My results demonstrate dispersing beavers are willing to travel long distances to find suitable habitat, and are particularly drawn to areas with previous beaver habitat manipulations. Any stream with year-round water and at least some streamside riparian vegetation should be considered a dispersal route, though the availability of suitable resting locations along that route may limit the ability of beavers to make long exploratory movements. I also observed a major pulse of dispersal and settlement during spring runoff, and this pulse may be magnified during years of exceptionally high runoff. The distinct spring runoff dispersal period offers an opportunity for restoration practitioners to take advantage of a large number of beavers seeking settlement sites. Although high waters may make working in the stream channel more difficult, implementing restoration site preparations, such as the construction of BDAs or rudimentary lodges, may be effective during high waters especially as waters begin to recede in early summer. Finally, project leaders should plan for dispersing beavers settling in new areas to move around the stream system considerably for many years as they deal with dam blow outs and localized resource depletion. Project areas should be large enough to accommodate frequent territorial shifts by beavers, and significant habitat manipulations may be necessary to promote long-term colonization of highly specific sites.

On-the-ground Habitat Assessment

In Chapter 2, I suggested habitat components that may be easily assessed within a stream or drainage based on publicly available datasets and analysis of aerial imagery. I further suggested habitat components to be assessed in the field in a relatively short time period and with simple measurement techniques. Once a specific restoration site or group of potential sites have been identified, the final step in site selection is to visit the areas in the field to check on fine-scale habitat conditions and look for opportunities and challenges that may not be measureable from remotely sensed data. Field visits allow project leaders to: 1) assess habitat changes that may have occurred after the most recent aerial imagery, 2) look for specific dam and lodge construction sites, 3) identify potential issues with predators both human and natural, and 4) begin outreach and communication to cope with neighboring land management issues. Field visits also provide the opportunity to validate geospatial modeling and check for sign of current or past beaver activity.

The results from Chapter 2 suggest field habitat assessments should include evaluation of water depths and channel structure that are conducive to successful dam and lodge construction. A diversity of water depths may be more critical to success than overall deeper waters, especially if beavers will need to build dams from scratch. Deep waters may only be useful if they are paired with an undercut bank where beavers can excavate a lodge entrance, so specific suitable lodge locations are critical to identify prior to restoration efforts. The presence of old beaver structures such as lodges or dams provides evidence of site suitability for occupancy (Vore 1993), and structures that can still be used or could be easily repaired may act as stepping stones for eventual long-term occupation. My observations indicate dispersing beavers use old lodges and bank dens almost exclusively both along the dispersal route and at the eventual settlement site if such structures are available. Restoration site assessments should also include an evaluation of stem sizes of preferred forage, and areas with smaller and more uniform stem sizes may be selected by beavers over areas with larger stem sizes. Smaller stems that are close to the water may be particularly important, and beavers will likely select a patch of smaller willows close to the water over larger forage species that require more energy to cut down, process, and transport back to the water.

Dispersing beavers may be particularly vulnerable to predation during dispersal, so field visits are an opportunity to assess potential dispersal routes to and from the restoration site. In the field, project leaders can assess the probability beavers will be able to reach the site naturally, and also can identify potential conflict areas where beavers may be drawn to settle before they get to the restoration site. If areas that may draw beavers away from the restoration site are on or near private land, cooperation with landowners will be critical to project success both to assure a safe route for dispersers to reach the site, and to manage beavers that eventually disperse from the project area if the project is successful. If a dispersal route is mostly devoid of daytime resting locations, rudimentary lodges may be needed along the potential dispersal route from the nearest source colony to promote beaver movement through the area. Daytime resting locations may be as simple as a large pile of branches with a cavity underneath large enough for a beaver to crawl into.

Conclusion

Beaver-mediated habitat restoration is increasing in popularity and has proven to be an effective and efficient form of stream restoration. As beaver restoration becomes more prevalent, project leaders will benefit from incorporating knowledge of beaver ecology into the restoration process. Habitat selection by beavers in restoration scenarios does not necessarily follow the same patterns as for beavers settling in optimal habitat, and stream-specific conditions must be carefully interpreted to select restoration sites that have the highest probability of success. Furthermore, beaver dispersal is a major factor influencing site selection, and understanding this process of beaver life history is critical to assessing current colony distributions and the potential for natural beaver occupancy in project areas. Well before project implementation, restoration practitioners should become familiar with the status of local beaver populations and their distribution on the landscape as well as available habitat in the project area and potential risks to that habitat in the short- and long-term. Working with beaver ecology and behavior has the potential to greatly improve beaver restoration project success, leading to dramatic habitat improvements and the reestablishment of ecosystem services in critical riparian and wetland habitats.

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APPENDICES

APPENDIX A

TABLES OF SUMMARY STATISTICS FOR BEAVER HABITAT CONDITIONS IN THE UPPER GALLATIN AND MADISON RIVER DRAINAGES

Table A1. Mean (±SD) habitat variables measured along stream segments (400-m) newly settled by beavers and segments that remained unsettled in the upper Gallatin and Madison River drainages, USA, 2015−2017.

Variable	Settled (n = 48)	Unsettled (n = 325)	*P*[a]
Sinuosity	1.36 (0.37)	1.26 (0.29)	0.031
Gradient (%)	1.1 (0.8)	1.3 (1.0)	0.22
Floodplain width (m)	181 (187)	155 (155)	0.87
Watershed size (km^2)	45.4 (34.1)	79 (108.4)	0.25
Distance to secondary channel (m)	308 (491)	383 (963)	0.90
Number of secondary channels	0.60 (0.68)	0.62 (0.76)	0.88
Width of woody riparian vegetation zone (m)	126 (177)	102 (106)	0.67
Canopy cover index (Score 1−3)	2.31 (0.43)	2.14 (0.53)	0.047
Forage height index (Score 1−3)	2.58 (0.68)	2.35 (0.7)	0.015
Forage biomass index	655.66 (1040.77)	475.94 (572.44)	0.33
Distance to active colony (m)	1633 (2021)	1769 (2009)	0.84
[b]Proportion sparse-willow wetlands	0.24 (0.25)	0.21 (0.21)	0.56
Proportion gravel bar wetlands	0.04 (0.09)	0.04 (0.09)	0.97
Proportion willow-dominate wetlands	0.16 (0.19)	0.14 (0.17)	0.65
Proportion waterbody wetlands	0.13 (0.07)	0.2 (0.16)	0.02

[a] *P*-values from Wilcoxan rank-sum test
[b] Proportions are from 30-m buffer around stream segments

Table A2. Mean (±SD) habitat variables measured along stream segments (400-m) in beaver-occupied streams in the upper Gallatin and Madison River drainages, USA, 2015−2017.

Variable	Gallatin (n = 354)	Madison (n = 259)	*P*[a]
Sinuosity	1.27 (0.24)	1.58 (0.56)	< 0.001
Gradient (%)	1.5 (1.1)	0.5 (0.6)	< 0.001
Floodplain width (m)	126 (87)	355 (300)	< 0.001
Watershed size (km^2)	85.5 (121.2)	59.0 (36.2)	0.010
Distance to secondary channel (m)	404 (1081)	118 (273)	< 0.001
Number of secondary channels	0.66 (0.74)	0.92 (0.93)	0.0013
Width of the woody riparian vegetation zone (m)	89 (71)	278 (255)	< 0.001
Canopy cover index (Score 1−3)	2.24 (0.52)	2.47 (0.52)	< 0.001
Forage height index (Score 1−3)	2.28 (0.71)	2.77 (0.43)	< 0.001
Forage biomass index	410.8 (333.6)	1524.5 (1545.6)	< 0.001
Distance to active colony (m)	1843 (2135)	328 (539)	< 0.001
[b]Proportion sparse-willow wetlands	0.21 (0.20)	0.21 (0.24)	0.17
Proportion gravel bar wetlands	0.03 (0.07)	0.04 (0.09)	0.70
Proportion willow-dominate wetlands	0.17 (0.19)	0.35 (0.27)	< 0.001
Proportion waterbody wetlands	0.18 (0.14)	0.2 (0.14)	< 0.001

[a] *P*-values from Wilcoxan rank-sum test
[b] Proportions are from 30-m buffer around stream segments

Table A3. Mean (±SD) habitat variables measured at stream segments (400-m) occupied by beaver colonies and unoccupied stream segments. Stream segments were classified based on beaver-use surveys in the upper Gallatin and Madison River drainages, USA, 2015−2017. Occupied segments were classified as occupied for at least one of the three years of study and do not include new settlement sites in previously unoccupied habitat.

Variable	Occupied (n = 229)	Unoccupied (n = 384)	*P*[a]
Sinuosity	1.61 (0.53)	1.28 (0.31)	< 0.001
Gradient (%)	0.7 (1.0)	1.3 (1.0)	< 0.001
Floodplain width (m)	316 (289)	167 (173)	< 0.001
Watershed size (km^2)	73.8 (83.2)	74.5 (102.9)	0.037
Distance to secondary channel (m)	158 (739)	358 (905)	< 0.001
Number of secondary channels	0.98 (0.92)	0.64 (0.76)	< 0.001
Width of the woody riparian vegetation zone (m)	260 (250)	115 (131)	< 0.001
Canopy cover index (Score 1−3)	2.63 (0.39)	2.17 (0.53)	< 0.001
Forage height index (Score 1−3)	2.64 (0.54)	2.39 (0.70)	< 0.001
Forage biomass index	1442.59 (1520.06)	546.62 (721.15)	< 0.001
Distance to active colony (m)	415 (1120)	1673 (1988)	< 0.001
[b]Proportion sparse-willow wetlands	0.19 (0.21)	0.22 (0.22)	0.71
Proportion gravel bar wetlands	0.03 (0.07)	0.03 (0.09)	0.56
Proportion willow-dominate wetlands	0.41 (0.24)	0.15 (0.18)	< 0.001
Proportion waterbody wetlands	0.19 (0.12)	0.19 (0.16)	0.071

[a] *P*-values from Wilcoxan rank-sum test

[b] Proportions are from 30-m buffer around stream segments

Table A4. Mean (±SD) habitat variables measured at relic beaver colonies and unoccupied stream segments (400-m) available to be settled by dispersing beavers. Stream segments were classified based on beaver-use surveys in the upper Gallatin and Madison River drainages, USA, 2015−2017.

Variable	Relic (n = 99)	Unoccupied (n = 274)	*P*[a]
Sinuosity	1.36 (0.44)	1.24 (0.23)	< 0.001
Gradient (%)	1.1 (0.8)	1.4 (1.0)	0.012
Floodplain width (m)	216 (211)	138 (131)	< 0.001
Watershed size (km^2)	57.7 (66.2)	80.8 (112.2)	0.84
Distance to secondary channel (m)	258 (475)	415 (1027)	0.26
Number of secondary channels	0.76 (0.83)	0.57 (0.71)	0.048
Width of the woody riparian vegetation zone (m)	157 (173)	86 (82)	< 0.001
Canopy cover index (Score 1−3)	2.25 (0.49)	2.13 (0.53)	0.052
Forage height index (Score 1−3)	2.45 (0.69)	2.35 (0.70)	0.17
Forage biomass index	778.74 (1024.1)	398.02 (406.49)	< 0.001
Distance to active colony (m)	1550 (1840)	1824 (2064)	0.16
[b]Proportion sparse-willow wetlands	0.25 (0.21)	0.20 (0.22)	0.021
Proportion gravel bar wetlands	0.04 (0.10)	0.03 (0.09)	0.45
Proportion willow-dominate wetlands	0.22 (0.21)	0.11 (0.15)	< 0.001
Proportion waterbody wetlands	0.16 (0.09)	0.20 (0.17)	0.47

[a] *P*-values from Wilcoxan rank-sum test
[b] Proportions are from 30-m buffer around stream segments

Table A5. Mean (±SD) habitat variables measured at stream segments (400-m) classified as active and abandoned beaver colonies compared to relic colonies and unoccupied stream segments. Stream segments were classified based on beaver-use surveys in the upper Gallatin and Madison River drainages, USA, 2015−2017.

Variable	Active/Abandoned (n = 243)	Relic/Unoccupied (n = 370)	*P*[a]
Sinuosity	1.61 (0.52)	1.27 (0.31)	< 0.001
Gradient (%)	0.8 (1.0)	1.3 (1.0)	< 0.001
Floodplain width (m)	321 (290)	158 (160)	< 0.001
Watershed size (km^2)	73.7 (84.5)	74.7 (102.8)	0.051
Distance to secondary channel (m)	143 (717)	375 (919)	< 0.001
Number of secondary channels	1.00 (0.92)	0.62 (0.75)	< 0.001
Width of the woody riparian vegetation zone (m)	268 (248)	104 (117)	< 0.001
Canopy cover index (Score 1−3)	2.61 (0.42)	2.16 (0.52)	< 0.001
Forage height index (Score 1−3)	2.65 (0.53)	2.37 (0.70)	< 0.001
Forage biomass index	1472.29 (1500.49)	493.22 (649.59)	< 0.001
Distance to active colony (m)	349 (996)	1764 (2012)	< 0.001
[b]Proportion sparse-willow wetlands	0.20 (0.22)	0.21 (0.22)	0.79
Proportion gravel bar wetlands	0.03 (0.06)	0.04 (0.09)	0.96
Proportion willow-dominate wetlands	0.41 (0.24)	0.14 (0.17)	< 0.001
Proportion waterbody wetlands	0.19 (0.12)	0.19 (0.15)	0.099

[a] *P*-values from Wilcoxan rank-sum test

[b] Proportions are from 30-m buffer around stream segments

Table A6. Model-averaged coefficient estimates from final modeling results investigating the influence of habitat variables on the probability a stream segment will be newly settled by beavers in the upper Gallatin and Madison River drainages in southwest Montana, USA, 2015−2017.

Variable	$\hat{\beta}$[a]	SE	(85% CI) - Lower	(85% CI) - Upper
Stream gradient[b]	-0.70	0.27	-1.09	-0.31
Sinuosity	0.14	0.16	-0.1	0.37
Canopy cover index[b]	0.58	0.22	0.27	0.89
Proportion sparse-willow wetlands[b]	0.36	0.23	0.02	0.70
Proportion waterbody wetlands[b]	-1.32	0.46	-1.98	-0.65
Proportion willow-dominate wetlands	0.03	0.23	-0.31	0.36
Distance to nearest active colony	0.09	0.27	-0.29	0.48

[a] Numerical model coefficients are standardized to compare relative importance. One unit = 1 SD.

[b] 85% confidence interval does not overlap 0 and indicates a significant effect on the probability of settlement by beavers

APPENDIX B

PREDICTING THE AGE-MASS RELATIONSHIP FOR BEAVERS IN SOUTHWEST MONTANA

Introduction

Humans and wildlife depend on riparian areas and wetlands to enhance landscape-scale water storage capacity and bolster the resilience and connectivity of ecosystems. An extensive body of scientific literature recognizes the habitat-modifying activities of beavers (*Castor canadensis*) as instrumental in the creation, expansion, and maintenance of healthy and productive riparian and wetland areas (Naiman et al. 1988, Collen and Gibson 2001, Wright et al. 2002, Cooke and Zack 2008). As a result, beavers are increasingly being used as a tool for cost-effective, proactive riparian and wetland habitat restoration, especially in the western United States where water resources are strained by increasing demand and ongoing drought (Baker 2003, Barnett et al. 2008, Hidalgo et al. 2009, Pollock et al. 2017). Projects aimed at recovering beaver populations in areas of their historic range are increasing in popularity and scope, and research directed towards understanding beaver population dynamics, habitat selection, and influence on ecosystems will be important in the future management of this species as well as the conservation of riparian and wetland habitats

Beavers are territorial mammals that live in well-defended colonies occupied most often by closely related family groups. Beaver colonies usually contain some combination of a mating pair of adults, kits, and yearlings (Muller-Schwarze 2011). In large colonies located in good habitat, sub-adult beavers between two and four years of age may also be present (McTaggart and Nelson 2003, Muller-Schwarze 2011). Because of this aspect of beaver life-history, researchers and restoration practitioners relying on live-captured beavers for their work will be capturing a wide range of beaver age classes in any given colony. Researchers may want to estimate the age of captured beavers to evaluate colony size and composition and to study age-specific processes such as dispersal and breeding. Restoration practitioners looking to translocate beavers may want to selectively remove beavers from a source colony without disrupting the breeding pair or translocating vulnerable kits. Additionally, restoration practitioners may want to monitor colonies established as part of a restoration effort to evaluate age composition of the colony and recruitment rates.

There are few reliable techniques for aging live beavers, and most require sedation or heavy restraint in order to safely gather measurements (Patric and Webb 1960, Layne 2003). Aging beavers via inspection of cementum annuli on cross-sections of teeth is the preferred method to age beavers, but is impossible with live animals (Van Nostrand and Stephenson 1964, Novak 1987). Many authors have proposed using the body mass of captured beavers to differentiate age classes (Bradt 1939, Hammond 1943, Patric and Webb 1960, Payne 1979, Van Deelen 1991, McTaggart 2002, Layne 2003). However, regional variation in growth rates driven by differing food resources and climatic conditions can cause the relationship between the age of beavers and body mass to vary widely across study areas (Table B1).

Table B1. Estimated age-mass (kg) relationships for beavers from various projects in North America, 1943–2018.

Authors	Location	Kits (0−1 yr)	Yearlings (1−2 yr)	Two-year-olds (2−3 yr)	Adults (> 3 yr)
Ritter and McNew, *this study*	Southwest Montana	< 6	6–14.5	14.5–20	> 20
Hammond (1943)	North Dakota	---	4.1–11.3	11.8–20.8	15.9–27.2
Townsend (1953)	Montana	3.6–5.4	9.1–11.8	> 13.6	---
Beer (1955)	Minnesota	< 4.5	5.4−11.8	> 13.6	> 13.6
Patric and Webb (1960)	New York	< 6.8	6.8−10.8	10.9−16.0	> 16
Brooks et al. (1980)	Massachusetts	< 6	6−11	11−15	> 15
Van Deelen (1991)	Western Montana	< 6.5	6.5−10.5	10.5−14.5	> 14.5
McTaggart (2002)	Central Illinois	3.2−11.4	10−19.1	15−23.6	> 15.5

Calibration of the age-mass relationship for beavers has been especially lacking in the western United States, where few studies have been conducted and all relied on small sample sizes of beavers from one or two drainages (Townsend 1953, Van Deelen 1991). Accurate estimation of the age-mass relationship for beavers in this region will improve current and future research projects in southwest Montana and similar habitats within the Greater Yellowstone Ecosystem (GYE). Additionally, practitioners of beaver reintroduction programs, which are most common in the western United States, would benefit from a reliable technique for aging live-captured beavers to determine colony composition and select appropriate individuals for release at restoration sites.

To address the aforementioned shortcomings in field-based age estimation for beavers, I initiated a project to estimate the age-mass relationship for beavers in southwest Montana using a robust sample size representing a broad geographic area.

Specifically, my objectives were to: 1) provide a region-specific calibration of the age-mass relationship for beavers inhabiting willow- and cottonwood-dominated streams and rivers, 2) evaluate drainage-level differences in the age-mass relationship for beavers, and 3) retroactively age beavers captured as part of a graduate research project on beaver dispersal and habitat selection in southwest Montana. This study will provide an accurate estimation of the age of beavers based on mass which will allow researchers to quickly and effectively age beavers in the field, saving time and resources and minimize handling time for captured animals.

Methods

I collected beaver carcasses and skulls from recreational trappers throughout southwest Montana during fall 2015–spring 2017. To make age-mass calibrations regional, I limited the sample to within 300 miles of Montana State University (Bozeman, MT). I contacted trappers through area biologists with the Montana Department of Fish, Wildlife, and Parks (MFWP), local game damage specialists, the Montana Trapper's Association newsletter and e-mail list, and e-mail lists for conservation and outdoor recreation groups in the area. I asked trappers to record the mass of each beaver they caught with the pelt on and provide the sex of the beaver if possible. Trappers generally weighed beaver carcasses just before skinning, and some beavers may have been more wet than others when mass was recorded. I did not feel it was reasonable to ask trappers to dry the beavers before determining mass so I was unable to control for this source of variation in masses, though I believe it would not significantly affect the results. Trappers submitted skulls or mandibles in plastic bags with the mass and sex written on the bag. I also did not ask trappers to record the exact geographic coordinates of beaver harvests; however, I obtained the general location of harvested beavers and grouped them by major river drainage (Figure B1).

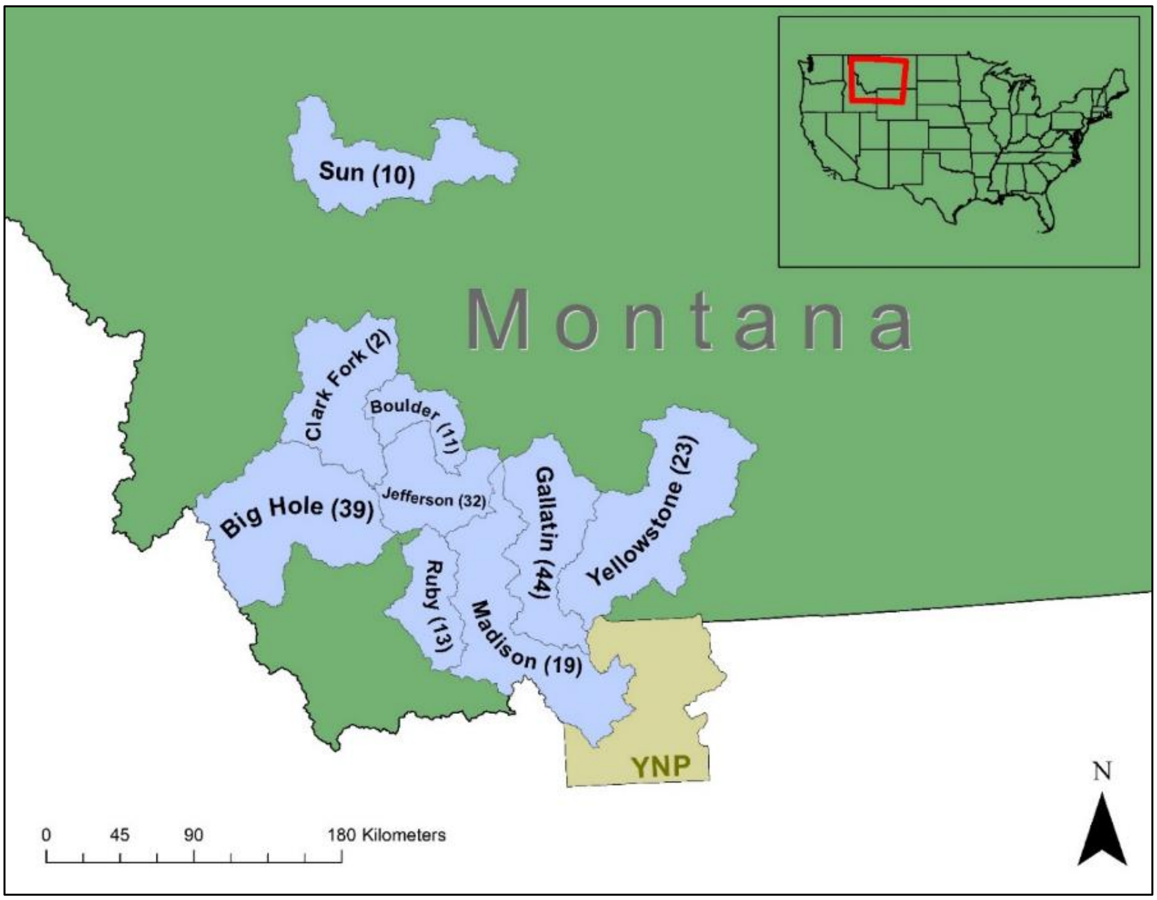

Figure B1: Major river drainages in southwest Montana, USA, where I obtained carcasses and skulls from trappers to estimate the age-mass relationship for beavers. The number of beavers submitted from each drainage are denoted in parentheses. No beavers were captured from within Yellowstone National Park (YNP).

I processed all samples at the Montana Department of Fish, Wildlife and Parks (MFWP) Wildlife Disease Lab in Bozeman, MT. I separated the lower mandible from the skull of each beaver and extracted molar teeth for use in age determination by cementum annuli. To extract the teeth, I allowed the mandibles to soak in water kept just below boiling point for ~ 3 minutes. I then wrapped the mandibles in cloth and struck them with a small hammer, targeting the thickest part of the mandible where the ridges coming off the condylar process and angular process meet. I was then able to extract teeth from the broken mandible parts without causing significant damage to the teeth that would have made age determination more difficult. I soaked teeth in 70% ethanol and then in Nolvasan Solution (Zoetis, Inc.; 0.8% concentration) for 30 seconds before drying the teeth on a paper towel and depositing them in uniquely marked coin envelopes. I submitted teeth to Matson's Laboratory in Manhattan, MT for aging via inspection of cementum annuli. The lab returned a best estimate of age in years for each beaver tooth sample assuming a common birth date of 1 June each year.

I used linear regression to evaluate the relationship between age and mass. I included an additive effect of drainage to test for differences in the average mass of beavers among major river drainages, and an interaction effect to test for differences in growth rates among drainages. I included eight major river drainages where sample sizes were large enough for drainage-specific estimates (Figure B1). I used data from all beavers in the sample to estimate the overall age-mass relationship for beavers across southwest Montana. I removed beavers from the Clark Fork River drainage for the drainage-specific analyses due to low sample size.

I constructed and analyzed models using R Statistical Computing Software (R Version 3.3.2, www.r-project.org, accessed 11 Feb 2018). The residuals of the response variable (age in years) were not normally distributed so I log-transformed the variable and examined residual plots to determine if the assumption of homoscedasticity was reasonably met with the transformation. I fit four linear models using the natural log of age as the response and tested a main effect of mass, an additive effect of drainage, an interaction between mass and drainage, and an intercept-only null model. I ranked models using Akaike's Information Criterion adjusted for small sample sizes (AIC_c). I evaluated the relative support for models in the candidate set based on model mass and number of parameters. I considered all models ≤ 2 ΔAIC_c from the top model to be parsimonious. Goodness of fit was evaluated for each competing model using adjusted R-squared. I used the coefficients from the top model to predict the age of beavers based on the entire range of beaver masses observed in the study area. I examined the means, standard deviations, and ranges of beaver masses representing each year of age to evaluate support for separation of ages based on the predictions from the top-ranked model. I used a Student's t-test to evaluate differences in mean log(mass) between subsequent ages.

Results

I acquired 174 beaver skulls and carcasses from 13 different trappers in southwest Montana during fall 2015–spring 2017. Beavers were taken from nine major river drainages (Figure B1). Not all trappers reported locations of trapping efforts to individual stream, but the sample of beavers were harvested from a minimum of 27 different streams. Due to low pelt prices, few trappers were targeting the species over the two years of the study. Although I directly contacted > 25 trappers, the majority of the samples came from eight individuals. Most of the beavers were trapped due to property damage complaints while the rest were trapped recreationally. I acquired an additional 19 beavers opportunistically during beaver activity surveys and live-capture trapping efforts for a related study on settlement site habitat selection, bringing the total sample size to 193.

Although beavers were captured in both the fall and the spring over the course of the study, all beavers were captured prior to 5 June each year, which was the assumed birth date used in age determination by cementum annuli. I felt confident the mass of beavers would not be drastically different between pre- and post-winter captures because overwinter mass loss in beavers is low (Smith and Jenkins 1997, McTaggart 2002), and most spring captures were late in the season when beavers had likely recovered from winter mass loss. Trappers recorded sex for 101 of the beavers (45 males, 56 females) but masses were highly similar between the sexes so I did not include sex as part of the modeling procedures. Males had a mean mass (±SE) of 36.7 (1.83) kg and females had a mean mass of 35.7 (1.82) kg.

The plot of the raw data suggested an asymptotic or pseudo-threshold relationship between age and mass, with beavers experiencing rapid growth early in life and slowed growth as they get older (Figure B2). Beavers in my sample typically ranged from 1−8 years old and weighed 2.3−31.3 kg, although one captured beaver was estimated at 11 years old. The distribution of ages was strongly skewed towards younger beavers between one and three years of age. Two-year-old beavers were the most common age making up 34% of the sample (Table B2).

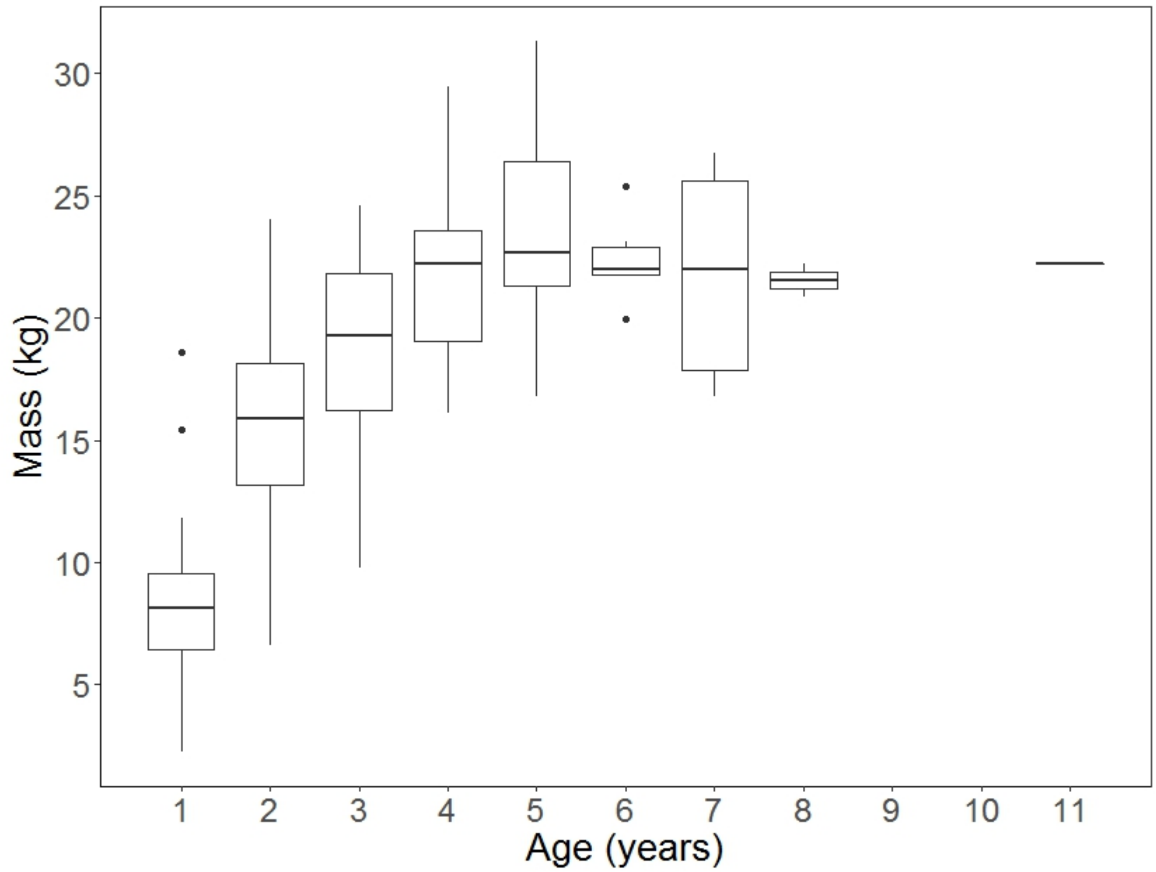

Figure B2. Relationship between age and mass for 193 beaver carcasses obtained during fall 2015–spring 2017 in southwest Montana, USA. Age was determined through inspection of cementum annuli on molars extracted from the lower mandibles.

Table B2. Distribution of ages and masses (kg) from 193 beaver carcasses collected throughout southwest Montana, USA, during fall 2015−spring 2017.

Age (years)	Number of samples	Mean mass (95% CI)	Range	*P*[a]
1	46	8.4 (7.5–9.3)	2.3–18.6	----
2	66	15.9 (15.0–16.9)	6.6–24.0	< 0.001
3	33	18.9 (17.6−20.1)	9.8−24.6	< 0.001
4	18	21.8 (20.1−23.6)	16.1−29.5	0.0092
5	11	23.7 (21.0−26.4)	16.8−31.3	0.26
6	6	22.4 (20.9−23.9)	20.0−25.4	0.41
7	10	21.8 (19.5−24.1)	16.8−26.7	0.68
8	2	---	20.9 and 22.2	---
9	0	---	---	---
10	0	---	---	---
11	1	---	22.2	---

[a] *P*-value result of Welch's t-test comparing mean beaver mass between each age-class and the mean mass of the previous age-class.

The top prediction equation using data pooled over all drainages was log(age) = -0.44589 + 0.079008 × mass (Adjusted R^2 = 0.63, SE = 0.37, N = 193). There was little model uncertainty among the candidate set of models (Table B3). The top-ranked model contained an additive effect of river drainage and accounted for 78% of the candidate set support. The 2nd-ranked model was not considered parsimonious but accounted for 22% of the model support and contained an interaction effect between drainage and age. Confidence intervals on the coefficient estimates for the top model indicated drainage-level differences in the mass of beavers across all ages (Figure B3). Beavers in the Yellowstone, Ruby, and Jefferson River drainages were larger overall than those in other drainages, while beavers from the Madison River drainage were smaller (Figure B4). Beavers from the Big Hole, Boulder, Sun, and Gallatin River drainages were all similar in size.

Table B3. Model selection results testing the influence of mass on age (years) for beavers in southwest Montana, USA, 2015–2017.

Model	K	AIC_c	ΔAIC_c	w_i	Cum w_i
mass + drainage	10	152.53	0.00	0.78	0.78
mass × drainage	17	155.09	2.56	0.22	1.00
mass	3	170.66	18.13	0.00	1.00
~ 1 (null model)	2	357.21	204.68	0.00	1.00

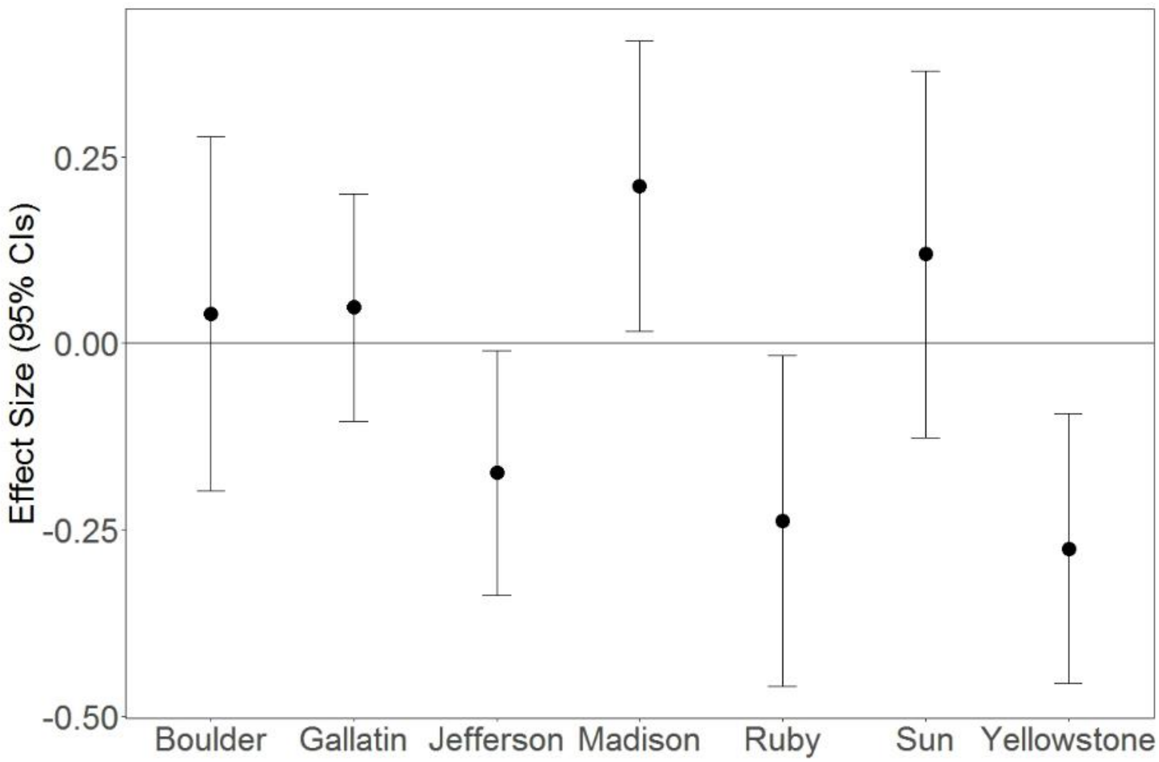

Figure B3. Effects plot for top-ranked model testing the influence of body mass on age for beavers from eight major river drainages in southwest Montana, USA, 2015–2017. The reference drainage was the Big Hole River drainage.

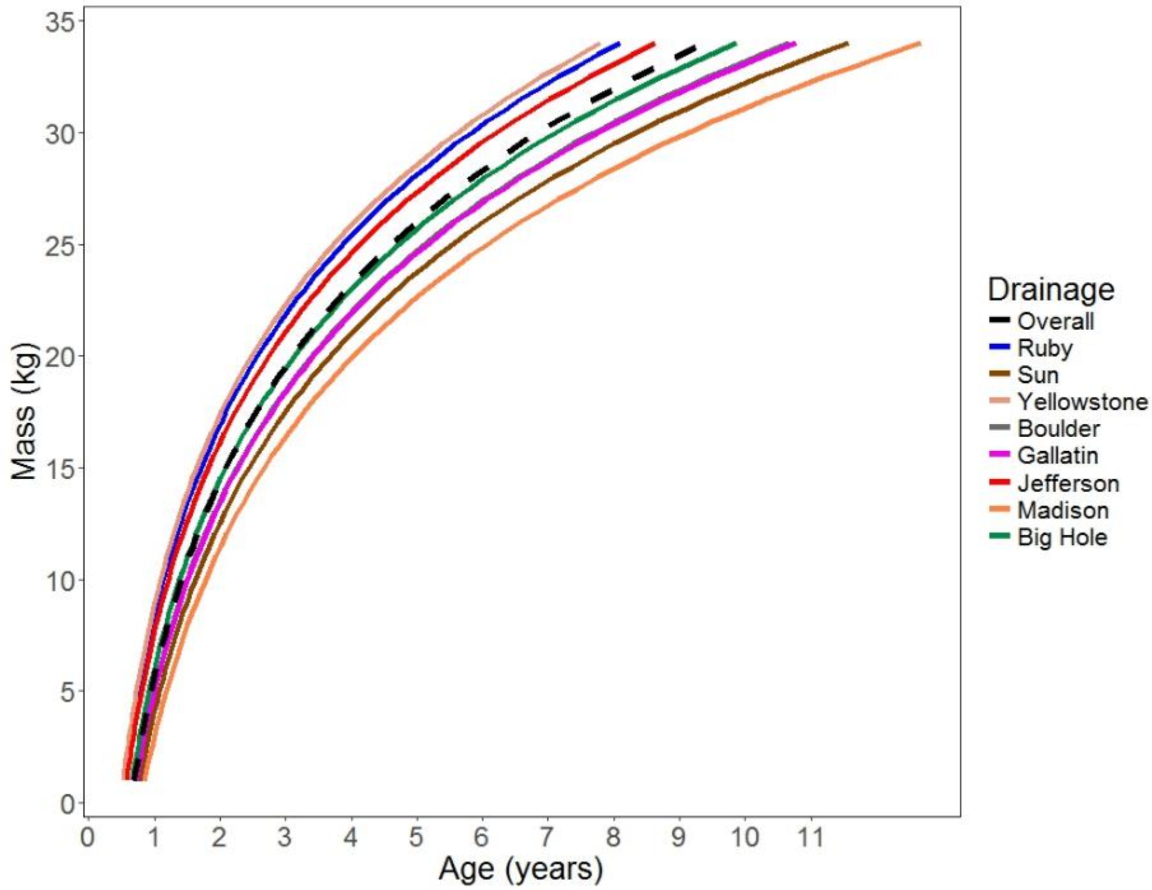

Figure B4. Estimated growth curves for beavers (n = 193) from eight major river drainage in southwest Montana, USA, 2015–2017.

Although beaver masses varied within age-classes, I was able to reliably separate one- and two-year-old beavers by mass, with reduced confidence in the separation of two- and three-year-old beavers as well as three- and four-year-old beavers (Table B2). Identification of beaver ages beyond four years was not possible using mass. The model with just the effect of mass had an adjusted R^2 value of 0.63 and was used to offer overall recommended mass ranges for beavers in southwest Montana (Table B1). However, this model was poorly supported in the candidate set, and the retention of drainage as a variable in the top model suggests mass ranges specific to individual river drainages are more accurate (Adj. $R^2 = 0.67$; Table B4).

Table B4. Recommended mass ranges (kg) for beavers in eight major river drainages in southwest Montana, USA.

Drainage	Kits	Yearlings	Two-year-olds	Adults
Madison	< 3	3−11.5	11.5−16.5	> 16.5
Sun	< 4.5	4.5−13	13−18	> 18
Gallatin	< 5	5−13.5	13.5−18.5	> 18.5
Boulder	< 5.5	5.5−14	14−18.5	> 18.5
Big Hole	< 6.5	6.5−14.5	14.5−19.5	> 19.5
Jefferson	< 8	8−16.5	16.5−21.5	> 21.5
Ruby	< 8.5	8.5−17	17−22	> 22
Yellowstone	< 9	9−17.5	17.5−22.5	> 22.5

Discussion

As expected, my results suggest beavers grow rapidly in the first 1–3 years of life then growth rates slow beyond three years of age. I could not reliably separate kits from one-year-old beavers using mass, but other authors have recommended kits vary from 3.2–11.4 kg (Table B1). My top model predicted beavers less than one year old are generally less than 5 kg, which is within the range of other studies. The reliability of my estimates of mass ranges decreased as beavers got older (Table B2). While separation of one- and two-year-old beavers was highly reliable, separation of two- and three-year-old beavers as well as three- and four-year-old beavers was only moderately reliable (Table B2). My results are consistent with other studies that have found age determination for live-captured beavers beyond three years of age difficult (Layne 2003).

The age distribution of my sample was skewed towards younger animals, and it is unclear if this represents an accurate age distribution for southwest Montana beavers overall. The age distribution of beavers gathered from trappers may not represent actual age distributions in a given area. Larson (1967) suggests beavers harvested by trappers may be skewed toward larger animals as trappers target beavers with more valuable furs. However, Novak (1977) found no bias in age distribution from trapper harvests in Ontario, Canada. McTaggart (2002) observed a similar age distribution as ours in Illinois where beavers were trapped with a more systematic protocol. Larson (1967) also noted a similar age distribution in Maryland from trapper-submitted beaver carcasses, but noted a drop in the number of two-year-old beavers which he attributed to those beavers being missed by trappers due to dispersal. Unlike his study, I found two-year-old beavers were the most common age submitted by trappers (Table B2). Due to the low market prices for beaver furs during my study, a majority of the beavers in my sample were trapped due to property damage complaints. Stream sections where beavers must be trapped due to property damage are commonly recurring issues where it is likely young, naïve beavers are repeatedly moving into the sites that appear to be open habitat. It is therefore possible my sample was biased towards younger animals which are more likely to have recently dispersed and settled in areas where they are not tolerated by humans.

Beavers in the Yellowstone, Ruby, and Jefferson River drainages were larger than in other drainages while beavers in the Madison River drainage were smaller (Figure B4). It is unclear why there were dissimilarities, but there are notable differences in environmental conditions among drainages. A large proportion of the beavers in the

Yellowstone, Ruby, and Jefferson River drainages came from colonies in or near spring creeks. Beavers in spring creeks may take advantage of stable water temperatures that enhance plant growth and limit ice cover which allows access to quality forage for a longer portion of the year compared to other drainages. Meanwhile, a large proportion of the Madison drainage sample came from the Hebgen Lake basin, a high-elevation plateau that often freezes several weeks earlier and thaws several weeks later than areas in other drainages or lower in the Madison drainage. It is possible the colder environment skewed the Madison drainage sample towards smaller animals as beavers in the Hebgen Lake basin are ice-bound for longer portions of the year and thus have a shorter season of plant growth to meet nutritional requirements.

I compared my overall growth curve to those of Payne (1979) and Van Deelen (1991) and found beavers grew at a faster rate in my study area (Figure B5). Payne (1979) examined beavers in Newfoundland but did not report on the food source or winter conditions associated with beaver habitat in his study area, making comparisons difficult. Van Deelen (1991) collected beavers in western Montana and incorporated data from Jackson (1990) in the same study area. Beavers in his study area live under similar climatic and habitat conditions to my study, with mountain streams flowing through willow-dominated riparian areas. Unlike Van Deelen (1991) a large portion of my sample came from spring creeks which may explain why my data resulted in faster estimated growth rates.

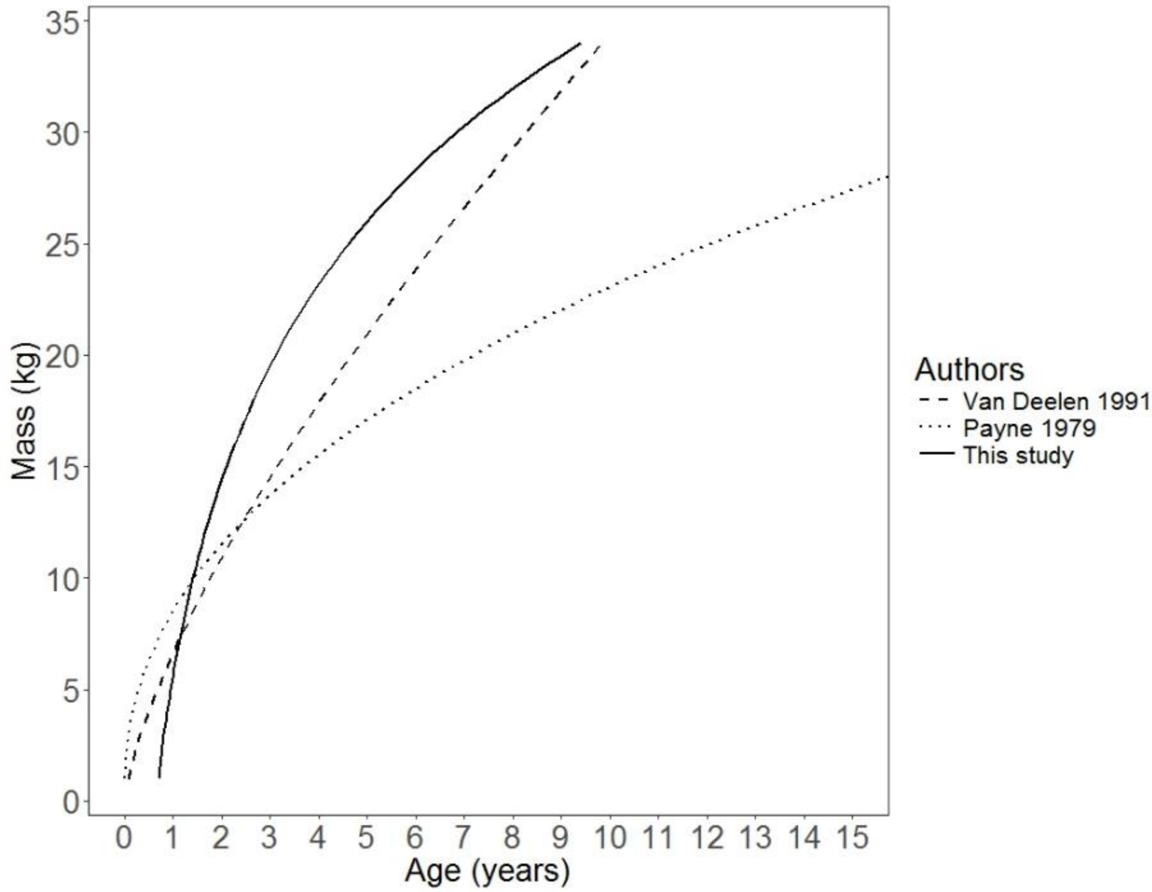

Figure B5. Estimates of the age-mass relationship for beavers from three studies in North America.

This study provides regionally calibrated growth curves allowing for estimation of the age of beavers by mass. Researchers, trappers, wildlife managers, and stream restoration practitioners can use the results of this project to more reliably age live-captured beavers. While my growth estimates were calculated from a relatively large sample size, there is still wide variation in beaver mass across ages which is likely due to differences in habitat conditions among individual colonies in a given drainage that allows members of some colonies to grow faster than others. I recommend future researchers acquire colony-specific locations for beavers if trappers are willing to provide such information. Colony membership information would allow for statistical analyses that account for cross-colony variation. The accuracy of age estimation may be increased if researchers gather other morphological measurements on captured beavers such as zygomatic breadth and tail dimensions (Patric and Webb 1960, Larson and Van Norstrand 1968, Layne 2003).

Acknowledgements

I would like to thank the Montana Chapter of The Wildlife Society for awarding me a grant to fund a major portion of this project. The Montana Agriculture Experiment Station at Montana State University provided additional funding. I also thank the Region 3 staff with the Montana Department of Fish, Wildlife, and Parks for use of their facilities and help with contacting trappers. I especially thank Jennifer Ramsey and Keri Carson with the MFWP Wildlife Lab for putting up with a great many frozen beavers. There were many trappers throughout the state that contributed to this project, both by submitting beaver skulls and by providing advice and additional contacts. A big thank you to Brian Stoner, Phil Hettinger, Rob Walker, Jim Van Norman, Vanna Boccadori, Tim McKenrick, Dean Waltee, Tom Barnes, Chad Dickinson, Craig Fager, Andy Weiser, Denny Schutz, Leroy Heinle, Toby Walrath, Bob Manners, Dave Visritch, Tater McKay, and Dave Murto.

APPENDIX C

INDIVIDUAL MOVEMENTS OF DISPERSING RADIO-MARKED BEAVERS IN THE UPPER GALLATIN AND MADISON RIVER DRAINAGES

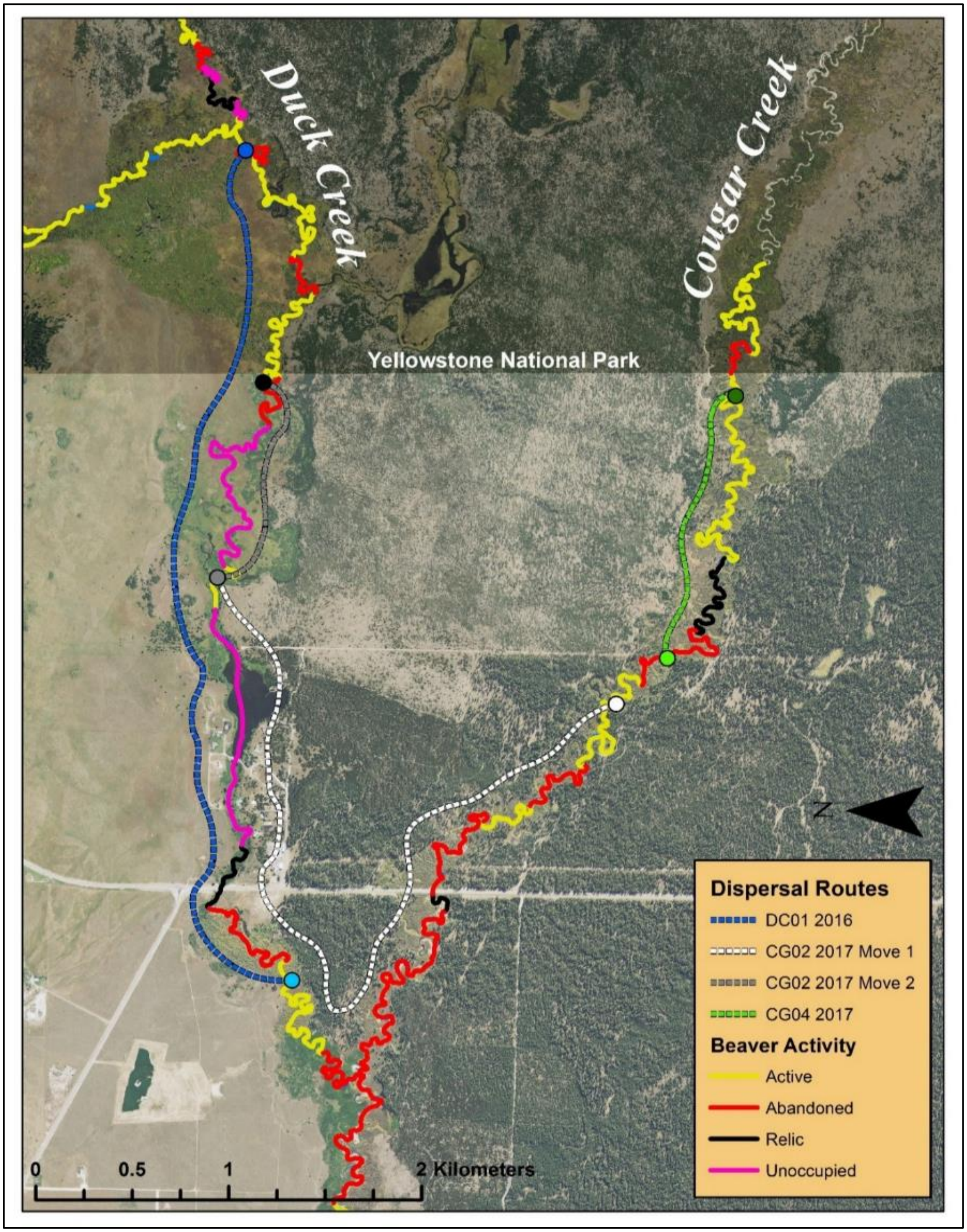

Figure C1. Dispersal movements of radio-marked beavers in Duck Creek and Cougar Creek in southwest Montana, USA, 2016–2017. "Beaver Activity" refers to the state of a stream segment in terms of beaver occupancy at the time the beavers dispersed. Lighter-colored dots represent the natal colony and darker-colored dots represent transient locations and settlement sites (terminal dots).

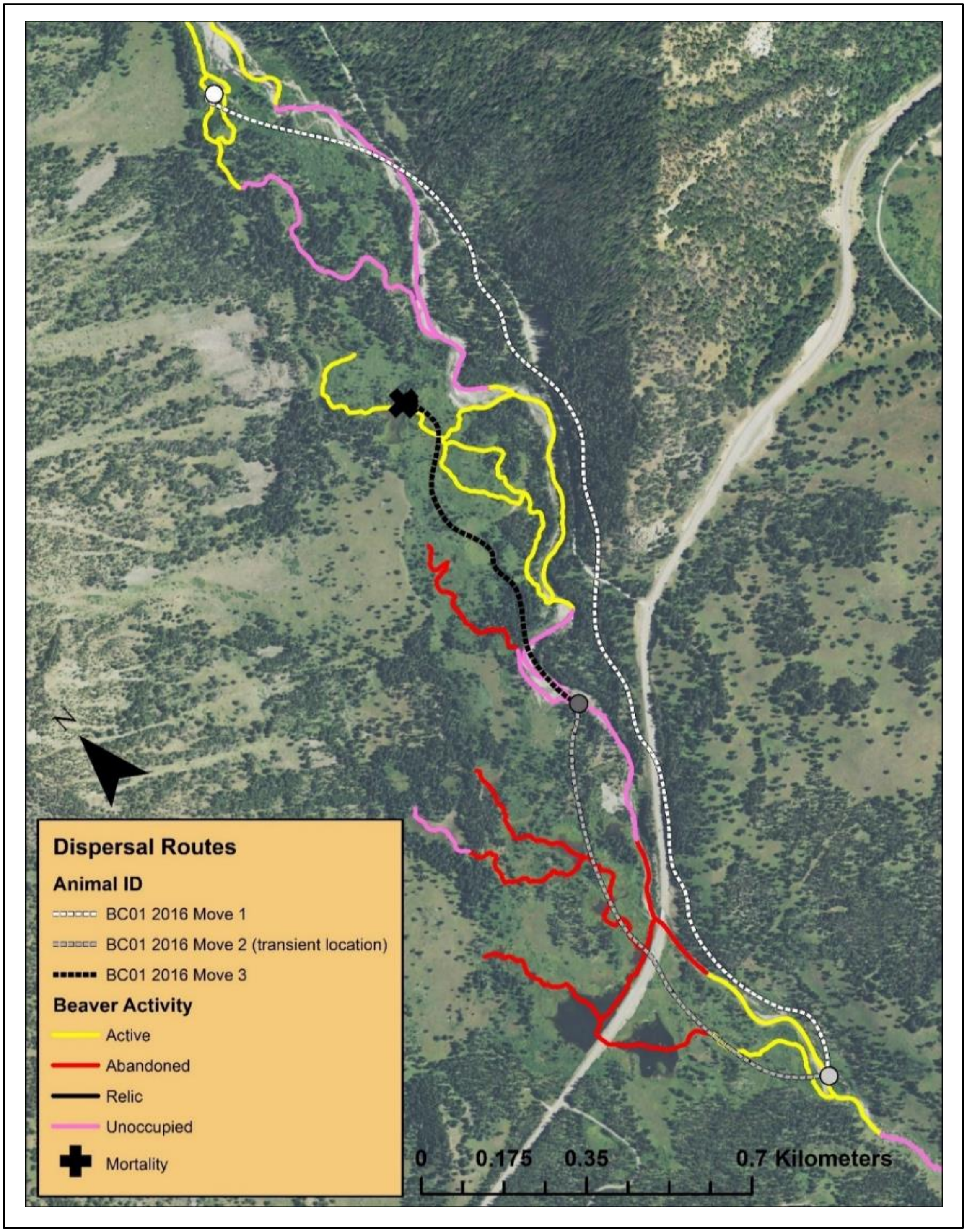

Figure C2. Dispersal movements of a radio-marked beaver in Beaver Creek in southwest Montana, USA, 2016–2017. “Beaver Activity” refers to the state of a stream segment in terms of beaver occupancy at the time the beaver dispersed. Lighter-colored dots represent the natal colony and darker-colored dots represent transient locations and settlement sites (terminal dots).

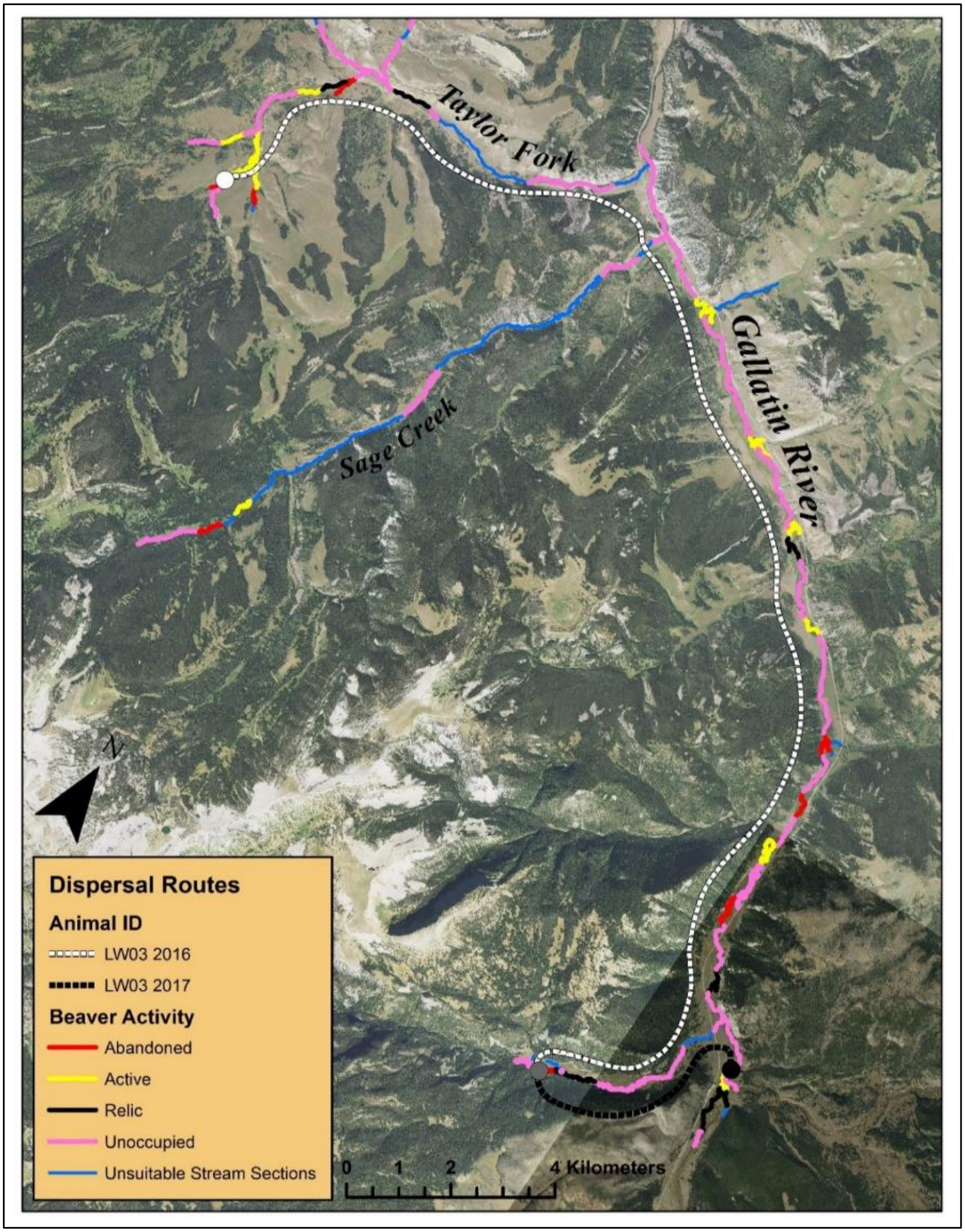

Figure C3. Dispersal movements of a radio-marked beaver in the upper Gallatin River drainage in southwest Montana, USA, 2016–2017. "Beaver Activity" refers to the state of a stream segment in terms of beaver occupancy at the time the beaver dispersed. Lighter-colored dots represent the natal colony and darker-colored dots represent transient locations and settlement sites (terminal dots).

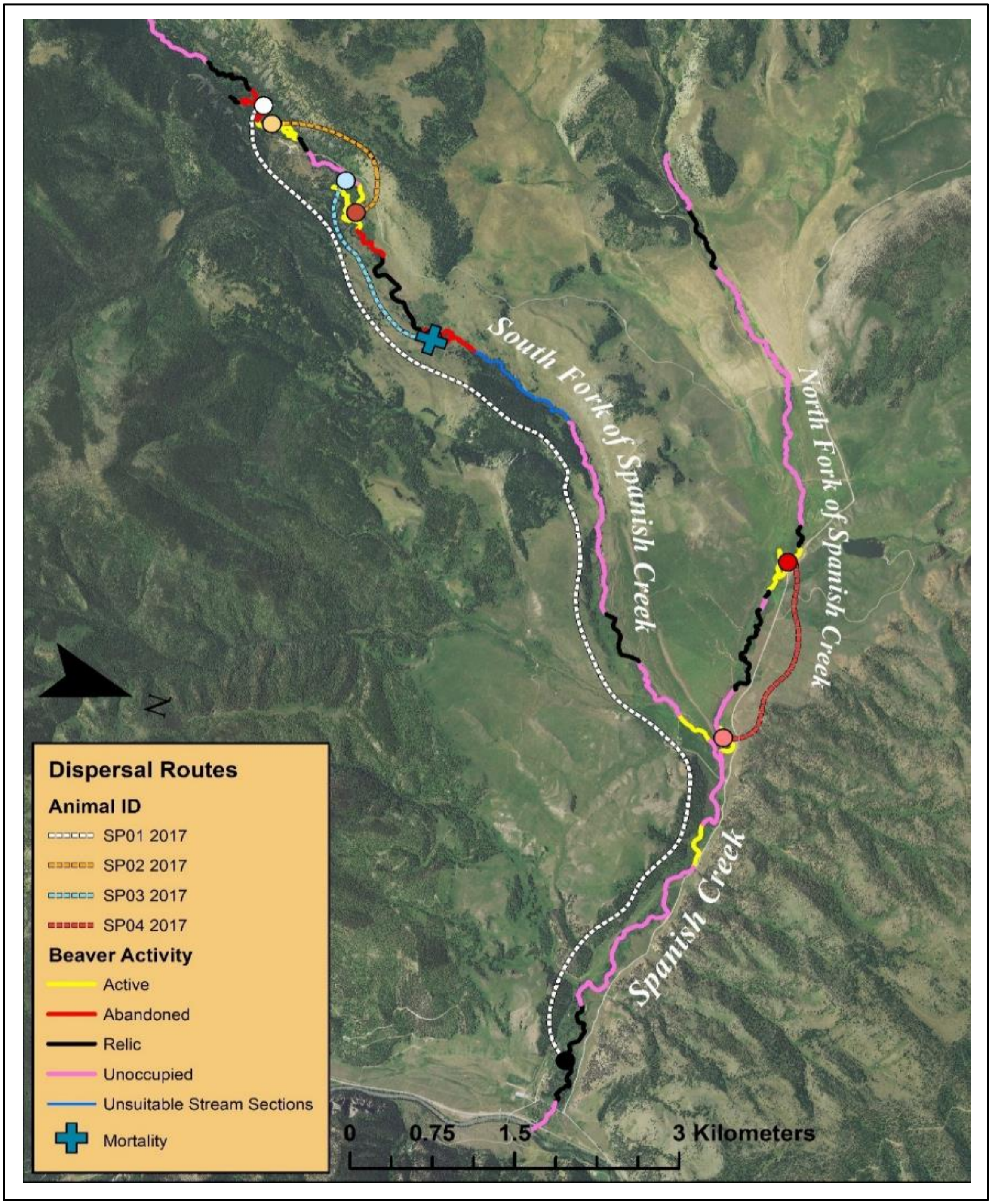

Figure C4. Dispersal movements of radio-marked beavers in the Spanish Creek drainage in southwest Montana, USA, 2016–2017. "Beaver Activity" refers to the state of a stream segment in terms of beaver occupancy at the time the beavers dispersed. Lighter-colored dots represent the natal colony and darker-colored dots represent transient locations and settlement sites (terminal dots).

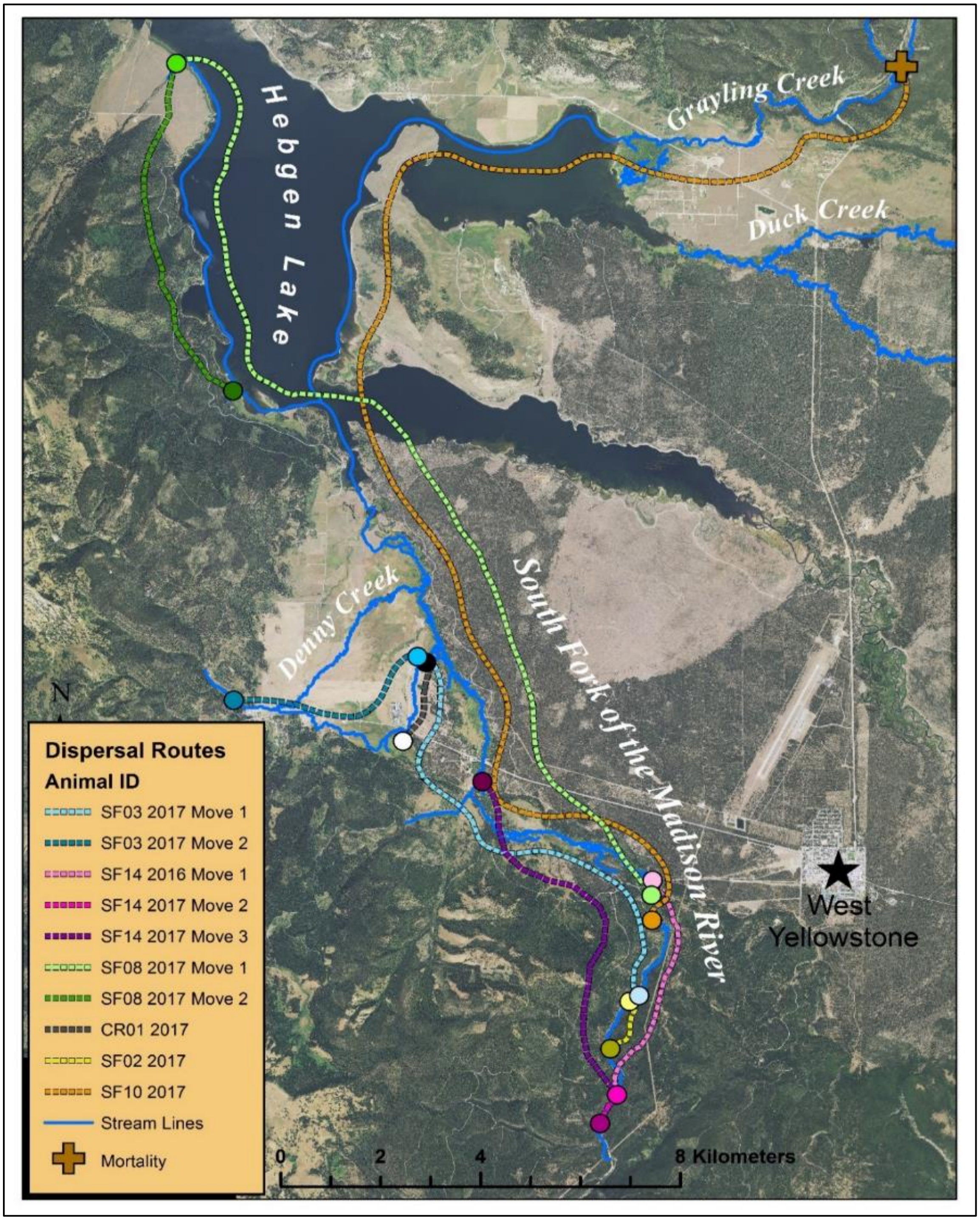

Figure C5. Dispersal movements of a radio-marked beavers in the South Fork of the Madison River drainage in southwest Montana, USA, 2016–2017. Lighter-colored dots represent the natal colony and darker-colored dots represent transient locations and settlement sites (terminal dots).

Table C1. Dispersal movements of radio-marked juvenile beavers in the upper Gallatin and Madison River drainages in southwest Montana, USA, 2016−2017. Dispersal date is the median date between the last day the beaver was detected at its natal colony and the first day it was detected outside the natal colony. “Total stream distance” is the sum of stream distances for all detected movements up to 31 Dec 2017 and includes distances traveled during exploratory movements by dispersing beavers. “Settlement type” refers to the beaver activity classification of the stream segment at the time it was occupied by the radio-marked beaver.

Dispersal date	Beaver ID	Drainage	Natal stream	Settlement stream	Dispersal-settlement interval (days)	Settlement type	Stream distance (km)	Straight-line distance (km)	Total stream distance
2 May 2016	BC01	Madison	Beaver Creek	Beaver Creek	150	Abandoned	2.0	1.5	3.3
13 Apr 2016	DC01	Madison	Duck Creek	Duck Creek	8	Relic	8.0	4.4	8.0
9 May 2016	LW03	Gallatin	Little Wapiti Creek	Bacon Rind Creek	---	Abandoned	41.3	18.3	49.0
3 May 2017	LW03	Gallatin	Bacon Rind Creek	Gallatin River	23	Active	7.0	3.0	7.0
7 May 2017	SF02	Madison	South Fork Madison River	South Fork Madison River	5	Active	1.4	1.1	5.3
29 Apr 2017	SF03	Madison	South Fork Madison River	Denny Creek	144	Abandoned	22.4	10.2	133.1

Table C1. Individual beaver movements (continued)

19 April 2017	SF08	Madison	South Fork Madison River	Cherry Creek	52	Abandoned	22.0	13.3	37.5
1 May 2017	SF10	Madison	South Fork Madison River	Grayling Creek	19	Active	42.3	18.4	42.3
7 Mar 2017	CG02	Madison	Cougar Creek	Duck Creek	117	Active	12.0	2.5	12.0
15 Apr 2017	CG04	Madison	Cougar Creek	Cougar Creek	15	Active	3.4	1.4	3.4
18 May 2017	CR01	Madison	Buttermilk Creek	Deep Well Ranch Spring	36	Relic	3.1	1.6	27.0
25 Nov 2016	SF14	Madison	South Fork Madison River	South Fork Madison River	9	Abandoned	6.3	4.4	6.3
29 May 2017	SP01	Gallatin	South Fork Spanish Creek	Spanish Creek	6	Relic	14.0	9.7	42.8
Unknown	SP02	Gallatin	South Fork Spanish Creek	South Fork Spanish Creek	---	Active	2.5	1.7	2.5

Table C1. Individual beaver movements (continued)

25 Mar 2017	SP04	Gallatin	North Fork Spanish Creek	North Fork Spanish Creek	1	Active	2.4	1.8	2.4
6 Sep 2017	SC01	Gallatin	Storm Castle Creek	Storm Castle Creek	26	Unoccupied	2.5	2.1	3.8
25 Mar 2017	SP04	Gallatin	North Fork Spanish Creek	North Fork Spanish Creek	1	Active	2.4	1.8	2.4
12 May 2017	SF14	Madison	South Fork Madison River	South Fork Madison River	138	Abandoned	0.7	0.7	147.3