

Wolf-Beaver Dynamics in a Southern Boreal Ecosystem

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Acknowledgments

My path to complete my Ph.D. studying wolves in Voyageurs has been unpredictable, circuitous, satisfying, and full of fond memories. Through this journey, I had many people who took chances on me and provided me with opportunities and experiences I was not deserving of, and many others whose friendship and encouragement continually refreshed my spirit.

The greatest pleasure of my graduate work has been the ability to do it with my closest friend, Austin Homkes. In 2015, I somehow convinced Austin to be a field assistant for me during my Master's work in Voyageurs National Park and we spent the 2015 field season (April to November) together doing all sorts of wolf-related research. We were both clueless—but in different ways—about what we were actually doing in Voyageurs during that time but despite that we both fell in love with the area, the research, and the wildlife. It is hard to believe that here we are now in our 6th field season together in Voyageurs. We have had the pleasure of doing things together that most friends could never dream of (e.g., collaring >60 wolves together, tagging dozens of wolf pups). Austin has shared every accomplishment and set back on the project with me. Austin has always been there to lift my spirit and cheer my soul in the low days as well as to celebrate the seemingly trivial day-to-day accomplishments on the good days of our project. Indeed, I cannot imagine what it would be like to do research in Voyageurs without him. Chris McCandless, at the end of his life, had an epiphany when he realized after venturing into the wilderness alone that “happiness is only real when shared”. I would have to agree and I am so happy, Austin, that I have been able to share so many prized moments with you while working on the project.

I am also deeply thankful that I crossed paths with (or more appropriately, was forced to live with) Sean Johnson-Bice. Sean, Austin, and I were placed in a Voyageurs National Park cabin together in 2015 and have been friends ever since. Indeed, Sean and I have only grown closer over the last 6 years while working on various research together, including the Voyageurs Wolf Project where he spent 3 seasons helping out. I have found substantial joy working with Sean, whose candour, enthusiasm, intellect, and humour allow us to disagree frequently—with Sean often challenging my ideas and me his—and yet be close friends. To me, Sean has been what C.S. Lewis described as the 2nd type of friend: “The Second Friend is the man who disagrees with you about everything...Of course, he shares your interests; otherwise he would not become your friend at all...He has read all the right books but has got the wrong thing out of every one. It is as if he spoke your language but mispronounced it. How can he be so nearly right and yet, invariably, just not right?...When you set out to correct his heresies, you find that he forsooth has decided to correct yours! And then you go at it, hammer and tongs, far into the night, night after night...each learning the weight of the other’s punches, and often more like mutually respectful enemies than friends. Actually (though it never seems so at the time) you modify one another’s thought; out of this perpetual dog-fight a community of mind and a deep affection emerge”. Suffice it to say, I am thankful for Sean’s deep friendship through everything.

Perhaps no one took a bigger gamble on me than John Stephenson at Grand Teton National Park. For some unknown reason, John selected me—an undergraduate between his junior and senior year at Hope College who had no prior research experience and relatively little documented backcountry experience, especially in mountainous terrain—

as one of two wolf research technicians in Grand Teton in Summer 2012. I look back and remain simply astounded I was even considered, let alone selected, for that position. Regardless of the reason, I am indebted to John because he opened doors for me by giving me experience that would have been hard to get otherwise at that stage in my career.

Dr. Shannon Barber-Meyer was the next person who took a chance on me. In late summer 2013, Shannon selected me as a technician to trap and collar wolves in the Boundary Waters. As someone who had no prior animal handling experience and limited trapping experience, I was hardly qualified. Yet, again, Shannon gave me an opportunity that ended up being formative, both personally and professionally, as I would spend the next 7 years trapping, collaring, and studying wolves in the Northwoods. Shannon has been a wonderful source of knowledge and enthusiasm throughout my Master's and Ph.D and I am really appreciative of the kindness and personal encouragement she has given me during this time.

As I look back, I do not think I really knew why I wanted to go to graduate school in the first place, other than I knew it was needed to progress in the wildlife field. After applying in vain to many Master's position (and feeling utterly dejected), I was finally—dare I say miraculously—offered a Master's position at Northern Michigan University by Dr. John Bruggink and Dr. Steve Windels. My Master's work was supposed to focus on beaver ecology in Voyageurs National Park but through some discussions I was able to convince John and Steve to let me study wolf-beaver interactions. My Master's was a period of tremendous growth intellectually and I learned so much about the academic world (publication process, grants, etc) from John and Steve. I appreciate John's gentle

and kind demeanour toward me, and I am thankful we continue to work together on wolves in Voyageurs to this day.

No one has influenced the trajectory of my academic and research pursuits more than Steve Windels. Steve and I have worked together for 7 years now (hard to believe!) and he co-advised me for my Master's and then also for my Ph.D. Steve gave me the most incredible and valuable gift I could have received during my graduate career: he gave me complete freedom to explore my interests, to figure things out, and to fail miserably (as Steve told me when I started my Master's, "the world is your oyster"). In April 2015, I arrived in Voyageurs National Park for my first and only field season of my Master's. I had no idea what I was actually supposed to do during my field season but I was excited. After conversations with Steve that April, it became apparent he was willing to let me do any fieldwork on wolves and beavers that interested me (so long as it did not require additional money or resources!). I was, in effect, cut loose. I started brainstorming all the things that interested me—wolf kill sites, visiting wolf dens, counting pups, collecting inordinate amounts of wolf scats, how wolves hunt beavers, etc—and set out to do them. Austin Homkes and I spent seemingly all day everyday that field season outdoors following wolves around. In that period, I felt just as Paul Errington did when he stated "I was a predator, myself, and lived close to the land". It was a time of indescribable joy and I am deeply thankful for that experience. Certainly, I had done little to convince Steve that my judgements were sound or my abilities sufficient, and was wholly undeserving of such innate trust. Yet, I am deeply thankful that Steve provided me the room to test myself and my abilities, to study the natural world unencumbered by

distractions or his expectations, to truly and completely immerse myself in a topic I found fascinating.

All this to say, I do not believe I would be where I am today without Steve giving me the freedom to explore what I wanted (not to mention, Steve put forth substantial resources so I could explore my interests). Steve's general support for my ideas and research pursuits during my Master's instilled a lot of confidence in me when I was just getting my feet wet in academia. At that time in my career, I really needed that kind of affirmation as I was really unsure of myself and my abilities. The confidence he helped to instill propelled me to and throughout my Ph.D. In addition, Steve has shared—in particular when I was just getting started and needed it most—many insights into the academic world and the steps needed to succeed in the field. No piece of advice has stuck with me more, and been more helpful to me, than when Steve told me at the beginning of my Master's: "Publications are currency and you want to collect currency because it makes everything easier". These words have undoubtedly proven true for me. Suffice it to say, Steve has helped and mentored me in tremendous ways over the past 7 years and who knows where I would be without him.

After I had finished my Master's, Steve introduced me to Dr. Joseph Bump who offered to advise me for my Ph.D at the University of Minnesota. I really did not want to live in the Twin Cities and was hesitant as I did not know Joe at all but after weighing my options, I decided it was the best place for me. Thank goodness I went there, if, for no other reason, than for the pleasure of working with Joe. I can say with certainty that Joe is about the best advisor anyone could ask for. Joe is intentional with his students, he cares about them and what is going on in their lives, and has their—as opposed to his own—

best interest in mind. Joe has been a wonderful mentor to me for so many reasons (of which I do not have space to enumerate all of them). In particular, Joe has always been an advocate for me (and his other graduate students) and I have never had a doubt that Joe was on my side. Further, Joe has provided me wonderful advice and sage counsel for handling a variety of issues ranging from funding, research, writing publications, the peer-review process, interacting with other professionals, and managing a fieldcrew. I have learned a lot and grown substantially as a professional through working with Joe. I am sincerely thankful for Joe's encouragement, guidance, and our intellectual discussions and occasional disagreements. His enthusiasm for my work, and the things I find interesting, has raised my confidence and morale more times than I can count. I undoubtedly made a great choice coming to the University of Minnesota. I am more than excited to continue working together on the Voyageurs Wolf Project for as long as we can.

I would like to thank Dr. Dave Mech whose continued interest in my research is humbling. Dave has read and provided feedback on the majority of manuscripts I have written to date and I really appreciate his keen eye and feedback. Dr. John Fieberg, who kindly agreed to be on my Ph.D. committee, was an excellent resource when I was on-campus and John is a top-notch instructor and teacher. I learned a wealth of information from him, and taking 2 classes from John was in itself worth coming to the Twin Cities for as well! Further, I would like to thank Drs. Greg and Kathy Murray from Hope College who were wonderful mentors to me in my undergraduate studies and who really fostered in me an interest in Ecology. There are numerous other people who have been

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I would like to thank all the family and friends who have been supportive throughout my graduate career. In particular, my parents, Dan and Kay Gable, who are simply amazing. My dissertation is dedicated to the both of you for your unending support and love. Without your help, I would not be where I am today. To both my sisters, Jess and Anna, who I unfortunately do not get to see as much as I want anymore. A big thanks to my grandparents on both sides and all my extended family.

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Lastly, and most importantly, I thank God who has made all of my successes, abilities, and accomplishments possible by opening doors and placing wonderful people and opportunities in my life. In my arrogance, I often convince myself that I have willed myself to success, that I—and I alone—somehow have earned it. As I look back, though, it is clear there were many gifts that facilitated my success which were not earned or deserved—including my upbringing, natural abilities, opportunities offered to me, etc. When I ponder this, I am truly humbled...“what is man that you are mindful of him?”. I am disappointed and saddened that I often fail to reflect and extend to others the kindness, love, and grace that has been extended to me.

Dedication

To my parents, Dan and Kay Gable, who have, through their continual encouragement, never-ending patience, and deep love, impacted my life in profound ways. Despite my many shortcomings, you have always cared for and loved me in ways I do not deserve.

Abstract

Predator-prey relationships can have wide-ranging ecological and landscape-level effects. Knowledge of these relationships is therefore crucial for understanding how changes in predator-prey communities affect ecosystems. Throughout much of the circumpolar boreal ecosystem, wolves are significant predators of beavers and beavers important prey for wolves, yet wolf-beaver dynamics remain poorly understood. My objective was to shed light on this predator-prey dynamic by studying wolf-beaver interactions in the Greater Voyageurs Ecosystem (GVE), a southern boreal ecosystem in Northern Minnesota. Specifically, I wanted to understand where and how wolves hunt beavers, what impact wolf predation has on beaver populations, and how wolf predation on beavers might impact ecosystem function.

By searching 11,817 GPS-clusters from 24 GPS-collared wolves during 2015-2019, I documented 748 instances where wolves attempted to ambush beavers and 214 instances where wolves killed beavers. Through this, I determined wolves are able to ambush beavers by anticipating the movements and behavior of beavers due to a fundamental understanding of beavers' sensory abilities. Further, wolves can strategically select ambushing locations by simultaneously accounting for abiotic and biotic factors, ultimately allowing wolves to counter beaver's defenses and exploit this unique prey.

The extent to which wolves influence beaver population change has been debated for decades despite a complete lack of quantitative data on the subject. I estimated, by determining kill and predation rates, that wolf packs can remove 38-42% of the beaver population in their territory in a year. Yet, in high-density beaver populations such as the

GVE, predation pressure appears to have little influence on beaver population dynamics because beaver populations can quickly compensate for predation.

Though wolves may not alter beaver population size, I demonstrate how wolves alter wetland creation and recolonization by killing dispersing beavers. By studying beaver pond creation and recolonization patterns, I determined that 84% of newly created and recolonized beaver ponds in the GVE remained occupied until the fall, whereas 0% remained active after a wolf killed the dispersing beaver that colonized that pond. By affecting where and when beavers engineer ecosystems, wolves alter all of the ecological processes that occur due to beaver-created impoundments.

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Chapter 1: The Forgotten Prey of an Iconic Predator: a Review of Interactions Between Grey Wolves and Beavers

ABSTRACT Predator-prey relationships can have wide-ranging ecological and landscape-level effects. Knowledge of these relationships is therefore crucial to understanding how the systems work and how changes in predator-prey communities affect these systems. Grey wolves *Canis lupus* can be significant predators of beavers *Castor* spp., and conversely, beavers can be important prey for wolves, but wolf-beaver dynamics in North America, Europe, and Asia are poorly understood. Our objectives were to synthesise current knowledge regarding wolf-beaver interactions and to identify knowledge gaps that should be targeted for study to increase our understanding of wolf-beaver dynamics. During the ice-free season, beavers are vulnerable to predation and can be the primary or secondary prey of wolves, but the factors that affect beaver consumption by wolves are complex and are likely dependent on biological and environmental factors. High beaver abundance can increase wolf pup survival, and beavers may subsidise wolves during periods of reduced ungulate abundance. Thus, many researchers have suggested that beaver densities adversely affect ungulate populations through apparent competition, though this remains largely untested. The effects of wolf predation on beaver population dynamics are poorly understood, as most assessments are lacking in quantitative rigor and are instead based on indirect methods (e.g., scat analysis), anecdotal evidence, or speculation. To understand the effect of predation on beaver populations fully, better estimates (e.g., from documented predation events) of wolf predation on beavers are necessary. Given the complexities of wolf-ungulate-beaver systems, fully understanding wolf-beaver dynamics will be challenging

and likely require long-term, intensive research of wolf, ungulate, and beaver population parameters. Understanding this dynamic has implications, not only for the conservation and management of wolves and beavers, but also for ungulate populations, which are affected by the numerical and functional responses of wolves in these same systems.

INTRODUCTION

Predator-prey relationships can have important ecological and landscape-level impacts. Knowledge of these relationships is therefore crucial to understanding how ecosystems function, and how changes in predator-prey communities can affect these systems (Pace et al. 1999). Grey wolves *Canis lupus* are apex predators that primarily kill and consume ungulates. Through predation or the fear thereof, wolves can impact the behaviour, movements, and abundance of ungulate prey (Mech et al. 2015). Wolves also hunt and kill non-ungulate prey that are seasonally abundant or easy to capture, such as salmon *Oncorhynchus* spp. (Watts and Newsome 2017), flightless moulting birds (Mech et al. 2015), and hares *Lepus* spp. (Peterson and Ciucci 2003). Abundant alternative prey can facilitate a numerical response in wolf populations (Mech 2007a), and may subsidise wolf populations during periods of low ungulate abundance (Andersone and Ozoliņš 2004). However, the relationships between wolves and alternate prey populations are poorly understood (Watts and Newsome 2017).

The American beaver *Castor canadensis* and the Eurasian beaver *Castor fiber* are semi-aquatic rodents that generally inhabit streams, rivers, ponds, and lakes with sufficiently deep water for them to swim, escape predators, and access forage (Novak 1987). Beavers are central-place foragers that forage away from a central body of water to access woody and herbaceous vegetation (Baker and Hill 2003). This central body of

water provides aquatic forage and refuge from predators, as beavers are generally vulnerable to predation when foraging terrestrially (Basey and Jenkins 1995).

Beavers have several natural predators (Appendix S1), but, with the exception of wolves, the impact of these predators on beaver populations is thought to be minor (but see Smith et al. 1994, Baker and Hill 2003). Predators presumably hunt and kill beavers using a variety of methods. For example, red foxes *Vulpes vulpes* ambush young beavers on shorelines (Kile et al. 1996), and brown bears *Ursus arctos* and black bears *Ursus americanus* dig into beavers' lodges to catch them (Smith et al. 1994, Rosell et al. 2005). Foraging behaviour can vary between individuals within predator populations, and some individuals might specialise on beavers. In Colorado, a cougar *Puma concolor* specialised on beavers, consuming ten times more individuals and spending six times more time in beaver habitats than would be expected based on availability (Lowrey et al. 2016). However, the role of predation on beaver behaviour and population dynamics is poorly understood and has received little attention.

Wolves and beavers are sympatric primarily in northern North America, northern Europe, and Siberian Asia, but the area in which they co-occur continues to increase, as wolf and beaver populations expand and recolonise their former ranges in North America and Europe (Fig. 1, Baker and Hill 2003). Prior to and during the 20th century, wolf distribution and abundance throughout much of North America and Europe was reduced due to persecution and systematic eradication (Boitani 2003). Wolves are currently distributed throughout most of Canada and Alaska, and have re-established populations in nine states in the USA (Mech 2017). In Europe, wolf populations have re-established themselves in some areas, but occur primarily in northern and eastern Europe;

fragmented populations occur in several countries in central and western Europe (Mech and Boitani 2010, Nowak et al. 2011). Wolves are still found throughout most of Asia, where their distribution has changed little through time (Boitani 2003, Mech and Boitani 2010). Beavers, which were historically widely distributed throughout North America, Europe, and Asia, have recovered from overexploitation prior to the 20th century and are occupying much of their former ranges (Halley et al. 2012, Cassola 2016). American beavers were also introduced to a few European countries (e.g. Finland and Russia; Parker et al. 2012). Eurasian beavers and wolves are sympatric in small areas in non-Siberian Asia (i.e., Mongolia and China; Halley et al. 2012) but we could not find information on wolf-beaver dynamics in these areas (Fig. 1).

In areas of sympatry, wolves can be significant predators of beavers, and conversely, beavers can be important prey for wolves (Newsome et al. 2016). Despite this, most wolf predation studies have focused on wolf-ungulate interactions, and ignored wolf-beaver dynamics (Gable et al. 2016), though many of these studies contain useful information about wolf predation on beavers. Given the ecological importance of wolves and beavers, understanding wolf-beaver dynamics is necessary to understand the systems where they co-occur. Furthermore, understanding the factors that impact wolf and beaver population change is important for conservation and management, especially when trying to mitigate human conflicts with these often controversial taxa. In light of this, our objective was to synthesise what is known about wolf-beaver dynamics, and to identify knowledge gaps for future study.

METHODS

We reviewed the literature using the search engines Google Scholar and Web of Science with the keywords “wolf beaver”, “*Castor canadensis Canis lupus*”, “*Castor fiber Canis lupus*”, “wolf predation beavers”, and “beaver predators”. We also used sources (journal articles, book chapters, books, MSc and PhD theses, and scientific and technical reports) known by the authors to include relevant information.

Beavers as Prey

Wolves and beavers generally co-occur in climates with strong seasonality, and beavers are vulnerable to predation when ice cover is absent (Fig. 1, 2). During the ice-free season, beavers forage terrestrially, maintain lodges and dams, scent-mark and defend territories, and in cold climates, often build food caches to help them survive the winter (Baker and Hill 2003). Consequently, predation of beavers by wolves is highest during the ice-free period (Table 1). When ice cover is present, beavers are relatively inaccessible to wolves as the ice is a protective barrier and beavers are seldom found above it (Smith and Peterson 1991). Nonetheless, wolves consume beavers that they catch above the ice during periods of open water or winter thaws (Mech 1966, Forbes and Theberge 1996). In milder climates, wolf predation can be relatively consistent year-round as beavers can forage terrestrially most of the year (Milne et al. 1989, Sidorovich et al. 2017).

When on land, beavers are thought to be easy prey for wolves as they lack the physical characteristics, agility, and speed necessary to defend themselves and escape from large predators (Mech 1970, Basey and Jenkins 1995, Mech et al. 2015). Due to this, beavers generally limit their terrestrial activities to close proximity of water (<40-100 m; Basey and Jenkins 1995, Graf et al. 2016). Beavers on land also must balance the

time and energetic returns of foraging at various distances from the water with the inherent predation risk when doing so (Novak 1987, Smith et al. 1994). However, some evidence suggests that predation risk largely influences whether beavers go on land or not, rather than the distance beavers travel once they are on land (Salandre et al. 2017). As habitat quality or food supply declines, beavers must either forage further from water, or find new suitable habitat, both of which can increase predation risk (Basey and Jenkins 1995). Although aquatic vegetation can constitute a substantial proportion of seasonal and annual beaver diets, it is unknown how abundant aquatic vegetation influences the time beavers spend foraging terrestrially, which may have implications for predation risk of beavers (Severud et al. 2013).

Beavers build structures and alter landscapes, in part to reduce predation risk. Beavers construct lodges or bank dens that provide protection from predators near water, and often build dams to flood large areas and create stable bodies of water (Rosell et al. 2005). However, lodge and dam construction and maintenance are labour-intensive and can increase predation risk for beavers conducting these activities (Gable et al. 2016). In larger lakes and rivers, beavers generally do not maintain dams and thus are dependent on sufficient water levels for their safety (Johnston and Windels 2015). Beavers also excavate channels to increase water access to food and decrease predation risk (Baker and Hill 2003).

Beavers are able to detect predator odours, and alter their foraging strategies and scent-marking behaviours to minimise encounters with predators (Smith et al. 1994, Rosell and Czech 2000, Severud et al. 2011). Moreover, beavers appear to exhibit an innate response to predators, probably due to the evolutionary relationship between

beavers and their predators (Rosell and Sanda 2006, Swinnen et al. 2015). Ultimately, avoiding fatal encounters with wolves is predicated on three factors: the ability of the beaver to detect the wolf, the distance between the beaver and the wolf, and the distance between the beaver and water (Basey and Jenkins 1995). However, not all encounters with wolves are fatal; several beavers in northern Minnesota, USA, have healed canine puncture tail wounds, presumably from wolves, the main predators of beavers in that system (S. Windels, unpublished data).

Beavers can be attractive prey for wolves during the ice-free season when wolves are frequently traveling alone or in small groups (Barber-Meyer and Mech 2015). Beavers are substantive (≤ 35 kg) prey that pose little risk to wolves compared to adult ungulates, which can require substantial risk and energy expenditure to kill (Mech 1970). Adult ungulates are less vulnerable to wolves during the ice-free season, and ungulate neonates, often protected by defensive mothers (Mech et al. 2015), are only highly vulnerable during the first few months of their lives (Metz et al. 2012). Beavers of all age classes, on the other hand, remain relatively available and vulnerable throughout the ice-free season. In fact, the number of beavers vulnerable to predation likely increases throughout the ice-free season as kits begin foraging on land during June–August. Further, consuming beavers can be beneficial to wolves by reducing individual parasite loads. In eastern Manitoba, cestode abundance in wolves was negatively related to the amount of beaver in wolf diets (Friesen and Roth 2016). The cost-benefit of killing beavers instead of ungulates is complex and is likely to depend on the interaction of several factors, including pack size, energetic requirements, prey densities and availability, and time of year (Table 1).

Where and How Wolves Hunt Beavers

Many researchers have speculated about how wolves hunt beavers (e.g., Mech 1966, Peterson and Ciucci 2003), but until recently (i.e., Gable et al. 2016), where and how wolves kill and hunt beavers was unknown, as observing wolves hunting beavers has proven difficult (Mech et al. 2015). Gable et al. (2016) searched clusters of Global Positioning System (GPS) locations from GPS-collared wolves to identify beaver kill sites and infer wolf hunting behaviour. Based on wolf behaviour in active beaver habitats (i.e., habitats occupied by beavers), Gable et al. (2016) concluded that a typical hunting strategy “consists of 3 components: 1) waiting near areas of high beaver use (e.g., feeding trails) until the beaver comes near shore or ashore, 2) using vegetation, the dam, or other habitat features for concealment, and 3) attacking the beaver by cutting off access to water, or immediately attacking the beaver (e.g., ambush).” Much of this conclusion was based on the fact that 63% of clusters visited in active beaver habitats were bed sites, not kill sites, suggesting that wolves were waiting for beavers, not solely encountering them opportunistically. These observations are consistent with those of Thurber and Peterson (1993), who observed a lone wolf that appeared to be hunting beavers during mid-winter thaws by bedding down next to beaver feeding trails. Similarly, Nash (1951) observed wolves stalking beavers near feeding trails. However, wolves certainly kill beavers opportunistically, but without direct observation it is challenging to determine how frequently that occurs (Gable et al. 2016).

Wolves appear to employ a variety of tactics to hunt beavers. Gable et al. (2016) documented six instances where wolves attacked beavers in the water and then killed them nearby on shore. This is particularly interesting, as it had been assumed that beavers

were safe from predators once they reached water (Basey and Jenkins 1995). Wolves dig into active beaver lodges, primarily in the winter (Peterson 1977, Forbes and Theberge 1996), but have not been confirmed to kill a beaver in this way (Mech et al. 2015). Although, wolves can successfully dig into lodges to scavenge on beavers that presumably died in the lodge (T. Gable, personal observation).

Wolves have been documented killing beavers in a variety of locations at different times of year. There appeared to be seasonal variation in where wolves were hunting beavers, based on where beaver kills occurred during the ice-free season in Voyageurs National Park, Minnesota, USA (Gable et al. 2016). More specifically, in the spring, wolves were hunting and killing beavers below beaver dams and on shorelines (58% of kills), whereas in the autumn, most kill sites (80%) occurred around feeding canals and trails. During winter, beavers are periodically caught on the ice near open waterways or when foraging above ice during mid-winter thaws (Mech 1966, Peterson 1977, Forbes and Theberge 1996). In northern Minnesota, wolves target and kill beavers in early spring from lodges on natural lakes when water levels are low (Smith and Peterson 1991, Gable et al. 2016). Future research would help clarify where and how wolves hunt beavers during different seasons in systems throughout the geographical range of wolves.

Wolf Diets: The Seasonal Importance of Beavers

Estimating wolf diets directly by identifying predation events during the ice-free season has proven challenging when wolves subsist primarily on small prey like beavers (Palacios and Mech 2010). Thus, our understanding of the role of beavers in wolf diets is based almost entirely on scat-based diet estimates (Table 1). Scat analysis is an indirect method of diet determination that provides only limited information on predation of

beavers by wolves (Peterson and Ciucci 2003). For example, this method cannot separate predation from scavenging, or be used to identify the way in which the beaver was killed (see previous section).

Beavers can be an important seasonal prey source for wolves, but only one study, in Belarus, has documented beavers as the primary year-round prey of wolves (V Sidorovich et al. 2017*b*; Table 1). The authors attributed this to relatively mild winters that facilitated year-round predation on beavers. By contrast, most systems where wolves and beavers co-occur experience cold and severe winters. Therefore, beavers cannot be a primary year-round food source, as they are much less vulnerable to predation during periods of ice cover, and typically constitute <15% of wolf diet estimates during the winter period (Forbes and Theberge 1996, Gogan et al. 2004). Nonetheless, beavers can be the primary or important alternate summer prey of wolves in many systems in North America (Table 1; Newsome et al. 2016). However, beavers appear to be a relatively minor food source for wolves in Europe, with the exception of Belarus and Latvia (Table 1).

Wolf consumption of beavers appears to fluctuate during the ice-free period. In North America, based on wolf diets examined at 1-2 month scales, there appear to be two periods of high beaver consumption: spring (April-May) and autumn (September-October; Fig. 2). We are unaware of wolf diet estimates examined at similar scales in European countries where beavers are significant prey. After ice-out in April or May, beaver consumption is high, as wolves target beavers that are foraging on land or maintaining dams (Gable et al. 2016). Beaver consumption decreases during June and July, as wolves primarily hunt and consume ungulate neonates (Van Ballenberghe et al.

1975, Fuller 1989, Gable et al. 2017a). In September and October, beavers become more vulnerable to predation, as they spend more time on land maintaining dams and lodges, or foraging on woody vegetation to build their winter food cache (Gable et al. 2016). Hall (1971) speculated that beaver consumption should be highest during the autumn because that is when beavers spend the most time foraging terrestrially and when the greatest number of beavers should be available, as kits are foraging alongside other colony members.

Although peaks in the consumption of beavers by wolves are likely influenced in part by beaver availability, they could also be influenced by wolf pack size, cohesion, and energetic demands (Metz et al. 2012). Indeed, beavers might be appealing prey, especially in areas with dense beaver populations, for small packs (e.g., breeding pair and a pup) or for wolves foraging individually, because of the cost-benefit of hunting beavers (Sand et al. 2016). Wolves in multi-prey systems prey selectively on specific species (Mech 1970, Potvin et al. 1988), but further research is necessary to determine if this is true with beavers. In Manitoba, Canada, beaver constituted 83% (based on stable isotope analysis) of the summer diet of one wolf but only 3-42% of the other 78 wolves examined, suggesting that some wolves specialise on beaver (Moayeri 2013).

Prey composition of adult wolf and pup diets can differ, which some suggest is a result of wolves selectively feeding pups particular prey (Bryan et al. 2006, Gable et al. 2017a). The reason for this is unknown but several possibilities have been suggested, such as the transportability of prey back to homesites, spatial and temporal abundance of prey in relation to homesites, and the nutritional value and parasite load of particular prey (Bryan et al. 2006, Steenweg et al. 2015). Sidorovich et al. (2017) stated that wolves were

selectively provisioning pups with beavers, as beaver composed 52% of pup diets but only 27% of adult diets. However, their results were probably biased, as they compared annual adult wolf diets (combined winter and summer diets) to presumably summer pup diets (Sidorovich et al. [2017] did not specify when pup scats were collected but ~May-August is when pup scats are generally distinguishable from adult scats; Gable et al. 2017). In Voyageurs National Park, there was no difference in beaver consumption between wolf pups and adults during May–August (Gable et al. 2017). Pup diets, though, have not been well studied (Bryan et al. 2006) and further research is necessary to determine whether wolves selectively provision pups with beaver.

The factors that impact beaver consumption are complex and likely dependent on both biological and environmental factors (Sidorovich et al. 2017). Several researchers have noted that consumption of beavers by wolves appears to be a functional response, where consumption increases as beaver density increases (Voigt et al. 1976, Peterson 1977, Tremblay et al. 2001, Sidorovich et al. 2017). On Isle Royale, Michigan, USA, a remote wolf-moose *Alces americanus*-beaver island system in Lake Superior, Romanski (2010) determined that there was a positive logarithmic relationship between annual beaver consumption by wolves (estimated via scat analysis) and beaver density (Figure 3). Although this is indicative of a Type II functional response (i.e., wolf consumption of beavers increased with increasing beaver density but approached an asymptote at high beaver densities), beaver density only explained 30% of the variation in beaver consumption, suggesting that other factors were influencing this dynamic. Romanski (2010) did not account for the effect of moose availability on beaver consumption, which may have explained some additional variation.

In more complex multi-ungulate prey systems, it has not been quantitatively demonstrated that beaver consumption by wolves is related to beaver density. Several authors have noted that beaver consumption was positively correlated with beaver density, but often increasing beaver consumption has coincided with declining ungulate populations (Hall 1971, Voigt et al. 1976, Mech and Karns 1977, Fuller and Keith 1980). Thus, whether increasing beaver in wolf diets was primarily the result of increasing beaver density, decreasing ungulate densities, or an interaction of the two is unknown. In an area of low white-tailed deer *Odocoileus virginianus* density in Quebec, Canada, moose were the primary summer prey (53% biomass) and beavers the secondary prey (29% biomass) of wolves (Potvin et al. 1988). Yet in an area of high deer density where deer, beaver, and moose densities were approximately eight times, four times, and two times higher than in the low-density area, respectively, beavers were the primary summer prey, constituting 44% of wolf diets. Thus, higher beaver density, not ungulate density, appeared to be driving consumption of beavers by wolves.

Environmental factors can also impact beaver consumption, by changing beavers' vulnerability to predators. Climatic events (e.g., droughts) that impact water levels can alter the distance beavers must forage from water and the depth of waterways (e.g., streams, feeding canals) beavers must travel through (Hall 1971). In Belarus, annual rainfall was negatively related to beaver consumption by wolves, and explained 34% of the variation in beaver consumption over a 15 year period (Sidorovich et al. 2017). Sidorovich et al. (2017) suggested that lower water levels in drier summers led to increased predation of beavers by wolves, presumably because beavers were more vulnerable when traveling through shallow waterways and had to travel further on land to

forage (Gable et al. 2016). However, Sidorovich et al. (2017) did not examine the relationship between rainfall and beaver densities, which has been shown to be influential (Campbell et al. 2012). Seasonal variation in water levels or ice cover can increase beaver vulnerability (Mech 1966, Forbes and Theberge 1996), but whether seasonal environmental factors result in an increase in predation on beavers by wolves over the ice-free season is unknown. For example, is beaver consumption higher during years with longer ice-free periods than during years with shorter ice-free periods? If so, expected changes resulting from global climate change (e.g., longer ice-free periods) in the wolf-beaver range may have profound effects on wolf-beaver dynamics (Campbell et al. 2012).

Understanding the role of all factors influencing beaver consumption by wolves is challenging. Temporal and spatial changes in factors such as prey density and availability likely influence when wolf consumption of beavers peaks, though more information is needed before larger conclusions about these patterns can be made. We suggest that researchers should primarily focus on understanding the effect of prey densities on consumption of beavers, and, when possible, they should include other covariates on environmental conditions (e.g., annual rainfall) and the demographic structure of wolf populations. To do this will require researchers to design studies that will accurately estimate wolf diets (see Gable et al. 2017a) and prey densities in the area(s) of interest.

Effects of Beaver Populations on Wolves

Understanding wolf-prey relationships is challenging, due to the complexities of studying predator-prey dynamics in multi-predator and multi-prey systems. Moreover, such research often requires long-term monitoring to understand the factors influencing population change of predators and prey. Some researchers have argued that intrinsic

factors (e.g., intraspecific strife) regulate wolf populations, especially at high densities (Cariappa et al. 2011, Cubaynes et al. 2014), but the most recent evidence suggests that wolf density is primarily a function of prey densities (McRoberts and Mech 2014, Mech and Barber-Meyer 2015). Thus, wolf density increases linearly (i.e., Type I numerical response) with increasing prey densities (Mech and Barber-Meyer 2015). To compare prey densities in multiple systems at large spatial scales, some researchers (e.g., McRoberts and Mech 2014) have used an ungulate biomass index (UBI) to express relative prey biomass. Typically, this is derived by assigning relative values to ungulates based on individual biomass (e.g., an individual white-tailed deer = 1 and a moose = 6, because a moose is six times the biomass of a white-tailed deer). Beavers have been ignored when quantifying prey abundance (Theberge and Theberge 2004), but we suggest that future studies examining the influence of prey abundance on wolf densities should include beavers. Beaver densities could easily be incorporated by assigning a UBI value of 0.2 to beavers, as the mean weight of beavers is 12.5–15 kg (Potvin et al. 1988, Gable et al. 2017a), roughly 20% of the weight of a deer. Beavers could compose a substantial proportion of total UBI when beaver densities are high (e.g., >5 beavers/km²) or when ungulate densities are low. Ultimately, this approach could elucidate whether or not wolf populations respond numerically to beaver densities, as has been suggested (Andersone 1999).

How beaver populations positively influence wolf populations is relatively unknown. Barber-Meyer et al. (2016) speculated that high beaver densities could supplement wolves during the ice-free season, ultimately leading to larger pack sizes via increased litter sizes, higher pup survival, and delayed dispersal. These hypotheses have

yet to be tested, but evidence suggests that high beaver densities can be critical to wolves during the pup-rearing season. On Isle Royale, Peterson (Peterson 1977) suggested that increased beaver densities resulted in high wolf pup survival during a period of decreased moose calf production. Similarly, in Algonquin Provincial Park, Southern Ontario, Canada, wolf packs in higher beaver density areas had higher pup survival and lower pup mortality from starvation than those in lower beaver density areas (Benson et al. 2013, 2015). Furthermore, wolves in lower beaver density areas showed reduced selection for water (i.e., beaver habitat), instead selecting for habitats to potentially maximise predation on moose calves (Benson et al. 2015).

One of the most important questions in wolf-ungulate-beaver systems is how beaver populations indirectly affect wolf predation on ungulate populations. Ultimately, dense beaver populations either 1) buffer ungulate populations from wolf predation, thus decreasing wolf predation on ungulate populations; 2) negatively affect ungulate populations by facilitating a numerical response by wolves, thus increasing wolf predation on ungulates (i.e., apparent competition, Latham et al. 2013); or 3) do not influence wolf predation on ungulates. Most evidence suggests that beaver densities negatively influence ungulate populations through apparent competition (Andersone 1999, Mech and Fieberg 2014), but much of this is speculative. Latham et al. (2013) suggested that high summer adult caribou *Rangifer tarandus* mortality was a result of wolves selecting beaver habitats in the summer, which led to increased spatial overlap between wolves and caribou, and consequently increased incidental predation of adult caribou by wolves. Mech and Karns (1977) thought that the wolf population in northeastern Minnesota was subsidised by the beaver population during a period of deer

decline, thus allowing the wolf population to remain larger than would be expected.

Andersone and Ozolins (2004) surmised that high beaver densities could keep depressed ungulate populations at low densities by increasing wolf pup survival, thus resulting in high predation of ungulates during the winter when beavers are unavailable.

Even if beaver populations do bolster summer wolf densities, whether this has a net positive or negative effect on ungulate populations is unknown. Forbes and Theberge (1996) thought that wolf populations in a moose-deer-beaver region of Algonquin Provincial Park were sustained, in part, by dense beaver populations, as wolf densities remained the same during periods when deer were abundant and when they were absent. Despite beavers apparently subsidising wolf populations, Forbes and Theberge (1996) concluded that wolves had little impact on moose populations in the area, as predation on moose calves was relatively low, and wolf predation was mostly on adults in poor condition and thus compensatory. It is possible that dense beaver populations could reduce summer predation of ungulates to the point that total annual predation of ungulates is actually lower than it would be when beaver densities are low (Theberge and Theberge 2004). That is, even though winter predation on ungulates might increase when beaver densities are high due to a numerical response in wolf populations, the reduction in predation on ungulates during the summer might exceed the increase in predation during the winter. This could be especially true if high beaver densities facilitated increased neonatal ungulate survival through reduced predation. However, if beaver populations are subsidising wolf populations, and then beaver populations decline substantially, predation on ungulates would be expected to increase markedly until the

wolf population decreased (Potvin et al. 1988). Thus, sustained high beaver densities might be necessary if beaver populations are to influence ungulate populations positively.

Impact of Wolf Predation on Beaver Populations

Cowan (1947) may have been the first to describe the possible effects of wolf predation on beaver populations, when he speculated that wolf predation had little impact on beaver populations until high-quality beaver forage (e.g., aspen *Populus* spp.) was unavailable, after which wolves could effectively reduce beaver populations. Unfortunately, in the 70 years since Cowan (1947) first discussed wolf-beaver dynamics, our understanding of wolf predation on beaver populations has advanced little, as most assessments are lacking quantitative rigor and are instead based on anecdotal evidence and speculation (e.g., Longley and Moyle 1963, Baker and Hill 2003). Much of this is due to the difficulties of estimating the number of beavers that wolves remove in a given time period. Unlike medium-sized to large ungulates, finding evidence of wolf-killed beavers is difficult, as wolves can almost wholly consume beavers in a short period (Palacios and Mech 2010).

Gable and Windels (2018) were the first to estimate kill rates and predation rates of beavers by wolves from confirmed predation events. They estimated that a GPS-collared breeding male wolf killed 22 beavers during a single ice-free season (kill rate = 0.095 beavers per day), which was 10% of the estimated beaver population in the wolf's 85 km² home range. Using that wolf's kill rate, they estimated that the pack (four adults, two pups) removed 38–42% of the beaver population (density = 0.47 lodges/km²) in the pack's home range. Despite this high predation rate, the beaver population still increased by 43% the following year, leading the authors to conclude that “the effect of wolf predation on a dense beaver population in a multi-prey system is minimal and that

changes in beaver population size are likely more influenced by other factors” such as food availability or water levels (Gable and Windels 2018).

Prior to the research by Gable and Windels (2018), all attempts to understand the effect of wolf predation on beaver populations quantitatively were based on indirect methods. The most common method has been to estimate how many beavers (and what proportion of the beaver population) wolves consumed during a given period by using estimates of the wolf population in an area, the percentage of wolf diet (estimated via scat analysis) that was beaver, and wolf food requirements (see Romanski 2010). Predation rates are calculated by dividing the estimated number of beavers killed by wolves by the estimated beaver population in an area. However, estimating predation via this method can be problematic, because it is dependent on accurate wolf diet and beaver population estimates for an area (discussed below), and involves assumptions about daily biomass intake by wolves and the mean weight of wolf-killed beavers.

Based on scat analysis, Romanski (2010) estimated that the wolf predation removed 137.4 beavers per year on Isle Royale during 1962–2009, which was 16% of the beaver population (density= 0.24 lodges/km²) per year. Thus, each wolf killed 5.8 beavers per year (average wolf population = 23.7). In some years, wolves removed an estimated 37–50% of the beaver population, leading Romanski (2010) to conclude that wolves were suppressing the beaver population to some extent. Wolves killed an estimated 545–1503 beavers per year in and around Algonquin Provincial Park (a 2700 km² study area), which was an estimated 7–19% of the beaver population (density = 0.4 lodges/km²) annually (Theberge and Theberge 2004). Theberge and Theberge (2004) estimated that each wolf killed anywhere between 8.5–23.5 beavers per year (average

wolf density was 2.4 individuals/100 km², a population of 64 wolves). They concluded that beaver recruitment alone was greater than the proportion of the beaver population consumed annually by wolves. However, the wolf diet and beaver population estimates used to estimate the effect of wolf predation on beavers in these studies are questionable, and should be taken cautiously (Gable and Windels 2018).

In Quebec, Canada, Potvin et al. (1992) monitored beaver populations before, during, and after wolf control measures. Based on scat analysis, wolves removed an estimated 15% of the beaver population (density = 1.1 lodges/km²) annually prior to wolf control measures, and each wolf killed on average 29.4 beavers per year. After a 60% reduction in wolf density following wolf control measures, beaver densities increased by 20% over a three year period. Within two years of the cessation of wolf control measures, the beaver population decreased to its original level. Beaver populations in adjacent control populations (where there was no wolf control) remained stable during the study, leading Potvin et al. (1992) to conclude wolves were having a stabilising effect on the beaver population.

Potvin et al. (1992) assumed that wolf predation acts primarily by reducing the number of beaver colonies, not the number of individuals per colony. If this is true, then one of two possible scenarios must occur: 1) wolves prey intensely on the beavers in specific lodges until all members of that colony are killed, or 2) the death of certain colony members (e.g., the breeding individuals) increases the probability that the lodge will be inactive the next year. However, the impact of predation on the demographic structure of beaver populations is unknown (Novak 1987). Some researchers have speculated that wolves primarily kill young or dispersing beavers (Longley and Moyle

1963, Fritts and Mech 1981) but there is no evidence for this. It is possible that predation, like hunting, selects for adult and pregnant female beavers (Parker et al. 2002). Thus, as has been done with ungulate species (e.g., Boyd et al. 1994), future researchers should compare the age-class distribution of wolf-killed beavers to that of the population as a whole (Novak 1987).

Substantial research is needed if we are to understand whether, how, and under what conditions wolves affect beaver populations. We suggest that researchers should design studies to identify beaver kills from GPS-collared wolves, as most kills from a collared wolf can be found. Using accelerometer data from GPS-collared wolves may aid in finding beaver kills, but further research is necessary (Wang et al. 2015). Ultimately, identifying kills will provide a more accurate metric of wolf predation on beavers than those derived from scat-based diet estimates. If future researchers do wish to estimate predation via scat-based diet estimates, then scats must be collected systematically in order to minimise biases in diet estimates (Gable et al. 2017a).

Researchers should also determine important beaver population-level parameters (active lodge densities and mean colony size) from their study areas, instead of using values from the literature. Indeed, accurate estimates of predation rates on beavers are highly dependent on these values (Baker and Hill 2003). Most researchers estimating beaver densities for studies of wolf predation have assumed that beaver colony size remained constant over time (Theberge and Theberge 2004, Romanski 2010), and thus that lodge densities accurately reflect population change (Potvin et al. 1992). However, colony size can fluctuate dramatically over time within a study area, and thus similar lodge densities might reflect different population levels (Baker and Hill 2003).

Researchers also commonly assume that active beaver lodge density estimates from past surveys are representative of the beaver densities during their study, even though the surveys were not spatially or temporally consistent with their study (e.g., Theberge and Theberge 2004). Like colony size, active lodge densities can fluctuate dramatically through time and space (Novak 1987, Parker and Rosell 2014). Aerial surveys of lodges or food caches are commonly used to estimate beaver densities (Novak 1987), but other methods based on observing beaver works from aerial photography or remote sensing data can be used (e.g., Johnston and Windels 2015).

Understanding Wolf-Beaver Dynamics

Wolves and beavers have been studied extensively as individual species, yet wolf-beaver dynamics remain poorly understood. High beaver densities may benefit wolf populations under certain conditions, but our understanding of these benefits and the underlying conditions is generally poor. Therefore, more research is needed to understand specifically how changes in beaver population densities affect various parameters (e.g., pup survival and dispersal) of wolf populations, and whether wolf populations respond similarly through space and time. Of utmost importance is understanding how wolves respond functionally and numerically to fluctuating ungulate and beaver densities in multi-prey systems. In North America, moose and caribou populations have declined dramatically in certain areas, and wolves have been implicated as a source of these declines (Michalski et al. 2011, Mech and Fieberg 2014). But what role do beavers play in these declines? Are beaver populations really subsidising wolf populations and exacerbating predation on large ungulates, as has been suggested (Latham et al. 2013, Mech and Fieberg 2014)?

Significant research is also necessary to understand the effect of wolf predation on beaver populations. Although scat-based diet estimates are important, direct estimates of wolf predation on beavers are necessary to understand fully the effect of predation on beaver populations (Gable et al. 2016). Considering all the research on wolves and their prey, our understanding of kill rates and predation rates of wolves on beavers, and the effects of wolf predation on beaver abundance, is surprisingly poor. The answers are likely dependent on a variety of conditions, such as total predation pressure, habitat quality, ungulate density, and beaver density. Given the complexity of wolf-ungulate-beaver systems, fully understanding wolf-beaver dynamics will be challenging, and is likely to require long-term, intensive research of wolf, ungulate, and beaver population densities and demographic parameters. However, understanding this dynamic has implications, not only for the conservation and management of both wolves and beavers, but also for ungulate populations, which are affected by the factors that influence changes in wolf populations.

Table 1. Percentage of wolf diet (estimated via scat, stomach content, kill site, and stable isotope analysis) comprised of beaver from wolf diet and predation studies in North America and Eurasia We estimated the mean percentage of wolf diet comprised of beaver for each study by averaging over meaningful temporal units (e.g., month) and wolf sampling units when possible (Gable et al. 2017). We have included studies in which beaver composed a non-trivial portion (>5%) of wolf diet. For studies where beaver constituted 1-5% of wolf diet, see Appendix S2.

Location	Diet Method	Wolf Sampling Unit ^a	Time Period Studied	Time Interval Studied ^b	Mean Beaver in Diet (%)	Range Beaver in Diet (%)	Role of Beaver in Wolf Diet	Beaver Density (lodges/km ²)	Reference
NORTH AMERICA									
Alaska, USA	Scat	Pop.	Summer	Annual	9	4-14	Alt		Ballard et al. 1987
	Scat	>1 Pop.	Jan-Dec	Seasonal	17*	14-24	Alt		Smith et al. 1987
	Scat	Pack	Jan-Dec	Annual	21*	13-28	Alt		Kohira and Rexstad 1997
	Scat	Pop.	Jan-Dec	Annual	11	11-12	Alt		Watts and Newsome 2017
Isle Royale National Park, Michigan, USA	Scat	Pop.	May-Oct	Annual	14	1-54	PS/Alt	0.28	Romanski 2010
Minnesota, USA	Scat	Pop.	Jan-Dec	Seasonal	16*	1-18	Alt	0.1	Frenzel 1974
	Scat	Pop.	May-Sept	Seasonal	10*	1-25	Alt		Van Ballenberghe et al. 1975

	Scat	Pop.	Apr-Oct	Month	11	1-19	Alt	~0.6	Fuller 1989
	Scat	Pop.	Jun-Aug	Seasonal	20		Alt		Barber-Meyer and Mech 2017
	Scat	Pop.	Jan-Dec	Seasonal	17*	7-35	Alt	~1	Gogan et al. 2004
	Scat	>1 Pop	Jan-Dec	Seasonal	11	2-30	Alt		Chenaux-Ibrahim 2015
	Scat	Pop.	Jun-Aug	Annual	7	5-9	Alt		Barber-Meyer and Mech 2017
	Scat	Packs	Apr-Oct	Annual	26	10-38	PS/Alt	~1	Gable et al. 2017a
Montana, USA	Scat	Pop.	Jan-Dec	Seasonal	5*	1-17	Alt		Arjo et al. 2002
Alberta, Canada	Scat	>1 pop.	Jan-Dec	Annual	7*	2-17	Alt		Cowan 1947
	Scat	Pack	Jun-Sept	Seasonal	37*	17-52	PS/Alt	0.24	Fuller and Keith 1980
	Scat	Pop.	Summer	Annual	11*	2-14	Alt		Carbyn 1983
	Scat	Pop	Jan-Dec	Annual	10*		Alt		James 1999
	Scat	Pop.	Jan-Dec	Seasonal	20	9-30	PS/Alt	1.54 ^d	Latham et al. 2013
British Columbia, Canada	Scat	Pop.	May-Oct	Annual	16*	8-22	Alt		Steenweg et al. 2015
	Isotope	Pop.	Summer		21		Alt		Merkle et al. 2017
Ontario, Canada	Scat	>1 Pop.	Summer	Annual	35*	7-59	PS/Alt		Pimlott et al. 1969
	Scat	>1 Pop.	May-Sept	Annual	60*	7-75	PS/Alt	~1-2	Voigt et al. 1976
	Scat	Pop.	May-Sept	Annual	49	35-63	PS/Alt		Theberge et al. 1978
	Scat	Pop.	Jan-Dec	Seasonal	37	13-60	PS/Alt		Krizan 1993
	Scat	>1 Pop.	Jan-Dec	Seasonal	12	8-15	Alt		Forbes and Theberge 1996
	Scat	1 Pop.	May-Aug	Seasonal	10	9-12	Alt	~0.4	Theberge and Theberge 2004
	Scat/ Stomach	Pop.	UNK	Annual	20	12-26	Alt		Wiwchar and Mallory 2012

Manitoba, Canada	Scat	Pop.	Apr-Oct	Seasonal	44*	24-82	PS/Alt		Hill 1979
	Scat	Pop.	Jan-Dec	Seasonal	17*	5-25	Alt	~1.1	Meleshko 1986
	Scat	Pop.	Jan-Dec	Seasonal	19*	10-35	Alt		Sallows 2007
	Isotope	Ind.	Sum.-Fall	Annual	15	3-83	PS/Alt		Moayeri 2013
	Isotope	Ind.	Sum.-Fall	Annual	11	5-20	Alt		Friesen and Roth 2016
	Scat	Pop.	Jan-Dec	Seasonal	~35*	~20-50	Alt		Naaykens et al. 2016
Saskatchewan, Canada	Isotope	Pop.	Sum.-Fall	Annual	8	4-17	Alt		Urton and Hobson 2005
Quebec, Canada	Scat	>1 Pop.	Jan-Dec	Annual	44	1-44	PS/Alt	3.7 ^d	Potvin et al. 1988
	Scat	>1 Pop.	May-Nov	Bi-month	19	9-23	Alt	0.23	Messier and Crête 1985
	Scat	Pack	Jun-Sept	Annual	12	2-33	Alt	0.08	Tremblay et al. 2001
Vancouver Island, Canada	Scat	Pack	Jan-Dec	Seasonal	~14*	~5-25	Alt		Milne et al. 1989
Yukon Territory, Canada	Scat	Pack	Summer	Annual	8*	0-9	Alt		Theberge and Cottrell 1977
	Scat	Pack	Summer		21*	0-63 ^e	PS/Alt		Hayes et al. 2016
EURASIA									
Belarus	Scat	Pop.	Jan-Dec	Seasonal	30	23-37	PA		Sidorovich et al. 2017
Germany	Scat	Pop.	Jan-Dec	Annual	10		Alt		Nitsche 2016

Latvia	Scat/ Stomach	Pop.	Summer	Seasonal	36		PS	Andersone 1999
	Scat	Pop.	Jan-Dec	Seasonal	8	3-13	Alt	Andersone and Ozoliņš 2004
	Stomach	Pop.	Jan-Dec	Annual	6		Alt	Žunna et al. 2009
Lithuania	Scat	Pop.	Annual	Seasonal	13	10-15	Alt	Spinkyte-Backaitiene and Petelis 2012
Russia	Scat	Pop.	Jan-Dec	Seasonal	10*	5-15	Alt	Mertz 1953

^a Wolf diet examined at the following scales: Ind. = individual; Pack = pack; Pop. = a single population; >1 Pop. = multiple populations.

^b Wolf diet examined at the following time intervals: Month = monthly; Bi-month = 2-month intervals; Seasonal = seasonally (e.g. winter, summer); Annual = annually (e.g., 1999) or over multiple years (e.g., 1997-1999).

^c Role of beaver in wolf diet: Alt = alternate prey, PS = primary prey during summer season, PA = primary annual prey.

^d Beavers/km²

^e Beavers and muskrats were combined, so this likely overestimates beaver

* Diets estimated using percent frequency of occurrence or percent volume as opposed to percent biomass. Generally, percent frequency of occurrence and percent volume overestimates the prevalence of beaver in wolf diets because more scats are produced per kg of beaver than per kg of larger prey as beavers have a larger proportion of indigestible material than larger prey (Weaver 1993).

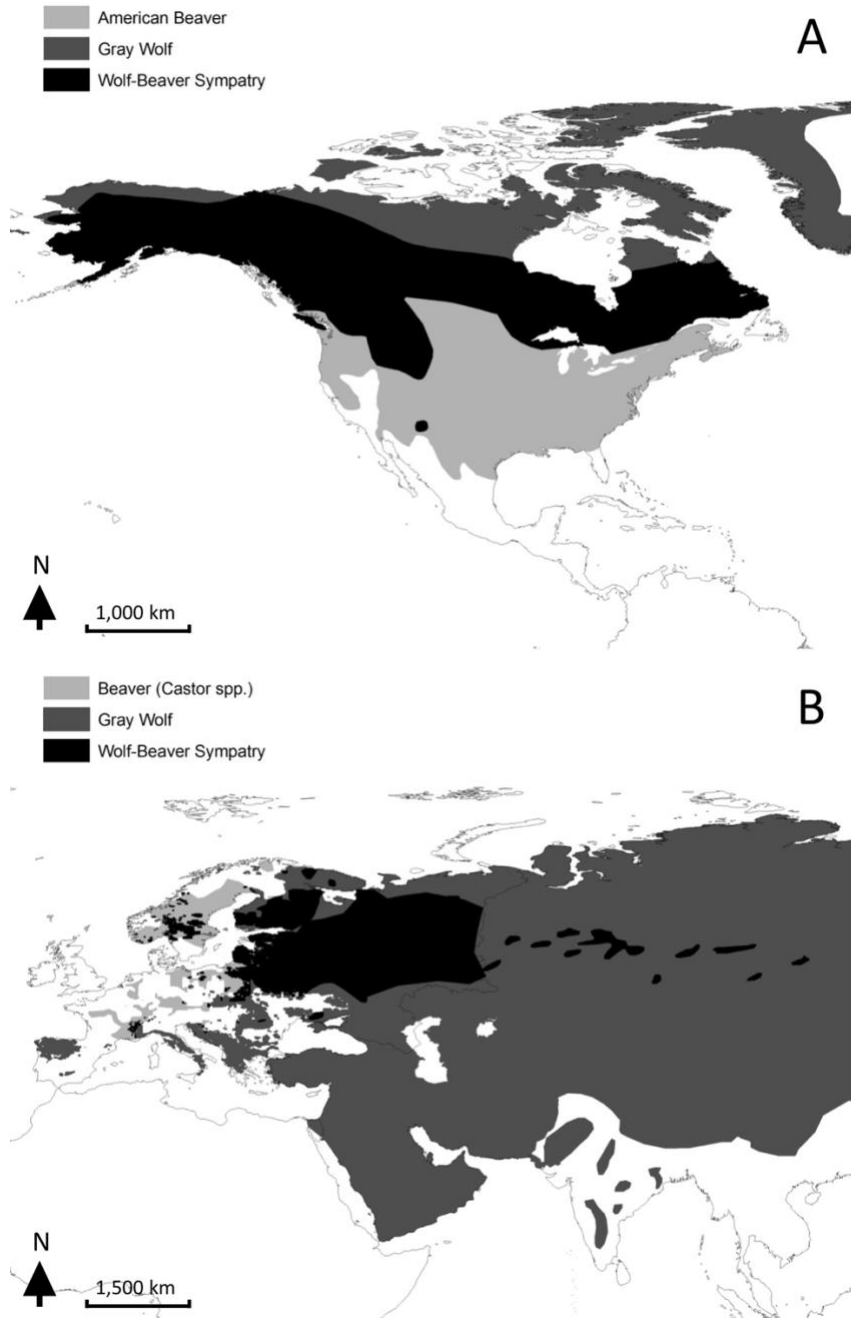


Figure 1. The geographical ranges of grey wolves *Canis lupus* and beavers *Castor* spp., and where the taxa co-occur, in North America (A), and Europe and Asia (B). Maps are based on data from the International Union for Conservation of Nature (Mech and Boitani 2010, Cassola 2016) and on unpublished data from Halley et al. (2017).

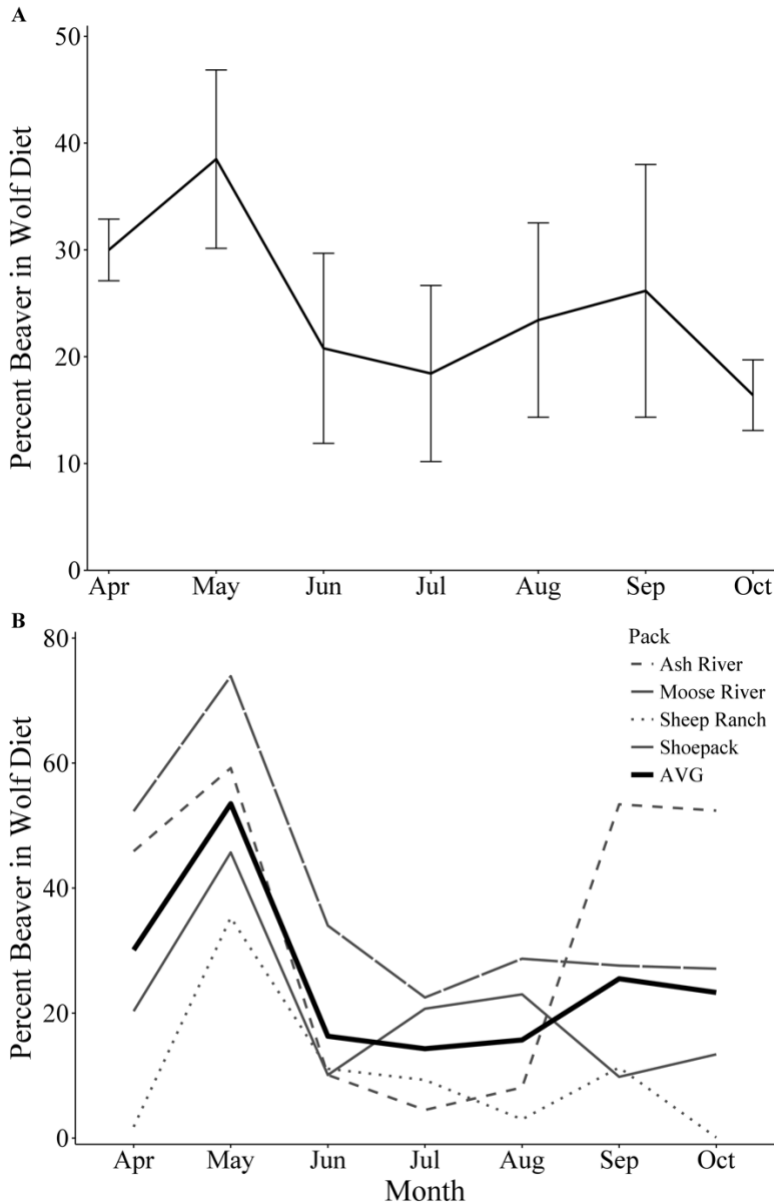


Figure 2. Mean monthly percentage (\pm standard errors) of scat-based grey wolf diets composed of beaver, based on seven studies (Pimlott et al. 1969, Hall 1971, Voigt et al. 1976, Messier and Crête 1985, Fuller 1989, Gogan et al. 2004, Theberge and Theberge 2004, Gable et al. 2017a) in North America (A), and monthly variation in the percentage of scat-based wolf diets composed of beaver in Voyageurs National Park, Minnesota, USA, in 2015 for four individual wolf packs (AVG = average; adapted from Gable et al. 2017a; B).

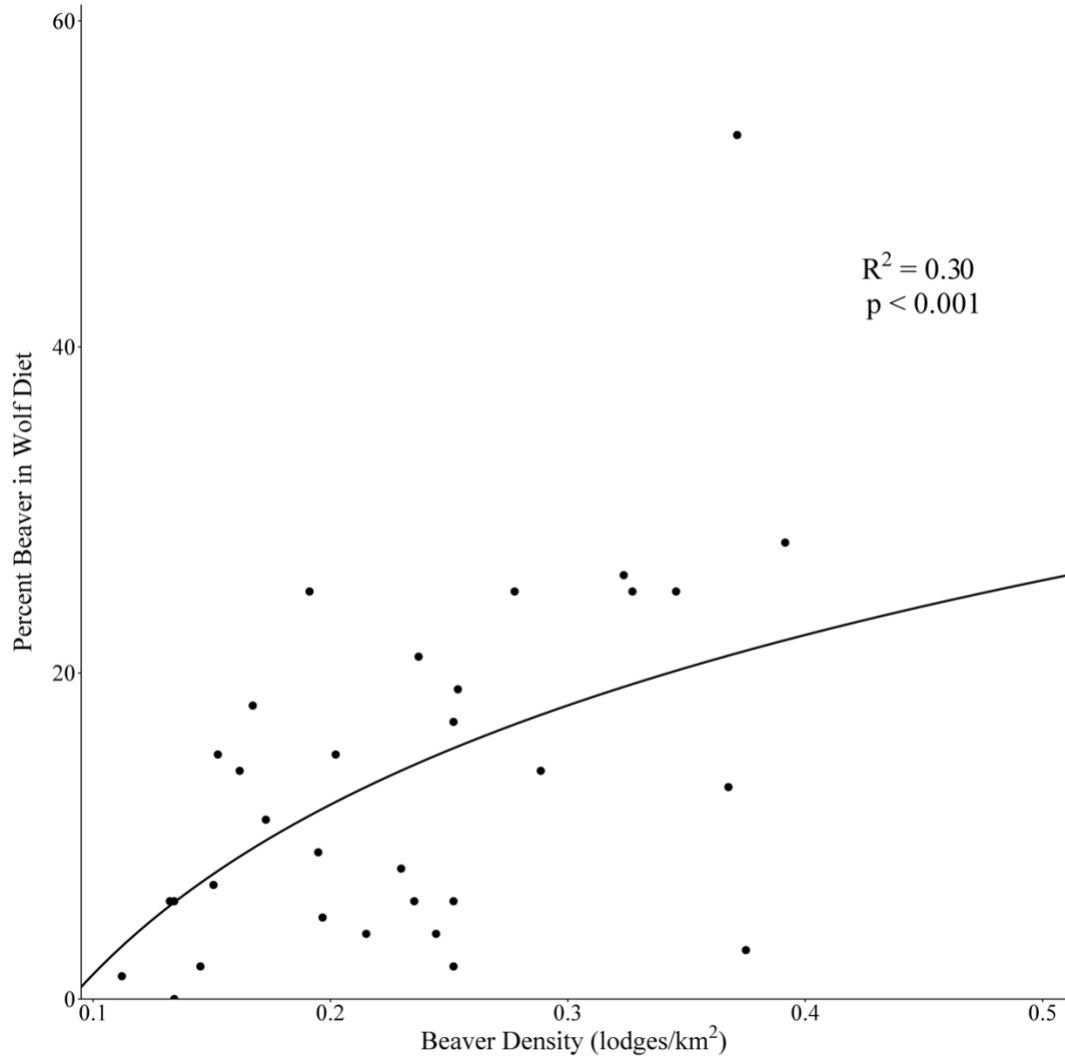


Figure 3. The relationship between the percentage of scat-based grey wolf diets comprised of beaver and beaver density on Isle Royale National Park, Michigan, USA, during 1962–2009 (each point represents one year; adapted from Romanski 2010).

Chapter 2: Kill Rates and Predation Rates of Wolves on Beavers

ABSTRACT Wolves (*Canis lupis*) can be primary predators of beavers (*Castor canadensis*), but little is known about wolf-beaver dynamics. We identified kills from 1 wolf (V009) of the Ash River Pack in Voyageurs National Park from 1 April to 5 November 2015 to provide direct estimates of wolf pack kill and predation rates of beavers. We documented 12 beaver kills by V009 during the 2015 ice-free season and estimated V009 killed 22 beavers during this period. Based on the number of beavers killed by V009, we estimated the Ash River Pack removed 80–88 beavers (kill rate of 0.085–0.095 beavers/wolf/day), which was 38–42% of the beaver population in their home range during the ice-free season. Even with this substantial level of predation in 2015, the beaver population in the Ash River Pack home range increased by an estimated 43% in 2016, which suggested dispersal from more densely populated adjacent areas likely compensated for the effects of wolf predation. We have presented the first direct estimate of wolf kill and predation rates on beavers, but more research is necessary to understand how wolf predation affects beaver populations under a variety of conditions.

INTRODUCTION

Scat analysis has been the most common method used to study wolf (*Canis lupus*) diets and predation because scats can often be collected with relatively little effort (Marucco et al. 2008, Newsome et al. 2016). Indeed, scat analysis provides valuable information about temporal and spatial variability in wolf diets. However, scat analysis is indirect and estimating the number of prey killed via scat analysis requires several assumptions about the energetic requirements of wolves and the size and digestibility of prey (Peterson and Ciucci 2003). This approach also assumes that all prey consumed are from direct

predation rather than a mixture of scavenged carcasses and animals killed via direct predation. Further, calculating metrics of predation (e.g., kill rates) in this manner assumes that the scats collected are representative of all scats deposited by a wolf population in a given period (Wachter et al. 2012, Gable et al. 2017a). For over a decade, researchers have attempted to obtain more direct estimates of predation by fitting wolves with global positioning system (GPS) collars and searching for kills in areas where there were clusters of GPS locations (Sand et al. 2005, Webb et al. 2008, Metz et al. 2011). This method has proven useful for locating kills of adult ungulates, but locating kills of small prey (e.g., beavers [*Castor canadensis*], ungulate neonates) has been challenging because wolves can consume small prey in a short period (Sand et al. 2008, Palacios and Mech 2010).

Beavers can be important seasonal prey for wolves in many systems in North America and Europe, generally constituting <30% diet biomass during the ice-free season (Voigt et al. 1976, Potvin et al. 1988, Anderson 1999, Latham et al. 2013, Sidorovich et al. 2017); however, wolf-beaver dynamics are poorly understood (Gable et al. 2016). The few attempts to understand wolf predation on beaver populations have been based on diet estimates from scat analysis because obtaining direct estimates of predation has been difficult (Potvin et al. 1992, Theberge and Theberge 2004, Romanski 2010). However, Potvin et al. (1992) also noted changes in beaver lodge density before, during, and after wolf removal. Nonetheless, the diet estimates used in these studies for calculating the number of beavers killed by wolves are suspect because the authors did not address many common biases that can affect the accuracy of scat-based diet estimates (Gable et al. 2017a). Additionally, the accuracy of the beaver population estimates used is

questionable because lodge density and colony size were not estimated annually for these study areas (Novak 1987, Baker and Hill 2003).

The estimates of predation rates (the proportion of the beaver population removed by wolves) from the studies by Potvin et al. (1992), Theberge and Theberge (2004), and Romanski (2010) have provided conflicting information about the effect of wolf predation on beaver populations. Theberge and Theberge (2004) estimated wolves removed 15% of the beaver population annually, and concluded that wolves had no effect on the beaver population as they thought recruitment was offsetting the number of beavers removed by wolves. Potvin et al. (1992) and Romanski (2010) reported similar predation rates (7–19% and 16%, respectively) but concluded that wolf predation was suppressing beaver populations to some extent as changes in wolf density appeared to be loosely associated with changes in beaver density.

Thus, direct estimates of predation rates and accurate wolf and beaver population estimates are necessary to understand the effect of wolf predation on beavers. Based on the beaver kill sites identified by investigating clusters of GPS locations from a wolf in Voyageurs National Park, Minnesota, USA, we estimated the magnitude of wolf predation on the beaver population in a single pack's home range. By doing so, we have provided the first direct estimate of wolf kill rates and predation rates of beavers.

STUDY AREA

Our study was conducted in and adjacent to Voyageurs National Park (VNP; 48°30' N, 92°50' W), an 882-km² protected area along the Minnesota-Ontario, Canada border (Fig. 1). Our study area extended from the southern edge of Kabetogama Lake, VNP, south into the Kabetogama State Forest, which is on the southern edge of the boreal forest and

part of the Laurentian Mixed Forest Province (Bailey 1980). The Kabetogama State Forest was managed for timber and is a mosaic of clear cuts, aspen (*Populus* spp.) and mixed forest stands, and wetlands. Beaver impoundments were abundant throughout our study area, and VNP had sustained high beaver densities for >40 years (Johnston and Windels 2015). Lakes in VNP froze during late October to mid-November with ice-out occurring during early April to early May (Kallemeyn et al. 2003). Winters in VNP were commonly long and severe, and summers hot and humid. Mean annual temperature and mean annual rainfall was 2.4° C and 63 cm, respectively (Johnston and Windels 2015). Voyageurs National Park is on the southern edge of the Canadian Shield. Maximum topographic relief is 80 m and gently sloping granitic ridges and steep rock faces are common.

White-tailed deer (*Odocoileus virginianus*) were common throughout our study area, with pre-fawn deer densities around 2–4 deer/km² (Gable et al. 2017b). Moose (*Alces americanus*) were rare with densities likely <0.05 moose/km² (Windels and Olson 2017). White-tailed deer, beavers, and other furbearers were legally harvested outside of VNP, but harvest was prohibited within the park. During this study, wolves in Minnesota were federally protected under the Endangered Species Act (Mech 2017). Summer wolf densities in the area were high (4–6 wolves/100 km²) with average summer home range of 115.8 km² and pack size of 5.5 wolves/pack in 2015 (Gable 2016). In 2015, ≥6 packs used part of VNP (VNP, unpublished data).

METHODS

In June 2013, we captured a breeding male wolf, V009, from the Ash River Pack (ARP) using a foothold trap. We immobilized V009 with 10 mg/kg ketamine and 2 mg/kg

xylazine using a syringe pole. Once immobilized, we fit V009 with a GPS telemetry collar (Lotek IridiumTrackM 1D, Lotek Wireless, Newmarket, Ontario, Canada). We reversed V009 with 0.15 mg/kg of yohimbine and monitored the wolf through recovery. All handling and processing of V009 followed Institutional Animal Care and Use Committee approvals by the United States National Park Service (protocol: MWR_VOYA_WINDELS_WOLF). For more details regarding handling procedures, see Gable et al. (2016).

We estimated V009 was 6–7 years old at capture based on tooth wear (Gipson et al. 2000), and thus was 8–9 years old in 2015. The fix interval of the GPS collar on V009 was set at 4 hours. In early May 2015, we switched the fix schedule remotely to 6 hours to conserve battery life. We searched clusters of GPS locations from V009 to document kill sites from 1 April to 5 November 2015. We defined clusters as consecutive locations within 200 m for ≥ 4 hours, and identified them using ArcGIS 10.2 (Environmental Systems Research Institute, Redlands, CA, USA). We searched clusters and identified kills using the same methods as Gable et al. (2016). We used ArcGIS to determine the number of clusters we did not search and to estimate how many of those were likely in active beaver habitats. We considered clusters to be in active beaver habitats if $\geq 50\%$ of cluster locations were < 30 m from water based on the typical distance of beaver kill sites to water (Gable et al. 2016, Lowrey et al. 2016). We estimated the number of beaver kills we missed by multiplying the number of unsearched clusters in active beaver habitats by the percentage of searched clusters in active beaver habitats at which there were beaver kills. We estimated the number of beavers killed by V009 during the ice-free season (1 Apr–20 Nov) by adding the beaver kills found and the estimated number of beaver kills

missed. We then estimated the number of beavers killed by the ARP during the ice-free season by multiplying the number of beavers killed by V009 by the number of individuals in the ARP. We estimated pack size using aerial mid-winter pack counts, remote cameras, and visual observations during 2015. We estimated the ARP home range during this period (1 Apr–20 Nov) based on GPS collar locations from V009 using the 95% adaptive kernel home range method with the Home Range Tools extension (Home Range Tools Version 2.0.20, <http://flash.lakeheadu.ca/~arodgers/hre/>, accessed 24 Aug 2017) for ArcGIS (Mills et al. 2006, Gable et al. 2016).

We sought to verify our estimates of predation by using scat-based monthly diet estimates from the ARP during April–October 2015. Gable et al. (2017a) provide information on scat collection and analysis. We estimated the number of beavers killed in a given month by multiplying the proportion of monthly diet biomass that was beaver by the estimated monthly biomass intake of the ARP and then dividing that by the digestible biomass of a beaver. The average weight of adult wolves in our study area was 28 kg (VNP, unpublished data) and we estimated average monthly pup weights based on Van Ballenberge and Mech (1975). We assumed biomass intake remained constant during the ice-free season at 0.09 kg/kg of wolf/day (Peterson and Ciucci 2003). We assumed the average wolf-killed beaver had 12.1 kg of digestible biomass based on the average weight of a wolf-killed beaver in our study area (15.5 kg; Gable 2016) and the percentage of a beaver carcass that was likely digestible (bones constitute 22% of carcass; Jankowska et al. 2005). Because we did not have scat-based estimates of beaver consumption for November, we used the mean April–October value.

In late October–early November 2015 and 2016, we conducted aerial censuses to locate all active beaver lodges in the ARP home range. We conducted censuses in a 2-seat tandem Top Cub at 180–215 m above the ground at about 112 kph in a flight pattern that ensured complete coverage of all potential beaver habitat. The observer and pilot identified active beaver lodges based on the presence of a food cache, fresh cuttings, or fresh mud on a lodge or dam (Johnston and Windels 2015). We often circled lodges ≥ 2 times to verify activity. Probability of detection for active lodges using our methodology is unknown, but previous work in VNP suggests that experienced observers can detect 90–100% of active lodges during searches (Johnston and Windels 2015).

We determined average beaver colony size in the ARP home range by live-trapping beavers in lake lodges in VNP (National Park Service Institutional Animal Care and Use Committee permit: MWR_VOYA_WINDELS_BEAVER). We placed 5 Hancock live traps around active beaver lodges for 3 nights (i.e., 15 attempted trap-nights) in September–October 2015 and 2016. We ear-tagged and handled beavers according to the procedures outlined in Windels (2013). Based on skull morphometrics and body size, we assigned beavers to 3 age classes: kits (~0.5 yr old), sub-adults (1.5–2.5 yr old), and adults (>2.5 yr old; Windels 2013). We assumed our live-trapping method generally caught most, but not all, beavers in a colony (Novak 1987). Thus, we estimated average colony size using Novak’s (Novak 1977) equation (Eq. 1) where average colony size is estimated based on the percent of the population that are kits, non-breeding sub-adults, breeding sub-adults, and breeding adults (Eq.1).

$$\frac{\% \text{ kits} + \% \text{ sub-adults} - \% \text{ breeding sub-adults}}{\% \text{ adults} + \% \text{ breeding sub-adults}} = \frac{N}{2 \text{ adults} + 0.12 \text{ non-breeding adults}}$$

Eq. 1

Novak's (1977) equation assumes that beaver colony structure generally consists of a breeding pair with non-breeding subordinate offspring. However, based on empirical data Novak (1977) estimated that 30% of sub-adults bred and on average each colony had 0.12 non-breeding adults. Because we live-trapped beavers we do not have estimates of these parameters so we used Novak's (1977) estimates. Thus, in Equation 1, N is the average number of juveniles per lodge (kits + sub-adults), and average colony size is $N + 2.12$ because there are 2 breeding adults per lodge plus 0.12 non-breeding adults.

RESULTS

We identified 120 clusters from wolf V009 from 1 April to 20 November 2015 (approximate ice-free season) via ArcGIS. The GPS collar successfully transmitted 87% (859/992) of the programmed fixes to the Lotek webservice. However, we were unable to recover the GPS collar to determine how many of the unsuccessfully transmitted fixes were stored on board the GPS collar. We searched 56 clusters from 1 April to 5 November 2015, with 29 occurring in active beaver habitats. Beaver kills were found at 12 (41%) of the clusters in active beaver habitats. We also located 1 beaver kill from V009 opportunistically (i.e., we found a fresh beaver kill opportunistically and GPS-collar data confirmed V009 was at this kill). We did not detect any kills that occurred outside of active beaver habitat. The home range of the ARP during April–November 2015 was 85 km² (Fig. 1). During our study the ARP consisted of 4 adults and 2 pups.

We identified 23 clusters using ArcGIS and satellite imagery that were in active beaver habitats but that we did not search. Based on the clusters searched in active beaver habitats, we estimated that beavers were killed at 41% of the unsearched clusters in active beaver habitats and that we missed 9 beaver kills. Thus, we estimated V009 killed 22 (13

+ 9) beavers during the ice-free season, which is a kill rate of 0.095 beavers/wolf/day. Based on the number of kills from V009, we estimated that the ARP killed 88 (22 beavers/wolf \times 4 wolves) beavers during the ice-free season. However, we estimated V009 was with ≥ 1 pack member at 15% (2) of beaver kills based on the suspected presence of other wolves at the kill site (Gable et al. 2016). We estimated this based on the number of kills from V009 where we identified wolf sign and prey remains that were not close to GPS collar locations from V009 (i.e., evidence of other wolves at the kill). Assuming that this overlap is indicative of all members in the ARP, then the ARP likely killed 80 beavers (20 beavers/wolf \times 4 wolves) during the ice-free season.

We estimated V009 killed 341 kg of beavers (22 beavers \times 15.5 kg/beaver) during the ice-free season, of which 266 kg was edible. We assumed V009 needed to consume 590 kg of food during the ice-free season (2.5 kg/day \times 234 days). Thus, beaver composed 45% of the diet of V009 during this time. However, this does not include the energetic demand of provisioning pups. We estimated, based on the average monthly weight of pups during the ice-free season (Table 1) and the energetic demand of wolves (0.09 kg/kg of wolf/day; Peterson and Ciucci 2003), that the pups increased the energetic demand of ARP by 2.0 kg/day (energetic requirement of pups = monthly weight \times 0.09 kg/kg of wolf/day \times 2 pups) during this period. Some evidence suggests wolf pups need 1.6 kg/pup/day (Van Ballenberghe and Mech 1975), which would mean ARP pups actually added 3.2 kg/day to the pack's requirements. If we assume that provisioning pups added an additional 0.5–1.0 kg/day to V009's energetic requirements, V009 would have had to consume 706–823 kg during our study period with beaver comprising 32–38% of the biomass consumed. These estimates are similar to the average proportion of

ARP diet biomass that was beaver based on scats (33%; Table 1). If V009 provided >1 kg/day to the pups then the percent of V009's diet that was beaver would be lower than our estimates.

We live-trapped 93 beavers at 28 active lake lodges ($\bar{x} = 3.3$ beavers/lodge ± 0.3 [SE]) in VNP in 2015 and 114 beavers at 34 active lake lodges ($\bar{x} = 3.3 \pm 0.4$ beavers/lodge) in 2016. Five of the active lodges trapped in 2015, and 6 trapped in 2016 were within ARP's 2015 home range. Of the beavers caught in 2015, 28 (30%) were kits, 40 (43%) were sub-adults, and 25 (27%) were adults. In 2016, 39 (34%) were kits, 42 (37%) were sub-adults, and 33 (29%) were adults. Using Novak's (1977) equation, we estimated average colony size to be 5.3 beavers/lodge in 2015 and 5.3 beavers/lodge in 2016 from live-trapping data. We identified 40 active beaver lodges (density = 0.47 lodges/km²) in the ARP home range during aerial censuses in late October–early November 2015 (Fig. 1). We censused this same area again in late October 2016 and identified 57 active lodges (0.67 lodges/km²), an increase of 43% from 2015.

Based on the number of active lodges and colony size, there were 188 beavers in ARP's home range in fall of 2015, and V009 removed an estimated 12% (22 beavers) of the beaver population during the ice-free season. Based on kill-site locations, V009 removed ≥ 1 beaver from 20% (8/40) of active lodges, and ≥ 2 beavers from 5% (2/40) of active lodges. Additionally, 1 of 13 kills appeared to be dispersing beavers that were not associated with an active lodge (Gable et al. 2016).

Based on scat analysis, beaver constituted 33% of average monthly diet biomass during the ice-free season (Table 1; Gable et al. 2017a). There was no difference ($\chi^2_1 = 0.88$, $P = 0.35$) between our estimates of the number of beavers removed by adult wolves

during the ice-free season based on scat analysis (76 beavers) or kills (80–88 beavers; Table 1). We estimated the ARP removed 38–42% of the beaver population during the ice-free season with a kill rate of 0.085–0.095 beavers/wolf/day.

DISCUSSION

To our knowledge, we have presented the first direct (i.e., from kill sites) estimate of kill rates (0.085–0.095 beavers/wolf/day) and predation rates (0.38–0.42, proportion of beaver population killed by wolves) of wolves on beavers. The predation rate (0.38–0.42) of beavers in the ARP home range in 2015 was nearly 2–3 times as high as the estimated annual mortality rate for beavers in lake habitats in VNP based on known fate of radio-marked individuals (0.14; 2006–2009) or mark-recapture of ear-tagged individuals (0.22; 2006–2014; Smith et al. 2016). However, Smith et al. (2016) only estimated mortality for beavers ≥ 2.5 years old and it is likely annual mortality would have been higher had younger age classes been included. Still, our results suggest that predation by wolves represents a significant portion of beaver mortality in our study area.

Despite the high level of predation, we estimated the beaver population in the ARP home range increased by 43% from 2015 to 2016. This is especially surprising as stable or growing beaver populations typically decrease when total annual mortality rates exceed 25–33% (Henry and Bookhout 1969, Payne 1984, 1989, Novak 1987, Potvin et al. 1992). Intense predation by black bears (*Ursus americanus*) on Stockton Island in Lake Superior caused a dramatic decline in the beaver population, but predation was likely exacerbated by a shortage of available food for bears on the island (Smith et al. 1994). In Norway, beaver (*Castor fiber*) populations declined by 46% after a 3-year spring hunting season removed 22–26% of the beaver population annually (Parker et al. 2002, Parker

and Rosell 2014). Wolves removed an estimated (via scat analysis) 15% of the beaver population annually in Quebec, Canada, but beaver populations remained stable (Potvin et al. 1992). The beaver density in the ARP home range was relatively high in 2015 compared to other parts of beaver range in Minnesota (S. K. Windels, VNP, unpublished data) but substantially lower than the densities (0.9–1.6 lodges/km²; VNP, unpublished data) in the rest of VNP in 2015 and 2016 (Fig. 1). However, beavers from densely populated regions of the park’s interior commonly disperse towards the margins of, or outside the park, including portions of the ARP home range (S. K. Windels, unpublished data). We suspect this dispersal may be compensating for the effect of wolf predation on the beavers in this area.

Over the past century beaver (*Castor* spp.) populations across North America and Europe have recovered rapidly from over-exploitation to the point that beavers in many areas are regarded as pests. Whether this rapid recovery of beaver populations was facilitated, in part, by the overall absence of many of the historical predators of beavers (mainly cougars [*Puma concolor*], bears [*Ursus* spp.] and wolves) is unknown. Some have suggested that wolves—the primary natural predator of beavers—can suppress beaver populations to some extent (Potvin et al. 1992, Romanski 2010), and that in the absence of wolves beaver populations become more irruptive (Hartman 1994). Our results suggest that wolf predation on dense beaver populations has minimal impact. For example, the 43% increase in beaver density in ARP from 2015 to 2016 was consistent with the 27% increase in beaver lodge density in VNP as a whole during the same period (VNP, unpublished data).

Estimating the proportion of the beaver population removed annually via wolf predation is challenging because estimating beaver population size is primarily done in fall when beavers are actively constructing and maintaining dams, lodges, and food caches (Baker and Hill 2003). However, using fall beaver population estimates to determine predation rates assumes beaver populations have already replaced all individuals killed by wolves during spring–fall prior to fall population estimates. That is, although wolves predominantly kill beavers from spring to fall, beaver population estimates reflect fall population size and thus could overestimate the magnitude of predation on the beaver population. Even if all predation of beavers by the ARP occurred prior to our beaver population estimates (which we know is not the case), the predation rate of beavers by ARP would still be high (0.27–0.29; predation rate = [80–88 beavers killed by wolves]/[212 beavers based on 2015 fall population estimate + 80–88 beavers killed by wolves prior to fall population estimate]).

Wolf V009 killed beavers at >20% (8) of the lodges in the ARP home range. At 2 of those lodges, V009 removed 2 beavers from the same lodge suggesting predation can affect some colonies more than others. If this is the case, then some colonies likely had >2–3 individuals killed by wolves, whereas other colonies likely had ≤ 1 beaver killed in 2015. If predation is evenly distributed across colonies, then each colony likely had approximately 2 members killed by wolves during the ice-free season.

Estimating the total number of prey killed by a pack of wolves during the summer can be difficult because wolves are frequently foraging as individuals (Demma et al. 2007, Metz et al. 2011, Barber-Meyer and Mech 2015). Further, how similar the diet of 1 pack member is to all other pack members is unknown in most cases. Because we only

have information from V009, we assumed that each pack member consumed the same number of beavers as V009. Pack members will hunt and kill small prey such as beavers together but how frequently this occurs is largely unknown (Palacios and Mech 2010). We estimated V009 was with ≥ 1 pack member at 2 beaver kills (Gable et al. 2016). If pack-member overlap at beaver kills for ARP was higher than this, then our pack-level predation rate is likely an overestimate.

Breeding individuals, such as V009, generally have a larger energetic demand during the ice-free season because they must obtain enough food for themselves and their pups (Mech and Boitani 2003). Thus, it is possible V009 might have killed more frequently than other wolves in the ARP. Wolf hunting success of large ungulate prey is generally a function of wolf sex and age (MacNulty et al. 2009*a, b*). Males are usually more successful hunters than females because they are generally larger, but whether males are better at hunting beavers is unknown (MacNulty et al. 2009*a*). In Latvia, the proportion of wolf diet that was beaver was higher in adult wolves (9% beaver) than 1–2-year-old wolves (3% beaver), and in males (13%) than females (3%; Žunna et al. 2009). If breeding individuals kill more small prey than other pack members or males are better at hunting beavers than females, our pack-level predation rate based on V009 is likely an overestimate.

Conversely, it is possible that we underestimated the number of beavers killed by ARP in 2015. By using 4–6-hour fix-interval clusters, we almost certainly missed kills because small prey can be killed and consumed in short periods (Webb et al. 2008, Palacios and Mech 2010, Gable et al. 2016). Indeed, we documented several beaver kills in VNP during 2016–2017 by wolves fitted with 20-minute fix-interval collars where

wolves remained at the kill <4 hours (T. D. Gable, VNP, unpublished data). Additionally, the GPS collar on V009 did not transmit 13% of fixes during our study so some clusters in active beaver habitats were almost certainly missed. Further, the proficiency of wolves hunting ungulates generally peaks around 3–5 years old and then decreases until death (MacNulty et al. 2009b). Whether this is true of wolves hunting beaver is unknown, but it suggests V009 could have been less proficient at hunting beavers than other pack members. Nonetheless, our estimates of predation rates from kills and scat analysis were similar, leading us to believe they are representative of wolf predation rates on the beaver population in the ARP home range during the ice-free season. Notably, wolves do kill beavers during the winter but at a much lower rate because beavers are mostly protected in their lodges or under the ice (Mech 1966, Peterson 1977, Forbes and Theberge 1996).

Although we only have estimates of kill and predation rates from a single collared wolf from a single pack, we suggest wolf predation can be a substantial source of mortality in beaver populations. Further research is needed to understand how wolf predation affects beaver populations temporally and spatially. Moreover, understanding whether mortality via wolf predation in beaver populations is compensatory or additive would help elucidate how wolf predation affects beaver populations (Mech and Peterson 2003). Because the beaver population responded rapidly to the substantial level of wolf predation, our results suggest that mortality via wolf predation could be compensatory. Mortality from human harvest can be compensatory in beaver populations (Payne 1984, 1989), and in Quebec harvest mortality appeared to compensate for reduced predation mortality following wolf removal (Potvin et al. 1992). Ultimately, the number of beavers removed by wolf predation is a function of beaver population size, wolf population size,

and individual wolf kill rates. However, individual kill rates of wolves on beavers could be influenced by wolf age and sex, ungulate availability, beaver density, and specialization or avoidance of beavers (Urton 2004, MacNulty et al. 2009*a, b*, Metz et al. 2012, Moayeri 2013). Thus, estimates of kill and predation rates of different wolves under a variety of conditions are necessary to understand the effect of wolf predation on beaver populations. We suggest long-term study of beaver populations, wolf populations, and wolf predation of beavers is necessary to understand how wolf predation affects beaver populations (Engeman et al. 2017).

MANAGEMENT IMPLICATIONS

Our results suggest that the effect of wolf predation on dense beaver populations in a multi-prey system is minimal and that changes in beaver population size are likely more influenced by other factors (e.g., food availability, precipitation). However, we suspect wolf predation on individual lodges could affect the social structure and persistence of colonies. Additional research is needed to understand how predation influences beaver populations at the colony and population scale under various ecological conditions.

Table 1. The number of beavers killed in 2015 by wolves in the Ash River Pack in Voyageurs National Park, Minnesota, USA using monthly estimates of the Ash River Pack (4 adults, 2 pups) biomass requirements and the monthly percent biomass of the Ash River Pack diet that was beaver based on scat analysis.

	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov ^a	Total
Adult wolf weight (kg)	28	28	28	28	28	28	28	28	
Pup weight (kg)	1	3	5	7	10	13	18	23	
Total pack weight (kg) ^b	114	118	122	126	132	138	148	158	
Biomass requirement (kg) ^c	308	329	329	352	368	373	413	284	2,756
Beaver in diet (%) ^d	46	60	10	5	8	53	52	33	
Beavers killed ^e	12	16	3	1	3	16	18	8	76

^aWe considered lakes frozen and beavers generally inaccessible after 20 Nov.

^bMonthly pack weight = (adult weight×4 adults) + (pup weight×2 pups).

^cBiomass requirements = pack weight×0.09 kg/kg of wolf/day (Peterson and Ciucci 2003).

^dPercent biomass of beaver in Ash River Pack diet from Gable et al. (2017a).

^eBeavers killed = (biomass requirement×beaver in diet)/12.1 (digestible biomass of beaver carcass; Jankowska et al. 2005, Gable et al. 2017a)

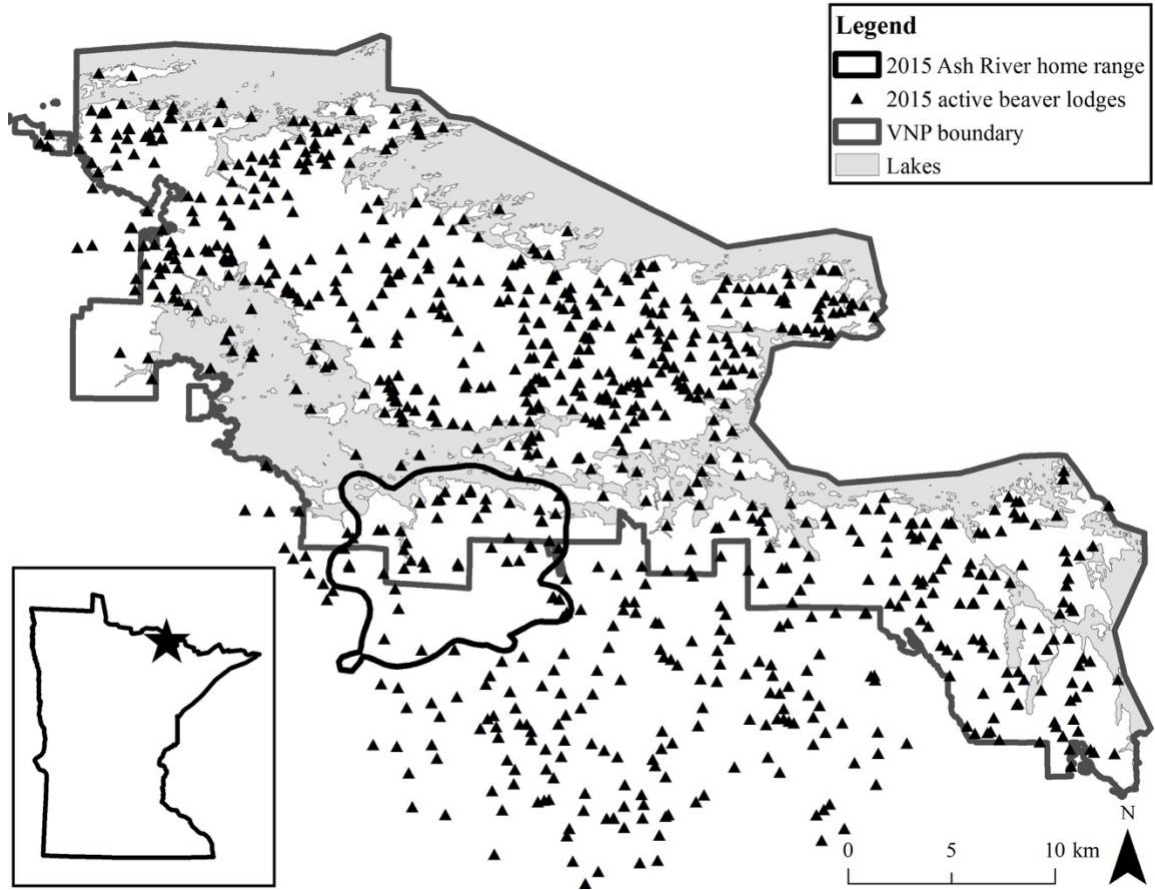


Figure 1. The 95% adaptive kernel home range of wolves in the Ash River Pack in Voyageurs National Park, Minnesota, USA. The black triangles represent all the active beaver lodges identified during the 2015 aerial beaver lodge census in and adjacent to Voyageurs National Park. The star in the inset marks the location of Voyageurs National Park in Minnesota.

Chapter 3: Do Wolves Ambush Beavers? Video Evidence for Higher-Order Hunting Strategies

ABSTRACT Over the past decade, there has been much debating about whether wolves possess high-order cognitive abilities that facilitate deliberate or cooperative hunting strategies such as ambush to capture prey. Beavers (*Castor canadensis*) can be important alternate or primary prey for wolves in North America and Europe, but no observations of wolves hunting and killing beavers exist. We describe the first documented observation of a gray wolf killing a beaver, an observation that has provided valuable insight into how beavers defend themselves when attacked by wolves, how wolves hunt beavers, and the predatory strategies and cognitive abilities of wolves. We suggest that wolves learn how to hunt beavers using high-order mental abilities combined with information learned from prior interactions with beavers.

INTRODUCTION

Wolves are cursorial predators that rely predominantly on outrunning and outlasting ungulate prey to kill them (Peterson and Ciucci 2003). There are a few anecdotal accounts, though, of wolves attempting to, or successfully ambushing prey such as caribou (*Rangifer tarandus*), muskox (*Ovibos moschatus*), arctic hares (*Lepus arcticus*) and Canada geese (*Branta canadensis*) (Mech et al. 2015, Nichols 2015). However, there is much skepticism about whether wolves use deliberate or cooperative hunting strategies such as ambush to capture prey (Peterson and Ciucci 2003, Muro et al. 2011, Escobedo et al. 2014, Mech et al. 2015).

Mech (2007b) suggested that wolves use higher-order mental processes to hunt and kill prey (defined as: “foresight [behaving appropriately for dealing with a future event], understanding [comprehending complex relationships], and planning [deciding to

behave in a way that considers information relevant to perceived outcome]”). There has been much debating whether or not the perceived cooperation between wolf pack members while hunting is evidence of these higher-order mental processes or advanced cognitive abilities (Escobedo et al. 2014, Mech et al. 2015). Computer simulations suggested that wolf-pack ambushing behavior, which might appear purposive or intentional, could be the result of wolves following simple rules instead of using advanced cognitive abilities (Muro et al. 2011). Such simulations were likely oversimplifications of wolf hunting behavior (Bailey et al. 2013) and did not incorporate the temporal and spatial complexities associated with ambush predation.

For most of the year, wolves hunt large ungulate prey cooperatively in packs (Peterson and Ciucci 2003). During late spring–early fall, wolf pack cohesion is reduced, and wolves commonly forage as individuals or in small groups within the pack (Demma et al. 2007, Metz et al. 2011, Barber-Meyer and Mech 2015). The decrease in pack cohesion during hunting coincides with the period when wolves use homesites (i.e., den and rendezvous sites) to raise pups, and when wolves are largely relying on smaller prey such as ungulate neonates, beavers (*Castor* spp.), and hares (*Lepus* spp.) (Gable et al. 2018b). Our understanding of wolf predation during this period is relatively poor (Palacios and Mech 2010, Metz et al. 2012, Gable and Windels 2018) as most wolf predation studies have occurred during winter when conditions are more conducive to finding wolf-killed prey and observing wolf hunting behavior (Mech et al. 2015).

Beavers are important alternate and primary prey for wolves from spring to fall (i.e., when ice-cover is absent) in many systems in northern North America and to a lesser degree, parts of Europe and Asia (Gable et al. 2018d). In areas with mild winters

(i.e., minimal ice-cover) wolves will hunt beavers all year, and as a result, beavers can be the primary annual prey of wolves in these areas (Milne et al. 1989, Sidorovich et al. 2017). Despite this, little is known about the interactions between wolves and beavers. In Voyageurs National Park, wolves appeared, based on where wolves killed beavers and how wolves spent time in beaver habitat, to hunt beavers by waiting for, and then ambushing beavers once they came on or near land (Gable et al. 2016). This indirect approach to understand how wolves hunt beavers was necessary because no documented observations of wolves killing beavers exist, despite the thousands of hours of wolf observations that have occurred around the world (Gable et al. 2016). Herein we describe the first observation of a gray wolf killing a beaver. Fortunately, this event was captured on video which allowed a detailed analysis of the behavior of both the wolf and the beaver during this encounter. Although this is only one observation, it provides extremely valuable information about wolf-beaver interactions and the complex hunting strategies that wolves are capable of.

METHODS AND RESULTS

In late October 2015, co-author Trent Stanger (TS) observed and recorded a video of a wolf hunting and killing a beaver while he was driving logging roads moose hunting in a remote, forested area outside of Remigny, Quebec (47° 46' N, 79° 12' W). In total his observation lasted about 15 minutes, and he recorded the last 4 minutes of the observation when the wolf attacked and killed a beaver (Video S1). On the day of the observation, the temperature was below freezing (<0° F), a light dusting of snow was on the ground, and there was no wind (Video S1). We have provided a detailed description of his account and put the corresponding time (min:sec) from the video in parentheses.

TS did not record the specific location or the direction he was driving when the observation occurred but a detailed map of the site where the encounter occurred is documented in Fig. 1. For simplicity we considered north to be the direction the wolf was facing when the video starts (Fig. 1, Video S1). We edited out 1 minute of the video (starting at 0:52) when the wolf moved into the forest and TS exited the car to observe on foot because the video was unstable and of poor quality.

TS was driving down a logging road around 10:00 a.m. in a pick-up truck when he noticed a wolf standing in the middle of the road facing away from him staring into the forest. TS stopped the truck about 50 m from the wolf and watched as the wolf stood for 6-7 minutes staring into the forest and down the road. The wolf then started trotting down the road for about 300-400 m before slowing down and starting to walk cautiously for a few meters. TS followed slowly in his truck about 50 m behind the wolf. The wolf then stopped—its head below its shoulders, tail somewhat lowered, and body still—and stared intently into the forest to the east of the road for 1-2 minutes (Fig. 2A). There was an active beaver pond about 15 m north/northeast of the wolf, and water from the pond had flooded the road about 10 m ahead of the wolf (Fig. 1). A small stream ran along about 1-2 m off the east side of the logging road, and fed into the southeast corner of the beaver pond.

After the wolf stood still for 1-2 minutes, TS slowly approached the wolf from behind in the truck but the wolf appeared unconcerned and continued staring into the forest (0:00-0:05). As TS got within 15-20 m of the wolf, the wolf took a few steps forward, briefly looked back at the truck, and then ran into the forest on the east side of the road (0:06-0:07). Two seconds later the wolf re-appeared on the road dragging a

struggling, medium-sized beaver out of the forest (0:08, Fig. 2B). Once on the road, the beaver escaped the wolf briefly (0:10) and started running across the road toward the forest on the west side of the road (Fig. 2C). The wolf quickly grabbed the beaver by the tail and dragged it back out into the road (0:12-0:14) where the wolf continued attacking the beaver. Throughout the attack, the beaver repeatedly tried to bite the wolf around the face. At one point (0:15-0:16) the beaver appeared to have successfully bitten the wolf on the shoulder, causing the wolf to briefly jump back and release the beaver (Fig. 2D). Over the first 30 seconds of the attack, the wolf was primarily biting and dragging the beaver by the base of the tail (Fig. 2E, 2F). When possible, though, the wolf tried to get ahold of the beaver by the abdomen in an apparent attempt to pin the beaver (Fig. 2F, 0:17-0:25; 0:42-0:46).

The beaver then appeared to escape the wolf for a few seconds (0:50) and run into the brush on the west side of the road where the wolf quickly caught it again. When the wolf and beaver disappeared into the brush (0:50), TS slowly approached in his truck, stepped out of the truck, and observed the wolf still attacking the beaver ~10 m off the road (0:55-3:00). The wolf appeared oblivious of TS observing the encounter only meters away. The beaver continued to fight the wolf, but appeared to quickly become more lethargic likely due to exhaustion and injury (1:00-2:00). Every time the beaver tried to move forward the wolf would grab the beaver by the tail and jerk it back. The wolf had largely subdued the beaver as the beaver was making minimal movements (1:58-2:36) until the beaver slowly turned over in an apparent attempt to defend itself or escape (2:37-2:38). The wolf, likely observing the beaver's lethargy, immediately grabbed the beaver by the head and neck (2:38-2:41), which likely killed the beaver as the beaver was

not observed moving again. Interestingly, this was the first time during the attack that the wolf attempted to bite the beaver's head. A few seconds after the beaver appeared dead, the wolf, with its muzzle covered in blood, noticed TS observing from the road (3:51) but appeared hesitant to leave the kill. TS then returned to his truck and left the area so as not to further disturb the wolf. We presume the wolf consumed the beaver but TS did not return to the kill after his observation.

In total, it took the wolf 3 minutes and 31 seconds to kill the beaver. The beaver was about 15 m upstream from the pond in the small creek when the wolf attacked it (Fig. 1). The beaver was likely traveling up this stream to access forage when it was attacked as there were no fresh-cuttings or other terrestrial beaver sign where the attack occurred but further upstream (~5 m) there were a few fresh-cut branches (Fig. 1).

DISCUSSION

To our knowledge this is the first recorded observation of a wolf hunting and killing a beaver (Mech et al. 2015, Gable et al. 2018*d*). Our rare observation provides valuable insight into how beavers defend themselves when attacked by wolves, how wolves hunt beavers, and the predatory strategies and cognitive abilities of wolves. Until now, observing wolves hunting beavers has been nearly impossible largely due to the dense riparian vegetation around most beaver habitats. In northern Manitoba, wolves were observed stalking beavers near feeding trails but unfortunately no other information about the observations is available (Nash 1951).

Beavers have been thought to be easily subdued once caught on land by wolves (Basey and Jenkins 1995, Mech et al. 2015), but our video suggests that beavers can be aggressive prey once attacked. Indeed, throughout the encounter the beaver continuously

tried to bite the wolf. Beavers have incredible bite strength combined with long, sharp incisors that could seriously injure or kill a wolf. In Calgary, Alberta, beavers mortally wounded a husky (*Canis familiaris*) and caused serious injury to 6 other dogs in 2010 (CBC News 2010). At one point the beaver successfully bit the wolf, which caused the wolf to briefly jump back and release the beaver (Fig. 2D). Ultimately, releasing the beaver was inconsequential in this encounter because the beaver was not close to water. When close to deep water, though, this defense could make the difference between the wolf killing the beaver and the beaver escaping into the water. In Voyageurs National Park, live-captured beavers have had healed puncture tail wounds presumably from wolves (the main predators of beavers in that system), indicating beavers do escape wolves even after being attacked on land (S. Windels, *unpublished data*). It is worth noting that the beaver (presumably a sub-adult) from our observation was not large (~10 kg). We can only surmise that large, adult beavers (~20-30 kg; Novak 1987, Baker and Hill 2003) could present a challenge for wolves, especially in areas such as Minnesota, Quebec, and Ontario, where wolves generally average <35 kg (see Table 5 in Theberge and Theberge 2004, Chenaux-Ibrahim 2015, S. Windels, *unpublished data*).

We can confirm that wolves do hunt and kill beavers by surprising and ambushing them (Fig. 2A). Wolves are not generally ambush predators (although see Mech 2007b), instead relying on outrunning and outlasting ungulate prey to kill them (Mech et al. 2015). Because of this most successful hunts of ungulate prey are simple and straightforward (Peterson and Ciucci 2003). However, our results suggest that wolves have a unique ability to switch between cursorial and ambush hunting strategies depending on the prey. Several authors (see Gable et al. 2016) have suggested that

wolves hunt beavers this way, but their inferences were based on indirect evidence (e.g., where wolves bed down in active beaver habitats, or kill sites). When actively hunting beavers, wolves likely wait concealed near areas of high beaver activity and ambush beavers once they come nearby (Gable et al. 2016). In Wisconsin, a wolf was observed successfully killing a beaver using this strategy (R. Schultz, *personal communication*). Although our recorded observation was of a wolf opportunistically encountering a beaver, there are similarities between this encounter and how wolves are thought to actively hunt beavers: 1) the wolf waited, albeit only a few minutes, after detecting the beaver for the beaver to get close, and 2) the wolf appeared to use vegetation along the roadside for concealment, which ultimately allowed the wolf to wait undetected until the beaver was within a few meters of the wolf (Fig. 2A).

Using vegetation for cover is an uncommon hunting strategy for cursorial canids (Bailey et al. 2013) but is likely necessary to successfully ambush beavers. Beavers have well-developed olfactory and auditory abilities that they use to detect and avoid predators (Novak 1987, Severud et al. 2011). Further, although beavers have poorly developed eyesight their vision is likely sufficient to detect predators at close distances (Novak 1987). Because beavers generally forage in close proximity to water and can detect predators over 15 m away, wolves only have a short window to catch beavers once they have been detected (Basey and Jenkins 1995). Thus to ambush a beaver, a wolf must get close enough to the beaver so that the beaver does not have adequate time to return to water after hearing, seeing, or smelling the wolf.

Our observation provides further evidence that wolves do have higher-order mental abilities that facilitate complex hunting strategies. Wolves are able to understand

causal relationships and adapt their cognitive abilities to their social environments (Lampe et al. 2017), and we think it is logical that these cognitive abilities extend to hunting strategy. The wolf's behavior suggests the wolf had detected the beaver 3-4 minutes prior to attacking (i.e., when the wolf went from a trot to a slow walk). However, instead of immediately attacking the beaver, the wolf slowly approached and waited for a few minutes. While the wolf was waiting on the road, we suspect the beaver was traveling upstream in the creek toward the wolf as it would be counterintuitive for the wolf to wait while the beaver traveled further downstream toward the safety of the pond. Indeed, the presence of fresh-cut branches further upstream from the attack site indicates that the beaver was likely moving up stream to access forage. The progression of this hunt suggests the wolf gathered information about its physical environment and the behavior of the beaver, processed this information (understanding), and then determined that its probability of success would increase by waiting instead of immediately attacking (foresight, planning). If the wolf had attempted to attack the beaver immediately after detecting the beaver, instead of waiting, it is possible the attempt would have been unsuccessful given how close the beaver was to the pond (<15 m; Basey and Jenkins 1995). The fact that the wolf waited for the beaver to move closer suggests that the wolf correctly interpreted and anticipated the beaver's behavior. In the end, this hunting strategy allowed the wolf to get within a few meters of the beaver, which was presumably unaware of the wolf. But how did the wolf know that the beaver would continue traveling up the small creek?

We think that hunting beavers is a learned behavior whereby wolves use higher-order mental abilities along with information learned from prior interactions with

beavers. Beavers are central place foragers that use feeding trails to access forage close (generally <50 m) to a central body of water (Baker and Hill 2003). Thus, beavers are unique prey for wolves given the short periods beavers spend on land in predictable areas (i.e., feeding trails, below dams) close to water. If wolves are to exploit beavers as a resource, having knowledge of terrestrial beaver behavior is advantageous, and arguably, necessary (Mech et al. 2015). We suspect that wolves are able to learn how beavers behave on land, can interpret beaver behavior, and employ hunting strategies to maximize success. Indeed, the fact that wolves will wait near areas of high beaver activity for hours to hunt beavers implies this is the case (Gable et al. 2016). Such a strategy requires prior knowledge of beaver behavior which is either learned from observing other wolves hunting beavers or through individual encounters with beavers. At what point, or how quickly, wolves learn how to hunt beavers is unknown. Learning different hunting strategies would be advantageous because it would allow wolves to exploit temporarily abundant alternate prey, or to persist during periods when primary ungulate prey are unavailable. Flexibility in hunting strategies has implications for predicting the functional role and conservation of wolves because carnivore hunting mode, specifically cursorial vs. ambush, is important to trophic control in ecosystems (Romero and Koricheva 2011).

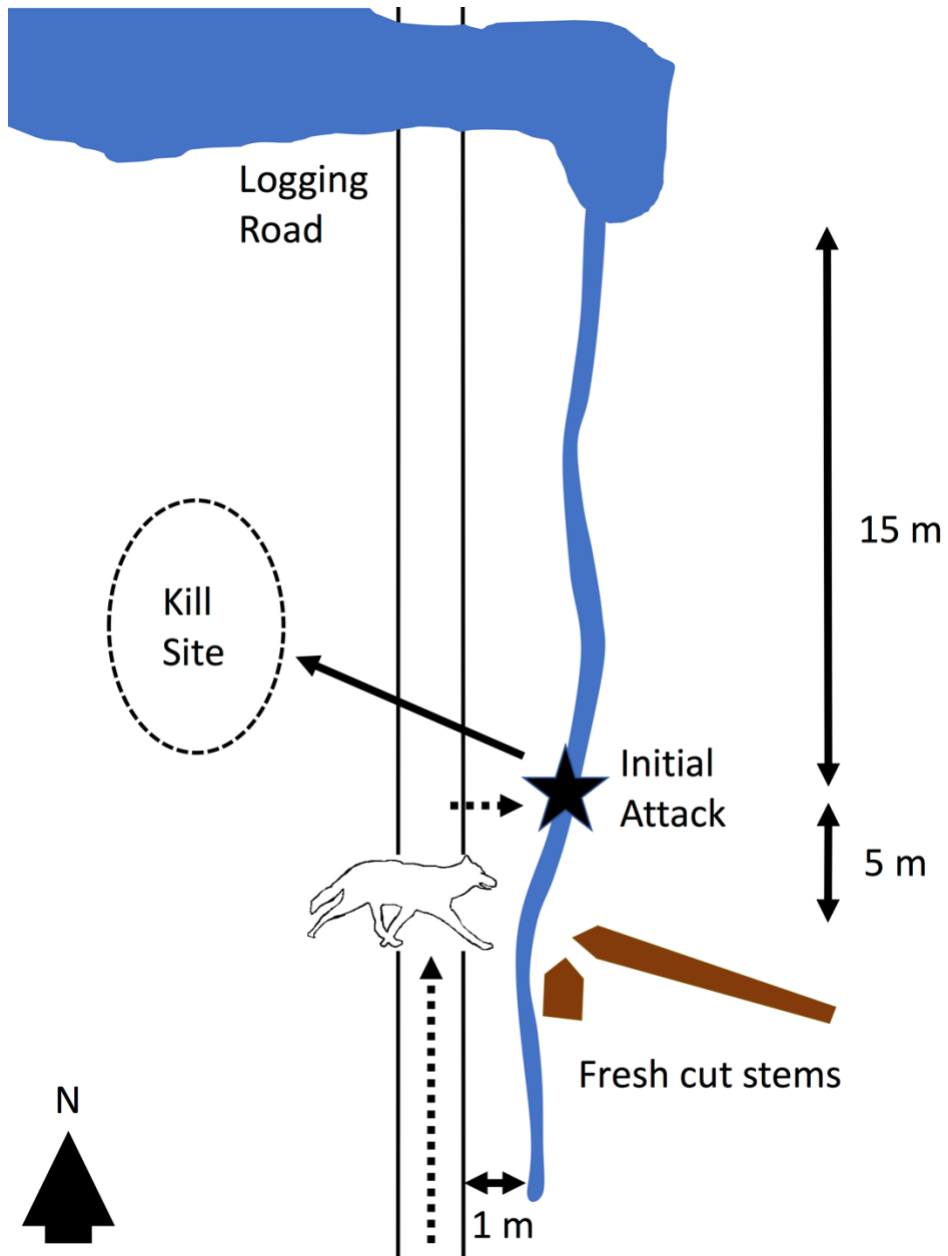


Figure 1. A map detailing how a wolf encountered, attacked, and killed a beaver that was upstream of an active beaver pond in a small creek. The dashed lines show the wolf's movement prior to the attack and the solid line shows the general movement of the wolf and beaver from the attack site to the kill site.



Figure 2. Progression of a wolf hunting a beaver: A) the wolf waiting for, and then ambushing the beaver, B) dragging the beaver out of a small stream and into the road, C) chasing the escaping beaver, D) briefly releasing the beaver after being bitten, E) attacking the beaver again shortly after releasing it, F) continuing to attack and subsequently kill the beaver.

Chapter 4: Wolves Choose Ambushing Locations to Counter the Defence

Mechanisms of their Prey

ABSTRACT Comprehensive knowledge of ambushing behaviour requires an understanding of where a predator *expects* prey to be, which is often unknowable because predators are ambushing mobile prey that exhibit complex and inconspicuous movements. Wolves are cursorial predators, but they use ambush strategies to hunt beavers. Terrestrial beaver activity is predictable because beavers use the same well-defined, conspicuous habitat features repeatedly. Thus, studying where wolves wait-in-ambush for beavers provides a unique opportunity to understand how predators select ambushing locations in relation to prey activity. We searched 11,817 clusters of GPS-locations from wolves in the Greater Voyageurs Ecosystem, Minnesota, and documented 748 ambushing sites and 214 instances where wolves killed beavers. Wolves appeared to select ambushing locations: 1) with olfactory concealment to avoid detection from the highly-developed olfactory senses of beavers; 2) close (generally <5 m) to beaver habitat features to take advantage of beavers' inability to visually detect motionless predators; and 3) farther from water (when possible), presumably to minimize the physical challenges of killing a beaver. The proportion of kills at each beaver habitat feature was different than the proportion of ambushing sites at each feature, indicating that capture and encounter rates, in addition to opportunistic predation, differ by habitat feature. Our results demonstrate that ambush predators can: 1) anticipate the movements and behaviour of their prey due to a fundamental understanding of their prey's sensory abilities and 2) strategically select ambushing locations by simultaneously accounting for

abiotic and biotic factors, ultimately allowing them to successfully counter their prey's defences.

INTRODUCTION

How predators hunt their prey provides insight into predator space use, energetics, and time budgets (Williams et al. 2014, Bryce et al. 2017). Predators are broadly categorized as either ambush predators (i.e., sit-and-wait or sit-and-pursue strategies) or cursorial predators (i.e., wide-ranging, active hunting strategy) (Preisser et al. 2007, Schmitz 2008, Miller et al. 2014). Because predation is a strong evolutionary force, understanding predator hunting mode and the strategies predators use to hunt prey can reveal the behavioural adaptations prey use to minimize fatal encounters with predators (Romero and Koricheva 2011, Kohl et al. 2019). Predators that ambush are more likely to lead to behavioural responses in prey compared to those that use cursorial strategies because an ambushing predator is concentrated in a localized area (i.e., the habitat domain of ambushing predators is generally smaller than coursing predators, Miller et al., 2014), allowing prey to ascertain information about the location of the predator and alter their behaviour accordingly (Schmitz 2008). Despite this, ambush hunting—in particular where and how predators decide to ambush prey—has received less attention and is more poorly understood than cursorial hunting behaviour (Rossoni and Niven 2020), likely due to the challenges of studying cryptic ambush behaviour (Li et al. 2003, González-Bernal et al. 2011).

Where predators choose ambushing locations is scale-dependent because predators must choose where to wait at both macrohabitat (where predators focus ambushing on a home-range scale) and microhabitat (the specific locations predators

choose to wait-in-ambush) scales (Rodríguez-Robles and Glaudas 2011, Clark et al. 2016). Macrohabitat selection by ambush predators is thought to be primarily a function of prey abundance, vulnerability, or accessibility (Hopcraft et al. 2005, Balme et al. 2007, Rodríguez-Robles and Glaudas 2011). When selecting ambush locations *within* macrohabitats (i.e., microhabitat selection), predators must balance the probabilities of: 1) being detected by prey (Li et al. 2003, Wilson 2007), 2) detecting their prey (Gall and Fernández-Juricic 2009), 3) encountering prey at a given location (i.e., encounter rates; Clark, 2004; González-Bernal et al., 2011), and 4) killing prey at that location should an encounter occur (i.e., capture rates; Shine & Li-Xin, 2002). Predators are likely under strong selective pressures to select optimal ambushing locations given the amount of time necessary to wait for and capture prey via ambushing (Du et al. 2009). Thus, optimal ambushing sites are generally considered those that maximize encounter and capture rates of prey while minimizing detection by prey (Wilson 2007, González-Bernal et al. 2011).

Systematically documenting ambushing behaviour is challenging, as many ambush predators are difficult to observe because they often rely on secrecy and concealment to hunt prey (Rodríguez-Robles and Glaudas 2011). Further, determining where predators anticipate or expect prey to appear is challenging, and often unknowable because ambush predators are often trying to hunt mobile prey that exhibit complex and inconspicuous movement patterns. Thus, relatively few studies have examined whether ambush strategies are specifically adapted to counter the anti-predator behaviours and defences of their prey. Although logistically challenging to document, such information is vital for a comprehensive understanding of the behavioural adaptations predators use to catch prey (Li et al. 2003) and where predators choose to wait-in-ambush.

Most research on ambushing behaviour has focused on how herpetofaunal and arachnid predators, and to a lesser degree avian, fish, and other invertebrate predators, select ambushing locations at the microhabitat scale. However, there is very little information on how terrestrial carnivores select ambushing locations at the microhabitat scale. Part of this is because these smaller taxa are easier to observe and study in the field relative to larger predators (e.g., Schraft et al. 2019). Additionally, smaller taxa are often well-suited for controlled experiments where ambushing behaviour can be examined under various conditions (Preisser et al. 2007, Schmitz 2008, Du et al. 2009, González-Bernal et al. 2011, Miller et al. 2014). Our understanding of carnivore ambushing behaviour is primarily based on anecdotal observations (Mech 2007*b*, Eads et al. 2010, Gable et al. 2018*a*) or by correlating predator movements or kill site locations with coarse biotic and abiotic metrics (e.g., habitat type, vegetation density, wind speed). For instance, researchers often assume that habitat selection by predators provides insight into where predators try to ambush prey (Hopcraft et al. 2005, Balme et al. 2007, Loarie et al. 2013), or that characteristics from kill sites are representative of where ambush predators choose to sit-and-wait (Lone et al. 2014, Donadio and Buskirk 2016, Lendrum et al. 2018). Such research might provide cursory insights into predator ambushing behaviour but precludes a fine-scale or detailed understanding of carnivore ambushing behaviour. Consequently, the fundamental questions of where and how carnivores choose to wait to ambush prey remain unanswered (González-Bernal et al. 2011).

Wolves (*Canis lupus*) are primarily cursorial predators, but they have highly flexible hunting strategies and can switch to ambushing when targeting alternate prey such as beavers (*Castor canadensis*) and freshwater fish (Gable et al. 2018*c, a*). Beavers

are important summer prey for wolves in many ecosystems, constituting up to 42% of wolf diets during spring-fall (Gable et al. 2017*a*, 2018*d*). Wolves—the primary natural predator of beavers across the circumboreal ecosystem (Gable et al. 2018*d*)—primarily hunt beavers as individuals, not as a pack (Gable et al. 2016, Gable and Windels 2018).

Beavers are unique prey for wolves given the short periods they spend on land close to water. When on land, beavers are primarily cutting woody vegetation for food and lodge/dam construction, building or repairing dams or lodges, or are creating and maintaining scent mounds that demarcate their territory (Baker and Hill 2003). Most notably, beavers use well-defined ‘feeding trails’, which rarely exceed 40-60 m, to access and cut woody vegetation (Jenkins 1975, Novak 1987, Salandre et al. 2017). Where beavers will be on land is predictable because they use the same habitat features repeatedly, and their terrestrial activity is conspicuous and confined to a small area (Baker and Hill 2003, Gable et al. 2018*a*, *d*). To minimize fatal encounters with predators on land, beavers primarily rely on their highly-developed olfactory senses to detect predators (Baker and Hill 2003, Rosell and Sanda 2006), and remain close to water to quickly escape should a predator be detected or encountered (Basey and Jenkins 1995, Campbell-Palmer and Rosell 2010, Gable et al. 2018*a*).

Although the general strategy wolves use to hunt and kill beavers (i.e., waiting-in-ambush) is relatively well understood (Gable et al. 2016, 2018*a*), specifics about how, when, and where wolves attempt to, and successfully do, ambush beavers are unknown. Fortunately, where wolves wait-in-ambush for beavers can be identified by searching clusters of locations from GPS-collared wolves (Gable et al. 2016). This approach allows us to determine not only where wolves choose to wait-in-ambush but also how they

choose ambushing locations relative to where they likely expect or anticipate beavers to be active on land (Gable et al. 2016, 2018*d*).

Our primary objective was to describe where and how wolves ambush beavers. Specifically, we sought to understand how wolves selected ambushing locations in relation to terrestrial beaver activity, water, and wind direction, and whether they killed beavers in the same habitats where they waited to ambush them. We expected wolves to select ambush locations that would allow them to counter the two main defence strategies of beavers: 1) using olfaction to detect predator odours (Campbell-Palmer and Rosell 2010), and 2) proximity to water to facilitate a quick escape (Basey and Jenkins 1995, Gable et al. 2018*a*). Thus, we hypothesized that wolves would choose ambushing locations with olfactory concealment (i.e., where the wind direction would not reveal the wolf's presence) and that would also be farther from water, when possible. We also expected wolves would choose ambushing locations close (<5 m) to beaver activity because beavers, which have poor eyesight, cannot visually detect motionless predators but can see pursuing predators from >15 m away (Basey and Jenkins 1995, Gable et al. 2018*a*). Finally, we expected to find differences between where wolves waited-in-ambush for, and killed, beavers, as previous work has shown that a certain, but unknown percent, of wolf-killed beavers are killed opportunistically (i.e., killed via opportunistic encounters) and not via ambushing (Gable et al. 2016).

METHODS

Our study was conducted as part of the long-term Voyageurs Wolf Project, located in the Greater Voyageurs Ecosystem (GVE), which is a southern boreal ecosystem which includes Voyageurs National Park and the area southerly adjacent to Voyageurs National

Park. For a detailed description of the study area, see Gable et al. (2016). During 2015-2019, we used foothold traps and cable restraints to capture wolves and fit them with 20-min-fix-interval GPS-collars (IACUC protocol: MWR_VOYA_WINDELS_WOLF). In 2015, 3 wolves were fitted with collars that took fixes every 4-12 hr instead of every 20 min (see Gable et al. [2016] for more details). We searched clusters of GPS-locations from collared wolves during April-November to identify predation events. In 2015, we only searched clusters where a wolf had remained within a 200- m area for ≥ 4 hr (see Gable et al. [2016]). Our objective in 2015 was to visit random GPS-clusters in beaver habitats because we primarily wanted to locate where wolves were killing beavers (Gable et al. 2016, Gable and Windels 2018). During 2016-2019, we adjusted our cluster criteria to be ≥ 2 consecutive locations (≥ 20 min) within a 200-m radius of one another (Gable et al. 2018c). In 2016-2017, we searched a random subset of clusters from GPS-collared wolves and in 2018-2019, we visited every cluster from GPS-collared wolves. The change in cluster criteria and percent of clusters searched represents our trial-and-error process to figure out how to successfully study wolf predation on small prey from spring to fall in a southern boreal ecosystem, which had proven difficult prior to our research (Palacios and Mech 2010, Gable et al. 2016). The change in our cluster criteria over time should not bias our results in regards to wolf hunting or predation behaviour on beavers, as clusters in beaver habitats were visited randomly from 2015-2017 and every cluster during 2018-2019 was searched (Gable et al. 2016, Gable and Windels 2018).

We systematically searched for evidence of predation events when at GPS-clusters. When we located wolf-killed beavers, we recorded the beaver habitat feature (e.g., feeding trails, dams) that the beaver was killed at or near (Gable et al. 2016). We

considered there to be 12 habitat features a beaver could be killed at (see Appendix 1 for descriptions of beaver habitat features). For more detailed information about our cluster and kill site investigations see Gable et al. (2016) or Gable et al. (2018c).

Beaver Hunting Attempts

We identified “beaver hunting attempts”—where wolves appeared to be waiting to ambush beavers, but where a kill was not found—when searching clusters of GPS-locations (Fig. 1; Gable et al., 2016). Generally speaking, a beaver hunting attempt was a tight cluster of wolf locations near fresh beaver activity (Appendix 2, 3, & 4). Specifically, we defined a beaver hunting attempt as ≥ 2 consecutive locations < 25 m apart, of which $> 50\%$ had to be ≤ 15 m from fresh beaver activity (e.g., fresh cuttings, mud on scent mound) (Gable et al. 2016). When we identified beaver hunting attempts, we searched intensively to find the specific spot (i.e., bed site) where the wolf had waited (Gable et al. 2016, Kusler et al. 2017). Wolf beds were characterized by a circular area of depressed vegetation or earth with wolf hairs scattered on the ground (see Appendix S2). We found bed sites at most hunting attempts; however, there were some attempts where we could not find a bed because of certain forest floor cover types (e.g., rock, compacted bare ground). If we could not find a bed site, we assumed that the bed site was at the centroid of the GPS-locations associated with that hunting attempt (Vogt et al. 2018), as most located bed sites were < 2 m from the centroid (T.D. Gable, pers. observation).

When we documented beaver hunting attempts, we recorded: 1) the beaver habitat feature(s) wolves were waiting by (Fig. 1), 2) the distance (m) between the wolf and the closest fresh beaver activity (i.e., how far the wolf was bedded down from where we surmised it expected beavers to be), 3) the distance (m) between the wolf and deep water

(>0.5 m deep), and 4) the time (beginning and end) the hunting attempt occurred based on GPS locations. When wolves waited by beaver feeding trails in 2018-2019, we measured the length of the trail to the nearest meter (this data was not recorded in 2015-2017). Additionally, we recorded videos of field investigations of most hunting attempt sites and created hand-drawn maps, based on field investigations, of each hunting attempt site to document pertinent information (e.g., where the wolf was waiting in relation to water and beaver activity, Fig. 1). The combination of the hunting attempt measurements, maps, and videos (see Appendix 2, 3, & 4) allowed us to thoroughly document this behaviour and determine where wolves were waiting to ambush beavers (Fig. 1).

For analysis and comparison, we assigned kills and hunting attempts to 6 broader beaver habitat feature categories (see Appendix 1 for definitions of categories): dams, foraging features, forest interior, lodges, shorelines, and waterways (e.g., streams and creeks). Wolves sometimes positioned themselves equidistant to 2-3 beaver habitat features during hunting attempts (e.g., a wolf bedded down next to a feeding trail below an active beaver dam). In such instances, we divided the attempt and assigned the resulting values to each feature the wolf waited next to (i.e., 1 attempt at 2 features = a value of 0.5 for each feature). We used a Fisher's Exact test to compare the habitat features where wolves waited to ambush beavers and where they killed beavers.

To assess the relationship between feeding trail length and the distance wolves waited from water, we used a generalized least squares (GLS) model with a power variance structure and included a random effect for individual wolves (Zuur et al. 2009). We used the 'lme4' package to fit the GLS model (Bates et al. 2015). We used a feeding trail index (index = bed site distance from water/feeding trail length) to assess the

distance wolves waited from water relative to the length of the feeding trail they were waiting next to. A feeding trail index >1 indicated that a wolf waited farther from water than the end of the feeding trail, whereas an index <1 indicates a wolf waited somewhere between water and the end of the trail. A feeding trail index of 1 indicates the wolf waited at the end of the trail. We fit these data with a locally weighted smoothing regression line to visualize the trend. All analysis was done in the program R version 3.5.2.

Wind direction and olfactory concealment

We used wind direction data collected hourly from a weather station in Voyageurs National Park (station name: VOYA-SB, station site code: 27-137-0034) to estimate wind direction during hunting attempts. We used both the mean hourly wind direction (in degrees) and overall range of wind direction during the attempt. If the attempt took <1 hr, we used the wind direction data from the nearest hour for our analysis. In a few instances, wind direction data were not available for specific periods so we used wind direction data recorded hourly at the Falls International Station at Falls International Airport (KINL), which is ~ 18 km west of Voyageurs National Park.

We then qualitatively evaluated whether wolves would have been detected via olfaction by beavers at each hunting attempt. Assessing whether a wolf would have been detected requires understanding not only how wolves positioned themselves relative to terrestrial beaver features that they waited by, but also how they positioned themselves relative to nearby aquatic features (e.g., ponds, streams, canals) that beavers used for travel to terrestrial features (Fig. 1). For instance, a wolf might correctly position itself relative to a beaver feature (e.g., feeding trail), given the wind direction, but if the wind blows the wolf's odour over the water that the beaver must travel through to reach that

feature, then the beaver would detect the wolf before it ever came ashore. We relied on the detailed information we recorded in the field (i.e., maps and videos of hunting attempts detailing pertinent beaver activity and where wolf bedded in relation to that) to assess whether the wolf would have been detected at each attempt (Fig. 1). In particular, we plotted the prevailing wind direction(s) during the attempt and assessed whether the wolf's odour plumes would have been dispersed over pertinent aquatic and terrestrial beaver features (see Fig. 1). Our hope in using these qualitative assessments was to understand whether wolves chose ambushing locations based on olfactory concealment. While our approach does not capture all of the nuances of wind turbulence and direction during hunting attempts, it allowed us to assess how wind direction influences ambushing behaviour at a much finer scale than any previous study we are aware of (Conover 2007, Cherry and Barton 2017).

When assessing how wolves waited in relation to wind direction, we categorized hunting attempts as: wolf likely undetected by beaver, wolf likely detected by beaver, or unknown (Fig. 1). Attempts assigned as 'unknown' were those where we were unable to make a clear decision due to a variety of different factors such as variable wind direction during the attempt, no wind during the attempt (wind direction was generally not recorded at weather station when wind speeds were <0.5 m/s), and uncertainty about how the beaver would have approached the location that the wolf was waiting-in-ambush. We calculated the percent of total attempts in each of these groups (likely detected, likely undetected, unknown) and used those percentages to assess how wolves chose to wait-in-ambush in relation to wind direction. We used percentile bootstrapping to get confidence

intervals for our detection estimates. We omitted a small number of attempts from our analysis because detailed information on the attempt was not recorded.

RESULTS

We searched 11,817 clusters of GPS-locations from 24 wolves during 2015-2019. In doing so, we documented 214 wolf-killed beavers and 748 beaver-hunting attempts (i.e., instances where wolves attempted to ambush beavers). Wolves generally waited-in-ambush 2.5–3.5 m (median-mean; SD=3.3) from beaver activity (Fig. 2) and 7–10.1 m (median-mean; SD=10.1) from water (Fig. 3). Wolves waited 3-4 m (median-mean; SD=3.5) from water when not waiting at feeding trails (Fig 3A). We measured 316 feeding trails that wolves bedded down along to ambush beavers. There was a positive relationship between the length of a feeding trail and the ambush site's distance from water (Fig. 4A; Distance to Water $\sim 4.31 + 0.44 \cdot \text{Feeding Trail Length}$; 95% confidence interval [CI] for B_0 and B_1 was 0.38-0.51 and 2.76-5.86, respectively; $p < 0.001$). At short trails (<9 m long, $n=47$), wolves generally waited beyond the end of the trail, whereas at trails >9 m long ($n=269$) wolves generally waited an average of 50-70% of the way down the trail (Fig 4B). At long feeding trails (>35- m long, $n=69$), wolves never waited beyond the end of the trail.

The proportion of hunting attempts at habitat features was different than the proportion of kills at those same features (Fig. 5, $p < 0.001$). In particular, 65% of beaver hunting attempts occurred around features beavers use for foraging (e.g., feeding trails, feeding canals, and feeding areas), whereas only 32% of kills occurred at these features. In contrast, 15% and 20% of kills occurred in the forest interior and at small waterways, respectively, but only 0% and 3% of all hunting attempts occurred at these features (Fig

5). Wolves focused much of their ambushing behaviour at feeding trails, as 49% ($n=368$) of all hunting attempts occurred near feeding trails.

When choosing ambush locations, wolves primarily (89% of hunting attempts; 95% CI=86%–91%) selected locations where beavers would likely have been unable to smell them. At 5% (95% CI: 3.7–7%) of hunting attempts, wolves waited where they likely would have been detected by beavers. We classified the remaining 6% of hunting attempts as unknown (95% CI: 4.4–7.9). Given that wolves primarily waited in a downwind or undetected position, we suspect that at most of these “unknowns” wolves were waiting in undetected or downwind positions. If we omit these unknowns (or assume that the other hunting attempts are representative of the unknowns), then wolves waited downwind or in undetected positions at 94% of hunting attempts and upwind or in detected positions at 6% of attempts. In 22 cases, we failed to record adequate data for such an assessment, so we omitted these from the olfactory analysis.

DISCUSSION

A mechanistic understanding of the ambushing behaviour of a predator requires an understanding of where a predator *expects* prey to be, which is often unknowable given the complexity of prey movement and behaviour. Understanding, with certainty, where wolves expected beavers to be is impossible. However, because beavers use the same, conspicuous habitat features repeatedly, their activity is predictable and we can reasonably infer where wolves expected beavers to appear when waiting-in-ambush (Appendix 2, 3, & 4). Because of this, we were able to simultaneously infer the behaviour of both predator and prey, as well as the influence of abiotic factors, providing rare

insight into how a terrestrial carnivore selects ambushing locations at the microhabitat scale.

Strategic Positioning to Counter Defences of Prey

Wolves appear to understand beaver behaviour and sensory abilities, and can select ambushing locations to counter beavers' defences. Beavers, due to poor eyesight and visual acuity, primarily detect predators via their highly-developed olfactory senses (Novak 1987, Campbell-Palmer and Rosell 2010). To prevent detection, wolves predominantly chose ambushing locations that likely had olfactory concealment where beavers could not detect them (we surmise that wolves were likely undetected at 89-94% of attempts). This suggests wolves have learned how wind disperses their own odour plumes, that beavers use olfaction to detect predators, and that selecting locations with olfactory concealment is necessary to ambush beavers. While this was expected, empirically demonstrating how wind direction influences the ambushing behaviour of carnivores has been difficult, at best, with most studies only able to correlate habitat selection or hunting success with wind speed or direction (Stander and Albon 1993, Conover 2007, Cherry and Barton 2017). As far as we know, this is the only study that has been able to demonstrate that carnivores choose ambushing locations with olfactory concealment from their prey (see Conover [2007] and Cherry and Barton [2017] for review of olfaction in predator-prey interactions).

Wolves appear to have learned that beavers cannot see a motionless predator (Gable et al. 2018a) and have likely adapted their ambushing strategies accordingly. Wolves generally waited close (1-5 m) to beaver features, commonly with little-to-no visual cover (Fig. 2, Video S2, Gable, unpublished data). Waiting close to a feature

minimizes the period between when wolves leave their ambushing location and when they encounter beavers, likely reducing the probability of beavers detecting pursuing wolves before being attacked. If beavers detected pursuing wolves, they could get closer to water and almost certainly increase their probability of escape once an attack is initiated (see Video S1 in Gable et al. 2018a). Thus, wolves, by waiting motionless in locations with olfactory concealment close to where beavers frequent, appear to understand beavers' sensory defences and deficiencies, and can select ambushing locations accordingly (Fig. 2). Indeed, a wolf in Quebec was observed using this strategy by waiting for a beaver to get within 2 m before attacking (Gable et al. 2018a).

In addition to accounting for the sensory defences of beavers, wolf ambushing strategies appear to have adapted to minimize the physical challenges of killing a beaver before it reaches water. Beavers can be challenging prey for a wolf to kill given their muscular stature and sharp incisors, the brief periods they spend on land, and the short distance a wolf has to catch and kill them before they can reach deep water (Gable et al. 2018d, a). Accordingly, we hypothesized that wolves would choose ambushing locations farther from water, when possible, to maximize the probability of killing a beaver by increasing the distance between the beaver and the safety of deep water. Our results support this hypothesis as the distance wolves waited from water was positively related to the length of beaver feeding trails where wolves waited-in-ambush (Fig. 4A). Interestingly, where wolves waited along feeding trails was also dependent, to a degree, on trail length (Fig 4B). There was substantial variability in the data (Fig. 4B) but some broad patterns exist. At short feeding trails, wolves generally waited at or beyond the end of the trail, but at longer trails wolves waited, on average, ~60% of the way down the

length of the trail. There were only a few instances of wolves waiting beyond the end of the feeding trail at longer trails (Fig 4B). We suspect wolves generally choose ambushing locations part way down feeding trails to allow the beaver to travel towards the end of the trail prior to attacking. By doing so, the wolf: 1) allows the beaver to reach the end of the trail (i.e., the maximum distance the beaver will go from water) before attacking, and 2) is between the beaver and water when it attacks. A wolf in Wisconsin was observed using this strategy; the wolf waited motionless near a feeding trail for a beaver to walk to the end of a 20 m trail before the wolf attacked and then killed the beaver (R. Schultz, pers. comm). We do not understand why wolves wait at the end or beyond the end of short feeding trails (or at short feeding trails altogether) but suspect wolves rarely kill beavers at short feeding trails.

Encounter Rates, Capture Rates, and Opportunism

Habitat-mediated differences in encounter and capture rates, in addition to opportunistic predation, likely explain why there is a difference between where wolves attempted to kill beavers, and where they actually were successful (Fig 5). Otherwise, the proportion of kills at each habitat should be similar to that of hunting attempts. When selecting ambushing locations, wolves must balance the probability of encountering a beaver (i.e., encounter rates) with the probability of killing a beaver if an encounter occurs (i.e., capture rates). Capture rates likely increase with increasing distance from water (Basey and Jenkins 1995, Gable et al. 2018*d*), whereas encounter rates likely vary by habitat feature. Unfortunately, gathering data on wolf encounter and capture rates of beavers is extremely challenging but is essential to understanding wolf ambush site selection and where wolves kill beavers. Wolves focus most ambushing efforts around

beaver foraging habitat features (Fig 5), suggesting that ambushing success rates—the product of encounter rates and capture rates—are higher at feeding trails relative to other features. Interestingly, though, only 32% of kills occurred around foraging features (compared to 65% of attempts). We suspect only part of this difference is likely attributable to capture and encounter rates, and that opportunistic predation on beavers explains some, if not most, of the disparity between where hunting attempts and kills occur. Most kills in the forest interior and along small waterways are likely the result of opportunistic encounters with dispersing beavers (Fig. 5, Gable et al. 2016). Beavers often disperse through small, shallow waterways or forested areas where they are readily killed by wolves because they have cannot access deep water to escape. However, beyond this, quantifying what percent of kills are opportunistic is difficult from GPS-collar data alone (Gable et al. 2016), and we do not know whether most beaver kills were the result of successful ambushes or opportunistic encounters. Ultimately, the inability to parse out opportunistic kills limits our ability to disentangle the extent to which encounter/capture rates and opportunism are driving the disparity between where attempts and kills are occurring. Developing methods using accelerometer data from GPS-collars could be beneficial toward this end (Gable et al. 2018*d*).

Our work has revealed that wolves primarily ambush beavers by waiting motionless near beaver features for substantial periods (>8-12 hr, Gable et al. 2016)—where they likely cannot see or hear beavers—in locations that account for wind direction, distance from beaver activity, distance from water, and the beaver habitat feature they are waiting next to (Figures 2–5). Yet, we still do not understand how wolves assess and decide where the best location to wait is. Wolves might select ambushing

locations based on the concentration of beaver odorants at habitat features—which generally corresponds to the recency or intensity of prey use (Conover 2007, Bytheway et al. 2013)—while simultaneously balancing the probability of encountering and capturing a beaver at certain features. Yet, understanding this is complicated by the fact that wolves must make both pond-level (where to wait around an active beaver pond) and territory-level (what pond to wait at) decisions when selecting ambushing locations (i.e., two-level spatial selection; Rodríguez-Robles & Glaudas, 2011). Thus, how wolves decide to wait at a particular location at a given pond, instead of a potentially better location at a different pond, remains unknown and is an outstanding challenge to understand empirically.

Prey Responses to Ambush Predators?

Determining how predators hunt their prey is crucial for understanding prey anti-predator behaviours (Preisser et al. 2007, Miller et al. 2014). Ambush predators probably foster behavioural responses or adaptations in their prey because prey, should they escape an encounter, can learn from the encounter and adjust their behaviour accordingly (Schmitz 2008). Several studies have examined how beavers alter their foraging and scent-marking behaviour when wolf odours (e.g., urine and feces) are placed directly on feeding trails (Engelhart and Müller-Schwarze 1995, Severud et al. 2011), cut vegetation (Salandre et al. 2017), or scent-mounds. While these studies have, in some instances, demonstrated that beavers can detect wolf odours, inference beyond that is limited because the study design(s) did not simulate how wolves actually hunt beavers. That is, the chemical cues often used (urine and faeces) do not match the intensity or type of sensory cue (Weissburg et al. 2014, Moll et al. 2017, Parsons et al. 2018) that beavers would likely

encounter in natural settings because wolves generally select ambushing locations in areas with olfactory concealment (e.g., downwind) from beavers and it seems rather implausible that wolves would urinate or defecate directly on the habitat features they were waiting by. This highlights the importance of understanding ambush hunting behaviour in order to design studies that adequately simulate natural predator-prey encounters (Peers et al. 2018, Prugh et al. 2019). Without accurate information on predator ambushing strategies, studies examining anti-predator behaviour run the risk of being biologically flawed because they fail to mimic how ambush predators hunt their prey, and consequently the strategies prey have evolved to avoid ambushing predators (Weissburg et al. 2014, Moll et al. 2017). Study designs that simulate natural predator-prey encounters and that account for different sensory cues at varying intensities will likely yield greater insights into how prey species rely on sensory cues for assessing predation risk (Prugh et al. 2019).

Identifying how ambushing carnivores influence the behaviour of their prey, and how their prey perceive predation risk of ambush predators, is challenging. Two common approaches for quantifying predation risk for prey of ambush predators are: 1) creating models that predict where kills are most likely to occur based on habitat characteristics at documented kill sites, and then assuming that habitats with higher probability of kill-occurrence have higher predation risk (Lone et al. 2014, Donadio and Buskirk 2016, Lendrum et al. 2018, Prugh et al. 2019); and 2) using GPS-locations from predators to predict predator space-use and assuming riskier habitats are those where predators spend the most time (Moll et al. 2017, Kohl et al. 2019). Our work suggests that where ambush predators successfully kill their prey can be different from where they hunt prey (Fig. 5),

which is likely a result of opportunistic predation as well as habitat-mediated variations in encounter and capture rates. If only one of these components was examined, we would not have fully captured wolf predation pressure on beavers. Thus, studies examining non-consumptive effects and predation risk of ambush predators on their prey should strive to account for where ambush predators attempt to and successfully kill their prey. Ideally, decoupling where and when ambush predators spend time waiting-in-ambush from where they spend time overall would be enlightening for understanding prey space use.

However, identifying ambushing attempts like we did would be extremely challenging, if not impossible, for many predator-prey systems. Given this, study designs that account for ambush predator space-use and where ambush predators make kills (e.g., Kohl et al. 2019) will likely be most useful approach for understanding how ambush predators influence prey behaviour.

General Insight into Ambush Site Selection and Behaviour

Our work shows how an ambush predator can select ambushing locations and adapt hunting behaviours in response to the anti-predator defences and behaviour of their prey. Due to the strong evolutionary pressure to select optimal ambushing-sites (Du et al. 2009, González-Bernal et al. 2011), ambush predators across various taxa likely have evolved ambush strategies that counter the defences and abilities of their prey. For example, *Phaeacius*, a sit-and-wait jumping spider, recognizes different prey species and changes its ambushing strategy based on the visual abilities of different prey (Li et al. 2003). In particular, *Phaeacius* remain stationary when ambushing prey that cannot visually detect a stationary spider whereas when hunting prey with exceptional eyesight, *Phaeacius* attempt to slowly and steadily move closer to their prey prior to launching an ambush (Li

et al. 2003). Indeed, the ability to select ambushing locations while avoiding detection requires ambush predators to account for the behaviour of their prey and how abiotic factors influence their preys' ability to detect predators. Furthermore, successfully ambushing prey requires predators to account for and predict how complex interactions between prey, the environment, and themselves will play out (Mech 2007*b*, Gable et al. 2018*a*). Whether such knowledge is innate, learned from conspecifics, or learned through prior interactions with prey is unknown, but such information would be valuable for understanding how hunting strategies persist in predator populations. Studying how ambushing strategies have evolved in response to prey defences is challenging, but we think our general approach could be useful for studying the ambushing behaviour of other sit-and-wait predators. Because ambush predators can affect the behaviour of their prey, understanding where and how, at a microhabitat scale, terrestrial carnivores ambush prey is important for understanding their functional role in ecosystems (Schmitz 2008, Romero and Koricheva 2011, Miller et al. 2014).

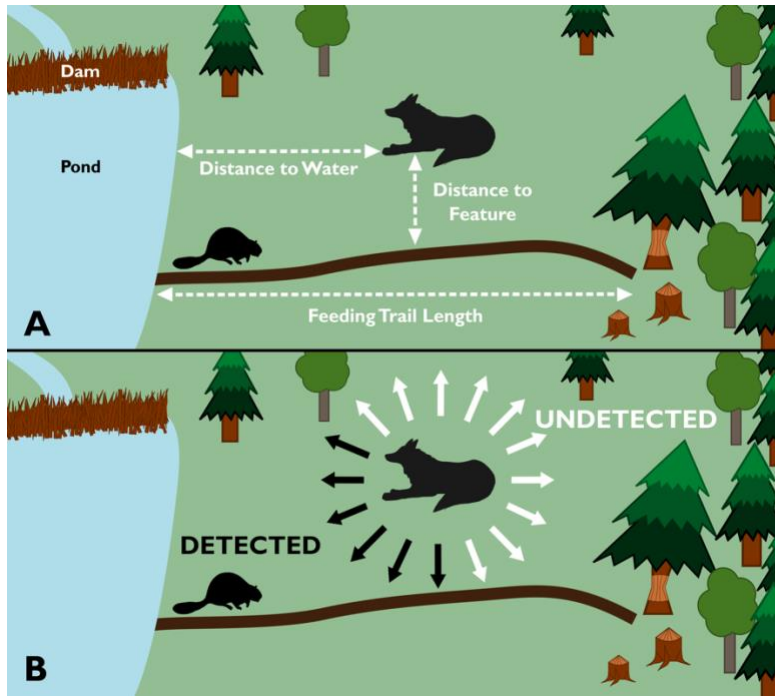


Figure 1. Diagram showing how we assessed whether wolves would have been likely detected or likely undetected by beavers at ambushing attempts. We first identified where the wolf was waiting-in-ambush based on bed-site location and then made a detailed map and video in the field of where the wolf waited in relation to terrestrial beaver habitat features (a feeding trail and dam in this example) as well as the aquatic features (a pond in this example; top panel, A). We then used the prevailing wind direction(s) during the hunting attempt based on the closest weather station to determine if the wolf's odour plume would have been blown over the terrestrial and aquatic beaver features (bottom panel, B). The white arrows indicate wind directions where we would have considered the wolf to likely have been undetected by beavers whereas black indicates wind directions where the wolf would likely have been detected. We assumed that once the beaver had traveled beyond the wolf, the wolf would be able to successfully ambush the beaver even if the beaver detected the wolf at that point.

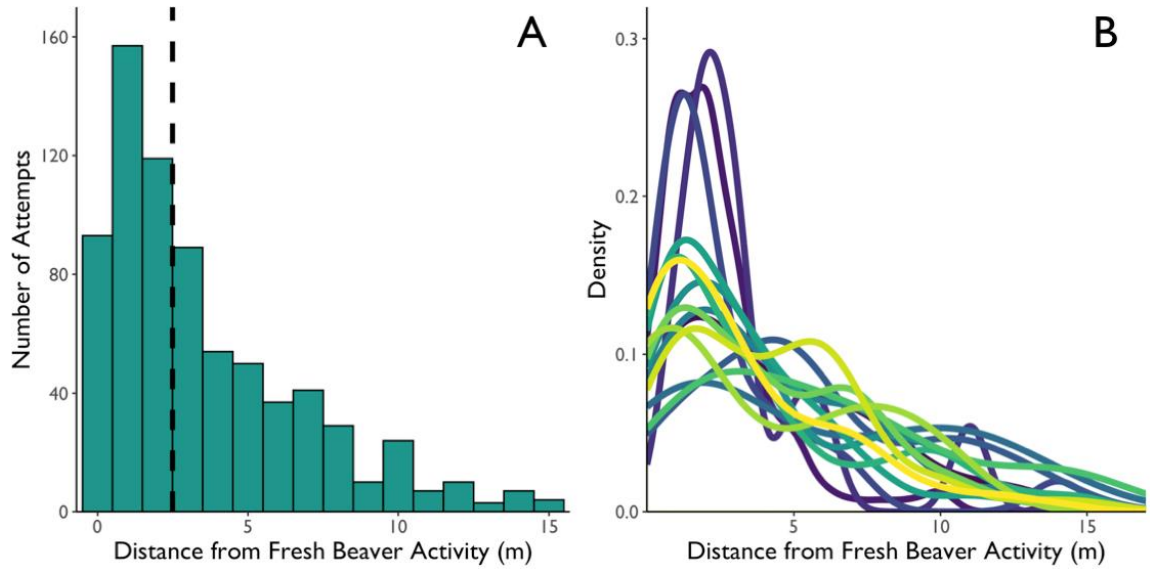


Figure 2. The distance from fresh beaver activity wolves waited-in-ambush when hunting beavers in the Greater Voyageurs Ecosystem, Minnesota, USA. Panel A shows the distribution of all (n=748) ambushing attempts documented between 2015-2019 and the dashed line represents the median. Panel B shows distribution of ambushing attempts from individual wolves (n=11) for which we documented >10 ambushing attempts (each line is a different wolf).

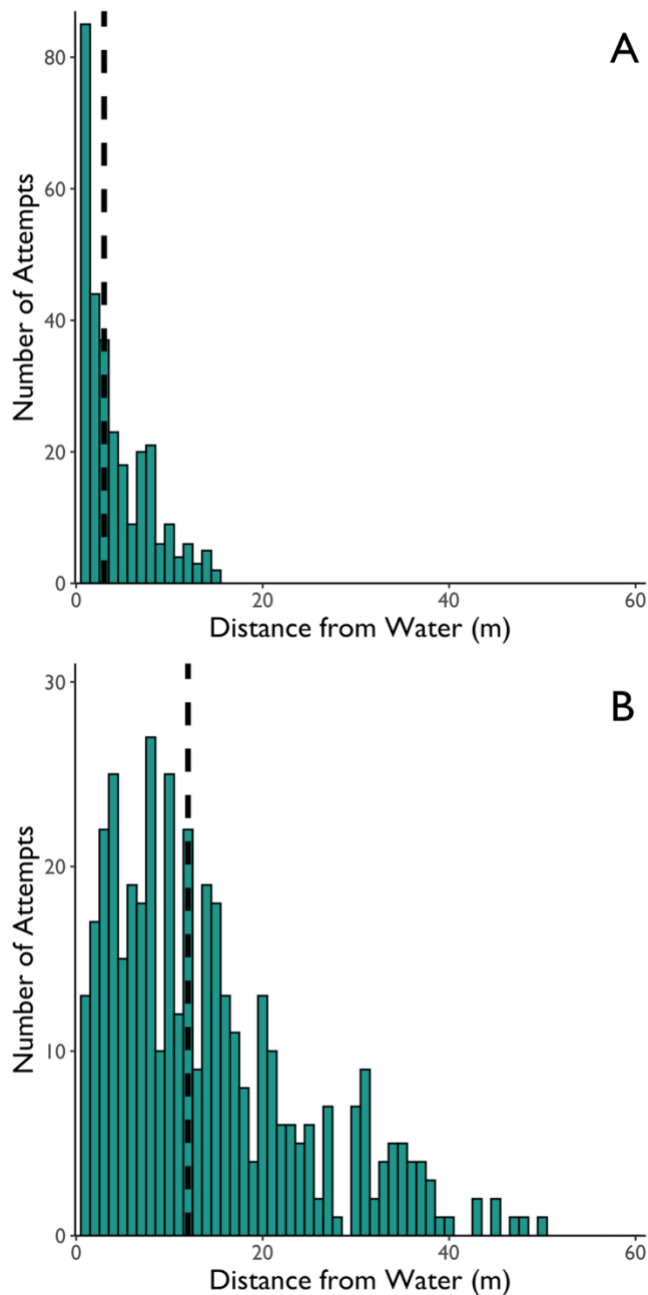


Figure 3. The distance from water wolves waited-in-ambush when hunting beavers in the Greater Voyageurs Ecosystem, Minnesota, USA. Panel A shows the distribution of all (n=317) ambushing attempts that were not along beaver feeding trails whereas Panel B shows the distribution of ambushing attempts along feeding trails (n=422). Dashed lines represent the median.

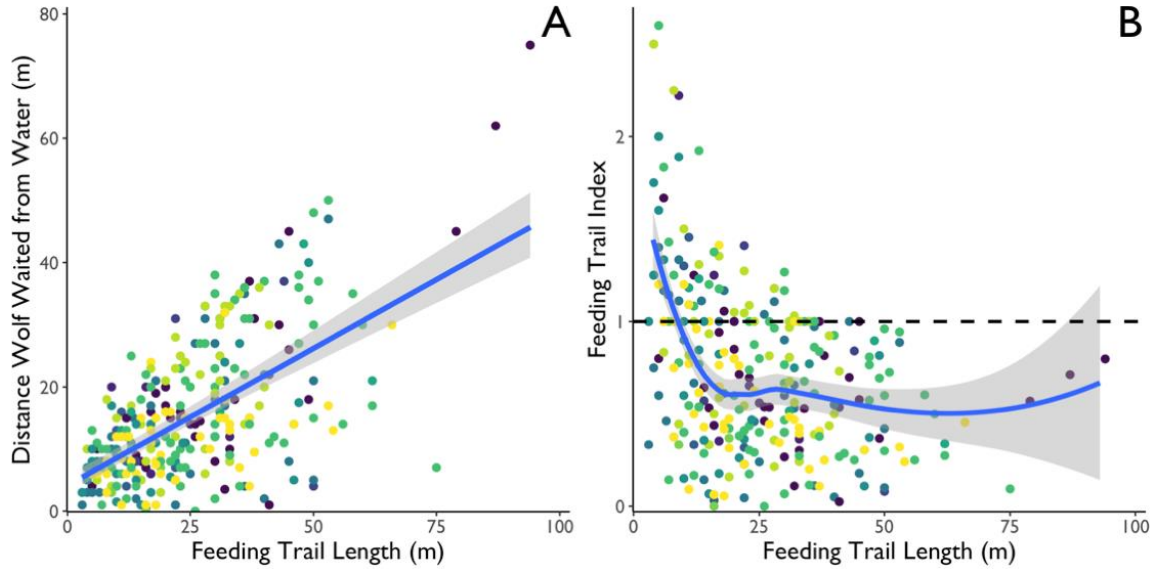


Figure 4. Where wolves choose to wait-in-ambush at beaver feeding trails in the Greater Voyageurs Ecosystem, Minnesota, USA based on 316 ambushing attempts from 2018-2019. The different colored points correspond to individual wolves ($n=11$ wolves).

Wolves wait farther from water as feeding trail length increases (A) but where they wait on a trail of a given length is dependent on trail length (B). The feeding trail index represents how far down a feeding trail relative to the length of the trail a wolf chose to wait-in-ambush (i.e., index = distance wolf waited from water/length of feeding trail).

Index values >1 indicate that a wolf waited further from water than the end of the feeding trail whereas index <1 indicate a wolf waited somewhere between water and the end of the trail. A feeding trail index of 1 (dashed line in Panel B) indicate the wolf waited at the end of the trail. Shading represents 95% confidence intervals.

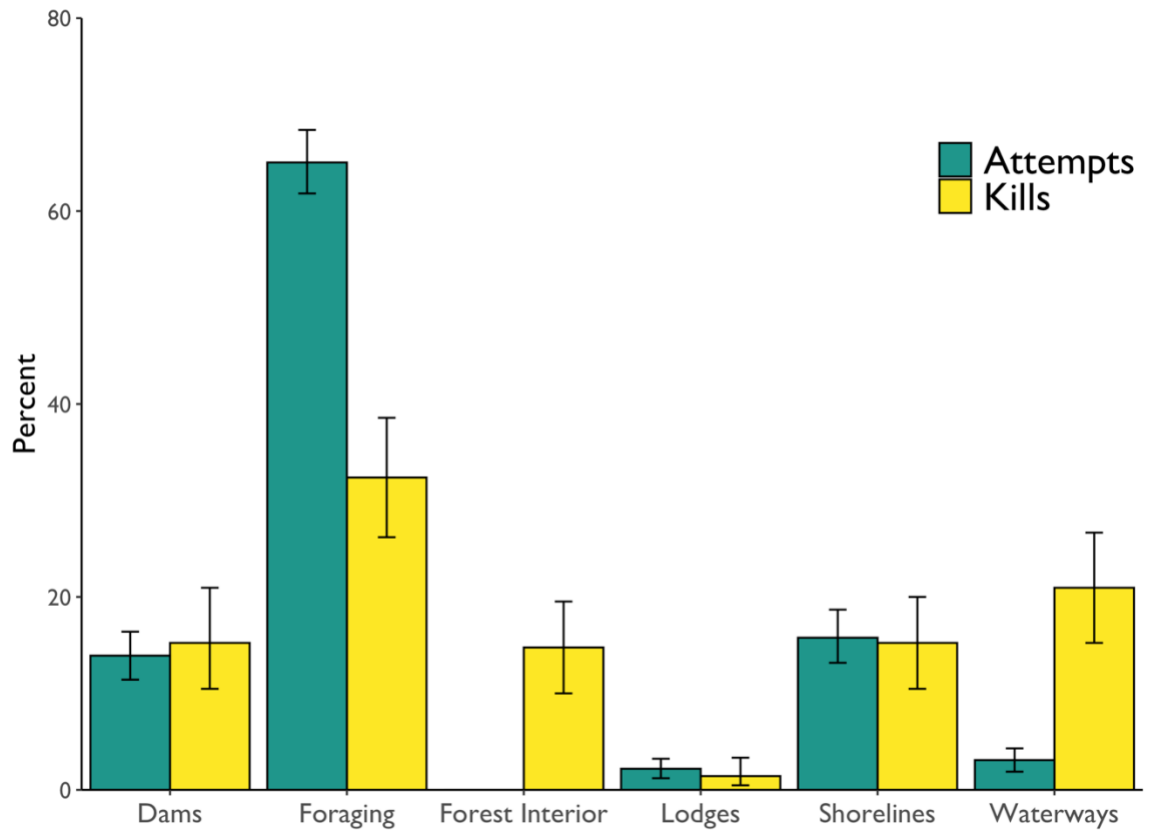


Figure 5. The habitat features where wolves attempted to ambush and successfully killed beavers in the Greater Voyageurs Ecosystem, Minnesota, USA during 2015-2019. The “foraging” habitat feature includes all attempts and kills around feeding trails, feeding areas, and feeding canals. The error bars represent 95% confidence intervals.

Chapter 5: Wolves use Cooperative Ambush Strategies to Hunt Beavers

ABSTRACT Cooperative hunting can confer fitness benefits by increasing foraging efficiency. We documented a breeding pair of wolves in the Greater Voyageurs Ecosystem of Minnesota using cooperative ambushing to hunt beavers. The breeding pair primarily chose to wait-in-ambush close to one another (<65 m) but on different beaver feeding trails, which appears optimal because: 1) feeding trails are where beavers are most active and vulnerable on land, 2) the probability that the pair encounters a beaver doubles, and 3) either wolf can quickly assist the other in killing a beaver. The cooperative ambush strategy these wolves used is either rare or undocumented for members of Carnivora but we suspect this behavior is widespread in areas of wolf-beaver sympatry. This observation demonstrates that novel insights into the natural history of even the most well-studied predators are possible when technological advancements (e.g., GPS-collars with high-intensity fix intervals) are combined with intensive fieldwork.

INTRODUCTION

Cooperative hunting involves two or more animals that act together to acquire a common prey (Boesch and Boesch 1989, Bailey et al. 2013). Cooperative hunting can confer fitness benefits by increasing hunting efficiency, allowing predators to exploit large prey that would be difficult to capture alone, or by reducing individual risk (MacDonald 1983, Packer and Ruttan 1988, Bailey et al. 2013). The trade-off when hunting cooperatively is that food is shared, and at times, some individuals might have reduced access to collaboratively-acquired food (e.g., social predators with a feeding hierarchy)(Packer and Ruttan 1988, Escobedo et al. 2014). Cooperative hunting ranges from passive hunting approaches, which requires no intentionality or awareness between animals hunting

together, up to coordinated and collaborative hunting strategies where cooperating animals intentionally align their actions to one another in time and space to capture prey (see Table 1 in Bailey et al. 2013). Collaborative hunting, which is considered the most complex form of cooperative hunting, is when “there is clear role differentiation resulting in team-like behavior...timing and positioning are much more strongly based on each other’s, rather than on the prey’s” (Bailey et al. 2013).

Wolves (*Canis lupus*) are cooperative, cursorial predators that primarily hunt and kill prey by outrunning and exhausting them (Mech et al. 2015). The amount of strategy or planning wolves use when hunting prey, and whether this is evidence of high-order cognitive abilities, has been debated for several decades (Mech and Peterson 2003, Mech 2007b, Muro et al. 2011, Gable et al. 2018a). Most wolf hunting sequences are straightforward and simple (Mech et al. 2015). However, there are multiple observations of wolves using collaborative hunting strategies that involve ambushing in an attempt to capture caribou (*Rangifer tarandus*; Haber 1977), musk ox (*Ovibos moschatus*; Mech 2007b), arctic hares (*Lepus arcticus*; Mech et al. 2015), and Canada geese (*Branta canadensis*; Nichols 2015). In several of these instances, wolf pack members chased prey toward one or more wolves that appeared to be waiting-in-ambush (Haber 1977, Mech et al. 2015, Nichols 2015). Despite these observations, wolves have not been considered ambush predators as reports of ambushing behavior have been relatively infrequent, and it is unknown whether the reports of ambushing behavior that do exist are simply artifacts of observer interpretation (Mech and Peterson 2003, Mech 2007b). Yet, recent work on wolf-beaver interactions demonstrates that wolves do use ambush hunting strategies and

are able to switch between cursorial and ambush strategies depending on the prey of interest (Gable et al. 2016, 2018a).

Beavers are important summer (i.e., the ice-free season) prey for wolves in many boreal ecosystems in North America and Eurasia (Gable et al. 2018d), with beavers constituting up to 42% of wolf pack diets (Gable et al. 2017a, 2018d) and up to 83% of individual wolf diets during this period (Moayeri 2013). Wolves primarily use wait-in-ambush hunting strategies to kill beavers. Specifically, wolves bed down next to areas with fresh beaver activity (e.g., feeding trails, beaver dams) and wait, sometimes >8-12 hr, for beavers to pass by (Gable et al. 2016, 2018a). Wolves appear to primarily hunt and kill beavers by themselves (Gable et al. 2016, Gable and Windels 2018) as most hunting and traveling by wolves during the summer is done individually (Barber-Meyer and Mech 2015, Gable et al. 2016, Gable and Windels 2018). However, how wolves hunt beavers has not received much study until recently, and there is much we do not understand about how wolves hunt beavers (Mech et al. 2015, Gable et al. 2018a). Herein, we document a breeding pair of wolves in the Greater Voyageurs Ecosystem (GVE) using cooperative ambushing strategies to hunt and kill beavers in Summer 2019.

STUDY AREA

The Moonshadow Pack home range is just south of Voyageurs National Park in the north-central Kabetogama State Forest (48°33'N, 92°90'W), which is in the southern portion of the GVE. The GVE is part of the Laurentian Mixed Forest Province and on the southern edge of the boreal forest (Bailey 1980). The southern portion of the GVE is actively managed for timber production, which results in a mosaic of clear cuts, young aspen (*Populus* spp.) stands, mature deciduous-coniferous stands, and wetlands (Gable et

al. 2018b). Logging roads and all-terrain vehicle trails are common throughout this area. White-tailed deer (*Odocoileus virginianus*) are common (pre-fawn densities 2-4 deer/km²; Gable et al. 2017b) throughout the GVE and moose (*Alces americanus*) are relatively rare in most of the GVE (<0.05 moose/km²; Windels and Olson 2019). The GVE supports a dense beaver population with densities generally ranging from 0.47 lodges/km² to >1 lodge/km² (Johnston and Windels 2015, Gable and Windels 2018). In 2019, beaver density in the Moonshadow Pack home range was 0.60 lodge/km² based on an aerial census in Fall 2019. Summer wolf densities in the area are ~4-6 wolves/100 km² with average summer home ranges of 116 km² (Gable et al. 2016). White-tailed deer and black bear (*Ursus americana*) hunting, and fur trapping are popular recreational activities in the Kabetogama State Forest but these activities are not permitted in Voyageurs National Park.

METHODS

The Moonshadow Pack had 4 members in Winter 2019. In May 2019, we captured 3 wolves from the Moonshadow Pack with foothold traps and fit them with 20-min-fix-interval Vectronic Vertex Plus GPS-collars. All capture and handling was approved by the National Park Service's Institute of Animal Care and Use Committee (IACUC protocol: MWR_VOYA_WINDELS_WOLF), and done in accordance with the American Society of Mammalogists guidelines for the use of wild mammals in research (Sikes and Bryan 2016). Acquisition and transmission rates of GPS-locations were >95-98%. The three wolves collared were the breeding female (BF hereafter), the breeding male (BM hereafter), and a 1-2 year-old subordinate male (SM hereafter; aged via tooth wear patterns Gipson et al. 2000). We searched clusters of GPS-locations—defined as ≥ 2

consecutive locations (≥ 20 min) within a 200 m radius of one another (Gable et al. 2018c)—to locate predation events and where wolves had bedded down to ambush beavers (hereafter referred to as “beaver hunting attempts”; Fig. 1). We searched all clusters of GPS-locations from each wolf from 3 days after capture until 29 October 2019, which was when most beaver ponds had iced over.

We identified “beaver hunting attempts”—where wolves were waiting to ambush beavers—when searching clusters of GPS-locations. Generally speaking, a beaver hunting attempt was a tight cluster of wolf locations near fresh beaver activity (Supplementary Video 1). Specifically, we defined a beaver hunting attempt as ≥ 2 consecutive locations < 25 m apart, of which $> 50\%$ had to be ≤ 15 m from fresh beaver activity (e.g., fresh cuttings, mud on scent mound) (Gable et al. 2016, Gable and Windels 2018). When we identified a beaver hunting attempt, we recorded detailed information about where and when the wolf chose to wait-in-ambush for beavers. When at hunting attempts, we searched intensively to find the specific spot (i.e., bed site) where the wolf had waited (Gable et al. 2016, Kusler et al. 2017). Wolf beds were characterized by a circular area of depressed vegetation or earth with wolf hairs scattered on the ground (see Supplementary Video 1). We found bed sites at most hunting attempts; however, there were some attempts where we could not find a bed because of the challenge of finding wolf beds on certain forest floor cover types. If we could not find a bed site, we assumed that the bed site was at the centroid of the GPS-locations in the cluster. We considered collared wolves to be involved in a cooperative beaver hunting attempt if they were waiting-in-ambush for beavers at the same pond/colony at the same time as another collared wolf. We assumed that two wolves from the same pack waiting-in-ambush at

the same pond at the same time was not coincidence and was consistent with cooperative hunting behavior as described and defined by Bailey et al. (2013).

When we documented beaver hunting attempts, we recorded: 1) the beaver habitat feature(s) (e.g., feeding trail, scent mounds) wolves were waiting by, 2) the distance (meters) between the wolf and the closest beaver activity (i.e., how far the wolf was bedded down from fresh beaver activity), 3) the distance (meters) between the wolf and deep water (>0.5 m deep), and 4) the time the hunting attempt occurred based on GPS-collar locations. When we documented a cooperative beaver hunting attempt, we measured the distance between where the two wolves waited-in-ambush. In addition to recording these measurements, we recorded a video of every hunting attempt during our field investigation (see Supplementary Video 1) and we also made hand-drawn maps of each hunting attempt to document where the wolves were waiting in relation to water and beaver activity (Fig. 1 and 2). The combination of the hunting attempt measurements, maps, and videos allowed us to thoroughly document this behavior and to understand where and how wolves were attempting to ambush beavers (Fig. 1).

We calculated the estimated time spent at beaver hunting attempts by taking the mean of the minimum and maximum possible time spent at hunting attempts (Gable et al. 2016, 2018c). We determined the minimum time at a beaver hunting attempt based on the time that occurred between the first and last location of each hunting attempt, and the maximum time by taking into account the fix interval prior to and after the first and last locations at the hunting attempt. We determined kill rates of wolves on beavers by dividing the number of beavers killed by a wolf by the number of days we searched GPS-clusters from that wolf.

RESULTS

We searched every cluster of GPS-locations from BF (breeding female) for 153 days (29 May 2019 to 29 Oct 2019), BM (breeding male) for 180 days (2 May 2019 to 29 Oct 2019), and SM (subordinate male) for 173 days (9 May 2019 to 29 Oct 2019). In total, we searched 605 clusters from BF, 806 clusters from BM, and 638 clusters from SM (Table 1). In doing so, we identified 50 beaver hunting attempts and 6 beaver kills from BF, 27 beaver hunting attempts and 7 beaver kills from SM, and 61 beaver hunting attempts and 14 beaver kills from BM. BF and BM cooperatively killed 3 beavers together (i.e., 3/6 kills by BF were made with BM, and 3/14 kills by BM were made with BF; see Fig. 2 for example of this). SM did not make any beaver kills with BF or BM. Every wolf in the pack primarily hunted and killed beavers by themselves (i.e., not with other collared wolves); BF made 70% of beaver kills and 84% of hunting attempts by itself, SM made 100% of kills and attempts by itself, and BM made 82% of kills and 87% of attempts by itself. Kill rates of beavers were 0.058, 0.039, and 0.098 beavers/day for BF, SM, and BM, respectively (Table 1).

We identified 8 cooperative beaver hunting attempts involving BF and BM (Fig. 1, Table 2). Cumulatively, 16% (8/50) and 13% (8/61) of all beaver hunting attempts made by BF and BM, respectively, were cooperative beaver hunting attempts. SM did not make any beaver hunting attempts with BF or BM. BF and BM started hunting beavers at the same time in all cooperative attempts except in 1 instance where BM joined BF 1.7 hr after BF had started a beaver hunting attempt. Similarly, BF and BM left all cooperative beaver hunting attempts at the same time except for 1 instance where BM left 2.3 hr

before BF. Cooperative beaver hunting attempts lasted (mean \pm SD) approximately 4.4 hr \pm 3.0 hr (range= 0.7–9.7 hr).

During cooperative beaver hunting attempts, BF and BM waited an average of 28 m \pm 20 m apart (SD; range= 6–64 m) with both wolves waiting on the same side of the body of water (e.g., pond, stream, river) (Fig 1, Table 2). Both wolves waited by beaver feeding trails during all cooperative hunting attempts, though the wolves waited by different feeding trails during 88% (7/8) of cooperative hunting attempts. In one instance, BF and BM waited-in-ambush on a feeding trail that forked with each wolf waiting at a different fork (Fig 1). We considered each fork of the trail to be a unique feeding trail. At 4 (50%) cooperative attempts both wolves waited the same distance from water, at 3 attempts BF waited closer to water than BM, and at 1 attempt BM waited closer to water than BF.

DISCUSSION

The breeding pair of the Moonshadow Pack used, by definition, cooperative ambush hunting strategies to hunt beavers (Boesch and Boesch 1989, Bailey et al. 2013). This is particularly fascinating because it demonstrates that wolves can synchronize, and likely coordinate, their ambushing behavior to catch prey (Fig. 1 & 2). In each cooperative hunting attempt, BF and BM related to one another in both time (both wolves started and ended most hunting attempts at same time) and space (wolves never >64 m apart at hunting attempts; Table 2) in a manner that is consistent with coordinated cooperative hunting (Boesch and Boesch 1989, Bailey et al. 2013). This cooperative wait-in-ambush hunting behavior by two individuals simultaneously is either quite rare or undocumented as we are unaware of other observations of canids or members of Carnivora engaging in

similar wait-in-ambush hunting strategies. Certainly, wolves and other social predators such as lions (*Panthera leo*) will use cooperative hunting strategies such as stalking-and-ambushing prey and driving prey towards other conspecifics that are waiting in ambush (Packer and Scheel 1991, Stander 1992, Mech et al. 2015), but this is categorically different than wolves waiting together for several hours next to beaver feeding trails. That is, two predators *passively* waiting in ambush together for prey to come near is different than predators *actively* waiting for conspecifics to direct prey toward them so they can ambush them.

Though we documented cooperative hunting attempts and cooperative beaver kills, we do not have direct evidence that BF and BM killed beavers using cooperative ambushing (i.e., it is possible that the 3 beaver kills by BF and BM were the result of opportunism when traveling together and not coordinated ambushing). This is due to the limitations of studying wolf predation behavior in densely forested ecosystems where visual observation of wolves ambushing beaver is extremely difficult (Gable et al. 2018d), and determining if beaver kills are the result of opportunism or ambushing from GPS-locations is not currently possible (Gable et al. 2016). We suspect that BF and BM did kill beavers using cooperative ambushing. Individual wolves successfully use ambush strategies and we think it is not only plausible, but likely, that two wolves that know how to ambush beavers alone would also be able to do so together as well. For example, on 19-20 September 2019, BF and BM made three cooperative hunting attempts before successfully killing a beaver on 20 September (Fig. 2, Table 2).

Cooperative hunting is thought to be primarily advantageous when individual foraging efficiency is low and/or prey are difficult to catch alone (Packer and Ruttan

1988). Beavers are almost certainly challenging prey for an individual wolf to catch and kill (Gable et al. 2018a), and the relatively low kill rates of wolves on beavers in a high beaver density ecosystem (the GVE) suggest that foraging efficiency is low. Based on this study and Gable and Windels (2018), which are the only available kill rates of wolves on beaver in the literature, a wolf kills 1 beaver every 10-25 days in the GVE. However, there is undoubtedly a cost-benefit to cooperatively ambushing beavers. The cost is that a beaver—‘small’ prey for wolves relative to ungulates (Peterson and Ciucci 2003)—must be shared between cooperating wolves (e.g., the 3 beaver kills that BF and BM made together). The benefit is that wolves, at least in this instance, effectively double their probability of encountering a beaver by hunting cooperatively. BF and BM almost always (88% [7/8] of attempts) chose to wait-in-ambush on different feeding trails but in close proximity (<65 m) to one another (Fig. 1). Beaver colonies are almost always using and maintaining >7-10 active feeding trails at any given point during the ice-free season (Gable, unpublished data). Wolves have to select one of these trails to wait by. This is a crucial decision because wolves only appear able to kill beavers at the feeding trail where they wait-to-ambush beavers. We have yet to document, out of the 214 beaver kills found, a single instance where a GPS-collared wolf waited-in-ambush at a specific feeding trail but ended up killing a beaver on a different feeding trail. This is likely because beavers, when on land, are able to detect rushing predators >15-18 m away (Basey and Jenkins 1995). Thus, in many scenarios, beavers likely are able to either retreat to water before a rushing wolf ever makes contact, or get close enough to water to escape a wolf after contact is made (Basey and Jenkins 1995, Gable et al. 2018a).

In addition to doubling the probability of an encounter, this type of cooperative ambushing almost certainly increases hunting success once a beaver is attacked. Beavers can be physically challenging prey for individual wolves to kill given: 1) their stout muscular stature and size (some adult beavers are as large, or larger, than adult wolves)(Gable et al. 2018a), 2) their sharp incisors and powerful bite strength (Stefen et al. 2016), and 3) the fact that beavers do not venture far from the safety of deep water (Basey and Jenkins 1995, Salandre et al. 2017). The margin for error when attacking beavers close to water is likely small. If a beaver manages to free itself for a few seconds, it would likely be able to reach water and escape in many scenarios (see Video S1 in Gable et al. [2018a]). By choosing feeding trails that were close to one another (<65 m), either wolf would have been able to quickly assist the other in a matter of seconds once an attack had started (Fig. 1). We suspect wolves assist in the attack once they observe or hear their partner engaged in an attack. If BF and BM had waited farther apart (e.g., on opposite sides of a beaver pond), their ability to help one another in any meaningful way would be limited. We would have considered—per our definition of a cooperative hunting attempt (see Methods)—two wolves waiting on opposite sides of a beaver pond to be engaged in a cooperative hunting attempt but our results suggest wolves primarily wait close together when ambushing cooperatively.

Cooperatively ambushing beavers is clearly not the primary hunting strategy wolves use to hunt and kill beavers. The Moonshadow Pack wolves were alone at >70% of all beaver kills and >84% of all beaver hunting attempts, which is consistent with previous research in the GVE (Table 1; Gable et al. 2016, Gable and Windels 2018). Thus, most of the time, the apparent benefits of cooperatively ambushing beavers do not

appear to be greater than the cost of sharing the kill with other pack members. We are optimistic that future research will be able to identify what must transpire for wolves to switch to using cooperative hunting strategies. We do not think it is coincidence that it was only the breeding pair (BF and BM) that cooperatively hunted and killed beavers (i.e., SM did not join). We suspect breeding pairs might be more likely to engage in this behavior because breeding individuals are more experienced at ambushing beavers than younger subordinate pack members, and have learned how, through previous shared experiences, to strategically work together, to increase their chance of success (similar to how wolves might learn to ambush musk oxen cooperatively; Mech 2007*b*). Furthermore, it is possible the breeding pair are willing to work together and share kills to feed their dependent pups, but unwilling to share kills with subordinate pack members who are not as involved or invested in raising pups. We should note that we do not know whether the uncollared 4th pack member hunted or killed beavers with other pack members. We suspect, given the lack of association between the other 3 GPS-collared pack members, that the uncollared wolf likely did not hunt or kill beavers frequently with other wolves.

The cooperative wait-in-ambush strategy that the breeding pair used appears to be ideal because: 1) feeding trails are where beavers are most active, and most vulnerable, on land (Gable et al. 2016), 2) the cumulative probability that the pair encounters a beaver is doubled, and 3) either wolf is able to quickly help when an attack occurs. Yet, our observation raises many interesting questions. In particular, is this behavior pervasive across all ecosystems where beavers are important prey for wolves? We suspect that this cooperative ambushing strategy is relatively widespread in areas of wolf-beaver sympatry—wolves in several different ecosystems understand how to ambush beavers

(Manitoba [Nash 1951], Minnesota [Gable et al. 2016], Isle Royale National Park [Thurber and Peterson 1993], Quebec [Gable et al. 2018a], Wisconsin [Gable et al. 2018a])—but simply has not been documented given the dearth of research on wolf-beaver interactions (Gable et al. 2018d).

Wolves are one of the most well-studied large predators in the world. However, our observation demonstrates that technological advancements (e.g., GPS-collars with high-intensity fix intervals) combined with intensive fieldwork—we spent an estimated 1,470 hours hiking 2,120 km to get to all GPS-clusters from these 3 wolves—can provide novel insights into the natural history of even well-studied species. Our hope is that our work will inspire comparative research in other ecosystems with wolf-beaver sympatry, and that this will eventually lead to a broader, more comprehensive understanding of wolf-beaver interactions and the predatory tactics wolves use to catch prey.

Table 1. Information on the beaver hunting behavior of three wolves from the same pack in the Greater Voyageurs Ecosystem, Minnesota.

Wolf	Pack Status ¹	Dates Followed	GPS-Clusters Searched	Individual Beaver Kills	Cooperative Beaver Kills	Kill Rate (kills/day) ²	Beaver Hunting Attempts	Cooperative Hunting Attempts
V072	BF	5/29/19-10/29/19	605	6	3	0.058	50	8
V077	SM	5/2/19-10/29/19	806	7	0	0.039	27	0
V079	BM	5/7/19-10/29/19	638	14	3	0.098	61	8

¹BF=breeding female, SM=subordinate male, BM=breeding male

²We combined kills made individually with those made cooperatively to estimate individual kill rates

Table 2. Specifics about 8 cooperative beaver hunting attempts made by the breeding pair of the Moonshadow Pack in the Greater Voyageurs Ecosystem, MN.

Hunting Attempt	Proximity (m) ¹	Breeding Female				Breeding Male			
		Start of Ambush	End of Ambush	Duration (hr) ²	Distance to Water (m)	Start of Ambush	End of Ambush	Duration (hr) ²	Distance to Water (m)
1	11	8/7/19 23:20	8/8/19 5:00	6.0	25	8/7/19 23:20	8/8/19 5:00	6.0	25
2	15	8/28/19 23:00	8/29/19 6:20	7.7	6	8/28/19 21:20	8/29/19 0:20	3.3	17
3	32	9/19/19 5:40	9/19/19 6:00	0.7	11	9/19/19 5:40	9/19/19 6:00	0.7	10
4	17	9/19/19 18:20	9/19/19 19:00	1.0	24	9/19/19 18:20	9/19/19 19:00	1.0	33
5	64	9/19/19 20:20	9/20/19 3:00	7.0	33	9/19/19 20:20	9/20/19 3:00	7.0	33
6	38	9/30/19 19:40	9/30/19 23:40	4.3	5	9/30/19 19:40	9/30/19 21:00	2.7	31
7	6	10/2/19 2:20	10/2/19 3:40	1.7	14	10/2/19 2:20	10/2/19 3:40	1.7	8
8	44	10/3/19 20:00	10/4/19 5:20	9.7	10	10/3/19 20:00	10/4/19 5:20	9.7	10

¹The distance between where the breeding female and breeding male waited-in-ambush at a cooperative beaver hunting attempt

² The amount of time the wolf spent waiting-in-ambush at a cooperative hunting attempt. We calculated the time spent at beaver hunting attempts by taking the mean of the minimum and maximum possible time spent at hunting attempts. We determined the minimum time at a beaver hunting attempt based on the time that occurred between the first and last location of each hunting attempt, and the maximum time by taking into account the fix interval prior to and after the first and last locations at the hunting attempt.

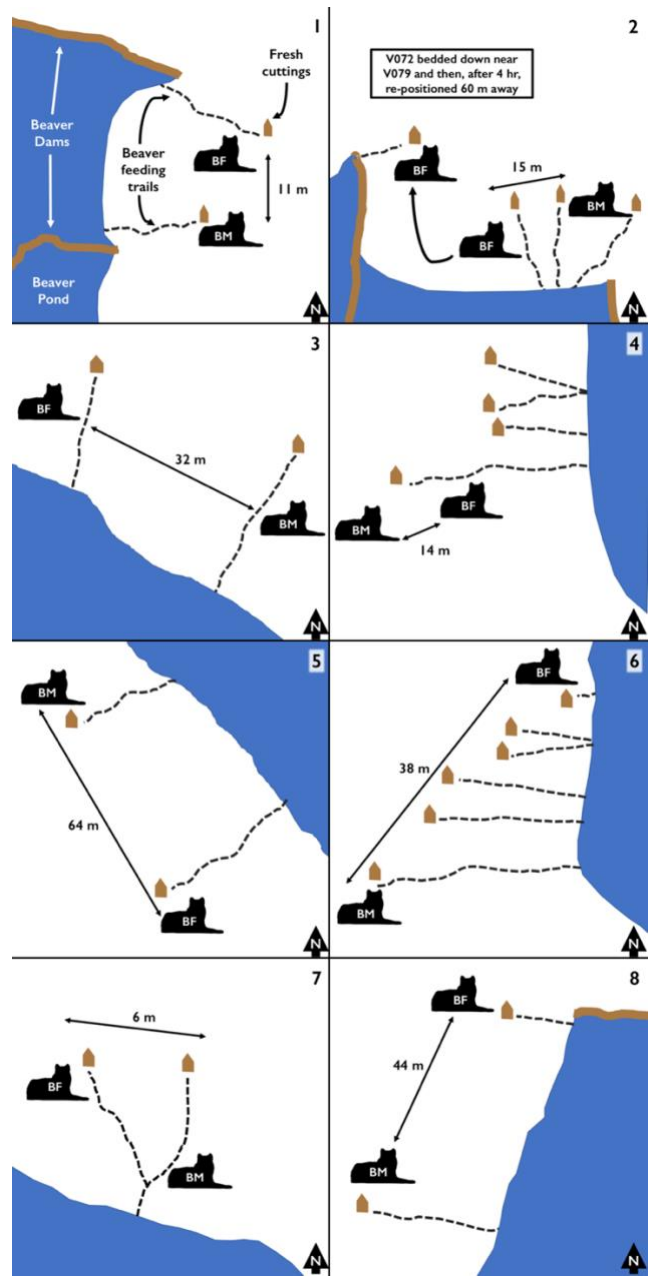


Figure 1. Diagrams of the 8 cooperative beaver hunting attempts made by the breeding female (BF) and the breeding male (BM) of the Moonshadow Pack, in the Greater Voyageurs Ecosystem, Minnesota. The blue polygons represent beaver ponds. Scale is relative to each panel. The number of the panel corresponds to the “hunting attempt” number in Table 2.

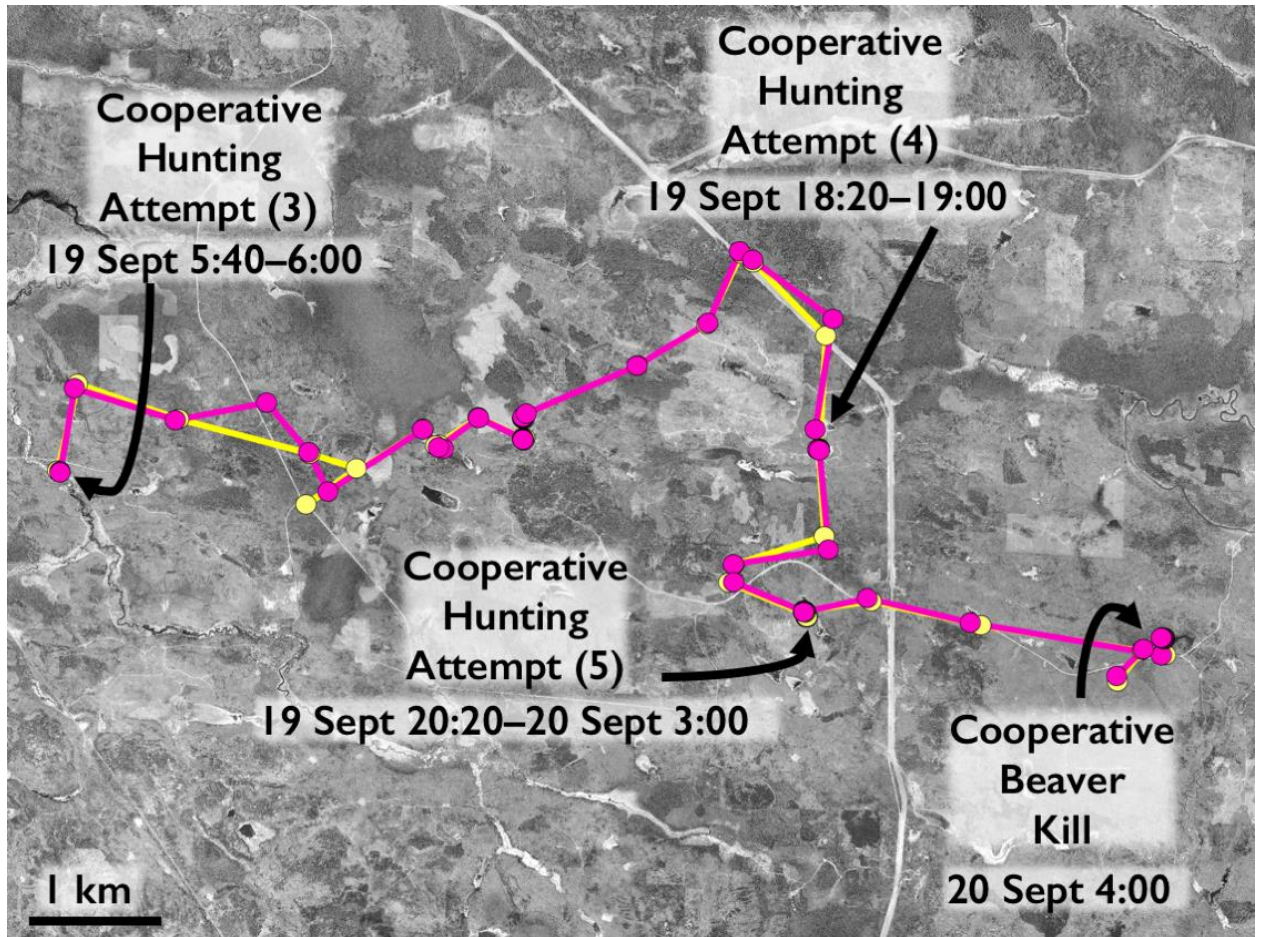


Figure 2. The GPS-locations of the breeding female (yellow) and breeding male (pink) of the Moonshadow Pack, during 19 Sept 2019 6:00–20 Sept 2019 6:00 in the Greater Voyageurs Ecosystem, Minnesota. The pair made three cooperative beaver hunting attempts during this period before successfully killing a beaver on 20 Sept 2019. The number in parentheses below each cooperative hunting attempt corresponds to the “hunting attempt” number in Fig.1 and Table 2.

Chapter 6: Outsized Effect of Predation: Wolves Alter Wetland Creation and Recolonization by Killing Ecosystem Engineers

ABSTRACT Gray wolves are a premier example of how large predators can transform ecosystems through trophic cascades. Yet, whether wolves change ecosystems as drastically as previously suggested has been increasingly questioned and criticized. We demonstrate how wolves alter wetland creation and recolonization by killing dispersing beavers. Beavers are ecosystem engineers responsible for most wetland creation throughout circumpolar boreal ecosystems. By studying beaver pond creation and recolonization patterns and wolf predation on beavers, we determined that 84% of newly created and recolonized beaver ponds remained occupied until the fall, whereas 0% of newly created and recolonized ponds remained active after a wolf killed the dispersing beaver that colonized that pond. By affecting where and when beavers engineer ecosystems, wolves alter all of the ecological processes (e.g., water storage, nutrient cycling, carbon sequestration, forest succession) that occur due to beaver-created impoundments. Our study demonstrates how predators have an outsized effect on ecosystems when they kill ecosystem engineers.

INTRODUCTION

Apex predators can directly and indirectly impact the behavior, spatial distribution, and abundance of prey populations, which may create cascading effects through lower trophic levels (Hebblewhite et al. 2005) and ultimately alter ecosystem processes such as energy flow and nutrient cycling (Schmitz 2008, Bump et al. 2009*b*). Large predators are thought to have outsized ecological effects primarily by reducing the abundance of their prey (i.e., density-mediated) or by altering the behavior of their prey via fear (i.e., behaviorally-mediated)—both of which can indirectly affect lower trophic levels via trophic cascades

(Ripple and Beschta 2012, Ford and Goheen 2015, Ripple et al. 2016). For example, orcas (*Orcinus orca*) reduce sea otter (*Enhydra lutris*) abundance, which has cascading effects on kelp forest communities (density-mediated trophic cascade) (Estes et al. 1998), while hawks (*Accipiter* spp.) alter the foraging behavior of jays (*Amphelocoma wollweberi*), which increases the breeding success of hummingbirds (*Archilochus alexandri*) (behaviorally-mediated trophic cascade) (Greeney et al. 2015). Quantifying the ecological impact of predators is valuable for understanding the functional role of predators in ecosystems and how that role changes in the face of anthropogenic factors that negatively influence large predator populations (e.g., habitat loss and fragmentation, climate change) (Ritchie et al. 2012). The ecological role of large predators and their purported ability to reshape entire ecosystems is frequently the primary justification for large predator conservation, restoration, and reintroduction (Allen et al. 2017, Engeman et al. 2017).

In North America, gray wolves (*Canis lupus*) are one of the premier examples of how large terrestrial predator populations can transform ecosystems through trophic cascades, although the extent to whether the mechanism is density- or behaviorally-mediated is debated (Estes et al. 2011, Ripple and Beschta 2012, Allen et al. 2017). Many have suggested that wolf-induced trophic cascades are the result of a landscape of fear (behaviorally-mediated), whereby wolves instill fear in their ungulate prey, which then alters the spatial and temporal distribution of ungulates (Laundré et al. 2001, Ripple and Beschta 2004). In northern Yellowstone National Park, USA, the primary study site of the wolf-trophic cascade literature (Ford and Goheen 2015), the landscape of fear has supposedly led to drastic changes in the duration, location, and intensity of ungulate

browsing (Laundré et al. 2001, Ripple and Beschta 2004, Kohl et al. 2018).

Cumulatively, these changes were thought to reduce ungulate overbrowsing in riparian areas, which led to increases in wildlife populations (e.g., songbirds, beavers [*Castor canadensis*]) dependent on riparian vegetation (Ripple and Beschta 2004, 2012). Further, the subsequent re-growth of riparian vegetation reduced erosion and ultimately affected the morphology and hydrology of streams by stabilizing stream banks (Beschta and Ripple 2006, 2012, 2019). This proposed ecological cascade—which was popularized in the online video “How Wolves Change Rivers”, viewed over 41 million times at time of writing—has been used to garner support for, and justify the conservation and recovery of, wolf populations worldwide (Allen et al. 2017, Mech 2017). Yet, whether wolves have the capacity to alter ecosystems as drastically as suggested has been increasingly questioned and criticized (Marshall et al. 2013, Ford and Goheen 2015, Allen et al. 2017, Mech 2017). Moreover, recent research suggests wolves primarily affect ecosystems through direct predation rather than indirectly through a landscape of fear (Kohl et al. 2018, Cusack et al. 2020).

Compared to the substantial dossier of Yellowstone research, relatively few studies have examined how wolf predation in boreal ecosystems—about 17% of Earth’s land surface area (Kasischke 2000)—affects lower trophic levels and ecosystem processes (Ripple et al. 2009). Wolves in boreal ecosystems rely on a different prey base than wolves in more arid, mountainous regions of North America (e.g., Greater Yellowstone Ecosystem). Importantly, wolves in boreal ecosystems generally rely, in part, on beavers during the summer for food (Gable et al. 2018a). Because beavers are ecosystem engineers that dramatically alter ecosystems (Table 1) by damming waterways

and creating impoundments that can persist for centuries (Jones et al. 1994, Rosell et al. 2005, Johnston 2015), there is potential for wolves to affect large-scale ecological processes through predation on beavers. For wolves to have such an effect, they would have to either 1) decrease beaver, and therefore impoundment, densities through predation (i.e., reducing survival and reproduction), 2) kill dispersing beavers, thereby altering the spatial and temporal distribution of newly-created or recolonized beaver impoundments, 3) kill certain beaver colony members (e.g., breeding individuals) that lead to increased colony abandonment, and consequently pond/dam failure (Gable et al. 2018*d*), or 4) alter the foraging or pond-creating behavior of beavers via a landscape of fear (i.e., non-consumptive risk effects; Say-Sallaz et al. 2019). Given that both wolves and beavers are well-studied and sympatric throughout most of the circumpolar boreal ecosystem, it is surprising that there is no information about how this apex predator-ecosystem engineer dynamic influences boreal ecosystem function (Gable et al. 2018*d*). Herein, we describe how wolves directly alter the persistence, and likely spatial distribution, of beaver ponds in a southern boreal ecosystem through predation on dispersing beavers. By impacting where and when beavers can engineer ecosystems, wolves alter all of the ecological processes (e.g., water storage, nutrient cycling, sediment deposition, forest succession; Table 1) that beaver-created impoundments affect.

STUDY AREA

This research is a part of the Voyageurs Wolf Project, a long-term research project studying wolf-prey interactions in the Greater Voyageurs Ecosystem (GVE), which is a 1,812-km² southern boreal ecosystem in Northern Minnesota (Fig. 1). The GVE (48°30' N, 92°50' W) borders Ontario to the north and the Boundary Water Canoe Area

Wilderness to the east. Voyageurs National Park constitutes the northern portion of the GVE whereas the central and southern portions of the GVE are predominantly a mix of U.S. Forest Service, state-owned, and timber company land (Homkes et al. 2020). The GVE is part of the Laurentian Mixed Forest Province and is typified by dense forests (coniferous, deciduous, and mixed) and abundant wetlands, lakes, and bogs interspersed with rocky outcrops and ridges from past glacial activity (Bailey 1980). Harvesting of timber or wildlife is not permitted in Voyageurs National Park but is common outside of the park. Mean annual precipitation in the GVE is 62 cm with 43 cm and 21 cm in the form of rain and snow, respectively (Kallemeyn et al. 2003). Topographic relief is not substantial (Fig. 1; maximum topographic relief is ~90-95 m) throughout the GVE but the mosaic of rock ridges, small draws, and lowlands provide ideal habitats for beavers to create dams that impound large areas (Johnston and Naiman 1990a).

The GVE has sustained a dense beaver population for >40 years with colony densities across the GVE generally >0.47-1.0 colonies/km² (Johnston and Windels 2015, Gable and Windels 2018). As a result, beavers have dramatically altered the landscape of the GVE by creating dams and impounding waterways. For example, a total of 7,175 beaver-created impoundments (both occupied and unoccupied) were visible from 2019 high-resolution aerial imagery of the GVE (Voyageurs Wolf Project, unpublished data) and beavers have impounded ~13% of the terrestrial landscape of Voyageurs National Park (Johnston and Naiman 1990b). The beaver population has remained relatively stable for many years, suggesting the population is at natural carrying capacity, though annual fluctuations in beavers population density do occur (Johnston and Windels 2015, Johnson-Bice et al. 2020).

The GVE has maintained high wolf densities (35-45 wolves/km²) for >30 years (Fox et al. 2001, Gogan et al. 2004, Gable et al. 2016) with wolf packs occupying the entirety of the GVE. White-tailed deer are the primary annual prey of wolves in the area. Beavers, due to their abundance, are important seasonal prey for wolves in the GVE with beaver constituting up to 42% of wolf pack diets during the ice-free season (April-October) when beavers are vulnerable to predation (Gable et al. 2017a). Predation of beavers during the ice-free season is widespread amongst wolf packs regardless of beaver density variation within wolf pack territories (Gable et al. 2017a). For example, beaver constituted 33% of the ice-free season diet of a pack in the lowest beaver density area (0.47 colonies/km²) of the GVE (Gable and Windels 2018). Though individual wolf packs can remove an estimated 38-42% of the beaver population within their territory, there is no evidence to suggest that wolves are suppressing or reducing beaver population densities in the GVE (Gable and Windels 2018, Gable et al. 2018d).

METHODS

To assess the ecological effects of wolf predation on dispersing beavers, we: 1) quantified wolf predation on dispersing beavers, 2) estimated how wolf predation affects the creation, recolonization, and persistence of beaver ponds, and 3) examined how wolf predation affects the number of ponds and volume of surface water stored in the Greater Voyageurs Ecosystem (GVE), Minnesota, a southern boreal ecosystem. To do so, we searched clusters of GPS-locations (20-min fix interval) from GPS-collared wolves to locate where wolves killed dispersing beavers and to estimate kill rates of wolves on dispersing beavers. When wolves killed dispersing beavers that had recently settled in an area—as determined by a newly constructed dam or a repaired existing dam—we

monitored the fate and occupancy of that pond annually both on foot and through aerial surveys. We compared the fate of these “wolf-altered ponds” (i.e., where a dispersing beaver created or recolonized a pond and was subsequently killed by a wolf) with newly-established “reference ponds” (i.e., where a dispersing beaver created or recolonized a pond) to assess how wolves affected the creation, recolonization, and persistence of beaver ponds. To evaluate the ecological effects of this process, we estimated the number of ponds that wolves alter annually in the GVE by using mean wolf density in the GVE, kill rates of dispersing beavers that had recently created or recolonized ponds, and the mean number of ponds maintained by a beaver colony in the GVE. We then used simulations to bound the uncertainty around our estimates and to describe how the number of beaver ponds altered by wolves would be expected to change with known parameter variability.

Clusters and Kill Rates

During 2015-2019, we captured wolves and fit them with 20-min-fix-interval GPS-collars (IACUC protocol: MWR_VOYA_WINDELS_WOLF). In 2015, a few wolves were fitted with collars that took fixes every 4-12 hr (see Gable et al. 2016 for more details). We searched clusters of GPS-locations from collared wolves during April-November to identify predation events. We considered a cluster to be ≥ 2 consecutive locations within a 200 m radius of one another (Gable et al. 2018c). When at clusters, we systematically searched for evidence of a predation event (Gable et al. 2016). When we found remains of a wolf-killed beaver, we assessed whether the beaver was a colony beaver (i.e., associated with established beaver colony), a not-settled dispersing beaver (i.e., not associated with a colony or pond), or a settled dispersing beaver (i.e., associated

with a recently created or recolonized dam/pond and occupying a wetland). Criteria used to classify a wolf-killed beaver in this way are outlined in Appendix 1. Because we were conservative in our assessment of what was a dispersing beaver and the status (settled vs. not settled) of the disperser, we are confident that the beavers examined in our analysis were dispersing individuals. Though, due to this, we likely excluded some dispersing beavers from our analysis. We used this information to estimate the percent of wolf-killed dispersing beavers that were settled when killed (denoted as $P_{settled}$ in the modeling approach described below).

We were only able to estimate kill rates of wolves on dispersing beavers (dispersing beaver/wolf/day; denoted as KR_{wolf} below) in 2018 and 2019, which is when we searched *all* clusters of GPS-locations from these wolves. Kill rates were determined by dividing the number of dispersing beavers killed by a wolf in 2018 and 2019 by the number of days we searched clusters for that wolf. We assumed this kill rate was representative of the wolf population in the GVE for 2018 and 2019. We determined the total number of dispersing beavers a typical wolf would kill in the GVE by multiplying the kill rate by the mean number of days a year that beavers are available to wolves (213 days; average ice-free season=April 1–October 31) (beavers are rarely killed during winter months). We did not determine kill rates for wolves followed from 2015 to 2017 because we only searched a subset of GPS-clusters and there is currently no reliable method to extrapolate wolf kill rates of small prey in summer from only a subset of searched GPS-clusters. We estimated 95% confidence intervals for kill rates using percentile bootstrapping.

Beaver Pond Fate

To understand how wolf predation of recently settled dispersing beavers affected the persistence of newly-created or recolonized ponds, we compared the fate of wolf-altered and reference ponds. Reference ponds were newly-created or recolonized ponds (<6 months old) with fresh beaver activity that were encountered and identified opportunistically on foot during May-September from 2015 to 2019 when searching clusters and conducting other fieldwork (we hiked >25,000–27,000 km and put in >15,000 hours of fieldwork over this 5-year period). As such, reference ponds should be a representative sample of newly-created or recolonized ponds and represent the fate of all newly-created/recolonized ponds in the GVE during the study period. We used data from reference ponds to estimate the probability of a newly-created or recolonized beaver pond remaining occupied until fall of that year (denoted as P_{occ} below) in the GVE. Reference ponds could become inactive for a variety of reasons (e.g. death of disperser via predation, disease, or starvation) but we had no way to assess this. That said, it is likely that a certain, potentially substantial, proportion of reference pond failure is attributable to wolf predation.

We assessed the fate of wolf-altered and reference ponds using aerial censuses in mid-to-late October during 2015-2019 (see Appendix 2 for details of aerial survey method). We also assessed the status of all wolf-altered ponds on foot 2-6 months after the predation event occurred, and reference ponds were visited multiple times per ice-free season as well. We quantified pond persistence by determining the percent of wolf-altered and reference ponds that remained active from the summer (May-Sept.) until the aerial fall survey of that year. Further, we monitored the status of wolf-altered and reference ponds via aerial fall surveys in each subsequent year after the pond was

colonized, which allowed a preliminary examination of the potential longer-term (1-4 years) effects of wolf predation on pond persistence and colonization.

Impact of Wolf Predation on Pond Creation and Water Storage

We then estimated how wolves impact beaver pond creation/recolonization and surface water storage in the GVE. Our general approach was to estimate the number of ponds altered per year (PA) by wolves by estimating the number of ponds that would have been created or recolonized by dispersing beavers had they not been killed by wolves. Specifically, we first estimated the total number of dispersing beavers killed by wolves per year in the GVE, then determined what proportion of those wolf-killed dispersers had started creating or recolonizing ponds, and from there estimated the number of ponds (PA) those dispersers would have created or recolonized had they not been killed; this is represented by Equation (1):

$$PA = W_{pop} \times KR_{wolf} \times P_{settled} \times BP_{beaver} \times P_{occ}$$

Equation 1

where W_{pop} is the number of wolves in the GVE, KR_{wolf} is the number of dispersing beavers killed per wolf per year, $P_{settled}$ is the proportion of wolf-killed dispersing beavers that started creating or recolonizing a pond prior to being killed, BP_{beaver} is the number of ponds maintained per active beaver colony in the GVE, and P_{occ} is the proportion of a newly-created or recolonized beaver pond remaining occupied until fall of that year in the GVE. We estimated the average number of wolves in the GVE by multiplying average annual wolf density in the GVE (40 wolves/1000 km²; Fox et al. 2001, Gogan et al. 2004, Gable et al. 2018b) by the total area of the GVE (1,812 km²). We estimated BP_{beaver} by recording the number of ponds actively maintained by a beaver colony (we sampled 74

colonies) during summer 2017 and 2018. Beaver colonies commonly maintain 1 or more ponds that are directly adjacent to the primary pond where their lodge is located.

We then used two different simulation approaches (frequentist and resampling [bootstrapping] approaches) to bound the uncertainty around our *PA* estimate and to understand how our estimate of *PA* changed with different, plausible parameter values. We did this to minimize the possibility of overestimating the magnitude of the effect wolves might have, and more importantly, to minimize the possibility of erroneously concluding wolves impacted pond creation when they were not. For the bootstrapping approach, we generated 100,000 plausible values, given the data collected, for each parameter by doing 100,000 bootstrapping iterations (i.e., resampling with replacement). In other words, we used the variability in the data collected on each parameter to generate plausible values of those parameters. We also incorporated variability in wolf population size (W_{pop}) in the GVE by generating 100,000 plausible wolf density values. We assumed wolf densities were uniformly distributed between 35-45 wolves/1000 km² (wolf densities in the GVE generally fluctuate between 35-45 wolves/1000 km²; Fox et al. 2001, Gogan et al. 2004, Gable et al. 2018b) and selected a value from that distribution per each of the 100,000 bootstrap iterations. We then multiplied the values generated during each bootstrap iteration (W_{pop} , KR_{wolf} , $P_{settled}$, BP_{beaver} , and P_{occ}) together (Eq 1) to yield 100,000 plausible estimates for the total number of ponds wolves altered (*PA*) in the GVE. We then selected the 2.5 and 97.5% highest values for our 95% bootstrap confidence interval (CI) of *PP*.

The frequentist approach consisted of generating plausible parameter values from a sample distribution—created using the mean and standard error for each parameter—

which could be multiplied together to yield plausible estimates of PA . That is, we generated plausible values for each parameter (W_{pop} , KR_{wolf} , $P_{settled}$, BP_{beaver} , and P_{occ}) and multiplied those values together (Eq 1), to yield a plausible estimate of PA in the GVE. We repeated this 100,000 times to get 100,000 estimates of PA . We should note that plausible W_{pop} values were generated from uniform distribution between 35-45 wolves/1000 km² (see above). We then selected the 2.5 and 97.5% highest values for our 95% frequentist CI of PA . We calculated a 99% CI using the same approach.

We estimated the volume of surface water wolves were displacing by preventing beaver pond creation by multiplying the number of ponds affected by wolves by the average volume of water stored in beaver ponds in the GVE (2,197 m³/pond; Karran et al. 2017). We used this singular estimate of surface water storage from Karran et al. (Karran et al. 2017)—who only measured a small sample of ponds—to coarsely estimate the overall magnitude of the effect wolves have on water storage; a more intensive study to estimate surface water storage in ponds would be needed to estimate displacement of water storage more precisely.

Results

By visiting 11,817 clusters of GPS-locations from wolves in the Greater Voyageurs Ecosystem (GVE) during 2015-2019, we documented 58 dispersing beavers killed by wolves. Eleven of these dispersing beavers (19%; 95% CI=10%-29%) had either constructed rudimentary dams ($n=6$) in an attempt to create a new pond, or started to recolonize drained ponds by repairing dams ($n=5$) that had blown out >1 yr prior (i.e., the dam was not functional and water was freely flowing downstream). Wolves, on average,

killed 0.021 dispersing beavers/wolf/day ($n=12$ wolves in 2018-2019), which is 4.5 dispersing beavers/wolf/year (95% CI=2.6–6.35 beavers/wolf/year).

We compared the fate of wolf-altered ponds (i.e., where a dispersing beaver started creating or recolonizing a pond and then was killed by a wolf) with reference ponds (i.e., where a dispersing beaver started creating or recolonizing a pond) to assess how wolves affected the creation, recolonization, and persistence of beaver ponds (Fig. 2, 3). Of 31 reference ponds, 84% (26/31; 95% CI= 71-97%) persisted to the fall after beaver colonization in the summer, whereas 0% (0/11) of wolf-altered ponds persisted to the fall (Fig. 2). All 11 wolf-altered ponds were non-functional by the fall, as the newly constructed or repaired dams had failed and water was flowing freely downstream. In other words, after a wolf killed a dispersing beaver that had created or recolonized a pond, our data indicates the pond remained inactive for >1 year 100% of the time (Fig. 3, 4). Of 22 reference ponds monitored for >1 yr, 69% (13/22; 95% CI=41-77%) were active in the fall of the following year, and 66% (11/16; 95% CI=44-88%) of reference ponds monitored >2 years were active after the second fall following creation or recolonization (Fig. 2). All wolf-altered ponds were inactive as of Fall 2019, except for two pre-existing ponds that were re-colonized 1 and 3 years after a wolf killed a dispersing beaver in that pond. Beaver colonies in the GVE maintained 1.7 ponds (95% CI=1.54-1.86).

In total, we estimate that wolves alter the establishment of ~88 ponds per year (95% and 99% frequentist CI: 33-162 ponds and 21-192 ponds, respectively; 95% and 99% bootstrap CI: 36-162 and 25-195 ponds, respectively) and the storage of 194,000 m³ of water per year (95% bootstrap CI: 79,100-355,900 m³; this assumes 2,197 m³ water

stored per pond Karran et al. 2017). Simulations suggest the number of ponds (and water stored) wolves alter in the GVE is largely a function of wolf kill rates of dispersing beavers and the proportion of wolf-killed dispersing beavers that had started creating or recolonizing ponds (Fig. 4, Fig. S1).

Discussion

We have demonstrated that wolves, by killing dispersing beavers that are unable to maintain the dams and ponds they had started creating or recolonizing, are able to alter riparian ecosystems (i.e., beaver pond creation, recolonization, and persistence, water storage; Fig 2 & 4). Because dispersing beavers are primarily solitary individuals (Mayer et al. 2020), the only way for a newly-created or recolonized pond to persist once a wolf kills a dispersing individual is if another dispersing beaver reaches that pond and continues to maintain the dam. Our work suggests such a scenario seldom occurs and that once a wolf kills a dispersing individual that new or recolonized pond remains unoccupied for the rest of that year. Our data suggests that the ecological effects caused by wolves disrupting beaver-mediated wetland creation might last for several years (Fig. 2).

Although wolves appear to alter beaver pond dynamics, we are not convinced that wolves reduce the total number of ponds at the landscape scale but rather alter the spatial and temporal distribution of ponds. There is little evidence to suggest that wolf populations are able to control or suppress beaver population densities in the Greater Voyageurs Ecosystem (GVE) (Gable and Windels 2018) or any other system (Gable et al. 2018*d*, Johnson-Bice et al. 2020). Instead, wolf predation appears compensatory in the GVE beaver population (Gable and Windels 2018). Given this, we suggest that wolves

likely alter the spatial distribution of 88 (95% CI=33-162) ponds per year, which equates to ~194,000 m³ of total surface water storage or one beaver pond per 22 km² in the GVE. Thus, the ecological importance of wolf predation on beavers might not be in influencing beaver population size, but rather by altering the spatio-temporal dynamics of where beavers engineer ecosystems. Notably, while we assumed wolves in the GVE are solitary predators that kill beavers individually during the summer (Demma et al. 2007, Gable et al. 2018*d*), the number of ponds wolves alter would decrease if prevalence of cooperative hunting by wolves during summer increased.

At the pond site scale, wolves radically alter the environment when they prevent the establishment of a new beaver pond or the recolonization of an old pond (Fig. 4). Beavers are predictable agents of disturbance within boreal forest ecosystems (Remillard et al. 1987, Nummi and Kuuluvainen 2013) due to the flooding associated with beaver engineering (Naiman et al. 1988), and the diverse ecological effects that result from beaver disturbance are exceptionally well-documented in the literature (Table 1). Wolves, by preventing the creation of entirely new ponds for at least 1-2 yr, can inhibit site-specific disturbances in boreal forests. That is, wolves prevent the conversion of a forest to a wetland and riparian ecosystem for >1-2 yr. When wolves kill a dispersing beaver that has recolonized an old pond, they directly affect the trajectory of ecological succession within that site and contribute to the increased environmental heterogeneity common within beaver-altered landscapes (Kivinen et al. 2020). Ecological succession generally ‘resets’ with beaver activity (Little et al. 2012), thus wolf prevention of beaver pond recolonization allows succession within that site to continue unabated for at least 1-2 more years and possibly longer (Fig. 2 & 4).

Although wolf alteration of beaver pond dynamics operates on a localized scale, the effects are likely influential at greater spatial and temporal scales. By influencing pond creation and recolonization, wolves contribute to the dynamic mosaic of abandoned and inundated ponds that increases environmental heterogeneity across space and time (Kivinen et al. 2020), ultimately influencing the spatial variation (Schlosser and Kallemeyn 2000), diversity (Bush et al. 2019), and richness (Stein et al. 2014) of species. This is similar to other small-scale ecological disturbances, such as tree tip-ups and the forest gaps they create (McClure and Lee 1993, Hart and Grissino-Mayer 2009), predator-killed carcasses (Wilmers et al. 2003, Bump et al. 2009a, Barry et al. 2019), predator dens and burrows (Eldridge and Whitford 2009, Gharajehdaghipour et al. 2016), termite mounds (Dangerfield et al. 1998), and ant hills (Folgarait et al. 2002, Frouz and Jilková 2008), that, due to their outsized ecological effects, influence landscape heterogeneity despite operating at small, seemingly trivial scales (Bump et al. 2009a). Even short-term, ephemeral disturbances such as vernal pools are important for biotic communities on landscape scales (Zedler 2003, Williams 2006).

Even if wolves only prevent pond creation or recolonization for short-time scales (<2-3 yr), wolves' effect on the spatial distribution of ponds at the landscape scale likely compounds over time because where wolves alter pond creation and recolonization almost certainly varies annually. In other words, we suspect wolves are not preventing pond creation and recolonization at the same 88 sites year after year but rather altering the creation and recolonization of *different* ponds each year (though there could be sites where wolves do frequently prevent beaver creation or recolonization). Thus, we suggest wolves' impact on pond creation and recolonization are akin to the cumulative ecological

effects of beaver pond creation articulated by Johnston and Naiman (1990a): “Although the area disturbed by an individual beaver pond is small...the cumulative disturbance of many beaver ponds over time results in extensive alteration” (p.1620). For example, in a 1-year period wolves might only alter the spatial distribution of 1 pond per 22 km² (88 ponds/yr) but over a 10-year period, wolves might affect 1 pond per 2.2 km² (88 ponds/yr*10 yr). While this example is almost certainly an oversimplification, it illustrates that wolves could have a substantial effect on the distribution of wetlands over time in the GVE, and in other systems where wolves and beavers are sympatric (see Fig. 1 in (Gable et al. 2018d)). Further, it highlights why long-term research is necessary to determine how interactions between this apex predator and ecosystem engineer ultimately shape wetland dynamics in boreal ecosystems.

Previous work from western North America suggests that wolves facilitate long-reaching behaviorally-mediated trophic cascades that ultimately affect riparian ecosystems and the geomorphology of waterways (Beschta and Ripple 2006, 2019), but this has been met with skepticism (Allen et al. 2017, Mech 2017). We, however, have identified and provided evidence for a well-defined mechanism by which wolves impact riparian ecosystems in boreal systems directly through predation (Fig. 4). Beavers, through their prolific ecosystem engineering, transform ecosystems wherever they establish ponds, creating abundant habitat for a variety of taxa and affecting large-scale ecological processes such as water storage, sedimentation, nutrient cycling, and carbon sequestration (Table 1) (Rosell et al. 2005). If beavers are the natural ecosystem ‘engineers’, creating wetlands across the circumpolar boreal ecosystem, then wolves can be thought of as a factor that directly influences such engineering by altering site-specific

beaver construction that in turn influences the spatial and temporal distribution of wetlands.

Large predators are thought to primarily have landscape-level ecological effects through density-mediated or behaviorally-mediated mechanisms. Here, we described a mechanism by which a large predator, through the outsized effects of direct predation on an ecosystem engineer, affected ecosystems without altering the density or behavior of their prey. The functional and numerical responses of predators to prey populations likely influence the ecological magnitude but the mechanism itself is independent of predator and prey densities. That is, predators can have outsized ecological effects by killing prey that have a disproportionately large role in ecosystem functioning (e.g., ecosystem engineers). Our work highlights yet another functional role of direct predation in ecosystems and should be helpful for understanding how the restoration of large predator populations across the world might impact ecosystems.

Table 1. The ecological benefits that ecosystem engineering by beavers creates in riparian ecosystems based on previous studies. All values (e.g., 200% greater, 2× higher) are in relation to reference (unmodified) sites sampled from the same study, or are in relation to sampled characteristics prior to ecosystem engineering by beaver. Superscripts indicate references, which are listed in Appendix 3. Although beavers often have deleterious (or no) effects on ecosystems, (e.g., references¹⁻⁷) we focus on the ecological benefits here for simplicity and space constraints.

Ecological benefits	Description of benefits due to ecosystem engineering by beavers
Ecosystem services	
Water runoff attenuation	Reduce peak stream discharge 30–100% ^{8,9} ; increase water residence time up to 230% ¹⁰
Groundwater recharge	Stabilize and even elevate groundwater levels ¹¹⁻¹³
Water purification	Greater pH values, acid-neutralizing capacity in ponds ¹⁴⁻¹⁶
Sediment deposition	Sedimentation rates up to 0.28 m yr ⁻¹ and 171 m ³ yr ⁻¹ ; up to 2000–6500 m ³ total sediment ¹⁷⁻¹⁹
Carbon (C) sequestration	Sequester and deposit C within sediment layers ^{2,20} ; up to 200% greater C storage ²¹
Nitrogen (N) sequestration	Increase N soil concentration up to 72% ²² ; remove 5-45% of watershed N loading ²³
Habitat alterations	
Stream geomorphology	
<i>Reduce incision</i>	Restore incised stream systems ^{24,25}
<i>Channels and pools</i>	Increase channel diversity ^{26,27} ; increase number (up to 1.4·) and depth (up to 1.6·) of pools ²⁸
Habitat heterogeneity	Increase habitat heterogeneity at local (site) ²⁹ , stream ³⁰ , and landscape ²⁵ scales
Water storage	Increase area of surface water on landscape up to 9· ³¹ ; store 2.5–11 km ³ water globally ³²
Benefits to plants and animals	
Mitigate effects of climate	Pond water buffers against effects of temperature increase, drought for animals ³¹
Wildlife	
<i>Large mammals</i>	Provide aquatic food resources and thermal cooling benefits ^{33,34}
<i>Semi-aquatic mammals</i>	Provide den sites, shelter, food resources ³⁵⁻³⁷ ; increased abundance and species richness ³⁸
<i>Small mammals</i>	Abundance 75–300% greater ^{39,40}
<i>Bats</i>	Foraging activity and use of beaver ponds 4–8· greater ^{41,42} ; up to 1/3 of roosts in ponds ⁴³
<i>Raptors</i>	83% of osprey (<i>Pandion haliaetus</i>) nests located in beaver ponds ³⁴
<i>Waterfowl</i>	Up to 3.4· greater species richness ⁴⁴ , 10· higher brood density ⁴⁵ , 50· greater abundance ⁴⁶
<i>Passerines</i>	Species richness 1.3–2· greater ^{47,48} ; provide essential snag tree cavities for nests ⁴⁹

<i>Amphibians</i>	Account for up to 81–100% of breeding sites ⁵⁰ ; annual production can increase 1.2–23 ⁵¹
<i>Reptiles</i>	Species richness up to 1.6· greater and species diversity 1.4· greater ⁵²
Fish	
<i>Salmonids</i>	Increase fish density up to 0.8/m, juvenile survival up to 52%, and production up to 175% ²⁸
<i>Other species</i>	Abundance up to 3· greater and species richness 1.2· greater ^{53,54}
Invertebrates	
<i>Aquatic</i>	Species richness up to 1.25–1.4 ^{55,56} , biomass density 2–5 ⁵⁷ , and abundance 235% greater ⁴⁰
<i>Terrestrial</i>	Abundance up to 26–60% greater ^{29,40}
<i>Both</i>	Pond succession influences community assemblages, increasing α-diversity at regional scale ⁵⁸
Plants	
<i>Aquatic</i>	Biomass density up to 20· greater ⁵⁶ ; species richness and diversity increase with pond age ⁵⁹
<i>Herbaceous</i>	Increase species diversity up to 28% and species richness 33–93% ^{60,61}
<i>Undifferentiated</i>	Increase cumulative (148%) and mean (46%) species richness ⁶²

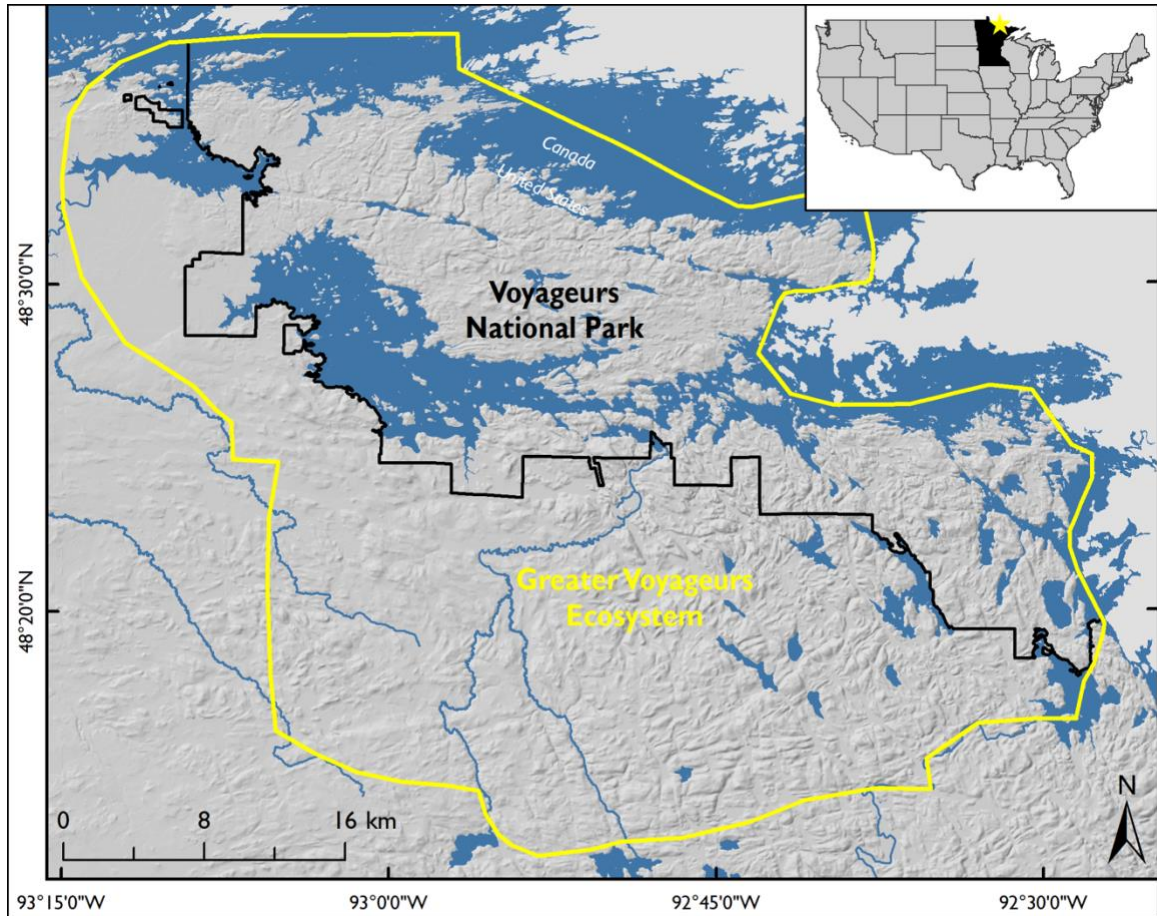


Figure 1. Map of the Greater Voyageurs Ecosystem (yellow polygon) in Northern Minnesota, USA, which is a 1,812-km² southern boreal ecosystem in Northern Minnesota (48°30' N, 92°50' W). Voyageurs National Park (black polygon) constitutes the northern portion of the GVE whereas the central and southern portions of the GVE are predominantly forest service, state-owned, and timber company land. The GVE is typified by dense forests (coniferous, deciduous, and mixed) and abundant wetlands, lakes, and bogs interspersed with rock outcrops and ridges from past glacial activity. The GVE has sustained high densities of wolves (35-45 wolves/1000 km²) and beavers (>0.47-1 colony/km²) for >30-40 years.

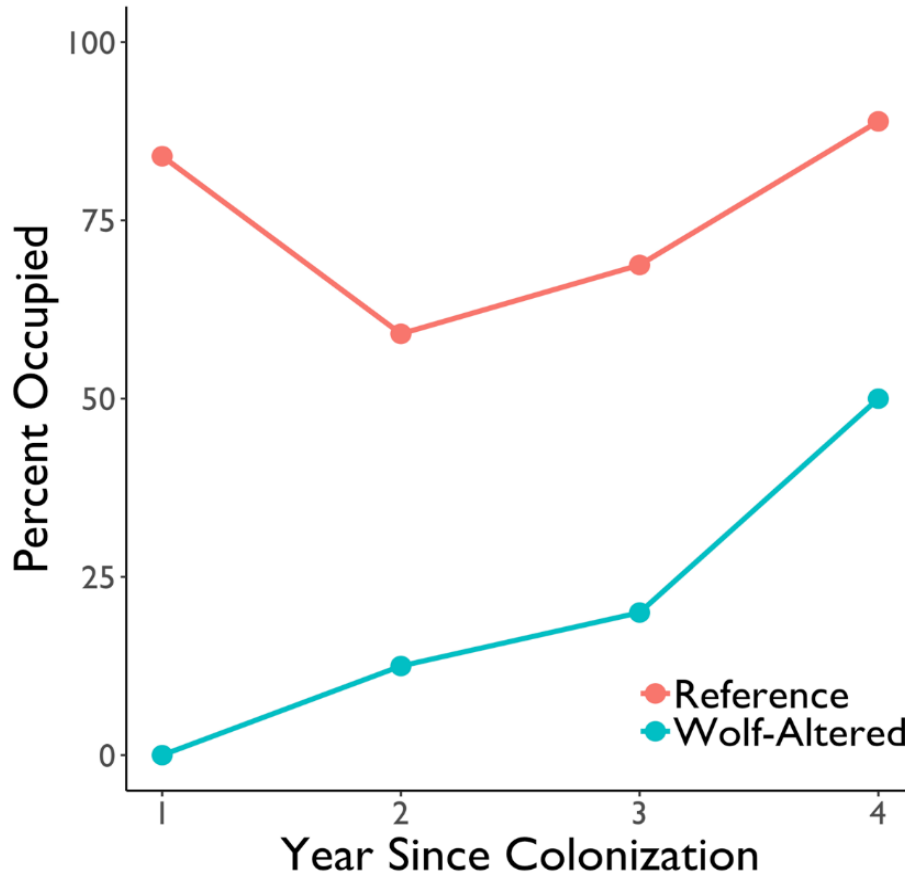


Figure 2. Occupancy of beaver ponds after creation or recolonization by dispersing beavers in the Greater Voyageurs Ecosystem (GVE), Minnesota during 2015-2019. Reference ponds (red line) are ponds that were created or recolonized by dispersing beavers during April-September of that year and identified opportunistically while conducting fieldwork whereas wolf-altered ponds (turquoise line). Reference ponds are a representative sample of newly-created and recolonized ponds in the GVE and thus should reflect the fate of all newly-created and recolonized ponds in the GVE. Wolf-altered ponds are ponds where dispersing beavers started creating or recolonizing a pond and then were subsequently killed by a GPS-collared wolf. Sample sizes for 1, 2, 3, and 4 ‘Years Since Colonization’ were 31, 22, 16, and 9 for reference ponds, and 11, 8, 5, and 4 for wolf-altered ponds, respectively.

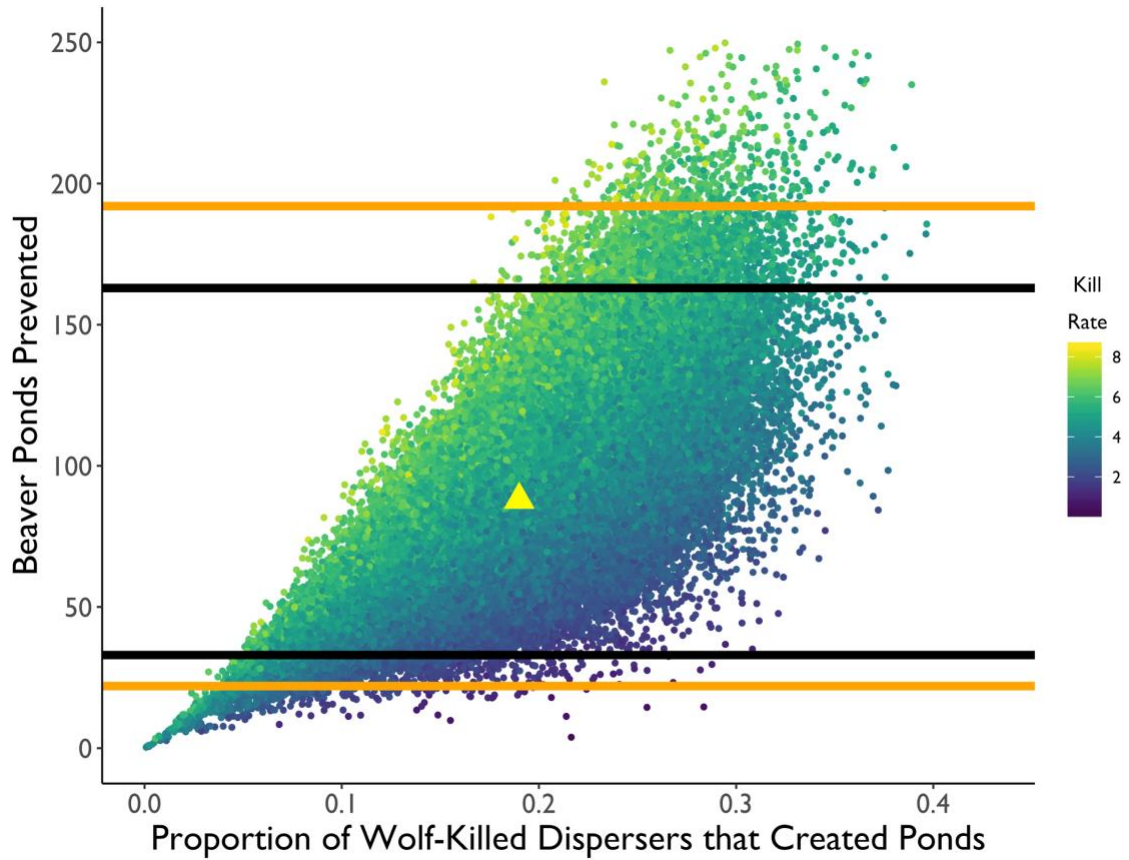


Figure 3. Relationship between the number of beaver ponds wolves prevented per year and the proportion of wolf-killed dispersing beavers that created ponds. Wolf kill rates of dispersing beavers (beavers/wolf/year) are represented in the color spectrum. Mean wolf kill rates of dispersing beavers in the GVE was 4.5 beavers/wolf/year (95% CI=2.6–6.35 beavers/wolf/year) and the proportion of wolf-killed dispersing beavers that created ponds was 0.19 (95% CI = 0.10-0.29). The yellow triangle represents our point estimate for the number of beaver ponds prevented. The solid black and orange lines represent the 95% and 99% confidence interval, respectively, of the beaver ponds prevented by wolves. Results were obtained by performing 100,000 simulations.

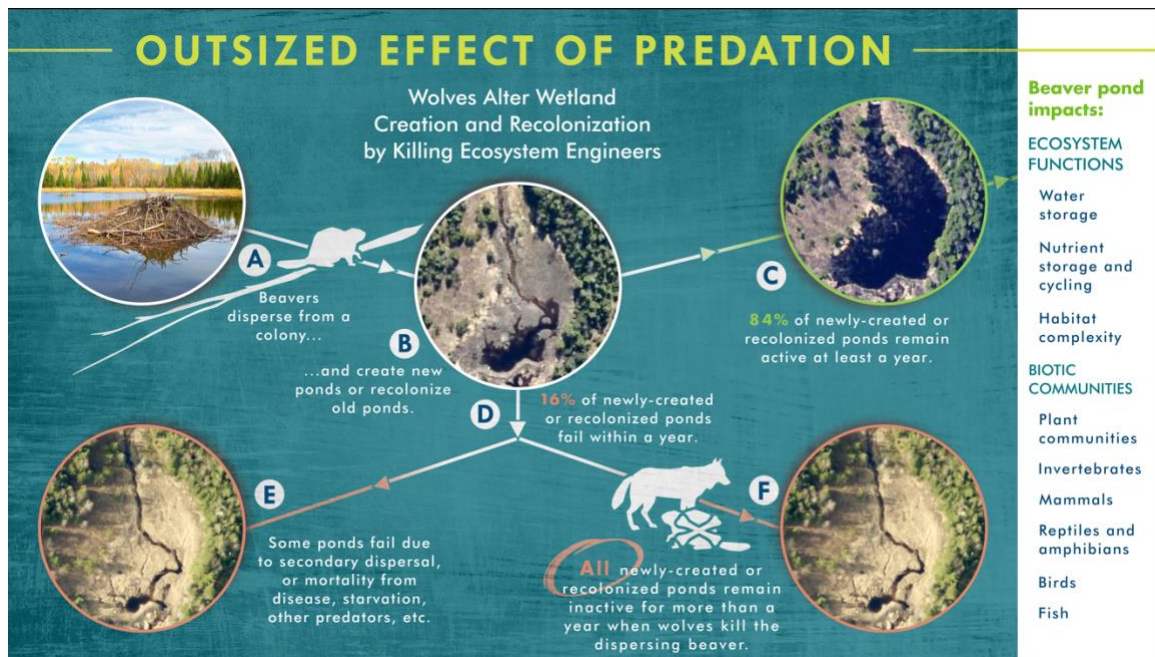


Figure 4. The fate of ponds created by dispersing beaver in the Greater Voyageurs Ecosystem, Minnesota. Dispersing beavers leave their colony (A) and eventually settle in an area where they create a new dam and pond or recolonize an existing pond by repairing a non-functional dam on a stream (B), either of which in turn creates a new pond. Dispersing beavers in these newly created ponds continue to occupy the pond 84% of the time until the winter of that year (C). By creating and occupying the pond, dispersing beavers initiate ‘ecosystem engineering’ that affects multiple species, habitats, ecosystem processes, and aquatic food communities (Table 1). However, 16% of the time beavers abandon the pond or die before winter of that year (D), which causes the dam to fail and the pond to drain (E, F). An unknown portion of these pond failures are not-related to wolf predation but other causes such as disease, habitat quality, or other predators (e.g., black bears) that either kill or cause the beaver to abandon the pond (E). Wolf predation is responsible for an unknown, but potentially substantial, proportion of these pond failures. After a wolf kills a dispersing beaver that has created a new pond,

our data indicates the pond remains inactive for >1 year 100% of the time (F). Note that photos in B, C, D, E, and F are of the same pond. Infographic credit A. Ostman.

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Appendices

Chapter 1 Appendices

Appendix S1. List of known predators of beavers (*Castor* spp.) in North America, Europe, and Asia. References are below the table.

Scientific name	Common Name	Source
<i>Accipiter gentilis</i>	Northern goshawk	Danilov 2009
<i>Alligator mississippiensis</i>	American alligator	Muller-Schwarze and Shulte 1999
<i>Aquila chrysaetos</i>	Golden eagle	Danilov 2009
<i>Canis familiaris</i>	Domestic dog	Rosell et al. 2005
<i>Canis latrans</i>	Coyote	Basey & Jenkins 1995
<i>Canis lupus</i>	Gray wolf	Gable et al. 2016
<i>Canis rufus</i>	Red wolf	Muller-Schwarze and Sun 2003
<i>Esox lucius</i>	Northern pike	Janiszewski et al. 2014
<i>Gulo gulo</i>	Wolverine	Baker and Hill 2003
<i>Haliaeetus albicilla</i>	White-tailed eagle	Danilov 2009
<i>Hugo taimen</i>	Taimen	Janiszewski et al. 2014
<i>Lontra canadensis</i>	River otter	Baker and Hill 2003
<i>Lynx canadensis</i>	Canada Lynx	Baker and Hill 2003
<i>Lynx lynx</i>	Eurasian Lynx	Rosell et al. 2005
<i>Lynx rufus</i>	Bobcat	Baker and Hill 2003
<i>Martes martes</i>	European marten	Janiszewski et al. 2014
<i>Neovision vison</i>	Mink	Baker and Hill 2003
<i>Nyctereutes procyonoides</i>	Raccoon dog	Janiszewski et al. 2014
<i>Puma concolor</i>	Cougar	Lowrey et al. 2016
<i>Ursus americanus</i>	Black bear	Smith et al. 1994
<i>Ursus arctos</i>	Brown bear	Rosell et al. 2005
<i>Vulpes vulpes</i>	Red fox	Kile et al. 1996

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Appendix S2. Percentage of wolf diet (estimated via scat, stomach content, kill site, and stable isotope analysis) comprised of beaver from wolf diet and predation studies in North America and Eurasia where beaver was a trivial component of wolf diet ($\leq 5\%$). We estimated the mean percentage of wolf diet comprised of beaver for each study by averaging over meaningful temporal units (e.g., month) and wolf sampling units when possible (Gable et al. 2017). See Table 1 for a list of studies where beavers composed a non-trivial portion of wolf diets ($>5\%$). References below the table.

Location	Diet Method	Wolf Sampling Unit ^a	Time Period Studied	Time Interval Studied ^b	Mean Beaver in Diet (%)	Range Beaver in Diet (%)	Role of Beaver in Wolf Diet	Beaver Density (lodges/km ²)	Reference
NORTH AMERICA									
Alaska, USA	Scat	1 Pop	Summer	Annual	<1*	0-1	Alt		Murie 1944
	Scat	1 Pop.	May-Jul	Annual	<4		Alt		Spaulding et al. 1998
	Scat	1 Pop.	May-Jun	Seasonal	1*		Alt		Lafferty et al. 2014
Michigan, USA	Kill Site ^d	Pop.	Dec-Apr	Annual	2		Alt		Vucetich et al. 2012
Minnesota, USA	Scat	Pop.	Apr-Sept	Annual	3		Alt	0.33	Fritts & Mech 1981
	Scat	Pop.	Mar-Nov	Annual	2*	0-3	Alt		Chavez and Gese 2005
Montana, USA	Kill site ^d	Pop.	Winter	Annual	1		Alt		Boyd et al. 1994

British Columbia, Canada	Scat	>1 Pop.	Summer		2.1		Alt	Darimont et al. 2004
EURASIA								
Belarus	Scat	Pop.	Jan-Dec	Annual	4	3-5	Alt	Sidorovich et al. 2003
Poland	Kill site ^d /	Pop.	Jan-Dec	Annual	1		Alt	Jedrzejewski et al. 2002
	Scat	>1 Pop.	Jan-Dec	Annual	1	0-5	Alt	Nowak et al. 2011
	Scat	Pop.	Annual		5		Alt	Jedrzejewski et al. 2012
Scandinavian Peninsula	Scat	Pop.	Jan-Dec	Annual	1	1-2	Alt	Muller 2006
	Kill site ^d	Pop.	Winter	Annual	1		Alt	Zimmerman et al. 2007
	Kill site ^d	Pop.	Jun-Sept	Annual	<3		Alt	Sand et al. 2008

^a Wolf diet examined at the following scales: Ind. = individual; Pack = pack; Pop. = a single population; >1 Pop. = multiple populations.

^b Wolf diet examined at the following time intervals: Month = monthly; Bi-month = 2-month intervals; Seasonal = seasonally (e.g. winter, summer); Annual = annually (e.g., 1999) or over multiple years (e.g., 1997-1999).

^c Role of beaver in wolf diet: Alt = alternate prey, PS = primary prey during summer season, PA = primary annual prey.

^d Percent of wolf diet that was beaver from kill site studies is based on the percent of all kills found that were beaver

* Diets estimated using percent frequency of occurrence or percent volume as opposed to percent biomass. Generally, percent frequency of occurrence and percent volume will overestimate the prevalence of beaver in wolf diets because more scats are produced per kg of beaver than per kg of larger prey because beavers have a larger proportion of indigestible material than larger prey (Weaver 1993).

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Chapter 3 Appendices:

Video S1: Video footage of the first documented observation of a wolf hunting a beaver.

Chapter 4 Appendices:

Appendix 1. Description of beaver habitat feature classes used for analysis.

Beaver Habitat Feature Definitions

We determined what habitat features wolves waited-in-ambush and killed beavers at based on the following definitions and categories. We used 12 specific habitat features that then can be condensed into 6 broader habitat features.

12 SPECIFIC BEAVER HABITAT FEATURES:

At Dam: Wolf was bedded down right on or next to an active beaver dam.

Below Dam: Wolf was bedded below (i.e., the downstream side) an active beaver dam.

Dam Crossing: wolf was bedded down to a trail that crossed an active beaver dam to reach a small waterway or pond below the dam. Dam crossings are used by beavers to travel to other bodies of water, not to forage. If there are cuttings at a trail that crosses a dam, then the trail should be considered a feeding trail.

Feeding Area: wolf was bedded down next to an area where beavers were foraging terrestrially but there were no clear and defined feeding trails. Usually feeding areas are strips of shorelines where beavers are actively cutting several trees within 10 m from shore.

Feeding Canal: wolf was bedded down next to a beaver-created canal that led to areas where beavers were foraging terrestrially.

Feeding Station: wolf was bedded down next to a recently used feeding station where beavers had sat on the shore stripping sticks and stems.

Feeding Trail: wolf was bedded down on and next to an active feeding trail

Forest Interior: wolf killed beaver in forest interior habitat (e.g., mature black spruce bog, cedar lowland, regenerating aspen stand) >100 m from active beaver colony.

Lodge: wolf was bedded down on, near, or at the base of an active beaver lodge

Pond Edge: wolf was bedded down on the shoreline of an active beaver pond. A pond is any body of water that is impounded by a beaver-created dam.

Shoreline: wolf was bedded down on the shoreline of a river or lake where there was recent, fresh sign of beaver activity (i.e., that a beaver(s) was inhabiting that stretch of shoreline

Scent Mound: wolf was bedded down by an recently used scent mound

Small Waterway: wolf was bedded down by a small creek, stream, or channel that connects two bodies of water.

6 BROADER HABITAT FEATURE CATEGORIES

Dams: includes all attempts in the At Dam, Below Dam, and Dam Crossing categories

Foraging Features: includes all attempts in the Feeding Trails, Feeding Areas, and Feeding Canals categories

Forest Interior: includes all attempts in the Forest Interior category

Lodges: includes all attempts in the Lodge category

Shorelines: includes all attempts in the Feeding Station, Pond Edge, Shoreline, and Scent Mound categories

Waterways: includes all attempts in the Small Waterways category

Appendix 2: Video taken in the field showing how beaver hunting attempts were identified and documented in the field.

Appendix 3: Video taken in the field showing how beaver hunting attempts were identified and documented in the field.

Appendix 4: Video taken in the field showing how beaver hunting attempts were identified and documented in the field.

Chapter 5 Appendices:

Supplementary Video 1: A video recorded when in the field detailing a cooperative beaver hunting attempt, and how we were able to locate these cooperative beaver hunting attempts based on GPS-locations from collared wolves. Video recorded in October 2019 in the Greater Voyageurs Ecosystem, Minnesota.

Chapter 6 Appendices:

Appendix 1: Method for determining whether a killed beaver was a colony beaver, settled dispersing beaver, or not settled dispersing beaver.

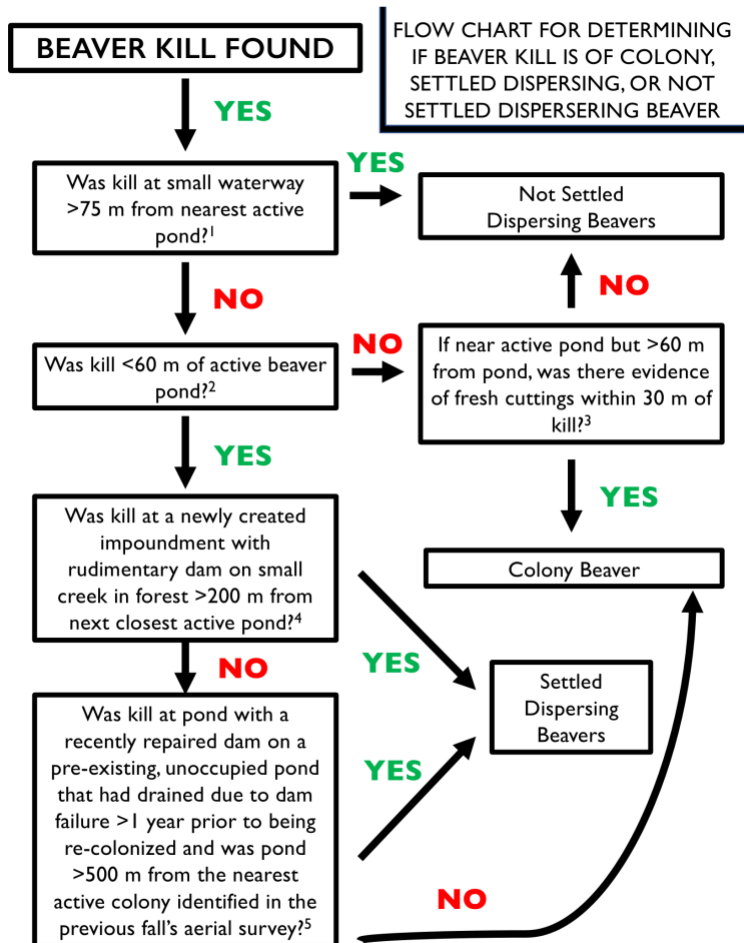


Fig. S1. Flowchart for determining whether a beaver killed by wolves was a colony beaver, settled dispersing beaver, or not settled dispersing beaver.

Rationale for the flow chart:

¹We did extensive mapping of beaver activity around active beaver ponds in 2017-2018.

We never documented beaver activity associated with an active colony >50 m away from the pond in a small waterway and there was no indication that colony beavers were

venturing this far away from the pond via water. To be conservative, however, we considered a kill to be of a colony beaver if the kill occurred in a small waterway <75 m from an active pond. We should note that we measured straight-line distance from a kill to the pond. However, most small waterways meander substantially, and 75 m straight-line distance generally equates to >100 m of small waterway length.

²Colony beavers rarely forage and travel beyond 60 m from the safety of water

³If a colony beaver did travel >60 m from water, it would be to forage. Thus, any beaver >60 m of water had to be within 30 m of fresh cuttings where beavers were clearly foraging to be considered a colony beaver

⁴Based on Gable et al. 2016

⁵We used these criteria so that we did not consider beaver colonies that moved 1-2 ponds upstream or downstream in a given year—which is common in the GVE—as dispersing individuals. Because we were conservative in our assessment of what was a dispersing

Appendix 2. Aerial beaver survey methods used to monitor beaver populations in the Greater Voyageurs Ecosystem.

Aerial beaver surveys were conducted in the Greater Voyageurs Ecosystem (i.e., in and around Voyageurs National Park) from October 2015 to 2019 as part of long-term monitoring protocols of beaver ecology in Voyageurs National Park, MN. All surveys were conducted by identifying active beaver lodges based on the presence of a food cache, fresh cuttings, or fresh mud on a lodge or dam. All surveys were flown in mid-October to early November in a 2-seat tandem Top Cub at 600–700 ft above the ground at a speed of approximately 70 mph (112 kph). We determined if a pond was occupied based on the presence of an active food cache, fresh mud on the lodge or dam, or fresh cuttings in and around the pond. Detection during our aerial beaver surveys was likely >95% because we used a free form, circling pattern that allowed us to circle ponds multiple times if we were uncertain about its occupancy status.

The observer (T.D.G. did all surveys from 2015-2019) recorded all survey data using a real-time mapping/GPS application (DNR Survey Application in ArcMap from 2015-2018 and Maps Plus application on an iPad in 2019). On the application, the observer could see the plane's location and track log as well as waterways and wetlands via high-resolution aerial imagery and all active beaver ponds that had been identified from 2000 to the year of the survey. Having this information allowed the observer to ensure that all potential beaver habitat was surveyed every year. Furthermore, to increase the accuracy and efficacy of our surveys, we created a survey grid (5 x 5 km grid cells) and we surveyed grid cells individually and would not move to the next grid cell until we were certain that we had thoroughly surveyed the current grid cell. We used a free-form

circling pattern for our surveys (Fig. S2), which allowed us to weave in and around as well as circle individual pond complexes as many times as needed to determine if the pond was active. When active lodges/colonies were identified, we recorded the location of the lodge/colony on the mapping/GPS-application. Given all of this, our survey results are highly accurate given the generally conspicuous nature of active beaver colonies and the survey design used.

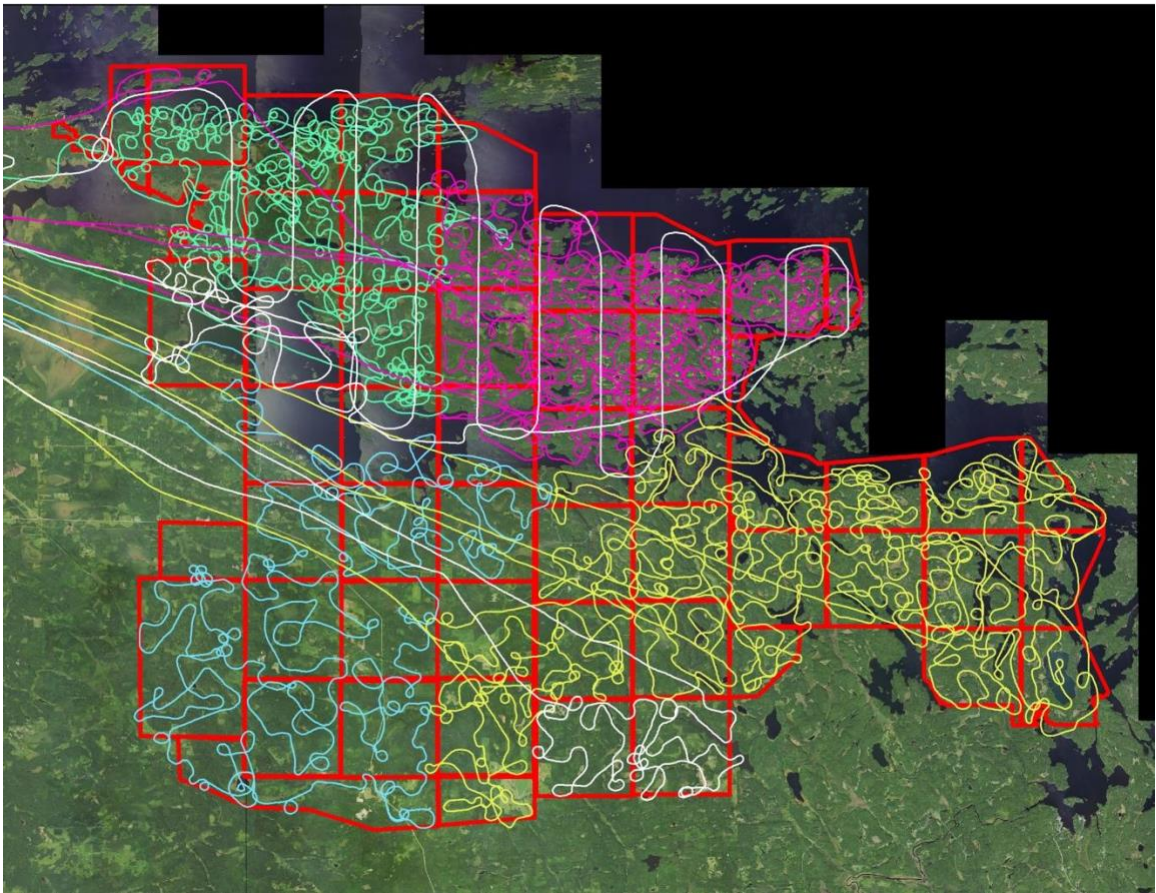


Fig S2. Survey flight tracks during 2019 aerial fall beaver survey in the Greater Voyageurs Ecosystem. The different colors correspond to different days flown. We overlaid a grid (red) on our study area and surveyed each grid cell individually.

Appendix 3. List of references cited in Table 1. The superscripts in Table 1 correspond to the number of each source below.

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