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REVIEW

The forgotten prey of an iconic predator: a review of interactions between grey wolves *Canis lupus* and beavers *Castor* spp.

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ABSTRACT

1. Predator–prey relationships can have wide-ranging ecological and landscape-level effects. Knowledge of these relationships is therefore crucial to understanding how these systems function 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.
2. 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.
3. 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.
4. 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.
5. 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.
6. Given the complexities 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 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 *Oncorhyncus* spp. (Watts & Newsome 2017), flightless moulting birds (Mech et al. 2015), and hares *Lepus* spp. (Peterson & Ciucci 2003). Abundant alternative prey can facilitate a numerical response in wolf populations (Mech 2007), and may subsidise wolf populations during periods of low ungulate abundance (Andersone & Ozoliņš 2004). However, the relationships between wolves and alternate prey populations are poorly understood (Watts & 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 & 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 & 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 & 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 & 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 & 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 & 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.

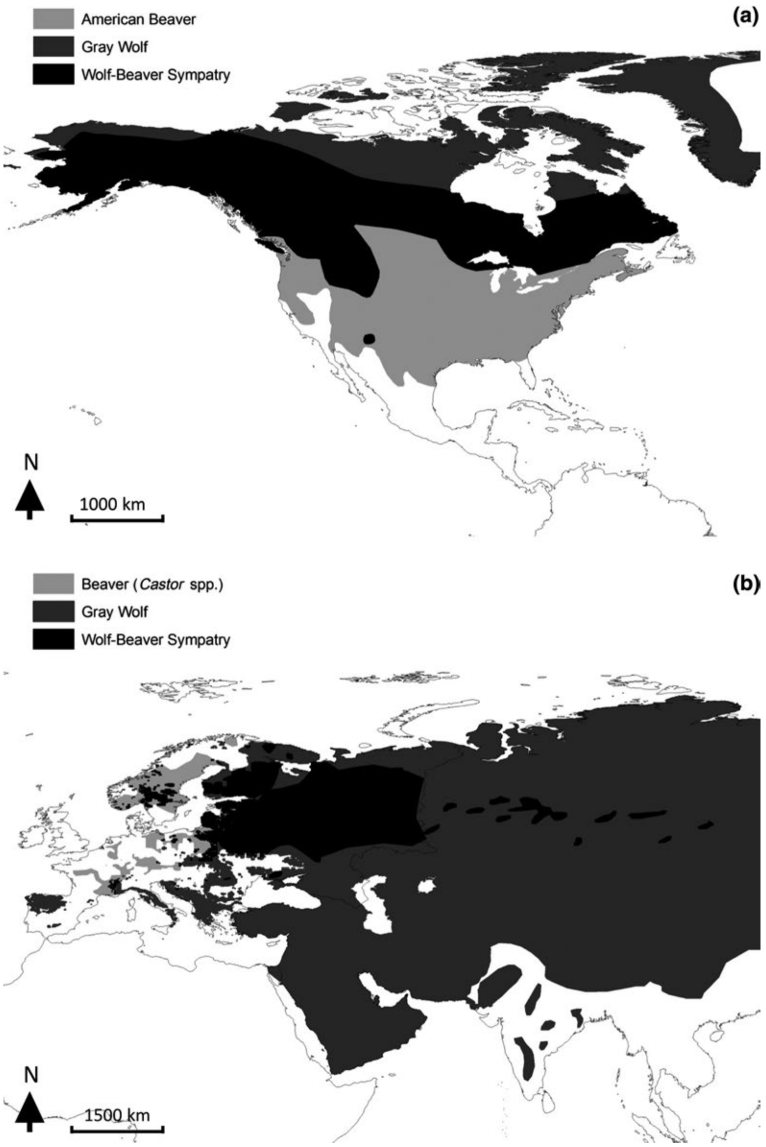

Fig. 1. The geographical ranges of grey wolves *Canis lupus* and beavers *Castor* spp., and where the taxa co-occur, in North America (a), and Europe and Asia (b). Maps are based on data from the International Union for Conservation of Nature (Mech & Boitani 2010, Cassola 2016) and on unpublished data from Halley et al.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

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 (Figs 1 and 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 & 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 & Peterson 1991). Nonetheless, wolves consume beavers that they catch above the ice during periods of open water or winter thaws (Mech 1966, Forbes & 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 large predators (Mech 1970, Basey & Jenkins 1995, Mech et al. 2015). Due to this, beavers generally limit their terrestrial

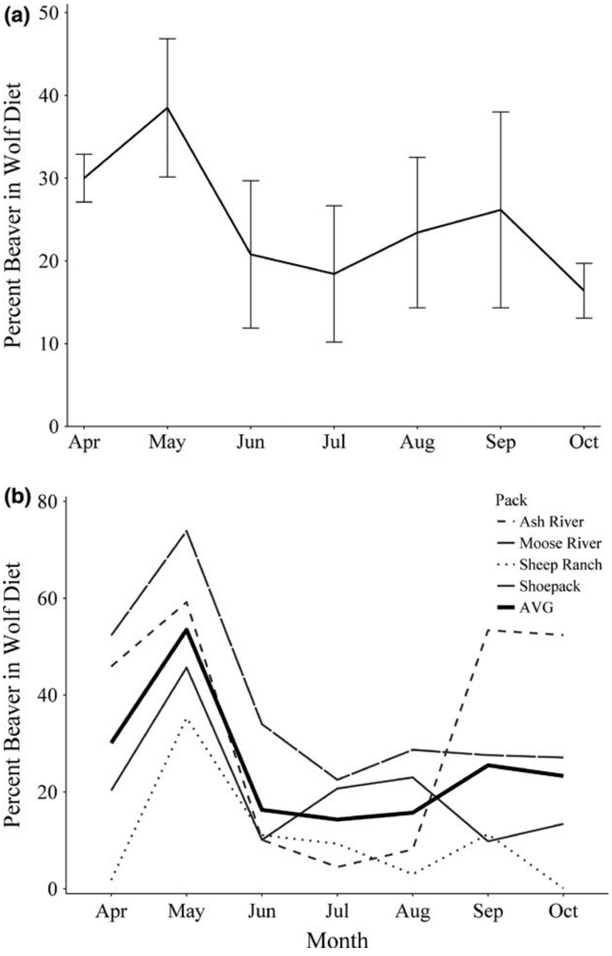

Fig. 2. Mean monthly percentage (±standard errors) of scat-based grey wolf diets composed of beaver, based on seven studies (Hall 1971, using raw data from Pimlott et al. 1969, Voigt et al. 1976, Messier & Crête 1985, Fuller 1989, Gogan et al. 2004, Theberge & Theberge 2004, and Gable et al. 2017) in 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. 2017; b).

activities to close proximity of water (<40–100 m; Basey & 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 & 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 (Wilsson 1971). 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 & Windels 2015). Beavers also excavate channels to increase water access to food and decrease predation risk (Baker & 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 & 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 & 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 & 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 & 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 (Wilsson 1971). Furthermore, 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 & 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 & 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 three 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 & Jenkins 1995). Wolves dig into active beaver lodges, primarily in the winter (Peterson 1977, Forbes & 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 & Theberge 1996). In northern Minnesota, wolves target and kill beavers in early spring from lodges on natural lakes when water levels are low (Smith & 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 & 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 & 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 (Sidorovich et al. 2017, 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 & 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 one to two 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

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 composed 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*	Time period studied	Time interval studied	Mean beaver in diet (%)	Range beaver in diet (%)	Role of beaver in wolf diet‡	Beaver density (lodges km^{-2})	References
North America									
Alaska, USA	Scat	Pop.	Summer	Annual	9	4–14	Alt		Ballard et al. (1987)
	Scat	>1 Pop.	January–December	Seasonal	17**	14–24	Alt		Smith et al. (1987)
	Scat	Pack	January–December	Annual	21**	13–28	Alt		Kohira and Rexstad (1997)
	Scat	Pop.	January–December	Annual	11	11–12	Alt		Watts and Newsome (2017)
Isle Royale National Park, Michigan, USA	Scat	Pop.	May–October	Annual	14	1–54	PS/Alt	0.28	Romanski (2010)
Minnesota, USA	Scat	Pop.	January–December	Seasonal	16**	1–18	Alt	0.1	Frenzel (1974)
	Scat	Pop.	May–September	Seasonal	10**	1–25	Alt		Van Ballenberghe et al. (1975)
	Scat	Pop.	April–October	Month	11	1–19	Alt	~0.6	Fuller (1989)
	Scat	Pop.	June–August	Seasonal	20		Alt		Paul (2002); Barber-Meyer and Mech (2016)
	Scat	Pop.	January–December	Seasonal	17**	7–35	Alt	~1	Gogan et al. (2004)
	Scat	>1 Pop	January–December	Seasonal	11	2–30	Alt		Chenaux-Ibrahim (2015)
	Scat	Pop.	June–August	Annual	7	5–9	Alt		Barber-Meyer and Mech (2016)
	Scat	Packs	April–October	Annual	26	10–38	PS/Alt	~1	Gable et al. (2017)
Montana, USA	Scat	Pop.	January–December	Seasonal	5**	1–17	Alt		Arjo et al. (2002)
Alberta, Canada	Scat	>1 pop.	January–December	Annual	7**	2–17	Alt		Cowan (1947)
	Scat	Pack	June–September	Seasonal	37**	17–52	PS/Alt	0.24	Fuller and Keith (1980)
	Scat	Pop.	Summer	Annual	11**	2–14	Alt		Carbyn et al. (1993)
	Scat	Pop	January–December	Annual	10**		Alt		James (1999)
	Scat	Pop.	January–December	Seasonal	20	9–30	PS/Alt	1.54§	Latham et al. (2013)
British Columbia, Canada	Scat	Pop.	May–October	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–September	Annual	60**	7–75	PS/Alt	~1–2	Voigt et al. (1976)
	Scat	Pop.	May–September	Annual	49	35–63	PS/Alt		Theberge et al. (1978)
	Scat	Pop.	January–December	Seasonal	37	13–60	PS/Alt		Krizan (1993)
	Scat	>1 Pop.	January–December	Seasonal	12	8–15	Alt		Forbes and Theberge (1996)
	Scat	1 Pop.	May–August	Seasonal	10	9–12	Alt	~0.4	Theberge and Theberge (2004)
	Scat/Stomach	Pop.	UNK	Annual	20	12–26	Alt		Wiwchar and Mallory (2012)

(Continues)

Table 1. (Continued)

Location	Diet method	Wolf sampling unit*	Time period studied	Time interval studied	Mean beaver in diet (%)	Range beaver in diet (%)	Role of beaver in wolf diet‡	Beaver density (lodges km^{-2})	References
Manitoba, Canada	Scat	Pop.	April–October	Seasonal	44**	24–82	PS/Alt		Hill (1979)
	Scat	Pop.	January–December	Seasonal	17**	5–25	Alt	~1.1	Meleshko (1986)
	Scat	Pop.	January–December	Seasonal	19**	10–35	Alt		Sallows (2007)
	Isotope	Ind.	Summer–Fall	Annual	15	3–83	PS/Alt		Moayeri (2013)
	Isotope	Ind.	Summer–Fall	Annual	11	5–20	Alt		Friesen and Roth (2016)
	Scat	Pop.	January–December	Seasonal	~35**	~20–50	Alt		Naaykens et al. (2016)
Saskatchewan, Canada	Isotope	Pop.	Summer–Fall	Annual	8	4–17	Alt		Urton and Hobson (2005)
Quebec, Canada	Scat	>1 Pop.	January–December	Annual	44	1–44	PS/Alt	3.7§	Potvin et al. (1988)
	Scat	>1 Pop.	May–November	Bi-month	19	9–23	Alt	0.23	Messier and Crête (1985)
	Scat	Pack	June–September	Annual	12	2–33	Alt	0.08	Tremblay et al. (2001)
Vancouver Island, Canada	Scat	Pack	January–December	Seasonal	~14**	~5–25	Alt		Milne et al. (1989)
Yukon Territory, Canada	Scat	Pack	Summer	Annual	8**	0–9	Alt		Theberge and Cotrell (1977)
	Scat	Pack	Summer		21**	0–63¶	PS/Alt		Hayes et al. (2016)
Eurasia									
Belarus	Scat	Pop.	January–December	Seasonal	30	23–37	PA		Sidorovich et al. (2017)
Germany	Scat	Pop.	January–December	Annual	10		Alt		Nitsche (2016)
Latvia	Scat/Stomach	Pop.	Summer	Seasonal	36		PS		Andersone (1999)
	Scat	Pop.	January–December	Seasonal	8	3–13	Alt		Andersone and Ozolinš (2004)
	Stomach	Pop.	January–December	Annual	6		Alt		Žunna et al. (2009)
Lithuania	Scat	Pop.	Annual	Seasonal	13	10–15	Alt		Spinkyte-Backaitiene and Petelis (2012)
Russia	Scat	Pop.	January–December	Seasonal	10**	5–15	Alt		Mertz (1953)

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).

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

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

§Beavers km^{-2}.

¶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).

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. 2018). 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 to be 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. a 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. 2017). 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. 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 (Fig. 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

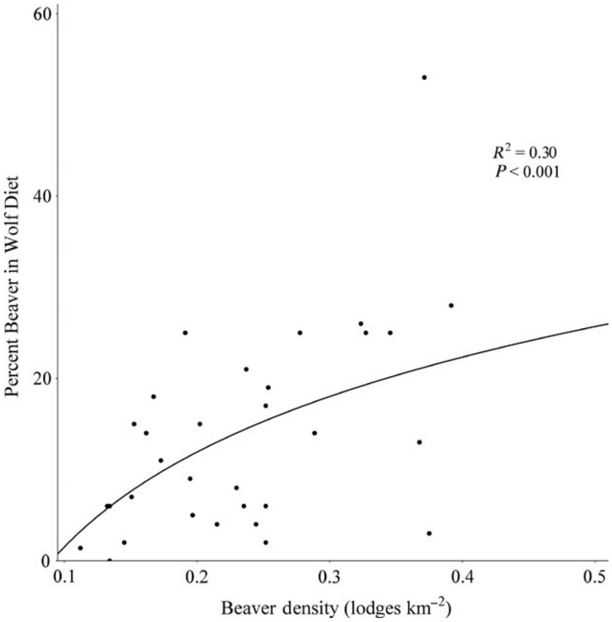

Fig. 3. The relationship between the percentage of scat-based grey wolf diets comprised of beaver and beaver density on Isle Royale National Park, Michigan, USA, during 1962–2009 (each point represents one year; adapted from Romanski 2010).

consumption has coincided with declining ungulate populations (Hall 1971, Voigt et al. 1976, Mech & Karns 1977, Fuller & 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 travelling 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 & 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. 2017) 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 in 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 & Mech 2014, Mech & Barber-Meyer 2015). Thus, wolf density increases linearly (i.e. Type I numerical response) with increasing prey densities (Mech & Barber-Meyer 2015). To compare prey densities in multiple systems at large spatial scales, some researchers (e.g. McRoberts & 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 & 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 a beaver is 12.5–15 kg (Potvin et al. 1988, Gable et al. 2017), 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 km^{-2}) 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 (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 & 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 Ozoliņš (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 & 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 facilitate 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 & Moyle 1963, Baker & 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 & Mech 2010, Gable et al. 2016).

Gable and Windels (2017) 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 km^2 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 km^{-2}) 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 & Windels 2017).

Prior to Gable and Windels (2017), 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 wolves removed 137.4 beavers per year on Isle Royale during 1962–2009, which was 16% of the beaver population (density = 0.24 lodges km^{-2}) 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 km^2 study area), which was an estimated 7–19% of the beaver population (density = 0.4 lodges km^{-2}) annually (Theberge & Theberge 2004). Theberge and Theberge (2004) estimated that each wolf killed anywhere between 8.5 and 23.5 beavers per year (average wolf density was 2.4 individuals/100 km^2, a population of 64 wolves). They concluded that beaver recruitment alone was likely 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 & Windels 2017).

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 km^{-2}) annually prior to wolf control measures, and each wolf killed an estimated 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, which lead Potvin et al. (1992) to conclude that 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 & Moyle 1963, Fritts & Mech 1981) but there is no evidence for this. It is possible that wolves, like human hunters, select 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. 2017).

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 & Hill 2003). Most researchers estimating beaver densities for studies of wolf predation have assumed that beaver colony size remained constant over time (Theberge & 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 & 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 & Theberge 2004). Like colony size, active lodge densities can fluctuate dramatically through time and space (Novak 1987, Parker & 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 & 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 (Wasser et al. 2011, Mech & 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 & 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 factors, 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.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

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

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 (≤5%).