



Note

Kill Rates and Predation Rates of Wolves on Beavers

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ABSTRACT Wolves (*Canis lupus*) 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. Published 2017. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS American beaver, *Canis lupus*, *Castor canadensis*, GPS clusters, gray wolf, kill rates, Minnesota, predation rates, predator-prey, Voyageurs National Park.

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

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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 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 was 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 ≥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

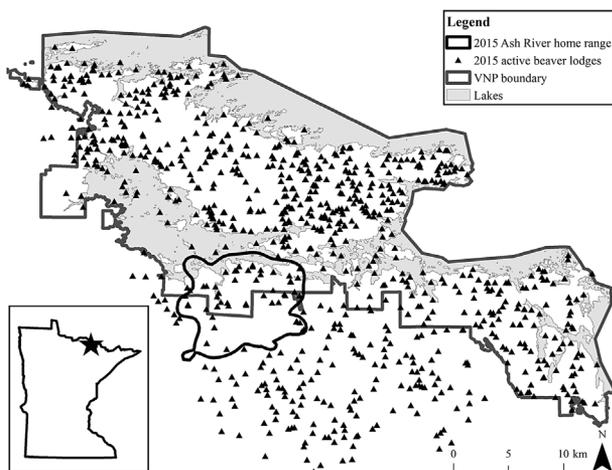


Figure 1. The 95% adaptive kernel home range of wolves in the Ash River Pack in Voyageurs National Park, Minnesota, USA. The black triangles represent all the active beaver lodges identified during the 2015 aerial beaver lodge census in and adjacent to Voyageurs National Park. The star in the inset marks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

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) provided 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 (S. K. Windels, 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 (2014). 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 2014). 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 (1977) equation (Equation 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 (Equation 1).

$$\frac{\% \text{ kits} + \% \text{ sub-adults} - \% \text{ breeding sub-adults}}{\% \text{ adults} + \% \text{ breeding sub-adults}} = \frac{N}{2.12} \quad (1)$$

Novak's (1977) equation assumes that beaver colony structure generally consists of a breeding pair with non-breeding subordinate offspring. Based on Novak (1977), we also estimated that 30% of sub-adults bred and on average each colony had 0.12 non-breeding adults. Thus, in Equation 1, N is the average number of subordinate offspring per lodge (kits + sub-adults), and average colony size is $N + 2.12$ because there are 2 breeding adults and 0.12 non-breeding adults per lodge.

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 aerial 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 (Van Ballenberghe and Mech 1975, 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 \pm 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 212 beavers in ARP's home range in fall of 2015, and V009 removed an estimated 10% (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 ($X_1^2 = 0.88$, $P = 0.35$) 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

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

^a We considered lakes frozen and beavers generally inaccessible after 20 November.

^b Monthly pack weight = (adult weight \times 4 adults) + (pup weight \times 2 pups).

^c Biomass requirements = pack weight \times 0.09 kg/kg of wolf/day (Peterson and Ciucci 2003).

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

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

density in the ARP home range was relatively high in 2015 compared to other parts of beaver range in Minnesota (S. K. Windels, 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 toward 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 (Müller-Schwarze and Sun 2003). 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 (S. K. Windels, 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. 2009a, 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. 2009a). 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. 2009a, 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.

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