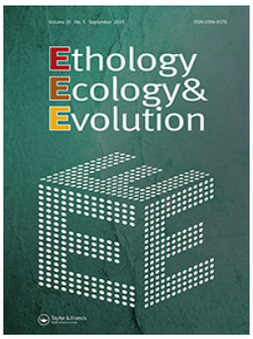

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Evidence that wolves use cooperative ambush strategies to hunt beavers

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Cooperative hunting can confer fitness benefits by increasing foraging efficiency. We documented a breeding pair of wolves in the Greater Voyageurs Ecosystem of Minnesota, USA that appeared to periodically use 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 advantageous because: (1) feeding trails are where beavers are most active and vulnerable on land, (2) the probability that the pair encounters a beaver is increased, and (3) either wolf can quickly assist the other in killing a beaver. The cooperative ambush strategy these wolves used appears rare for most social Carnivora but we hypothesize this behavior is widespread in areas of wolf-beaver sympatry. This observation demonstrates that novel insights into the natural history of even well-studied predators are possible when technological advancements are combined with intensive fieldwork.

KEY WORDS: predation, hunting strategy, sit-and-wait, ambush, GPS-cluster, kill site, *Castor canadensis*, *Canis lupus*.

INTRODUCTION

Cooperative hunting involves two or more animals that act together to acquire a common prey (Boesch & Boesch 1989; Bailey et al. 2013). Cooperative hunting can confer fitness benefits by increasing hunting efficiency, allowing predators to exploit large prey that are difficult to capture alone, or by reducing individual risk (MacDonald 1983; Packer & 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 & Ruttan 1988; Escobedo et al. 2014). Cooperative hunting ranges from passive hunting approaches that require no intentionality or awareness between animals hunting together, up to coordinated and collaborative hunting

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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

[1]BF = breeding female, SM = subordinate male, BM = breeding male.
[2]We combined kills made individually with those made cooperatively to estimate individual kill rates.

strategies where cooperating animals intentionally align their actions to one another in time and space (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 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 (Mech & Peterson 2003; Mech 2007; 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 2007), arctic hares (*Lepus arcticus*; Mech et al. 2015), and Canada geese (*Branta canadens*is; Nichols 2015). In most 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 artifacts of observer interpretation (Mech & Peterson 2003; Mech 2007). Yet, recent work on wolf-beaver interactions demonstrates wolves do use ambush strategies and are able to switch between cursorial and ambush strategies depending on prey species (Gable et al. 2016, 2018a, 2021; Bump et al. 2022).

Beavers are important summer (i.e. the ice-free season) prey for wolves in many ecosystems in North America and Eurasia (Gable et al. 2018a), constituting up to 42% of wolf pack diets (Gable et al. 2017, 2018a) and up to 83% of individual wolf diets during this period (Moayeri 2013). Wolves primarily hunt and kill beavers alone (Gable et al. 2016; Gable & Windels 2018), as most movement by wolves during the summer is done individually (Barber-Meyer & Mech 2015; Gable et al. 2016; Gable & Windels 2018).

Wolves often 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). Gable et al. (2021) documented 748 instances where wolves waited-in-ambush for beaver and demonstrated that wolves choose ambush locations to counter and capitalize on the sensory abilities of beavers. However, how wolves hunt beavers has not received much study until recently, though there is much we still do not understand (Mech et al. 2015; Gable et al. 2018a). Herein, we document a breeding pair of wolves using cooperative ambushing strategies to hunt beavers.

MATERIAL AND METHODS

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 Greater Voyageurs Ecosystem (GVE), Minnesota, USA. The GVE is part of the Laurentian Mixed Forest Province and on the southern edge of the boreal forest (Bailey 1980; Gable et al. 2018b). The GVE supports a dense beaver population with densities generally ranging from 0.47 lodges/

km^2 to > 1 lodge/km^2 (Johnston & Windels 2015; Gable & Windels 2018). In 2019, beaver density in the Moonshadow Pack home range was 0.60 lodge/km^2 based on an aerial census in Fall 2019.

Clusters, kill sites, and beaver hunting attempts

The Moonshadow Pack had four members in Winter 2019. In May 2019, we captured three 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 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). When at clusters, we searched a 20 m radius around each GPS-location in the cluster. We searched all clusters of GPS-locations from each wolf from 3 days after capture until 29 October 2019, when most beaver ponds had iced over.

We identified ambush locations, which we refer to as "beaver hunting attempts" below, using the methods described in Gable et al. (2021). This approach successfully identified 748 ambushing locations from 28 different wolves, which illuminated clear patterns of behavior (see fig 5 in Gable et al. 2021) and demonstrated this is a valid method to study wolf ambushing behavior of beavers.

In short, we identified "beaver hunting attempts" – where wolves waited-in-ambush for beavers – when searching clusters of GPS-locations. Generally speaking, a beaver hunting attempt was a tight cluster of wolf locations near fresh beaver activity (Video 1 in Supplemental Data). Specifically, we defined a beaver hunting attempt as ≥ 2 consecutive locations < 25 m apart, of which > 50% were ≤ 15 m from fresh beaver activity (e.g. fresh cuttings) (Gable & Windels 2018; Gable et al. 2021; Bump et al. 2022). When at hunting attempts, we searched intensively to find the specific spot (i.e. bed site) where the wolf 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 therein (see Video 1 in Supplemental Data). We found a bed at most hunting attempts; however, there were some attempts where we could not find a bed because of the challenge of finding beds on forest floors without vegetation. If we could not find a bed, we assumed that the bed 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) that 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. For each attempt, we also measured the distance between where the two wolves waited-in-ambush. In addition, we recorded a video of every hunting attempt during our field investigation (see Video 1 in Supplemental Data) and drew maps of each hunting attempt to document where the wolves were waiting in relation to water and beaver activity (Figs 1–2). The combination of hunting attempt measurements, maps, and videos allowed us to document this behavior in detail (Fig. 1).

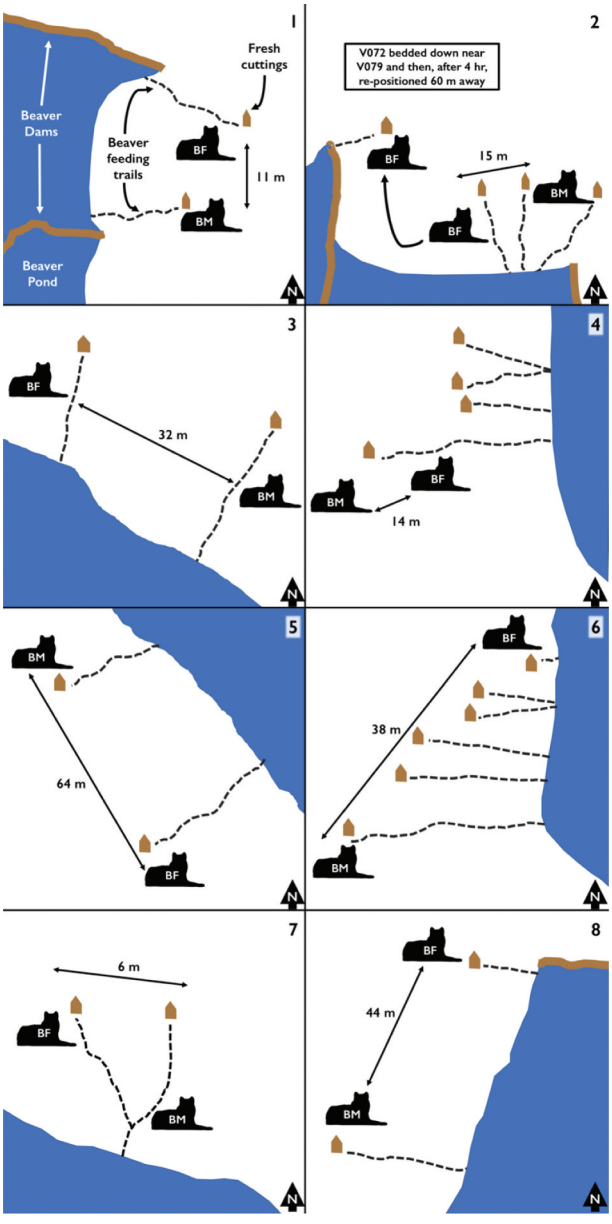

Fig. 1. — Diagrams of the eight cooperative beaver hunting attempts made by the breeding female (BF) and the breeding male (BM) of the Moonshadow pack, in the Greater Voyageurs Ecosystem, Minnesota. The polygons represent beaver ponds. Scale is relative to each panel. The number of the panel corresponds to the "hunting attempt" number in Table 2.

We calculated the estimated time wolves spent at beaver hunting attempts by recording 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 period (days) we searched GPS-clusters from that wolf. We considered wolves to have cooperatively killed beavers when two or more collared wolves were first at a kill site (< 200 m from kill) at the same time based on GPS-locations.

RESULTS

We searched every cluster ($n = 2{,}047$) of GPS-locations from BF (breeding female) for 153 days (29 May 2019 to 29 October 2019), BM (breeding male) for 180 days (2 May 2019 to 29 October 2019), and SM (subordinate male) for 173 days (9 May 2019 to 29 October 2019). In total, we searched 604 clusters from BF, 805 clusters from BM, and 638 clusters from SM (Table 1). We searched clusters 5.9 days on average after the cluster occurred. In doing so, we identified 49 beaver hunting attempts and 10 beaver kills from BF, 28 beaver hunting attempts and seven beaver kills from SM, and 62 beaver hunting attempts and 16 beaver kills from BM. BF and BM cooperatively killed three beavers together (i.e. 3/10 kills by BF were made with BM, and 3/16 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 81% of kills and 87% of attempts by itself. Kill rates of beavers were 0.057, 0.039, and 0.105 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% (8/49) and 13% (8/62) 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 one 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 one instance where BM left 2.3 hr before BF. Cooperative beaver hunting attempts lasted approximately 4.4 ± 3.0 hr (mean ± SD; range = 0.7–9.7 hr).

During cooperative beaver hunting attempts, BF and BM waited an average of 28 m ±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 four (50%) cooperative attempts both wolves waited the same distance from water, at three attempts BF waited closer to water than BM, and at one attempt BM waited closer to water than BF.

Table 2.

Specifics about eight cooperative beaver ambush attempts made by the breeding pair of the Moonshadow pack in the Greater Voyageurs Ecosystem, Minnesota.

		Breeding female				Breeding male			
Hunting attempt	Proximity (m)[1]	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

[1]The 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.

DISCUSSION

The breeding pair of the Moonshadow Pack appeared to periodically use, by definition, cooperative ambush strategies to hunt beavers (Boesch & Boesch 1989; Bailey et al. 2013). In each cooperative hunting attempt, BF and BM related to one another in both time and space in a manner that is evident of coordinated cooperative hunting (Boesch & Boesch 1989; Bailey et al. 2013). This cooperative wait-in-ambush hunting behavior by two individuals appears rare as we struggled to find similar observations of canids or members of Carnivora engaging in similar hunting strategies. Certainly, wolves and other social predators will use cooperative hunting strategies such as stalking-and-ambushing prey and driving prey towards other conspecifics waiting in ambush (Packer & Scheel 1991; Stander 1992; Mech et al. 2015), but this is categorically different than wolves waiting together for 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. The most similar observation to ours that we are aware of was by Schaller (1972) who observed two lionesses waiting "crouched, tense for a rush" in a thicket near a water hole for 7.3 hr. After 7 hr, one lioness unsuccessfully rushed a gazelle at the waterhole while the other lioness remained stationary.

Though we do have evidence of 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 three 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 in densely forested ecosystems where visual observation of wolves ambushing beaver is extremely difficult (Gable et al. 2018d), and distinguishing if beaver kills are the result of opportunism or ambushing from GPS-locations is not currently possible (Gable et al. 2016, 2021). However, 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 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 & 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 foraging efficiency is low. Based on this study and Gable and Windels (2018), a wolf kills one 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 adult ungulates (Peterson & Ciucci 2003) – must be shared between cooperating wolves. The benefit is that wolves likely increase 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 generally use multiple feeding trails at any given time during the ice-free season. Wolves have to select one of these trails at which to wait. This is a crucial decision because wolves only appear able to kill beavers at the feeding trail where they wait-in-ambush. Out of the 214 beaver kills found during 2015–2019, we did not document a single instance where a wolf waited-in-ambush at a specific

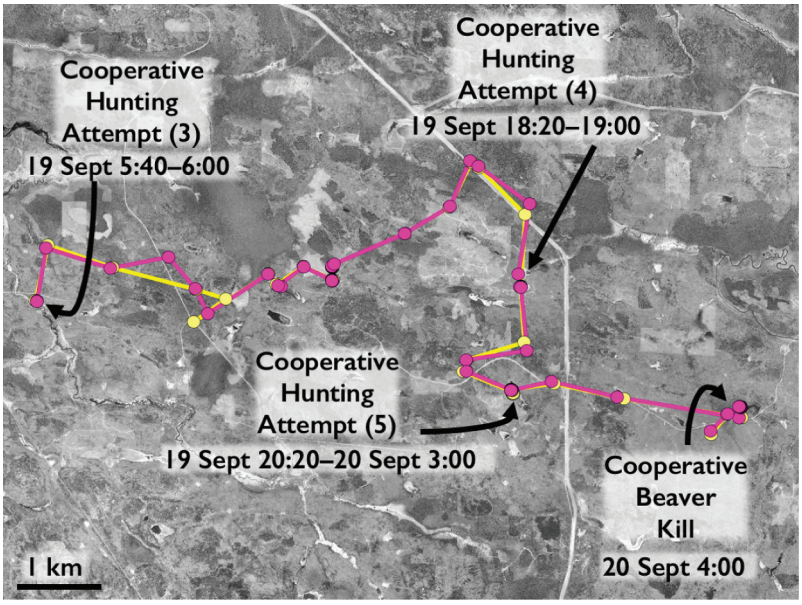

Fig. 2. — The GPS-locations of the breeding female and breeding male of the Moonshadow pack, during 19–20 September 2019 in the Greater Voyageurs Ecosystem, Minnesota. The pair made three cooperative beaver hunting attempts during this period before successfully killing a beaver on 20 September 2019. The number in parentheses below each cooperative hunting attempt corresponds to the "hunting attempt" number in Fig. 1 and Table 2.

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 & 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 & Jenkins 1995; Gable et al. 2018a).

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 & Jenkins 1995; Salandre et al. 2017). The margin for error when attacking beavers close to water is likely small (Gable et al. 2021). 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 manner of seconds once an attack had started (Fig. 1). 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.

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 & 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 wolves. We do not think it is coincidence that only the breeding pair (BF and BM) cooperatively hunted and killed beavers (i.e. SM did not join). We suspect breeding pairs might be more likely to hunt cooperatively 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). 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 fourth pack member hunted or killed beavers with other pack members. We suspect, given the lack of association between the other three GPS-collared pack members, that the uncollared wolf likely did not hunt or kill beavers frequently with other wolves.

Our observation raises many interesting questions. In particular, is this behavior pervasive across all ecosystems where beavers are important prey for wolves? We hypothesize that this cooperative ambush 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. 2021), Isle Royale National Park (Thurber & Peterson 1993), Quebec (Gable et al. 2018a), Wisconsin (Gable et al. 2018)] – but it 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 hr hiking 2,120 km to assess all GPS-clusters from these three 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.

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DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

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SUPPLEMENTAL DATA

Video 1: A video 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, USA. Video can be accessed here: https://doi.org/10.1080/03949370.2023.2248608

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