BIOLOGY LETTERS

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Cite this article: Gross AD, Gable TD, Homkes AT, Winnett-Murray K, Woodside R, Bump JK, Murray KG. 2026 Wolves increase germination speed and success of blueberries. *Biol. Lett.* **22**: 20260279.
https://doi.org/10.1098/rsbl.2026.0279

Received: 7 January 2026
Accepted: 8 July 2026

Subject Category:
Community Ecology

Subject Areas:
ecology, ecosystem, plant science, evolution

Keywords:
seed dispersal, ecosystem effects, endozoochory, *Canis lupus*, frugivory

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Supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.8605320.

THE ROYAL SOCIETY PUBLISHING

Wolves increase germination speed and success of blueberries

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Seed dispersal plays a key role in facilitating important ecological processes that reduce plant competition, parasitism and predation while promoting gene flow and biodiversity. In many ecosystems across North America and Eurasia, wolves consume fruits when available. However, the impact of wolf consumption on seeds, particularly germination success and speed, remains unknown. We extracted blueberry seeds from wolf scats and fresh fruits in the Greater Voyageurs Ecosystem, Minnesota, USA, where wolves forage extensively on blueberries in summer. We grew seeds under controlled conditions to assess if blueberry seeds deposited in wolf scat germinate more rapidly and successfully than seeds from berries alone (control). Seeds that passed through wolf digestive tracts had higher germination success and speed than controlled seeds. This pattern suggests blueberries receive positive benefits passing through wolf gastrointestinal systems. This finding, in combination with wolves' propensity to travel long distances in short periods, indicates wolves are likely effective long-distance dispersers of blueberry seeds. Thus, our findings reveal another way wolves are likely connected to larger ecological processes in boreal ecosystems, and possibly other ecosystems where wolves consume fruits.

1. Introduction

Seed dispersal plays a key role in facilitating important ecological processes. Among these are plant reproduction and recruitment, migration and colonization of new landscapes, all of which reduce competition, parasitism and predation while promoting gene flow and biodiversity [1–4]. One mechanism by which seeds are dispersed is endozoochory, the process of animals ingesting seeds and depositing them in their faeces. In this mutualism, animals receive fitness benefits by consuming plant-based foods, and plants receive fitness benefits from animals by having seeds dispersed [5,6]. The passage of seeds through gastrointestinal systems (hereafter, guts) of animals often increases germination success by reducing seed dormancy—a process often initiated by chemical and/or mechanical scarification of seed coats. Further, when passing through guts, seeds are surrounded by faecal material, which acts as fertilizer and protects seeds from pathogens following defaecation [7,8]. For instance, numerous carnivorous mammals, including bears, civets and pine martens, have positive effects on seed germination success after gut passage [9–11].

Wolves (*Canis lupus*) are opportunistic generalists who mostly consume ungulate prey. However, wolves occasionally switch to non-ungulate prey when such prey is readily available and/or primary ungulate prey is less available [12,13]. Further, in a variety of ecosystems across North America and Eurasia, wolves consume fruits and berries when available, especially during peak

abundance [14,15]. One of the most thoroughly studied examples of wolf frugivory is from the Greater Voyageurs Ecosystem (GVE), Minnesota, where wolves commonly forage on wild blueberries (primarily *Vaccinium angustifolium*), and to a lesser extent raspberries (*Rubus idaeus*), in summer [16,17]. During peak berry season (July–August) in the GVE, berries constitute up to 83% of weekly diets of adult wolves and over 30% of pup diets [17,18]. Additionally, wolves in the GVE will regurgitate berries for pups, suggesting berries may be seasonally important foods for provisioning pups in southern boreal ecosystems [19].

Although berries can be seasonally important for wolves in the GVE, the impact of wolf consumption on berry seeds remains unknown. Seed passage through canid guts can have positive, negative and neutral effects on germination success and speeds, though these effects can be species-specific [20–23]. Thus, we aimed to determine whether wolves increase germination speed and success rates by consuming berries and then depositing them in scats.

2. Methods

The GVE is a 2338 km^2 southern boreal forest ecosystem that encompasses Voyageurs National Park, and a large area south of the park made up of federal, state, county, timber company and privately owned lands. Dense deciduous, coniferous and mixed forests are interspersed with plentiful wetlands, bogs and lakes. Blueberries are abundant in the GVE from early-to-mid-July to mid-August [19] and are primarily found in open coniferous forests, rock outcrops and hilltops and logged/burned black spruce (*Picea mariana*) bogs.

During summers of 2017 and 2018, we opportunistically collected five fresh, likely 1–2 days old, wolf scats (three in 2017, two in 2018) in the GVE that were primarily or entirely filled with digested fruits. We also collected 'control' seeds from intact fruits from 10 wild blueberry plants per year in the GVE in 2017, 2018 and 2019.

Notably, storage conditions and periods between seed collection and their use in germination trials varied somewhat among treatments and years. After drying for three to four weeks at ambient temperature, wolf scats were stored at −15°C for 134 (2017) and 127 (2018) days before seeds were extracted by hand. Seeds extracted from individual wolf scats were germinated in separate trials ($n = 5$). Seeds collected for the 'control' treatments in 2017 were collected in late July, frozen within the intact fruits at −15°C for 43 days, dehydrated and shipped at ambient temperature (11 days) and then frozen again at −15°C for 144 days before extraction from fruits by hand. Seeds collected for the control treatments in 2018 were collected in late July, extracted from fruits by hand, dried, stored (and shipped) at ambient temperature for 98 days, and then stored at −15°C for 97 days before use in germination trials. Seeds collected for the control treatment in 2019 were collected in late July, extracted, dried, stored and shipped at ambient temperature for 120 days and then stored at −15°C for 265 days before use in germination trials.

For germination trials in a laboratory setting, we first excluded any immature seeds or empty seed coats via floating in water and visually examined before placing randomly chosen subsets of seeds on moist filter paper (Whatman no. 2) in 90 ×15 mm Petri dishes. For the treatment group (i.e. seeds from wolf scats), we used 200 seeds from each wolf scat collected in 2017 and 100 and 102 seeds from the two scats collected in 2018. For the control group (i.e. seeds from fresh fruits), we used 200 seeds from each of the 2017 and 2018 trials and 84 control seeds from the 2019 trial. Petri dishes with seeds were maintained in a Conviron E15 growth chamber (Conviron USA, Pembina, North Dakota, USA) on a 16 h light : 8 h dark cycle at 60% relative humidity and with temperature alternating between 21.5 and 9.5°C during light and dark periods. We used full-spectrum fluorescent lights, providing approximately 500 µmol m^{-2} s^{-1} in the 400–700 nm range as measured with a Decagon AccuPAR ceptometer (Decagon Devices, Pullman, Washington, USA). We watered seeds daily for 60 days and scored them as germinated when the radicle emerged from the seed coat by approximately 0.5 mm. We removed any seeds that developed fungal contamination throughout each trial. Notably, the difference in sample sizes for treatment and control samples between years was simply due to changes in our capacity.

(a) Statistical analyses

We compared germination success of seeds that passed through wolf guts with that of control seeds using Fisher's exact tests. We derived 95% confidence intervals (CI) for our estimates using equation (2.1), where $\hat{p}$ is the proportion of seeds that germinated and n is the total number of seeds.

$$\hat{p} \pm 1.96 * \sqrt{\frac{\hat{p}\,(1-\hat{p})}{n}}. \tag{2.1}$$

To compare cumulative germination curves of wolf-ingested versus control seeds, we used log-rank tests. To examine differences in germination speed between treatment groups, we created Kaplan–Meier curves via the survfit() function in the 'survival' package in program R, and calculated median time to germination to quantify germination speed [24,25]. We used the survfit() function to calculate median time to germination—the time it took for 50% of seeds to germinate—using all seeds (germinated and ungerminated) and using only seeds that germinated, the latter of which is particularly meaningful because it allowed us to examine how passage of seeds through wolf guts influences the speed of germination independent of its effects on germination success [10,26]. Notably, we attempted to use a Cox proportional hazards model to quantify germination speed, but our data did not meet model assumptions of proportional hazards based on a Schoenfeld individual test (i.e. the hazard ratio between groups was not constant over time) [27]. All analyses were conducted in the program R [28], and we assumed $\alpha = 0.05$.

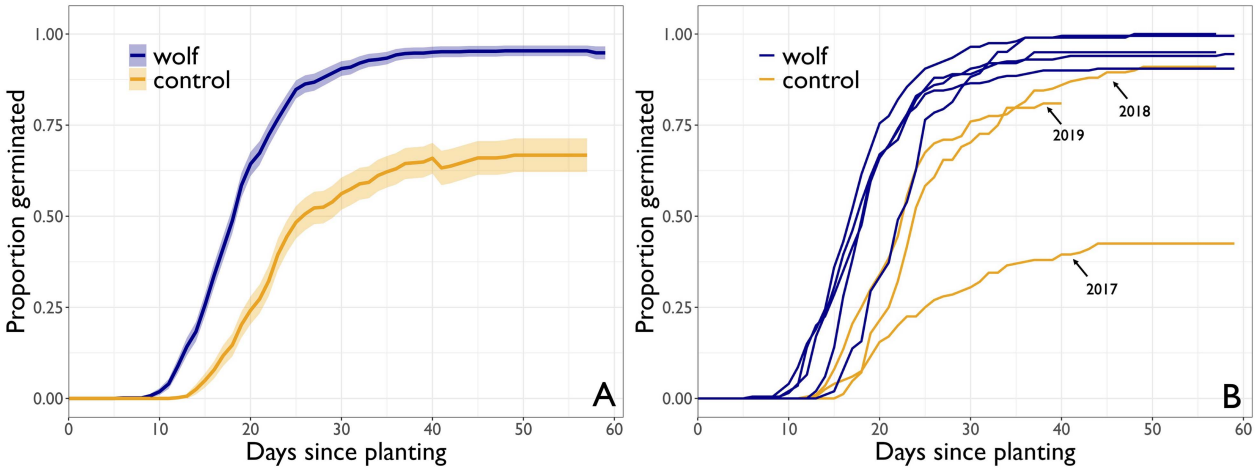

Figure 1. The cumulative germination curves for blueberry seeds that passed through wolf guts (wolf) and those that did not (control) based on seeds collected in the Greater Voyageurs Ecosystem, Minnesota, USA. Panel A shows cumulative germination curves for all blueberry seeds that passed through wolf guts (wolf). The control line represents overall germination for all control seed data from 2017, 2018 and 2019. The shaded ribbon around each line is the 95% CI. Panel B shows cumulative germination curves for each Petri dish trial (each line is a trial) of blueberry seeds. All seeds extracted from an individual wolf scat were grown in a single trial (i.e. we extracted seeds from five scats and therefore there are five trials), whereas all 'control' seeds were grown in trials based on the year the seeds were collected from wild blueberry bushes (i.e. three trials). Notably, the 2019 trial was stopped at 40 days due to shutdowns from the COVID-19 pandemic.

3. Results

Overall, the 802 seeds that passed through digestive tracts of wolves had higher germination success (96%, 95% CI = 94–97%) than the 484 control seeds (69%, 95% CI = 65–73%; Fisher's exact test results: $p < 0.001$, odds ratio = 9.45), indicating passage through wolf guts increased germination success by 27% (figure 1A). Further, based on a log-rank test and Kaplan–Meier curves, the cumulative germination curve for seeds that passed through wolf guts was different from the cumulative germination curve of control seeds (log-rank test, $p < 0.0001$, $\chi^2 = 276$), indicating that the seeds that passed through wolf guts germinated faster than control seeds (figure 1A). Median time to germination for all wolf-ingested seeds (germinated and ungerminated) was 19 days (95% CI: 18–19 days; $n = 766$ germinated seeds) and for all control seeds 26 days (95% CI: 25–30 days; $n = 335$ germinated seeds).

Although there was some variability among trials of seeds from wolf scats, all trials had similar cumulative germination curves and all had high germination success (91–100%; figure 1B). By contrast, there was marked variability among control trials from 2017, 2018 and 2019. The 2017 trial had low germination success with only 42% of control seeds germinating. The 2018 and 2019 trials, however, had higher germination success of 91% and 81%, respectively (figure 1B). Notably, the 2019 trial was planted in Spring 2020 and ended early due to a shutdown from the COVID-19 pandemic. Nonetheless, the cumulative growth curve for the 2019 trial had reached or was close to reaching an asymptote, indicating that, at most, germination success would only have increased slightly if the trial had not been interrupted (figure 1B).

Given the variability among control trials, we examined whether germination success of seeds that passed through wolf guts differed from that of the best-performing control trial (2018). We found that seeds that had passed through wolf guts had higher germination success than the best-performing control trial (Fisher's exact test: $p < 0.05$, odds ratio: 2.10), and that wolf-ingested seeds, based on a log-rank test and Kaplan–Meier curves, germinated faster than the best-performing control trial (log-rank test: $p < 0.0001$, $\chi^2 = 43.8$; figure 2A). Wolf-ingested seeds had a germination rate 5% greater than the best-performing control trial. Median time to germination for all wolf-ingested seeds (germinated and ungerminated) was 19 days (95% CI: 18–19 days; $n = 766$ germinated seeds) and for the best-performing control trial 23 days (95% CI: 22–24 days; $n = 182$ germinated seeds).

We further compared germination speeds between wolf-ingested seeds and those from the best-performing control trial by examining only the speed of germination for the seeds that germinated (figure 2B). Of germinated seeds, wolf-ingested seeds germinated faster than the best-performing control trial based on a log-rank test and Kaplan–Meier curves (log-rank test: $p < 0.0001$, $\chi^2 = 54.4$). Further, median time to germination for wolf-ingested seeds was 22% shorter than the best-performing control trial (figure 2B) with wolf-ingested seeds and the best-performing control trial having a median time to germination 18 days (95% CI = 18–19), and 23 days (95% CI = 22–23 days), respectively.

4. Discussion

Wild blueberry seeds that pass through the digestive tracts of wolves have higher germination success and germinate more rapidly than control seeds, indicating that consumption by wolves facilitates the germination of blueberry seeds. Passage through wolf guts likely enhances blueberry seed germination via chemical and/or mechanical scarification [7,8] that facilitates perception of

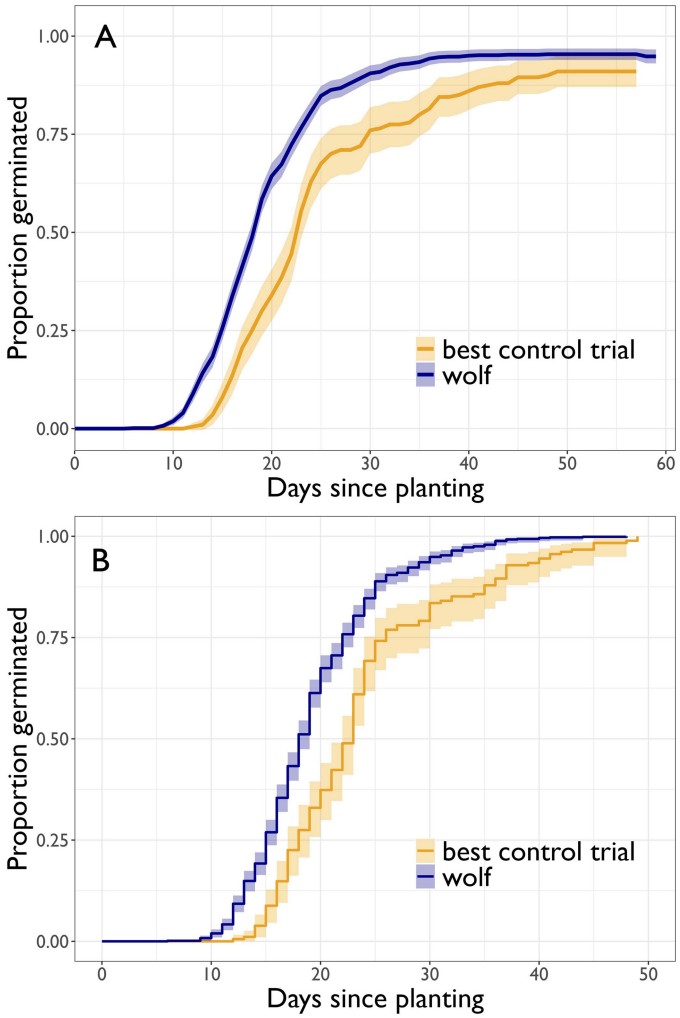

Figure 2. Comparison of cumulative germination curves for blueberry seeds that passed through wolf guts and seeds from the best-performing control trial (2018) based on seeds collected in the Greater Voyageurs Ecosystem, Minnesota, USA. Panel A shows the cumulative germination curve for all seeds (germinated and ungerminated) in each treatment, whereas Panel B shows Kaplan–Meier curves for only the seeds that germinated, a way to visualize germination speed independently of germination success. The shaded ribbon around each line represents the 95% CI.

germination cues or water uptake. Further, the faecal material contained in wolf scats likely creates a microenvironment that may have a fertilizing effect on blueberry seeds and perhaps protects them from harmful pathogens [7,8].

Although our results clearly indicate passage through wolf guts increased germination speed and success of blueberry seeds, we are less certain about the extent of these increases. Our uncertainty stems from the variability in germination speed and success rates in our control trials (figure 1B). In particular, the 2017 control trial had considerably lower germination success (42%) than the other two control trials (81–91%) for unknown reasons. We suspect differences among control trials were due to differences in seed extraction as well as storage procedures and durations. If we assume the best-performing control trial is indicative of germination success of blueberries, then passage through wolf guts increased overall germination success by 5% (96% vs. 91% for control). If we pool data from all control trials together and assume that it is representative, then passage through wolf guts increased overall germination success by 27% (96% vs. 69% for control). Even if wolves only increase germination success by 5%, that could be considerable in terms of plants propagated, given that blueberry-filled wolf scats are numerous and widespread during summer months in the GVE [16,18].

Our work reveals wolves are the largest canid known to enhance germination speed and success of seeds from fruits they have consumed. Many smaller canids that occupy mesocarnivore roles, such as golden jackals (*Canis aureus*), coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*), routinely consume berries and other fruits when available [29–31]. Yet, the effect of seed ingestion by canids on germination success seems species-specific. For instance, several studies have found that passage of fruits/seeds through digestive tracts of red foxes and coyotes increased germination speed and success [32–34]. However, passage of fruits/seeds through the digestive tracts of dogs (*Canis lupus familiaris*), coyotes, gray foxes (*Urocyon cinereoargenteus*), crab-eating foxes (*Cerdocyon thous*) and several other canids decreased or had no effect on germination success and speed [21,35–39]. Yet, to our knowledge, there has not been any research examining how wolves influence germination of seeds from fruits, likely because (1) wolves are apex predators that primarily kill larger-bodied prey, (2) wolves have narrower dietary breadth than most canids that have positive effects on germination of seeds and (3) wolves' seasonal frugivorous tendencies were not well documented until recently [16,18,19]. Our work illustrates the largest extant canid, despite being highly carnivorous, can have

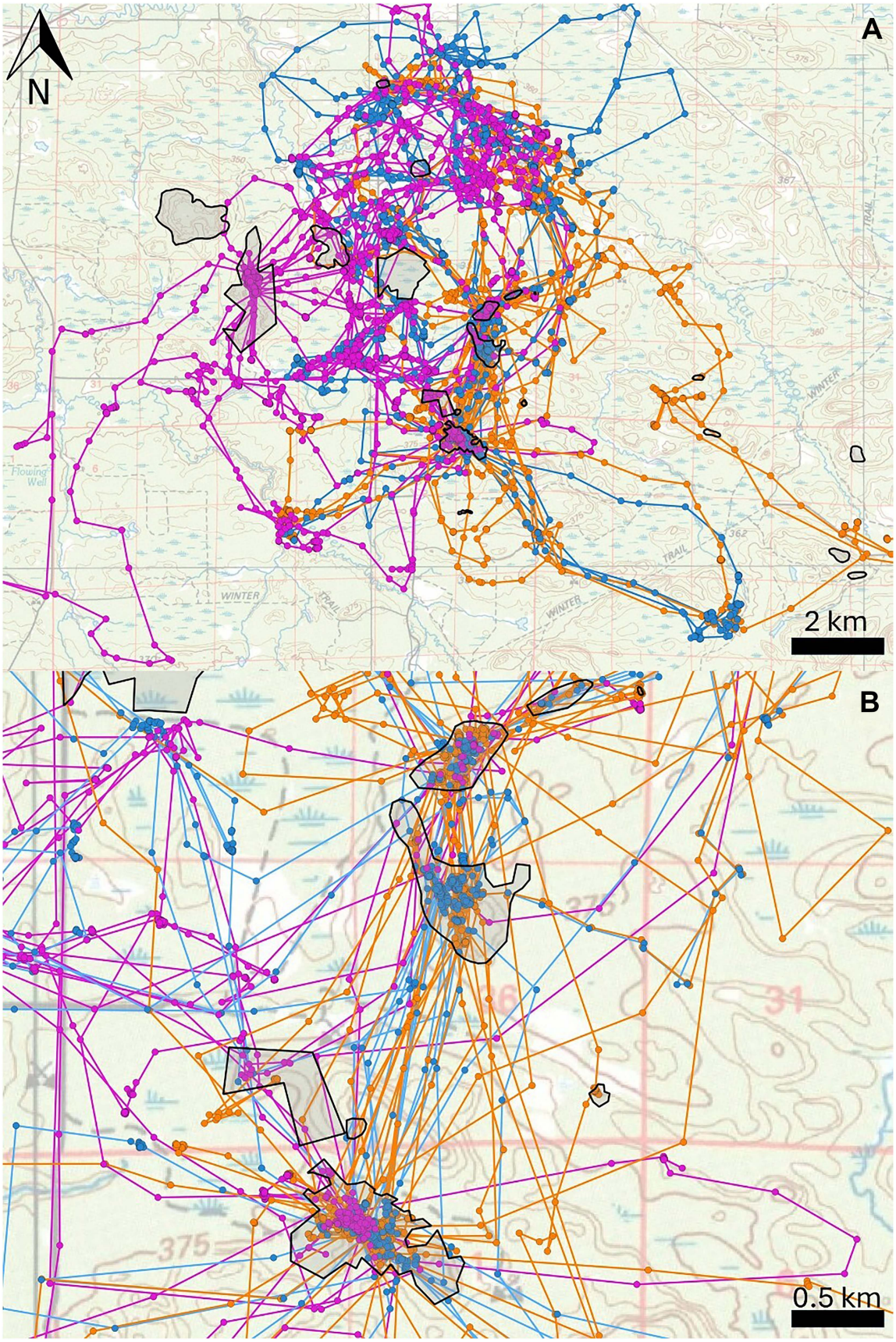

Figure 3. GPS locations of three wolves in the same pack in the Greater Voyageurs Ecosystem, Minnesota, USA, during 10 July–16 August 2024, when all were foraging extensively on blueberries. Each colour is a different wolf, and the black outlined polygons are known blueberry patches within the territory. Panel A illustrates the movement of these wolves in and around berry patches within their territory. Panel B is a zoomed-in example illustrating the intensive amount of time and travel between berry patches.

positive effects on the germination of seeds from some fruits. Notably, our findings are based on seeds extracted from five scats over 2 years from an unknown number of individual wolves (scats could all be from a single wolf or five different wolves). Although we suspect individual wolves likely have similar effects on germination success and speed of blueberries, future work examining the effects of individual wolves on germination success and speed would be useful for a more complete understanding of how wolves influence blueberry germination.

Our findings detail another way wolves are connected to larger ecological processes in boreal ecosystems [40–43]. Through the simple act of consuming blueberries, wolves may facilitate the propagation of blueberry plants by dispersing blueberry seeds, which have higher probabilities of germinating, across large areas. Wolves regularly travel long distances, can make large daily movements [44,45] and therefore could be meaningful dispersers of seeds beyond local distribution. Most wolves in the GVE consume blueberries every year [16,17] and forage in different berry patches throughout their territory (figure 3) [46], transporting blueberry seeds from one area to other berry patches, which may have multiple effects. Seed dispersal by wolves may increase the genetic diversity of berry patches, which could increase the resilience of blueberry patches to pests and pathogens [7,8]. Additionally, wolves may initiate colonization of new berry patches in different habitats within their territories such as in recently disturbed habitats (e.g. clear-cut rock ridges or bogs, burned forests).

How long wolves retain blueberry seeds in their guts before deposition is unknown, and determining gut retention times would be valuable for understanding how far wolves disperse berry seeds. Even if seeds were retained for 1–2 h, wolves could disperse them over long distances, given they can travel 8.7 km h^{-1} [47] (figure 3). Recent work in a southern boreal ecosystem in Minnesota estimated wolves retained fungal spores in their guts for 16.1 h after consuming spore-carrying small mammals (49% of wolf scats examined contained spores), enabling wolves to disperse fungal spores an estimated 3.5 km on average [43]. Thus, our findings, in combination with this research, highlight an underappreciated ecological role of wolves in boreal systems: as seed and spore dispersers.

Wolves consume fruits in a variety of different systems outside the GVE. For instance, scat analyses of wolves in northern Italy and Quebec have shown blueberries, apples (*Malus* spp.), blackberries (*Rubus* spp.) and pears (*Pyrus* spp.) to be important seasonal food sources for wolves [14,15]. Evaluating if wolves have similar positive effects on germination speed and success of fruit seeds in systems outside of the GVE would be valuable for determining if this pattern is ubiquitous across other systems and for other fruit species. Further, assessing whether blueberry seeds deposited by wolves germinate more rapidly and more successfully in outdoor plots would elucidate whether the experimental patterns we documented are reflected in natural, more dynamic settings. For instance, in natural settings, germination is a complex, dynamic process where many factors such as the microhabitat seeds are deposited in, as well as the aggregation of seeds in individual scats, likely influence germination speed and success [48–51]. Thus, such studies could further illuminate the extent to which wolves are connected to and influence the dynamics of fruit seed dispersal in ecosystems. Regardless of how large the effect of wolves on seed dispersal is, our findings highlight another way in which wolves appear to be connected to larger ecological processes in boreal forests [40–43].

Ethics. We captured and collared wolves for this research per the University of Minnesota's Institutional Animal Care and Use Committee (protocols: UMN protocol no. 2207-40241A).

Data accessibility. We have provided all data used in this manuscript in our submission as electronic supplementary material so that editors and reviewers can examine it. All data associated with this manuscript will be archived to the Data Repository of the University of Minnesota (DRUM), and can be accessed at the following link: https://hdl.handle.net/11299/281651.

Supplementary material is available online [52].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. A.D.G.: data curation, formal analysis, investigation, visualization, writing—original draft, writing—review and editing; T.D.G.: conceptualization, formal analysis, funding acquisition, methodology, project administration, resources, visualization, writing—review and editing; A.T.H.: data curation, investigation, methodology, resources, writing—review and editing; K.W.-M.: data curation, formal analysis, investigation, methodology, project administration, resources, writing—review and editing; R.W.: data curation, formal analysis, investigation, methodology, writing—review and editing; J.K.B.: funding acquisition, project administration, resources, writing—review and editing; K.G.M.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, resources, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. Data used in this manuscript were the result, in part, of Cooperative Agreement P17AC01116 between the National Park Service and the University of Minnesota. We thank the Minnesota Environment and Natural Resources Trust Fund, the University of Minnesota, Hope College, Rainy Lake Conservancy, the Van Sloun Foundation, Manitou Fund, Summer Fund, Voyageurs Conservancy, International Wolf Center, the National Wolfwatcher Coalition, Wildlife Science Center, Vectronic-Aerospace and >10 600 individual donors who have supported the work of the Voyageurs Wolf Project.

Acknowledgements. We thank the National Park Service/Voyageurs National Park and all park staff —including Dr Steve Windels—involved in wolf research and monitoring efforts since 2012. We thank many hard-working volunteers and technicians for their efforts on the Voyageurs Wolf Project team.

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