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Research Article

Born to die: pack and population level estimates of wolf pup survival and recruitment in the Greater Voyageurs Ecosystem

Andrea Hynes[1], Thomas D. Gable[2], Austin T. Homkes[2], Joseph K. Bump[2] and John G. Bruggink[1]

[1]Department of Biology, Northern Michigan University, Marquette Michigan, MI, USA
[2]Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, Minneapolis Minnesota, MN, USA

Correspondence: Thomas D. Gable (thomasd.gable@gmail.com)

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Wolf pup *Canis lupus* survival is a key driver of wolf population dynamics that remains poorly understood, especially in forested systems, because wolf pups are difficult to monitor. We used a combination of pup counts at dens and remote camera observations to estimate annual survival and recruitment of wolf pups in the Greater Voyageurs Ecosystem, MN, USA, from 2019 to 2025. We estimated recruitment for 33 packs over 92 pack-years and survival for 23 litters from 13 packs. Mean annual pup recruitment was 1.27 pups per pack, and mean annual pup survival was 0.29. Annual wolf pup recruitment and survival rates were highly variable among years and packs, which is likely a result of differences in food availability and the ability of breeding animals to acquire sufficient prey to provision dependent pups. Pup survival was negatively related to litter size. Although most (71%) wolf pups born during our study did not survive their first biological year, the population remained relatively stable, suggesting that recruitment rates were sufficient to sustain the high-density wolf population over time. Our work underscores the potential of integrative monitoring approaches to advance the understanding of wolf reproductive ecology.

Keywords: *Canis lupus*, forested ecosystem, litter size, mortality, prey abundance, remote camera

Introduction

Changes in the abundance, survival, and recruitment of neonatal wildlife can substantially impact population structure, density, growth rates, and long-term population viability (Mills et al. 2008, Gude et al. 2012, Dybala et al. 2013, Cubaynes et al. 2014). Thus, understanding neonatal vital rates is important for interpreting wildlife population dynamics and developing effective conservation and management strategies (Chitwood et al. 2017, Drummond et al. 2019, Gable et al. 2024b). However, obtaining data on neonatal survival often presents significant challenges, as neonates in many taxa are cryptic, difficult to capture, and particularly vulnerable compared

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to other life history stages (Murray and Patterson 2006, Pike et al. 2008, Chitwood et al. 2017). As a result, monitoring efforts tend to be costly, labor-intensive, and invasive, especially for wide-ranging carnivores like gray wolves *Canis lupus*, which occur at low densities and are difficult to observe directly (Murray and Patterson 2006, Engebretsen et al. 2023). Wolves are nevertheless among the most well-studied carnivores in the Northern Hemisphere, in part because they are apex predators that can influence the behavior and populations of prey, and at times, influence ecosystem processes to a degree (Brice et al. 2022, Gable et al. 2023a, b, Wilmers et al. 2025). Even so, important knowledge gaps remain, as estimating wolf pup survival has been a persistent challenge across most of their range (Fuller et al. 2003, Mills et al. 2008, Gable et al. 2024b).

Several aspects of wolf biology and behavior complicate efforts to monitor wolf pups, particularly in forested systems (Fuller et al. 2003, Mills et al. 2008, Gable et al. 2024b). Pups are typically born in early spring and generally remain in or near dens for the first eight weeks of life (Mech and Boitani 2003). Locating active dens and reliably observing pups is difficult in dense, forested landscapes where visibility is limited, and even when dens are found and visited, some pups may remain hidden in inaccessible areas (Person and Russell 2009, Smith et al. 2017, Gable et al. 2024b). Moreover, breeding females frequently move pups among multiple dens during the early weeks of life, further complicating monitoring efforts during the denning period (Packard 2003, Argue et al. 2008). As pups become more mobile throughout summer, the pack commonly moves them among various rendezvous sites and pups can be elusive until they are large enough to accompany adults (Van Ballenberghe and Mech 1975, Packard 2003, Mills et al. 2008). By six months of age, pups are approaching adult size, and accurately distinguishing pups from adults often requires close-range observation (Peterson and Page 1988). However, because most wolf populations inhabit forested landscapes where even adult wolves are rarely seen, observing pups remains particularly difficult.

Researchers have employed a variety of methods to estimate wolf pup survival with varying degrees of efficacy. Early work primarily relied on capture-mark-recapture, radio telemetry, and visual observations – particularly aerial counts in winter – to monitor pups (Van Ballenberghe et al. 1975, Fritts and Mech 1981, Peterson et al. 1984, Hayes and Harestad 2000). However, limitations in available technology often meant that monitoring did not begin until pups were large enough to be fitted with very high frequency (VHF) collars, and later, global positioning system (GPS) collars, typically at four to six months of age (Van Ballenberghe and Mech 1975, Fuller 1989, Reichmann and Saltz 2005). More recently, advances in collar design have allowed for the use of expandable VHF/GPS collars on pups as young as four weeks old, enabling researchers to begin monitoring at an earlier stage (Swingen 2021). In some cases, researchers have also used surgically implanted VHF transmitters to collect detailed data on wolf pup movement and survival (Crawshaw et al. 2007, Argue et al. 2008, Mills et al. 2008). Although implanted transmitters can yield fine-scale data, using them is logistically demanding and comparatively invasive, which may explain why they have not been more widely adopted. Non-invasive techniques, such as genetic identification from scat samples, have also become increasingly common tools for monitoring pups and estimating their survival (Ausband et al. 2017, Jacobs and Ausband 2019). Despite advances in technology and the development of improved monitoring techniques, relatively few estimates of annual pup survival are available, and changes in survival over time remain largely undocumented across much of gray wolf range.

Where data are available, evidence suggests that wolf pup survival is highly-variable both within and among regions. For example, mean wolf pup survival rates reported over a 23-year period in Alaska, USA, were relatively high and stable (0.70–0.91), whereas estimates from Poland over a 37-year period have been lower and more variable (0.26–0.68; Peterson et al. 1984, Jędrzejewska et al. 1996, Mech et al. 1998, Nowak et al. 2008). In the northern Great Lakes Region of North America, annual pup survival rates have ranged widely – from 0.29 in Wisconsin to 0.48 in Minnesota and 0.80 in Ontario (Fuller 1989, Mills et al. 2008, Wydeven et al. 2009, Table 1). Knowledge of the ecological and demographic factors that drive such variation in pup survival and recruitment, both within and across regions, remains limited despite decades of wolf research because of the difficulties associated with estimating pup survival.

Our objective was to estimate annual wolf pup survival and recruitment rates in the Greater Voyageurs Ecosystem, a densely forested region of northern MN, USA, using a combination of pup counts at dens (located via GPS-collared adults) and observations from remote cameras (Gable et al. 2024b). Specifically, we examined how wolf pup survival and recruitment varied over time and across packs in an attempt to understand the factors that could be influencing these important population metrics – information and data that are limited for wolf populations in the Great Lakes region of North America, and most ecosystems. Pairing existing monitoring techniques – namely pup counts at dens and remote camera technologies – offers a promising integrative approach for addressing many of the challenges associated with monitoring wolf pups in forested landscapes.

Study area

The Greater Voyageurs Ecosystem (GVE) in northern MN, USA, covers ~2338 km^2 of land just south of the Canadian border (Gable et al. 2024a, Fig. 1). The dense forest ecosystem of the GVE is predominantly composed of mixed deciduous and coniferous trees that are interspersed with rocky ridges and wetlands. Voyageurs National Park comprises 882 km^{2}of the northern portion of the GVE (National Park Service 2016). The protected land within the park is dominated by mature forests that have experienced minimal disturbance since the park was created in 1975. The southern portion of the GVE is a mixture of state, federal, county, and

Table 1. A summary of wolf pup survival rates compiled from a review of available literature. The literature search was conducted primarily using Google Scholar with keywords such as 'wolf pups,' 'survival,' and 'recruitment,' and by reviewing references cited in relevant literature. Details include study locations, study years, mean wolf pup survival rates, reported ranges of survival rates (where available), age when pups were first observed or counted, the reported period of survival estimates from birth, and the primary methods of observation used.

Location	Years	Mean survival rate	Reported range of survival	Age of pups when first observed or counted	Reported period of survival estimate[a]	Method of observation	Source
Alaska	1975–1981	0.82	0.57–0.97	~ 2 months	6 months	Visual[b]	Ballard et al. 1987
Kenai Alaska	1976–1981	0.70		~ 6 months	12 months	Visual and VHF telemetry	Peterson et al. 1984
Denali Alaska	1986–1998	0.91[c]		UNK[d]	4 months	Visual	Mech et al. 1998
Alaska	1987–1991	0.86[e]	0.81–0.90	Not observed[f]	5 months	Visual	Adams et al. 2008
Yukon	1990–1994	0.75		Not observed[f]	12 months	Visual	Hayes and Harestad 2000
Montana	1982–1994	0.85		~ 3 months	7 months	Visual	Pletscher et al. 1997
Yellowstone	1996–2010	0.68	0.29–0.85	2 weeks	12 months	Visual	Stahler et al. 2013
Idaho	2008–2014	0.47[g]	0.29–0.62[g]	~ 3 months	12 months	Genetic sampling	Ausband et al. 2017
Wisconsin	1979–2007	0.29	0.14–0.58	UNK[d]	12 months	Visual and VHF telemetry	Wydeven et al. 2009
Minnesota	1969–1972	0.44		UNK[d]	6 months	Visual and VHF telemetry	Van Ballenberghe et al. 1975
Minnesota	1972–1977	0.43		UNK[d]	12 months	Visual	Fritts and Mech 1981
Minnesota	1980–1986	0.48		UNK[d]	6 months	Visual	Fuller 1989
Minnesota	2017–2021	0.57		4–5 weeks	12 months	Expandable VHF collars	Swingen 2021
Minnesota	2019–2025	0.29	0.07–0.50	3–5 weeks	12 months	Den visit/remote cameras	This study
Alberta	1975–1978	0.69[c]		UNK[d]	4 months	Visual	Fuller and Keith 1980
Ontario	2002–2011	0.65	0.25–0.75	3–8 weeks	12 months	Implanted transmitters	Benson et al. 2013
Ontario	2004–2005	0.80	0.50–1.0[h]	4–6 weeks	6 months	Implanted transmitters	Mills et al. 2008
Poland	1975–1993	0.26		UNK[d]	12 months	Visual	Jędrzejewska et al. 1996
Poland	1996–2003	0.68		UNK[d]	6 months	Visual	Nowak et al. 2008
Poland	2001–2012	0.50		UNK[d]	6 months	Visual	Nowak and Myslajek 2016
Belarus	1975–1993	0.15		UNK[d]	12 months	Visual	Jędrzejewska et al. 1996
Belarus	1999–2014	0.55[h]	0.0–1.0[h]	UNK[d]	6 months	Visual	Sidorovich et al. 2017

[a] This column indicates the period for which each study estimated survival. For example, '12 months' means the authors presented survival estimates from birth until pups were 12 months old. Notably, in some instances, a study did not begin observing pups until they were 3 months old (or older) and thus, almost certainly overestimate survival because the authors assumed no pup mortality occurred until after they began observing pups.[b] Visual observation may also include howl surveys and track counts.[c] Retrieved from Fuller et al. 2003.[d] These studies did not provide specific ages of pups at first observation, but rather described ages of pups in general and broad terms (e.g. authors stated pups were observed during summer), often because pups were of a range of ages when first observed. In some instances, the age when pups were first observed was not reported at all. Survival estimates from these studies should be interpreted cautiously because many lacked rigorous approaches to estimating survival, likely overestimated survival by excluding early mortality (as pups were often a few months old or older at first observation), and/or provided insufficient detail to assess the reliability of the estimates.[e] The mean survival rate was not reported; the value was calculated as the average of the reported range.[f] In these cases, studies did not observe pups but rather used placental scars from dead female wolves and assumed these were indicative of litter size. The authors then determined survival by taking the number of pups recruited up to a given point and dividing it by the average litter size (as determined by placental scars) and assumed that the resulting number was indicative of pup survival rates.[g] Survival estimates were calculated using supplemental material in Ausband et al. 2017.[h] Rates represent survival range among litters or packs

privately-owned lands that are subject to a variety of uses. A significant portion of the southern GVE is actively logged, which has resulted in forest habitats that are a patchwork of wetlands, clear cuts, regenerating stands of aspen (*Populus* spp.), and mature deciduous-coniferous stands.

Over the past decade, wolf densities in the GVE have remained relatively high during winter, with an average density of 59 wolves 1000 km^{-2} (Gable et al. 2025). Packs are generally small, with a mean size of 4.0 wolves per pack during 2019–2025. About 19–22 packs have territories entirely or largely within the GVE, depending on the year (Gable et al. 2025). Wolves in the GVE primarily prey on white-tailed deer *Odocoileus virginianus*, but North American beavers *Castor canadensis* serve as an important secondary food source, particularly during the spring to fall (Gable et al. 2018, Gable et al. 2023b). Parturition of wolf pups typically occurs around 11 April based on denning movement behaviors, and during the pup-rearing season (April–August), pups are reared almost exclusively by the breeding pair (Gable et al. 2023b).

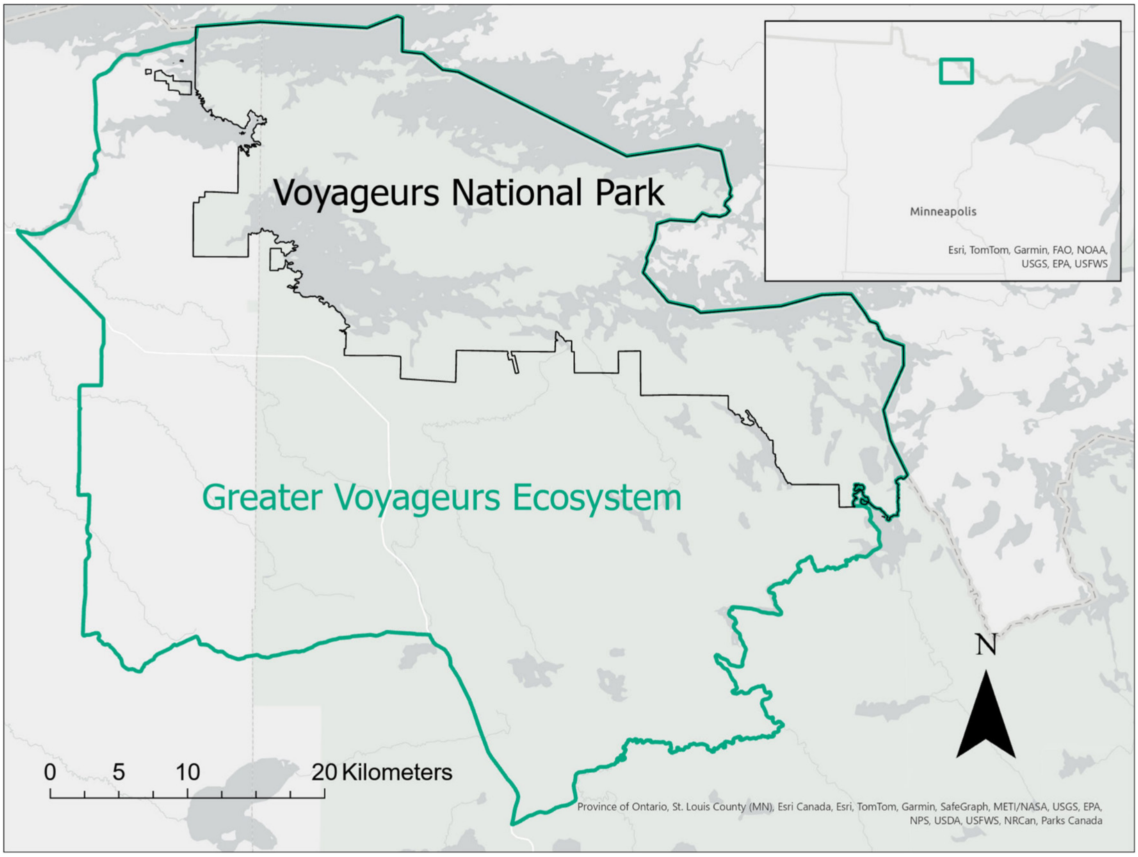

Figure 1. The Greater Voyageurs Ecosystem (green line) in northern Minnesota, USA. The black line is the Voyageurs National Park border.

Material and methods

Pup monitoring

Beginning in the spring (1 May) of each year (2019–2024), we trapped adult wolves using rubber-padded foothold traps and fitted them with GPS collars (Gable et al. 2023b, 2024b). Trapping occurred across multiple wolf pack territories within the study area, though not all territories were trapped in every year. GPS collars were programmed to record locations every 20 min or 6 h, depending on the individual. To locate active wolf dens, we examined the movements of GPS-collared adult wolves (Walsh et al. 2016). We visited dens in the first two weeks of May when wolf pups were 3–5 weeks old to determine litter sizes (Mills et al. 2008, Person and Russell 2009, Gable et al. 2024b). Upon locating dens, we removed pups from dens, recorded the number of pups in each litter, and then returned all pups to their dens (Mills et al. 2008, Gable et al. 2024b).

We deployed 2–5 Browning Spec Ops model (models used: Advantage, Edge, Elite HP4, Elite HP5; Browning, Morgan, UT) remote cameras outside of all dens to record videos of pups after handling. Cameras were set to record 20 s of video with a 1-s delay between triggers. When den shape or size prevented the observation or removal of all pups, we used video footage recorded at the dens to confirm or adjust the initial count (Person and Russell 2009, Gable et al. 2024b). In two instances, we used video footage of pups captured opportunistically in late April and early May to determine litter sizes (Gable et al. 2024b). All capture and handling of pups and adults was evaluated and approved by Institutional Animal Care and Use Committees of the National Park Service and the University of Minnesota (protocols: MWR_VOYA_WINDELS_WOLF and UMN 2207-40241A).

To obtain observations of wolf packs and their pups, we deployed remote cameras (primarily Browning SpecOps model cameras, though some Reconyx Hyperfires were used during 2019–2021) in strategic locations throughout wolf pack territories (Ausband et al. 2022, Gable et al. 2023b). We deployed from ~60 to ~220 cameras per year, increasing the number of cameras we deployed as we studied an increasing number of packs (Gable et al. 2022, 2023a). Cameras, triggered by passive infrared motion sensors, were set to record 20 s of video, with a 1-s delay between trigger events. We placed cameras in areas we thought wolves were likely to travel (i.e. along roads, snowmobile trails, hiking and game trails, and at beaver dams) to maximize wolf pup observations (Gable et al. 2022, 2023a, 2024b). Pups were distinguishable from adults in camera footage throughout the year based upon size, pelage, and facial structure (Peterson and Page 1988, Gable et al. 2024b).

We observed wolves on remote cameras frequently throughout the winter survey period (1 December–10 April). On average, we recorded 31 observations of ≥ 2 pack members in a given pack traveling together during the winter survey period, which amounted to an observation of multiple pack members once every 4.2 days during the 131-day winter survey period. On average, 42% (n = 13) of those were independent observations of the pack at its full composition (i.e. all pack members including pups). Notably, because we observed pack members frequently, we could readily identify most individuals in the pack by unique fur patterns and other unique physical features (e.g. scars). Thus, if a given, known pack member was not present in an observation but was present in previous and subsequent observations, we still considered the observation informative for our pack size and recruitment estimates. For instance, if on different days we captured an observation of a breeding pair and two pups (a pack count of 4 wolves), then an observation of a breeding female and two pups (a count of 3), and then another observation of the breeding male and two pups (another count of 3), followed shortly thereafter by multiple observations of the breeding male, the breeding female, and both pups (counts of 4 wolves), we would consider the two counts of 3 wolves to functionally be counts of 4 wolves because we recognized all 3 wolves in both observations, knew which wolves were undetected or missing, and knew these undetected wolves were part of the pack. In other words, we used 'functional observations' similar to this example when we could: 1) identify all wolves in an observation and therefore knew which pack member(s) was not observed in a given count, and 2) determine that the 'undetected' individual(s) was part of the pack both before and after an observation. We did this because in such instances these partial pack counts, put in the proper context, were highly-informative for overall pack size and recruitment estimates and yielded the most rigorous data on pack structure and size possible. Thus, when we state we had an average of 13 independent observations of a pack at its full composition (all pack members including pups), we mean observations when all wolves in a pack were visually present as well as functional observations (Gable et al. 2024a, 2025). Similar approaches have been employed in other camera trap studies, where partial detections are aggregated across sequential captures and individual identification is used to account for undetected pack members, ensuring accurate pack size estimates (Mattioli et al. 2018, Jiménez et al. 2023).

Estimating recruitment

We defined recruitment as the number of pups that survived their first biological year (11 April–10 April the following year) (Gude et al. 2012, Gable et al. 2024b). To estimate annual recruitment, we divided the total number of pups observed at the end of the biological year by the number of packs in the sampled population. We assessed recruitment using ≥ 3 independent observations (i.e. observations recorded on different days) of each pack during the winter survey period, when pack cohesion is highest (Peterson et al. 1984, Fuller 1989, Gable et al. 2024b). In a few instances, when camera observations were of insufficient quality to conclusively determine the number of pups in a given pack, we used the minimum number of observed pups to estimate recruitment.

Because pups could not be directly observed on 11 April each year, we assumed that those surviving through at least January were recruited (Gude et al. 2012, Gable et al. 2024b). In most instances, we had numerous observations of all living pups in each pack through late March and early April. Thus, whenever possible, we used the most recent data available to estimate recruitment. For a few packs, high-quality data were only available through the end of January; in these cases, we assumed that the pups surviving through January were recruited into the population. Although mortality risk is high for pups in late summer and fall, it decreases substantially by winter, making survival through January a strong indicator of recruitment (Fuller et al. 2003, Gable et al. 2024b). Furthermore, wolf pack size, which reflects recruitment, changes little in the GVE from December to April (Gable et al. 2022, Cassidy et al. 2023).

We used linear regression to examine whether there was a positive relationship between litter size and the number of pups recruited in packs.

Estimating survival

We defined annual pup survival as the proportion of pups born that survived their first biological year (Benson et al. 2013). Because we could only count the number of pups born in packs whose active dens we located (i.e. using GPS locations and in 2 instances by visiting previously used dens) our pup survival estimates were based on a smaller sample size (n = 23) than our recruitment estimates (n = 95). We estimated annual pup survival by dividing the total number of pups recruited at the end of the biological year by the number of pups born at the start of the biological year. In two packs, we were unable to determine the number of surviving pups with certainty because camera footage lacked sufficient quality to conclusively identify pups. In these instances, we used the minimum number of observed pups to calculate survival rates (Gable et al. 2024b, Table 2). To account for unequal sampling among years (e.g. due to challenges in maintaining GPS collar deployment across multiple packs), we first calculated annual survival and recruitment rates, then averaged these annual estimates to generate overall estimates of survival and recruitment for the duration of our study. We used binomial logistic regression to examine the relationship between litter size and pup survival. We did not include a random intercept for year or pack because of the small sample sizes from individual packs and years. We used an alpha-level of 0.05 for all significance tests. All analyses were conducted with the program R (ver. 4.3.1, www.r-project.org), using the 'ggplot2', 'scales', 'MASS', 'performance', and 'ggpubr' packages.

Table 2. Annual litter sizes, number of pups recruited at the end of the biological year, and the proportion of pups that survived in 13 wolf packs in the Greater Voyageurs Ecosystem, Minnesota, USA, from 2019 to 2025.

Year	Pack	Litter size	Pups recruited	Survival rate
2019–2020	Bowman Bay	7	1	0.14
2019–2020	Moonshadow	6	0	0.00
2019–2020	Wiyapka Lake	5	1	0.20
2020–2021	Cranberry Bay	4	1	0.25
2020–2021	Fawn Crick	2	1	0.50
2020–2021	Half-Moon	4	0	0.00
2020–2021	Lightfoot	7	0	0.00
2020–2021	Paradise	4	0	0.00
2020–2021	Wiyapka Lake	6	0	0.00
2021–2022	Cranberry Bay	4	3	0.75
2021–2022	Half-Moon	8	0	0.00
2021–2022	Lightfoot	5	4	0.80
2021–2022	Paradise	5	2	0.40
2021–2022	Windsong	2	2	1.00
2021–2022	Wiyapka Lake	6	3	0.50
2022–2023	Bluebird Lake	6	0	0.00
2022–2023	Paradise	5	1	0.20
2022–2023	Wiyapka Lake	6	2	0.33
2023–2024	Blood Moon	4	0	0.00
2023–2024	Half-Moon	7	3	0.43
2023–2024	Vermilion River	4	3	0.75
2024–2025	Thuja	5	4	0.80
2024–2025	Windsong	3	0	0.00

Results

Recruitment

We estimated recruitment for 33 packs across 92 pack-years during 2019–2025 (Fig. 2). Annual proportions of packs that produced pups but failed to recruit any pups ranged from 0.15 to 0.60 over the six-year study. The proportions of packs that did not produce pups in a given year ranged from 0.0 to 0.21. We could not confirm from camera footage whether pups were produced in 6 packs during the study (Table 3). Annual pack-level recruitment ranged from 0 to 5 pups per pack with a mean of 1.27 (95% confidence interval [CI] = 0.46–2.08) pups recruited per pack across the six-year study (Fig. 2). For packs that produced pups (i.e. excluding packs that did not produce pups and those with unknown pup production) mean recruitment was 1.49 (CI = 0.55–2.42) pups per pack. Recruitment varied considerably from year to year, with mean annual recruitment rates of 0.43 pups per pack in 2019–2020, 0.42 pups per pack in 2020–2021, 2.31 pups per pack in 2021–2022, 1.71 pups per pack in 2022–2023, 1.72 pups per pack in 2023–2024, and 1.00 pups per pack in 2024–2025 (Fig. 3). We found no relationship between litter size and the number of pups recruited per pack ($F = 0.010$ df = 1, 23, $p = 0.923$, $R^2 < 0.001$).

Survival

We estimated the survival of 115 wolf pups from 23 litters in 13 packs from April 2019 to April 2025 (Fig. 4). Litter size ranged from 2 to 8 pups with a mean litter size of 5.0 pups per litter (CI = 4.32–5.68) (Table 2). Pup survival was negatively related to litter size ($\beta = -0.358$, $p = 0.015$, Fig. 5), with each additional pup in a litter reducing the odds of pups in that litter surviving by about 30% (odds ratio = 0.70). Annual pup survival rates were 0.11 in 2019–2020 (n = 18 pups), 0.07 in 2020–2021 (n = 27 pups), 0.47 in 2021–2022 (n = 30 pups), 0.18 in 2022–2023 (n = 17 pups), 0.40 in 2023–2024 (n = 15 pups), and 0.50 in 2024–2025 (n = 8 pups) (Fig. 3). The six-year mean of annual survival rate was 0.29 (CI = 0.09–0.49) but wolf pup survival rates were highly variable among litters and years (Fig. 4). If survival was calculated as mean annual recruitment (1.27 pups per pack) divided by mean litter size (5.0 pups per pack), then annual pup survival would have been 0.25, strikingly similar to our primary way of estimating pup survival as described above.

Discussion

Most wolf pups (71%) born in the GVE during our study did not survive their first biological year, and the annual pup survival rate of 0.07 we observed in 2020–2021 is, to our knowledge, the lowest annual wolf pup survival rate reported. Mean estimates of pup survival from our study were marginally lower than survival estimates from other studies in the Great Lakes Region (Table 1). However, previous estimates from this region were based on shorter timeframes (e.g. six months), likely resulting in higher survival rates than our annual survival rate estimates. Additionally, several studies that reported pup survival rates lacked early litter counts (i.e. when pups were ≤ 5 weeks old) and relied instead on counts of pups from later observations ($\geq$ 8–12 weeks since birth) as approximations of litter size (Fritts and Mech 1981, Fuller 1989, Table 1). However, because some pups almost certainly died prior to these observations, this approach almost certainly overestimated survival rates by underestimating the number of pups born (Gable et al. 2024b, Hynes 2024).

Despite comparatively low and highly-variable wolf pup survival and recruitment rates, the Greater Voyageurs Ecosystem supported one of the highest sustained densities of wolves recorded in North America (mean density from 2019 to 2025 was 55 wolves 1000 km^{-2}; Gable et al. 2025). All evidence indicates that the GVE has sustained a stable, dense wolf population for decades, though annual fluctuations in population density are common and such fluctuations are driven, in large part, by changes in pup survival and recruitment. For instance, in years when recruitment was higher (1.7–2.3 pups per pack), wolf density was higher ($\bar{x} = 62$ wolves 1000 km^{-2}) whereas in years when recruitment was lower ($\leq$ 1 pup per pack), wolf density was considerably lower ($\bar{x} = 45$ wolves 1000 km^{-2}; Gable et al. 2025). Thus, while wolf populations undoubtedly declined when survival/recruitment was low (e.g. pup survival rates of 0.07), our data illustrate that wolf populations can maintain high and stable densities even when pup recruitment and survival rates are, on average, relatively low. For example, during three years

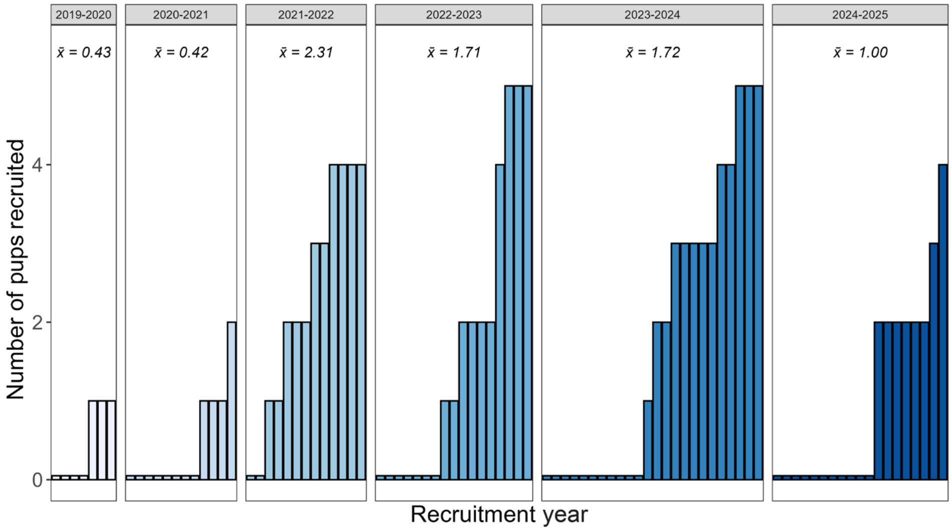

Figure 2. The number of wolf pups recruited annually from 92 litters of wolf pups in 33 packs within the Greater Voyageurs Ecosystem, Minnesota, USA, from 2019 to 2025. Each bar represents a wolf pack. Annual means of pups recruited per pack are shown below each year label.

of our study (2022–2024), when pup survival averaged 0.36 and recruitment averaged 1.9 pups per pack, the population remained near 60 wolves 1000 km^{-2} – a notably high-density wolf population (Mech and Barber-Meyer 2015).

Low pup survival rates appear to be more common in regions where wolf pack sizes are small. Indeed, pup survival rates appear positively related to pack size, in part because non-breeding individuals in larger packs can help guard and provision pups (Stahler et al. 2013, Ausband et al. 2017). Packs without helpers, as observed in the GVE where pups are predominantly provisioned by their parents (Gable et al. 2023b), tend to have lower pup survival rates than packs with helpers. Most evidence indicates that differences in average pack size across larger geographical areas (e.g. the Great Lakes Region versus the Greater Yellowstone Ecosystem) are largely a function of the body size of the primary prey species, with wolf packs in areas with larger-bodied prey generally larger than those in areas with smaller-bodied prey (Fuller et al. 2003, Barber-Meyer et al. 2016). Larger packs are generally better at killing prey, especially large-bodied prey like moose *Alces americanus* and bison *Bison bison* than smaller packs (MacNulty et al. 2014). Yet, in general, the biomass acquired per wolf from kills decreases with increasing pack size (Schmidt and Mech 1997, Barber-Meyer at al. 2016). Thus, the body size of prey appears to modulate when and where the cost of increasing pack members (i.e. decreased biomass acquisition per wolf) exceeds the benefits of more pack members (increased hunting success/kill rates of prey), which, in turn, appears to influence pup survival rates. Indeed, broadly speaking, it seems probable that the ultimate driver of pup survival and recruitment across ecosystems is the body size of prey and its relationship to biomass acquisition per wolf, which likely explains why pup survival and pack size are generally lower in areas with smaller prey, such as the GVE and Wisconsin, where wolves largely subsist on white-tailed deer, and higher in areas with larger prey, such as Yellowstone National Park, Idaho, and Alaska, where wolves largely subsist on elk *Cervus canadensis*, bison, or moose (Table 1).

Wolf pup survival rates in the GVE varied dramatically among years, and we suspect that much of this variation was driven by differences in resource availability and the ability of breeding animals to acquire sufficient biomass to provision dependent pups (Harrington et al. 1983, Gable et al. 2023b). Interestingly, the lowest and highest pup survival rates we documented occurred in consecutive years (0.07 in 2020–2021, and 0.50 in 2021–2022), which indicates that wolves in the GVE have the capacity to rapidly respond to changing conditions. This pattern is likely the result of adult

Table 3. Summary of annual pup production and recruitment outcomes for wolf packs in the Greater Voyageurs Ecosystem, Minnesota, USA, from 2019 to 2025.

Year	No. of packs studied	Proportion of packs that produced pups but failed to recruit	Proportion of packs that did not produce pups	No. of packs with unknown pup production
2019–2020	7	0.50	0.0	1
2020–2021	12	0.60	0.17	0
2021–2022	13	0.15	0.0	0
2022–2023	17	0.23	0.18	1
2023–2024	24	0.24	0.17	3
2024–2025	19	0.47	0.21	0

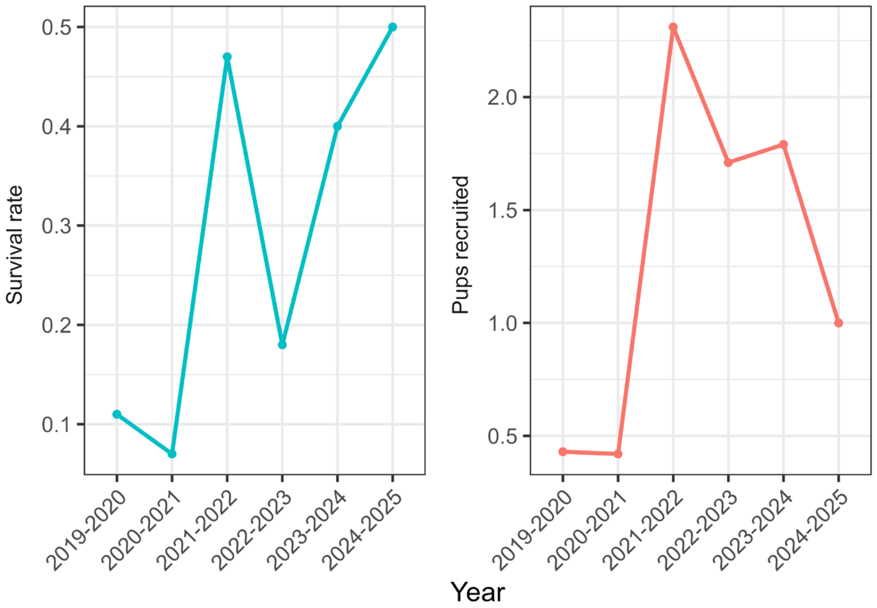

Figure 3. Annual survival rates of wolf pups at the population level and mean number of wolf pups recruited per pack in the Greater Voyageurs Ecosystem, Minnesota, USA, from 2019 to 2025.

wolves modifying their provisioning behavior in response to annual fluctuations in prey abundance (white-tailed deer and beavers). When prey become less abundant, breeding wolves in the GVE appear to prioritize satisfying their own nutritional needs over those of their pups, effectively redirecting effort from current reproductive success toward future breeding opportunities (Gable et al. 2023b). Indeed, continued investment in a litter during unfavorable conditions may be detrimental to the lifetime reproductive success of the breeders (Verboven and Tinbergen 2002). Because pups are largely unable to procure their own food and depend almost entirely on adults to provision them, most pups likely starve to death during periods of prey scarcity (Mech and Goyal 1993, Fuller et al. 2003, Gable et al. 2023b). Thus, through their ability to adjust provisioning behavior and influence pup survival, adult wolves – particularly breeding individuals – likely play a crucial role in maintaining the wolf population at or near a level that prey populations can support (Gable et al. 2023b). Therefore, changes in prey abundance that influence biomass acquisition rates of wolves may be the primary driver of inter-annual variation in pup survival and, consequently, recruitment within wolf populations.

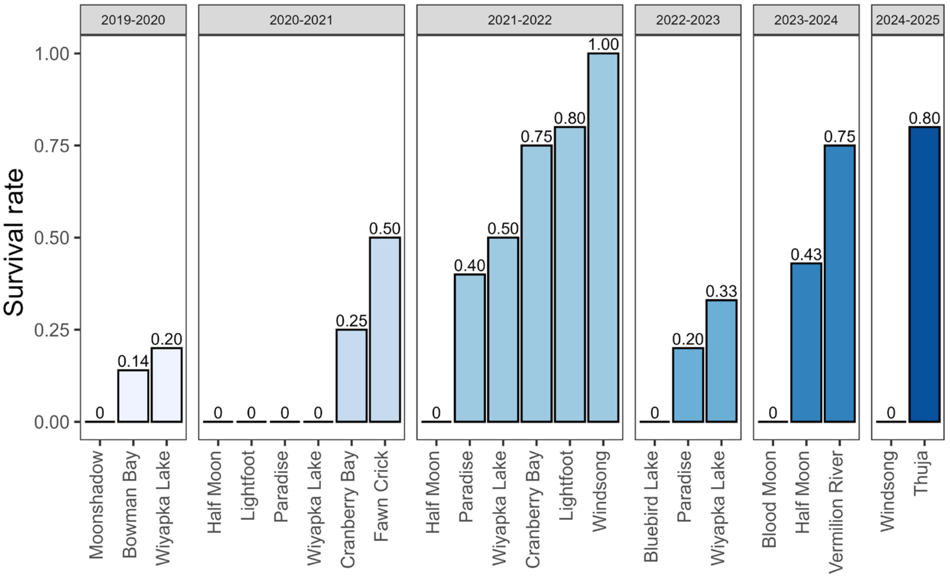

Figure 4. Annual survival rates of 23 litters of wolf pups from 13 packs in the Greater Voyageurs Ecosystem, Minnesota, USA, from 2019 to 2025.

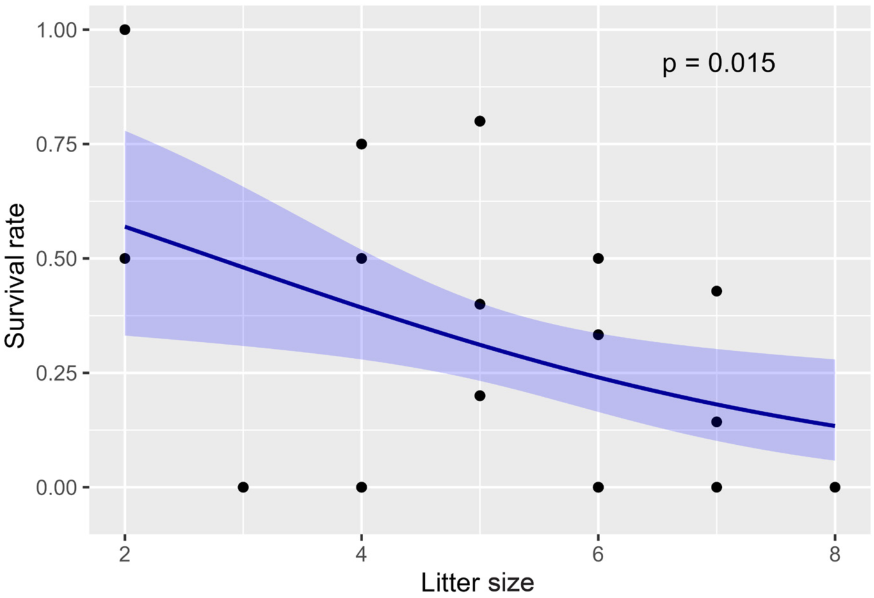

Figure 5. The relationship between litter size and pup survival in the Greater Voyageurs Ecosystem, Minnesota, USA, from 2019 to 2025.

Differences in age, experience, and physical condition among breeding wolves likely explain, to some degree, interpack variation in pup survival and recruitment. The substantial variation we observed among neighboring packs in the GVE within the same years may reflect such differences, particularly in the age and experience of breeders (Fig. 6). Similar patterns have been reported in sympatric carnivores, where offspring survival is often lower among younger, less-experienced breeders than among older, more experienced breeders (Meijer et al. 2011, Marneweck et al. 2019, Engebretsen et al. 2024). Additionally, body mass of adult female wolves, which increases with age and is closely correlated with age of primiparity, also has a significant impact on pup survival, with heavier females experiencing greater success in rearing pups (Stahler et al. 2013). Larger body size in wolves of both sexes is also associated with greater hunting success, suggesting that larger wolves may be better able to provision pups (MacNulty et al. 2009a). Although wolves typically gain experience in both hunting and pup rearing as they age, reproductive senescence can begin in wolves around 4–6 years of age, while predatory senescence, which can constrain prey acquisition and affect the ability of adults to provision pups, may begin even earlier (MacNulty et al. 2009b, Stahler et al. 2013, Sparkman et al. 2016). Therefore, packs with inexperienced or older breeders may have higher rates of pup mortality than adjacent packs whose breeders are in their prime. Furthermore, most wolves in the GVE are solitary predators during the pup-rearing season and there is significant variability in the hunting behavior and hunting success of individual wolves during the summer (Bump et al. 2022, Gable et al. 2023b). Variation in hunting ability and success among wolves almost certainly influences the extent to which breeding wolves are able to provision pups (Gable et al. 2023b). Thus, differences in physical and behavioral traits among individual breeding wolves likely contribute to the substantial variability in pup survival among neighboring packs within a given year.

Additionally, variation in pup survival may also reflect differences in fecundity and seasonal resource availability. Litter size is often a function of winter prey abundance and availability, with larger litters more common following winters when prey was more abundant (Harrington et al. 1983, Fuller et al. 2003). In contrast, survival and recruitment rates within a given population appear to be predominantly influenced by summer prey abundance (Fuller et al. 2003, Gable et al. 2023b). We found that pup survival was negatively related to litter size, undoubtedly due to greater demand for limited resources in large litters – particularly during summer, when prey is typically less available to wolves (Lodberg-Holm et al. 2021, Fig. 5). We found no relationship between litter size and recruitment rates, which suggests that the number of pups that can be successfully recruited each year is independent of litter size and is driven predominantly by the abundance and availability of prey during summer.

Our method for estimating survival and recruitment assumes that pups who were not recruited into a pack died, rather than dispersed. Although wolf pups have been documented dispersing as early as 15 weeks of age, dispersal events during the first year of life are infrequent and generally considered exceptions (Mills et al. 2008, Morales-González et al. 2022). Jimenez et al. (2017) found that only 2% of wolf pups in the Rocky Mountains, USA, dispersed, and noted that dispersal prior to 11 months was uncommon, a finding similar to dispersal patterns of wolves in Scandinavia (Nordli et al. 2023). Similarly, pups accounted for only 4% of dispersing wolves studied in Idaho, USA (Ausband et al. 2017). In contrast, Mills et al. (2008) reported that the dispersal rates of pups from Algonquin Provincial Park, Ontario, Canada, was at least 6%, and may have been as high as 18%. However, we are unaware of any other study reporting

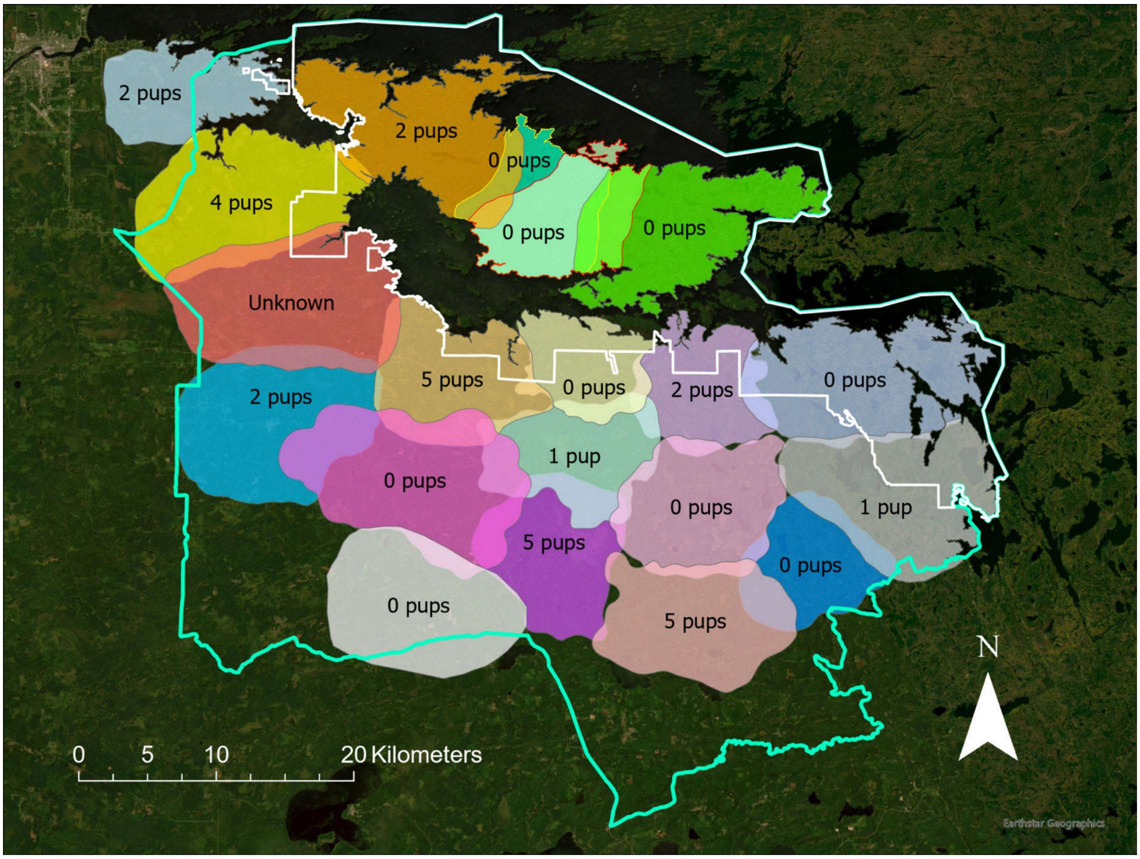

Figure 6. The number of wolf pups recruited by 20 packs in the Greater Voyageurs Ecosystem (GVE), Minnesota, USA, in 2022–2023. The green line indicates the GVE boundary, and the white line delineates the border of Voyageurs National Park. Colored polygons represent estimated wolf pack territories derived from GPS collar data, historical territory size, and remote camera data.

similarly high pup dispersal rates. Indeed, in the Great Lakes Region < 5% of pups from several studies dispersed, and these were all near one year of age at the time of dispersal (Treves et al. 2009). Although some pups in our study may have dispersed in their first year of life, available information on pup dispersal suggests that dispersal rates were likely very low and would not have altered our results in a meaningful way. Additionally, average pack sizes in the GVE, and therefore the number of surviving pups in each pack, rarely changed from late December to April (Cassidy et al. 2023, Gable et al. 2023a, 2024b, 2025), indicating that if dispersal occurred during winter, it was very rare. Thus, we think it reasonable to assume that almost all decreases in the number of surviving pups in a pack can be attributed to mortality.

Our approach to monitoring enabled us to readily study annual wolf pup survival and recruitment in a forested ecosystem, which has heretofore been difficult. We are convinced that the method we employed to estimate survival and recruitment could be effective in many similar ecosystems, offering researchers a feasible and less invasive (i.e. compared to fitting small pups with collars or surgically implanting transmitters) alternative for estimating and monitoring pup survival and recruitment, particularly in long-term studies (Fuller et al. 2003, Gable et al. 2023a). By studying wolf pups almost exclusively through observations from remote cameras, we were able to examine patterns in interannual variation in pup survival and recruitment that have previously proven enigmatic. The considerable variability in survival rates we observed among packs and years highlights how little is known about patterns in pup survival and the need for a better understanding of the reproductive ecology of wolves. Over two decades ago, Fuller et al. (2003, p. 191) stated that pup survival 'was probably the single greatest enigma in wolf biology today.' Although significant advancements have been made since then, pup survival has remained one of the most elusive aspects of wolf biology due to the difficulty of observing wolf pups. However, new approaches and technologies are improving our ability to estimate pup recruitment and survival, and we are optimistic that with more data on recruitment and survival within and across study areas, we can gain a better understanding of what ultimately drives spatiotemporal patterns in pup survival.

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Author contributions

Andrea Hynes: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (equal); Methodology (equal); Software (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Thomas D. Gable**: Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing – review and editing (equal). **Austin T. Homkes**: Data curation (equal); Funding acquisition (supporting); Investigation (equal); Methodology (supporting); Project administration (supporting); Resources (equal); Supervision (supporting); Writing – review and editing (supporting). **Joseph K. Bump**: Funding acquisition (equal); Project administration (equal); Writing – review and editing (supporting). **John G. Bruggink**: Funding acquisition (supporting); Project administration (supporting); Resources (supporting); Supervision (equal); Writing – review and editing (equal).

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Data availability statement

Data are available from the Data Repository for the University of Minnesota (DRUM), https://hdl.handle.net/11299/277747 (Hynes et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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