Greater Voyageurs Ecosystem Wolf Pack and Population Size Report

2021 - 2022

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2021-2022 Pack and Population Summary

During 2021-2022, we estimated the area of 9 wolf pack home ranges/territories and estimated the size of 14 wolf packs based on an average of 7.3 independent observations of each pack at the estimated size (i.e., the number of wolves we determined were in a given pack).

The 2021-2022 survey effort — in terms of number of packs and territories studied — tied 2020-2021 as the most intensive survey effort to date in the Greater Voyageurs Ecosystem, Minnesota (Fig. 1).

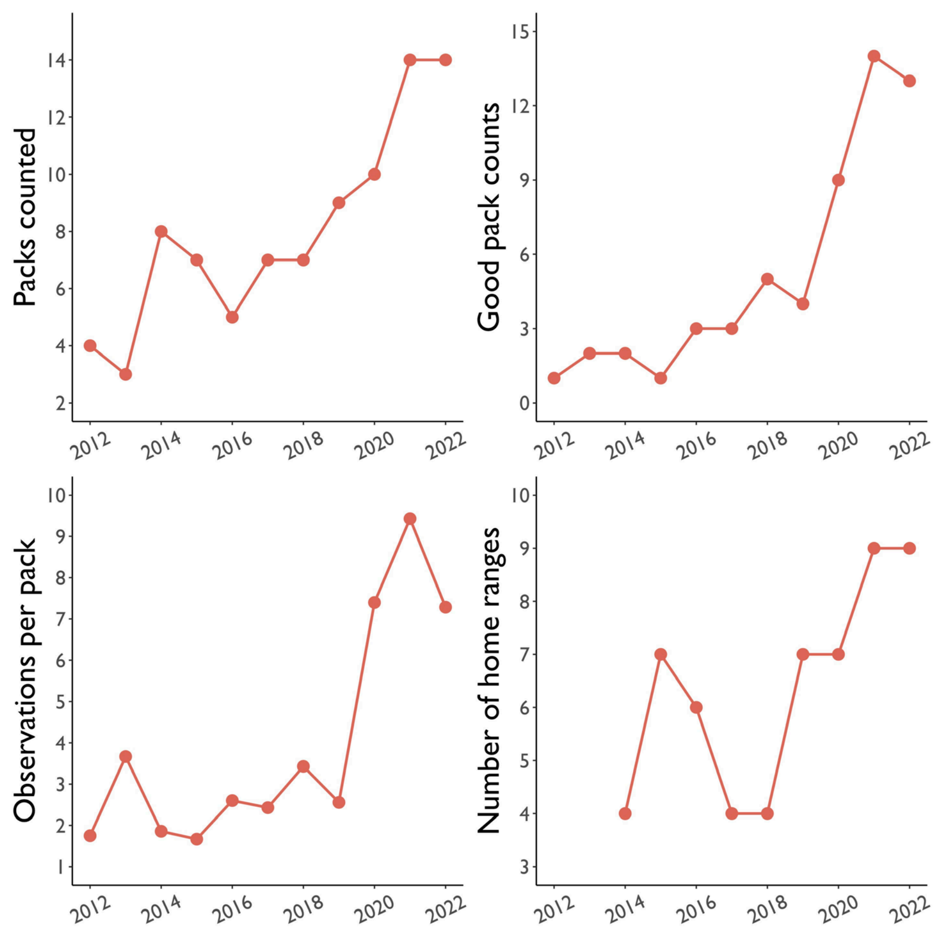


Figure 1. The number of wolf packs (upper left) and pack home ranges (upper right) studied during 2012-2022, as well as indicators of the quality of wolf pack size estimates during this time (lower two graphs). The number of observations per pack (lower left) refers to the number of independent observations of each pack at a given size (e.g., a value of 7.3 in 2022 indicates that, on average, we had 7.3 independent observations of each pack at their estimated size). We considered a "good pack count" to be when we had 3 or more independent observations of a specific pack their estimated size.

This year marks the 3rd straight year of a sustained, intensive effort to collect data on more wolf packs, obtain better estimates of pack size, and understand the wolf population of the GVE in more detail (Fig. 1).

Prior to 2019, the estimated size of many packs were based on 1 or 2 independent observations per pack. The lack of repeated observations likely introduced error because 1 or 2 observations might not be representative of actual pack size (Barber-Meyer 2022). Beginning in 2019, we deployed a large remote camera array across the study area to increase the number of independent observations of each pack. This approach has been highly effective and we have averaged 7.4, 9.8, and 7.3 independent observations of each pack at the estimated size in 2019-2020, 2020-2021, and 2021-2022, respectively. For comparison, the average annual number of independent observations per pack at their estimated size during 2012-2018 was 2.5 with a maximum of 3.7 observations per pack in 2013.

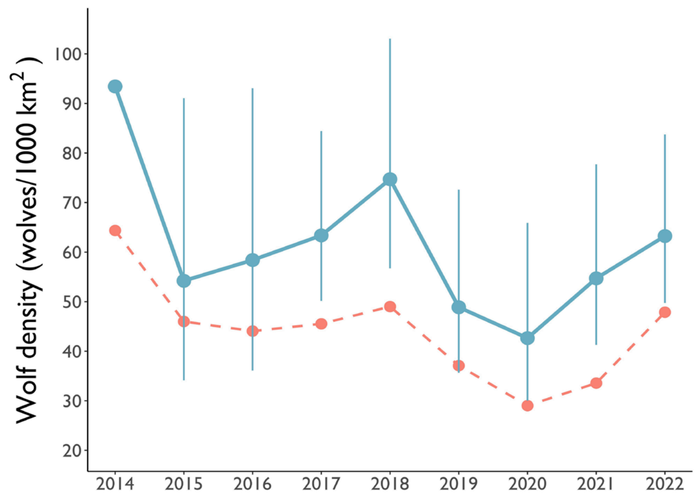


Figure 2. Wolf density estimates (blue points) for the Greater Voyageurs Ecosystem from 2014 to 2022. The error bars represent 95% confidence intervals. The red points and dashed red line represent wolf pack density if density was calculated solely by dividing mean wolf pack size by mean home range size (i.e., if density estimates did not account for pack home range overlap or lone wolves).

We estimate that wolf population density in the Greater Voyageurs Ecosystem in 2021-2022 was 63.2 wolves/1000 km^2 (95% confidence interval: 50.3-83.8 wolves/1000 km^2). This density represents a 16% increase in population density from 2020-2021 and a 48% increase from the recent population low in 2019-2020 of 42.7 wolves/1000 km^2 (Fig. 2).

The increase in population density is largely attributable to increased pup survival, which likely increased pack size.

Pack size was 3.1 wolves per pack in both 2019-2020 and 2020-2021 but increased substantially to 4.7 wolves per pack in 2021-2022 (Fig. 3). Our preliminary estimates indicate 52% (min-max survival estimates: 47-57%) of pups survived last year, which stands in stark contrast to 2020-2021 when we estimated only 7% (4-11%) of pups survived.

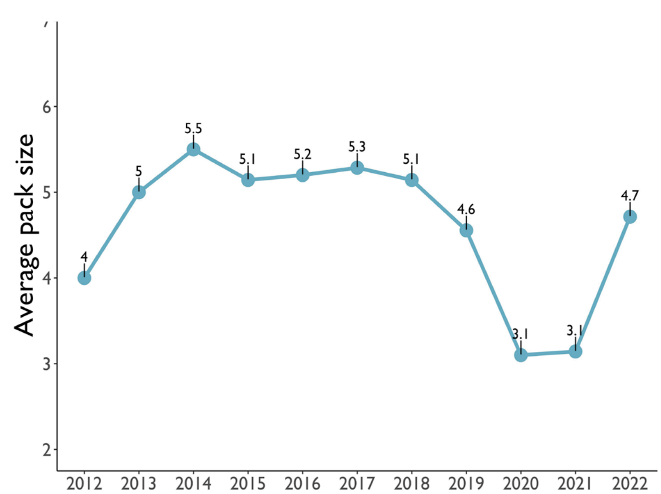


Figure 3. Wolf pack size estimates for the Greater Voyageurs Ecosystem, Minnesota from 2012 to 2022.

Wolf Density in the Greater Voyageurs Ecosystem: 2012-2022

Rigorous estimates of wolf population density during the current monitoring period (2012-2022) have been lacking, even though wolf population metrics (pack size, home range size, etc.) have been collected since 2012 and 2013 (Fig. 4 & 5). Although some density estimates do exist (e.g., 40-60 wolves/1000 km²; Gable et al. 2016), these were coarse at best. As such, it was clear that a more robust and quantitatively-rigorous density estimate was needed to understand current and historical wolf population density in the GVE (Table 1). Further, reliable density estimates are necessary for future efforts to understand the factors that influence population change through time.

To this end, we developed a standardized, quantitative method to estimate annual wolf density in the GVE (see end of the report for description of methods used). We then used all available data from 2012 to 2022 to calculate annual wolf density in the GVE during this period (Fig. 2). We had sufficient data to calculate annual wolf density during 2015-2022, and made some assumptions to estimate density for 2013-2014. We did not have sufficient data to reasonably estimate wolf density during 2012-2013.

Although wolf density has varied annually in the GVE since 2014, there is no indication that density is increasing or decreasing with time (Fig. 2). In other words, the population has remained relatively stable and current population density (63.2) is close to the average population density [61.5 wolves/1000 km²] over the past 9 years in the GVE.

Notably, the average density of wolves in the GVE during this period represents some of the highest sustained densities of gray wolves reported (Mech and Barber-Meyer 2015). The Northern Range in Yellowstone National Park had average wolf densities of 54 wolves/1000 km² from 1998 to 2012, including 7 years where wolf density exceeded 65 wolves/1000 km². Similarly, the wolf population in Isle Royale National Park surpassed densities >50 wolves/1000 km² in some years (Vucetich and Peterson 2004). Wolf densities in individual wolf pack territories have, on occasion, reached 106-308 wolves/1000 km² (Mech and Tracy 2004, McRoberts and Mech 2014) but there is little evidence of wolf populations remaining at these densities for long-periods.

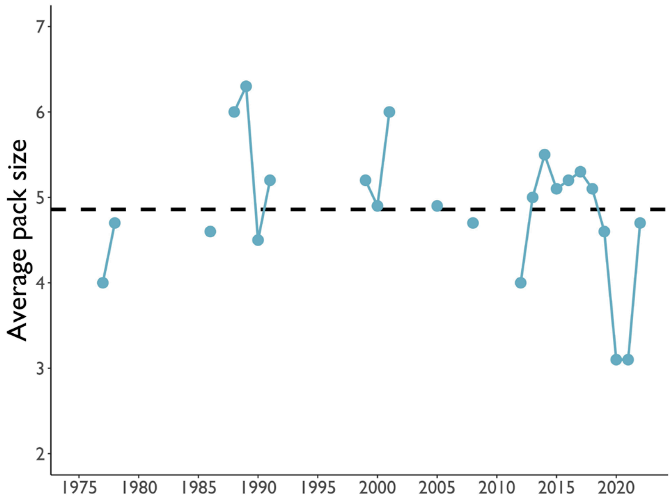


Figure 4. Mean wolf pack size in the Greater Voyageurs Ecosystem (GVE), Minnesota from 1975 to 2022. Dashed line represents long-term average. Pack size estimates from 1977-1978 (Hardwig 1978), 1985-1986 (archived map by Voyageurs National Park biologist Glen Cole), 1987-1991 (Gogan et al. 2004), 1998-2001 (Fox et al. 2001), 2005 (Fox 2006), and 2008 (Ethier and Sayers 2008).

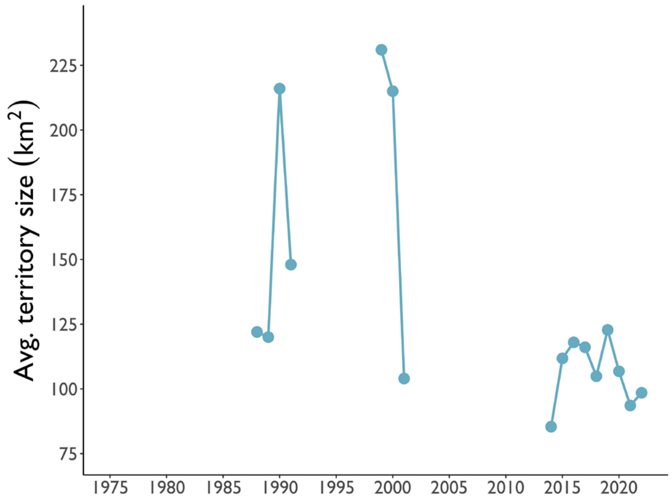


Figure 5. Mean home range size in the Greater Voyageurs Ecosystem, Minnesota from 1975 to 2022. Data from 1987-1991 and 1998-2001 are from Gogan et al. (2004) and Fox et al. (2001), respectively. Home ranges from 1987 to 2001 were estimated using telemetry data and minimum convex polygons whereas home ranges from 2014-2022 were estimated using GPS-location data and kernel density estimators.

Table 1. Available data on wolf pack size, home range size, and population density in the Greater Voyageurs Ecosystem, Minnesota from 1977 to 2022. We are not aware of any data on wolf population metrics prior to 1977 for the Greater Voyageurs Ecosystem.

Year	Pack Size Data	Home Range Data	Density Estimates	Source
1977-1978	X			Hardwig 1978
1986	X			Cole 1986 map*
1988-1991	X	X	X	Gogan et al. 2004
1999-2001	X	X	X	Fox et al. 2001
2005	X			Fox 2006
2008	X			Ethier and Sayers 2008
2012-2022	X	X	X	This study

**Map by Glen Cole in Voyageurs National Park archives that had pack size estimates for 4 packs during 1985-1986*

Current and Historical Wolf Density in the Greater Voyageurs Ecosystem

Wolf density during 2014-2022 was substantially higher than that reported by the two previous studies in the GVE (Fig. 6). During 1987-1991 and 1998-2001, wolf population density was estimated to be 33.5 wolves/1000 km² (Gogan et al. 2004) and 38.6 wolves/1000 km² (Fox et al. 2001), respectively. However, we do not think wolf population density has increased—or at least increased substantially—over the past 35 years. Instead, the disparity in density from previous studies and ours likely stems from the coarser survey methods used in previous studies. Both previous studies of wolves in the GVE relied predominantly on VHF locations from collared wolves and aerial observations of wolf packs during winter to derive population estimates. VHF locations helped delineate territories while aerial observations allowed biologists to count the number of wolves in each pack. Winter track counts and opportunistic observations augmented and informed some pack-level data in both studies.

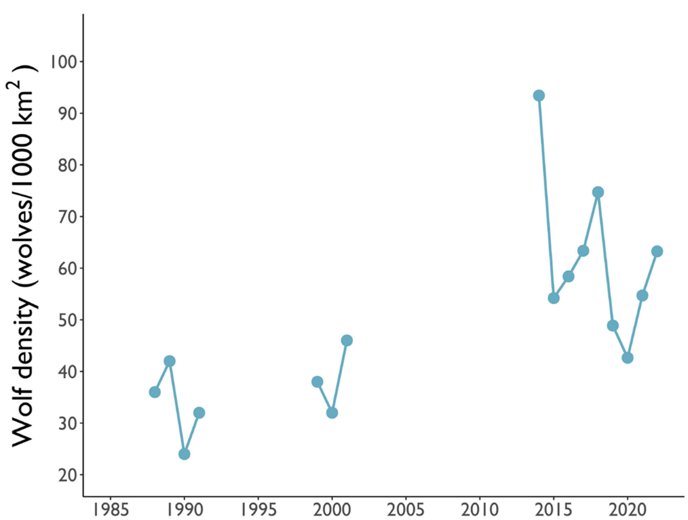


Figure 6. Wolf density in the Greater Voyageurs Ecosystem, Minnesota from 1987 to 2022. Data from 1987-1991 and 1998-2001 are from Gogan et al. (2004) and Fox et al. (2001), respectively.

We think there is little reason, given trends in prey density, to expect wolf density to be higher now than it has been over the past 35 years. Wolf population density is primarily a function of prey density with denser prey populations facilitating denser wolf populations (Fuller et al. 2003, McRoberts and Mech 2014, Mech and Barber-Meyer 2015). White-tailed deer are the primary annual prey for wolves in the GVE with beavers being an important secondary prey. White-tail deer density in the GVE has remained between 2-4.6 deer/km² for the past 35 years, though deer density was higher (3-4.6 deer/km²) during 1987-2001 than it has been over the past decade (2.0-3.2 deer/km²; (Gable et al. 2017). Beaver populations have remained at very high but relatively stable densities of ~1 colony/km² since 1987, though transect data suggests densities have decreased slightly since the 1990s (Johnston and Windels 2015). Notably, the GVE has supported a low density moose population for decades (<0.15 moose/km²; Windels and Olson 2019) but wolves rarely kill moose in the GVE (Gogan et al. 2004, Gable et al. 2017).

Wolf population metrics from the previous two studies indicate pack size and home range size have decreased since 1987-2001 (Fig. 4 & 5). Average pack size during 2012-2022 was 4.6 wolves/pack compared to 5.5 wolves/pack and 5.3 wolves/pack in 1987-1991 and 1998-2001, respectively. Similarly, average home range size was 106.4 km² during 2012-2022 compared to 152 km² and 183 km² during 1987-1991 and 1998-2001, respectively. This pattern is perplexing because wolves typically adjust home range size based on prey density (i.e., smaller territories at higher prey densities and vice versa) (Kittle et al. 2015, Sells et al. 2021). Yet, as mentioned above, prey density was higher during the previous two study periods than the current period (Gable et al. 2017) suggesting that territories in 1987-2001 should have been smaller, not substantially larger, than they currently are. However, we think the differences in territory size between the current study and previous studies can easily be explained by five factors: 1) differences in location/fix interval, 2) method used to delineate home ranges, 3) smaller sample size in earlier studies, 4) inability to remove extra-territorial locations and determine social status of wolves, and 5) inclusion or exclusion of large lakes in density estimates.

As mentioned above, previous studies had to rely on VHF locations to estimate territory boundaries. More specifically, the size of territories during earlier studies were delineated using relatively few VHF locations (an average of only 58 VHF locations during 1987-1991, and even fewer locations on average for home ranges during 1998-2001). By contrast, the majority of wolves during our current study period were fitted with GPS-collars that recorded locations every 20 minutes providing >10,000-14,000 GPS- locations per summer to estimate home ranges. Even wolves fitted with collars that took locations every 2-12 hr provided more detailed location data than previous studies. More intensive GPS-locations yield fine-scale insight into home range boundaries (Mills et al. 2006) while also making it easier to identify and remove extra-territorial forays and to assess the social status of collared wolves (Burch et al. 2005). Limited location data (e.g., VHF data) can make it difficult to determine whether collared wolves are foraying outside of their home range or if collared individuals are lone or pack wolves—both of which can impact population density estimates (Burch et al. 2005). Given all of this, home ranges during the current period are almost certainly more accurate than previous studies because of intensive GPS-collar data (Fig. 7).

We estimated home ranges using a kernel density approach as opposed to the minimum convex polygon (MCP) approach that was used in the two previous studies (Fig. 7). The kernel density approach provides a more nuanced and detailed home range polygon/estimate than MCPs. MCP home ranges often overestimate territory size because they only yield coarse polygons that do not account for nuances in home range shape (Nilsen et al. 2008). MCP home ranges are particularly problematic because they do not conform well to the contours of shorelines, which are often territory boundaries for wolves in the GVE. For example, even with our intensive GPS-location data, MCP home ranges for wolves during the current study period were 6% larger than kernel home ranges. The difference in home range size would undoubtedly alter density estimates (e.g., we could have under-estimated density by as much as 6% if we had used MCPs instead of kernel home ranges).

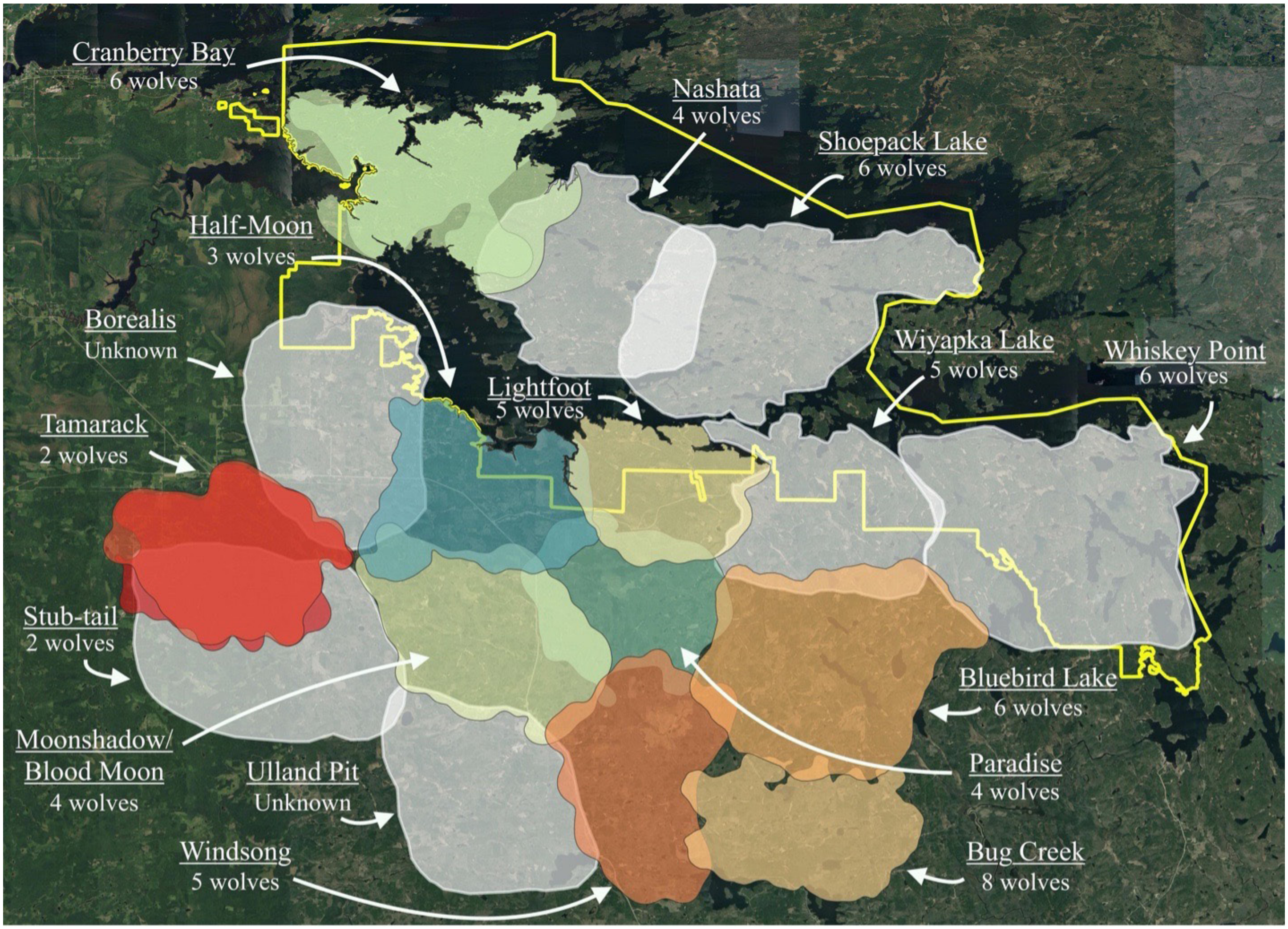


Figure 7. The known and estimated home ranges of 16 wolf packs in the Greater Voyageurs Ecosystem, Minnesota from April 2021 to April 2022. Colored polygons represent known wolf pack home ranges (n=9) based on GPS-collar data from April 2021 to April 2022. Notably, there are two home range polygons for both the Tamarack and Cranberry Bay Pack because we had two wolves collared in each pack (a home range polygon for each wolf in the pack).White polygons represent pack home ranges (n=7) that we estimated using a combination of remote camera data, historical home range data, and data on neighboring wolf pack home ranges. These home ranges were only estimated for visualization purposes and were not used for any analyses or density calculations.

Because of the relatively few VHF locations for each wolf and the inability to frequently observe wolves, previous studies almost certainly included locations of extra-territorial forays in home range estimates (e.g., see Locator Lake Pack in Figure 2 of Fox et al. [2001]), which would substantially inflate some MCP home range estimates (Burch et al. 2005). For the same reasons, earlier studies likely considered some wolves to be pack wolves when they were in actuality lone wolves. For example, Fox et al. (2001) considered one wolf with a home range of 444 km^2 to be a pack wolf. This home range is substantially larger than the next largest home range ever documented in the GVE and given the pattern of locations was almost certainly a lone wolf or a 'floater' (see Fig. 2 of Fox et al. [2001]). Fox et al. (2001) used this data to represent the home range of this pack for two consecutive years—representing 2 of the 11 home ranges estimated during this study—which is likely why 1998-1999 and 1999-2000 have abnormally large annual home range estimates (Fig 5).

Of course, these kind of decisions are completely understandable given the data available at the time of this work. We certainly are in a privileged position to be able to re-assess these data after observing fine-scale GPS-collar data from wolves in the GVE for multiple years. However, the inability to control for these aspects combined with small sample sizes are almost certainly why there is substantial volatility (Fig. 6) in home range size from one year to the next in both earlier studies.

Lastly, both previous studies included the area of the largest 4 lakes (Rainy, Kabetogama, Namakan, and Sand Point) in the GVE when calculating wolf densities. These four lakes comprise 281 km^2 or roughly 16% of the GVE (1,800 km^2) and 32% of Voyageurs National Park (882 km^2). However, wolves do not, except on rare occasion, venture out into the lake or onto the islands of these lakes during the ice-free season (7-8 months of the year). Even during winter, wolves spend relatively little time out on the ice with most activity restricted to land. Thus, we think it makes little biological sense to include the area of these large lakes in home range and population density calculations (a la (Powell and Mitchell 2012)). Furthermore, doing so would lead to a substantial underestimate of wolf population density. For instance, home range estimates for packs that bordered the large lakes during 2014-2022 were 16% smaller after we removed the area of large lakes from their estimated home ranges.

By simply using a kernel home range estimator and removing large lakes, we estimate that home ranges during the previous studies could be at least ~25% smaller based on the data from the current study period. If we are correct, home ranges from 1987-1991 and 1998-2001 could plausibly be below 114 km^2 and 137 km^2, respectively. Of course, home range estimates would likely decrease even more if there was more intensive location data from wolves during these periods. Any decrease in home range size would, in turn, lead to an increase in population density of a similar magnitude.

Thus, it seems unlikely that wolf densities during the previous two studies were significantly different than current wolf densities.

Individual Pack Summaries:

Below are individual summaries on the data collected for each wolf pack during the Winter 2021-2022 monitoring period. The summaries provide an explanation of the size of each pack and how we arrived at that estimate.

Blood Moon/Moonshadow

Wolf V079, the breeding male of the Moonshadow pack, died of natural causes in January 2022. The cause of death was starvation, possibly exacerbated by other health-related complications (necropsy is pending). V079 was clearly not maintaining a territory for most of January 2022 prior to death. Between December 1, 2021 and January 3, 2022, we had 5 observations of V079 traveling around with other pack members in the Moonshadow territory. By late January, a new pack was in the territory led by a wolf with distinctive coloration that could easily be identified on trail cameras (we collared this male wolf, dubbed “Y1T”, in May 2022).

This new pack, called the “Blood Moon Pack”, had 4 individuals in it: Wolf Y1T, an older-looking female wolf, and two younger wolves that looked very much like 9-11 month old pups. We feel confident that Y1T is not from a pack we have studied given his distinctive appearance but are unsure about the other 3 wolves. We think it is possible the female and two pups were Moonshadow Pack members and that Y1T simply usurped V079 to take over the pack. The older female does bear some resemblance to the V079’s mate in 2021 and some Moonshadow pups were still alive as of late December 2021/early January 2022. However, we will need to obtain genetic samples to confirm. On the other hand, Blood Moon could be completely unrelated to the Moonshadow Pack. Regardless, Y1T and the older female appear to be the dominant pair of the pack.

We did get two observations on January 3, 2022 and January 29, 2022 of 5 wolves in this pack traveling together. In the latter observation, Wolf Y1T was present. However, 3 subsequent observations in February and 1 on April 1st showed 4 wolves traveling together. As such, we feel comfortable that, based on these observations, that the pack is 4 wolves. Worth noting, we also had two observations of 4 wolves in the Moonshadow Pack (V079 was present in both observations) in December 2021.

The dominant male of the Blood Moon Pack, Wolf Y1T

The dominant male of the Blood Moon Pack, Wolf Y1T, with a subordinate pack member

Wolf Y1T, the dominant male, playing with the two subordinate pack members of the Blood Moon Pack

Bluebird Lake

We had several observations of the Bluebird Lake Pack during winter but the number of wolves traveling together waffled between 4 to 6 wolves throughout the winter. However, we conclude that the pack had 6 wolves in it because: 1) we had more observations of 6 wolves (n=4) together than we did 4 (n=2) or 5 (n=3), and 2.) the 4 observations of 6 wolves were spread out through the winter (Feb 4, Feb 8, Mar 2, and March 12).

The Bluebird Lake Pack was 8 wolves (5 adults and 3 pups) for most of late summer and fall in 2021. The pack appears to have lost two members between fall and winter. These could either have been pups that died or other subordinates who dispersed or died during this period. Unfortunately, we do not know how many pups the pack produced in 2021 or how many survived until adulthood.

The breeding pair of the Bluebird Lake Pack is Wolf P0C (breeding male) and Wolf V052 (breeding female). Both wolves were observed in most observations of the pack that we had during winter. We confirmed V052 was breeding female and produced litter of pups from trail cameras and a den visit in Spring 2022.

Interestingly, the Bluebird Lake Pack is the only pack that decreased in size from the prior winter. In Winter 2020-2021, the pack was 8 wolves strong. However, Bluebird Lake was much larger than any other pack studied in Winter 2020-2021 and we would have been surprised to see an already large pack increase in size again.

Two Bluebird Lake pups and 1 subordinate adult in Fall 2021

The breeding male, wolf P0C, and the breeding female, wolf P3S (V052), of Bluebird Lake in January 2022

An unknown ear tagged wolf in Bluebird Lake Pack territory

A subordinate Bluebird Lake wolf running down trail in February 2022

Subordinate Bug Creek wolf in early April 2022

Bug Creek

This past winter was the first time we conducted pack counts for the Bug Creek Pack (or the wolves that have occupied that general area). Much of the impetus for this was because we collared a subordinate wolf (Wolf P1T) in the pack that was still part of the pack during the past winter. However, given camera-related challenges, we only deployed a few cameras throughout the territory and instead focused most of our efforts on other packs we have studied more consistently.

We did not get an abundance of observations of the Bug Creek pack but enough to feel confident in our estimate of 8 wolves in the pack. We had two observations of 8 wolves in February and then another great daytime observation of 8 wolves in early April. We had two other observations (one in February and one in March) of 7 wolves.

Wolf B5E, the breeding male, with a large wound on his back leg and abdomen in February 2022

All four Cranberry Bay pups in October 2021

Cranberry Bay

The Cranberry Bay Pack was 6 wolves in Winter 2021-2022. During late fall and early December, the pack was larger at 7 wolves but by mid-January had decreased to 6 wolves. From January 19, 2022 to April 1, 2022, we had 8 observations of 6 wolves traveling together, including one really nice daytime observation on April 1 of all 6 wolves together, including V083 and V084 (the breeding pair). In this observation, V084 was noticeably pregnant. The pack composition during the winter was the breeding pair (V083 and V084) and 4 subordinate wolves. Wolves V083 and V084 produced a litter of 4 pups in Spring 2021 and all 4 pups survived until late fall or early winter as we have a clear video sequence of all 4 pups together.

During fall and early winter, the pack clearly had 7 members, indicating that there was an additional subordinate wolf in the pack at that time that was not a pup of the year (i.e., 2 breeding individuals + 4 pups + 1 subordinate wolf= 7 wolves). We do not know why the pack decreased from 7 to 6 wolves in early winter. The subordinate wolf could have died or dispersed meaning that the pack was the breeding pair plus their 4 pups in winter. In this scenario, all 4 pups survived. Alternatively, a pup could have died or dispersed and the pack could have been the breeding pair, 3 pups, and 1 other subordinate wolf. Regardless, the Cranberry Bay pack had very high pup survival in 2021 (75-100%).

We did have two really odd observations of 10 wolves and 7 wolves on the night of March 2 and early morning of March 3 on cameras along the Chain of Lakes snowmobile trail. Each observation was at night and consisted of wolves running full speed past the camera. These observations are curious because we had no other observations of 10 wolves for any pack during our monitoring period and all other observations during this time indicate the Cranberry Bay Pack was 6 wolves.

We think the most likely explanation for these interesting observations is that wolves from the Cranberry Bay and Nashata Packs were in a territorial skirmish with one pack chasing wolves from the other pack. Both of these observations were close to the border of the Cranberry Bay and Nashata Pack territories, where we had observations of both packs during the monitoring period. An observation of 10 wolves makes sense in this regard because the Cranberry Bay Pack was 6 wolves and the Nashata Pack was 4 during winter. The observation of 7 occurred hours after the observation of 10 wolves and is hard to know exactly how to interpret this. One possibility is that there were some wolves that had given up on the pursuit/conflict at this point, or some wolves had simply taken another route and did not pass by the camera.

Almost the entire Cranberry Bay Pack in early December 2021

Three Cranberry Bay pups scent-rolling in Fall 2021

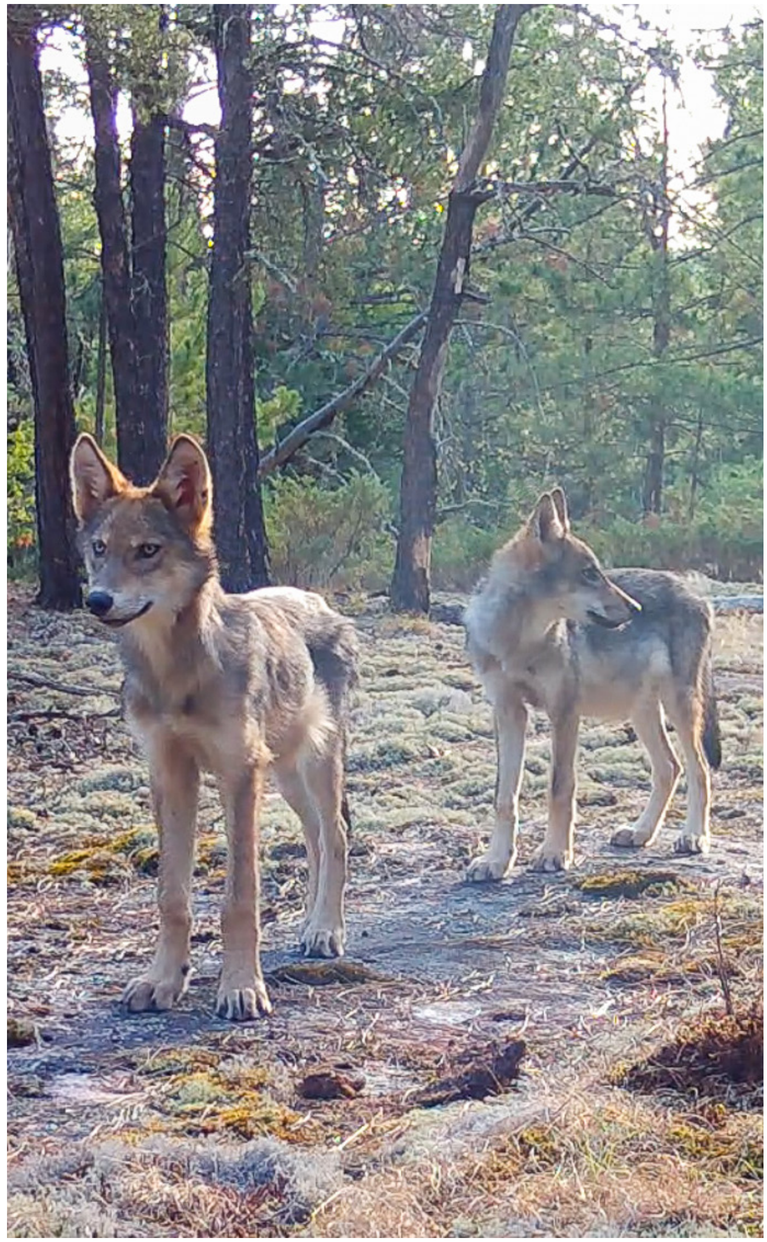
A subordinate Cranberry Bay wolf in early April 2022

Half-Moon

The Half-Moon Pack was 3 wolves during Winter 2021-2022: Wolf V094 (breeding male), the breeding female, and a pup. We had 7 independent observations of this pack throughout the winter giving us high confidence in this estimate.

Notably, we are assuming that the 3rd wolf in the pack is a pup and not another subordinate wolf. During Winter 2020-2021, the Half-Moon Pack was 3 wolves: V094, his mate, and Pup46 (a 3-year-old wolf we ear-tagged as a pup in 2018). The third wolf this past winter clearly was not Pup46 as it did not have small blue ear-tags. Thus, we presume, and think it more likely, that this 3rd wolf was a pup that survived as opposed to another subordinate wolf who joined the pack.

Regardless, the Half-Moon Pack was an enigma of sorts this past year. Wolf V094 and his mate produced a litter of 8 pups in Spring 2021 and at least 7 of these were still alive as of August 2021. And yet, somehow between August 2021 and December 2021, all of these pups but presumably 1 had died. This is the same pattern we observed in 2020 when all 4 Half-Moon pups survived through August but were dead by December. We simply find the pattern somewhat surprising and striking.



Two Half-Moon pups at a rendezvous site in August 2021

Half-Moon subordinate on the left, V094 in the center center, and female in the far right

Lightfoot

Estimating the size of the Lightfoot Pack this past winter was a real challenge. In late January, Wolf V071, the breeding male of the pack, was attacked and killed by other wolves. V071's death appeared to trigger some instability in the pack because after his death, we rarely got wolves traveling around as a social unit, and the few observations we got ranged from 1-5 wolves. In December, prior to V071's death, we had one observation of 5 wolves (V071 being one of the 5) and two others of 4 wolves. After V071's death, we had one clear observation of 5 wolves and then another observation of 4 wolves passing the camera together with a 5th wolf lagging behind by about 30 minutes. We considered the latter observation to be a count of 5 wolves.

Altogether, we had 3 observations of 5 wolves during the winter monitoring period. Thus, we considered the Lightfoot Pack to be 5 wolves. In reality, we suspect that the Lightfoot Pack was probably 6 wolves prior to V071's death and 5 wolves after his death. Granted, these are likely minimum estimates.

In Spring 2021, the Lightfoot Pack, which was just a breeding pair, produced 5 pups. All five of these pups were still alive as of November 2021 (we had two different observations of V071 and 6 other wolves together). A pack of 6 wolves in December would be the breeding pair plus 4 pups. However, given the scant observations of the Lightfoot Pack, it is possible all 5 pups survived and the pack was 7 wolves prior to V071's death and then 6 wolves after it. Our observations for the Lightfoot Pack simply are not conclusive and it is possible we undercounted the pack by 1 wolf.

Interestingly, we have no evidence to suggest that the breeding female found another mate during winter after V071 died and doubt that she produced a litter of pups (if she is even still in the territory). We collared 3 yearling wolves (two were PIT-tagged as pups) from the Lightfoot Pack in May 2022. We have since searched all the GPS-clusters from these 3 wolves and have not found any evidence of a den or rendezvous site. We also conducted howl surveys in the Lightfoot territory to identify pups and did not get any response. What becomes of the Lightfoot Pack going forward will be quite interesting to observe.

Three Lightfoot pups in August 2021

Nashata

We had many observations of the Nashata Pack this winter but the number of wolves traveling together fluctuated between 4 and 5 wolves. Most observations of 5 wolves were in December and January with most observations of 4 wolves occurring in mid-to-late winter. In total, we had 9 independent observations of 4 wolves and 5 observations of 5 wolves. Only 4 wolves were observed in all 3 observations of the pack in March.

Given all of this, we think 4 wolves is the most appropriate pack count for the Nashata Pack. We suspect that a 5th member observed with the pack in early winter might have dispersed in mid-to-late winter or simply stopped associating much with the pack. This kind of behavior is no uncommon with subordinate wolves in mid-to-late winter based on what we have seen from collared individuals (e.g., Wolf V057 from Moose River Pack in 2018 or V045 from Shoepack Lake in 2015).

The Nashata Pack produced their first litter of pups in 2021. Unfortunately, we do not know how many were born in the litter but we captured footage of 4 pups traveling with adult packs members in late summer and early fall. Two of these pups were still alive as of early December but the pups were becoming difficult to distinguish from adult pack members at that point.

We can safely conclude that at least one or two of these pups survived. In Winter 2020-2021, the Nashata Pack was 4 wolves: the breeding pair, Wolf V074, and another subordinate. However, we do not have any video footage of V074 by himself or with other pack members after Winter 2020-2021 indicating that V074 either dispersed from the pack or died during spring to mid-summer 2021. Thus, at most, 3 pack members from Winter 2020-2021 were part of the Nashata Pack during this past winter (2021-2022). We know the breeding pair of the Nashata Pack is still intact as both the breeding male and female are easy to identify by coat coloration and physical characteristics. If the 3rd wolf from Winter 2020-2021 remained in the pack during this past winter, then at least 1 pup survived (i.e., 2 breeding member + 1 remaining pack member + 1 surviving pup). If that 3rd wolf from Winter 2020-2021 left the pack, then is it possible two pups survived.

Our suspicion is that the 4 wolves in the pack during this past winter were the breeding pair plus two surviving pups. We suspect that the "5th" member observed in early winter was the subordinate wolf from Winter 2020-2021 who dispersed/disassociated from the pack in mid-to-late winter. Of course, this is speculative but seems the most likely scenario, based on our prior experience and observations, in which we consistently get 4 wolves together and then a few additional observations where another wolf is present a few times in early-to-mid winter.

We did have a few observations of the breeding female from the Nashata Pack in early April where she was clearly pregnant and one in which she had distended nipples indicating she was nursing. The year 2022 marks the second year in a row where 3 packs on the Kabetogama Peninsula likely produced pups. During 2015-2019, we had only documented two packs on the Kab Peninsula.

A pup and adult from the Nashata Pack in October 2021

A yearling Paradise Pack wolf with food in its mouth in April 2022

Paradise

The Paradise Pack was 4 wolves during Winter 2021-2022. The pack consisted of the breeding pair, Wolves V077 (male) and V085 (female), and then two pups. The Paradise Pack had 5 pups in Spring 2021 but only two of these survived. This survival rate was higher than 2020 when all 4 pups in the pack died before reaching 3 months of age. We are very confident in this estimate as we had 14 independent observations of the pack at this size.

Notably, the Paradise Pack territory shifted and grew starting in late Summer 2021 when the Huron Pack dissolved. The Paradise Pack had initially carved out a small territory in 2020 that overlapped substantially with the 4 neighboring wolf packs. However, with the dissolution of the Huron Pack in August 2021, the Paradise Pack effectively took over much of the Huron territory and reduced the amount of overlap with other neighboring packs to the north and west (i.e., Half-Moon, Lightfoot, and Moonshadow/Blood Moon).

The breeding pair of the Paradise Pack—Wolves V077 and V085—in Fall 2021

Shoepack Lake

The number of wolves in the Shoepack Lake Pack was difficult to determine because we did not get a consistent count of the same number of individuals in the pack throughout the winter. Instead, the average number of individuals traveling together decreased from December until April. In December, we had 1 observation of 8 wolves and two of 7 wolves. We never observed 8 wolves together after early December and the only other observation of 7 wolves was on February 9, 2022. In the February 9 observation, the breeding male of Shoepack was seen mounting Wolf V036, the breeding female, indicating the breeding pair of the pack was still intact. After February 9, we had 1 observation of 6 wolves on February 26, an observation of 5 wolves on March 11, and 11 observations of 2-4 wolves. A few of the observations in late winter were clearly a different social unit/pack as there was an uncollared wolf with two-green ear-tags traveling with other wolves. Aside from V036 who only has 1 green ear-tag, there are no ear-tagged wolves in the Shoepack Lake Pack. Thus, these are either a wandering group of wolves, the pack to the east of Shoepack that was trespassing, or a pack that recently took over the Shoepack Lake territory. The latter seems unlikely as we had an observation on April 2, 2022 of 4 wolves, two of which appear to be V036 and her mate.

Given the variability in pack counts, we concluded that average pack size during the winter monitoring period (Dec 1 to April 10) was 6 wolves. The pack was clearly larger than 6 wolves in early December through mid-February and possibly smaller than 6 wolves in late March or early April. However, on April 25, outside of our winter monitoring period, we had an observation of 5 Shoepack wolves together just west of Shoepack Lake. The lead wolf was clearly the breeding male of the pack. Wolf V036 was absent but she very likely would have been at den with pups at that time. Thus, this observation provides additional evidence that Shoepack Lake was 6 wolves (5 wolves + V036).

Notably, the Shoepack Lake Pack has been a very difficult pack to get consistent pack size estimates for over the past 3 winters. Much of this difficulty is due to the lack of trails through the Shoepack Lake territory and that the trails that exist are on the periphery of the pack territory. It would be advantageous to locate other areas in the territory that the pack consistently uses. However, doing so will be an outsized challenge given the difficulty of accessing much of the territory during winter.

A Shoepack Lake wolf in November 2021

Multiple Shoepack Lake members in the fall 2021

Stub-Tail Pack

The Stub-tail Pack was two wolves—presumably a breeding pair— in Winter 2021-2022. The female of the pair has a deformed tail that is readily noticeable on trail camera footage and made it very easy to know when we were observing this pair. In total, we had 11 observations of the two wolves in the Stub-tail Pack spread across the entire winter monitoring period.

For context: we started getting observations of the Stub-tail pair in the Tamarack Pack territory beginning in Summer 2021. At that point, the Tamarack Pack occupied the territory and the Stub-tail pack appeared to be a wandering nomadic pair of wolves. The Tamarack Pack continued to occupy the territory until mid-fall or so, before the Stub-tail Pack eventually took over the Tamarack territory forcing the Tamarack Pack to move north and occupy a small territory sandwiched between Highway 53 and the northern edge of the Stub-tail Pack territory.

The breeding female of the Stub-tail Pack carrying a fawn leg in June 2022. The Stub-tail Pack was named for this female's stubby, somewhat deformed tail that is very obvious on remote cameras

Wolves B0C and B1T, the breeding pair of the Tamarack Pack, in Winter 2021-2022

Tamarack

The Tamarack Pack was only a breeding pair during Winter 2021-2022 consisting of wolves B0C (male) and B1T (female). We had 5 observations of the pair together during the winter monitoring period and we never observed another wolf traveling with the pair.

The pair had produced at least 1 pup in Spring 2021 that we observed on camera footage several times throughout Summer to Fall 2021. However, the pup did not survive to winter and so the pack remained a breeding pair. We do not know how many pups in total were produced in Spring 2021 unfortunately.

The presumed death of the pup was an omen of things to come. Indeed, The Tamarack Pack had a tumultuous fall and winter. First, the Stub-tail Pack took over the Tamarack Pack territory forcing the Tamarack Pack into a new territory to the north of their former territory. Then, in early March, Wolf B1T, the breeding female of the pack, was illegally shot and killed. The death of B1T was the nail-in-the-coffin, so to speak, for the Tamarack Pack. Shortly after B1T was killed, Wolf B0C left the territory and started wandering far and wide. In other words, the death of B1T resulted in B0C becoming a lone wolf, and was the end of the Tamarack Pack.

Windsong

The Windsong Pack had 5 wolves in it during Winter 2021-2022. The pack consisted of the breeding pair (Wolf V087 and his mate), a 2-year-old subordinate wolf (Wolf O0C and sibling of V087), and two pups (Pup59 and Pup60). We had 5 independent observations of this pack throughout the winter.

The count of 5 wolves during winter was reinforced in May 2022 when Pup59 and Pup60 were killed for depredation purposes on the Sheep Ranch. Those two pups in addition to Wolf V087, the breeding female, and O0C makes 5 wolves. Thus, both remote camera as well as GPS-collar/mortality data confirmed the pack had 5 wolves.

Windsong was only 3 wolves (V087, breeding female, and O0C) in Winter 2020-2021. The pack then produced a litter of two pups (Pup59 and 60) in Spring 2021, both of which survived until they were lethally removed on the Sheep Ranch for depredation purposes.

A Windsong yearling play bowing in January 2022

Three Windsong wolves in October 2022. The ear-tagged wolf is Wolf O0C, a 2 year old wolf. On either side of him are the two pups that the pack successfully reared

Likely the breeding male of the Whiskey Point Pack in May 2022

Whiskey Point

We do not have as good of data on the Whiskey Point Pack as we would have liked. In past years, we had numerous observations of this pack traveling the Grassy Bay snowmobile portage but that was not the case this year. Additionally, the cameras we had out in this area were not functioning properly for some of the winter and we might have missed some observations. However, we think we have enough to feel relatively comfortable with our estimate.

The only observation we had of the Whiskey Point Pack was of 6 wolves on February 8, 2022. In this observation, there was one wolf in front of the camera and then 5 wolves far in the distance on the ice. We also received one report from a member of the public who observed 6 wolves on the ice of Sandpoint Lake.

In Winter 2020-2021, the newly-formed Whiskey Point Pack consisted of two wolves (the breeding pair). However, the pair produced pups in Spring 2021 and we had two different observations of 4 pups following an adult in Fall 2021 (Sept 25 and Oct 3). We would expect a pack of 6 wolves if all four pups survived until winter. We suspect that is likely what occurred and why there were two observations of 6 wolves in the pack during winter.

Our pack count is a minimum estimate. We know there were 6 wolves in the pack during the winter but there could have been additional wolves not on camera during that observation. We think this is unlikely given the other data we have (e.g., number of pups observed in the fall) but we cannot entirely rule it out.

Wiyapka Lake pup in the fall of 2021

Wiyapka Lake

We had really solid data on the Wiyapka Lake Pack from this past winter. We observed 5 wolves traveling together on 11 different instances. The pack composition was the breeding pair (V076 and her mate) and 3 pups. In Winter 2020-2021, Wiyapka Lake was only 3 wolves (V076 and her mate plus their 1.5 year old offspring, Wolf V095). In Spring 2021, V095 left the pack and subsequently died on the north shore of Rainy Lake in June 2021. Thus, the only remaining wolves in the pack were V076, her mate, and their new litter of pups, of which 3 survived to adulthood.

Two Wiyapka Lake pups playing with a deer leg in February 2022

The breeding male and female, V076, of Wiyapka Lake. V076 is clearly nursing

Methods

Pack Size

During 2012-2019, wolf pack size was estimated in winter via a combination of several approaches that included aerial observations, remote cameras, snow tracking, and opportunistic observations. During this period, there was no specific survey approach. The primary approach was to get as many observations of wolf packs or their tracks when possible. However, this was not a sustained or standardized survey effort but rather depended on a variety of factors such as staff and pilot availability, weather conditions, wolves with functioning collars, other competing research and monitoring objectives, and logistical support.

Survey effort during 2012-2019 was variable from year to year but certainly much lower than survey effort from 2020 to 2022. A typical annual survey effort during 2012-2018 consisted of flying several times a winter (ranging from <1 survey per week to <1 survey per month depending on the year) in an attempt to observe wolf packs that had a radio-collared pack member. In addition, 24-30 remote cameras were placed in and around Voyageurs National Park on snowmobile trails or other linear features that wolves were thought to frequent during the winter. When fresh tracks were encountered during winter fieldwork or during aerial surveys, the number of wolves traveling together were recorded when discernable. In other words, winter track counts were opportunistic and not systematic.

In 2020-2022, we increased survey effort to provide a more robust estimate of pack size and to survey more wolf packs. Specifically, we strategically deployed between 100-200 remote cameras in wolf pack territories to get repeated video observations of wolf packs during winter. Importantly, we ceased using aerial surveys or any opportunistic track counts to estimate pack size. However, we did take into account any opportunistic observations of wolf packs. We primarily used Browning Spec Ops cameras (models included the Advantage, Edge, and Elite HP4) and programmed cameras to take 20 second videos with a 1 second delay between videos.

We estimated pack size during our winter monitoring period which we defined as December 1 to April 11. We considered the end of the winter monitoring period as April 11 because that is average parturition date for wolves in the GVE and when we would generally expect packs to stop traveling as a cohesive social group. Our objective was to get repeated independent observations of the same pack at the same size during the monitoring period. We considered observations to be independent if they were on a different day than any other observations of that pack. Multiple independent observations of the same size for each pack provides highly-reliable and accurate pack size estimates. Generally, we considered >3 independent observations of the same size to be a reliable pack count (Fig. 1).

Estimating Home Ranges

To estimate home ranges, we caught wolves via rubber-padded foothold traps and fit them with GPS-collars. All capture and handling of wolves was approved by the National Park Service's and University of Minnesota's Institutional Animal Care and Use Committee (protocols: MWR_VOYA_WINDELS_WOLF and UMN 1905-37051A).

We primarily estimated home range size for wolf packs using GPS-collar data from May 1 to October 31. Wolf pack home ranges in the GVE appear more stable in summer (the ice-free period) than they are in winter. During winter, wolf home ranges in the GVE are prone to small shifts and changes and are less stable than they are in the summer, likely because wolf movements change based on where deer congregate and on intraspecific pressures from neighboring packs. Wolf home ranges appear to stabilize during spring to fall because deer are likely more dispersed across their territory and intraspecific competition is lowest during the summer (Mech and Barber-Meyer 2017).

Furthermore, most wolves studied during summer are fitted with GPS-collars that take locations every 20 minutes during the summer period before the collars switch to taking 6 hour locations. Wolves fitted with collars that take 20-min fixes yield high-resolution GPS-collar data on wolf movements during summer, which is ideal for estimating home ranges and certainly superior to using longer fix-interval GPS data from the winter. That said, GPS-location data was limited for some wolves during summer for a variety of reasons including fall capture dates and collars with sustained low fix rates (12 or 24 hr). In these scenarios, we estimated home ranges using winter locations or a combination of summer and winter locations. We did not estimate home ranges for wolves that were fitted with VHF collars in 2012-2014 because location data were sparse and not comparable to the GPS-collar data we had from other wolves in subsequent years (2014-2022). As a result, we only present data on home range size from 2014 to 2022.

We used locations from GPS-collared wolves to estimate kernel home ranges for each pack (Fig. 7). More specifically, we used 99% kernel home ranges for wolves with 20-min-fix-interval GPS-collars and then 95% kernel home ranges for wolves with GPS-collars that had longer fix intervals (most others had 4, 6, or 12 hr-fix-interval collars). We calculated home ranges differently because the data from wolves with 20-min-fix-intervals had substantially higher resolution than collars with longer fix intervals. Thus, the periphery of territories was much clearer because of the amount of GPS-location data (~2,180 locations/month). As a result, kernel density home ranges fit the location data exceptionally well and a 99% kernel home range was more representative of than a 95% home range. With longer fix-intervals, however, there was more uncertainty due to substantially fewer GPS-locations and we decided a 95% kernel home range was more appropriate. We removed locations associated with extra-territorial forays prior to developing kernel density home ranges (Burch et al. 2005, Powell and Mitchell 2012, Mancinelli and Ciucci 2018).

We removed the area of kernel home ranges that overlapped the 4 large lakes—Kabetogama, Rainy, Namakan, and Sand Point— in the Greater Voyageurs Ecosystem (Fig. 7). Wolves do not use the large lakes as part of their home range during the ice-free periods (~April to November) and rarely, if ever, swim out to the islands in these large lakes. Thus, these lakes are hard territorial boundaries for most of these packs for the majority of the year (~April to November). Even when ice forms, wolves spend relatively little time out on the ice with most activity on the ice near the shorelines of these major lakes or on the small islands close to the mainland. As such, removing any territory overlap with these major lakes seems more logical than including territory that overlaps the lakes. Notably, we did not remove the area of smaller lakes that were entirely contained within pack territories.

Quantifying Home Range Overlap

Although wolves are highly territorial, wolf pack home ranges frequently overlap to some extent (Fig 7). When using metrics such as mean pack and home range size to estimate density, quantifying home range overlap is necessary to avoid underestimating density (Erb et al. 2020). However, for most wolf pack home ranges, we only had partial knowledge of neighboring packs (i.e., we did not have current home range data for each pack every year) so we devised an approach that allowed us to account for overlap when estimating density without having perfect knowledge of all home range overlap in our study area.

Our approach consisted of calculating the average spatial overlap of one home range on another using all available home range data for a given year (we refer to this metric as 'pack-on-pack overlap' hereafter). We then estimated the number of neighbors that known wolf pack home ranges likely had using a combination of known and historical wolf pack territory locations. We then multiplied pack-on-pack overlap by the average number of neighboring packs to yield the average home range area that a typical wolf pack overlaps with other wolf packs. To incorporate this into density estimates, we divided the spatial overlap by two (i.e., because two packs shared the area of overlap) and subtracted the result from the average home range size (see equation below). In a few instances, 3 pack home ranges overlapped but the area of the overlap was minor (<1-2 km²) so we were not concerned about incorporating this into our estimates as it would have little-to-no effect (Fig. 7).

Calculating Density

We calculated wolf density (wolves/1000 km²) using data on pack size, home range size, and pack-on-pack overlap. Specifically, we used the following equation:

$$Density = \frac{PS \div \left(HR - \left(\frac{Ovlp * Nb}{2}\right)\right)}{0.85} * 1000$$

where PS is mean pack size, HR is mean home range size, Ovlp is mean pack-on-pack overlap, and Nb is the mean estimated number of neighboring packs that a typical wolf pack has. We assumed that lone wolves constituted 15% of the population and thus divided the density of pack wolves (which is calculated via the numerator in the equation above) by 0.85 to yield overall wolf density (Erb and Humpal 2020).

We used a non-parametric bootstrapping approach to obtain 95% confidence intervals for our density estimates (Fieberg et al. 2020). To do this, we generated 1,000 plausible values, given the data collected, for each parameter (HR, PS, Ovlp, Nb) by doing 1,000 bootstrapping iterations (i.e., resampling with replacement). We calculated density using the values generated during each bootstrap iteration to yield 1,000 plausible density estimates. We then selected the 2.5% and 97.5% highest density values for our 95% confidence interval (Gable et al. 2020). We used simple linear regression to assess whether there was any trend or change in annual pack size, home range size, or density with time during 2012-2022.

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Report designed by Dani Freund

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Austin Homkes and Lucas Beck inserting a microchip into the pup's scruff to track it


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