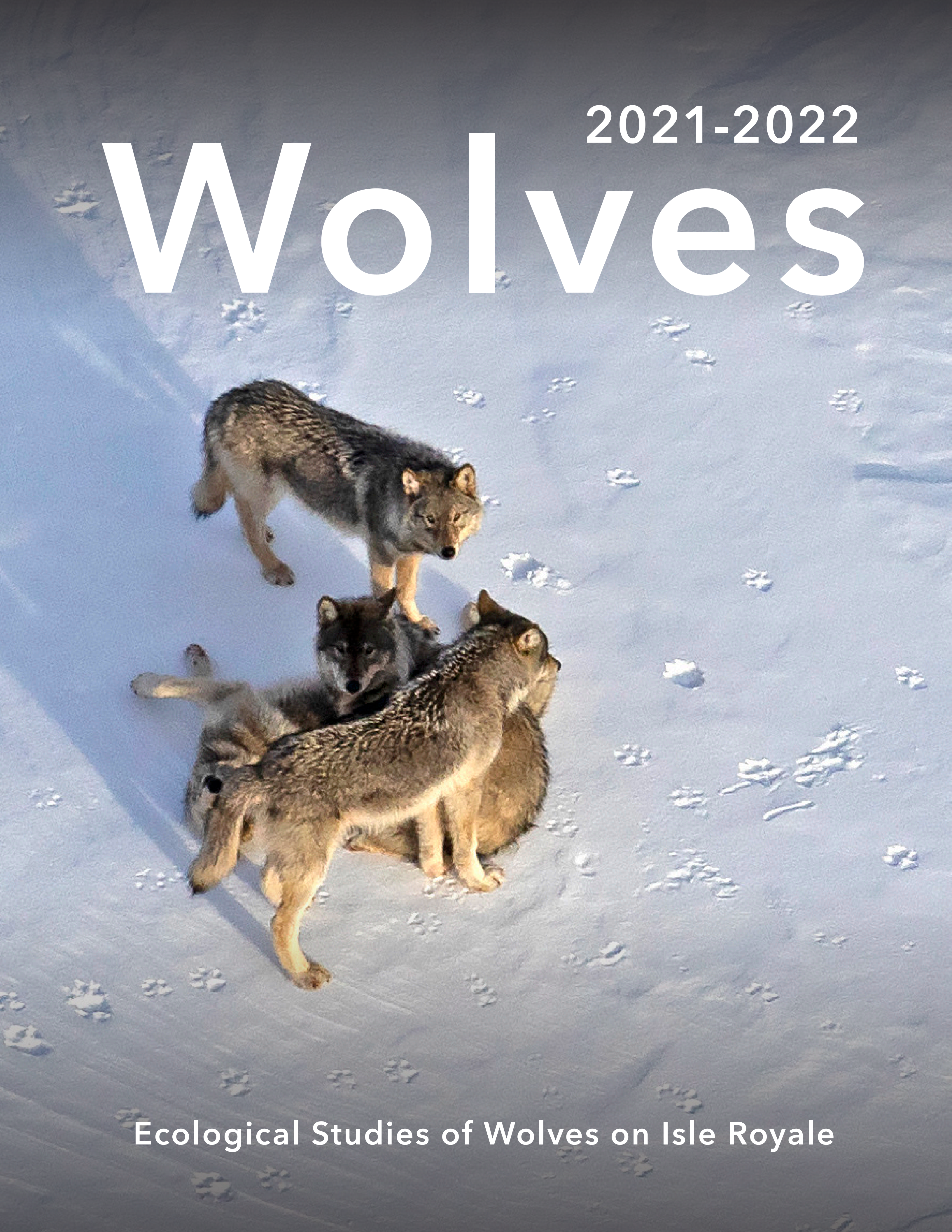
2021-2022

Wolves



Ecological Studies of Wolves on Isle Royale

> These magnificent animals [wolves] serve important roles in our Great Lakes ecosystems, and they show us that dedication to family is not unique to humans.

Dana Nessel, Michigan Attorney General

Ecological Studies of Wolves on Isle Royale

Annual Report 2021-2022

by

Sarah R. Hoy, Rolf O. Peterson, and **John A. Vucetich**
College of Forest Resources and Environmental Science,
Michigan Technological University,
Houghton, Michigan USA 49931-1295

April 2022

Front cover photograph: Two pups from the eastern pack try to rouse packmates for play.

Support and Contributions

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Ken Vrana of the Isle Royale Institute has been of critical value for helping organize our Moosewatch research expeditions. We gratefully acknowledge the contributions, personal time, and financial assistance of the volunteer members of our Moosewatch expeditions:

Team IA–Michael George (leader), Seth Shannon, Tyler Shannon, Peter Wegner, Adrienne Detanico, and Annette Matzen
Team IB–Lynn Anne Vesper (leader), Erik Freeman, Bob Bollinger, Leta Landucci, and Alex Vaeth
Team IC–Clay Ecklund (leader), John Warming, Marshall Weimer, Lada Zednik, and Hal Hanson
Team ID–Wayne Shannon (leader), Ron Eckoff, Larry Fuerst, Mike LaMotte, and Ron Porritt

Team IIA–Lynn Anne Vesper (leader), Patrick Huver, Erik Freeman, and Velda Hammerbacher
Team IIB–Marcy Erickson (leader), Lauren Ross, Emily Betyl, Jason Rehfeldt, and Dennis Zielinski
Team IIC–Loreen Niewenhuis (leader), Joceline Pasaylo, Julie Ann Timmer, Zan Ceely, and April Willbur
Team IID–Chris Woeltje (leader), Jim Clink, Steve Leatherman, Lucas Baldesberger, and Janiene Licciardi

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Team IIIB–David Conrad (leader), Mel Tracy, Megan Horodko, Susan Ritter, and Frank Tester
Team IIIC–Lynn Anne Vesper (leader), Becky Martin, Alec Martin, Inaki Abella-Gutierrez, and Hal Evensen

Team IVA–Karen Bacula (leader), Josette Lory, Cathy Pumford, Joe Hemming, and John Stryker
Team IVB–Erin Parker (leader), Erik Freeman, David Rolfes, and Antonette St. Pierre
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To learn more about how you can join one of our research expeditions, visit **isleroyalewolf.org** and click "Contribute & Participate." Tax-deductible donations to support continuing research on Isle Royale wolves and moose can be sent to Wolf-Moose Study, Michigan Tech Fund, Michigan Technological University, 1400 Townsend Drive, Houghton, Michigan 49931-1295. Thank you to all who help!

Results reported here are preliminary and, in some cases, represent findings of collaborators; please do not cite without consulting the authors. Specifically, genetic analysis of wolf DNA was conducted by collaborators Dr. Kristin Brzeski and Samuel Hervey (MTU), who are funded by the U.S. National Park Service and also working in partnership with researchers at other institutions. For any questions about genetic analyses, please contact the principal investigator on this project, Brzeski, at kbrzeski@mtu.edu. The views expressed here do not necessarily reflect those of the U.S. National Park Service or the U.S. National Science Foundation.

Ecological Studies of Wolves on Isle Royale

SUMMARY OF FIELD OPERATIONS

Over the past year, fieldwork resumed at pre-pandemic levels. In February 2022, the wolf population was likely comprised of 28 wolves. This is an increase from the next most recent estimate of 12-14 wolves, made 24 months earlier in March 2020 (Fig. 1). The wolf population appears to be primarily organized as two main social groups—an eastern pack consisting of at least 13 wolves and a western pack most likely consisting of 13 wolves—and two wolves that may not be part of either pack. There is evidence that pups were born to both packs in April 2021. For context, there is also evidence that one litter of pups was born in 2019 and two litters were born in 2020. Wolves appear to be an important cause of mortality for moose once again. In particular, this past year, the proportion of the moose population killed by wolves (i.e., the predation rate) was 8.7 percent. That rate is almost twice as high as the predation rate observed in 2020 (4.5 percent) and it is the highest predation rate observed since 2011. Overall, the new population of wolves on Isle Royale appear to be well-established and functioning healthily. Over the past year, the U.S. National Park Service (NPS) continued its efforts to outfit a small proportion of the wolf population with GPS radio collars to help monitor the recovering population.

The estimated abundance of moose declined by 28 percent, from 1,876 to 1,346, between February 2020 and February 2022. Longer-term population trends suggest that the moose population had increased greatly over an eight-year period (2011-2019) but then started to decline over the last few years. The decline in moose abundance is likely a consequence of several factors, including higher predation rates by wolves, severe burdens of parasites (winter ticks), and a shortage of winter forage, indicated in part by an unusually high number of moose dying from malnutrition over the past two years. That shortage of winter forage, specifically balsam fir, is likely due to a combination of intense browsing by moose in previous years and recent defoliation due to budworm (moth larvae) in some regions of the park. In February 2022, 19 moose were outfitted with GPS collars so their movements and behavior can be monitored, adding to the 45 moose radio-collared between 2019 and 2020.

For more information, visit isleroyalewolf.org and "Wolves and Moose of Isle Royale" on Facebook and Instagram.

PERSONNEL AND LOGISTICS

In April 2021, Sarah Hoy, Rolf Peterson, and John Vucetich assisted the NPS with efforts to outfit wolves with GPS collars. Sarah Hoy, Rolf Peterson, and pilot Don L. Murray (UpNorth Aerials, Two Harbors, Minnesota) assisted the NPS with efforts to outfit wolves with GPS collars in February 2022.

In summer 2021, we conducted ground-based fieldwork from early May through mid-October. Rolf Peterson, John Vucetich, and Sarah Hoy directed that fieldwork with assistance from Carolyn Peterson and Leah Vucetich. Fieldwork pertaining to moose-balsam fir interactions was conducted in summer by graduate student Olivia Bailey and undergraduate students Neveah Pifer, Jacklyn Lenten, Vincent Dockery, Benjamin Miller, and Grace Erba. Additional summer fieldwork was carried out by Isabella Evavold, Dick Murray, and Erik Freeman. Don Murray flew a fixed-wing aircraft to download data from GPS collars on moose in May and July. That effort was aided by Jill Podominick Murray. Don Murray and Rolf Peterson conducted an aerial survey to estimate the number of active beaver sites in October 2021.

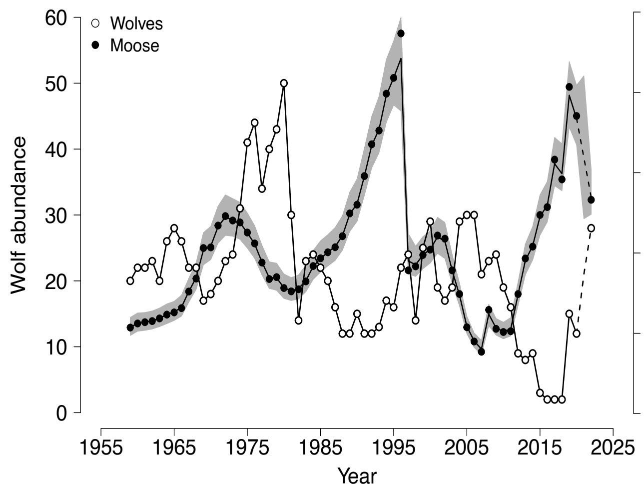


Fig. 1 *Fluctuations in the abundance of wolves and moose in Isle Royale National Park, 1959-2022. Wolf population estimates (open circles) and moose population estimates (filled circles) were based on aerial surveys during winter (January-March). Additional estimates of moose abundance (solid line) and confidence intervals (gray shaded area) were derived from a Gompertz state-space model that emphasizes population processes associated with density dependence and sampling error (Hoy et al. in press, Functional Ecology). Note that estimates of wolf and moose abundance are not available for last year, March 2021, as winter fieldwork could not take place due to the COVID-19 pandemic. Those missing data are the reason why a dashed line connects the most recent estimates of wolf and moose abundance (2022) with the previous estimate (2020). The sudden increase in wolf abundance between 2018 and 2019 is the result of wolves being translocated to the island from populations in Michigan, Minnesota, and Ontario, Canada, as part of NPS efforts to reestablish a healthy wolf population.*

During the summer field season, many park staff, other researchers, and visitors (especially Jay and Terry Brasher) contributed key observations and reports of wolf signs and moose bones. Several dozen Moosewatch volunteers participated in weeklong cross-country treks, searching for moose bones. Elizabeth Valencia (NPS) also provided valuable administrative support over the past year.

Lab work included updating the curation of wolf and moose bone collections working in partnership with Martin Hobmeier and Brian Hoduski from the NPS. Lab work was led by Leah Vucetich, Grace Parikh, and John "Moose" Henderson with the assistance of Allie Johnson, Erik Freeman, Tom Offer-Westort, Nathan Coleman, Carly Zielinski, Otti Brueshaber, Molly Powers, Sarah Arnold, J.T. Boudreau, Haleigh Bonk, Adam Awanda, Zoie Schafer, Michael Yuchasz, Sage Haney, and Chance Spencer.

The annual winter study was conducted during 25 January to 6 March 2022. Winter fieldwork was led by Rolf Peterson and Sarah Hoy, with key contributions provided by Don Murray. Ky and Lisa Koitzsch, Isabella Evavold, and Brenna Cassidy provided daily fieldwork on skis to collect data on moose and balsam fir. NPS employees Mark Romanski, Anthony Richno, Lynette Potvin, and Jacob Bonessi provided important logistical assistance throughout the winter study.

An effort to outfit moose with GPS collars took place between 23 and 27 February, headed by Sarah Hoy, Mark Romanski (NPS), and Seth Moore (Grand Portage Band of Lake Superior Chippewa). This effort was greatly aided by Rolf Peterson, Don Murray, wildlife veterinarians Jenny Powers and Michelle Verrant (NPS), Scott Ratchford (Colorado State University and NPS), Samuel Hervey (MTU), and pilot Harry Hensberg, Roy Hensberg, and Gary Tracy (Helicopter Wildlife Services [Heliwild]).

Fig. 2 *A large group of wolves were seen feeding on a moose on the ice near Daisy Farm at the east end of the Isle Royale National Park on 7 February. After that large group of wolves had left the area, Ky and Lisa Koitzsch visited the kill site to determine the age and sex of the dead moose and to collect scat samples from wolves for genetic analysis. Photo credit: Ky and Lisa Koitzsch.*

Fig. 3 *The wolf on the left, facing away from the camera, is 19M. The wolf on the right, facing the camera, is a recently collared young female wolf thought to have been born on Isle Royale. These two wolves were observed to be traveling together during the breeding season (late February and early March) at the east end of the island.*

THE WOLF POPULATION

Population Size and Social Organization

By early March 2022, the wolf population was likely comprised of 28 wolves, which is approximately double the number of wolves estimated to be on the island two years ago, when the last survey of wolf abundance took place (Fig. 1).

The population was primarily organized into two packs—one living at each end of the island. Each pack was composed of core members and other members that spent time away from the core group. The eastern pack is comprised of at least 13 wolves (including 12M). That estimate of 13 wolves is based on observations of a large group of wolves seen feeding on a moose carcass near Daisy Farm by Ky and Lisa Koitzsch on the afternoon of 7 February (Fig. 2). Specifically, close scrutiny of images and video of that large group of wolves revealed that nine wolves were non-collared. Four wolves with GPS collars were also known to have visited the kill site. That large group of wolves was also observed to still be at the kill site early in the morning on 8 February.

In addition to the 13 wolves of the eastern pack, we observed evidence that two other wolves spent time within the eastern pack's territory during February. The first of these wolves is 19M, a collared male wolf translocated from upper Michigan to Isle Royale in September 2019. During aerial survey flights, we observed 19M on several occasions during late February and early March within the territory of the eastern pack, but he tended to associate with just one other wolf (a young female) during the breeding season and not with the rest of the eastern pack (Fig. 3). The second of these wolves is non-collared and was observed to be traveling alone on the morning of 8 February. This non-collared wolf was observed cautiously approaching the Daisy Farm kill site a few hours after the large group of wolves had left the area. This wolf's behavior and caution strongly suggest it was not a secure member of the eastern pack. Together, those observations suggest that at least 13 wolves were in the eastern pack and most likely 15 wolves were present at the east end in early February.

The western pack is likely comprised of 13 wolves (including 7M). That estimate is based on three observations from the morning of 2 February:

- fresh tracks of at least seven wolves traveling near Lake Desor;
- fresh tracks of at least two wolves at a kill site near Houghton Point; and
- the beds and fresh tracks of what appear to have been at least four wolves at a site near Senter Point, where two moose had been killed.

Although we did not directly observe wolves at these three locations, it is unlikely that the tracks observed at Lake Desor, Houghton Point, and Senter Point were made by the same wolves because the tracks were fresh (made after snowfall and 50-knot winds on the evening of 1 February), and we followed each set of tracks and found that they were not interconnected. It is also unlikely that these tracks were left by wolves from the eastern pack, because we also observed fresh tracks from a large number of wolves in the eastern pack's territory on 2 February. We also directly observed large groups of wolves in the eastern pack's territory a few days shortly before and after 2 February.

Taking those considerations into account, the best estimate of wolf abundance on Isle Royale in February 2022 is 28 wolves, which includes 13 wolves in the western pack, 13 wolves in the eastern pack, plus an additional two wolves in the eastern region which were not thought to be associated with the eastern pack. However, if the non-collared wolf seen behaving cautiously by the Daisy Farm kill on 8 February was one of the wolves that left fresh tracks at the west end during the count on 2 February, then it would reduce the wolf abundance estimate to 27 wolves. Alternatively, it is also possible that the estimate of 28 wolves is a slight underestimate given that the counts of wolves from beds and tracks seen in three locations at west end locations on 2 February were all minimum counts. Additionally, on several occasions we observed wolves that were traveling alone—which may or may not have been among the 28 wolves that we accounted for. In the near future, more insight about this estimate of wolf abundance will be gained through genetic analysis conducted by Brzeski and Hervey (MTU) of DNA extracted from fecal samples collected this past winter.

GPS-Collared Wolves

Over the past year, researchers at MTU assisted the NPS with their efforts to outfit wolves with GPS collars. In spring 2021, five wolves were captured and outfitted with GPS collars, one of which was a male wolf (12M) translocated from Michipicoten Island, Ontario, to Isle Royale in early March 2019. 12M was captured in the same location (eastern region) as three other wolves: one female and two male wolves, which were all born on Isle Royale in April 2020. Genetic analysis performed by Brzeski and Hervey (MTU) confirmed that the two young males and female were the offspring of 12M and 15F, the socially bonded pair that held a territory at the east end during the 2020 winter field season. Note that any offspring of 12M and 15F are inbred, as 12M and 15F are brother and sister (Hervey et al. 2021, Conservation Genetics, 22: 913-296). A fifth wolf, a young male born on Isle Royale in April 2020, was outfitted with a GPS collar in the western region. Genetic analysis confirmed that this individual was the offspring of 1F, a female translocated from northern Minnesota in October 2018, and 7M, a male translocated from Michipicoten Island in March 2019. During the 2020 winter field season, we observed that 1F and 7M were a socially bonded pair that held a territory at the west end. Note that 7M is the full sibling of both 12M and 15F (Hervey et al. 2021, Conservation Genetics, 22: 913-296); as such, the young wolf collared in the western region is the cousin of the three young wolves collared in the eastern region.

In winter 2022, another small group of wolves were captured and outfitted with new GPS collars—some of those wolves had previously worn collars (Fig. 4).

Wolf Reproduction

Five litters of pups are thought to have been born on Isle Royale since wolves were translocated to the island (a time period that spans three breeding seasons).

- In April 2019, one litter was born at the west end of Isle Royale. Specifically, at least two pups are thought to have been born to 14F, a female wolf translocated from Michipicoten Island in March 2019. Those pups were most likely conceived on Michipicoten and survived until at least nine months of age (see front


Fig. 4. *The left panel shows a male wolf who was outfitted with a new GPS collar this past winter. The right panel shows the same wolf bedded down in the snow near Lake Desor two years earlier, on 6 March 2020. At that time, this male was observed to be living alone at the west end of Isle Royale.*

cover of last year's annual report). For further details, see annual reports published by MTU (Hoy et al. 2020) and NPS (Romanski et al. 2020).

- In April 2020, at least two litters were born. Field observations and genetic analysis suggests that one of these litters was born to 12M and 15F, which were known to hold a territory at the east end in 2019-2020, and the other litter was born to 7M and 1F, which were known to hold a territory at the west end in 2019-2020. Importantly, pups born to the eastern pack are inbred, as 12M and 15F are siblings. Furthermore, all the wolves born on Isle Royale since 2019 have at least one parent from the Michipicoten family group. Most notably, 14F is either the mother or grandmother of all wolves born on Isle Royale because 7M, 12M, and 15F are all the offspring of 14F (Hervey et al. 2021).
- In April 2021, a litter was likely born to each of the island's two packs. Evidence for the litter born to the western pack includes images of a wolf pup captured by a park visitor at a beach on the west end of Isle Royale in June. Evidence for the litter born to the eastern pack includes tracks and scats of pups found at two locations (near Lake Richie and Conglomerate Bay) at the eastern end of Isle Royale in July and August. Additionally, this past winter, Ky and Lisa Koitzsch also observed and took images of at least one non-collared nine-month-old pup in the territory of the eastern pack (Fig. 5).

Fig. 5 *A wolf that appeared to be a nine-month-old pup was observed to be traveling and playing with two larger wolves on the ice by Daisy Farm on 8 February 2022. Photo credit: Ky and Lisa Koitzsch.*

During the 2022 winter study, we did not document any of the known breeding females (14F, 1F, or 15F), but we did observe the two males that bred in previous years: 12M (east end) and 7M (west end). At the west end of the island, we observed courtship behavior (genital sniffing) between 7M and a non-collared female on 25 February 2022, and tracks indicated that they probably copulated on 28 February. At the east end of the island, we observed courtship behavior between a male wolf who was collared in April 2021 and a non-collared female. We also observed 19M exhibiting courtship behavior with a young female who was collared in February 2022 (see Fig. 3). We did not observe 12M exhibiting courtship behavior with any female wolves. These observations suggest that litters of wolf pups may be born at both the east and west ends of the island in April 2022.

Wolf Survival

During winter 2022, we did not observe any wolves whose appearance was consistent with F193, who had been the last surviving wolf of the previous Isle Royale wolf population prior to the translocation of wolves in 2018. We assume that F193 is most likely dead, in part because she would have turned 11 years old in May 2021, which is exceptionally old for a wild wolf.

In May 2021, wolf skeletal remains were found at several sites (located within 200 m of each other) near McGinty Cove at the western end of Isle Royale. The remains appeared to be from two wolves that died six to eight weeks before they were found. One of the dead wolves is likely to be 11F (based on an ear-tag found nearby), who was a female wolf translocated from Michipicoten Island to Isle Royale in March 2019. During February and March 2020, 11F was observed traveling and exhibiting courtship behavior with 16M, a male wolf translocated from Wawa, mainland Ontario. This socially bonded pair is noteworthy because 11F was a grey wolf and 16M was an unrelated black wolf (see Fig. 5 in annual report for 2019-2020). Moreover, this pair regularly swam out to smaller islands off Isle Royale's southwestern shore during the winter of 2020 (for details, see annual report for 2019-2020). Examination of the teeth of the unidentified dead wolf suggest it was an adult aged approximately two to five years old. Therefore, the unidentified wolf is unlikely to be one of the pups born on Isle Royale in 2020, nor is it likely to be F193, 14F, or 9M, as those wolves would all be older than seven years. Genetic analysis of tissue samples collected from the dead wolf will be conducted by Brzeski and Hervey (MTU) to confirm the identity of this wolf.

Of the 19 wolves that were translocated to Isle Royale between October 2018 and September 2019, one wolf left the island across an ice bridge (3F), three wolves were known to be alive as of March 2022 (7M, 12M, 19M),

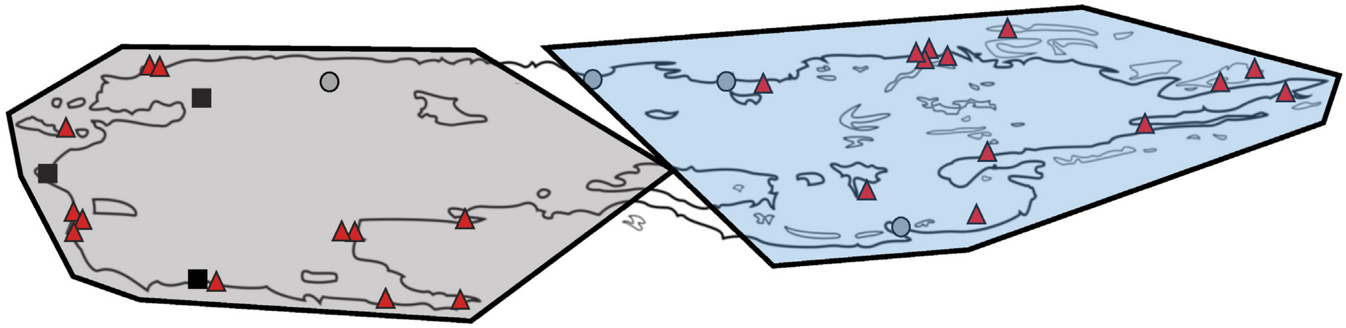


Fig. 6 *Minimum convex polygons representing territories of the western pack (grey polygon) and eastern pack (blue polygon) based on observations of wolves and wolf tracks during winter study (25 January to 3 March). Points indicate locations where we detected dead moose. The 25 red triangles are locations of moose killed by wolves during winter study. The three black squares indicate the carcasses of moose that died of causes other than wolf predation during winter study. The four grey circles represent moose that died shortly before the start of winter study.*

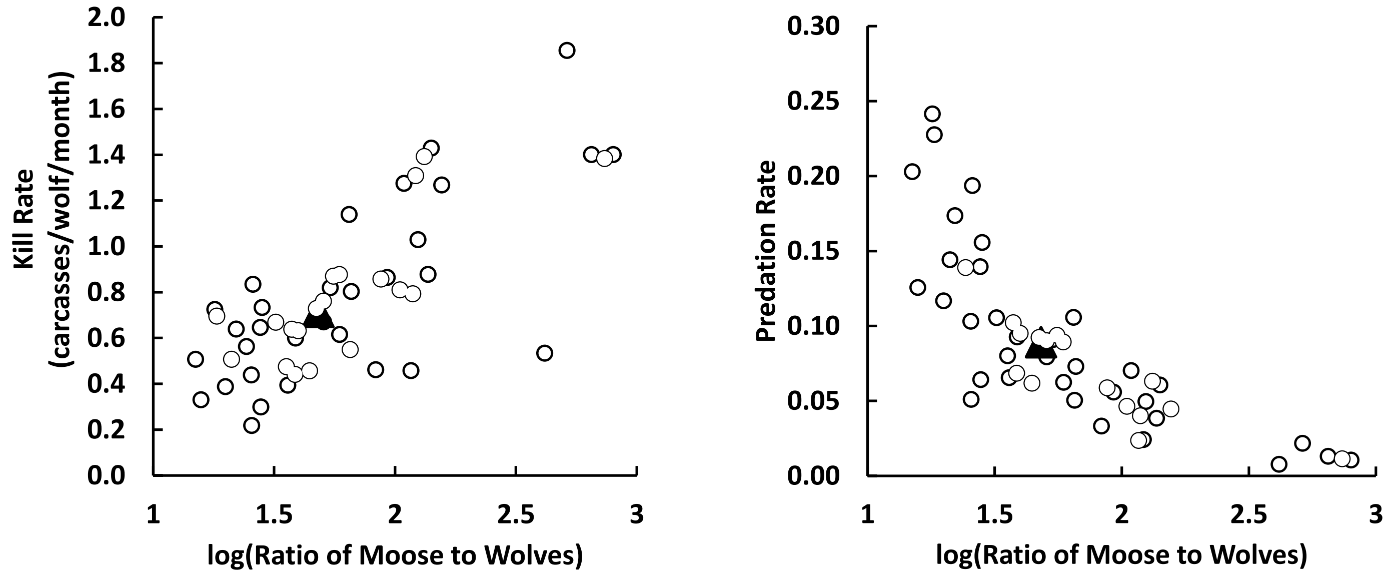


Fig. 7 *The ratio of wolves to moose in relationship to the rate at which wolves acquired prey on a per-capita basis (i.e., kill rate, left panel) and the proportion of the moose population killed by wolves (i.e., predation rate, right panel) for the period, 1971-2022. The black triangle indicates the observation for 2022.*

nine are known to have died (4F, 5F, 11F, 18F, 20F, 8M, 6M, 10M, and one as-yet-unidentified wolf), and the fate of the remaining seven translocated wolves is unknown (1F, 14F, 15F, 9M, 13M, 17M, 16M). Note that the wolf assigned the translocation ID number 2F is not included in the aforementioned account because that wolf died on the mainland before it could be released into the Isle Royale population.

Carcass Utilization Rates

The per-capita rate of prey acquisition (sometimes equated with the per-capita kill rate) is a statistic that describes the rate at which a predator acquires food. That statistic is calculated as the number of carcasses from which the wolves fed, divided by the number of wolves, divided by the number of days over which the carcasses were acquired. This winter, we discovered the remains of 25 moose which appeared to have been killed by wolves during a 38-day period (25 January to 3 March, Fig. 6). We also found the remains of another four moose that may have been killed by wolves before the start of winter study and three other moose that died from causes other than wolf predation. All of these sites will be examined during summer fieldwork to gain additional insights.

Those observations indicate that this year's rate of prey acquisition is 0.71 moose per wolf per month (assuming 25 moose fed on by 28 wolves over 38 days). That kill rate is similar to the long-term average per-capita kill rate of 0.7 (±0.04 SE) observed between 1971 and 2011 (the period prior to the wolf population's recent collapse). That kill rate is also consistent with expectations based on the ratio of moose to wolves on Isle Royale (Fig. 7, left panel). For context, the rate of prey acquisition in 2020 was estimated to be 1.27 moose per wolf per month (see the 2019-2020 annual report for details). The higher kill rate observed in 2020 is most likely because wolves lived in small groups in 2020, which tend to lose a larger portion of their kills to scavengers and therefore kill at higher per-capita rates than wolves in larger groups (Vucetich et al. 2004, Animal Behaviour, 67: 1117).

THE MOOSE POPULATION

The 2022 moose census (conducted during 30 January to 23 February) resulted in an estimated abundance of 1,346 moose (Fig. 1). The 80 percent confidence intervals on this estimate are [1,056, 1,654], and the 90 percent confidence intervals are [925, 1,842]. Moose density was lowest in the western portion of Isle Royale (1.46 moose/km^2), slightly higher in the middle of the island (2.25 moose/km^2), and notably higher at the far east end of the island (4.51 moose/km^2, Fig. 7). This is the first time in five decades that the density of moose in the middle of the island is higher than in the western region.

The estimate of 1,346 moose is based on a sightability correction factor of 52 percent. In recent years, we have estimated sightability during the survey on the basis of trials with collared moose (Fig. 9), which involved recording the frequency that collared moose were detected on census plots. In 2022, we were able to conduct only one trial due to collared moose not being on census plots during surveys and limited flight time (which was constrained by poor weather). While a single trial represents an inadequate basis for estimating sightability, other considerations allow for a more useful estimate. Specifically, interannual variability in sightability is importantly influenced by the effect of snow conditions on the habitat selection of moose. For example, when snow is deep and difficult to travel through, moose tend to exhibit stronger preference for being in thick conifer cover where snow tends to be less deep, but where moose are more difficult to detect from aircraft. Snow conditions have been similar during the past three surveys (2022, 2020, and 2019), and we had been able to conduct considerably more sightability trials in 2019 and 2020. Specifically, in 2019, we detected 26 moose in 53 trials. In 2020, we detected 11 moose in 19 trials. In 2022, we detected one moose in one trial. Collectively, the trials from all three years lead to an estimated sightability of 52 percent (=38/73).

To provide context, it can be useful to know what the estimated abundance of moose would have been if the sightability trials led to a different estimate of sightability (e.g., 10 percent lower or higher than 52 percent). Specifically, a sightability of 42 percent would have yielded an estimate of 1,660 moose, and a sightability of 62 percent would have yielded an estimate of 1,132 moose. Importantly, the 80 percent confidence intervals for abundance under the assumption of 52 percent sightability (i.e., [1,056, 1,654]) includes (or nearly includes) the point

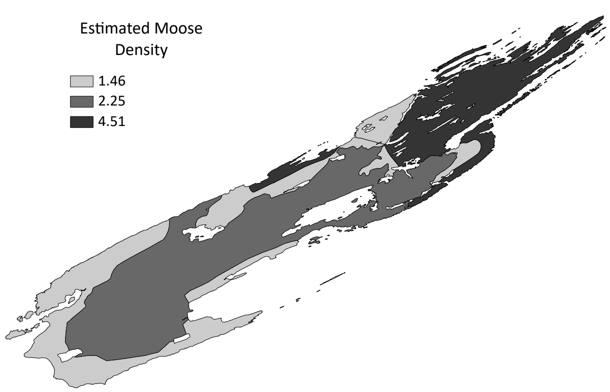


Fig. 8 *The density of moose on Isle Royale during winter 2022 was lower in the western portion of Isle Royale and highest in the eastern portion of Isle Royale (dark grey shaded). Estimates are based on aerial surveys of 91 plots that comprised 17 percent of the main island area. This map was produced by Emma Jones (MTU).*

Fig. 9 *A cow moose that was outfitted with a GPS collar near Beaver Island at the west end of Isle Royale in February 2022. The collars record the animal's location every 30 minutes. We can use that location data to determine whether collared moose were located on any of the moose census plots at the same time that we were conducting the aerial surveys. During aerial surveys, we record whether any moose observed on census plots are wearing collars. We then use this data to determine the rate at which we are successful at detecting collared moose and generate an estimate of sightability.*

estimates of abundance for sightabilities of 42 percent and 62 percent.

This estimated abundance of moose will be refined in future years when the population's demography can be statistically "reconstructed" using data collected by examining dead moose. More precisely, when we locate the remains of a moose that died within the last year or two, we can determine how old that individual was (by counting cementum lines in its teeth). Once we know both when an individual died and how old it was, we can determine the year that the individual was born and which years it was alive in the population. For example, if we find the remains of a four-year-old moose that died in 2020, then we know that individual was born in 2016 and must have also been alive in the population in 2019, 2018, and 2017. When this information can be obtained for a sufficiently large number of dead moose, it is possible to use reconstruction analysis to estimate the number of moose that were alive in the population (Hoy et al. 2020, Functional Ecology, 34: 203-216). However, reconstruction-based estimates of abundance for a particular year (say 2022) cannot be calculated until most of the moose living during that year have died. In the meantime, the best available point estimate of moose abundance for 2022 is 1,346.

This winter's estimated abundance of 1,346 moose is 28 percent lower than the estimated abundance for winter 2020 (1,876 moose), which is the last time that moose abundance was estimated. That two-year rate of decline is equivalent to the population having declined by

15.3 percent in each of the past two years. Taking account of statistical uncertainties, it is reasonable to infer that the moose population grew rapidly for a number of years (2010-2019) and started to decline in recent years (Fig. 1).

In general, populations decline due to one or both of the following reasons: (i) a reduction in the rate at which calves are born and survive to adulthood (i.e., recruitment rate); and (ii) a reduction in the rate at which adult moose survive from one year to the next (i.e., adult survival rate). When a moose population declines as much as we have observed, it is commonly the case that both recruitment and adult survival rates have declined. Next, we review evidence suggesting that declines in both rates have occurred over the past year due to a combination of higher predation rates by wolves, a shortage of food in winter—specifically balsam fir—and severe burdens of a parasite—winter ticks (*Dermacentor albipictus*).

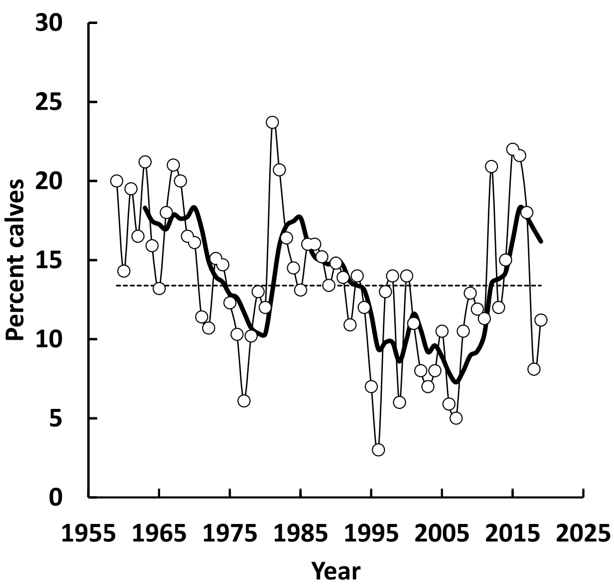


Fig. 10 *Long-term trends (1959-2022) in the percentage of the moose population that are nine-month-old calves. The 50-year average (13.4 percent) is marked by the dashed line, and the thicker line represents the five-year moving average.*

A useful indicator of recruitment rates is the percentage of moose seen on survey plots that were calves, as calves surviving to nine months of age are likely to be recruited into the population. In 2022, calves represented only 4 percent of the 135 moose counted on survey plots. Using general methods for calculating confidence intervals for proportions, the 90 percent confidence intervals for that observation are 1.4 percent and 7.6 percent. For context, this winter's estimate of 4 percent is well below the long-term average recruitment rate of 13 percent observed for this study system (Fig. 10). Recruitment rates were also below average in 2019 and 2020, which is consistent with the moose population having started to decline in recent years. Lastly, in years when recruitment rates are high we tend to observe more cows raising twins, but this winter only one cow was observed to be raising twins.

A useful indicator of adult survival rate for a given year is the number of moose that are known to have died from causes such as wolf predation or malnutrition. Each summer and winter we search for the remains of dead moose, and this past year (summer 2021 and winter 2022) we found the remains of 69 moose that died within the last year. Of those 69 moose, 41 moose were killed by wolves, 21 appeared to have died from malnutrition, two died due to accidents (falls into old mine pits), and another five died of unknown causes. While 30 percent of moose died from malnutrition in this recent sample, in a typical year less than 5 percent of moose that we discover die from malnutrition. The unusually high number of moose that starved to death in 2021-2022 suggest that a shortage of food has importantly impacted adult survival over the past year. The inference that moose are experiencing a food shortage is supported by observations that the growth of balsam fir saplings, the main winter food source for moose, was especially poor last year and many saplings had died. The poor growth and death of fir saplings was in part due to intense browsing pressure by moose in previous years and also because of a recent outbreak of spruce budworm (*Choristoneura fumiferana*, see **VEGETATION** section).

The overall impact of wolf predation on the moose population is indicated by predation rate, which is the proportion of the moose population killed by wolves. This statistic is equal to the per-capita kill rate multiplied by the ratio of wolves to moose and then extrapolated throughout the year (according to methods described in Vucetich et al. 2011, Journal of Animal Ecology 80: 1236-1245). This year's calculations indicate a predation rate of 8.9 percent (Fig. 7, right panel), which is close to the long-term average predation rate of 9.9 percent (±0.8 percent SE) observed between 1971 and 2011 (the period prior to the wolf population's recent collapse). For additional context, this rate is almost twice as high as the rate observed in 2020 (4.5 percent) and it is the highest predation rate observed since 2011. This year's estimate of predation rate suggests that wolf predation has also importantly impacted changes in moose abundance this past year and probably during the previous year.

Fig. 11 *The left panel shows a close-up image of winter ticks on the skin of a bull moose that was outfitted with a GPS collar near Beaver Island at the west end of Isle Royale in February 2022. The irritation caused by bites from these hematophagous (blood-sucking) parasites causes moose to intensively groom themselves, which results in damage to their winter coat of hair. When moose break or damage large parts of their winter coats, they have greater difficulty thermoregulating (staying warm), especially during cold winters. The right panel is an image of the same bull moose shown in the left panel. The bull had lost or damaged large patches of its winter coat, especially near the shoulder region. This bull died on 14 April 2022, seemingly from malnutrition.*

During spring 2021 and winter 2022, we observed that moose were severely affected by winter ticks (Fig. 11). When moose acquire large numbers of winter ticks (i.e., individuals may have >20,000 ticks), the blood loss can cause moose to become anemic and result in substantial energetic costs for moose, which can ultimately reduce the chance of female moose successfully raising calves and may also impact adult survival. The irritation caused by tick bites compels moose to groom intensely enough to result in significant damage to (and loss of) their winter coat (Fig. 11). Consequently, we have monitored the severity of winter tick infestation for moose since 2001 by photographing moose in spring, digitizing each side profile, and calculating the proportion of hair loss. This past summer and winter field season, we observed moose with significant amounts of hair loss, and ground-based field crew regularly found winter ticks in beds left by moose in the snow. Recent analysis of hair loss data suggests that tick burdens for moose tend to be importantly influenced by weather (Hoy et al. 2021, Frontiers in Ecology and the Environment). Specifically, tick burdens tend to be greater following hotter summers, presumably because warmer temperatures may accelerate the development of tick eggs and increase egg survival. Moreover, years when moose were severely impacted by ticks also tended to coincide with years when the predation rate was high. That positive relationship between severe tick burdens and predation rate could potentially arise if moose with severe parasite burdens are more vulnerable to predators, such as wolves. Therefore, it seems that severe winter tick burdens may be exacerbating the effects of food shortages and high levels of wolf predation on moose population dynamics.

In sum, it seems that moose demography is now driven by a combination of high levels of wolf predation, winter ticks, and a depleted winter food source caused by overbrowsing in previous years and spruce budworm.

Collared Moose

In February 2019, around the time that wolves were first being translocated to Isle Royale, a new collaborative project began that involved outfitting 20 cow moose with GPS collars. In 2020, we advanced that project by collaring another 25 moose (19 cows and six bulls). This past winter, we deployed GPS collars on another 19 moose (13 cows and six bulls). Thus, in total, we have outfitted 64 moose (52 cows and 12 bulls) with collars. We focused on predominately outfitting cows with collars because cows produce and care for calves and therefore help us gather additional information about interannual variation in recruitment rates.

The collars regularly record each moose's location and upload that location data via satellite to an online database, allowing researchers to track each animal's movements remotely (Fig. 12). Each collar is also equipped with sensors that record the animal's activity levels and ambient temperature every five minutes. An important aim of this project is to assess the influence of predation on moose now that the wolf population has been restored. Other aims include gaining a better understanding of how activity levels and habitat selection are related to a moose's nutritional condition, various aspects of their diet, and weather conditions. Collared moose are also providing an opportunity to develop a sightability model that will be useful for assessing the likelihood of seeing moose during the aerial census in winter. Additionally, the data collected through this project will be valuable for comparing the health and behavior of the Isle Royale moose population with the mainland moose population on the reservation lands of the Grand Portage Band of Lake Superior Chippewa. Grand Portage sits on the northwest shore of Lake Superior and experiences similar interannual variability in winter severity and summer heat as Isle Royale. However, the moose population in Grand Portage faces some additional challenges that don't occur

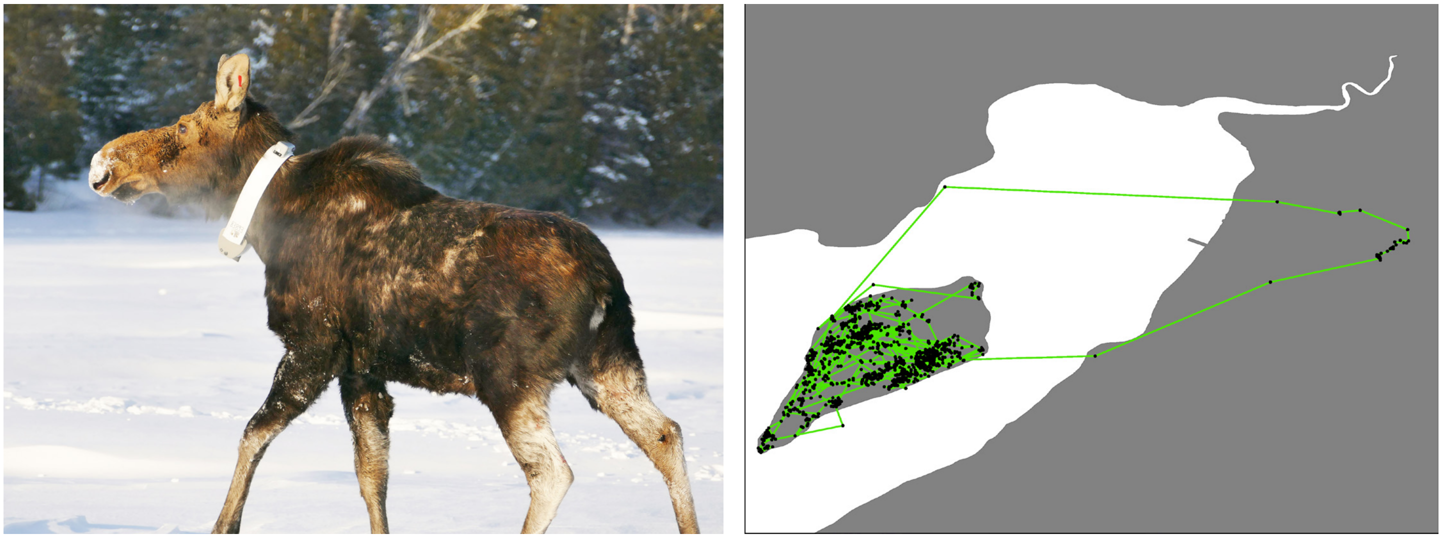


Fig. 12 *The left panel shows a cow moose outfitted with a GPS collar on 24 February 2022 near Beaver Island at the west end of Isle Royale. The right panel shows movements of that cow between 25 February and 25 April, revealing that she left Beaver Island only once in the two months after she was collared (map prepared by J. Terry-Shindelman). This past winter, we observed a high density of moose on Beaver Island (at least 12 moose in an area of approximately 0.22 km^2) and significant browsing damage to balsam fir saplings that had previously escaped intensive browsing by moose.*

on Isle Royale due to the presence of other species on the mainland, such as black bear, which prey on moose calves, and white-tailed deer, which carry parasites (e.g., brainworm—*Parelaphostrongylus tenuis*) that are fatal to moose.

Of the 64 moose that have been outfitted with GPS collars, 28 moose are currently alive with functional collars and the collars on 19 cows are no longer functional (mostly individuals collared in 2019), presumably due to depleted batteries or other malfunctions. Another 14 moose (nine cows and five bulls) are known to have died. Specifically, two cows are thought to have been killed by wolves, one cow died giving birth, one bull died from an injury sustained during the rut, and three bulls and six cows appear to have died of malnutrition. The cause of death for another bull that died three days after it was outfitted with a GPS collar is not known, but when the bull was outfitted with a collar it appeared to be in poor health. In addition to those 14 dead moose, three more moose are thought to be dead insomuch as the GPS data from those animals suggests they have not moved for a prolonged period and it is unlikely that the collars broke or slipped off the animals. We plan to perform necropsies on those moose to gain insights about their deaths.

Of the 24 moose collared in 2019-2020 that still had functioning collars in early February 2022, 11 of them were tracked by Ky and Lisa Koitzsch, Brenna Cassidy, and Isabella Evavold. They were tracked to determine which moose were raising calves and to collect urine (yellow snow) and fecal pellet samples. We also collected samples of balsam fir from saplings that the collared moose had fed on. The fir samples will provide insights about the quality of forage available to moose. The pellet and urine samples will be analyzed to determine individuals' diet and to assess biomarkers of individuals' health. Ultimately, these data will be used to answer questions about relationships among habitat selection, foraging behavior, and individuals' body condition, as well as how those interrelationships affect survival and reproductive success.

We are grateful to Helicopter Wildlife Services (Heliwild) for deploying collars on moose and to the NPS, National Parks of Lake Superior Foundation, and Grand Portage Band of Lake Superior Chippewa for providing funding to support this GPS-collaring project.

VEGETATION

Balsam fir is the primary forage species for moose in winter, typically representing about 50 percent of moose diet. Because the density of moose on Isle Royale has been well above average for several consecutive years, concerns have grown about the impact of moose browsing on balsam fir growth and recruitment (i.e., the rate that young fir saplings become mature cone-producing trees). To assess those impacts of moose browsing, each year (May and June) we measure the height that fir saplings grew during the previous summer and monitor the rate at which moose browse the terminal leader (main growing stem) of saplings found in multiple locations. Browsing of the terminal leader is especially important because that is how saplings gain the height necessary to grow out of the reach of moose and into the forest canopy. Furthermore, it can take multiple years for saplings to recover and develop new terminal leaders after being terminally browsed, and fir trees shorter than 3 m typically don't produce seeds (necessary for the next generation of fir trees). We have been making these summer measurements on fir each year over the past decade.

The average height growth attained by saplings during the 2020 growing season was 8.5 cm, which is approximately half the average height growth observed in 2014 and 2015 (around 20 cm) when the number of moose on the island was substantially lower. Furthermore, those measurements show that browse rate has been high in each of the past four years (Fig. 13). Specifically, moose had terminally browsed 83 percent of the fir saplings we examined along an 11-km-long transect at the west end of the island. We also observed that moose had broken off the tops of many young fir saplings that had previously escaped severe moose browsing (saplings taller than 175 cm) both along the 11-km-long transect and in other regions of the park. In particular, moose had broken the tops off a large number of regenerating fir trees along the shoreline of Beaver Island. When moose break the tops off of fir trees, it represents an especially severe setback to height growth. In short, in some areas of Isle Royale, it appears as though moose are currently breaking or browsing the main growing stems of fir saplings faster than the trees can recover and replace them, and this issue has been getting progressively worse each year since 2017.

Balsam fir also faced an additional challenge this past summer—a significant infestation of spruce budworm, which is the larval stage of a moth. Budworm was observed to have defoliated both young and mature balsam fir on Isle Royale this past summer. The impact of budworm was especially severe in the eastern region of Isle Royale, where the impact of moose browsing on fir is typically less severe. Budworm damage to trees ranged from defoliation of the current year's growth to almost complete defoliation of nearly all a tree's needles and buds (Fig. 13). Most mature trees lacked any cones, and in some regions many young fir saplings were dead or dying. It is too early to know the long-term impacts of this budworm outbreak. Nevertheless, the cumulative effects of budworm defoliation and intensive moose browsing during recent years have likely resulted in less winter forage for moose this past winter. White spruce trees (*Picea glauca*) were also observed to be impacted by budworm, and although spruce is seldom eaten by moose, spruce trees represent an important source of food for other wildlife.

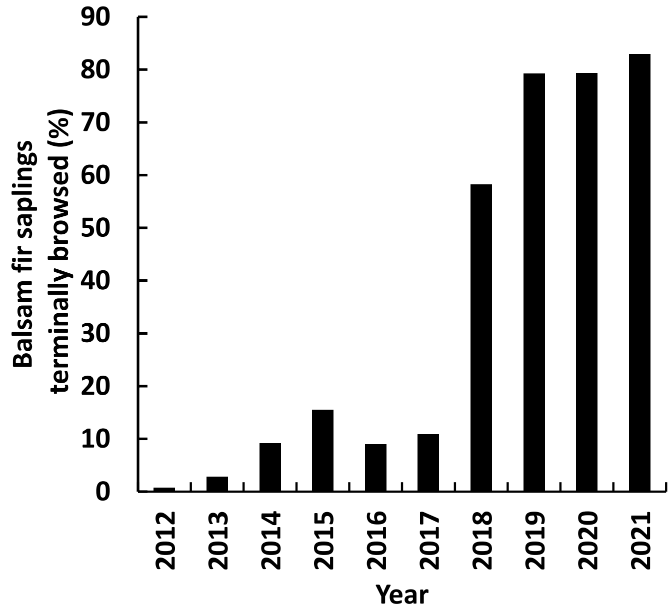


Fig. 13 *When balsam fir saplings grow to a height of 175 cm, their main growing stem (terminal leader) is on the cusp of being beyond the reach of browsing moose. Such trees are likely to grow into the canopy and mature into reproductive adults (i.e., cone-producing trees). Since 2012, we have monitored the growth of saplings that are taller than 175 cm along an 11-km-long transect that coincides with the Huginnin Trail at the west end of Isle Royale. The top panel shows the percentage of balsam fir saplings terminally browsed by moose, 2012 to present. Between 2012 and 2017, moose had terminally browsed only a small proportion of saplings taller than 175 cm. However, from 2017-2019, there was a dramatic increase in the number of saplings that were terminally browsed by moose in a manner that would have arrested their height growth. The bottom panel shows defoliation of balsam fir needles caused by spruce budworm.*
Photo credit: Ky and Lisa Koitzsch.

OTHER WILDLIFE

Winter observations of red foxes yielded a fox abundance index of 15.9, which is similar to 2020 (the last year when the index of fox abundance was observed, Fig. 14). Populations of their primary prey, snowshoe hares, appear to have increased slightly this past year (Fig. 14) after having remained at a similar level of abundance over the last five years. In the near future, foxes are expected to fare better due to the recovering wolf population, which provides moose carcasses that foxes can scavenge.

Aerial counts of active beaver colonies occurred periodically in past decades. However, since 2006, aerial counts have been completed at least once every two years. The results of those recent aerial surveys suggest that the beaver population remained at around 100 active colonies between 2006 and 2012, but then increased dramatically between 2014 and 2018 (the period after the wolf population had collapsed, but before wolves were reintroduced). In previous reports, we predicted that predation rates on beaver would increase following the reintroduction of wolves and lead to a reduction in the number of active beaver colonies or a reduction in the number of beavers living in each beaver colony. In line with that prediction, the results of the 2021 aerial survey suggest that the beaver population has decreased slightly from 506 active colonies in 2020 to 457 colonies in 2021 (Fig. 15).

During winter 2022, field crew observed marten tracks in the Daisy Farm and Windigo areas. Otters were observed to be present on 58 of the square-mile sections which comprise Isle Royale. Lastly, there were notably fewer

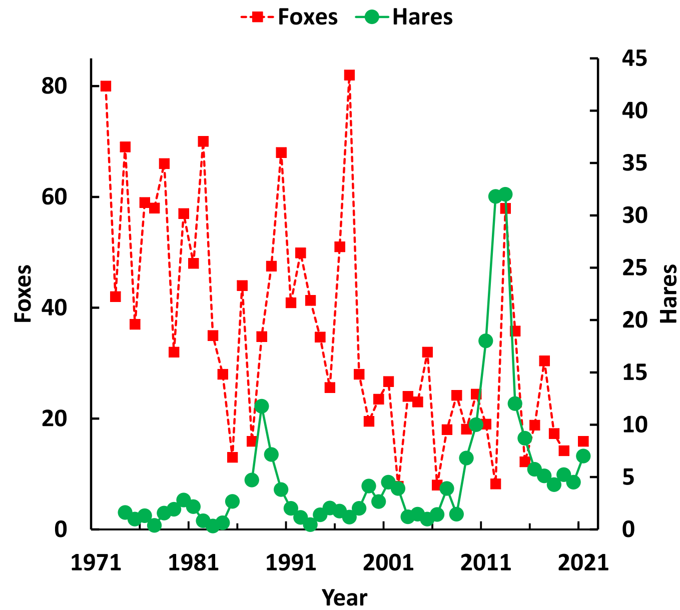


Fig. 14 *Indices of abundance for red foxes and snowshoe hares on Isle Royale, 1974 to present. The hare index is the number of hares seen per 100 km of summer hiking. The fox index is the sum of the maximum number seen at sites of moose carcasses plus the number seen otherwise per 100 hours of flight time.*

observations of red squirrels, siskins, and crossbills than in previous years, perhaps because of fewer cones due to the budworm outbreak.

WEATHER AND ICE

The winter of 2022 was characterized by cold temperatures, significant ice cover, deep and uncompacted snow, and high winds. Temperatures averaged 12.2°F and remained below freezing for all but four days during winter study (Fig. 16, top panel). During most nights and early mornings, temperatures were below 0°F or in single digits. There was expansive and thick ice cover between Isle Royale's main island and the smaller islets within the park. Additionally, ice cover on Lake Superior averaged over 50 percent throughout late February and early March. There also appeared to be an ice bridge connecting Isle Royale to the mainland for a few days during winter study. Snow depth gradually increased over the study, resulting in snow depths (average 26 inches) that were somewhat deeper than the long-term average (18 inches) observed during winter study (Fig. 16, middle panel). The sustained cold temperatures meant that the snow did not compact as much as it commonly does. Deep and unconsolidated snow made it difficult to ski and snowshoe to data collection

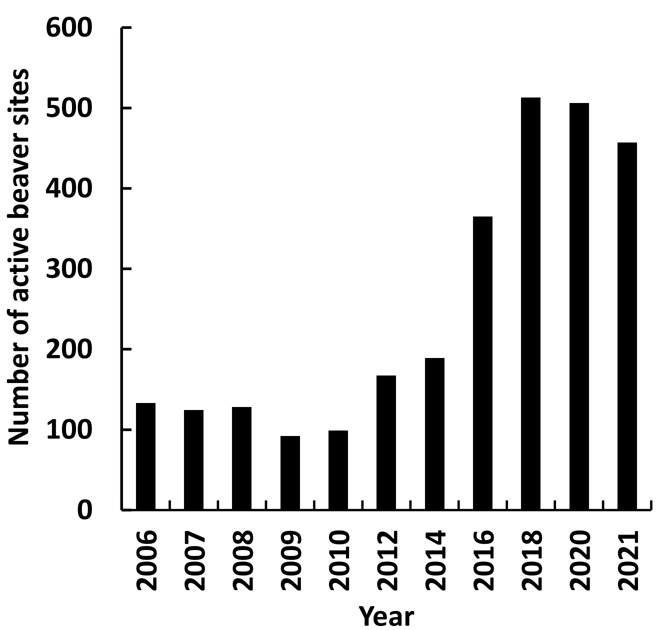


Fig. 15 *The number of active beaver colonies has been estimated during aerial surveys at least every other year since 2006 (data collected in partnership with and funded by NPS). During 2006-2010, there were approximately 100 active sites, and wolf predation was probably the primary limiting factor. After the wolf population collapsed in 2012, the beaver population increased greatly and then declined slightly in the past 12 months.*

sites, and the deep snow, combined with extreme wind chill on many days, made it especially challenging to carry out ground-based fieldwork. High winds during January and February greatly limited the number of days that aerial surveys could be conducted. The high winds also contributed to unusually large and hard snow drifts all over Washington Harbor, making it challenging to maintain suitable areas where fixed-wing aircraft could take off and land.

The deep and unconsolidated snow resulted in both wolves and moose frequently traveling along shorelines. Additionally, expansive ice cover allowed wolves to frequently visit smaller islets along Isle Royale's north shore and southwestern end.

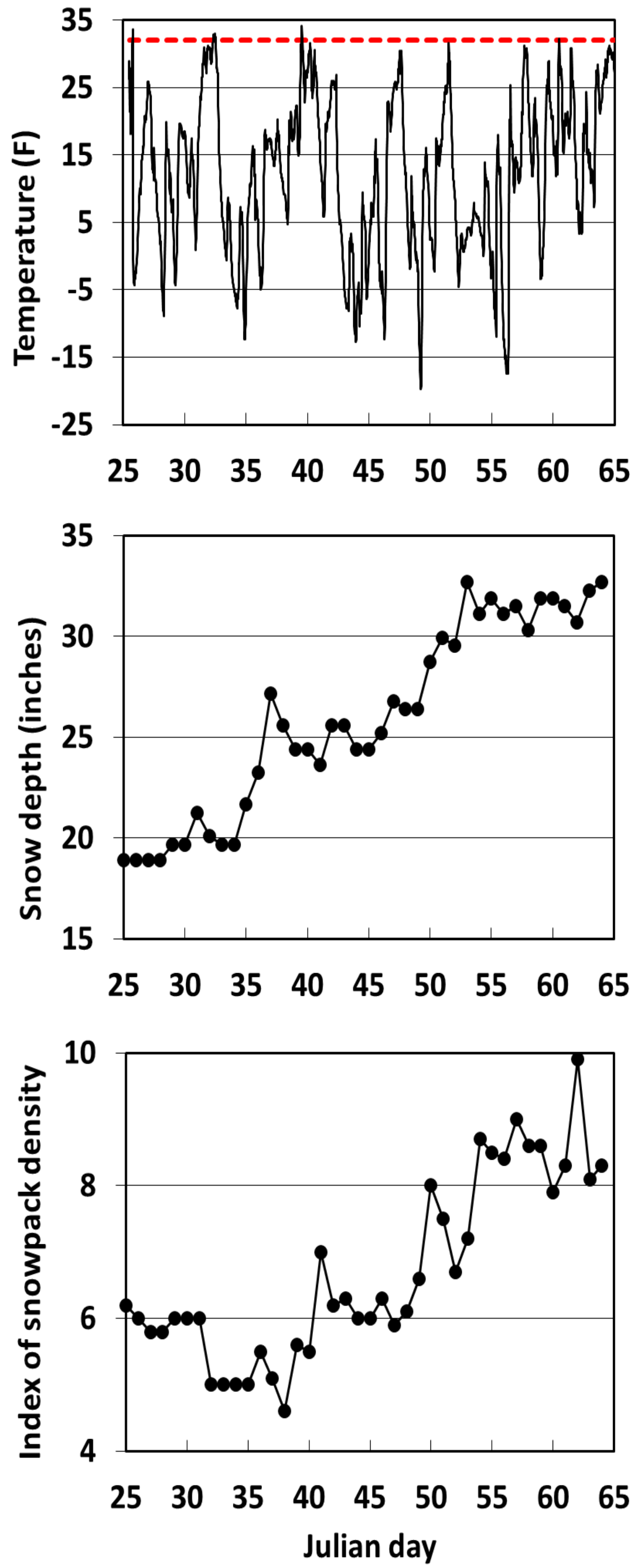
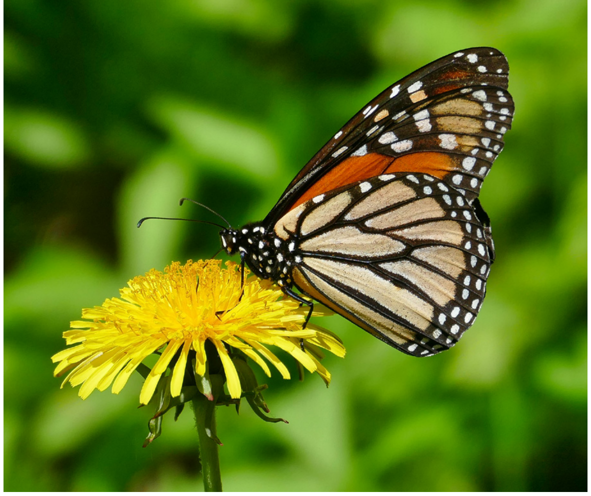


Fig. 16 *Daily temperature (top), snow depth (middle), and daily snowpack density (bottom) during the 2022 winter study on Isle Royale. Density was estimated as the Ramsonde hardness value, calculated using a penetrometer. The dashed line in the top panel indicates freezing point.*

Back cover photograph: A bull moose is pictured at a mineral lick at the west end of Isle Royale in June 2021.

Appendix—The table below summarizes the data contained in the 2021-2022 annual report.

Variable/parameter	2021/2022 Estimate	Notes
Wolf abundance	28 wolves	Based on winter observations of wolves and tracks from ground and aircraft in winter.
Moose abundance	1,346 moose	Based on stratified random sampling method involving counting moose on census plots in winter. (In 2022, we observed 135 moose on 91 plots.)
Moose recruitment rate	4%	Based on observing that only five of the 135 moose observed on census plots were calves.
Per-capita kill rate	0.71	Based on evidence that 25 moose were fed on by 28 wolves over a 38-day period and methods described in Vucetich et al. (2011).
Predation rate	8.90%	Calculated as that annual per-capita kill rate (0.71) multiplied by the ratio of wolves to moose (28 wolves to 1,346 moose).
Terminal browsing on balsam fir	83%	Based on data collected along Huginnin Loop transect.
Fox index	15.9	Calculated as the sum of two indices: (i) fox observations per 100 hours of flying in winter, and (ii) the total number of foxes seen on kills. (This year, we observed 9.6 foxes per 100 hours of flying and a total of six foxes on kills.)
Hare index	7.0 hares /100 km hiked	Based on observing 85 hares whilst hiking 1,215 km in summer.
Beaver	457 colonies	Based on aerial surveys to detect beaver food caches in fall.
Otter	Present in 58 sections	Based on observations of otter tracks mapped at a scale of square-mile sections during aerial surveys.
Average snow depth	26 inches	Based on daily measurements at Windigo during winter study.
Average temperature	12.2°F	Based on daily measurements at Windigo during winter study.
Average Ramsonde hardness (snow density)	6.7	Based on daily measurements at Windigo during winter study.



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