

2022-2023

Wolves



Ecological Studies of Wolves on Isle Royale



“...to redress the extinction crisis, we need to...be better at telling stories and better at politics.”

Mike Phillips (2022), executive director of the Turner Endangered Species Fund and the recipient of the 2021 Aldo Leopold Memorial Award from The Wildlife Society



Ecological Studies of Wolves on Isle Royale

Annual Report 2022-2023

by

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Front cover photograph: Three wolves from the East Pack, including two pups, look down a hill towards other pack members as they confront a moose.

Support and Contributions

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Note that in last year's report we inadvertently forgot to acknowledge the contribution made by Janet L. Parker.

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Team IA—Wayne Shannon (leader), Hal Hanson, Ron Porritt, Annie Matzen, Larry Fuerst, and Erik Freeman

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Team IC—Clay Ecklund (leader), Ken Lemieux, Matt Anderson, Sophie Busch, and Mike Kaszyca

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Team IIA—Julie Ann Timmer Wiest (leader), Zan Ceeley, Laura Saher, and Jim Clink

Team IIB—Trevor Peterson (leader), Erik Freeman, Patrick Huver, and Steve Leatherman

Team IIC—Loreen Niewenhuis (leader), April Willbur, Allison Burnett, and Liana Vital

Team IID—Karen Bacula (leader), John Algiere, Richard Gerity, and Sam Kaiser

Team IIIA—Michael George (leader), Megan Spencley, Bradley Spencley, Bill Kennis, and Wesley (Mike) Viilo

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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 made online at mtu.edu/givenow/?desig=1816_Wolf_Moose_Fund or 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!

The results reported here are preliminary and, in some cases, may represent findings of collaborators; please do not cite without consulting the authors. The views expressed here do not necessarily reflect those of the U.S. National Park Service or the U.S. National Science Foundation. Photographs in this report were provided by Isabella Evavold, Brenna Cassidy, Garrett Craig, Sarah Hoy, and Rolf Peterson.

Ecological Studies of Wolves on Isle Royale

SUMMARY

In February 2023, the wolf population was likely composed of 31 wolves. This is a slight increase from last year's estimate of 28 wolves (Fig. 1). The wolf population includes an East Pack with 11 wolves, a West Pack with five wolves, three groups of at least three wolves each, and several other wolves that are either loners or only loosely affiliated with one of the smaller groups. There is evidence that pups were born into three, possibly four, litters in April 2022. For context, no litters are thought to have been born between 2015 and 2018. However, following the translocation of wolves to Isle Royale between 2018 and 2019, one litter was born in 2019, two litters were born in both 2020 and 2021, and possibly four litters were born in 2022. Thus, the reproductive success of the wolf population has steadily increased over the last five years. The per-capita kill rate, which is an indication of the rate that wolves acquire food, was 0.52 moose per wolf per month. That rate is somewhat lower than last year's estimate of 0.71, but similar to what is expected given the number of wolves and moose currently on the island.

The estimated abundance of moose is 967, which is a 28 percent decline from last year's estimate of 1,346. Longer-term population trends suggest that the moose population had increased greatly over an eight-year period (2011-2019) but then started to decline rapidly over the last few years. The proportion of the moose population that is newly recruited individuals (i.e., nine-month-old calves in February) was 1.7 percent, which is very low compared to the long-term average. Predation rate was estimated to be 10 percent, which is similar to last year's estimate and close to the long-term average. While predation and low recruitment were important contributors to the moose decline, starvation also played an important role.

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

PERSONNEL AND LOGISTICS

In summer 2022, 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 Allie Johnson, graduate student Jasmine Terry-Shindelman, and undergraduate students Finn Swaty, Yujin Kim, Morgan Halley-Gluesing, and Otti Brueshaber. Additional summer fieldwork was carried out by Isabella Evavold, Ron Eckoff, Dick Murray, and Erik Freeman. Pilot Don Murray (UpNorth Aerials, Two Harbors, Minnesota) flew a fixed-wing aircraft to download data from GPS collars on moose in May. Don Murray and Rolf Peterson conducted an aerial survey to estimate the number of active beaver sites in October 2022.

During the summer field season, many park staff, other researchers, and visitors contributed key observations and

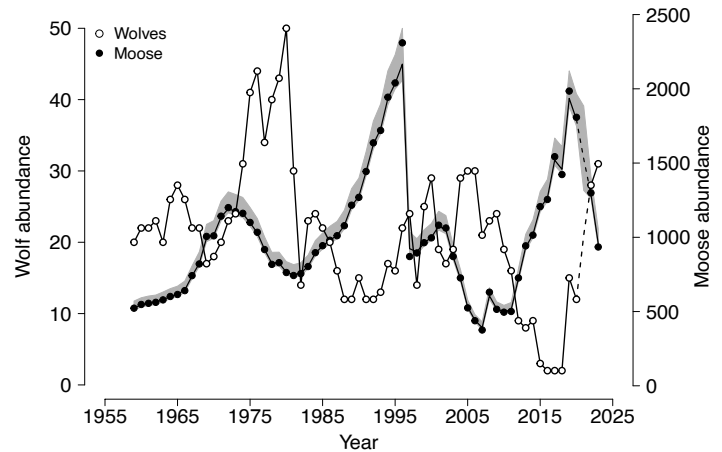


Fig. 1 Fluctuations in the abundance of wolves (open circles) and moose (filled circles) in Isle Royale National Park between 1959 and 2023. Abundance estimates are based on aerial surveys during winter. Additional estimates of moose abundance (solid line) and 90 percent Bayesian credible intervals (gray shaded area) were derived from a Gompertz state-space model (Hoy et al. 2020). The Gompertz model estimated abundance to be 989 moose [918, 1,080] in 2023. Surveys to estimate wolf and moose abundances did not take place in 2021 because of the COVID-19 pandemic, which is why a dashed line connects the estimates of abundance between 2020 and 2022. The increase in wolf abundance between 2018 and 2019 is the result of 19 wolves being translocated to the island.

reports of wolf signs and moose bones. Several dozen Moosewatch volunteers participated in weeklong cross-country treks, searching for sites where moose had been killed by wolves or died from other causes.

Lab work included updating the curation of wolf and moose bone collections in partnership with Martin Hobmeier and Brian Hoduski from the U.S. National Park Service (NPS). Lab work also included preparation and chemical analysis of balsam fir samples. Lab work was led by Leah Vucetich, John "Moose" Henderson, Jasmine Terry-Shindelman, and Allie Johnson, with the assistance of Erik Freeman, Janet Parker, Martina Friedeberg, Matt Anderson, Nathan Coleman, Zoie Schafer, J.T. Boudreau, Sarah Arnold, Carly Zielinski, Otti Brueshaber, Adam Awanda, Michael Yuchasz, Sage Haney, Chance Spencer, Adam Waltman, Noah Spranger, Zoe Riordan, Emma Tebo, Madolin Yuchasz, and Annamarie Wood.

In 2023, the 64th annual winter study was conducted during 20 January to 7 March. Winter fieldwork was led by Rolf Peterson and Sarah Hoy, with key contributions provided by pilot Don Murray (UpNorth Aerials). Isabella Evavold and Brenna Cassidy provided daily fieldwork on skis to collect data on moose and balsam fir. Important transportation and logistical assistance were provided by Wiskair helicopters, Don Murray, George Desort, Leah Vucetich, Brian McLaren, Jim Wiinanen, Isabella Evavold, Lynette Potvin (NPS), and several other employees at Isle Royale National Park. Brent Patterson

(Ontario Ministry of Natural Resources and Forestry) and the crew of Helicopter Wildlife Services provided important observations. Elizabeth Valencia (NPS) also provided valuable administrative support over the past year.

THE WOLF POPULATION

Population Size and Social Organization

In January 2023, the wolf population was likely composed of 31 wolves, which is an 11 percent increase from last year's estimate of 28 wolves (Fig. 1). The population included an East Pack with 11 wolves, a West Pack with five wolves, three groups of at least three wolves each, and several other wolves that were either loners, pairs, or only loosely affiliated with one of the three smaller groups.

The inference that the East Pack was composed of 11 wolves and West Pack was composed of five wolves is based on having regularly and consistently observed a group of 11 wolves in the eastern region and a group of five wolves in the western region throughout winter study. On 28 January, we experienced snow conditions that were excellent for finding and following tracks of lone wolves and smaller groups of wolves. In particular, we conducted an observation flight about six hours after a snowfall. On that day, the East Pack was at a kill site near McCargoe Cove and the West Pack was at a kill site west of Hay Bay. For that reason, the detection of additional wolves (via visual observation or tracks) on 28 January represents evidence for additional wolves which were not closely affiliated with either the East Pack or West Pack. These detections are detailed hereafter and were all made on 28 January, except where noted otherwise:

- Three wolves were directly observed at Tobin Harbor. The identity of one of those wolves was known because he wore a GPS collar.
- One wolf was directly observed at Brady Cove. The identity of that wolf was known because she wore a GPS collar.

- One wolf was directly observed on Washington Harbor on 28 January. However, inspection of wolf tracks in that same area on the morning of 29 January suggest there were two wolves.
- Two wolves were detected near Chippewa Harbor, one by direct observation and one by tracks traveling in a direction opposite of the wolf that was directly observed.
- Three wolves were detected by observing tracks near Moskey Basin.
- Three wolves were detected by observing tracks inland from Little Todd Harbor.
- One wolf was detected by observing tracks coming from the northeast near Hay Point. The tracks turned inland about three miles away from a kill site where the West Pack was located. There were no tracks on Hay Bay or in other forest clearings between this single wolf track and the West Pack's kill site.

The observations outlined in these bullet points likely represent different wolves because they were all made within a short period (approximately eight hours) and are separated by reasonable distances from each other, and from the East Pack and West Pack. As a result, winter observations suggest that there are very likely 31 wolves: 11 in the East Pack, five in the West Pack, and 15 in smaller groups (Fig. 2).

The density of wolves living in the eastern and western halves of Isle Royale has changed over the past year. Last winter (February 2022) in the eastern half of the island, we observed a large group of 13 wolves (the East Pack, which included 12M) and two other wolves that did not belong to the East Pack. By contrast, this winter we observed a large group of 11 wolves in the East Pack (which continues to include 12M) and nine other wolves living in smaller groups or alone. These observations suggest that although the number of wolves in the East Pack may have declined

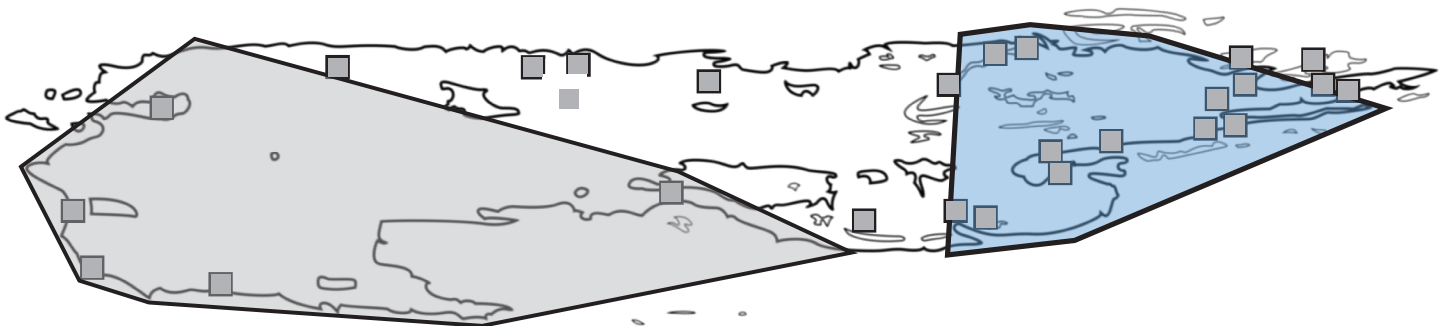


Fig. 2 The gray squares are locations where we observed small groups of wolves (two to five wolves) which were not affiliated with the East Pack or West Pack (even when inside the territories of these established packs). Minimum convex polygons are shown, which represent territories of the West Pack (gray polygon) and East Pack (blue polygon) based on observations of wolves during winter study (22 January to 7 March).

slightly (by 15 percent, from 13 to 11 wolves) over the past year, the overall density of wolves living in the eastern half of Isle Royale increased by around 33 percent, from 15 to 20 wolves.

Understanding the dynamics of the wolves in the western half of Isle Royale over the past year is more complicated. Last year, we observed a total of 13 wolves in the western half of the island based on evidence of a group of seven wolves (the West Pack, which included 7M), a group of four wolves, and a group of two wolves observed in three different locations on the same day. However, there is some uncertainty about the extent to which these three groups represent a single pack because weather conditions greatly limited the time we spent conducting aerial surveys in 2022. If the 13 wolves observed in the western region in 2022 represented a single pack, then there has been a substantial decline in the number of wolves in the West Pack over the past year: an approximately 62 percent decline, from 13 to five wolves. By contrast, if the 2022 observations represented the West Pack (which included 7M) and one or more other groups, then there has been a moderate decline in the size of the West Pack (which continues to include 7M in 2023): a 29 percent decline from seven to five wolves. However, if one were not concerned about whether wolves living in the western region represented one or more packs, then it is useful to note that the density of wolves living in the western region has only declined slightly (by 15 percent) over the past year, from 13 wolves in 2022 to 11 wolves in 2023.

In addition to the East Pack and West Pack, our observations this past winter suggest that another pack has formed. We regularly observed a small group of wolves in the middle of the island, in the vicinity of Little Todd Harbor and Todd Harbor. For context, the wolf population commonly consisted of three stable packs prior to the recent translocation of wolves to Isle Royale.

Wolf Reproduction

In 2022-2023, the annual recruitment rate for the wolf population was estimated to be 25 percent, which is similar to the long-term average rate of 28 percent observed between 1970 and 2011 (the period before the wolf population collapsed due to inbreeding). That annual recruitment rate is based on observations that: (i) there were 28 wolves in the population in 2022; (ii) the West Pack and East Pack both produced three pups in 2022, which survived to winter 2023; and (iii) wolves toward the middle of the island produced at least one pup, which survived to winter 2023. More precisely, on multiple occasions during winter study 2023, we observed several wolves that appeared to be pups in both the East Pack and West Pack (Fig. 3). Prior observations during the breeding season in 2022 suggest that 7M is likely the father of the litter born to the West Pack in April 2022 and that 12M is likely the father of the litter born to the East Pack. Additionally, we observed one pup in a group of four wolves near Mount Siskiwit in the middle of the island. That group of four wolves did not appear to be affiliated with either the East Pack or West Pack.

In addition to the three litters mentioned above, direct observations of the behavior of 19M and a collared female during the breeding season in 2022 (see Fig. 3 in last year's annual report) strongly suggest the pair mated and likely produced a litter in April 2022. However, when we observed that collared female this winter she did not have any pups with her. The significance of whether 19M and the collared female produced surviving offspring is that 19M was translocated from Michigan. That Michigan heritage is notable because five of the six wolves that are thought to be the parents of pups born on Isle Royale between 2019 and 2022 are all from the Michipicoten lineage (7M, 9M, 12M, 14F, 15F) and the other wolf is from the northern Minnesota lineage (1F). We suspect the female with 19M is the offspring of 12M and 15F from the East Pack and was



Fig. 3 Left image shows wolf pups in the East Pack on 6 March and right image shows pups from the West Pack on 17 February.

born on Isle Royale in May 2020. This assumption is based on having regularly observed the female to be living within the East Pack's territory during winter 2022, and having observed that 12M and 15F were a bonded pair during the 2020 breeding season (see the 2019-2020 annual report).

In summary, we observed evidence suggesting that three or possibly four litters were born during the spring of 2022: one at the west end, two litters at the east end, and probably another in the middle of the island. Litters born to both the established packs (East Pack and West Pack) resulted in at least six pups surviving until winter 2023, while the other two litters may have resulted in only one or no surviving pups.

During the 2023 breeding season, we observed evidence of four, possibly five breeding females. Observations were either estrous blood left in the snow of a wolf bed or tracks in the snow that were indicative of mating between wolves. We observed:

- Estrous blood and tracks indicative of mating left by members of the West Pack south of Washington Harbor on 17 February. We assume that the breeding male is 7M (Fig. 4) because he was observed in this area at this time and he is thought to have been the breeding male in the West Pack since 2020;
- Estrous blood at Duncan Bay left by a female wolf traveling with a collared male wolf and another unknown wolf on 19 February. We suspect that the collared male is the offspring of 1F and 7M, wolves that held a territory at the west end in 2020;
- Tracks indicative of mating at Moskey Basin left by members of the East Pack on 2 March. We assume that the breeding male may be 12M, a wolf we observed in this area that is thought to have been the breeding male in the East Pack since 2020; and
- Estrous blood and tracks indicative of mating at McCargoe Cove on 25 February. Tracks indicated the presence of just two wolves. These are not likely to be the same group of three wolves seen at Duncan Bay on 19 February because that group was observed between Three Mile Campground and Tobin Harbor on 25 February. This mated pair is also unlikely to belong to the East Pack, because the East Pack was observed in the Amygdaloid Island/Robinson Bay area on 24 February and tracks suggest the East Pack did not travel toward McCargoe Cove on 25 February.

In addition to the listed observations of four breeding females, on 19 February we also saw estrous blood in a bed at Moskey Basin that appeared to be from a female wolf traveling alone. The identity of this female is not known, but she is unlikely to be the same female in estrus detected in the group of three wolves at Duncan Bay that same day. Because female wolves are typically only in estrus for around 9-15 days, it is plausible that she is the



Fig. 4 Both images are of wolf 7M, who is thought to have been the breeding male of West Pack since 2020.

same female that mated at Moskey Basin on 2 March (14 days later) or the same female that mated at McCargoe Cove on 25 February (six days later). If this female in estrus is not one of the females that mated at either McCargoe or Moskey, then there are potentially five breeding females.

Wolf Survival

In 2022-2023, the annual survival rate was estimated to be 86 percent, which is higher than the long-term average annual survival rate of 74 percent observed on Isle Royale between 1970 and 2011. For additional context, the annual survival rate of adult wolves living in wilderness areas in Minnesota is estimated to be around 79 percent (Barber-Meyer et al. 2021 *Biological Conservation*). Our estimate of 86 percent is based on observing that there were 28 wolves in February 2022 but only 24 adult wolves in February 2023, and the assumption that no wolves traveled from the island to the mainland or vice versa during the past year. Also note that if we have underestimated how many of the 31 wolves on the island were pups this past winter, then the annual survival rate estimate would be lower than 86 percent and the annual recruitment rate would be higher than 25 percent.

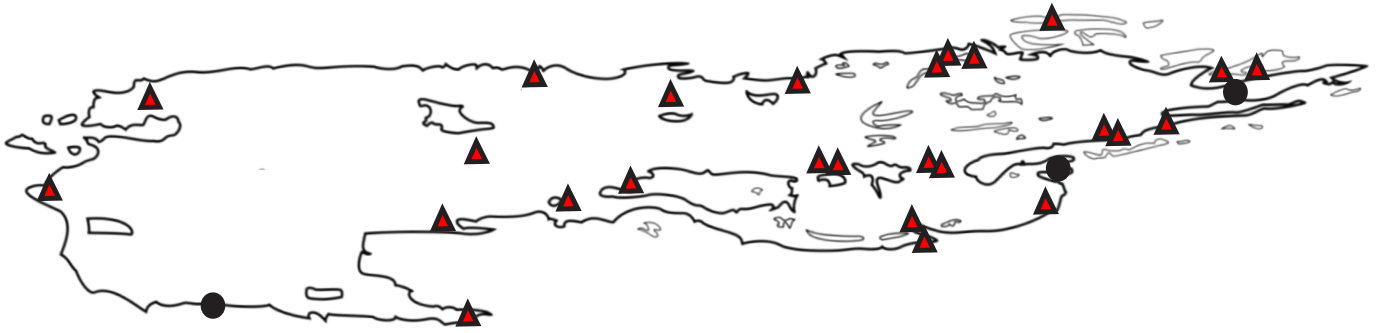


Fig. 5 The 26 red triangles show where we detected moose killed by wolves during winter study. The black circles represent moose that died shortly before winter study.



Fig. 6 These images were taken the morning of 24 January 2023 and show wolves from the East Pack shortly after they killed a moose near the shoreline by Chippewa Harbor. That morning, all 11 members of the East Pack were resting in small clearings on a ridgetop, just a few hundred meters away from the kill site. Fresh tracks and blood in the snow suggest that the wolves had recently chased the moose down toward the shoreline and killed it, as opposed to having scavenged the carcass.

Of the 19 wolves translocated to Isle Royale between 2018 and 2019, we only observed two during winter 2023: 7M (Fig. 4) appears to be continuing as the breeding male in the West Pack, and 12M is probably still the dominant breeding male in the East Pack. When interpreting that observation, it is important to note two things. First, the fate of several of the translocated wolves is unknown because their GPS collars stopped functioning or fell off (see the 2021-2022 annual report). Second, most wild wolves do not live beyond 4.5 years old. All of the translocated wolves would be older than six years by March 2023 because they were at least two years old when they were brought to Isle Royale (NPS report 2022). Consequently, it would be surprising if a large number of the translocated wolves were still alive.

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 26 moose killed by wolves during a 49-day period (15 January to 4 March, Fig. 5). Available evidence suggests that each of those 26 moose were killed by wolves (Fig. 6), as opposed to being scavenged by wolves. Each one of these dead moose will be carefully examined in spring 2023 to gain additional insights about their age and health.

These observations indicate that this year's rate of prey acquisition is 0.52 moose per wolf per month (assuming 26 moose were fed on by 31 wolves over 49 days). That rate is lower than the long-term average rate of 0.70 (± 0.04 SE) observed between 1971 and 2011 (the period prior to the wolf population's recent collapse). However, that estimated rate is consistent with expectations based on the ratio of moose to wolves on Isle Royale (Fig. 7, left panel).

In summary, the current wolf population is demographically secure, in the sense that wolf abundance, vital rates, and kill rate indicate that the population is well-established. However, the social organization of the wolf population appears to be quite dynamic. For context, prior to the translocation of wolves to Isle Royale in 2018, the wolf population had most commonly consisted of three stable packs and a number of lone wolves typically representing about 10 percent of the population's total size. By contrast, over the past 12 months, the population appears to be characterized by three or possibly four reproducing groups, of which only two seem to have well-established territories (Fig. 2). Over the past year, we continued our long-term efforts to collect wolf scat samples from which DNA can be extracted, and analysis of those genetic samples (along with samples collected by the NPS and other collaborators) will provide more insights about wolf abundance and vital rates. That genetic research is being led by Dr. Kristin Brzeski and Sam Hervey (both MTU).

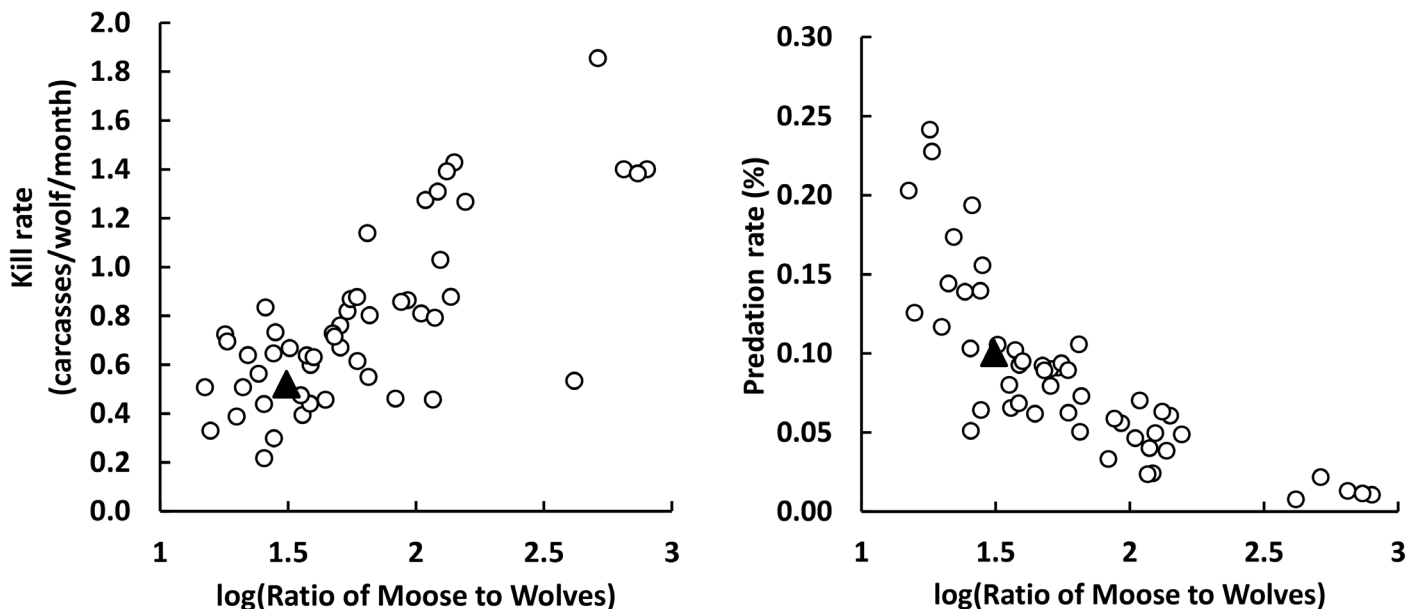


Fig. 7 The ratio of moose to wolves in relationship to the rate at which wolves acquired prey on a per-capita basis (i.e., kill rate, left panel) and the proportion of the moose population killed by wolves (i.e., predation rate, right panel) for the period, 1971-2023. The black triangles indicate observations for 2023.

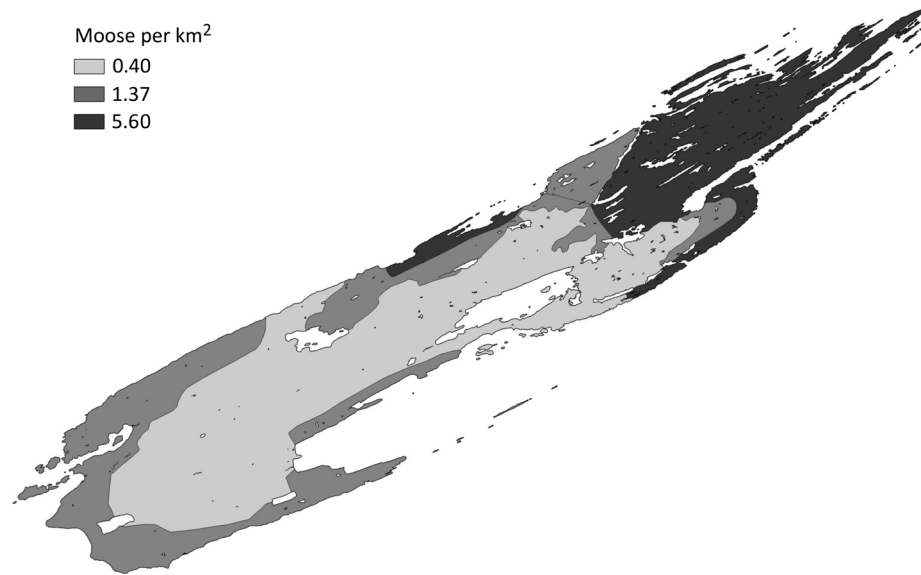


Fig. 8 The estimated density of moose on Isle Royale during winter 2023. Estimates are based on aerial surveys of 91 plots that comprised 17 percent of the main island's area. This map was produced by Jasmine Terry-Shindelman (MTU).

THE MOOSE POPULATION

The 2023 moose census was conducted during 22 January to 1 February and resulted in an estimated abundance of 967 moose (Fig. 1). The 80 percent confidence intervals on this estimate are [712, 1,240], and the 90 percent confidence intervals are [602, 1,413]. Moose density was lowest in the middle portion of Isle Royale (0.40 moose/km²), higher in the western portion (1.37 moose/km²), and highest in the eastern portion (5.60 moose/km², Fig. 8).

We estimated moose abundance on the assumption of a 52 percent sightability correction factor given that weather and survey conditions were good or excellent for the majority of the census (e.g., overcast, low winds, complete snow coverage). Additional rationale for using a 52 percent sightability is given in the 2021-2022 annual report. For context, it can be useful to know what the estimated abundance would have been if a different sightability factor had been assumed (e.g., 10 percent lower or higher than 52 percent). A sightability of 42 percent would yield an estimate of 1,197 moose, and a sightability of 62 percent would yield an estimate of 810 moose. Importantly, the 80 percent confidence intervals for abundance under the assumption of 52 percent sightability (i.e., [712, 1,240]) includes the point estimates of abundance for correction factors of 42 percent and 62 percent. This estimated abundance of moose will be refined in future years by using a method known as "reconstruction" which is described in more detail in the 2021-2022 annual report.

This winter's estimated abundance of 967 moose is 28 percent lower than last year's estimate (1,346 moose). That decline is one of the largest by percentage and absolute numbers ever observed on Isle Royale. Furthermore, the population has declined by 54 percent since 2019, when the moose population appears to have peaked at around 2,000 moose. The average annual per-capita rate of population change during this four-year period has been -17 percent/year. Taking account of statistical uncertainties

in moose counts, it is reasonable to infer that the moose population grew rapidly for a number of years (2010-2019) and started to decline rapidly in recent years (Fig. 1).

The population decline observed over the past four years is comparable to a large population collapse in the mid-1990s, in that both decreases were of similar magnitudes. However, the current collapse occurred over four years, whereas the collapse in the mid-1990s largely occurred over a single year and was associated with an especially severe winter.

The large rate of population decline is consistent with observing a very low recruitment rate. Of the 116 moose sighted during our aerial survey, only two were calves, representing a recruitment rate of 1.7 percent. The 80 percent and 90 percent confidence intervals on that estimate are [0.5 percent, 4.5 percent] and [0.3 percent, 5.3 percent], respectively. This is the lowest recruitment rate ever observed on Isle Royale (Fig. 9). For context, the long-term average recruitment rate is approximately 13 percent. Furthermore, the recruitment rate has been below average for each of the past four years, which is consistent with the moose population having significantly declined in recent years. Other evidence that recruitment rates are lower this year comes from observations of whether GPS-collared female moose were accompanied by calves in winter. Specifically, we observed 0.27 calves per cow in 2023, down from 0.40 calves per cow in 2020. Lastly, when recruitment rates are high, we tend to observe more cows raising twins, but this winter we saw no twins.

In addition to the moose population declining partly due to low recruitment rates, we also observed evidence that the survival of adult moose has declined in recent years. Part of that evidence comes from monitoring the survival of adult moose outfitted with GPS collars, which has declined by around 30 percent over the last four years. More precisely, estimates of annual survival were: 100 percent in 2019, 92 percent in 2020, 87 percent in 2021, and 70 percent in 2022.

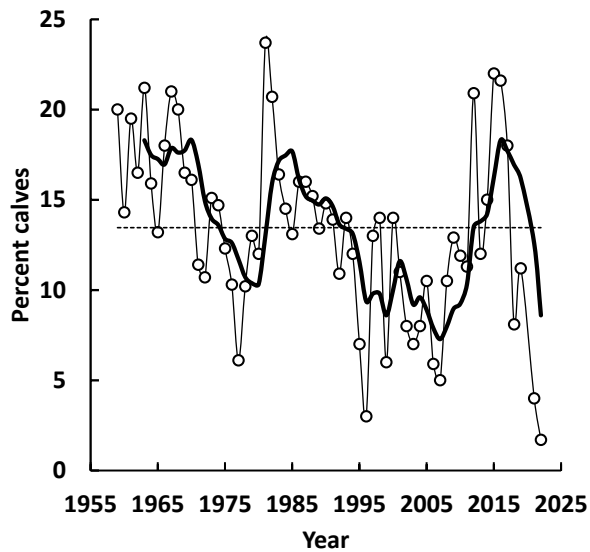


Fig. 9 Long-term trends (1959-2022) in the percentage of the moose population that represents nine-month-old calves. The 63-year average (13.5 percent) is marked by the dashed line, and the thicker line represents the five-year moving average.

Wolf predation is one factor that influences both the recruitment of calves and the survival of adult moose on Isle Royale. 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). This year’s calculations indicate a predation rate of 10 percent, which is:

- about what is expected given the ratio of moose to wolf abundance on Isle Royale (Fig. 7, right panel);
- 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); and
- slightly higher than last year’s estimate of 8.9 percent.

Although this year’s predation rate is the highest rate observed since 2011, predation accounts for only a portion of the decline in moose abundance over the last year.

Necropsies of moose over the last few years suggest that starvation continues to be an important cause of mortality. Each summer and winter, researchers, students, and volunteers have conducted extensive searches for the remains of moose that died over the past year. Of the 76 dead moose examined in winter and spring 2022, 46 percent starved. Similarly, of the 69 dead moose examined in 2021, 30 percent starved. In a typical year, less than 5 percent of moose that we necropsy have died from starvation. We also observed high levels of starvation for moose outfitted with GPS collars. Of the 10 collared moose that died over the past year, 70 percent starved, 20 percent were killed by wolves (Fig. 10), and 10 percent died from unknown causes.



Fig. 10 The remains of a female moose killed by the West Pack near Cumberland Point on the night of 2 February 2023. This moose was outfitted with a GPS collar in February 2022 and had spent the majority of the past year in the Cumberland Point area. The carcass was scavenged by foxes by the time that field crew arrived to investigate (photos taken on 7 February by Isabella Evavold and Brenna Cassidy).

Together, the above evidence suggests that in the past two years, for every moose killed by wolves, one to three other moose died from malnutrition. Allowing for various uncertainties, those calculations are reliable enough to conclude that starvation was an important drag on the population, and very likely starvation was more important than predation. The elevated rates of starvation this past year are a continuance of a pattern that we first detected several years ago in 2019 (see Fig. 11 of the 2019-2020 annual report).

The unusually high number of moose that starved between 2019 and 2022 suggests that moose are experiencing an ongoing shortage of food. Evidence of a food shortage is supported by long-term monitoring of the growth and status of balsam fir saplings, which are typically the main source of food for moose on Isle Royale during the winter. For the last three years, the growth of balsam fir saplings has become increasingly poor and many saplings have died, 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). This past winter, we also observed moose browsing more frequently on cedar than in previous years and that moose were stripping bark from mature aspen and balsam fir trees. Both of those observations suggest that foraging moose cannot find a sufficient amount of fir twigs and foliage.

Winter severity, specifically snow depth, is another factor that can influence both the foraging behavior and nutritional condition of moose and thereby affect the rate at which moose populations increase or decrease. For example, moose tend to be more nutritionally stressed in years with deep snow because it is more energetically

costly for moose to move around, and deep snow can limit a moose's ability to find food (Hoy et al. 2021). Although this winter was characterized by average snow depth (46 cm), the winters of 2020 and 2022 were characterized by above average snow depth (66 cm), which may have contributed to evaluated levels of starvation and declines in moose abundance in recent years.

To summarize, the large decline in moose abundance is—demographically speaking—the result of low recruitment rate and high mortality rate. Those vital rates are the combined results of moderate levels of predation and high rates of starvation.

Collared Moose

Since 2019, a total of 64 moose (52 cows and 12 bulls) have been outfitted with GPS collars as part of a collaborative project to assess how the restoration of the wolf population has impacted moose. Outfitting moose with GPS collars also allows us to gather information about interannual variation in recruitment and adult survival rates (see earlier sections) and to gain a better understanding of how activity levels and habitat selection are related to a moose's nutritional condition, various aspects of their diet, weather conditions, and predation risk.

Of those 64 collared moose, 13 are still alive with functional collars, 18 have died, and the fate of the remaining 33 is currently unknown because their collars either stopped functioning or dropped off. Of the 18 moose that died: 11 (61 percent) died from starvation, three (17 percent) were killed by wolves, one (5.5 percent) died from an injury sustained during the rut, one (5.5 percent) died from complications while giving birth, and the causes of



Fig. 11 Moose have been outfitted with GPS collars to better understand their habitat selection and foraging behavior, and how those behaviors affect the individuals' body condition, calf recruitment, and survival.

death for two moose (11 percent) are unknown. Thus, over the four-year study period, starvation, as opposed to wolf predation, appears to be the primary cause of mortality for collared moose whose fate was known.

This past winter, 12 collared moose (10 cows and two bulls) were tracked by 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. The pellet and urine samples will be analyzed to determine individuals' diet and to assess biomarkers of the individuals' health. We also track moose to find sites where moose have spent time foraging and collect samples of foliage that moose have been browsing on to provide insights about the quality of forage available to moose. 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 factors affect survival and recruitment of calves (Fig. 11).

VEGETATION

Balsam fir is the primary forage species for moose in winter—typically representing about 50 percent of a moose's diet (Parikh et al. 2017). Over the last decade, concerns were raised about how balsam fir growth and recruitment (i.e., the rate that young fir saplings become mature cone-producing trees) were being negatively impacted by high levels of moose browsing. To assess those impacts of moose browsing, each summer we monitor the growth and browsing status of balsam fir saplings at multiple locations across the eastern and western regions of Isle Royale. For example, since 2012 we have monitored fir saplings taller than 175 cm along a 15-km-long transect (representing a 10-ha area) at the west end of the island. At this site, we have focused on fir saplings taller than 175 cm because that is the height beyond which the tree's main growing stem (terminal leader) is on the cusp of being out of the reach of browsing moose, and saplings are more likely to grow into mature, cone-producing trees. On this transect, we attach a small metal tag with a unique number to any sapling that grows taller than 175 cm so that each tree is individually identifiable. Each spring, we record whether the tree is still alive, the total height of the tree, how much it grew during the previous growing season, and whether its main growing stem (terminal leader) had been browsed during the past year. 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 leaders after being terminally browsed.

In the spring of 2022, we found that 49 (of 581) tagged saplings had died over the last year. Of the 532 tagged saplings that survived, 17 had grown taller than 3 m. By contrast, 264 tagged saplings had heights below 175 cm, either because moose had bent and broken off the top part of the tree or because the top part of the tree had died due to intense moose browsing in previous years. Thus, a large proportion (50 percent) of fir saplings have experienced

a huge setback to their height growth over the past year (Fig. 12, top panel). Of the 251 saplings that were still alive and between 1.75 m and 3 m tall, eight had no obvious main growing stem (due to browsing in previous years) and another 123 had their terminal leaders browsed by moose during the past year. Thus, moose had browsed 51 percent of the terminal leaders that were available and within their reach. That level of terminal browsing by moose is somewhat lower than it has been for the past five years, but is still notably higher than the level observed between 2012 and 2017 (Fig. 12, bottom panel). During the 2022 growing season, the average height growth attained by unbrowsed saplings shorter than 175 cm was 6.4 cm, which is well below the average annual height growth of 19 cm observed between 2015 and 2017. The patterns described above for fir saplings along this transect were also observed at many other locations within the western region of Isle Royale.

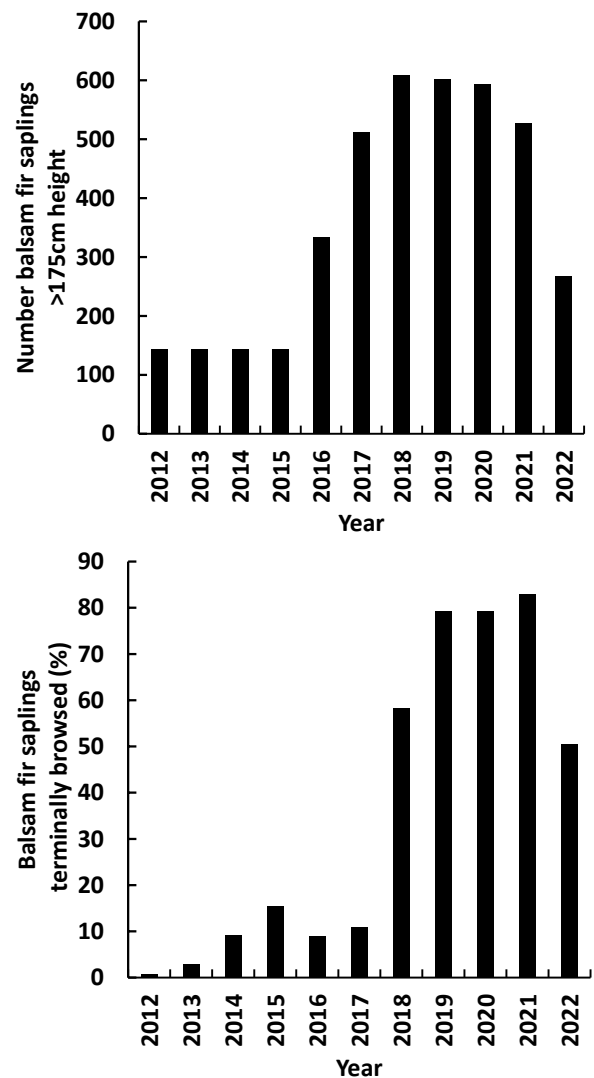


Fig. 12 Since 2012, we have monitored fir saplings taller than 175 cm along a 15-km-long transect that coincides with the Huginnin Trail at the west end of Isle Royale. Over the past year, there has been a significant decrease in the number of fir saplings over 175 cm tall (top panel). Between 2012 and 2017, moose terminally browsed only a small proportion (less than 20 percent) of saplings taller than 175 cm (bottom panel). However, after 2017 there was a dramatic increase in the number of saplings that were terminally browsed by moose in a manner that arrested their height growth.

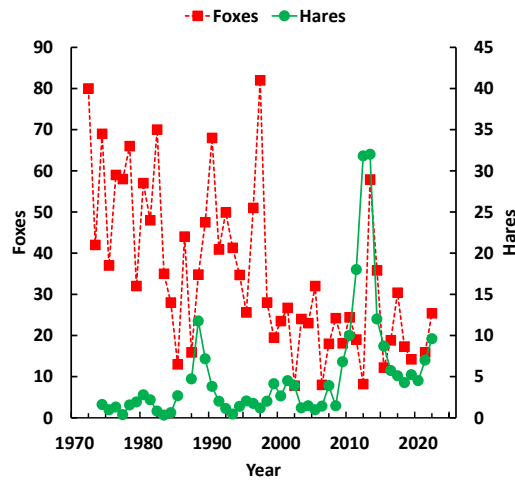


Fig. 13 Indices of abundance for red foxes and snowshoe hares on Isle Royale, 1974-present. The hare index is the number of hares seen per 100 km of summer hiking. The fox index is the sum of the maximum number seen at sites of moose carcasses plus the number seen otherwise per 100 hours of flight time.

In addition to moose browsing impacting the growth and mortality of balsam fir trees, during the summer of 2022 we continued to observe that fir saplings had been at least partly defoliated by spruce budworm, the larval stage of a moth. The impact of budworm was more severe in the eastern region of Isle Royale. The cumulative effects of budworm defoliation and intensive moose browsing during recent years likely resulted in less winter forage for moose this past winter.

In summary, the status of balsam fir saplings continues to deteriorate and this issue has been getting progressively worse each year since 2017. The high levels of browsing that saplings experienced across recent years have resulted in fir saplings that are substantially shorter and exhibit especially poor growth compared to five years ago. That fir trees have experienced a significant setback in height growth and grew very little over the past year is significant because trees shorter than 3 m typically don't produce seeds (necessary for the next generation of fir trees).

OTHER WILDLIFE

Winter observations of red foxes from aircraft yielded a fox abundance index of 25.4, which is higher than last year's estimate of 15.9 (Fig. 13). Populations of their primary prey, snowshoe hares, increased for the second year in a row to 9.6 hares seen per 100 km hiked, which is double the number of hares seen in 2020 (Fig. 13).

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. Those surveys suggest that the beaver population remained at around 100 active colonies during 2006-2012, but then increased dramatically during 2014-2018 (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

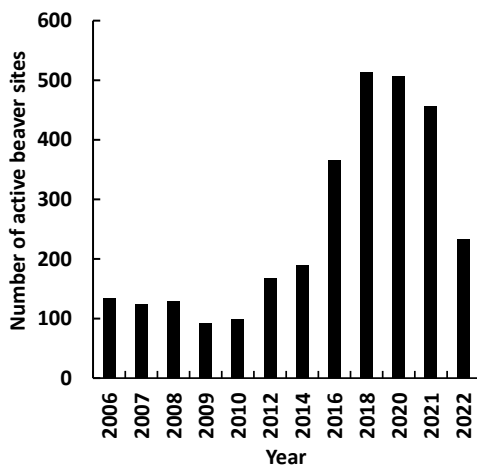


Fig. 14 Since 2006, the number of active beaver colonies has been estimated during aerial surveys at least once every two years (data collected in partnership with and partly funded by the NPS). During 2006-2010, there were approximately 100 active sites, and wolf predation may have been an important limiting factor. After the wolf population collapsed in 2012, the beaver population increased rapidly until wolf restoration in 2018-2019. Since then, beavers have declined, particularly in the past year.

line with that prediction, the results of the 2022 aerial survey suggest that the beaver population has decreased by approximately 50 percent over the last year, from 457 active colonies in 2021 to 233 colonies in 2022 (Fig. 14).

During winter 2023, our field crew observed marten tracks in the Windigo, Grace Creek, Middle Point, and Huginnin Loop areas at the west end, but no marten tracks were observed at the east end. Otters were observed on 83 of the (square-mile) sections of which Isle Royale is composed.

We regularly observed bald eagles during this past winter and also observed a golden eagle scavenging on the carcass of a moose killed by wolves (Fig. 15). This is only the second time since 1959 that a golden eagle has been observed at Isle Royale during winter.



Fig. 15 Notable wildlife sightings this past winter. Top panel: A golden eagle and red fox scavenging on the carcass of a moose. While it is common to see bald eagles, ravens, and red foxes feeding on the remains of moose, this is only the second time that a golden eagle has been observed in winter. Bottom panel: A black fox (melanistic form of the red fox) chewing on the ribs and vertebrae of a moose carcass. This past winter we observed a black fox on four different occasions, whereas in a typical winter we observe one or no black foxes.

WEATHER AND ICE

This winter was characterized by below-average ice cover. Ice concentration on Lake Superior was estimated to be 5 percent at the start of winter study and it remained below 20 percent for the duration of the winter (NOAA, coastwatch.glerl.noaa.gov/ice). For context, last winter ice concentration averaged 50 percent. At no point was there an ice bridge connecting Isle Royale to the mainland this winter.

Temperatures were relatively mild compared to last winter. They averaged -7.8°C in 2023 (compared to the average of -10.8°C in 2022) and remained below 0°C on all but three days during winter study (Fig. 16, left panel). Snow depth averaged 45 cm, which is similar to the long-term average of 46 cm, but substantially less than the average of 66 cm observed in the winters of 2020 and 2022 (Fig. 16, middle panel). The average snowpack density, estimated as the Ramsonde hardness value, was 15.8 in 2023; it was 6.7 in 2022 (Fig. 16, right panel). Thus, this winter was characterized by less deep, but more densely packed snow than last year.

In general, weather conditions were favorable for conducting aerial surveys this winter. Furthermore, by mid-January the ground was completely covered in snow, which is beneficial when counting moose on survey plots.

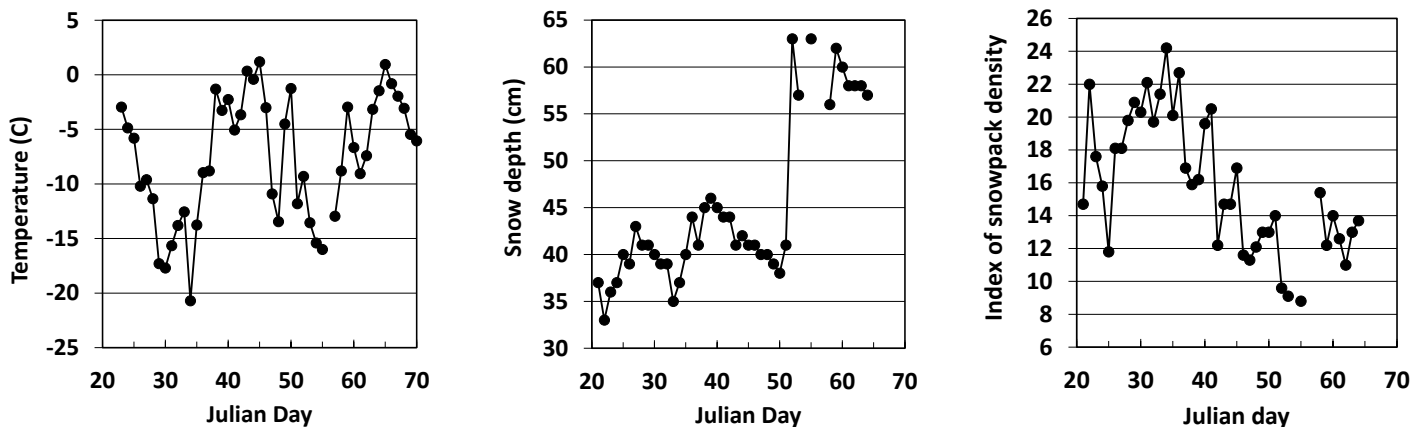


Fig. 16 Average of the daily maximum and daily minimum temperature (left), snow depth (middle), and daily snowpack density (right) during the 2023 winter study on Isle Royale. Density was estimated as the Ramsonde hardness value calculated using a penetrometer.

Appendix—The table below summarizes the data contained in the 2022-2023 annual report.

Variable/parameter	2022/2023 Estimate	Notes
Wolf abundance	31 wolves	Based on winter observations of wolves and tracks from ground and aircraft in winter.
Moose abundance	967 moose	Based on stratified random sampling method involving counting moose on census plots in winter.
Moose recruitment rate	1.7%	Based on the number of moose which were calves on census plots.
Per-capita kill rate	0.52 moose killed, per wolf, per month	Based on evidence that 26 moose were fed on by 31 wolves over a 39-day period.
Predation rate	10%	Calculated as that annual per-capita kill rate multiplied by the ratio of wolves to moose.
Terminal browsing on balsam fir	51%	Based on data collected along Huginnin Loop transect.
Fox index	25.4	Calculated as the sum of two indices: (i) fox observations per 100 hours of flying in winter, plus (ii) the total number of foxes seen on kills.
Hare index	9.6 hares per 100 km hiked	Based on observing the number of hares seen per 100 km hiked in summer.
Beaver	233 colonies	Based on aerial surveys to detect beaver food caches and other fresh activity in fall.
Otter	Present in 83 sections	Based on observations of otter tracks mapped at a scale of square-mile sections during aerial surveys
Average snow depth	45 cm	Based on daily measurements at Windigo during winter study.
Average temperature	-7.8°C	Based on daily measurements at Windigo during winter study.
Average Ramsonde hardness (snow density)	15.8	Based on daily measurements at Windigo during winter study.

Back cover photograph: A bull moose bedded down amongst blue bead lilies in spring.





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