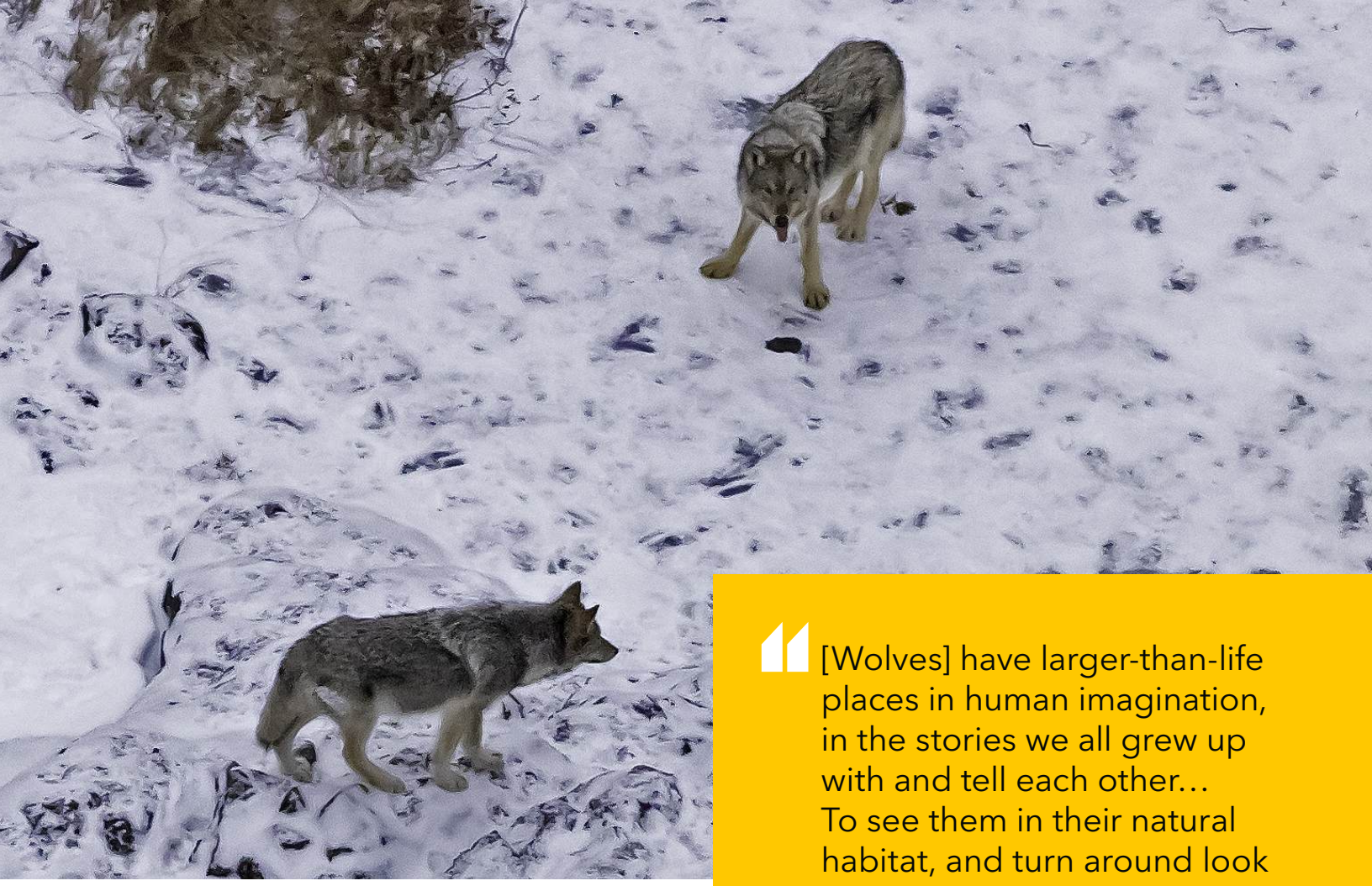
2023-2024

Wolves

Ecological Studies of Wolves on Isle Royale



> [Wolves] have larger-than-life places in human imagination, in the stories we all grew up with and tell each other… To see them in their natural habitat, and turn around look curiously at us…is really, really a special moment that I will treasure for my entire life.

– Colorado Governor Jared Polis after participating in Colorado Parks and Wildlife's release of five gray wolves onto public land in December 2023 (*CBS News Colorado*)

Ecological Studies of Wolves on Isle Royale

Annual Report 2023-2024

by

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April 2024

Support and Contributions

During the past year, major support for these studies was received from the National Park Service (CESU Task Agreement Numbers: P22AC00193, P18AC00331, and P24AC00220), National Science Foundation (DEB-1939399), McIntire Stennis, Robert Bateman Endowment at the Michigan Tech Fund, James L. Bigley Revocable Trust, the Suzanne Scott and Larry Fuerst Isle Royale Endowment Fund, the Wolf-Moose Foundation, and Detroit Zoological Society.

For the period, 1 January 2023 through 31 January 2024, additional contributions were received from the following organizations and individuals: Carol A. Argentati, Dianne Ashley and John Bumby, Dorthey L. Behrend, Ann and Darrel Bimberg, Jerry and Jennifer Boeckman, Bob J. Bollinger, Joseph V. Brazie, Emily Bretl, Linda Brewster, Sheri A. Buller, Anna Burke, Michelle Campbell, Zan Ceeley and Laura Christensen, Alison J. Clarke, Patricia Clements, Donald C. Close, Ryan and Linda Collier, Joel Dalton, Jacob W. Depper, Francis DeRoos, Adrienne Detanico, Detroit Zoological Society, Jennifer Dietzen, Elizabeth H. Donoghue, Natalie L. Dorrler-Hyde, Bruce Dziadzio, Ronald and Barbara Eckoff, James Eder, Susan Elsner, Larry Fuerst and Suzanne Scott, General Motors Corporation, Michael George, Donald and Loretta Gossett, Edith N. Greene, Amanda Griggs, Randolf A. Gschwind, Steven and Lila Hammer, Hal W. Hanson, John and Heidi Harlander, Marley Hatfield, Mollie Hilliard, Jeffrey Holden and Sandra Noll, Joshua Hunter, Robert and Sally Irmiger, Isle Royale & Keweenaw Parks Association, Megan Kaiser, Bruce Kehl, WK Kellogg Foundation, Kathleen Keup, Sandra Khalil, Dr. Paul Myron Kotila, Dylan Kwast, Scott Lamparski, John R. Lane, Robert Latta, Steven Leatherman, Dana and Donna Lowell, William and Nicole Maier, Lisa Martin, Annette Matzen, Michael and Linda Meetz, Paul S. Mueller, Mark Mullican, Sarah Mullican, Richard and Beatrice Murray, Paul and Anne Nagi, Joseph Olenik, Oxie Farm, Michael and Karl Palmer, Janet L. Parker, Mary G. Peters, Rolf and Carolyn Peterson, Steven Pope, Jason and Hannah Porritt, Ronald and Julie Porritt, Carolyn Raski, Kathleen Rhodes, Jay Richardson, Robert and Darcy Rutkowski, Jeffrey Sailor, Salesforce Inc., Matthew Sanford, Patrick J. Schafer, John and Linda Schakenbach, Jesse A. Scott, Seth and Jodie Shannon, Tyler and Rachell Ann Shannon, Joan Silaco, Alec Smith, Gregg and Judy Smith, Stantec Consulting Services Inc., Russell and Barbara Tabbert, United Health Group, Cecilia R. Vanden Heuvel, Bridgett VonHoldt, Stephen Vrla, Leah and John Vucetich, John Warming, David K. Weaver, Paul and Emily Weber, April L. Willbur, Dawn Williams, Shane Williams, Cindy Wills, and Albert and Frances Wilson.

Karen Bacula has been of critical value for helping to 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–Loreen Niewenhuis (leader), April Wilbur, and Zan Ceeley
Team IB–Clay Ecklund (leader), Adrienne Detanico, Seth Shannon, and Tyler Shannon
Team IC–Bob Bollinger (leader), Matt Sanford, and John Warming
Team ID–Wayne Shannon (leader), Ron Porritt, Michael George, Annette Matzen, Anne Nagi, and Joe Olenik

Team IIA–Lynn-Anne Vesper (leader), Jennifer Dietzen, Michael Campbell, Josh Hunter, Shane Williams, and Jon Jonas
Team IIB–Karen Bacula (leader), Dawn Williams, Sarah Mullican, Mark Mullican, and Steve Leatherman
Team IIC–Patrick Huver (leader), Garrett Craig, Marley Hatfield, Steven Pope, and Sandra Carlson

Team IIIA–Julie Weist (leader), Stephen Vrla, and Elizabeth Donoghue
Team IIIB–Jeff Holden (leader), Cecelia Vanden Heuvel, Anna Burke, Alec Smith, Scott Lamparski, and Jacob Depper
Team IIIC–Erin Parker (leader), Amanda Griggs, and Robbie Latta

Team IVA–Stephen Vrla (leader), Megan Kaiser, Dylan Kwast, Jesse Scott, Cindy Wills, and Bruce Dziadzio
Team IVB–Karen Bacula (leader), Kathy Keup, Natalie Dorrler-Hyde, and Emily Bretl

Moosewatch for Educators–Karen Bacula (leader), Kyle Lorditch, Becky Cassel, Drew Denzin, Ed Thomas, Alina Soha, Carlie Hacha, and Roy Moffitt

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.

Ecological Studies of Wolves on Isle Royale

SUMMARY

In January 2024, the best estimate of wolf population size was 30 wolves, which is similar to last year's estimate of 31 wolves (Fig. 1). For context, in 2022 there were estimated to be 28 wolves in the population—thus, the number of wolves in the population is thought to have remained relatively stable over the last few years. The wolf population likely includes a West Pack with at least four wolves, a Middle Pack with seven wolves, an East Pack with 13 wolves, and a Northeast Pack with five wolves, and one wolf at the east end of the island which appeared to be living alone. At least three litters of pups were born in April 2023, given that we saw at least one nine-month-old pup amongst wolves in the Middle Pack, East Pack, and Northeast Pack. We found no evidence suggesting that pups were born to the West Pack in April 2023. It is important to note that this year's survey of the wolf population took place over a two-week period, as opposed to the usual seven-week period, meaning that wolf abundance, pack sizes, and demography are estimated on the basis of fewer observations than is typical (Fig. 1). The reason for the unusually short survey period this winter was a prolonged period of above-freezing temperatures, which impacted ice conditions on the harbor and made the ice unsuitable for the survey aircraft to land upon.

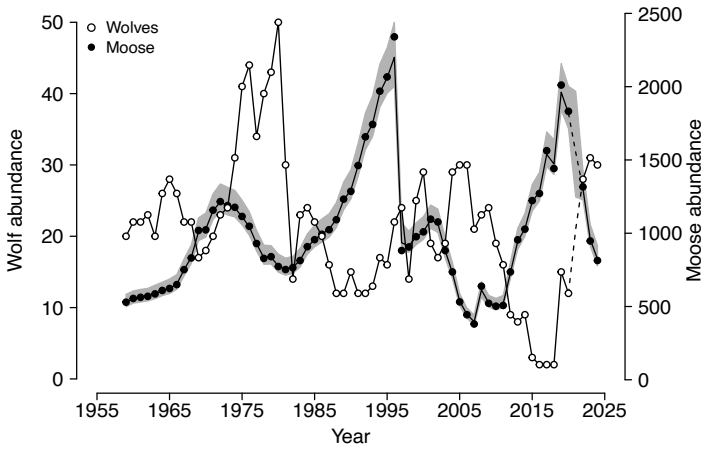

Fig. 1 *Fluctuations in the abundance of wolves and moose in Isle Royale National Park, 1959-2024. Wolf and moose population estimates are based on aerial surveys during winter (January-March). Estimates of moose abundance and 95 percent Bayesian credible intervals (gray shaded area) were derived from a Gompertz state-space model (Hoy et al. 2020). Note that surveys to estimate wolf and moose abundance did not take place in 2021 because of the COVID-19 pandemic. Those missing data are the reason why a dashed line connects the estimates of wolf and moose abundance between 2020 and 2022. The sudden increase in wolf abundance between 2018 and 2019 is the result of 19 wolves being translocated to the island.*

The estimated abundance of moose is 840, which is a 14 percent decline from last year's estimate (Fig. 1). Longer-term population trends suggest that the moose population had increased greatly over an eight-year period (2011-2019), but then declined over the last five years. The estimated proportion of the moose population that is newly recruited individuals (i.e., nine-month-old calves) was 5.5 percent, which is higher than last year's estimate of 1.7 percent, but still substantially lower than the long-term average recruitment rate of 13 percent. That low recruitment rate partly explains why the moose population has continued to decline over the past year. The density of moose continued to be highest at the east end of the island. Predation by wolves seems to be an important factor contributing to the decline in moose abundance.

For more information, go to **isleroyalewolf.org** and visit "Wolves and Moose of Isle Royale" on Facebook (**facebook.com/wolvesandmooseofisleroyale**) and Instagram (**instagram.com/wolvesandmooseofisleroyale**).

PERSONNEL AND LOGISTICS

In summer 2023, 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 Jack Schafer, Wesley McGee, Louis Good, and Suellen Ronk. Additional summer fieldwork was carried out by Ron Eckoff, Dick Murray, and Jay and Terry Brasher. During the summer field season, many park staff and visitors contributed key observations and 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 of other causes.

Lab work continued to include updating the curation of wolf and moose bone collections in partnership with Martin Hobmeier and Anne Lewellen from the U.S. National Park Service (NPS). That lab work was led by Leah Vucetich, Sarah Arnold, and Zoie Schafer with the assistance of Jack Schafer, J.T. Boudreau, Robby MacKinnon, Madelyn Dechane, Danica Wrobel, and Ella Roach. Lab work also included the analysis of balsam fir samples led by Jasmine Terry-Shindelman and Sarah Arnold.

In 2024, the 65th annual winter study was conducted during 19 January to 31 January. Winter fieldwork was led by Rolf Peterson and Sarah Hoy, with key contributions provided by pilot Don L. Murray (UpNorth Aerials). Isabella Evavold and Amelia Evavold provided daily fieldwork on skis to collect data on moose and balsam fir. Important transportation assistance was provided by Wisk Air Helicopters Ltd. and Alex Schmidt (NPS). The U.S. National Weather Service in Marquette, Michigan, provided information about daily weather and ice conditions over a four-week period between January and February, which was valuable for planning aerial survey work and other fieldwork activities.

THE WOLF POPULATION

In January 2024, the best estimate is that the wolf population consisted of 30 wolves, which included four packs and one wolf living alone (Fig. 1). That estimate is partly based on observing:

- tracks of at least four wolves from the West Pack;
- direct observations of at least 13 wolves from the East Pack;
- direct observations of at least two wolves from the Middle Pack; and
- direct observations of a wolf traveling alone near Moskey Basin.

Those observations were all made on a single day (20 January) and indicate that the population consisted of a minimum of 20 wolves. However, two additional observations made on 26 January indicate that the minimum of 20 wolves is an underestimate of the wolf population's abundance. First, we observed at least seven wolves in the Middle Pack, suggesting that the population consisted of at least 25 wolves. Second, we observed what appeared to be a fourth pack at the far east end of the island (Northeast Pack) consisting of at least five wolves. This second observation (along with the first observation) suggests that the population likely consists of at least 30 wolves.

Those observations suggest that the best estimate of wolf abundance is 30. However, it is important to consider that estimate in light of the unprecedentedly brief monitoring period. Specifically, the record-breaking warm temperatures meant we could only conduct aerial surveys over a two-week period in January (see Weather and Ice). For context, we typically conduct aerial surveys over a seven-week period. As a result of this unusually short monitoring period, there is a risk of double counting or missing some wolves. However, additional insights about the wolf population are likely to come from the genetic analysis of DNA extracted from scat and tissue samples that we collected over the past year. That genetic research is being led by Dr. Kristin Brzeski and Sam Hervey (both MTU). In the paragraphs below, we summarize what has been learned about the wolf populations over the past year.

The West Pack consisted of at least four wolves. That inference is based on repeatedly seeing fresh tracks left by a group of at least four wolves in January around the Huginnin Loop, Feldtmann Lake Trail, and Grace Creek areas, and along the southwestern shore between Lake Halloran and Houghton Point. For context, last year we estimated that the West Pack contained five wolves. This winter, we found the remains of three moose which appeared to have been killed by wolves within the West Pack's territory. We did not find any evidence that a litter of pups was born in the West Pack in April 2023. This past summer, a dead wolf was found within the West Pack's territory. More precisely, on 3 June 2023, a wolf was found floating in the water near the shore by Huginnin Cove Campground (Fig. 2). Examination of that wolf revealed that it was a young adult female which likely died in late May. There were several deep puncture wounds on her neck (Fig. 2), and wounds on her face, ear, and groin area. All of those injuries are consistent with the female having been killed by another wolf or wolves. Other than those wounds, the female appeared to be in good condition.

Fig. 2 *Young adult female wolf found dead near the shore of Huginnin Cove Campground in June 2023. The wolf's injuries were consistent with having been killed by other wolves.*

The female wolf had never been captured and outfitted with ear-tags or a GPS/radio collar. Tissue and hair samples were collected for genetic analysis and to provide further insights about the identity of this female wolf, such as whether she was likely an offspring of the West Pack or another pack.

The Middle Pack consisted of seven wolves, which are thought to include a breeding pair plus several nine-month-old pups (Fig. 3, top panel). That inference is based on several observations of a group of wolves feeding on the carcass of a young adult moose which had been killed on the ice at the western end of Lake Siskiwit. Two of the wolves in this pack had ear-tags and a GPS/radio collar, and at least one of the wolves in this group had a rope-tail (a tail which appears to be much thinner than usual), a trait that we have observed before in wolves born to the East Pack, but not the West Pack. On 22 January 2024, we visited a moose carcass on Lake Siskiwit to collect scats from the wolves that had been feeding on it (Fig. 3, bottom panel). Genetic analysis of those scats may provide further insights about the identity of the wolves which formed Middle Pack.

Fig. 3 *Top image: Seven wolves from Middle Pack on the ice at Siskiwit Lake on 26 January 2024. Bottom image: Pilot Don Murray (UpNorth Aerials) collecting samples from the remains of a young adult moose that wolves from the Middle Pack were observed to be feeding upon on the ice at Siskiwit Lake on 22 January 2024. Scat samples from wolves that were feeding on the moose carcass were also collected for genetic analysis.*

The East Pack is thought to consist of at least 13 wolves. That inference is based on observing a group of eight and a group of five wolves in very close proximity to each other near a recent kill (Fig. 4) and wolf tracks connecting the two groups. For context, we estimated that there were 11 wolves and 13 wolves in the East Pack in 2022 and 2023, respectively. At least two wolves in the East Pack had been outfitted with ear-tags and GPS/radio collars in prior years, and at least one of those wolves was a nine-month-old pup. This winter, we found the remains of two moose that were probably killed by the East Pack. Specifically, on the ice at Chippewa Harbor, we saw the remains of a moose that had been killed shortly before the start of winter study, and we also observed wolves considered to be from the East Pack resting on the ice near this kill during winter study. Additionally, on the morning of 20 January 2024, we observed the East Pack feeding on the carcass of a moose that they had killed a few hours earlier, in a swampy area just east of Lake Mason.

The Northeast Pack is thought to consist of at least five wolves. That inference is based on observing four wolves feeding on the carcass of a five-day-old kill by Tobin Creek on 26 January 2024 (Fig. 5). On that same day and time, we also saw another wolf with a full stomach on Tobin Harbor, which we assume was part of the group that was feeding on the Tobin Creek kill a short distance away. None of the wolves that were seen in the Tobin Creek/Harbor area were outfitted with ear-tags or a GPS/radio collar. At least one of those four wolves seen feeding on the Tobin Creek kill was a nine-month-old pup.

In addition to the four packs described above, we also saw a single wolf traveling along the ice between Daisy Farm and Moskey Basin on 20 January 2024 (on that same day and time the East Pack wolves were near the kill by Lake Mason). We checked on that lone wolf several times, and it still appeared to be alone and traveling in a different direction from the East Pack's location. Therefore, we assume this wolf is not closely affiliated with the East Pack. Additionally, on 26 January 2024, we saw a lone wolf walking along the ice between Daisy Farm and Moskey Basin—again, that wolf was not traveling toward or away from the areas where we had seen the East Pack previously, or toward or away from the group of wolves seen at the Tobin Creek/Harbor area that same day. Based on those observations, we conclude that there was at least one wolf which appeared to be alone at the east end of the Isle Royale in late January.

Fig. 4 *Wolves from the East Pack walking and resting on the ice just north of where they had killed a moose near Lake Mason on the morning of 20 January 2024.*

In summary, our observations suggest that this winter the wolf population likely consisted of 30 wolves, including four territorial packs: a West Pack with at least four wolves, a Middle Pack with at least seven wolves, an East Pack with at least 13 wolves, and a Northeast Pack with at least five wolves, as well as one wolf living alone. For context, in 2023 the wolf population consisted of 31 wolves, including three packs, and several other wolves that were either loners, pairs, or only loosely affiliated with packs. In 2022, the population consisted of 28 wolves and included only two well-established packs. Therefore, the abundance of wolves on Isle Royale appears to have stabilized between 28 and 31 wolves over the past three years. There is evidence that three litters were born in April 2023—in the Middle Pack, East Pack, and Northeast Pack—but we did not find any evidence suggesting that the West Pack produced a litter. For context, last year we observed evidence suggesting that three or possibly four litters were born in April 2022. Our observations in 2024 suggest that wolves killed at least seven moose over an approximately three-week period in January. All of those moose were killed along the southern portion of Isle Royale (Fig. 6). Several of those kills appeared to be the result of wolves chasing moose out onto the ice—where wolves would likely have an advantage because of the lack of snow covering the ice and the lack of traction that moose hooves have on glare ice.

Fig. 5 *Four wolves thought to belong to the Northeast Pack were observed to be feeding on the carcass of a moose by Tobin Creek on 26 January 2024.*

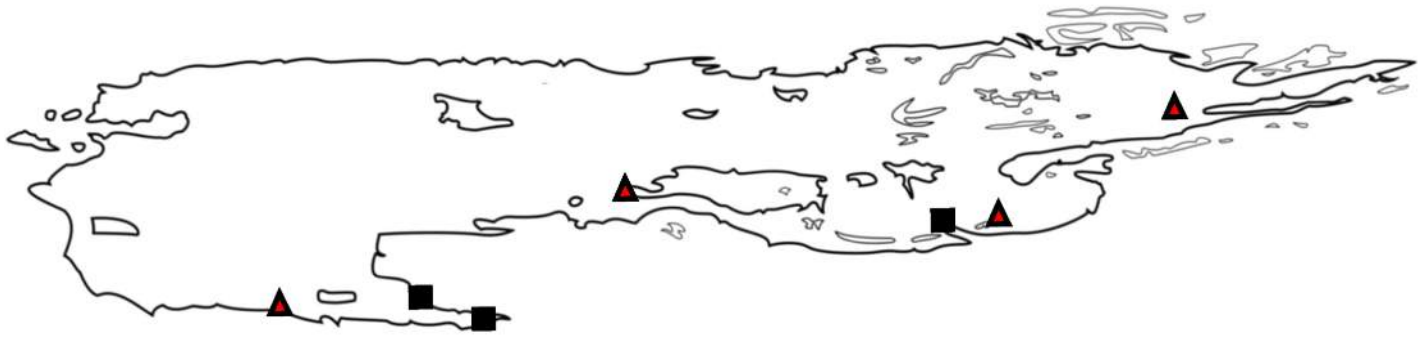

Fig. 6 *Map showing the locations of dead moose found during winter study. The four red triangles show locations where we detected moose killed by wolves during 19-26 January. The black squares represent locations where moose were killed shortly before the start of winter study.*

THE MOOSE POPULATION

The 2024 moose census was conducted during 22-27 January and resulted in an estimated abundance of 840 moose (95 percent Bayesian Credible Interval, BCI = [761, 938], see Fig. 1). Moose density was estimated to be lowest in the western portion of Isle Royale (0.99 moose/km^2), slightly higher in the middle portion of the island (1.28 moose/km^2), and highest in the eastern portion of the island (2.41 moose/km^2, Fig. 7).

We estimated moose abundance on the assumption of an 80 percent sightability correction factor. The rationale for selecting that correction factor is based on noting that over 80 percent of the moose that we observed on survey plots this winter were easy to detect from the survey plane because the moose were in areas which were open or had deciduous cover (i.e., areas with no foliage to obscure the view of moose in winter). By contrast, last year only 30 percent of the moose that we detected on survey plots were in open areas or areas with deciduous cover. The high visibility of moose this year can be attributed to weather conditions being ideal for flying and counting moose throughout the census (e.g., overcast skies and low winds) and the unusual snow conditions this winter. More precisely, in a typical year snow tends to be deepest in open areas and areas with deciduous cover, and moose tend to spend less time in those areas because deep snow makes it more energetically costly for moose to move around and forage. However, this year there was an absence of snow cover until approximately 11 January and very low snow depth (less than 28 cm) afterward, meaning that moose could easily move around and forage in more open/deciduous areas. Using a sightability correction factor of 80 percent is consistent with the findings of Peterson and Page (1983) at Isle Royale, and assessments of conditions affecting moose sightability during surveys in Alaska (Oehlers et al. 2012 in Alces) and British Columbia (Quayle et al. 2001 in Alces). Nevertheless, it can also be useful to know what the estimated abundance would be if a different sightability correction factor had been assumed. A sightability of 70 percent would have yielded an estimate of 952 moose (95 percent BCI = [685, 841]), and a sightability of 90 percent would have yielded an estimate of 749 moose (95 percent BCI = [860, 1,056]). Finally, the estimated abundance of 840 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 840 moose is 14 percent lower than last year's estimate. For context, the moose population is estimated to have declined by around 28 percent between 2022 and 2023. Therefore, the rate of decline has slowed over the past 12 months. Overall, the abundance of moose has declined by almost 60 percent since 2019, when the moose population appears to have peaked at just over 2,000 moose. In other words, the average annual per capita rate of population change during this five-year period has been –12 percent/year. Taking account of statistical uncertainties, it is reasonable to infer that the moose population grew rapidly for a number of years (2010-2019) and has declined substantially in recent years (Fig. 1).

The continued decline in moose abundance is consistent with having observed a low recruitment rate. Of the 127

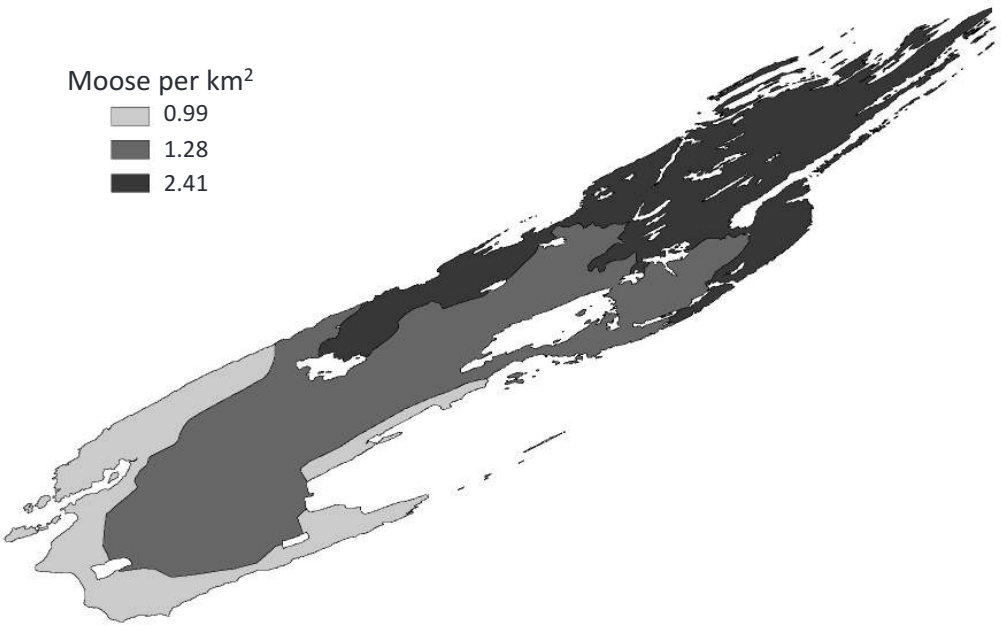

Fig. 7 *The estimated density of moose on Isle Royale during winter 2024. Estimates are based on aerial surveys of 91 plots that comprised 17 percent of the main island's area.*

moose seen on survey plots during the aerial census, only seven were nine-month-old calves, representing a recruitment rate of 5.5 percent (95 percent CI = 2-11 percent). This year's recruitment rate of 5.5 percent is higher than last year's estimate of 1.7 percent, but still substantially lower than the long-term average of 13.3 percent moose recruitment (Fig. 8). Furthermore, the recruitment rate has been well below average for each of the past five years, which is consistent with the moose population having declined significantly in recent years. Other evidence that recruitment rates are low this year comes from noting that when recruitment rates are high, we tend to observe cows raising twins—however, we did not observe any cows with twins this winter.

Over the past year, the proportion of adult moose dying from malnutrition has dramatically declined, and the proportion dying from wolf predation has greatly increased. That inference is based on necropsies of moose which died during the past year. Each year, we conduct extensive searches for the remains of dead moose, and we carefully examine those remains to determine the causes of death. In a typical year, over 75 percent of moose die from wolf predation and less than 5 percent die from malnutrition. That statistic provides context for what we have seen in recent years:

- In 2021, 59 percent (of 69 necropsied moose) died from wolf predation and 30 percent died from malnutrition.
- In 2022, 48 percent (of 76 moose) died from wolf predation and 46 percent died from malnutrition.
- In 2023, 92 percent (of 26 moose) died from wolf predation and only 4 percent died from malnutrition.

Those observations suggest that over the past year there has been a notable increase in the proportion of moose killed by wolves and a decline in the proportion dying from malnutrition—back to levels that are similar to long-term averages. (Note that we do not have estimates of wolf per capita kill rates or predation rate on moose for this winter because of the unusually short winter study period.)

In summary, over the past year the moose population has continued to decline, which is partly attributable to low recruitment of calves. This decline in moose abundance and recruitment rate represents an ongoing pattern which we first observed in 2019—although the rate of decline over the past year is notably lower than in previous years. While malnutrition appeared to be a very important cause of mortality for adult moose between 2019 and 2022, there has been a substantial decline in the proportion of moose dying from malnutrition over the past year. Wolf predation is once again the primary cause of mortality for adult moose.

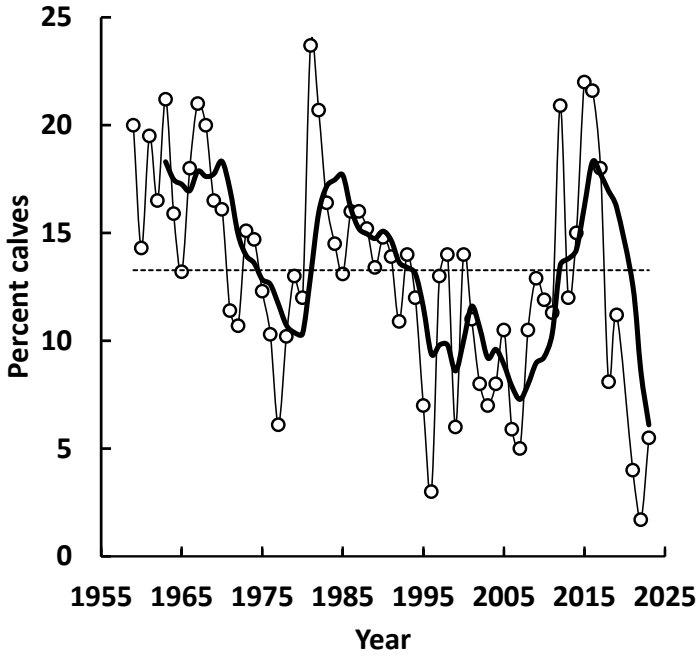

Fig. 8 *Long-term trends (1959-2023) in the percentage of the moose population that are nine-month-old calves. The 64-year average (13.3 percent) is marked by the dashed line, and the thicker line represents the five-year moving average.*

RESEARCH HIGHLIGHT

What Studying Moose Bones for 60 Years Teaches Us about Diseases in Humans

For over 60 years, researchers, students, and citizen scientists have been searching for the remains of moose which died from natural causes on Isle Royale (Fig. 9) and conducting necropsies to understand how and why the health and abundance of the moose population changes over time. In addition to conducting necropsies to determine the cause of death for each moose (i.e., predation or malnutrition), we also carefully check each moose's skeletal remains to look for signs of several bone diseases. Those long-term efforts resulted in a new study, published earlier this year in the journal Osteoarthritis & Cartilage, which investigated links among three chronic bone diseases known to affect both humans and other mammals, including moose: periodontitis, osteoporosis, and osteoarthritis.

Periodontitis (periodontal disease) is caused by bacterial infections in the gums and bone surrounding teeth. In more severe cases, periodontitis leads to a loss of the bone surrounding teeth and ultimately tooth loss (Fig. 10). Osteoporosis is a loss of bone mineral density, which occurs when the rate that new bone cells form is slower than the rate at which old bone cells are broken down. Osteoporosis tends to result in bones being more fragile and more likely to break or fracture (Fig. 11). Osteoarthritis is a progressive and often disabling disease caused by degeneration of cartilage in joints, such as hip joints (Fig. 12). As people get older, they are more likely to develop periodontitis, osteoporosis, and osteoarthritis. These three diseases are thought to have a negative impact on quality of life for millions of people around the world and place a huge burden on health and social care systems. Consequently, there is an urgent need to better understand the links among these diseases and the factors that cause them.

Fig. 9 *Each summer, teams of students, and citizen scientists participate in one-week-long "Moosewatch" expeditions which involve backpacking across Isle Royale and searching for the remains of dead moose.*

For decades, doctors have suspected that there are important links between these three bone diseases. However, it can be complicated to study links between these diseases in humans because the likelihood of getting these diseases can also be influenced by a wide variety of confounding risk factors—such as whether or not a person is obese, smokes cigarettes, drinks alcohol, has a poor-quality diet, or has good access to healthcare. However, many of those confounding risk factors (e.g., obesity, smoking, alcohol consumption) do not apply to wild animals, such as moose on Isle Royale.

In total, the new study assessed both the prevalence and severity of each of the three diseases in over 2,000 adult moose which died between 1958 and 2021. The key finding of the study was that individuals which had periodontitis were much more likely to have severe forms of osteoarthritis and osteoporosis. More precisely, female moose with periodontitis were 88 percent more likely to have severe osteoarthritis and more than twice as likely to have severe osteoporosis than female moose which didn't have periodontitis. Similarly, male moose with

Fig. 10 *Top image: The upper row of teeth (molars) on a moose which did not exhibit signs of periodontal disease (degradation and loss of the bone surrounding the teeth). Bottom image: The upper row of teeth on a moose which had severe periodontal disease, causing loss of the bone surrounding the teeth to such an extent that the moose lost a molar.*

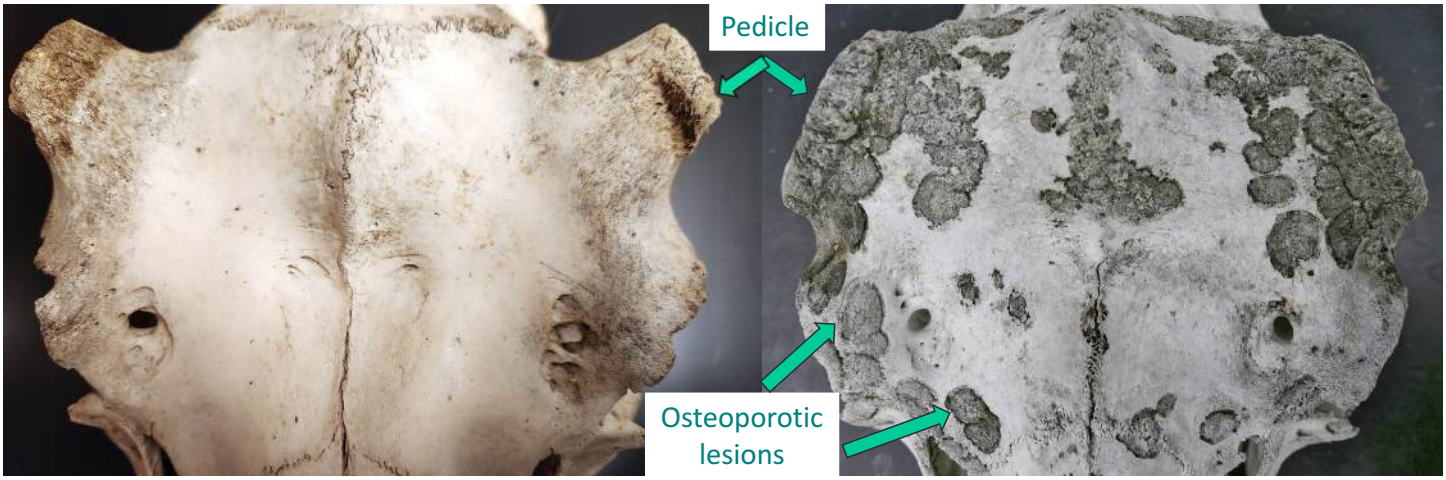

Fig. 11 *Left image: The skull of a healthy young bull moose whose skull did not exhibit any signs of osteoporosis. Right image: The skull of a bull moose whose skull is covered in osteoporotic lesions, especially around the pedicles (place where antlers attach to the skull). Moose with osteoporotic lesions tend to have lower bone density (i.e., osteoporosis) in other parts of their skeleton.*

periodontitis were 63 percent more likely to have severe osteoarthritis and more than three times as likely to have severe osteoporosis than male moose which didn't have periodontitis.

While the study on moose didn't evaluate the cellular mechanisms underlying the links between these three diseases, it is thought that periodontitis may increase the risk that individuals will develop osteoporosis and osteoarthritis because of the impact that the bacterial pathogens causing periodontitis have on proinflammatory cytokines. Proinflammatory cytokines are small proteins secreted by cells in the immune system; these cytokines can cause inflammation and tissue destruction, which may exacerbate the process of osteoarthritis in joints. These proinflammatory cytokines can also impair cells in the body that grow and heal existing bones, whilst also increasing the activity of cells that break down bones—thereby leading to individuals having a greater risk of osteoporosis.

Whatever the underlying mechanism may be, this new research adds to a growing body of evidence suggesting that diseases such as periodontitis, which affect the health of teeth and gums, increase the risk of individuals developing other serious health conditions, including: diabetes, strokes, cardiovascular disease, and pneumonia. In doing so, the research highlights the importance of developing and maintaining good oral hygiene habits. It also highlights the value of striving to achieve a broad understanding of linkages between bone diseases which is applicable across species.

This new study is the result of a collaboration between Sarah Hoy, John Vucetich, Leah Vucetich, and Rolf Peterson from MTU; Mary Hindelang, a former PhD student from MTU; and Virginia Kraus and Janet Huebner from the Duke Molecular Physiology Department and Department of Medicine at Duke University School of Medicine.

Fig. 12 *Top image: A healthy hip socket on a moose pelvis. Bottom image: A severely arthritic hip socket on a moose pelvis.*

VEGETATION

Balsam fir is a common and important tree species in boreal forest ecosystems and is also the primary forage species for moose in winter (representing about 50 percent of their winter diet). Over the last decade, concerns have been raised about how balsam fir growth and recruitment (i.e., the rate that young fir saplings become mature cone-producing trees) was 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 2014 we have tagged and monitored balsam fir saplings—which were at least 175 cm tall at the time they were tagged—along an 11-km-long transect (representing a 10-ha area) at the west end of the island. We initially focused on fir saplings taller than 175 cm along this transect because 175 cm 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. Additionally, saplings taller than 175 cm are more likely to grow into mature, cone-producing trees. (Note that once a sapling is taller than 300 cm, its terminal leader is beyond the reach of a moose and the tree is likely to start producing cones in the near future.) Each spring, we record whether each tagged sapling is still alive, the total height of the sapling, how much it grew during the previous growing season, and whether its terminal leader was 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 2023, we observed that moose had browsed 31 percent of terminal leaders available and within their reach. (That estimate excludes saplings with heights greater than 300 cm and saplings that did not have a terminal leader because it had been browsed in previous years). That level of terminal browsing by moose is somewhat lower than the browse rates we have observed over the past six years, but approximately double the browse rate observed between 2014 and 2017 (Fig. 13, left panel).

Over the past five years, we observed evidence strongly suggesting that high levels of moose browsing has negatively impacted the survival, growth, and recruitment of young fir saplings. Specifically, we have observed:

- There has been a steady increase in the number of saplings dying each year, from less than 1 percent in 2019 to over 9 percent in 2023 (Fig. 13, right panel). In total, 22 percent of all tagged fir saplings (n = 647) that we monitor are now dead.
- There has been a decline in the number of new saplings that are over 175 cm in height. Specifically, between 2015 and 2018, we observed a total of 464 new saplings growing to be over 175 cm in height. However, since 2019, we have observed a total of only 40 new saplings reaching 175 cm in height.
- A large proportion of saplings that were once over 175 cm in height have since experienced a large

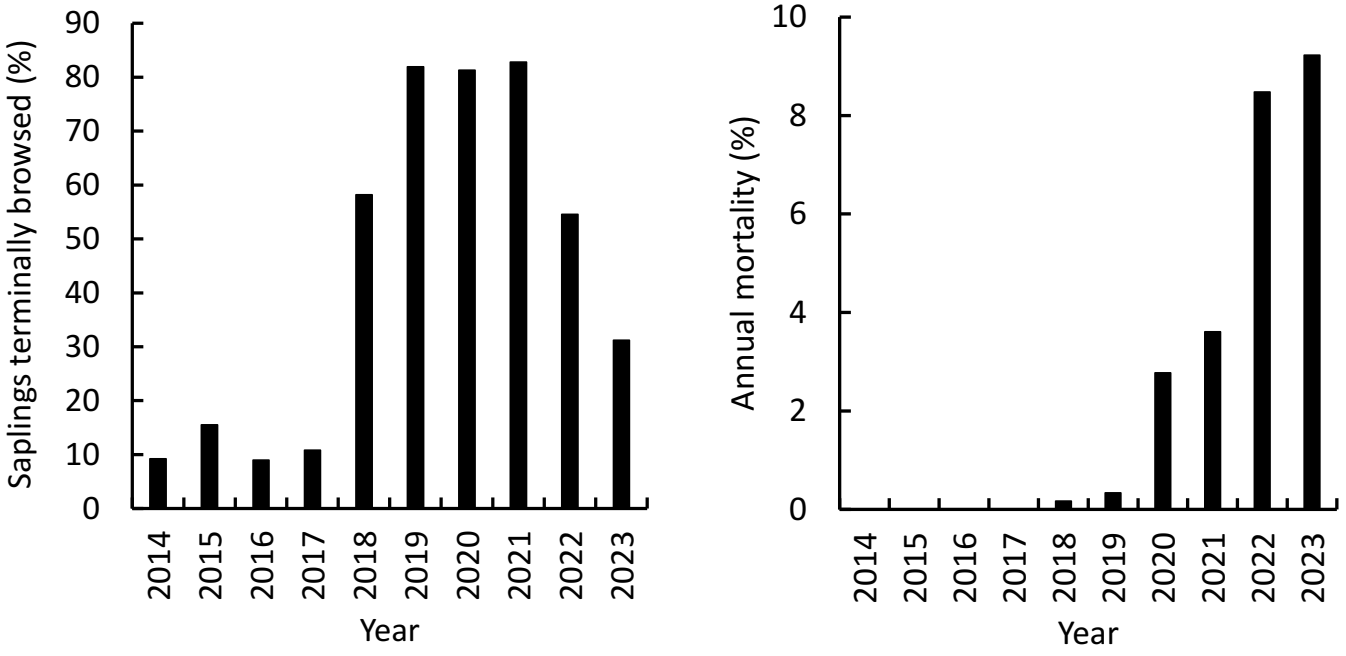

Fig. 13 *Left panel: The percentage of tagged balsam fir saplings whose terminal leader (main growing stem) was browsed by moose each year along a 11-km-long transect. Right panel: The percentage of tagged balsam fir saplings which died each year along the same 11-km-long transect.*

setback in growth. More precisely, 56 percent of the tagged fir saplings that we measured in 2023 (which were still alive) now have heights below 175 cm. The reason for that setback in growth is 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. Together, the increase in mortality and setback in growth has resulted in a steady decline in the number of saplings taller than 175 cm over the past five years.

- Less than 3 percent of the tagged saplings that we monitored in 2023 had heights greater than 300 cm, and the percentage of saplings over 300 cm in height has not changed substantially over time. This is noteworthy because trees less than 300 cm typically do not produce cones (necessary for the next generation of trees).
- The annual growth of terminal leaders (which were not browsed by moose) has also declined substantially over the past five years. For example, between 2015 and 2017, the mean annual growth of leaders was between 18.4 cm and 19.9 cm. However, since 2019, the mean annual growth of leaders was between 3.5 cm and 8.4 cm. In other words, the growth of leaders which escaped moose browsing is about two to four times less than it was prior to 2018.

Together, those findings suggest that high levels of moose browsing in previous years has severely limited fir growth and survival, and that the likelihood of fir saplings growing into mature canopy trees has been greatly reduced in recent years. That strong negative impact on fir sapling recruitment is noteworthy because many mature canopy fir trees (which produce cones) have died in this same region over the last few decades. More precisely, 479 mature balsam fir trees were tagged along the same 11-km-long transect (representing a 10-ha area) in 1988, and each year since then, we record whether each mature tree is still alive. In 2023, we observed that only 27 (5.6 percent) of these mature trees were still alive. In summary, the status of balsam fir across parts of the island continues to deteriorate and this issue has been getting progressively worse each year since 2018. Lastly, it is important to note that in addition to moose browsing, spruce budworm had a notable impact on the growth and survival of balsam fir between 2020 and 2022.

OTHER WILDLIFE

We are unable to estimate our index of fox abundance and otter presence this year given the unusually short winter survey period. However, it is relevant to note that during our aerial surveys, we observed a maximum of two foxes scavenging on moose carcasses, and two other foxes not on carcasses. We also observed a red fox and a black fox around the Windigo area. The red fox in the Windigo area appeared to be blind in one eye and is suspected to have glaucoma (Fig. 14, top panel).

Over the last year, populations of snowshoe hares decreased slightly from an estimated 9.6 hares seen per 100 km hiked during the summer of 2022 to 4.39 hares seen per 100 km hiked during the summer of 2023. We regularly observed bald eagles during this past winter and saw a maximum of five mature bald eagles feeding on the carcass of a moose (Fig. 14, bottom panel).

Fig. 14 *Top image: A red fox which was regularly seen around the Windigo area over the past year. The fox appeared to be blind in one eye. We shared a photograph of the fox with a local veterinarian (Brandon Hajdo-Fernandez) who suspects that the fox has glaucoma. Bottom image: Five mature bald eagles and a raven fed on the carcass of a moose that died along the south shore in late January 2024.*

WEATHER AND ICE

This year was a strong El Niño year in the Pacific Ocean and Western Hemisphere, which resulted in prolonged periods of above-freezing temperatures and below-average ice cover and snow depth this winter. Specifically, ice concentrations on Lake Superior were estimated to be 7 percent or less throughout January and into February—which is very close to the minimum value observed since 1973 (NOAA, coastwatch.glerl.noaa.gov/ice). At no point was there an ice bridge connecting Isle Royale to the mainland.

Temperatures were unusually mild and there were several days when nightly minimum temperatures did not drop below freezing. Overall, temperatures averaged –2.8°C during 19-30 January 2024 (Fig. 15, top panel). For context, between mid- and late January, temperatures averaged –11°C in 2023 and –10°C in 2022. Snow depth averaged 26 cm during winter study (Fig. 15, center panel). For context, snow depth averaged 39 cm and 49 cm between mid- and late January in 2023 and in 2022, respectively. Most snowfall occurred during a short period in mid-January. The average snowpack density, estimated as the "Ramsonde hardness" value, was 2.8 in 2024, in contrast to average values of 18.3 in 2023 and 5.9 in 2022 (Fig. 15, bottom panel). Thus, this winter was characterized by unusually warm temperatures and very little snow.

The unusually long period of above-freezing temperatures and low amount of ice coverage severely limited our ability to conduct aerial surveys this winter. More precisely, weather conditions meant that aerial surveys could only take place over a two-week period in January this winter, whereas we typically conduct surveys over a seven-week period between January and early March. This unusually short survey period occurred because the prolonged period of above-freezing temperatures reduced both the quality and thickness of ice covering the northeast end of Washington Harbor, where the survey plane takes off, lands, and is kept when not in use. Toward the end of January, several holes and cracks started to appear in the ice near the shoreline of the harbor, and slush and standing water started to accumulate on top of the ice—making it less suitable for aircraft operations (Fig. 16, left panel). On 29 January 2024, out of an abundance of caution, the decision was made to temporarily move the survey plane off the deteriorating ice and onto land (Fig. 16, right panel). That decision was made because above-freezing temperatures were expected to continue for several more days, and weather conditions had not been good enough (i.e., low visibility and cloud ceilings) for the pilot to fly back to the mainland between 27 and 29 January. The weather forecast for the next few days (30 January to

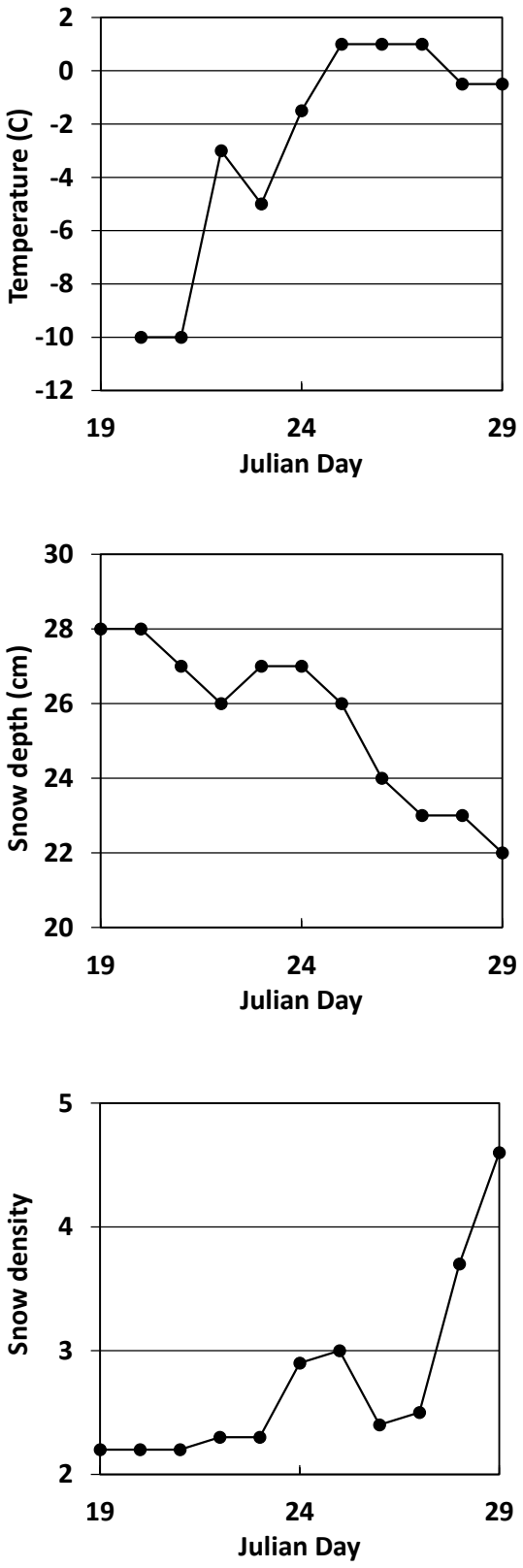

Fig. 15 *Average of the daily maximum and daily minimum temperature (top panel), snow depth (center panel) and daily snowpack density (bottom panel) during the 2024 winter study on Isle Royale. Density was estimated as the "Ramsonde hardness" value calculated using a penetrometer.*

Fig. 16 *Left image: Ice conditions on Washington Harbor on 27 January 2024 after three consecutive nights when temperatures did not drop below freezing. The warm temperatures resulted in a lot of standing water and slush on top of the ice. Right image: The survey plane (an Aeronca Champion) was temporarily moved onto land on 29 January.*

2 February) also suggested that weather conditions would not be good enough to allow for a flight back to the mainland. Fortunately, on the morning of 30 January, weather conditions turned out to be better than originally forecast, and the survey plane and pilot (UpNorth Aerials) were able to return to northern Minnesota.

Following the departure of the survey aircraft, it was decided that all winter fieldwork operations should be suspended. On 31 January 2024, all field crew returned to the mainland via helicopter (Wisk Air Helicopters Ltd.). (Note that travel via helicopter is not dependent on having good ice conditions). In early February, weather predictions suggested that sufficiently cold temperatures may return to Lake Superior and perhaps allow for the condition of ice on the harbor to improve by mid-February—offering some hope that aerial survey work could resume. However, the cold temperatures that were initially predicted did not materialize.

The circumstances and events described in this section are unprecedented. This year was the first time in 65 years that the survey plane has ever been moved onto land and that winter fieldwork operations have needed to conclude more than five weeks early due to poor ice conditions. We are grateful to the National Weather Service in Marquette, Michigan, for providing detailed daily weather reports for Isle Royale, which helped us plan fieldwork activities.

Appendix—The table below summarizes the data contained in the 2023-2024 annual report.

Variable/parameter	2023/2024 Estimate	Notes
Wolf abundance	30 wolves	Based on winter observations of wolves and tracks from ground and aircraft in winter.
Moose abundance	840 moose	Based on a stratified random sampling method involving counting moose on census plots in winter.
Moose recruitment rate	5.5%	Based on the number of moose which were calves on census plots.
Per-capita kill rate	–	Not estimated due to limited winter survey period.
Predation rate	–	Not estimated due to limited winter survey period.
Terminal browsing on balsam fir	31%	Based on data collected along Huginnin Loop transect.
Fox index	–	Not estimated due to limited winter survey period.
Hare index	4.39 hares per 100 km hiked	Based on observing the number of hares seen per 100 km hiked in summer.
Beaver	–	Not estimated.
Otter	–	Not estimated due to limited winter survey period.
Average snow depth	25.5 cm	Based on daily measurements at Windigo during winter study.
Average temperature	2.8°C	Based on daily measurements at Windigo during winter study.
Average Ramsonde hardness (snow density)	2.75	Based on daily measurements at Windigo during winter study.

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