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Ecological Studies of Wolves on Isle Royale, 2018-2019

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Ecological Studies of Wolves on Isle Royale

Wolves

2018-2019

"To see these wolves disappear into the forests of Isle Royale and to have an opportunity to start a new generation of wolves on the island, fulfilled a major objective in the first year of reestablishing the population."

- Phyllis Green, Superintendent, Isle Royale National Park, following the release of four wolves relocated from Ontario in March 2019

Ecological Studies of Wolves on Isle Royale

Annual Report 2018–2019

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Team I/IIA–Wayne Shannon (leader), Larry Fuerst, Ron Porritt
Team I/IIB–Barrett Warming and Clay Ecklund (leaders), Hal Hanson, Tom Offer-Westort
Team I/IIC–Thomas Rutti (leader), Michael George, Cathy More, Loreen Niewenhuis, Julie Timmer
Team I/IID–Joe Olenik and Chris Woeltje (leaders), Erik Freeman, Dan Goyen, Mark Kanitz, John Warming
Team IIIA–Jeff Holden and David Conrad (leaders), David Beck, Brianna LaBelle-Hahn, Scott Lamparski, Bonnie Verant
Team IIIB–Jason Deutsch (leader), Jim Arduin, Ryan Bottorf, Jim Clink, Erik Freeman, EuYew Tan
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Team IVA–Karen Bacula (leader), Mark Ode, Dylan Sweers, Greg Sweers
Team IVB–Paul Buzzard (leader), Irene Fiala, Erik Freeman, David Rolfes, John Wojciechowski

To learn more about how you can join one of our research expeditions, visit www.isleroyalewolf.org and click "Contribute & Participate." Tax-deductible donations to support continuing research on Isle Royale wolves and moose can be sent to Wolf-Moose Study, Michigan Tech Fund, Michigan Technological University, 1400 Townsend Drive, Houghton, Michigan 49931-1295. Thank you to all who help!

The results reported here are preliminary and, in some cases, represent findings of collaborators; please do not cite without consulting the authors. The views expressed here do not necessarily reflect those of the US National Park Service or the US National Science Foundation.

Ecological Studies of Wolves on Isle Royale

SUMMARY

Between 2009 and 2016 the wolf population dwindled from 24 to two wolves and remained at two until this past year. In June 2018 the US National Park Service (NPS) decided to restore wolf predation in Isle Royale National Park. In early October 2018 the NPS and the Grand Portage Band of Lake Superior Chippewa led an effort that moved one male and three female wolves from Minnesota to Isle Royale. The male died about a month later. The NPS reported the proximate cause of death as pneumonia. One of the females left the island in late January 2019 by crossing an ice bridge to the mainland. In March 2019 the NPS and Ontario Ministry of Natural Resources and Forestry led an effort that moved seven male and four female wolves from Ontario, Canada. The last two island-born wolves of Isle Royale also survived the past year, bringing the total number of wolves on Isle Royale to 15 by the end of March 2019 (eight males and seven females, Figure 1). Aerial observations suggested that the new wolves had not yet formed solid or stable social bonds by the end of winter study 2019, which is not surprising given how little time has passed since their arrival. The moose

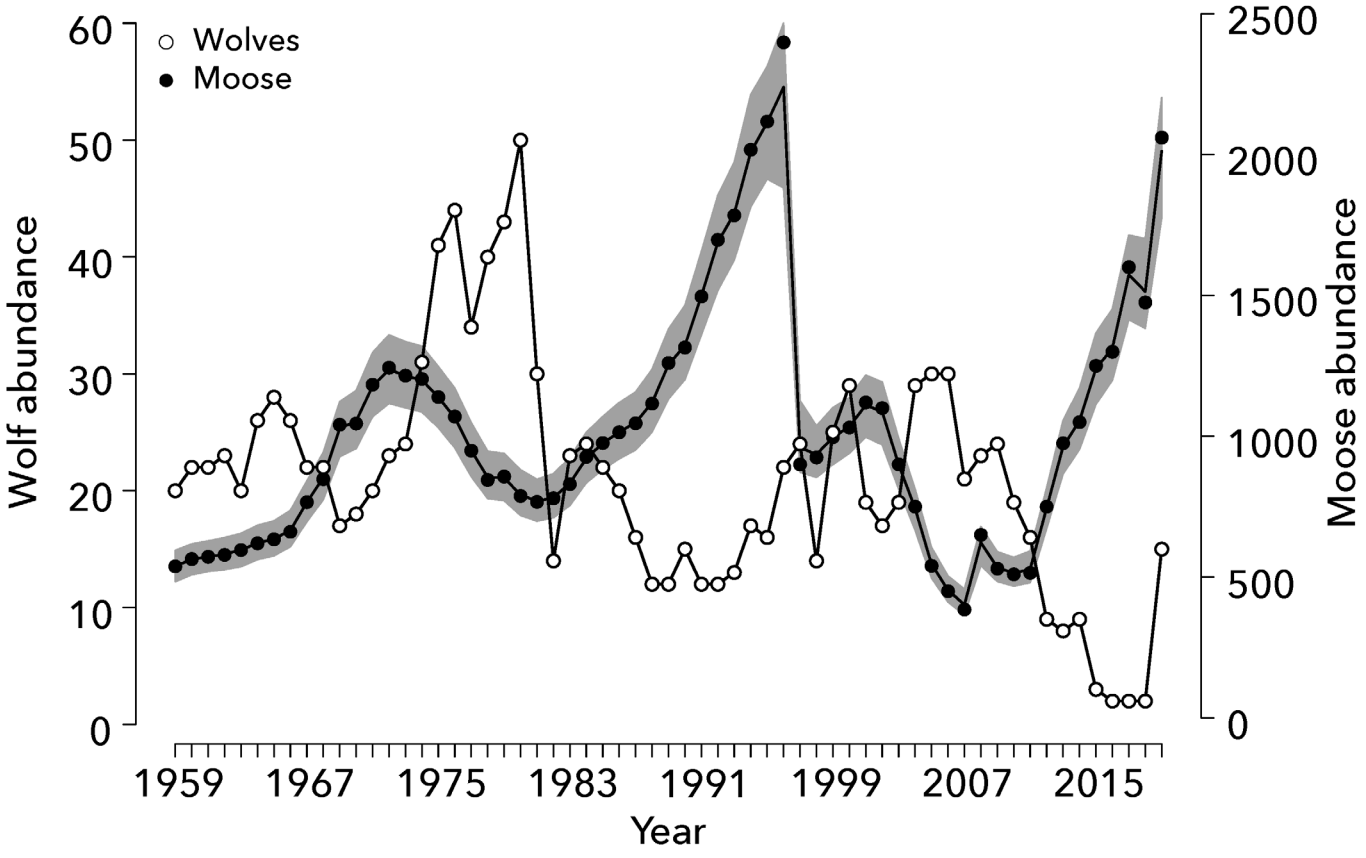

Figure 1. *Wolf and moose fluctuations in Isle Royale National Park, 1959–2019. Wolf population estimates (open circles) were based on aerial surveys during winter (January-March). The sudden increase in wolf abundance in 2019 is the result of wolves being translocated to the island from northeastern Minnesota and Ontario, Canada, as part of the NPS efforts to reestablish a healthy wolf population. Moose population estimates (filled circles) during 1959–2001 were based on population reconstruction from recoveries of dead moose, whereas estimates from 2002 to 2019 were based on aerial surveys. Additional estimates of moose population estimates (lines) and confidence intervals (gray shaded area), were derived from a Gompertz state-space model that emphasizes population processes associated with density dependence and age structure, as well as sampling error (Hoy et al. in press,* Functional Ecology*). By contrast, the confidence intervals reported in the main text emphasize sampling error associated with aerial survey.*

population increased to an estimated 2,060. The average annual growth rate of the population for the past eight years has been 19percent. The newly arrived wolves have been on Isle Royale for too brief a time for them to have significantly influenced the demography of the moose population. The impact of the moose population on vegetation is increasingly apparent. In February 2019, 20 female moose were outfitted with GPS radio-collars as part of a project to better understand how the arrival of new wolves will impact moose demography and behavior.

BACKGROUND

Isle Royale National Park is a remote island, 15 miles from Lake Superior's northwest shoreline. The Isle Royale wolf population typically varied from 18 to 27 animals, organized into three packs. The moose population usually numbered between 700 and 1,200 moose. The wolf-moose project of Isle Royale, now in its 61st year, is the longest continuous study of any predator-prey system in the world.

Moose first arrived on Isle Royale in the early 1900s, then increased rapidly in a predator-free environment. For 50 years, moose abundance fluctuated dramatically, limited by bottom-up factors (i.e., forage availability, winter ticks, and various weather influences). Wolves established themselves on Isle Royale in the late 1940s by crossing an ice bridge between the island and mainland Ontario. Researchers began annual observations of wolves and moose on Isle Royale in 1958–1959.

Isle Royale provides an outstanding venue for ecosystem science. That is, Isle Royale's wolves and moose are isolated from mainland populations most of the time, and the population fluctuations we observe are due primarily to births and deaths, not the movements of animals to and from the island. Also, the small number of mammal species provides a simpler system for study. The wolves are the only predator of moose on Isle Royale, and their effect on the moose population is relatively easy to monitor and understand. Moose are essentially the only food for wolves, although beaver are a significant food source at times. Finally and importantly, human impact is limited in the sense that people do not hunt wolves or moose, or harvest the forest.

The original purpose of the project was to better understand how wolves affect moose populations. The project began during the darkest hours for wolves in North America—humans had driven wolves to extinction in large portions of their former range. The hope was that knowledge about wolves would replace hateful myths and form the basis for a wiser relationship with wolves.

After six decades, the Isle Royale wolf-moose project continues. Today, wolves prosper again in several regions of North America. But our relationship with wolves in many parts of the world is still threatened by hatred, and now we face new questions, profound questions about how to live sustainably with nature. The project's purpose remains the same: to observe and understand the dynamic fluctuations of Isle Royale's wolves and moose, in the hope that such knowledge will inspire a new, flourishing relationship between humans and our natural world.

Many of the project's discoveries are documented at **www.isleroyalewolf.org.**

PERSONNEL AND LOGISTICS

In summer 2018, 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. Summer interns Isabella Evavold, Ryann Rich, Madeline Witt, and Nicolas Wilson did widespread field work on moose-balsam fir interactions, and additional field work was carried out by Joellen Saugrich, Joe Lazzari, Cheyanne Boucher, and Jeff Selans. Leah Vucetich also led a number of people working in the lab, especially Shallen Gurtler, Max Keyzers, Christian Stevens, Eli Paulen, Rachel Christensen, Tori Engler, Noah Yaks, and Tanner Barnes.

During the course of 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 week-long cross-country treks, searching for moose bones. In 2019, the annual winter study was delayed and shortened by the federal government shutdown. The winter field work, led by Rolf Peterson and Sarah Hoy, started on February 2 and continued until March 4. Ky and Lisa Koitzsch provided a month of daily field work on skis to collect data on moose and balsam fir. Pilot Don L. Murray (UpNorth Aerials, Two Harbors, Minnesota) piloted the primary research aircraft

during February 1–5 and February 13—March 4. Pilot Don E. Glaser (Arctic Wings, Willow, Alaska), provided a second aircraft during February 5–18. National Park Service staff Ryan Wetelainen, Sarah Pikora, Lynette Potvin, Mike Ausema, and Mark Romanski participated in the winter study, as well as Superintendent Phyllis Green and NPS veterinarian Jenny Powers. In January, Green opened up the winter facility with Rob Bell and Jason Killoran in preparation for wolf translocation from Ontario. Matt Uphaus, Marley Cheno, and Robert Glaser provided ground transportation on the mainland. Kevin Miller (US Department of Agriculture Wildlife Services), NPS pilot Jim Hummel, and National Parks of Lake Superior Foundation videographer Daniel Cojanu, also participated in this year's winter study. Cojanu documented the winter field work in video. GPS collaring of moose was accomplished with collaborators Tiffany Wolf (Veterinary Medicine, University of Minnesota), Seth Moore (director of Biology and Environment, Grand Portage Band of Lake Superior Chippewa), Lynette Potvin, Mark Romanski (NPS), and the following crew from Quicksilver, Inc.—Mark Stott (pilot), Andrew Orlando, and Tom Zaczkowski.

THE WOLF POPULATION

The number of wolves on Isle Royale fluctuated greatly (between two and 15 wolves) throughout fall 2018 and winter 2019.

- Prior to September, the population was comprised of two island-born wolves. They are the highly inbred, M183 and F193, who are father and daughter as well as being half siblings.
- In late September and early October, four Minnesota-born wolves (one male and three females) were released on Isle Royale.
- In late October, the male Minnesota-born wolf died.
- On January 31, one of the Minnesota-born female wolves (translocation ID: 004F) departed the island by crossing the ice-bridge to mainland Canada, leaving the Isle Royale wolf population with four wolves (two island-born wolves and two Minnesota-born females).
- During February 26-March 1, four Canadian-born wolves were released onto the island. They included a male and female captured near Wawa, Ontario; and two males from Michipicoten Island, Ontario. One of the wolves was a breeding-male on Michipicoten.
- During March 23, seven more wolves were released on Isle Royale. These include three males and three females from Michipicoten Island and another male captured near Wawa, Ontario. One of the wolves had been a breeding-female on Michipicoten.
- All reintroduced wolves were outfitted with GPS enabled radio-collars that collect GPS locations six times per day. This GPS data will be closely monitored by the NPS.

Figure 2. *In 2019, the wolf population continues to include the island-born father-daughter pair (who also shared the same mother; so they are half-siblings), M183 (left image) and F193 (right image), now 10 years old and eight years old, respectively.*

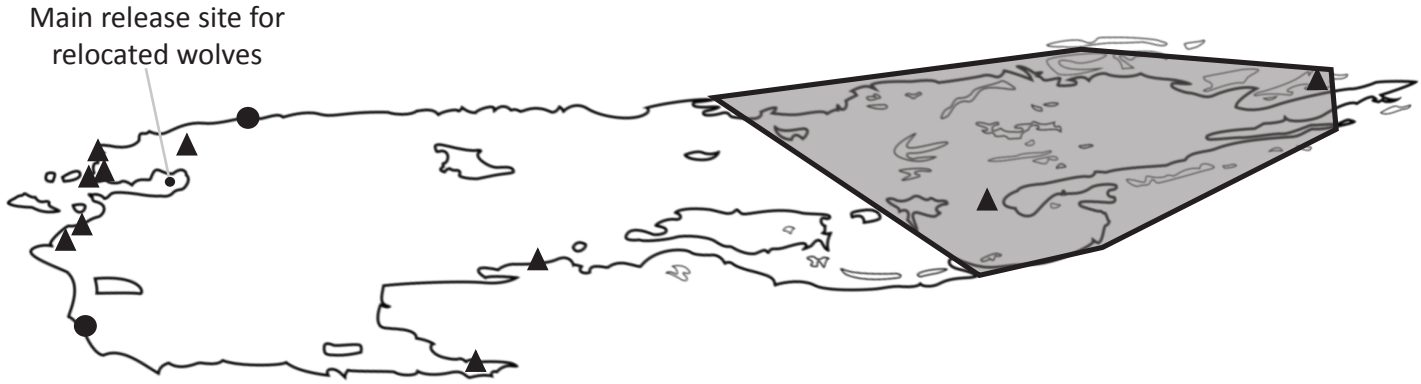

Figure 3. *During the winter study of 2019, the island-born wolves continued to travel throughout their usual territory (gray overlay) at the east end of Isle Royale. The four wolves (the island-born pair M183 and F193, and the two Minnesota-born females) were estimated to have killed a total of 10 moose over a 41-day period, January 21–March 2 (triangles). They also fed on the carcasses of two moose dying by accident or malnutrition (filled circle).*

At the end of March, a total of 15 wolves are known to be on the island: two island-born wolves (one male and one female), two Minnesota-born wolves (two females), eight Ontario-born wolves from Michipicoten Island (five males and three females) and three Ontario-born wolves from the mainland (two males and one female). The NPS plans for restoring wolf predation are flexible enough to allow additional wolves to be moved to Isle Royale, as deemed appropriate, over the next two to four years.

The two island-born wolves, M183 and F193, are now 10 years old and eight years old, respectively (Figure 2). They both originated in the Chippewa Harbor Pack, born to the same mother (i.e., half-siblings). The female is also the daughter of the male, so any offspring from this pair would be extremely inbred and unlikely to survive. The pair have not successfully raised any young (one pup born in 2014 probably died at nine months of age). In winter 2019, the island-born wolves remained together as a strongly bonded, territorial pair. They continue to occupy a territory at the eastern end of Isle Royale (Figure 3). The pair was undoubtedly aware of the arrival of new wolves on the island (resulting from translocation in fall 2018) as their tracks overlapped occasionally.

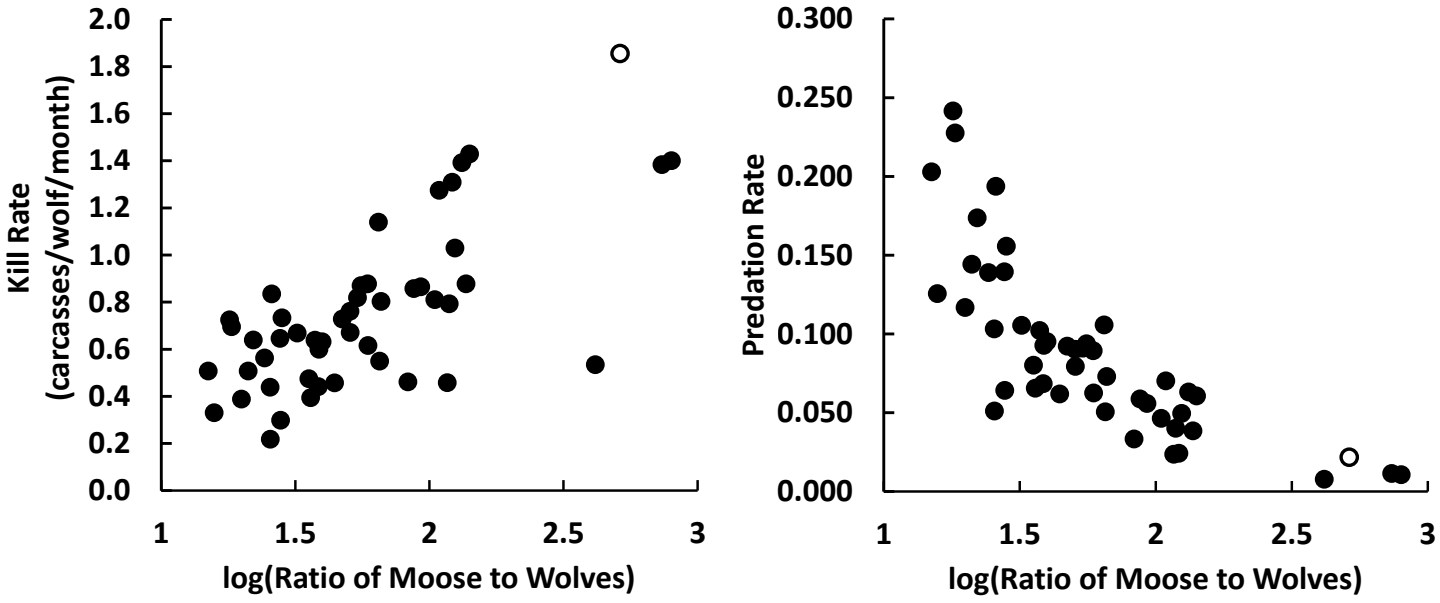

Figure 4. *Relationship between the ratio of moose-to-wolves and kill rate, the number of moose consumed per wolf per month (left panel), and predation rate (right panel) on Isle Royale, 1971-2019. White data point corresponds to 2019.*

Figure 5. *An extensive and long-lasting ice bridge formed between the island and mainland which spanned almost the entire length of the north shore between January 29 and March 8. Photographs show the ice-conditions at the northwest end of the island (left) and across Lake Superior towards Canada (right) on February 2, around the time that the Minnesota-born female wolf (translocation ID: 004F) left the island.*

During early winter 2018–2019 (prior to early March), the wolf population contained three females and one male. The island-born pair remained together at the east end of the island. The two Minnesota-born females remained alone, at the far west end of the island through February. These two females, new to the island, killed moose calves on their own. They were unusually sedentary throughout February when mating usually occurs. They may have been positioning themselves for maximum exposure to any males that might travel the shorelines at the west end (see section Will there be wolf pups in 2019?). However, the male Ontario-born wolves did not start arriving on the island until the very end of the breeding season and shortly thereafter. The movements and activity of all Minnesota-born and Ontario-born wolves will be closely monitored over the upcoming months via their GPS-collars by the NPS.

During this year's winter field season, we detected the carcasses of 12 moose, including at least one moose that appeared to have died of malnutrition and one that died in an accidental fall (Figure 3). We plan for Moosewatch volunteers to visit all these sites in May and June.

The per-capita rate of prey acquisition (sometimes known as 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 year, the acquisition rate may be estimated from having observed four wolves throughout a 41-day period, during which we detected those wolves having killed 10 moose (Figure 3). This corresponds to approximately 1.9 moose per wolf per month. That kill rate is 30 percent greater than the next highest kill rate that we have ever observed (1971–2019, see Figure 4, left panel). For context, that kill rate is 2.5 times greater than the long-term average kill rate of 0.7 (+/- 0.04 SE) between 1971 and 2011, the period prior to the wolf population's recent collapse. The high kill rate value is likely attributable to: (i) very high ratio of moose-to-wolves, (ii) small group sizes among wolves, and (iii) the possibility of detecting kills at a higher rate than is typical due to the presence of GPS-collared wolves. Because of the last reason, some caution is warranted in interpreting this estimate of kill rate. Nevertheless, the estimate is useful enough to conclude that the wolves are likely well fed.

Figure 6. *The island-born father-daughter pair (M183 and F193) closely inspected tracks and scent marks that appeared to have been left by unknown wolves. Photograph taken February 16.*

The impact of a predator population on a prey population is indicated by the predation rate, which is the proportion of moose killed by wolves. This statistic is equal to the kill rate multiplied by the ratio of wolves-to-moose and then extrapolated throughout the year (according to methods described in Vucetich et al. 2011; *Journal of Animal Ecology* 80, 1236–1245). When the ratio of wolves-to-moose is very low, as it was during most of the winter field season (i.e., 4:2060), then the predation rate is determined almost entirely by the ratio, rather than the kill rate. Even with a high estimate of kill rate, predation rate—expressed as a percentage of moose—is still very low. The calculations indicate a predation rate of 2.2 percent, which is higher than in previous years, but still far below the long-term average (Figure 4, right panel). For context, the long-term average predation rate is 9.9 percent (+/- 0.8 SE) between 1971 and 2011 (the period prior to the wolf population's recent collapse). We expect predation rate to remain relatively low, until either: (i) wolf abundance increases considerably, or (ii) moose abundance decreases due to limited availability of browse.

With new wolves arriving on the island in autumn 2018 and winter 2019, the fate of the two remaining island-born wolves and their response to the newcomers is of great interest. Favorable weather and tracking conditions in February provided a valuable window to observe the noncollared, island-born pair that have continued to hold forth on Isle Royale for most of the past decade. The pair remained tightly bonded and highly territorial. At the start of winter study 2019 (February 2), the Minnesota-born wolves had traveled throughout the east end, and it's likely that all the wolves knew about each other, even if they hadn't come face to face.

The winter was characterized by an extensive and long-lasting ice bridge during February 2019. One female Minnesota-born wolf (translocation ID: 004F) used the ice bridge to leave the island on January 29, skirting open cracks in new ice to make the traverse to the mainland (Figure 5).

On February 13, tracks of an unknown wolf were observed near Daisy Farm, the day after the island-born pair had been observed scent-marking the same area. On February 19, the island-born pair was observed in Lane Cove inspecting tracks that appeared to have been left by an unknown wolf (Figure 6), possibly different from the first unknown wolf as its tracks were very large. (We investigated both sets of tracks from the ground—giving us reason to think they were left by different-sized wolves.) On the same day, 10 miles to the southwest of Lane Cove, we followed tracks of three wolves off and on for 50 miles, beginning along the north shore of Isle Royale, then continuing all the way to the southwest end, on and over a couple offshore islands, around to the south shore of the island where the wolves fed on a moose carcass (which probably died from malnutrition). The tracks then continued along the shore to Houghton Point, at which point the tracks were lost as they crossed the vast expanse of ice covering Siskiwit Bay. The island-born pair spent much of February 19-25 patrolling their territory, following the unknown-wolf tracks (Figure 7) and leaving prominent double

Figure 7. *The island-born pair (M183 and F193) remained tightly bonded and highly territorial. The pair spent much of late February patrolling their territory (left), and following tracks left by unknown wolves (right).*

Figure 8. *Female Minnesota-born wolf (translocation ID: 003F) was located via telemetry on March 1 and found bedded down on the shoreline at the west end of the island (left). Although she has spent most of her time alone since she arrived on the island, she has managed to kill moose calves and was evidently well fed during winter study 2019 (right).*

scent-marks along the way. During the week that remained of the winter study, we flew the shorelines and much of the eastern interior, but found no more tracks that appeared to be from unknown wolves.

It can be difficult to draw inferences from observing tracks when those tracks do not lead to directly observing the wolves that made them. However, it's highly unlikely that these unknown wolf tracks could have been left by either of the two Minnesota-born female wolves because GPS data from these collared wolves places them at the other end of the island during this period. Our best (though fallible) inference is that several wolves arrived to Isle Royale by crossing the ice bridge and then returned to the mainland after spending approximately a week on Isle Royale in February. If that inference is incorrect and one or more of these putative wolves remained on Isle Royale, then there is a good chance of detecting their presence within the next 12 months through fecal DNA. Alternatively, if one or more of these putative wolves contributes reproductively to the island, then that contribution will eventually be detected through the fecal DNA of their offspring.

Will there be wolf pups in 2019?

Although the gray wolf is one of the most studied wild mammals on Earth, there are significant gaps in knowledge about some aspects of their lives. Dr. Cheryl Asa, an endocrinologist from the St. Louis

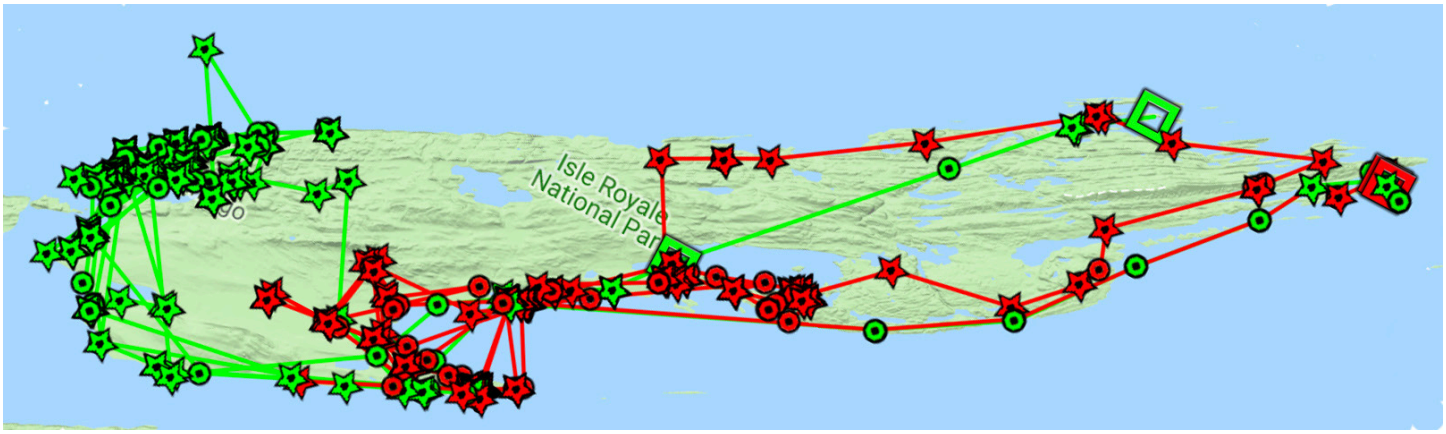

Figure 9. *Movement patterns of the two Minnesota-born female wolves, translocation ID: 001F (shown in green) and 003F (shown in red), between January 15 and March 4, 2019. GPS collar data were provided by NPS. These wolves each spent most of February alone, and sedentary, on the shoreline extremities of the west end, but also traveled together at times.*

Figure 10. *On February 19, the island-born female wolf (F193) was observed scent marking while her father (M183) inspected her readiness to mate (left image). As seen in 2017 and 2018, the island-born female soundly rejected the courtship advances of her father during the 2019 mating season (right image taken on February 26).*

Zoo, recently pointed out, "We don't know what triggers ovulation in wolves . . . ", when asked if female wolves without access to males during their annual estrus might ovulate again a few weeks later. While she doubted that a second estrus was likely, she also pointed out that there can be great variation in the timing of estrus for a given individual, and she wouldn't rule out a female breeding in March. While the peak in mating for wolves on Isle Royale has typically been the third week of February, we have seen evidence of mating from late January through early March in prior years.

For most of the 2018–2019 winter, only one male and three females were present in the population. The two females introduced in autumn 2018 spent most of February alone and rather sedentary on the shoreline along the Island's west end (Figure 8). Both females killed moose calves and evidently had ample food. They also did not venture away from the island in search of a mate, even when a solid ice bridge connected the island to the mainland throughout February. Both Minnesota-born females left an extensive web of tracks that would be impossible for a male wolf to overlook if it happened along the shore. During winter study, the travels of the Minnesota-born females, as indicated by their GPS collars, showed only occasional overlap with the island-born pair at the northeast end of the island (Figure 9).

Meanwhile, the island-born pair seemed to have remained tightly bonded. The female of this pair did not (to our knowledge) have access to any other males on February 26 when she exhibited signs of estrus. During this time she was closely tended and inspected by her long-time partner (and father). Nevertheless, the female soundly rejected the courtship advances of her father based on three extended observations between February 19 and 26 (Figure 10).

Mating could have occurred between the Ontario-born female and male wolves that were captured at the same location near Wawa at the end of February, or on Michipicoten Island before translocation to Isle Royale. At this point, only time will tell if wolf pups are born in 2019.

THE MOOSE POPULATION

The 2019 moose census (conducted between February 4 and 22) resulted in an estimated abundance of 2,060 moose (Figure 1). The 80 percent confidence intervals on this estimate are [1,618; 2,529], and the 90 percent confidence intervals are [1,420; 2,816]. The estimated abundance (2,060) corresponds to an average growth rate of 19 percent each year, over the past eight years (i.e, since 2011 when there was an estimated 515 moose). That rate of growth is consistent with a moose population growing in a manner limited only by their life history and not by predation, food, or weather. Moose density was lowest in central Isle Royale (2.3 moose/km2), greater at the west end, (4.5 moose/km2) and greatest at the east end of Isle Royale (6.9 moose/km2).

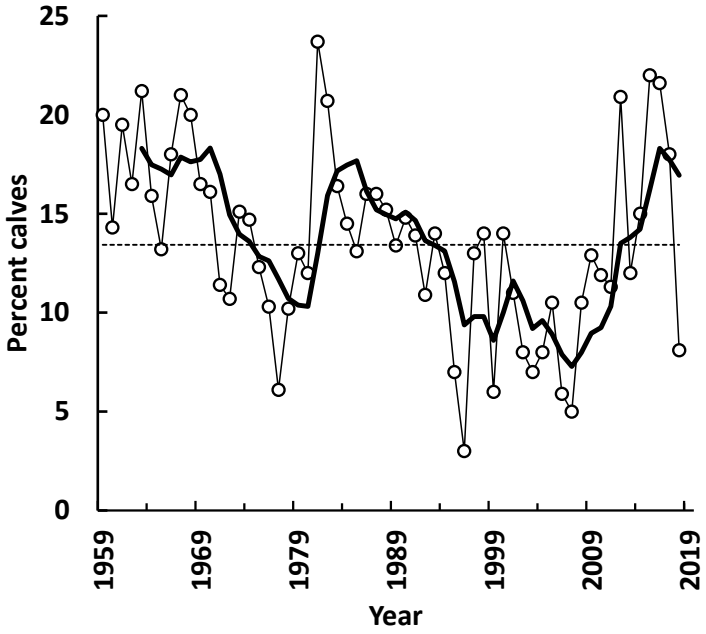

Figure 11. *Long-term trends (1959–2019) in the percentage of the total moose population that are eight-month old calves. The 50-year average (13.4 percent) is marked by the dashed line, and the thicker line represents the five-year moving average.*

Overall counting conditions were similar to those of last year. While last year was characterized by a thick snow crust, this year was characterized by deep, uncompacted snow. Both conditions result in poor counting conditions because moose concentrate in habitats where the snow is less deep. Those habitats also happen to be characterized by densely growing stands of conifer, where moose are especially difficult to see from the plane, compared to the more open habitats they tend to occupy in the absence of deep or crusted snow. In each of the two previous years we used a 59 percent sightability correction factor. The rationale for using that correction factor is explained in the 2016–2017 and 2017–2018 annual reports.

This year we estimated the sightability correction factor to be 49 percent. This estimate of sightability is based on the frequency with which we detected radio-collared moose, which should be considered only an approximation. (Details about the radio-collared moose are described below.) To estimate sightability, we found the approximate location of collared moose as indicated by radio signal. Then we flew a flight pattern (overlapping circles) over this location at a search intensity of 10-15 minutes/km2. This is the flight pattern and search intensity used when counting moose on survey plots during the moose census. If the collared moose was not visually observed after such a search, the search intensity was increased to 30-45 minutes/km2. Between February 18 and 26, we conducted 51 independent trials—i.e., attempts to visually observe moose whose radio-collar signal was detected, plus two additional trials when collared animals happened to be survey plots during the moose census. We observed the moose on 26 occasions of the 53 trials yielding a sightability estimate of 49 percent. There was little improvement when search intensity was three times greater than the census level (55 percent). In the near future we will estimate sightability using collared moose following procedures similar to Giudice et al. 2012 (*Journal of Wildlife Management,* 76:75-87). Doing so will provide the most robust estimates of sightability possible. For now, the estimate of 49 percent is the most reasonable estimate available.

In 2019, 8.1 percent of the 222 moose classified on census plots were calves. Using basic assumptions for calculating confidence intervals for proportions, the 90 percent confidence intervals for that observation are [5.1 percent; 11.5 percent]. As such, it seems reasonable to conclude that recruitment is substantively lower than in the past two years and non-trivially lower than the long-term average (Figure 11). Because reduced recruitment cannot be attributable

Figure 12. *Cow moose (ID#: 18) was outfitted with a GPS enabled radio-collar in Tobin Creek on February 16, after which she moved over to Robinson Bay, where this photograph was taken on February 27. The female showed a considerable degree of hair loss.*

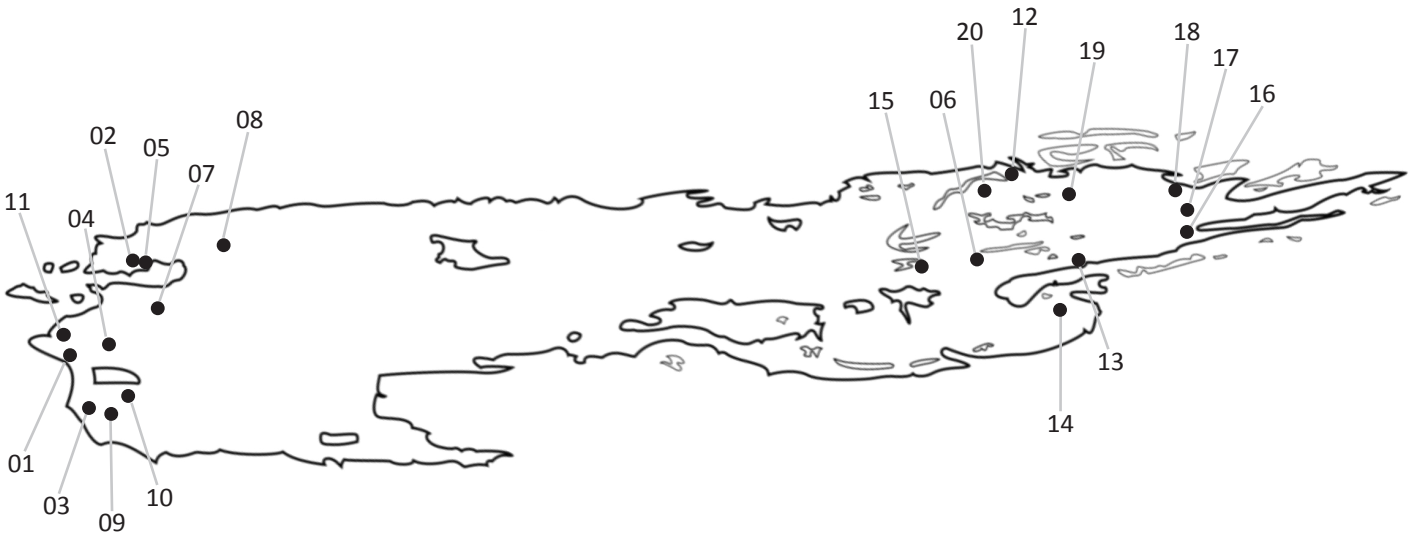

Figure 13. *Location of all 20 GPS-collared cow moose (with individual ID#) at Isle Royale on February 20, a few days after capture and release.*

to predation, we infer that the decline is an early sign of food stress in the moose population. Some food stress during the past year may be attributable to the late arrival of spring green-up in May and June of 2018. The nutritional stress associated with a delayed spring green-up comes around the time that cow moose give birth and begin lactating. The unusually deep, and uncompacted snow this winter (~3 feet) may also have contributed to moose being more nutritionally stressed this year by making it more difficult for moose to find food above the snowline, and to move between areas in search of suitable food. Additional food stress could also be due, in part, to the large number of moose in the population and the impact that high moose densities are having on the abundance of winter forage. During the 2018–2019 field seasons, we observed an extremely high level of moose browsing damage to balsam fir saplings, the main winter food source for moose on Isle Royale (see Vegetation section). Data collected this winter (by Ky and Lisa Koitzsch) revealed that moose had eaten almost 100 percent of the new branches produced by the fir saplings during the 2018 growing season—with the exception of branches protected below the snowline. Such extreme levels of browsing damage are possibly the result of moose densities remaining at high levels over the last five years.

To have estimated a low recruitment rate is at odds with having estimated a high population abundance and population growth rate. The discrepancy may be attributable to having underestimated moose abundance last year (see *Annual Report 2017–2018* for details). And it is plausible that this year's point estimate for abundance (2,060) is an overestimate. That moose abundance may have been overestimated this year and underestimated last year is further suggested by the pattern of predictions provided by the Gompertz state-space model (see solid line in Figure 1), which generates abundance estimates that explicitly account for observation error (i.e., error due to imperfect detection of moose). At the same time, it is plausible that the estimate (2,060 moose) is accurate and the discrepancy arises from having underestimated recruitment. If recruitment was underestimated, it would be due to calves—for some unknown reason—being differentially less visible than other kinds of moose this year compared to other years. In any case, the discrepancy does not weaken the more general inference that the moose population has been growing rapidly for nearly a decade and is well above the long-term average.

Collared moose

For the first time in several decades, moose were outfitted with GPS enabled radio-collars in Isle Royale National Park. The collars record the animals GPS location every 30 minutes. The main purpose of the GPS collaring project is to complement ongoing studies led by the wolf-moose project and fill gaps in our understanding of moose responses to predation, forage abundance, and climate. More precisely, it represents an important first step to help the NPS assess the impacts of predator restoration to the ecosystem.

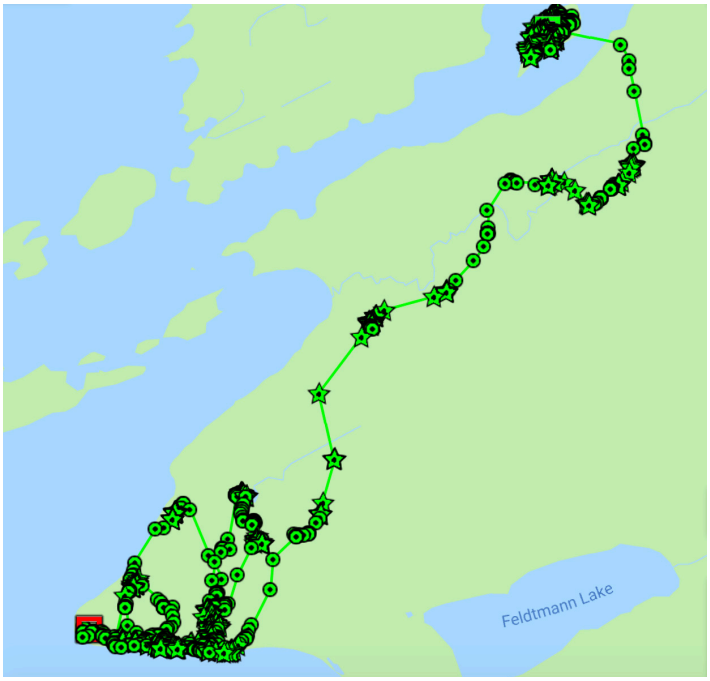

Figure 14. *Cow moose (ID#: 01) illustrates movements of moose in late winter, between February 20 and March 20. Most of the nearly 1,400 locations are overlapping at fir-rich habitat on Beaver Island (where she spent two weeks), or near Cumberland Point, where she could move readily along the frozen shoreline.*

The collaring project also begins a unique collaboration to compare the health and dynamics of the moose population in Isle Royale National Park, alongside a neighboring population of collared moose on the mainland on the reservation lands of the Grand Portage Band of Lake Superior Chippewa.

A total of 20 female moose were outfitted with GPS enabled collars over a four-day period. On February 13, eight moose were captured (via anesthesia darting from a helicopter) and outfitted with collars at the west end of the island, around the Washington Harbor and Feldtman Lake areas. On February 14, two more animals were collared at the west end, near Windigo, and two moose were collared at the east end, around the Daisy Farm area. Collaring efforts had to be suspended on February 15 because of 50-knot winds. On February 16, eight more moose were collared at the east end.

To briefly summarize, the collaring procedure involved spotter planes (piloted by Glaser and Murray) identifying the locations of candidate animals for collaring. Moose were then anesthetized (via a dart) by the helicopter capture team from Quicksilver, Inc. A wildlife veterinarian (Wolf) and wildlife biologist (Moore) then assisted the helicopter capture team to collect biological samples (i.e., blood, hair, urine, and feces), assess moose health (body fat and winter tick load), and fit the animal with the GPS collar. Each moose was then administered drugs to reverse the anesthesia. After about two minutes, the animals awoke and walked away (Figure 12). The animal's recovery was monitored both on the ground by the wildlife veterinarian and wildlife biologist and from the air by the spotter planes. The collared animals redistributed themselves over surprisingly large areas at the west and east ends of the island (Figure 13), where they will be the focus of intense study over the next three years (Figure 14).

The above collaring efforts were led by Rolf Peterson, Sarah Hoy, and John Vucetich from Michigan Technological University, as part of a unique partnership with the National Park Service, University of Minnesota, and the Grand Portage Band of Lake Superior Chippewa. The main collaborators on this project were: Mark Romanski and Lynette Potvin, Natural Resources Management Division personnel for Isle Royale National Park; Seth Moore, director of biology and environment for Grand Portage Band of Chippewa, who has studied mainland moose populations in Grand Portage, Minnesota, since 2009; Tiffany Wolf, a wildlife veterinarian and research epidemiologist from the University of Minnesota, who co-leads moose research with Moore in Grand Portage. The helicopter capture team was Mark Stott (pilot), Andrew Orlando, and Tom Zaczkowski from Quicksilver, Inc.

For the past 18 years, we have monitored the severity of winter tick infestation by photographing moose in spring, digitizing each side profile and calculating the proportion of hair loss. There is considerable variation in the extent of hair loss observed between individuals within a given year, and also among years (Figure 15).

VEGETATION

Terrestrial

For the past century, balsam fir, a characteristic boreal tree species, has been impacted by moose browsing during the winter. In particular, moose browsing is one factor underlying a 75 percent decline in the number of mature fir trees since 1846 (reduced from 36 percent to 9 percent of all trees, based on original

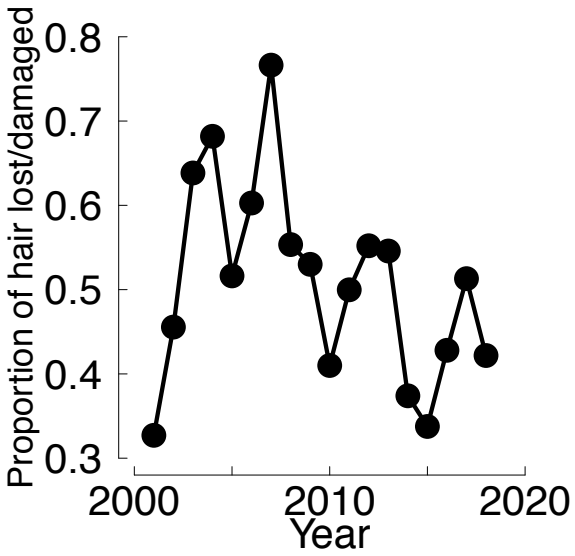

Figure 15. *Photographs of moose in spring provide annual information on extent of hair loss caused by winter ticks. There is a considerable amount of variation in the extent of hair loss between individuals within a given year. Top photograph shows a yearling male with only a small degree (8 percent) of hair loss on shoulders, whereas the photo below shows a mature male that has lost or damaged 98 percent of the hair on his body and neck. Both photographs were taken in late May 2018. Graph shows the average extent of hair loss for moose in the Isle Royale population each year, over the last 18 years (2001–2018).*

land survey and modern-day US Forest Service estimates). Under the dense hardwood canopy at the west end of Isle Royale, where fir is further limited by light and germination sites, moose browsing has largely eliminated the regeneration of fir trees over the past 100 years. In the absence of regeneration, balsam fir would eventually disappear from most of Isle Royale. At the west end of the island in the late 2000s, long-suppressed fir trees, often decades-old but still less than a meter tall, began to grow because browsing by moose was reduced. Moose browsing was reduced because wolves, buoyed by genetic rescue a decade earlier, preyed on moose at a higher level than previously seen on Isle Royale.

The future status of balsam fir is critically dependent on the growth and survival of new regenerating trees as >90 percent of the mature canopy trees on the west end have died in the past 30 years. In 1988, 473 mature balsam fir trees were tagged along a transect approximately 10 miles in length (representing a 10-ha area) at the west end. Only 28 (6 percent) of these tagged mature trees remained in 2018. By 2017, there were more than 500 newly emerging fir trees (trees >175cm in height) along the same transect. These newly emerging fir trees were also tagged in recent years. However, by spring 2018 moose had terminal browsed (i.e., browsed of the main growing stem) almost 60 percent of the tagged newly emerging fir trees (up from 5 to 10 percent in previous years, Figure 16). By February 2019, browsing pressure had increased yet again, and it was virtually impossible for our winter field crew to find accessible fir stems that had not been seriously browsed. Balsam fir provides about half of all moose food during winter, and the deterioration of fir growth has impacted moose behavior at the west end of the island. Specifically, in the deep snow conditions of 2019, moose congregated in high numbers in the two areas at the west end—Beaver Island and the Hay Bay area—where fir regeneration is abundant (probably because of historic forest disturbance).

Aquatic

While it has long been known that moose are prodigious underwater foragers, determining the underwater impacts of moose browsing continues to be an important research challenge. In the past decade, a native floating-leafed plant called watershield *(Brasenia schreberi)* provided some insights on how moose affect aquatic communities. Watershield, a

plant that can quickly grow over much of the surface of ponds and shallow lakes, is highly favored by both moose and beavers. In the late 2000s, when moose were reduced by wolf predation, watershield emerged from obscurity to become the dominant aquatic plant in five ponds at the east end of Isle Royale, covering as much as 90 percent of the water surface. Moose increasingly congregated in these ponds to feed on watershield. As the moose population grew between 2012 and 2017, watershield was steadily diminished. By 2018, watershield had once again declined to the point where it was not readily found in aquatic areas. Lake Ojibway, the pond with the greatest abundance of watershield, was found partially drained in May 2018 (Figure 17). The beaver dam that had been holding back Lake Ojibway since the 1950s, blew out in November 2017 and it was not repaired by beavers. Beavers had been well-established in Lake Ojibway for decades and they evidently relied heavily on aquatic plants as there was little evidence of

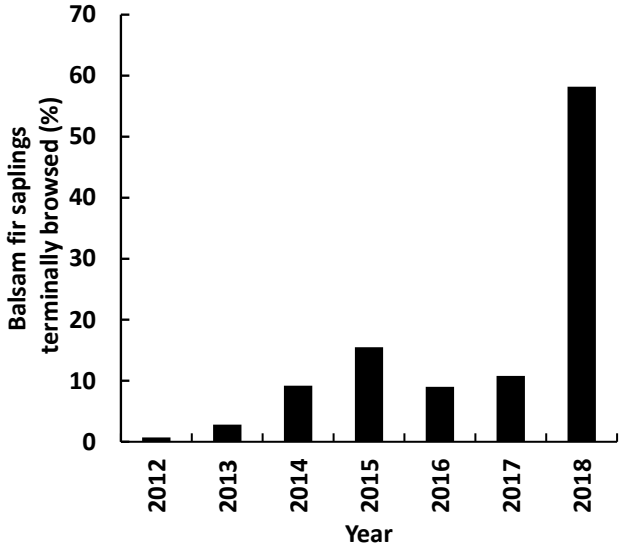

Figure 16. *In 2018, moose had terminally browsed (i.e., eaten the main growing stem) 58 percent of the 608 balsam fir saplings, which had reached a height of >175 cm along a 10 mile transect between Windigo and Huginnin Cove at the west end of Isle Royale. This represents the highest level of terminal browsing ever recorded since we began tagging and monitoring these newly emerging fir trees in 2012.*

Figure 17. *Lake Ojibway was formed when the area was flooded by beavers in the early 1950s, but in November 2017 the main beaver dam failed and much of the lake drained.*

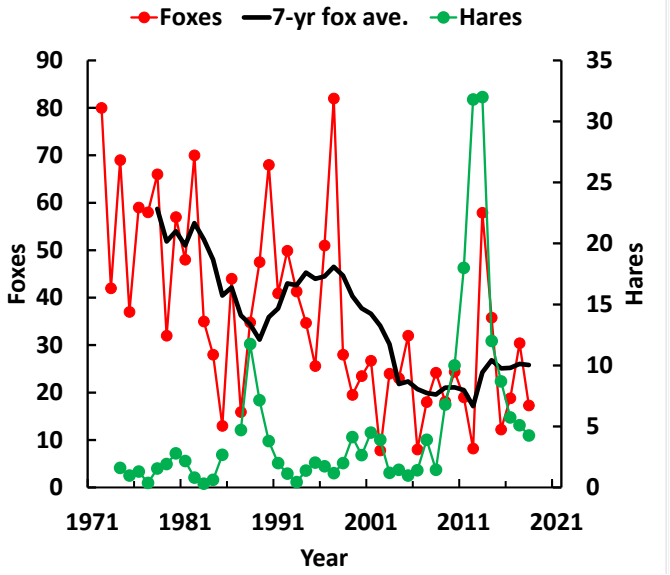

Figure 18. *Indices of abundance for red foxes and snowshoe hares on Isle Royale, 1974–2019. The hare index is the number of hares observed per 100 km hiked during the summer. The fox index is the number of foxes seen from the survey aircraft during winter study, the sum of the maximum number seen at kills plus the number seen otherwise per 100 hours flight time. The thick black line is a moving average, highlighting a longer-term trend in fox abundance.*

tree-cutting by beavers in the late 2000s. However, in 2018 beavers stopped occupying the lake, presumably these beavers were either killed by wolves or they relocated to somewhere else with a higher availability of aquatic plants.

OTHER WILDLIFE

During winter 2019, the tracks of marten were observed at Windigo and several other nearby locations, as well as two sites at the east end of the island. Marten sign was not observed between 1959 and 1990; however, since 1991, marten sign has been observed every year but three.

Red foxes were relatively uncommon in 2018–2019, as were their primary prey snowshoe hares (Figure 18). Foxes are expected to fare much better over the winter as the wolf population grows and provides more moose carcasses that can be used by scavengers, such as foxes and ravens.

An aerial count of active beaver colonies was conducted by Rolf Peterson (observer) and Don Murray (pilot), using float-equipped Aeronca Champ aircraft in October 2018. The 2018 survey resulted in the highest estimate of active beaver sites ever recorded for Isle Royale, 541 sites, which is consistent with the increasing beaver population documented since 2012 (Figure 19).

WEATHER, CLIMATE AND ICE

The winter of 2019 was noteworthy for extensive ice on Lake Superior and unusually deep, uncompacted, powdery snow during the February period of the winter study. Extreme cold and calm winds in January allowed the formation of an extensive ice bridge connecting Isle Royale to the mainland by February 2, and that bridge increased in extent until the winter study ended on March 4. Temperatures did not increase above freezing during winter study, and there were virtually no crusts in the snow profile (Figure 20). With such extensive ice and deep snow inland, wolf travel was concentrated on the Lake Superior shore, and moose were restricted to areas with thick conifer canopy where the snow was less deep.

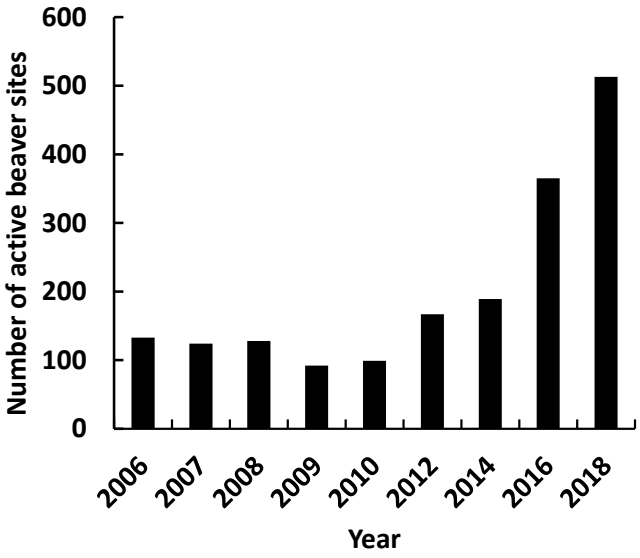

Figure 19. *The number of active beaver colonies has been estimated during aerial surveys at least every other year since 1974. During 2006–2010 there were around 100 active sites, and intensive wolf predation was probably the primary limiting factor. After the wolf population collapsed in 2012, the beaver population has consistently increased.*

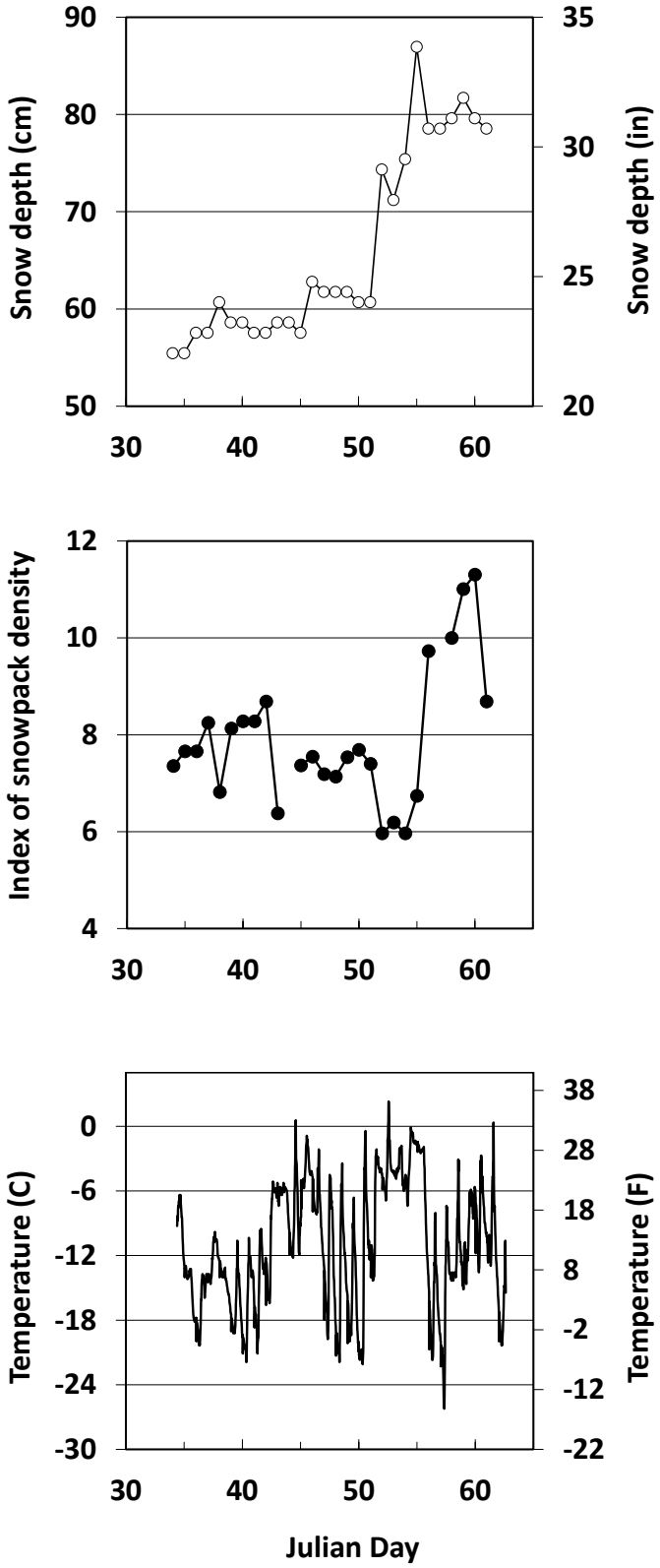

Figure 20. *Snow depth (daily, top graph), snowpack density (daily, middle graph), and ambient temperature (one-hour intervals, bottom graph) during the 2019 winter study on Isle Royale. The relative density of the snowpack was estimated as the "Rammsonde hardness" value calculated using a penetrometer.*

"Caring for ecosystems requires farsightedness....where certain species are destroyed or seriously harmed, the values involved are incalculable."
- Pope Francis, *Laudato si'*, encyclical on the environment and human ecology

Tax-deductible donations to support continuing research on Isle Royale wolves and moose can be sent to:

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